Evolutionary Biology

Understanding Evolutionary Processes

Melody Glover

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Preface

This book aims to help a broader range of students by exploring a wide variety of significant topics related to this discipline. It will help students in achieving a higher level of understanding of the subject and excel in their respective fields. This book would not have been possible without the unwavered support of my senior professors who took out the time to provide me feedback and help me with the process. I would also like to thank my family for their patience and support.

The sub-field of biology that is concerned with the study of evolutionary processes is referred to as evolutionary biology. The diversity of life on Earth is produced by evolutionary processes such as common descent, natural selection and speciation. Evolutionary biology makes use of principles from various fields like genetics, systematics, palaeontology and ecology. Some of the major sub-fields within this discipline are evolutionary ecology and evolutionary developmental biology. Evolutionary ecology seeks to take the evolutionary history of species as well as their interactions into consideration while studying ecology. Evolutionary developmental biology is involved in the comparison of the developmental processes of different organisms in order to understand the evolution of developmental processes and ancestral relationships between them. This book presents the complex subject of evolutionary biology in the most comprehensible and easy to understand language. Some of the diverse topics covered in this book address the varied branches that fall under this category. It will provide comprehensive knowledge to the readers.

A brief overview of the book contents is provided below:

Chapter – What is Evolutionary Biology?

The branch of biology that studies evolutionary processes which are responsible for producing diversity of life on the earth is known as evolutionary biology. This is an introductory chapter which will introduce briefly all the diverse aspects of evolutionary biology.

Chapter – Types of Evolution

The change in heritable characteristics in successive generations of biological populations is known as evolution. Different types of evolution include the evolution of cell, evolution of sexual reproduction and the evolution of biological complexity. The aim of this chapter is to explore these types of evolution to provide an extensive understanding of the subject.

Chapter – Fundamental Concepts of Evolutionary Biology

The fundamental concepts of evolutionary biology include genetic drift, natural selection, evolvability, modern synthesis, common descent and polyploidy. This chapter has been carefully written to provide an easy understanding of these concepts of evolutionary biology.

Chapter – Processes in Evolutionary Biology

There are numerous processes which are studied within the field of evolutionary biology. A few of them are co-operation, speciation, adaptation, adaptive radiation, parallel evolution, molecular evolution, coevolution, macroevolution, microevolution, etc. All these diverse processes have been carefully analyzed in this chapter.

Chapter – Fields Related to Evolutionary Biology

Evolutionary physiology, experimental evolution, population genetics, paleontology, phylogenetics are some of the fields that are studied in association with evolutionary biology. All these diverse fields related to evolutionary biology have been carefully analyzed in this chapter.

Melody Glover

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What is Evolutionary Biology?

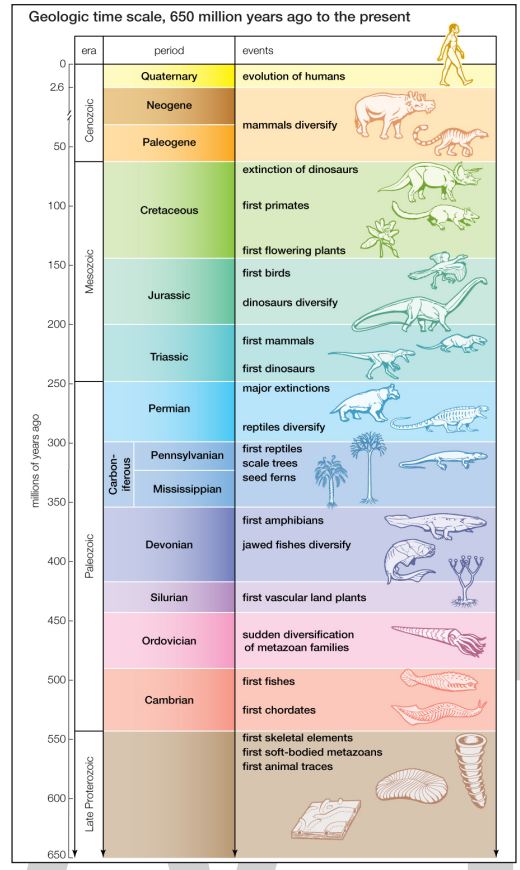
The branch of biology that studies evolutionary processes which are responsible for producing diversity of life on the earth is known as evolutionary biology. This is an introductory chapter which will introduce briefly all the diverse aspects of evolutionary biology.

Evolution

Evolution is the 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 millimetre in diameter, to stately sequoias, rising 100 metres (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 metres (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 shrewlike 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 geologic time scale from 650 million years ago to the present, showing major evolutionary events.

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-favourable 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.

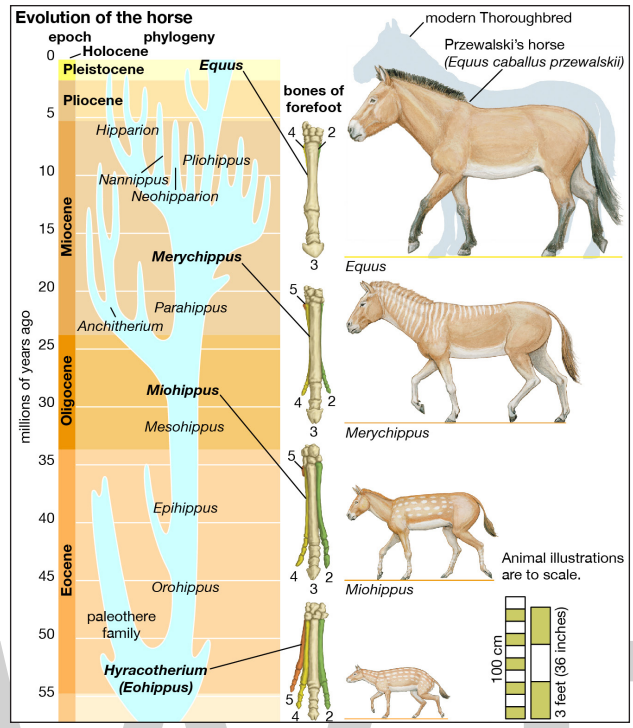
The Fossil Record

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.



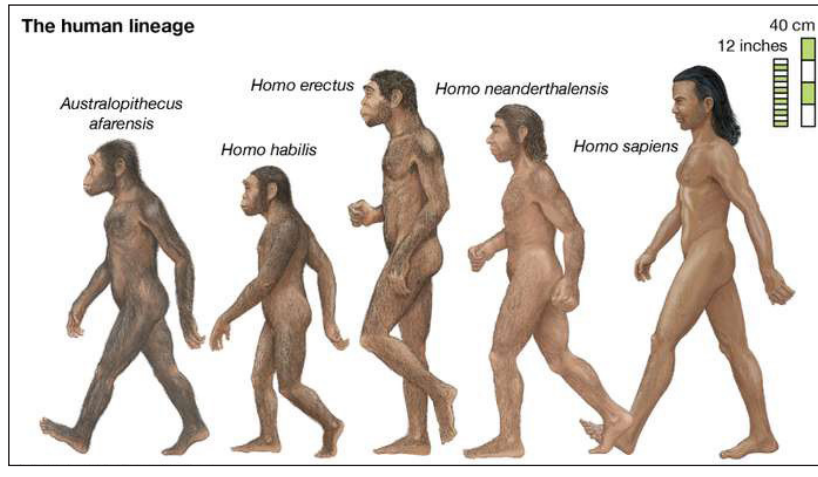
Evolution of the horse.

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.



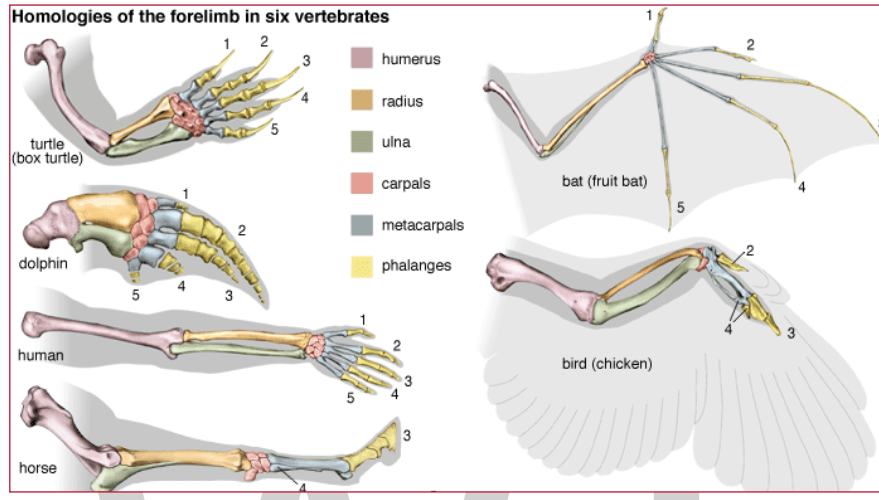
Five hominins—members of the human lineage after it separated at least seven million to six million years ago from lineages going to the apes—are depicted in an artist's interpretations. All but Homo sapiens, the species that comprises modern humans, are extinct and have been reconstructed from fossil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

Structural Similarities

The skeletons of turtles, horses, humans, birds, and bats are strikingly similar, in spite of the different ways of life of these animals and the diversity of their environments. The correspondence, bone by bone, can easily be seen not only in the limbs but also in every other part of the body. From a purely practical point of view, it is incomprehensible that a turtle should swim, a horse run, a person write, and a bird or a bat fly with forelimb structures built of the same bones. An engineer could design better limbs in each case. But if it is accepted that all of these skeletons inherited their structures from a common ancestor and became modified only as they adapted to different ways of life, the similarity of their structures makes sense.

Comparative anatomy investigates the homologies, or inherited similarities, among organisms in bone structure and in other parts of the body. The correspondence of structures is typically

very close among some organisms—the different varieties of songbirds, for instance—but becomes less so as the organisms being compared are less closely related in their evolutionary history. The similarities are less between mammals and birds than they are among mammals, and they are still less between mammals and fishes. Similarities in structure, therefore, not only manifest evolution but also help to reconstruct the phylogeny, or evolutionary history, of organisms.



Homologies of the forelimb among vertebrates, giving evidence for evolution. The bones correspond, although they are adapted to the specific mode of life of the animal. (Some anatomists interpret the digits in the bird's wing as being 1, 2, and 3, rather than 2, 3, and 4.)

Comparative anatomy also reveals why most organismic structures are not perfect. Like the forelimbs of turtles, horses, humans, birds, and bats, an organism's body parts are less than perfectly adapted because they are modified from an inherited structure rather than designed from completely "raw" materials for a specific purpose. The imperfection of structures is evidence for evolution and against antievolutionist arguments that invoke intelligent design.

Embryonic Development and Vestiges

Darwin and his followers found support for evolution in the study of embryology, the science that investigates the development of organisms from fertilized egg to time of birth or hatching. Vertebrates, from fishes through lizards to humans, develop in ways that are remarkably similar during early stages, but they become more and more differentiated as the embryos approach maturity. The similarities persist longer between organisms that are more closely related (e.g., humans and monkeys) than between those less closely related (humans and sharks). Common developmental patterns reflect evolutionary kinship. Lizards and humans share a developmental pattern inherited from their remote common ancestor; the inherited pattern of each was modified only as the separate descendant lineages evolved in different directions. The common embryonic stages of the two creatures reflect the constraints imposed by this common inheritance, which prevents changes that have not been necessitated by their diverging environments and ways of life.

The embryos of humans and other nonaquatic vertebrates exhibit gill slits even though they never breathe through gills. These slits are found in the embryos of all vertebrates because they share as common ancestors the fish in which these structures first evolved. Human embryos also exhibit by the fourth week of development a well-defined tail, which reaches maximum length at six weeks.

Similar embryonic tails are found in other mammals, such as dogs, horses, and monkeys; in humans, however, the tail eventually shortens, persisting only as a rudiment in the adult coccyx.

A close evolutionary relationship between organisms that appear drastically different as adults can sometimes be recognized by their embryonic homologies. Barnacles, for example, are sedentary crustaceans with little apparent likeness to such free-swimming crustaceans as lobsters, shrimps, or copepods. Yet barnacles pass through a free-swimming larval stage, the nauplius, which is unmistakably similar to that of other crustacean larvae.

Embryonic rudiments that never fully develop, such as the gill slits in humans, are common in all sorts of animals. Some, however, like the tail rudiment in humans, persist as adult vestiges, reflecting evolutionary ancestry. The most familiar rudimentary organ in humans is the vermiform appendix. This wormlike structure attaches to a short section of intestine called the cecum, which is located at the point where the large and small intestines join. The human vermiform appendix is a functionless vestige of a fully developed organ present in other mammals, such as the rabbit and other herbivores, where a large cecum and appendix store vegetable cellulose to enable its digestion with the help of bacteria. Vestiges are instances of imperfections—like the imperfections seen in anatomical structures—that argue against creation by design but are fully understandable as a result of evolution.

Biogeography

Darwin also saw a confirmation of evolution in the geographic distribution of plants and animals, and later knowledge has reinforced his observations. For example, there are about 1,500 known species of Drosophila vinegar flies in the world; nearly one-third of them live in Hawaii and nowhere else, although the total area of the archipelago is less than one-twentieth the area of California or Germany. Also in Hawaii are more than 1,000 species of snails and other land mollusks that exist nowhere else. This unusual diversity is easily explained by evolution. The islands of Hawaii are extremely isolated and have had few colonizers—i.e, animals and plants that arrived there from elsewhere and established populations. Those species that did colonize the islands found many unoccupied ecological niches, local environments suited to sustaining them and lacking predators that would prevent them from multiplying. In response, these species rapidly diversified; this process of diversifying in order to fill ecological niches is called adaptive radiation.

Each of the world's continents has its own distinctive collection of animals and plants. In Africa are rhinoceroses, hippopotamuses, lions, hyenas, giraffes, zebras, lemurs, monkeys with narrow noses and nonprehensile tails, chimpanzees, and gorillas. South America, which extends over much the same latitudes as Africa, has none of these animals; it instead has pumas, jaguars, tapir, llamas, raccoons, opossums, armadillos, and monkeys with broad noses and large prehensile tails.

These vagaries of biogeography are not due solely to the suitability of the different environments. There is no reason to believe that South American animals are not well suited to living in Africa or those of Africa to living in South America. The islands of Hawaii are no better suited than other Pacific islands for vinegar flies, nor are they less hospitable than other parts of the world for many absent organisms. In fact, although no large mammals are native to the Hawaiian islands, pigs and goats have multiplied there as wild animals since being introduced by humans. This absence

of many species from a hospitable environment in which an extraordinary variety of other species flourish can be explained by the theory of evolution, which holds that species can exist and evolve only in geographic areas that were colonized by their ancestors.

Molecular Biology

The field of molecular biology provides the most detailed and convincing evidence available for biological evolution. In its unveiling of the nature of DNA and the workings of organisms at the level of enzymes and other protein molecules, it has shown that these molecules hold information about an organism's ancestry. This has made it possible to reconstruct evolutionary events that were previously unknown and to confirm and adjust the view of events already known. The precision with which these events can be reconstructed is one reason the evidence from molecular biology is so compelling. Another reason is that molecular evolution has shown all living organisms, from bacteria to humans, to be related by descent from common ancestors.

A remarkable uniformity exists in the molecular components of organisms—in the nature of the components as well as in the ways in which they are assembled and used. In all bacteria, plants, animals, and humans, the DNA comprises a different sequence of the same four component nucleotides, and all the various proteins are synthesized from different combinations and sequences of the same 20 amino acids, although several hundred other amino acids do exist. The genetic code by which the information contained in the DNA of the cell nucleus is passed on to proteins is virtually everywhere the same. Similar metabolic pathways—sequences of biochemical reactions —are used by the most diverse organisms to produce energy and to make up the cell components.

This unity reveals the genetic continuity and common ancestry of all organisms. There is no other rational way to account for their molecular uniformity when numerous alternative structures are equally likely. The genetic code serves as an example. Each particular sequence of three nucleotides in the nuclear DNA acts as a pattern for the production of exactly the same amino acid in all organisms. This is no more necessary than it is for a language to use a particular combination of letters to represent a particular object. If it is found that certain sequences of letters—planet, tree, woman—are used with identical meanings in a number of different books, one can be sure that the languages used in those books are of common origin.

Genes and proteins are long molecules that contain information in the sequence of their components in much the same way as sentences of the English language contain information in the sequence of their letters and words. The sequences that make up the genes are passed on from parents to offspring and are identical except for occasional changes introduced by mutations. As an illustration, one may assume that two books are being compared. Both books are 200 pages long and contain the same number of chapters. Closer examination reveals that the two books are identical page for page and word for word, except that an occasional word—say, one in 100—is different. The two books cannot have been written independently; either one has been copied from the other, or both have been copied, directly or indirectly, from the same original book. Similarly, if each component nucleotide of DNA is represented by one letter, the complete sequence of nucleotides in the DNA of a higher organism would require several hundred books of hundreds of pages, with several thousand letters on each page. When the "pages" (or sequences of nucleotides) in these "books" (organisms) are examined one by one, the correspondence in the "letters" (nucleotides) gives unmistakable evidence of common origin.

The two arguments presented above are based on different grounds, although both attest to evolution. Using the alphabet analogy, the first argument says that languages that use the same dictionary—the same genetic code and the same 20 amino acids—cannot be of independent origin. The second argument, concerning similarity in the sequence of nucleotides in the DNA (and thus the sequence of amino acids in the proteins), says that books with very similar texts cannot be of independent origin.

The evidence of evolution revealed by molecular biology goes even farther. The degree of similarity in the sequence of nucleotides or of amino acids can be precisely quantified. For example, in humans and chimpanzees, the protein molecule called cytochrome c, which serves a vital function in respiration within cells, consists of the same 104 amino acids in exactly the same order. It differs, however, from the cytochrome c of rhesus monkeys by 1 amino acid, from that of horses by 11 additional amino acids, and from that of tuna by 21 additional amino acids. The degree of similarity reflects the recency of common ancestry. Thus, the inferences from comparative anatomy and other disciplines concerning evolutionary history can be tested in molecular studies of DNA and proteins by examining their sequences of nucleotides and amino acids.

The authority of this kind of test is overwhelming; each of the thousands of genes and thousands of proteins contained in an organism provides an independent test of that organism's evolutionary history. Not all possible tests have been performed, but many hundreds have been done, and not one has given evidence contrary to evolution. There is probably no other notion in any field of science that has been as extensively tested and as thoroughly corroborated as the evolutionary origin of living organisms.

The Science of Evolution

The Gene Pool

The gene pool is the sum total of all the genes and combinations of genes that occur in a population of organisms of the same species. It can be described by citing the frequencies of the alternative genetic constitutions. Consider, for example, a particular gene (which geneticists call a locus), such as the one determining the MN blood groups in humans. One form of the gene codes for the M blood group, while the other form codes for the N blood group; different forms of the same gene are called alleles. The MN gene pool of a particular population is specified by giving the frequencies of the alleles M and N. Thus, in the United States the M allele occurs in people of European descent with a frequency of 0.539 and the N allele with a frequency of 0.461—that is, 53.9 percent of the alleles in the population are M and 46.1 percent are N. In other populations these frequencies are different; for instance, the frequency of the M allele is 0.917 in Navajo Indians and 0.178 in Australian Aboriginals.

The necessity of hereditary variation for evolutionary change to occur can be understood in terms of the gene pool. Assume, for instance, a population in which there is no variation at the gene locus that codes for the MN blood groups; only the M allele exists in all individuals. Evolution of the MN blood groups cannot take place in such a population, since the allelic frequencies have no opportunity to change from generation to generation. On the other hand, in populations in which both alleles M and N are present, evolutionary change is possible.

Genetic Variation and Rate of Evolution

The more genetic variation that exists in a population, the greater the opportunity for evolution to occur. As the number of gene loci that are variable increases and as the number of alleles at each locus becomes greater, the likelihood grows that some alleles will change in frequency at the expense of their alternates. The British geneticist R.A. Fisher mathematically demonstrated a direct correlation between the amount of genetic variation in a population and the rate of evolutionary change by natural selection. This demonstration is embodied in his fundamental theorem of natural selection: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time."

This theorem has been confirmed experimentally. One study employed different strains of Drosophila serrata, a species of vinegar fly from eastern Australia and New Guinea. Evolution in vinegar flies can be investigated by breeding them in separate "population cages" and finding out how populations change over many generations. Experimental populations were set up, with the flies living and reproducing in their isolated microcosms. Single-strain populations were established from flies collected either in New Guinea or in Australia; in addition, a mixed population was constituted by crossing these two strains of flies. The mixed population had the greater initial genetic variation, since it began with two different single-strain populations. To encourage rapid evolutionary change, the populations were manipulated such that the flies experienced intense competition for food and space. Adaptation to the experimental environment was measured by periodically counting the number of individuals in the populations.

Two results deserve notice. First, the mixed population had, at the end of the experiment, more flies than the single-strain populations. Second, and more relevant, the number of flies increased at a faster rate in the mixed population than in the single-strain populations. Evolutionary adaptation to the environment occurred in both types of population; both were able to maintain higher numbers as the generations progressed. But the rate of evolution was more rapid in the mixed group than in the single-strain groups. The greater initial amount of genetic variation made possible a faster rate of evolution.

Measuring Gene Variability

Because a population's potential for evolving is determined by its genetic variation, evolutionists are interested in discovering the extent of such variation in natural populations. It is readily apparent that plant and animal species are heterogeneous in all sorts of ways—in the flower colours and growth habits of plants, for instance, or the shell shapes and banding patterns of snails. Differences are more readily noticed among humans—in facial features, hair and skin colour, height, and weight—but such morphological differences are present in all groups of organisms. One problem with morphological variation is that it is not known how much is due to genetic factors and how much may result from environmental influences.

Animal and plant breeders select for their experiments individuals or seeds that excel in desired attributes—in the protein content of corn (maize), for example, or the milk yield of cows. The selection is repeated generation after generation. If the population changes in the direction favoured by the breeder, it becomes clear that the original stock possessed genetic variation with respect to the selected trait.

The results of artificial selection are impressive. Selection for high oil content in corn increased the oil content from less than 5 percent to more than 19 percent in 76 generations, while selection for low oil content reduced it to below 1 percent. Thirty years of selection for increased egg production in a flock of White Leghorn chickens increased the average yearly output of a hen from 125.6 to 249.6 eggs. Artificial selection has produced endless varieties of dog, cat, and horse breeds. The plants grown for food and fibre and the animals bred for food and transportation are all products of age-old or modern-day artificial selection. Since the late 20th century, scientists have used the techniques of molecular biology to modify or introduce genes for desired traits in a variety of organisms, including domestic plants and animals; this field has become known as genetic engineering or recombinant DNA technology. Improvements that in the past were achieved after tens of generations by artificial selection can now be accomplished much more effectively and rapidly (within a single generation) by molecular genetic technology.

The success of artificial selection for virtually every trait and every organism in which it has been tried suggests that genetic variation is pervasive throughout natural populations. But evolutionists like to go one step farther and obtain quantitative estimates. Only since the 1960s, with the advances of molecular biology, have geneticists developed methods for measuring the extent of genetic variation in populations or among species of organisms. These methods consist essentially of taking a sample of genes and finding out how many are variable and how variable each one is. One simple way of measuring the variability of a gene locus is to ascertain what proportion of the individuals in a population are heterozygotes at that locus. In a heterozygous individual the two genes for a trait, one received from the mother and the other from the father, are different. The proportion of heterozygotes in the population is, therefore, the same as the probability that two genes taken at random from the gene pool are different.

Techniques for determining heterozygosity have been used to investigate numerous species of plants and animals. Typically, insects and other invertebrates are more varied genetically than mammals and other vertebrates, and plants bred by outcrossing (crossing with relatively unrelated strains) exhibit more variation than those bred by self-pollination. But the amount of genetic variation is in any case astounding. Consider as an example humans, whose level of variation is about the same as that of other mammals. The human heterozygosity value at the level of proteins is stated as H = 0.067, which means that an individual is heterozygous at 6.7 percent of his genes, because the two genes at each locus encode slightly different proteins. The human genome contains an estimated 20,000–25,000 genes. This means that a person is heterozygous at no fewer than 30,000 × 0.067 = 2,010 gene loci. An individual heterozygous at one locus (Aa) can produce two different kinds of sex cells, or gametes, one with each allele (A and a); an individual heterozygous at two loci (AaBb) can produce four kinds of gametes (AB, Ab, aB, and ab); an individual heterozygous at n loci can potentially produce 2_n different gametes. Therefore, a typical human individual has the potential to produce $2^{2,010}$, or approximately 10^{605} (1 with 605 zeros following), different kinds of gametes. That number is much larger than the estimated number of atoms in the universe, about 10^{80}.

It is clear, then, that every sex cell produced by a human being is genetically different from every other sex cell and, therefore, that no two persons who ever existed or will ever exist are likely to be genetically identical—with the exception of identical twins, which develop from a single fertilized ovum. The same conclusion applies to all organisms that reproduce sexually; every individual represents a unique genetic configuration that will likely never be repeated again. This enormous

reservoir of genetic variation in natural populations provides virtually unlimited opportunities for evolutionary change in response to the environmental constraints and the needs of the organisms.

The Origin of Genetic Variation: Mutations

Life originated about 3.5 billion years ago in the form of primordial organisms that were relatively simple and very small. All living things have evolved from these lowly beginnings. At present there are more than two million known species, which are widely diverse in size, shape, and way of life, as well as in the DNA sequences that contain their genetic information. What has produced the pervasive genetic variation within natural populations and the genetic differences among species? There must be some evolutionary means by which existing DNA sequences are changed and new sequences are incorporated into the gene pools of species.

The information encoded in the nucleotide sequence of DNA is, as a rule, faithfully reproduced during replication, so that each replication results in two DNA molecules that are identical to each other and to the parent molecule. But heredity is not a perfectly conservative process; otherwise, evolution could not have taken place. Occasionally "mistakes," or mutations, occur in the DNA molecule during replication, so that daughter cells differ from the parent cells in the sequence or in the amount of DNA. A mutation first appears in a single cell of an organism, but it is passed on to all cells descended from the first. Mutations can be classified into two categories—gene, or point, mutations, which affect only a few nucleotides within a gene, and chromosomal mutations, which either change the number of chromosomes or change the number or arrangement of genes on a chromosome.

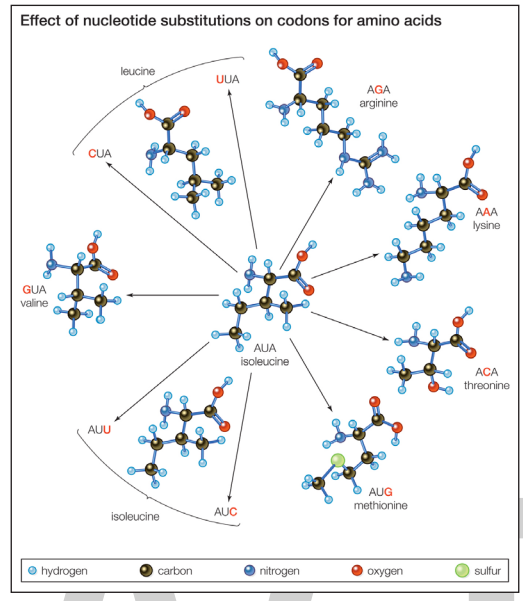
Gene Mutations

A gene mutation occurs when the nucleotide sequence of the DNA is altered and a new sequence is passed on to the offspring. The change may be either a substitution of one or a few nucleotides for others or an insertion or deletion of one or a few pairs of nucleotides.

The four nucleotide bases of DNA, named adenine, cytosine, guanine, and thymine, are represented by the letters A, C, G, and T, respectively. A gene that bears the code for constructing a protein molecule consists of a sequence of several thousand nucleotides, so that each segment of three nucleotides—called a triplet or codon—codes for one particular amino acid in the protein. The nucleotide sequence in the DNA is first transcribed into a molecule of messenger RNA (ribonucleic acid). The RNA, using a slightly different code (represented by the letters A, C, G, and U, the last letter representing the nucleotide base uracil), bears the message that determines which amino acid will be inserted into the protein's chain in the process of translation. Substitutions in the nucleotide sequence of a structural gene may result in changes in the amino acid sequence of the protein, although this is not always the case. The genetic code is redundant in that different triplets may hold the code for the same amino acid. Consider the triplet AUA in messenger RNA, which codes for the amino acid isoleucine. If the last A is replaced by C, the triplet still codes for isoleucine, but if it is replaced by G, it codes for methionine instead.

The effect of base substitutions, or point mutations, on the messenger-RNA codon AUA, which codes for the amino acid isoleucine is shown in the above figure. Substitutions (red letters) at the first, second, or third position in the codon can result in nine new codons corresponding to six

different amino acids in addition to isoleucine itself. The chemical properties of some of these amino acids are quite different from those of isoleucine. Replacement of one amino acid in a protein by another can seriously affect the protein's biological function.



Point mutation.

A nucleotide substitution in the DNA that results in an amino acid substitution in the corresponding protein may or may not severely affect the biological function of the protein. Some nucleotide substitutions change a codon for an amino acid into a signal to terminate translation, and those mutations are likely to have harmful effects. If, for instance, the second U in the triplet UUA, which codes for leucine, is replaced by A, the triplet becomes UAA, a "terminator" codon; the result is that the triplets following this codon in the DNA sequence are not translated into amino acids.

Additions or deletions of nucleotides within the DNA sequence of a structural gene often result in a greatly altered sequence of amino acids in the coded protein. The addition or deletion of one or two nucleotides shifts the "reading frame" of the nucleotide sequence all along the way from the point of the insertion or deletion to the end of the molecule. To illustrate, assume that the DNA segment CATCATCATCATCAT is read in groups of three as CAT-CAT-CAT-CAT-CAT. If a nucleotide base—say, T—is inserted after the first C of the segment, the segment will then be read as CTA-TCA-TCA-TCA-TCA. From the point of the insertion onward, the sequence of encoded amino acids is altered. If, however, a total of three nucleotides is either added or deleted, the original reading frame will be maintained in the rest of the sequence. Additions or deletions of nucleotides in numbers other than three or multiples of three are called frameshift mutations.

Gene mutations can occur spontaneously—that is, without being intentionally caused by humans. They can also be induced by ultraviolet light, X-rays, and other high-frequency electromagnetic radiation, as well as by exposure to certain mutagenic chemicals, such as mustard gas. The consequences of gene mutations may range from negligible to lethal. Mutations that change one or even several amino acids may have a small or undetectable effect on the organism's ability to survive and reproduce if the essential biological function of the coded protein is not hindered. But where

an amino acid substitution affects the active site of an enzyme or modifies in some other way an essential function of a protein, the impact may be severe.

Newly arisen mutations are more likely to be harmful than beneficial to their carriers, because mutations are random events with respect to adaptation—that is, their occurrence is independent of any possible consequences. The allelic variants present in an existing population have already been subject to natural selection. They are present in the population because they improve the adaptation of their carriers, and their alternative alleles have been eliminated or kept at low frequencies by natural selection. A newly arisen mutant is likely to have been preceded by an identical mutation in the previous history of a population. If the previous mutant no longer exists in the population, it is a sign that the new mutant is not beneficial to the organism and is likely also to be eliminated.

This proposition can be illustrated with an analogy. Consider a sentence whose words have been chosen because together they express a certain idea. If single letters or words are replaced with others at random, most changes will be unlikely to improve the meaning of the sentence; very likely they will destroy it. The nucleotide sequence of a gene has been "edited" into its present form by natural selection because it "makes sense." If the sequence is changed at random, the "meaning" rarely will be improved and often will be hampered or destroyed.

Occasionally, however, a new mutation may increase the organism's adaptation. The probability of such an event's happening is greater when organisms colonize a new territory or when environmental changes confront a population with new challenges. In these cases the established adaptation of a population is less than optimal, and there is greater opportunity for new mutations to be better adaptive. The consequences of mutations depend on the environment. Increased melanin pigmentation may be advantageous to inhabitants of tropical Africa, where dark skin protects them from the Sun's ultraviolet radiation, but it is not beneficial in Scandinavia, where the intensity of sunlight is low and light skin facilitates the synthesis of vitamin D.

Mutation rates have been measured in a great variety of organisms, mostly for mutants that exhibit conspicuous effects. Mutation rates are generally lower in bacteria and other microorganisms than in more complex species. In humans and other multicellular organisms, the rate typically ranges from about 1 per 100,000 to 1 per 1,000,000 gametes. There is, however, considerable variation from gene to gene as well as from organism to organism.

Although mutation rates are low, new mutants appear continuously in nature, because there are many individuals in every species and many gene loci in every individual. The process of mutation provides each generation with many new genetic variations. Thus, it is not surprising to see that, when new environmental challenges arise, species are able to adapt to them. More than 200 insect and rodent species, for example, have developed resistance to the pesticide DDT in parts of the world where spraying has been intense. Although these animals had never before encountered this synthetic compound, they adapted to it rapidly by means of mutations that allowed them to survive in its presence. Similarly, many species of moths and butterflies in industrialized regions have shown an increase in the frequency of individuals with dark wings in response to environmental pollution, an adaptation known as industrial melanism.

The resistance of disease-causing bacteria and parasites to antibiotics and other drugs is a consequence of the same process. When an individual receives an antibiotic that specifically kills the bacteria causing the disease—say, tuberculosis—the immense majority of the bacteria die, but one in a million may have a mutation that provides resistance to the antibiotic. These resistant bacteria will survive and multiply, and the antibiotic will no longer cure the disease. This is the reason that modern medicine treats bacterial diseases with cocktails of antibiotics. If the incidence of a mutation conferring resistance for a given antibiotic is one in a million, the incidence of one bacterium carrying three mutations, each conferring resistance to one of three antibiotics, is one in a trillion; such bacteria are far less likely to exist in any infected individual.

Chromosomal Mutations

Chromosomes, which carry the hereditary material, or DNA, are contained in the nucleus of each cell. Chromosomes come in pairs, with one member of each pair inherited from each parent. The two members of a pair are called homologous chromosomes. Each cell of an organism and all individuals of the same species have, as a rule, the same number of chromosomes. The reproductive cells (gametes) are an exception; they have only half as many chromosomes as the body (somatic) cells. But the number, size, and organization of chromosomes varies between species. The parasitic nematode Parascaris univalens has only one pair of chromosomes, whereas many species of butterflies have more than 100 pairs and some ferns more than 600. Even closely related organisms may vary considerably in the number of chromosomes. Species of spiny rats of the South American genus Proechimys range from 12 to 31 chromosome pairs.

Changes in the number, size, or organization of chromosomes within a species are termed chromosomal mutations, chromosomal abnormalities, or chromosomal aberrations. Changes in number may occur by the fusion of two chromosomes into one, by fission of one chromosome into two, or by addition or subtraction of one or more whole chromosomes or sets of chromosomes. (The condition in which an organism acquires one or more additional sets of chromosomes is called polyploidy.) Changes in the structure of chromosomes may occur by inversion, when a chromosomal segment rotates 180 degrees within the same location; by duplication, when a segment is added; by deletion, when a segment is lost; or by translocation, when a segment changes from one location to another in the same or a different chromosome. These are the processes by which chromosomes evolve. Inversions, translocations, fusions, and fissions do not change the amount of DNA. The importance of these mutations in evolution is that they change the linkage relationships between genes. Genes that were closely linked to each other become separated and vice versa; this can affect their expression because genes are often transcribed sequentially, two or more at a time.

Dynamics of Genetic Change

Genetic Equilibrium: The Hardy-Weinberg Law

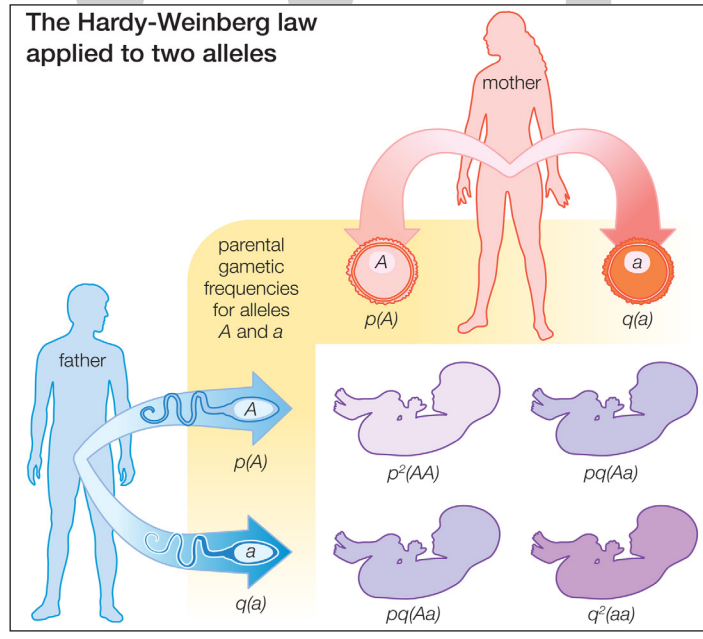
Genetic variation is present throughout natural populations of organisms. This variation is sorted out in new ways in each generation by the process of sexual reproduction, which recombines the chromosomes inherited from the two parents during the formation of the gametes that produce the following generation. But heredity by itself does not change gene frequencies. This principle is stated by the Hardy-Weinberg law, so called because it was independently discovered in 1908 by the English mathematician G.H. Hardy and the German physician Wilhelm Weinberg.

The Hardy-Weinberg law describes the genetic equilibrium in a population by means of an algebraic equation. It states that genotypes, the genetic constitution of individual organisms, exist in certain frequencies that are a simple function of the allelic frequencies—namely, the square expansion of the sum of the allelic frequencies.

If there are two alleles, A and a, at a gene locus, three genotypes will be possible: AA, Aa, and aa. If the frequencies of the alleles A and a are p and q, respectively, the equilibrium frequencies of the three genotypes will be given by $(p + q)^2 = p^2 + 2pq + q^2$ for AA, Aa, and aa, respectively. The genotype equilibrium frequencies for any number of alleles are derived in the same way. If there are three alleles A_1, A_2, and A_3 with frequencies p, q, and r, the equilibrium frequencies corresponding to the six possible genotypes will be calculated as follows:

$$(p+q+r)^2 = p^2(A_1A_1) + q^2(A_2A_2) + r^2(A_3A_3) + 2pq(A_1A_2) + 2pr(A_1A_3) + 2qr(A_2A_3).$$

The figure shows how the law operates in a situation with just two alleles. Across the top and down the left side are the frequencies in the parental generation of the two alleles, p for A and q for a. As shown in the lower right of the figure, the probabilities of the three possible genotypes in the following generation are products of the probabilities of the corresponding alleles in the parents. The probability of genotype AA among the progeny is the probability p that allele A will be present in the paternal gamete multiplied by the probability p that allele A will be present in the maternal gamete, or p2. Similarly, the probability of the genotype aa is q2. The genotype Aa can arise when A from the father combines with a from the mother, which will occur with a frequency pq, or when a from the father combines with A from the mother, which also has a probability of pq; the result is a total probability of 2pq for the frequency of the Aa genotype in the progeny.



There is no change in the allele equilibrium frequencies from one generation to the next. The frequency of the A allele among the offspring is the frequency of the AA genotype (because all alleles

in these individuals are A alleles) plus half the frequency of the Aa genotype (because half the alleles in these individuals are A alleles), or $p^2 + pq = p(p + q) = p$ (because $p + q = 1$). Similarly, the frequency of the a allele among the offspring is given by $q^2 + pq = q(q + p) = q$. These are precisely the frequencies of the alleles in the parents.

The genotype equilibrium frequencies are obtained by the Hardy-Weinberg law on the assumption that there is random mating—that is, the probability of a particular kind of mating is the same as the frequency of the genotypes of the two mating individuals. For example, the probability of an AA female mating with an aa male must be p^2 (the frequency of AA) times q^2 (the frequency of aa). Random mating can occur with respect to most gene loci even though mates may be chosen according to particular characteristics. People, for example, choose their spouses according to all sorts of preferences concerning looks, personality, and the like. But concerning the majority of genes, people's marriages are essentially random.

Assortative, or selective, mating takes place when the choice of mates is not random. Marriages in the United States, for example, are assortative with respect to many social factors, so that members of any one social group tend to marry members of their own group more often, and people from a different group less often, than would be expected from random mating. Consider the sensitive social issue of interracial marriage in a hypothetical community in which 80 percent of the population is white and 20 percent is black. With random mating, 32 percent ($2 \times 0.80 \times 0.20 = 0.32$) of all marriages would be interracial, whereas only 4 percent ($0.20 \times 0.20 = 0.04$) would be marriages between two blacks. These statistical expectations depart from typical observations even in modern society, as a result of persistent social customs that for evolutionists are examples of assortative mating. The most extreme form of assortative mating is self-fertilization, which occurs rarely in animals but is a common form of reproduction in many plant groups.

The Hardy-Weinberg law assumes that gene frequencies remain constant from generation to generation—that there is no gene mutation or natural selection and that populations are very large. But these assumptions are not correct; indeed, if they were, evolution could not occur. Why, then, is the law significant if its assumptions do not hold true in nature? The answer is that it plays in evolutionary studies a role similar to that of Newton's first law of motion in mechanics. Newton's first law says that a body not acted upon by a net external force remains at rest or maintains a constant velocity. In fact, there are always external forces acting upon physical objects, but the first law provides the starting point for the application of other laws. Similarly, organisms are subject to mutation, selection, and other processes that change gene frequencies, but the effects of these processes can be calculated by using the Hardy-Weinberg law as the starting point.

Processes of Gene-frequency Change

Mutation

The allelic variations that make evolution possible are generated by the process of mutation, but new mutations change gene frequencies very slowly, because mutation rates are low. Assume that the gene allele A_1 mutates to allele A_2 at a rate m per generation and that at a given time the frequency of A_1 is p. In the next generation, a fraction m of all A_1 alleles become A_2 alleles. The

frequency of A_1 in the next generation will then be reduced by the fraction of mutated alleles (pm), or $p_1 = p - pm = p(1 - m)$. After t generations the frequency of A_1 will be $p_t = p(1 - m)^t$.

If the mutations continue, the frequency of A_1 alleles will gradually decrease, because a fraction of them change every generation to A_2. If the process continues indefinitely, the A_1 allele will eventually disappear, although the process is slow. If the mutation rate is 10^{-5} (1 in 100,000) per gene per generation, about 2,000 generations will be required for the frequency of A_1 to change from 0.50 to 0.49 and about 10,000 generations for it to change from 0.10 to 0.09.

Moreover, gene mutations are reversible: the allele A_2 may also mutate to A_1. Assume that A_1 mutates to A_2 at a rate m, as before, and that A_2 mutates to A1 at a rate n per generation. If at a certain time the frequencies of A_1 and A_2 are p and q, respectively, after one generation the frequency of A_1 will be $p_1 = p - pm + qn$. A fraction pm of allele A_1 changes to A_2, but a fraction qn of the A_2 alleles changes to A_1. The conditions for equilibrium occur when $pm = qn$, or $p = n/(m + n)$ Suppose that the mutation rates are $m = 10^{-5}$ and $n = 10^{-6}$; then, at equilibrium, $p = 10^{-6}/(10^{-5} + 10^{-6}) = 1/(10 + 1) = 0.09$, and $q = 0.91$.

Changes in gene frequencies due to mutation occur, therefore, at rates even slower than was suggested above, because forward and backward mutations counteract each other. In any case, allelic frequencies usually are not in mutational equilibrium, because some alleles are favoured over others by natural selection. The equilibrium frequencies are then decided by the interaction between mutation and selection, with selection usually having the greater consequence.

Gene Flow

Gene flow, or gene migration, takes place when individuals migrate from one population to another and interbreed with its members. Gene frequencies are not changed for the species as a whole, but they change locally whenever different populations have different allele frequencies. In general, the greater the difference in allele frequencies between the resident and the migrant individuals, and the larger the number of migrants, the greater effect the migrants have in changing the genetic constitution of the resident population.

Suppose that a proportion of all reproducing individuals in a population are migrants and that the frequency of allele A_1 is p in the population but pm among the migrants. The change in gene frequency, Δp, in the next generation will be $\Delta p = m(p_m - p)$.If the migration rate persists for a number t of generations, the frequency of A_1 will be given by $pt = (1 - m)t(p - p_m) + p_m$.

Genetic Drift

Gene frequencies can change from one generation to another by a process of pure chance known as genetic drift. This occurs because the number of individuals in any population is finite, and thus the frequency of a gene may change in the following generation by accidents of sampling, just as it is possible to get more or fewer than 50 “heads” in 100 throws of a coin simply by chance.

The magnitude of the gene frequency changes due to genetic drift is inversely related to the size of the population—the larger the number of reproducing individuals, the smaller the effects of

genetic drift. This inverse relationship between sample size and magnitude of sampling errors can be illustrated by referring again to tossing a coin. When a penny is tossed twice, two heads are not surprising. But it will be surprising, and suspicious, if 20 tosses all yield heads. The proportion of heads obtained in a series of throws approaches closer to 0.5 as the number of throws grows larger.

The relationship is the same in populations, although the important value here is not the actual number of individuals in the population but the "effective" population size. This is the number of individuals that produce offspring, because only reproducing individuals transmit their genes to the following generation. It is not unusual, in plants as well as animals, for some individuals to have large numbers of progeny while others have none. In marine seals, antelopes, baboons, and many other mammals, for example, a dominant male may keep a large harem of females at the expense of many other males who can find no mates. It often happens that the effective population size is substantially smaller than the number of individuals in any one generation.

The effects of genetic drift in changing gene frequencies from one generation to the next are quite small in most natural populations, which generally consist of thousands of reproducing individuals. The effects over many generations are more important. Indeed, in the absence of other processes of change (such as natural selection and mutation), populations would eventually become fixed, having one allele at each locus after the gradual elimination of all others. With genetic drift as the only force in operation, the probability of a given allele's eventually reaching a frequency of 1 would be precisely the frequency of the allele—that is, an allele with a frequency of 0.8 would have an 80 percent chance of ultimately becoming the only allele present in the population. The process would, however, take a long time, because increases and decreases are likely to alternate with equal probability. More important, natural selection and other processes change gene frequencies in ways not governed by pure chance, so that no allele has an opportunity to become fixed as a consequence of genetic drift alone.

Genetic drift can have important evolutionary consequences when a new population becomes established by only a few individuals—a phenomenon known as the founder principle. Islands, lakes, and other isolated ecological sites are often colonized by one or very few seeds or animals of a species, which are transported there passively by wind, in the fur of larger animals, or in some other way. The allelic frequencies present in these few colonizers are likely to differ at many loci from those in the population they left, and those differences have a lasting impact on the evolution of the new population. The founder principle is one reason that species in neighbouring islands, such as those in the Hawaiian archipelago, are often more heterogeneous than species in comparable continental areas adjacent to one another.

Climatic or other conditions, if unfavourable, may on occasion drastically reduce the number of individuals in a population and even threaten it with extinction. Such occasional reductions are called population bottlenecks. The populations may later recover their typical size, but the allelic frequencies may have been considerably altered and thereby affect the future evolution of the species. Bottlenecks are more likely in relatively large animals and plants than in smaller ones, because populations of large organisms typically consist of fewer individuals. Primitive human populations of the past were subdivided into many small tribes that were time and again decimated by disease, war, and other disasters. Differences among current human populations in the allele

frequencies of many genes—such as those determining the ABO and other blood groups—may have arisen at least in part as a consequence of bottlenecks in ancestral populations. Persistent population bottlenecks may reduce the overall genetic variation so greatly as to alter future evolution and endanger the survival of the species. A well-authenticated case is that of the cheetah, where no allelic variation whatsoever has been found among the many scores of gene loci studied.

The Operation of Natural Selection in Populations

Natural Selection as a Process of Genetic Change

Natural selection refers to any reproductive bias favouring some genes or genotypes over others. Natural selection promotes the adaptation of organisms to the environments in which they live; any hereditary variant that improves the ability to survive and reproduce in an environment will increase in frequency over the generations, precisely because the organisms carrying such a variant will leave more descendants than those lacking it. Hereditary variants, favourable or not to the organisms, arise by mutation. Unfavourable ones are eventually eliminated by natural selection; their carriers leave no descendants or leave fewer than those carrying alternative variants. Favourable mutations accumulate over the generations. The process continues indefinitely because the environments that organisms inhabit are forever changing. Environments change physically—in their climate, configuration, and so on—but also biologically, because the predators, parasites, competitors, and food sources with which an organism interacts are themselves evolving.

Mutation, gene flow, and genetic drift are random processes with respect to adaptation; they change gene frequencies without regard for the consequences that such changes may have in the ability of the organisms to survive and reproduce. If these were the only processes of evolutionary change, the organization of living things would gradually disintegrate. The effects of such processes alone would be analogous to those of a mechanic who changed parts in an automobile engine at random, with no regard for the role of the parts in the engine. Natural selection keeps the disorganizing effects of mutation and other processes in check because it multiplies beneficial mutations and eliminates harmful ones.

Natural selection accounts not only for the preservation and improvement of the organization of living beings but also for their diversity. In different localities or in different circumstances, natural selection favours different traits, precisely those that make the organisms well adapted to their particular circumstances and ways of life.

The parameter used to measure the effects of natural selection is fitness, which can be expressed as an absolute or as a relative value. Consider a population consisting at a certain locus of three genotypes: A_1A_1, A_1A_2, and A_2A_2. Assume that on the average each A_1A_1 and each A_1A_2 individual produces one offspring but that each A_2A_2 individual produces two. One could use the average number of progeny left by each genotype as a measure of that genotype's absolute fitness and calculate the changes in gene frequency that would occur over the generations. (This, of course, requires knowing how many of the progeny survive to adulthood and reproduce.) Evolutionists, however, find it mathematically more convenient to use relative fitness values—which they represent with the letter w—in most calculations. They usually assign the value 1 to the genotype with the highest reproductive efficiency and calculate the other relative fitness values proportionally. For the example just used, the relative fitness of the A_2A_2 genotype would be w = 1 and that of each

of the other two genotypes would be w = 0.5. A parameter related to fitness is the selection coefficient, often represented by the letter s, which is defined as s = 1 – w. The selection coefficient is a measure of the reduction in fitness of a genotype. The selection coefficients in the example are s = 0 for A_2A_2 and s = 0.5 for A_1A_1 and for A_1A_2.

Selection Against one of the Homozygotes

Suppose that one homozygous genotype, A_2A_2, has lower fitness than the other two genotypes, A_1A_1 and A_1A_2. (This is the situation in many human diseases, such as phenylketonuria [PKU] and sickle cell anemia, that are inherited in a recessive fashion and that require the presence of two deleterious mutant alleles for the trait to manifest.) The heterozygotes and the homozygotes for the normal allele (A_1) have equal fitness, higher than that of the homozygotes for the deleterious mutant allele (A_2). Call the fitness of these latter homozygotes 1 – s (the fitness of the other two genotypes is 1), and let p be the frequency of A_1 and q the frequency of A_2. It can be shown that the frequency of A_2 will decrease each generation by an amount given by $\Delta q = -spq^2/(1-sq^2)$. The deleterious allele will continuously decrease in frequency until it has been eliminated. The rate of elimination is fastest when s = 1 (i.e., when the relative fitness w = 0); this occurs with fatal diseases, such as untreated PKU, when the homozygotes die before the age of reproduction.

Because of new mutations, the elimination of a deleterious allele is never complete. A dynamic equilibrium frequency will exist when the number of new alleles produced by mutation is the same as the number eliminated by selection. If the mutation rate at which the deleterious allele arises is u, the equilibrium frequency for a deleterious allele that is recessive is given approximately by $q = \sqrt{u/s}$ which, if s = 1, reduces to $q = \sqrt{u}$.

The mutation rate for many human recessive diseases is about 1 in 100,000 ($u = 10^{-5}$). If the disease is fatal, the equilibrium frequency becomes $q \cong \sqrt{10^{-5}} = 0.003$, or about 1 recessive lethal mutant allele for every 300 normal alleles. That is roughly the frequency in human populations of alleles that in homozygous individuals, such as those with PKU, cause death before adulthood. The equilibrium frequency for a deleterious, but not lethal, recessive allele is much higher. Albinism, for example, is due to a recessive gene. The reproductive efficiency of albinos is, on average, about 0.9 that of normal individuals. Therefore, $s = 0.1$ and $q = \sqrt{u/s} = \sqrt{10^{-5}/10^{-1}} = 0.01$ or 1 in 100 genes rather than 1 in 300 as for a lethal allele.

For deleterious dominant alleles, the mutation-selection equilibrium frequency is given by $p = u/s$, which for fatal genes becomes $p = u$. If the gene is lethal even in single copy, all the genes are eliminated by selection in the same generation in which they arise, and the frequency of the gene in the population is the frequency with which it arises by mutation. One deleterious condition that is caused by a dominant allele present at low frequencies in human populations is achondroplasia, the most common cause of dwarfism. Because of abnormal growth of the long bones, achondroplastics have short, squat, often deformed limbs, along with bulging skulls. The mutation rate from the normal allele to the achondroplasia allele is about 5×10^{-5}. Achondroplastics reproduce only 20 percent as efficiently as normal individuals; hence, s = 0.8. The equilibrium frequency of the mutant allele can therefore be calculated as $p = u/s = 6.25 \times 10^{-5}$.

Overdominance

In many instances heterozygotes have a higher degree of fitness than homozygotes for one or the other allele. This situation, known as heterosis or overdominance, leads to the stable coexistence of both alleles in the population and hence contributes to the widespread genetic variation found in populations of most organisms. The model situation is:

Genotype	A_1A_1	A_1A_2	A_2A_2
Fitness(w)	$1-s$	1	$1-t$

It is assumed that s and t are positive numbers between 0 and 1, so that the fitnesses of the two homozygotes are somewhat less than 1. It is not difficult to show that the change in frequency per generation of allele A_2 is $\Delta q = pq(sp - tq)/(1 - sp^2 - tq^2)$ An equilibrium will exist when $\Delta q = 0$ (gene frequencies no longer change); this will happen when sp = tq, at which the numerator of the expression for Δq will be 0. The condition $sp = tq$ can be rewritten as $s(1 - q) = tq$ (when $p + q = 1$), which leads to $q = s/(s + t)$. If the fitnesses of the two homozygotes are known, it is possible to infer the allele equilibrium frequencies.

One of many well-investigated examples of overdominance in animals is the colour polymorphism that exists in the marine copepod crustacean Tisbe reticulata. Three populations of colour variants (morphs) are found in the lagoon of Venice; they are known as violacea (homozygous genotype $V^V V^V$), maculata (homozygous genotype $V^M V^M$), and violacea-maculata (heterozygous genotype $V^V V^M$). The colour polymorphism persists in the lagoon because the heterozygotes survive better than either of the two homozygotes. In laboratory experiments, the fitness of the three genotypes depends on the degree of crowding, as shown by the following comparison of their relative fitnesses:

Genotype	Fitness in low crowding	Fitness in high crowding
$V^v V^v$	0.89	0.66
$V^v V^M$	1	1
$V^M V^M$	0.90	0.62

The greater the crowding—with more competition for resources—the greater the superiority of the heterozygotes. (In this example, the colour trait serves a genetic marker—individuals heterozygous for the marker have higher fitness, but whether this is due to the colour per se is not known.)

A particularly interesting example of heterozygote superiority among humans is provided by the gene responsible for sickle cell anemia. Human hemoglobin in adults is for the most part hemoglobin A, a four-component molecule consisting of two α and two β hemoglobin chains. The gene Hb^A codes for the normal β hemoglobin chain, which consists of 146 amino acids. A mutant allele of this gene, Hb^S, causes the β chain to have in the sixth position the amino acid valine instead of glutamic acid. This seemingly minor substitution modifies the properties of hemoglobin so that homozygotes with the mutant allele, Hb^SHb^S suffer from a severe form of anemia that in most cases leads to death before the age of reproduction.

The Hb^S allele occurs in some African and Asian populations with a high frequency. This formerly was puzzling because the severity of the anemia, representing a strong natural selection against homozygotes, should have eliminated the defective allele. But researchers noticed that the Hb^S allele occurred at high frequency precisely in regions of the world where a particularly severe form of malaria, which is caused by the parasite Plasmodium falciparum, was endemic. It was hypothesized that the heterozygotes, Hb^{AHbS}, were resistant to malaria, whereas the homozygotes Hb^{AHbA} were not. In malaria-infested regions then the heterozygotes survived better than either of the homozygotes, which were more likely to die from either malaria (Hb^{AHbA} homozygotes) or anemia (Hb^{SHbS} homozygotes). This hypothesis has been confirmed in various ways. Most significant is that most hospital patients suffering from severe or fatal forms of malaria are homozygotes Hb^{AHbA}. In a study of 100 children who died from malaria, only 1 was found to be a heterozygote, whereas 22 were expected to be so according to the frequency of the Hb^S allele in the population.

The table shows how the relative fitness of the three β-chain genotypes can be calculated from their distribution among the Yoruba people of Ibadan, Nigeria. The frequency of the Hb^S allele among adults is estimated as q = 0.1232. According to the Hardy-Weinberg law, the three genotypes will be formed at conception in the frequencies p^2, $2pq$, and q^2 which are the expected frequencies given in the table. The ratios of the observed frequencies among adults to the expected frequencies give the relative survival efficiency of the three genotypes. These are divided by their largest value (1.12) in order to obtain the relative fitness of the genotypes. Sickle cell anemia reduces the probability of survival of the Hb^{SHbS} homozygotes to 13 percent of that of the heterozygotes. On the other hand, malaria infection reduces the survival probability of the homozygotes for the normal allele, Hb^{AHbA}, to 88 percent of that of the heterozygotes.

Table: Fitnesses of the three genotypes at the sickle cell anemia locus in a population.

	Genotype			Total	Frequency of Hb^S
	Hb^AHb^A	Hb^AHb^S	Hb^SHb^S		
Observed number	9,365	2,993	29	12,387	
Observed frequency	0.7560	0.2416	0.0023	1	0.1232
Expected frequency	0.7688	0.2160	0.0152	1	0.1232
Survival efficiency	0.98	1.12	0.15		
Relative fitness	0.88	1	0.13		

Frequency-dependent Selection

The fitness of genotypes can change when the environmental conditions change. White fur may be protective to a bear living on the Arctic snows but not to one living in a Russian forest; there an allele coding for brown pigmentation may be favoured over one that codes for white. The environment of an organism includes not only the climate and other physical features but also the organisms of the same or different species with which it is associated.

Changes in genotypic fitness are associated with the density of the organisms present. Insects and other short-lived organisms experience enormous yearly oscillations in density. Some genotypes

may possess high fitness in the spring, when the population is rapidly expanding, because such genotypes yield more prolific individuals. Other genotypes may be favoured during the summer, when populations are dense, because these genotypes make for better competitors, ones more successful at securing limited food resources. Still others may be at an advantage during the long winter months, because they increase the population's hardiness, or ability to withstand the inclement conditions that kill most members of the other genotypes.

The fitness of genotypes can also vary according to their relative numbers, and genotype frequencies may change as a consequence. This is known as frequency-dependent selection. Particularly interesting is the situation in which genotypic fitnesses are inversely related to their frequencies. Assume that two genotypes, A and B, have fitnesses related to their frequencies in such a way that the fitness of either genotype increases when its frequency decreases and vice versa. When A is rare, its fitness is high, and therefore A increases in frequency. As it becomes more and more common, however, the fitness of A gradually decreases, so that its increase in frequency eventually comes to a halt. A stable polymorphism occurs at the frequency where the two genotypes, A and B, have identical fitnesses.

In natural populations of animals and plants, frequency-dependent selection is very common and may contribute importantly to the maintenance of genetic polymorphism. In the vinegar fly Drosophila pseudoobscura, for example, three genotypes exist at the gene locus that codes for the metabolically important enzyme malate dehydrogenase—the homozygous SS and FF and the heterozygous *SF*. When the *SS* homozygotes represent 90 percent of the population, they have a fitness about two-thirds that of the heterozygotes, SF. But when the SS homozygotes represent only 10 percent of the population, their fitness is more than double that of the heterozygotes. Similarly, the fitness of the *FF* homozygotes relative to the heterozygotes increases from less than half to nearly double as their frequency goes from 90 to 10 percent. All three genotypes have equal fitnesses when the frequency of the S allele, represented by p, is about 0.70, so that there is a stable polymorphism with frequencies $p^2 = 0.49$ for *SS*, $2pq = 0.42$ for *SF*, and $q^2 = 0.09$ for *FF*.

Frequency-dependent selection may arise because the environment is heterogeneous and because different genotypes can better exploit different subenvironments. When a genotype is rare, the subenvironments that it exploits better will be relatively abundant. But as the genotype becomes common, its favoured subenvironment becomes saturated. That genotype must then compete for resources in subenvironments that are optimal for other genotypes. It follows then that a mixture of genotypes exploits the environmental resources better than a single genotype. This has been extensively demonstrated. When the three Drosophila genotypes mentioned above were mixed in a single population, the average number of individuals that developed per unit of food was 45.6. This was greater than the number of individuals that developed when only one of the genotypes was present, which averaged 41.1 for SS, 40.2 for SF, and 37.1 for *FF*. Plant breeders know that mixed plantings (a mixture of different strains) are more productive than single stands (plantings of one strain only), although farmers avoid them for reasons such as increased harvesting costs.

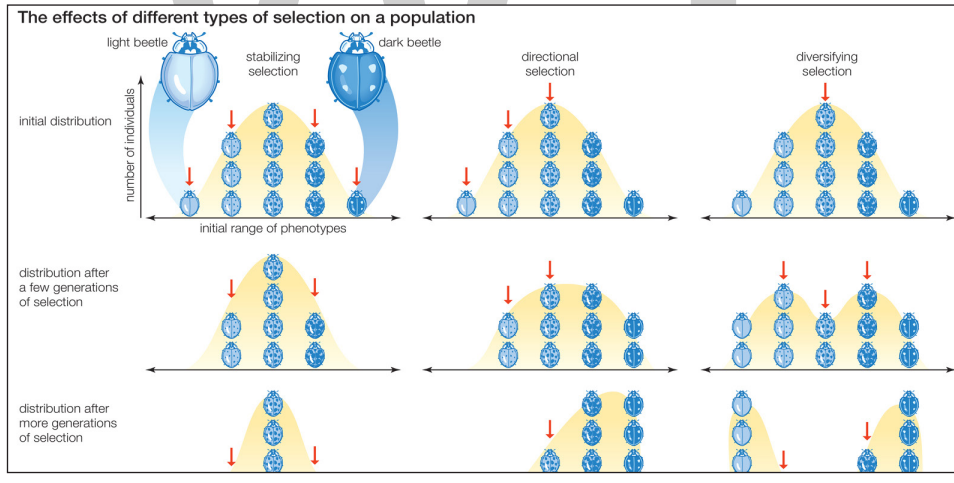
Sexual preferences can also lead to frequency-dependent selection. It has been demonstrated in some insects, birds, mammals, and other organisms that the mates preferred are precisely those that are rare. People also appear to experience this rare-mate advantage—blonds may seem attractively exotic to brunets, or brunets to blonds.

Types of Selection

Stabilizing Selection

Natural selection can be studied by analyzing its effects on changing gene frequencies, but it can also be explored by examining its effects on the observable characteristics—or phenotypes—of individuals in a population. Distribution scales of phenotypic traits such as height, weight, number of progeny, or longevity typically show greater numbers of individuals with intermediate values and fewer and fewer toward the extremes—this is the so-called normal distribution. When individuals with intermediate phenotypes are favoured and extreme phenotypes are selected against, the selection is said to be stabilizing. The range and distribution of phenotypes then remains approximately the same from one generation to another. Stabilizing selection is very common. The individuals that survive and reproduce more successfully are those that have intermediate phenotypic values. Mortality among newborn infants, for example, is highest when they are either very small or very large; infants of intermediate size have a greater chance of surviving.

In the figure above, the downward arrows point to those phenotypes against which selection acts. Stabilizing selection (left column) acts against phenotypes at both extremes of the distribution, favouring the multiplication of intermediate phenotypes. Directional selection (centre column) acts against only one extreme of phenotypes, causing a shift in distribution toward the other extreme. Diversifying selection (right column) acts against intermediate phenotypes, creating a split in distribution toward each extreme.



Three types of natural selection, showing the effects of each on the distribution of phenotypes within a population.

Stabilizing selection is often noticeable after artificial selection. Breeders choose chickens that produce larger eggs, cows that yield more milk, and corn with higher protein content. But the selection must be continued or reinstated from time to time, even after the desired goals have been achieved. If it is stopped altogether, natural selection gradually takes effect and turns the traits back toward their original intermediate value.

As a result of stabilizing selection, populations often maintain a steady genetic constitution with respect to many traits. This attribute of populations is called genetic homeostasis.

Directional Selection

The distribution of phenotypes in a population sometimes changes systematically in a particular direction. The physical and biological aspects of the environment are continuously changing, and over long periods of time the changes may be substantial. The climate and even the configuration of the land or waters vary incessantly. Changes also take place in the biotic conditions—that is, in the other organisms present, whether predators, prey, parasites, or competitors. Genetic changes occur as a consequence, because the genotypic fitnesses may shift so that different sets of alleles are favoured. The opportunity for directional selection also arises when organisms colonize new environments where the conditions are different from those of their original habitat. In addition, the appearance of a new favourable allele or a new genetic combination may prompt directional changes as the new genetic constitution replaces the preexisting one.

The process of directional selection takes place in spurts. The replacement of one genetic constitution with another changes the genotypic fitnesses at other loci, which then change in their allelic frequencies, thereby stimulating additional changes, and so on in a cascade of consequences.

Directional selection is possible only if there is genetic variation with respect to the phenotypic traits under selection. Natural populations contain large stores of genetic variation, and these are continuously replenished by additional new variants that arise by mutation. The nearly universal success of artificial selection and the rapid response of natural populations to new environmental challenges are evidence that existing variation provides the necessary materials for directional selection.

A light gray peppered moth (Biston betularia) and a darkly pigmented variant rest near each other on the trunk of a soot-covered oak tree.

Against this background, the light gray moth is more easily noticed than the darker variant.In modern times human actions have been an important stimulus to this type of selection. Human activity transforms the environments of many organisms, which rapidly respond to the new environmental challenges through directional selection. Well-known instances are the many

cases of insect resistance to pesticides, which are synthetic substances not present in the natural environment. When a new insecticide is first applied to control a pest, the results are encouraging because a small amount of the insecticide is sufficient to bring the pest organism under control. As time passes, however, the amount required to achieve a certain level of control must be increased again and again until finally it becomes ineffective or economically impractical. This occurs because organisms become resistant to the pesticide through directional selection. The resistance of the housefly, Musca domestica, to DDT was first reported in 1947. Resistance to one or more pesticides has since been recorded in several hundred species of insects and mites.

Another example is the phenomenon of industrial melanism, which is exemplified by the gradual darkening of the wings of many species of moths and butterflies living in woodlands darkened by industrial pollution. The best-investigated case is the peppered moth, Biston betularia, of England. Until the middle of the 19th century, these moths were uniformly peppered light gray. Darkly pigmented variants were detected first in 1848 in Manchester and shortly afterward in other industrial regions where the vegetation was blackened by soot and other pollutants. By the middle of the 20th century, the dark varieties had almost completely replaced the lightly pigmented forms in many polluted areas, while in unpolluted regions light moths continued to be the most common. The shift from light to dark moths was an example of directional selection brought about by bird predators. On lichen-covered tree trunks, the light-gray moths are well camouflaged, whereas the dark ones are conspicuously visible and therefore fall victim to the birds. The opposite is the case on trees darkened by pollution.

Against the background of a lichen-covered oak tree, a darkly pigmented peppered moth (Biston betularia) stands out, while the light gray moth (left) remains inconspicuous.

Over geologic time, directional selection leads to major changes in morphology and ways of life. Evolutionary changes that persist in a more or less continuous fashion over long periods of time are known as evolutionary trends. Directional evolutionary changes increased the cranial capacity of the human lineage from the small brain of Australopithecus—human ancestors of three million years ago—which was less than 500 cc in volume, to a brain nearly three times as large in modern humans. The evolution of the horse from more than 50 million years ago to modern times is another well-studied example of directional selection.

Diversifying Selection

Two or more divergent phenotypes in an environment may be favoured simultaneously by diversifying selection. No natural environment is homogeneous; rather, the environment of any plant or animal population is a mosaic consisting of more or less dissimilar subenvironments. There is heterogeneity with respect to climate, food resources, and living space. Also, the heterogeneity may be temporal, with change occurring over time, as well as spatial. Species cope with environmental heterogeneity in diverse ways. One strategy is genetic monomorphism, the selection of a generalist genotype that is well adapted to all the subenvironments encountered by the species. Another strategy is genetic polymorphism, the selection of a diversified gene pool that yields different genotypes, each adapted to a specific subenvironment.

There is no single plan that prevails in nature. Sometimes the most efficient strategy is genetic monomorphism to confront temporal heterogeneity but polymorphism to confront spatial heterogeneity. If the environment changes in time or if it is unstable relative to the life span of the organisms, each individual will have to face diverse environments appearing one after the other. A series of genotypes, each well adapted to one or another of the conditions that prevail at various times, will not succeed very well, because each organism will fare well at one period of its life but not at others. A better strategy is to have a population with one or a few genotypes that survive well in all the successive environments.

If the environment changes from place to place, the situation is likely to be different. Although a single genotype, well adapted to the various environmental patches, is a possible strategy, a variety of genotypes, with some individuals optimally adapted to each subenvironment, might fare still better. The ability of the population to exploit the environmental patchiness is thereby increased. Diversifying selection refers to the situation in which natural selection favours different genotypes in different subenvironments.

The efficiency of diversifying natural selection is quite apparent in circumstances in which populations living a short distance apart have become genetically differentiated. In one example, populations of bent grass can be found growing on heaps of mining refuse heavily contaminated with metals such as lead and copper. The soil has become so contaminated that it is toxic to most plants, but the dense stands of bent grass growing over these refuse heaps have been shown to possess genes that make them resistant to high concentrations of lead and copper. But only a few metres from the contaminated soil can be found bent grass plants that are not resistant to these metals. Bent grasses reproduce primarily by cross-pollination, so that the resistant grass receives wind-borne pollen from the neighbouring nonresistant plants. Yet they maintain their genetic differentiation because nonresistant seedlings are unable to grow in the contaminated soil and, in nearby uncontaminated soil, the nonresistant seedlings outgrow the resistant ones. The evolution of these resistant strains has taken place in the fewer than 400 years since the mines were first opened.

Protective morphologies and protective coloration exist in many animals as a defense against predators or as a cover against prey. Sometimes an organism mimics the appearance of a different one for protection. Diversifying selection often occurs in association with mimicry. A species of swallowtail butterfly, Papilio dardanus, is endemic in tropical and Southern Africa. Males have yellow and black wings, with characteristic tails in the second pair of wings. But females in many

localities are conspicuously different from males; their wings lack tails and have colour patterns that vary from place to place. The explanation for these differences stems from the fact that P. dardanus can be eaten safely by birds. Many other butterfly species are noxious to birds, and so they are carefully avoided as food. In localities where P. dardanus coexists with noxious butterfly species, the P. dardanus females have evolved an appearance that mimics the noxious species. Birds confuse the mimics with their models and do not prey on them. In different localities the females mimic different species; in some areas two or even three different female forms exist, each mimicking different noxious species. Diversifying selection has resulted in different phenotypes of P. dardanus as a protection from bird predators.

Sexual Selection

Mutual attraction between the sexes is an important factor in reproduction. The males and females of many animal species 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.

A pair of red deer stags (Cervus elaphus) competing for possession of a female in the rutting season.

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 northern sea 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.

Kin Selection and Reciprocal Altruism

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.

Members of a group of Japanese macaques grooming each other. Grooming is a type of altruistic behaviour that can extend even to unrelated individuals when the behaviour is reciprocal and the giver's costs are smaller than the recipient's benefits.

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.

Patterns and Rates of Species Evolution

Evolution within a Lineage and by Lineage Splitting

Evolution can take place by anagenesis, in which changes occur within a lineage, or by cladogenesis, in which a lineage splits into two or more separate lines. Anagenetic evolution has doubled the size of the human cranium over the course of two million years; in the lineage of the horse it has reduced the number of toes from four to one. Cladogenetic evolution has produced the extraordinary diversity of the living world, with its more than two million species of animals, plants, fungi, and microorganisms.

The most essential cladogenetic function is speciation, the process by which one species splits into two or more species. Because species are reproductively isolated from one another, they are independent evolutionary units; that is, evolutionary changes occurring in one species are not shared with other species. Over time, species diverge more and more from one another as a consequence of anagenetic evolution. Descendant lineages of two related species that existed millions of years ago may now be classified into quite different biological categories, such as different genera or even different families.

The evolution of all living organisms, or of a subset of them, can be seen as a tree, with branches that divide into two or more as time progresses. Such trees are called phylogenies. Their branches represent evolving lineages, some of which eventually die out while others persist in themselves or in their derived lineages down to the present time. Evolutionists are interested in the history of life and hence in the topology, or configuration, of phylogenies. They are concerned as well with the nature of the anagenetic changes within lineages and with the timing of the events.

Phylogenetic relationships are ascertained by means of several complementary sources of evidence. First, there are the discovered remnants of organisms that lived in the past, the fossil record, which provides definitive evidence of relationships between some groups of organisms. The fossil record, however, is far from complete and is often seriously deficient. Second, information about phylogeny comes from comparative studies of living forms. Comparative anatomy contributed the most information in the past, although additional knowledge came from comparative embryology, cytology, ethology, biogeography, and other biological disciplines. In recent years the comparative study of the so-called informational macromolecules—proteins and nucleic acids, whose specific sequences of constituents carry genetic information—has become a powerful tool for the study of phylogeny.

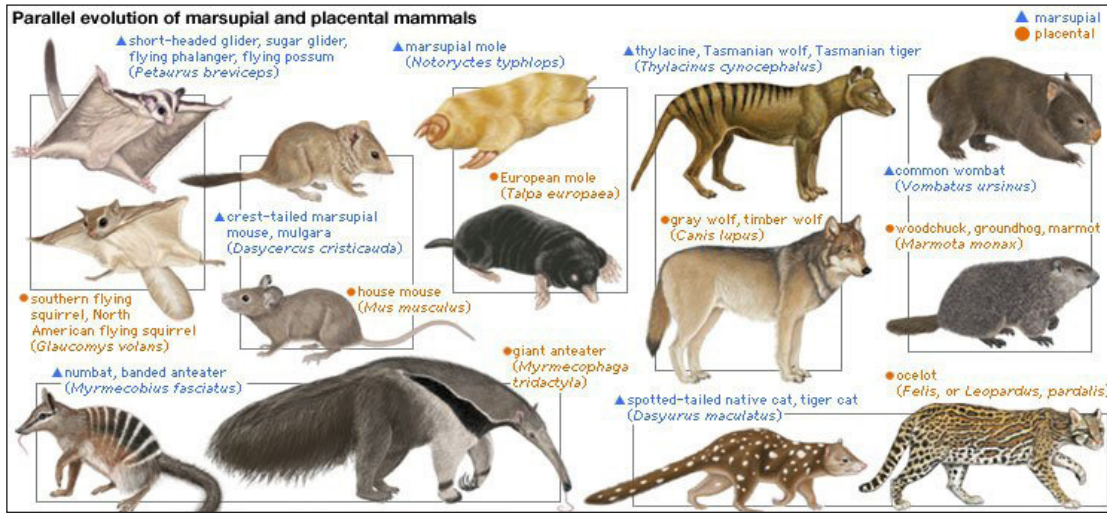
Morphological similarities between organisms have probably always been recognized. In ancient Greece Aristotle and later his followers and those of Plato, particularly Porphyry, classified organisms (as well as inanimate objects) on the basis of similarities. The Aristotelian system of classification was further developed by some medieval Scholastic philosophers, notably Albertus Magnus and Thomas Aquinas. The modern foundations of biological taxonomy, the science of classification of living and extinct organisms, were laid in the 18th century by the Swedish botanist Carolus Linnaeus and the French botanist Michel Adanson. The French naturalist Lamarck dedicated much of his work to the systematic classification of organisms. He proposed that their similarities were due to ancestral relationships—in other words, to the degree of evolutionary proximity.

The modern theory of evolution provides a causal explanation of the similarities between living things. Organisms evolve by a process of descent with modification. Changes, and therefore differences, gradually accumulate over the generations. The more recent the last common ancestor of a group of organisms, the less their differentiation; similarities of form and function reflect phylogenetic propinquity. Accordingly, phylogenetic affinities can be inferred on the basis of relative similarity.

Convergent and Parallel Evolution

A distinction has to be made between resemblances due to propinquity of descent and those due only to similarity of function. Correspondence of features in different organisms that is due to inheritance from a common ancestor is called homology. The forelimbs of humans, whales, dogs, and bats are homologous. The skeletons of these limbs are all constructed of bones arranged according to the same pattern because they derive from a common ancestor with similarly arranged forelimbs. Correspondence of features due to similarity of function but not related to common descent is termed analogy. The wings of birds and of flies are analogous. Their wings are not modified versions of a structure present in a common ancestor but rather have developed independently as adaptations to a common function, flying. The similarities between the wings of bats and birds are partially homologous and partially analogous. Their skeletal structure is homologous, due to common descent from the forelimb of a reptilian ancestor; but the modifications for flying are different and independently evolved, and in this respect they are analogous.

Features that become more rather than less similar through independent evolution are said to be convergent. Convergence is often associated with similarity of function, as in the evolution of wings in birds, bats, and flies. The shark (a fish) and the dolphin (a mammal) are much alike in external morphology; their similarities are due to convergence, since they have evolved independently as adaptations to aquatic life.



Parallel evolution of marsupial mammals and placental mammals.

Taxonomists also speak of parallel evolution. Parallelism and convergence are not always clearly distinguishable. Strictly speaking, convergent evolution occurs when descendants

resemble each other more than their ancestors did with respect to some feature. Parallel evolution implies that two or more lineages have changed in similar ways, so that the evolved descendants are as similar to each other as their ancestors were. The evolution of marsupials in Australia, for example, paralleled the evolution of placental mammals in other parts of the world. There are Australian marsupials resembling true wolves, cats, mice, squirrels, moles, groundhogs, and anteaters. These placental mammals and the corresponding Australian marsupials evolved independently but in parallel lines by reason of their adaptation to similar ways of life. Some resemblances between a true anteater (genus Myrmecophaga) and a marsupial anteater, or numbat (Myrmecobius), are due to homology—both are mammals. Others are due to analogy—both feed on ants.

Parallel and convergent evolution are also common in plants. New World cacti and African euphorbias, or spurges, are alike in overall appearance although they belong to separate families. Both are succulent, spiny, water-storing plants adapted to the arid conditions of the desert. Their corresponding morphologies have evolved independently in response to similar environmental challenges.

Homology can be recognized not only between different organisms but also between repetitive structures of the same organism. This has been called serial homology. There is serial homology, for example, between the arms and legs of humans, between the seven cervical vertebrae of mammals, and between the branches or leaves of a tree. The jointed appendages of arthropods are elaborate examples of serial homology. Crayfish have 19 pairs of appendages, all built according to the same basic pattern but serving diverse functions—sensing, chewing, food handling, walking, mating, egg carrying, and swimming. Although serial homologies are not useful in reconstructing the phylogenetic relationships of organisms, they are an important dimension of the evolutionary process.

Relationships in some sense akin to those between serial homologs exist at the molecular level between genes and proteins derived from ancestral gene duplications. The genes coding for the various hemoglobin chains are an example. About 500 million years ago a chromosome segment carrying the gene coding for hemoglobin became duplicated, so that the genes in the different segments thereafter evolved in somewhat different ways, one eventually giving rise to the modern gene coding for the α hemoglobin chain, the other for the β chain. The β chain gene became duplicated again about 200 million years ago, giving rise to the γ hemoglobin chain, a normal component of fetal hemoglobin (hemoblobin F). The genes for the α, β, γ, and other hemoglobin chains are homologous; similarities in their nucleotide sequences occur because they are modified descendants of a single ancestral sequence.

There are two ways of comparing homology between hemoglobins. One is to compare the same hemoglobin chain—for instance, the α chain—in different species of animals. The degree of divergence between the α chains reflects the degree of the evolutionary relationship between the organisms, because the hemoglobin chains have evolved independently of one another since the time of divergence of the lineages leading to the present-day organisms. A second way is to make comparisons between, say, the α and β chains of a single species. The degree of divergence between the different globin chains reflects the degree of relationship between the genes coding for them. The different globins have evolved independently of each other since the time of duplication of their ancestral genes. Comparisons between homologous genes or proteins within a given organism

provide information about the phylogenetic history of the genes and hence about the historical sequence of the gene duplication events.

Whether similar features in different organisms are homologous or analogous—or simply accidental—cannot always be decided unambiguously, but the distinction must be made in order to determine phylogenetic relationships. Moreover, the degrees of homology must be quantified in some way so as to determine the propinquity of common descent between species. Difficulties arise here as well. In the case of forelimbs, it is not clear whether the homologies are greater between human and bird than between human and reptile, or between human and reptile than between human and bat. The fossil record sometimes provides the appropriate information, even though the record is deficient. Fossil evidence must be examined together with the evidence from comparative studies of living forms and with the quantitative estimates provided by comparative studies of proteins and nucleic acids.

Gradual and Punctuational Evolution

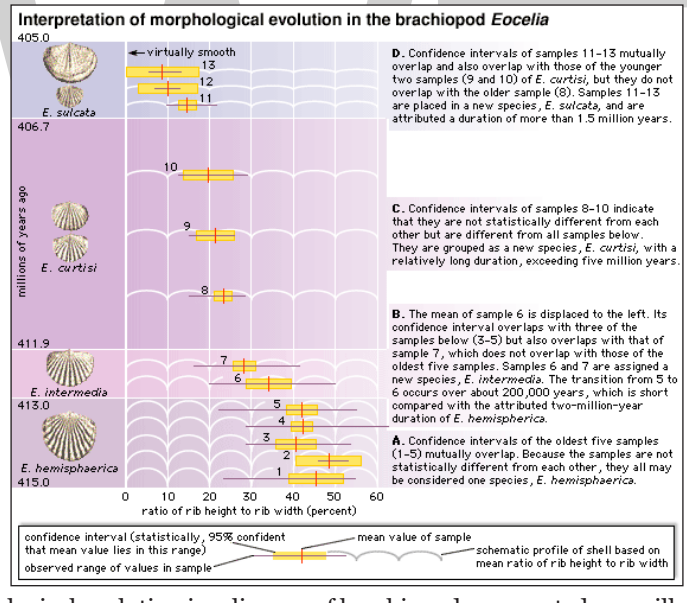
The fossil record indicates that morphological evolution is by and large a gradual process. Major evolutionary changes are usually due to a building-up over the ages of relatively small changes. But the fossil record is discontinuous. Fossil strata are separated by sharp boundaries; accumulation of fossils within a geologic deposit (stratum) is fairly constant over time, but the transition from one stratum to another may involve gaps of tens of thousands of years. Whereas the fossils within a stratum exhibit little morphological variation, new species—characterized by small but discontinuous morphological changes—typically appear at the boundaries between strata. That is not to say that the transition from one stratum to another always involves sudden changes in morphology; on the contrary, fossil forms often persist virtually unchanged through several geologic strata, each representing millions of years.

The apparent morphological discontinuities of the fossil record are often attributed by paleontologists to the discontinuity of the sediments—that is, to the substantial time gaps encompassed in the boundaries between strata. The assumption is that, if the fossil deposits were more continuous, they would show a more gradual transition of form. Even so, morphological evolution would not always keep progressing gradually, because some forms, at least, remain unchanged for extremely long times. Examples are the lineages known as “living fossils”—for instance, the lamp shell Lingula, a genus of brachiopod (a phylum of shelled invertebrates) that appears to have remained essentially unchanged since the Ordovician Period, some 450 million years ago; or the tuatara (Sphenodon punctatus), a reptile that has shown little morphological evolution for nearly 200 million years, since the early Mesozoic.

Some paleontologists have proposed that the discontinuities of the fossil record are not artifacts created by gaps in the record but rather reflect the true nature of morphological evolution, which happens in sudden bursts associated with the formation of new species. The lack of morphological evolution, or stasis, of lineages such as Lingula and Sphenodon is in turn due to lack of speciation within those lineages. The proposition that morphological evolution is jerky, with most morphological change occurring during the brief speciation events and virtually no change during the subsequent existence of the species, is known as the punctuated equilibrium model.

Whether morphological evolution in the fossil record is predominantly punctuational or gradual is a much-debated question. The imperfection of the record makes it unlikely that the issue will be settled in the foreseeable future. Intensive study of a favourable and abundant set of fossils may be expected to substantiate punctuated or gradual evolution in particular cases. But the argument is not about whether only one or the other pattern ever occurs; it is about their relative frequency. Some paleontologists argue that morphological evolution is in most cases gradual and only rarely jerky, whereas others think the opposite is true.

Much of the problem is that gradualness or jerkiness is in the eye of the beholder. Consider the evolution of shell rib strength (the ratio of rib height to rib width) within a lineage of fossil brachiopods of the genus Eocelia. Results of the analysis of an abundant sample of fossils in Wales from near the beginning of the Devonian Period is shown in the figure. One possible interpretation of the data is that rib strength changed little or not at all from 415 million to 413 million years ago; rapid change ensued for the next 1 million years, followed by virtual stasis from 412 million to 407 million years ago; and then another short burst of change occurred about 406 million years ago, followed by a final period of stasis. On the other hand, the same record may be interpreted as not particularly punctuated but rather a gradual process, with the rate of change somewhat greater at particular times.



Morphological evolution in a lineage of brachiopods, presented as an illustration of the ambiguity in interpreting whether the process is gradual or punctuational.

From the statistical analysis of fossil shells detailed in steps A through D, one may conclude that periods of essentially no change in shell rib strength, each lasting millions of years, are interspersed with comparatively short bursts of rapid change. From another point of view, however, one may see the same record as evidence of an unbroken process of evolution in which the rate of change speeds up somewhat at particular times.

The proponents of the punctuated equilibrium model propose not only that morphological evolution is jerky but also that it is associated with speciation events. They argue that phyletic evolution—that is, evolution along lineages of descent—proceeds at two levels. First, there is

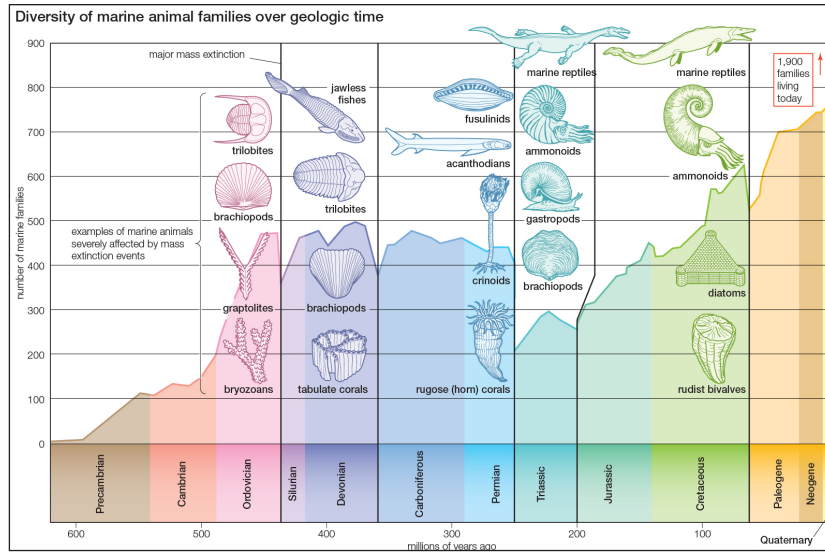
continuous change through time within a population. This consists largely of gene substitutions prompted by natural selection, mutation, genetic drift, and other genetic processes that operate at the level of the individual organism. The punctualists maintain that this continuous evolution within established lineages rarely, if ever, yields substantial morphological changes in species. Second, they say, there is the process of origination and extinction of species, in which most morphological change occurs. According to the punctualist model, evolutionary trends result from the patterns of origination and extinction of species rather than from evolution within established lineages.

Speciation involves the development of reproductive isolation between populations previously able to interbreed. Paleontologists discriminate between species by their different morphologies as preserved in the fossil record, but fossils cannot provide evidence of the development of reproductive isolation—new species that are reproductively isolated from their ancestors are often morphologically indistinguishable from them. Speciation as it is seen by paleontologists always involves substantial morphological change. This situation creates an insuperable difficulty for resolving the question of whether morphological evolution is always associated with speciation events. If speciation is defined as the evolution of reproductive isolation, the fossil record provides no evidence that an association between speciation and morphological change is necessary. But if new species are identified in the fossil record by morphological changes, then all such changes will occur concomitantly with the origination of new species.

Diversity and Extinction

The current diversity of life is the balance between the species that have arisen through time and those that have become extinct. Paleontologists observe that organisms have continuously changed since the Cambrian Period, more than 500 million years ago, from which abundant animal fossil remains are known. The division of geologic history into a succession of eras and periods is hallmarked by major changes in plant and animal life—the appearance of new sorts of organisms and the extinction of others. Paleontologists distinguish between background extinction, the steady rate at which species disappear through geologic time, and mass extinctions, the episodic events in which large numbers of species become extinct over time spans short enough to appear almost instantaneous on the geologic scale.

Best known among mass extinctions is the one that occurred at the end of the Cretaceous Period, when the dinosaurs and many other marine and land animals disappeared. Most scientists believe that the Cretaceous mass extinction was provoked by the impact of an asteroid or comet on the tip of the Yucatán Peninsula in southeastern Mexico 65 million years ago. The object's impact caused an enormous dust cloud, which greatly reduced the Sun's radiation reaching Earth, with a consequent drastic drop in temperature and other adverse conditions. Among animals, about 76 percent of species, 47 percent of genera, and 16 percent of families became extinct. Although the dinosaurs vanished, turtles, snakes, lizards, crocodiles, and other reptiles, as well as some mammals and birds, survived. Mammals that lived prior to the event were small and mostly nocturnal, but during the ensuing Paleogene and Neogene periods they experienced an explosive diversification in size and morphology, occupying ecological niches vacated by the dinosaurs. Most of the orders and families of mammals now in existence originated in the first 10 million–20 million years after the dinosaurs' extinction. Birds also greatly diversified at that time.



The diversity of marine animal families since late Precambrian time.

The data for the curve comprise only those families that are reliably preserved in the fossil record; the 1,900 value for living families also includes those families rarely preserved as fossils. The several pronounced dips in the curve correspond to major mass-extinction events. The most catastrophic extinction took place at the end of the Permian Period.

Several other mass extinctions have occurred since the Cambrian. The most catastrophic happened at the end of the Permian Period, about 251 million years ago, when 95 percent of marine species, 82 percent of genera, and 51 percent of families of animals became extinct. Other large mass extinctions occurred at or near the end of the Ordovician (about 444 million years ago, 85 percent of marine species extinct), Devonian (about 359 million years ago, 70–80 percent of species extinct), and Triassic (about 200 million years ago, nearly 80 percent of species extinct). Changes of climate and chemical composition of the atmosphere appear to have caused these mass extinctions; there is no convincing evidence that they resulted from cosmic impacts. Like other mass extinctions, they were followed by the origin or rapid diversification of various kinds of organisms. The first mammals and dinosaurs appeared after the late Permian extinction, and the first vascular plants after the Late Ordovician extinction.

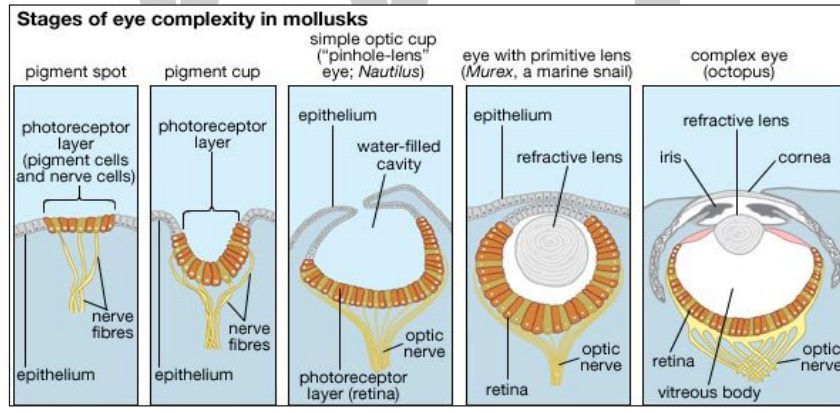
Background extinctions result from ordinary biological processes, such as competition between species, predation, and parasitism. When two species compete for very similar resources—say, the same kinds of seeds or fruits—one may become extinct, although often they will displace one another by dividing the territory or by specializing in slightly different foods, such as seeds of a different size or kind. Ordinary physical and climatic changes also account for background extinctions—for example, when a lake dries out or a mountain range rises or erodes.

New species come about by the processes. These processes are largely gradual, yet the history of life shows major transitions in which one kind of organism becomes a very different kind. The earliest organisms were prokaryotes, or bacteria-like cells, whose hereditary material is not segregated into a nucleus. Eukaryotes have their DNA organized into chromosomes that are membrane-bound in the nucleus, have other organelles inside their cells, and reproduce sexually. Eventually, eukaryotic multicellular organisms appeared, in which there is a division of function among

cells—some specializing in reproduction, others becoming leaves, trunks, and roots in plants or different organs and tissues such as muscle, nerve, and bone in animals. Social organization of individuals in a population is another way of achieving functional division, which may be quite fixed, as in ants and bees, or more flexible, as in cattle herds or primate groups.

Because of the gradualness of evolution, immediate descendants differ little, and then mostly quantitatively, from their ancestors. But gradual evolution may amount to large differences over time. The forelimbs of mammals are normally adapted for walking, but they are adapted for shoveling earth in moles and other mammals that live mostly underground, for climbing and grasping in arboreal monkeys and apes, for swimming in dolphins and whales, and for flying in bats. The forelimbs of reptiles became wings in their bird descendants. Feathers appear to have served first for regulating temperature but eventually were co-opted for flying and became incorporated into wings.

Eyes, which serve as another example, also evolved gradually and achieved very different configurations, all serving the function of seeing. Eyes have evolved independently at least 40 times. Because sunlight is a pervasive feature of Earth's environment, it is not surprising that organs have evolved that take advantage of it. The simplest "organ" of vision occurs in some single-celled organisms that have enzymes or spots sensitive to light, which helps them move toward the surface of their pond, where they feed on the algae growing there by photosynthesis. Some multicellular animals exhibit light-sensitive spots on their epidermis. Further steps—deposition of pigment around the spot, configuration of cells into a cuplike shape, thickening of the epidermis leading to the development of a lens, development of muscles to move the eyes and nerves to transmit optical signals to the brain—all led to the highly developed eyes of vertebrates and cephalopods (octopuses and squids) and to the compound eyes of insects.



The figure above shows, steps in the evolution of the eye as reflected in the range of eye complexity in living mollusk species (left to right): a pigment spot, as in the limpet Patella; a pigment cup, as in the slit shell mollusk Pleurotomaria; the "pinhole-lens" eye of Nautilus; a primitive lensed eye, as in the marine snail Murex; and the complex eye—with iris, crystalline lens, and retina—of octopuses and squids.

While the evolution of forelimbs—for walking—into the wings of birds or the arms and hands of primates may seem more like changes of function, the evolution of eyes exemplifies gradual advancement of the same function—seeing. In all cases, however, the process is impelled

by natural selection's favouring individuals exhibiting functional advantages over others of the same species. Examples of functional shifts are many and diverse. Some transitions at first may seem unlikely because of the difficulty in identifying which possible functions may have been served during the intermediate stages. These cases are eventually resolved with further research and the discovery of intermediate fossil forms. An example of a seemingly unlikely transition is namely, the transformation of bones found in the reptilian jaw into the hammer and anvil of the mammalian ear.

Evolution and Development

Starfish are radially symmetrical, but most animals are bilaterally symmetrical—the parts of the left and right halves of their bodies tend to correspond in size, shape, and position. Some bilateral animals, such as millipedes and shrimps, are segmented (metameric); others, such as frogs and humans, have a front-to-back (head-to-foot) body plan, with head, thorax, abdomen, and limbs, but they lack the repetitive, nearly identical segments of metameric animals. There are other basic body plans, such as those of sponges, clams, and jellyfish, but their total number is not large—less than 40.

The fertilized egg, or zygote, is a single cell, more or less spherical, that does not exhibit polarity such as anterior and posterior ends or dorsal and ventral sides. Embryonic development is the process of growth and differentiation by which the single-celled egg becomes a multicellular organism.

The determination of body plan from this single cell and the construction of specialized organs, such as the eye, are under the control of regulatory genes. Most notable among these are the Hox genes, which produce proteins (transcription factors) that bind with other genes and thus determine their expression—that is, when they will act. The Hox genes embody spatial and temporal information. By means of their encoded proteins, they activate or repress the expression of other genes according to the position of each cell in the developing body, determining where limbs and other body parts will grow in the embryo. Since their discovery in the early 1980s, the Hox genes have been found to play crucial roles from the first steps of development, such as establishing anterior and posterior ends in the zygote, to much later steps, such as the differentiation of nerve cells.

The critical region of the Hox proteins is encoded by a sequence of about 180 consecutive nucleotides (called the homeobox). The corresponding protein region (the homeodomain), about 60 amino acids long, binds to a short stretch of DNA in the regulatory region of the target genes. Genes containing homeobox sequences are found not only in animals but also in other eukaryotes such as fungi and plants.

All animals have Hox genes, which may be as few as 1, as in sponges, or as many as 38, as in humans and other mammals. Hox genes are clustered in the genome. Invertebrates have only one cluster with a variable number of genes, typically fewer than 13. The common ancestor of the chordates (which include the vertebrates) probably had only one cluster of Hox genes, which may have numbered 13. Chordates may have one or more clusters, but not all 13 genes remain in every cluster. The marine animal amphioxus, a primitive chordate, has a single array of 10 Hox genes. Humans, mice, and other mammals have 38 Hox genes arranged in four clusters, three with 9 genes each and one with 11 genes. The set of genes varies from cluster to cluster, so that out of the

13 in the original cluster, genes designated 1, 2, 3, and 7 may be missing in one set, whereas 10, 11, 12, and 13 may be missing in a different set.

The four clusters of Hox genes found in mammals originated by duplication of the whole original cluster and retain considerable similarity between clusters. The 13 genes in the original cluster also themselves originated by repeated duplication, starting from a single Hox gene as found in the sponges. These first duplications happened very early in animal evolution, in the Precambrian. The genes within a cluster retain detectable similarity, but they differ more from one another than they differ from the corresponding, or homologous, gene in any of the other sets. There is a puzzling correspondence between the position of the Hox genes in a cluster along the chromosome and the patterning of the body—genes located upstream (anteriorly in the direction in which genes are transcribed) in the cluster are expressed earlier and more anteriorly in the body, while those located downstream (posteriorly in the direction of transcription) are expressed later in development and predominantly affect the posterior body parts.

Researchers demonstrated the evolutionary conservation of the Hox genes by means of clever manipulations of genes in laboratory experiments. For example, the ey gene that determines the formation of the compound eye in Drosophila vinegar flies was activated in the developing embryo in various parts of the body, yielding experimental flies with anatomically normal eyes on the legs, wings, and other structures. The evolutionary conservation of the Hox genes may be the explanation for the puzzling observation that most of the diversity of body plans within major groups of animals arose early in the evolution of the group. The multicellular animals (metazoans) first found as fossils in the Cambrian already demonstrate all the major body plans found during the ensuing 540 million years, as well as four to seven additional body plans that became extinct and seem bizarre to observers today. Similarly, most of the classes found within a phylum appear early in the evolution of the phylum. For example, all living classes of arthropods are already found in the Cambrian, with body plans essentially unchanged thereafter; in addition, the Cambrian contains a few strange kinds of arthropods that later became extinct.

Reconstruction of Evolutionary History

DNA and Protein as Informational Macromolecules

The advances of molecular biology have made possible the comparative study of proteins and the nucleic acids, DNA and RNA. DNA is the repository of hereditary (evolutionary and developmental) information. The relationship of proteins to DNA is so immediate that they closely reflect the hereditary information. This reflection is not perfect, because the genetic code is redundant, and, consequently, some differences in the DNA do not yield differences in the proteins. Moreover, this reflection is not complete, because a large fraction of DNA (about 90 percent in many organisms) does not code for proteins. Nevertheless, proteins are so closely related to the information contained in DNA that they, as well as nucleic acids, are called informational macromolecules.

Nucleic acids and proteins are linear molecules made up of sequences of units—nucleotides in the case of nucleic acids, amino acids in the case of proteins—which retain considerable amounts of evolutionary information. Comparing two macromolecules establishes the number of their units that are different. Because evolution usually occurs by changing one unit at a time, the number

of differences is an indication of the recency of common ancestry. Changes in evolutionary rates may create difficulties in interpretation, but macromolecular studies have three notable advantages over comparative anatomy and the other classical disciplines. One is that the information is more readily quantifiable. The number of units that are different is readily established when the sequence of units is known for a given macromolecule in different organisms. The second advantage is that comparisons can be made even between very different sorts of organisms. There is very little that comparative anatomy can say when organisms as diverse as yeasts, pine trees, and human beings are compared, but there are homologous macromolecules that can be compared in all three. The third advantage is multiplicity. Each organism possesses thousands of genes and proteins, which all reflect the same evolutionary history. If the investigation of one particular gene or protein does not resolve the evolutionary relationship of a set of species, additional genes and proteins can be investigated until the matter has been settled.

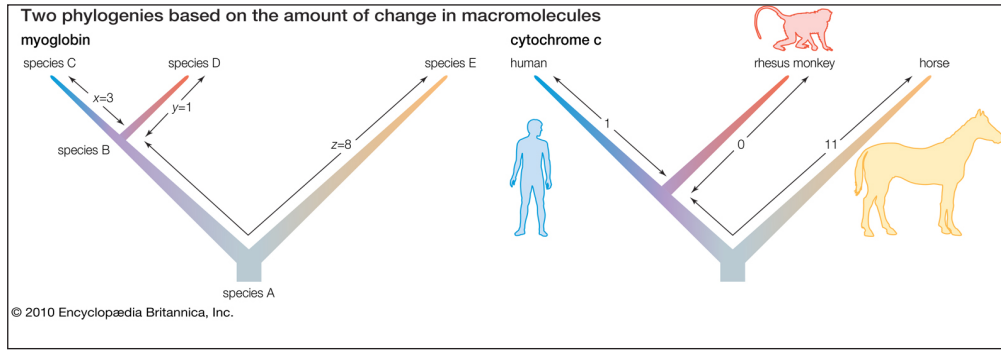
Informational macromolecules provide information not only about the branching of lineages from common ancestors (cladogenesis) but also about the amount of genetic change that has occurred in any given lineage (anagenesis). It might seem at first that quantifying anagenesis for proteins and nucleic acids would be impossible, because it would require comparison of molecules from organisms that lived in the past with those from living organisms. Organisms of the past are sometimes preserved as fossils, but their DNA and proteins have largely disintegrated. Nevertheless, comparisons between living species provide information about anagenesis.

The following is an example of such comparison: Two living species, C and D, have a common ancestor, the extinct species B . If C and D were found to differ by four amino acid substitutions in a single protein, then it could tentatively be assumed that two substitutions (four total changes divided by two species) had taken place in the evolutionary lineage of each species. This assumption, however, could be invalidated by the discovery of a third living species, E, that is related to C, D, and their ancestor, B, through an earlier ancestor, A. The number of amino acid differences between the protein molecules of the three living species may be as follows:

C and D = 4

C and E = 11

C and E = 9



In the figure above, (Left) amount of change in the evolutionary history of three hypothetical living species (C, D, and E), inferred by comparing amino-acid differences in their myoglobin molecules. All three species have the same earlier ancestor (A). (Right) phylogeny of the human, the rhesus

monkey, and the horse, based on amino-acid substitutions in the evolution of cytochrome c in the lineages of the three species.

The left side of the figure proposes a phylogeny of the three living species, making it possible to estimate the number of amino acid substitutions that have occurred in each lineage. Let x denote the number of differences between B and C, y denote the differences between B and D, and z denote the differences between A and B as well as A and E. The following three equations can be produced:

$$x + y = 4$$
$$x + z = 11$$
$$y + z = 9$$

Solving the equations yields x = 3, y = 1, and z = 8.

As a concrete example, consider the protein cytochrome c, involved in cell respiration. The sequence of amino acids in this protein is known for many organisms, from bacteria and yeasts to insects and humans; in animals cytochrome c consists of 104 amino acids. When the amino acid sequences of humans and rhesus monkeys are compared, they are found to be different at position 66 (isoleucine in humans, threonine in rhesus monkeys) but, identical at the other 103 positions. When humans are compared with horses, 12 amino acid differences are found, but, when horses are compared with rhesus monkeys, there are only 11 amino acid differences. Even without knowing anything else about the evolutionary history of mammals, one would conclude that the lineages of humans and rhesus monkeys diverged from each other much more recently than they diverged from the horse lineage. Moreover, it can be concluded that the amino acid difference between humans and rhesus monkeys must have occurred in the human lineage after its separation from the rhesus monkey lineage.

Evolutionary Trees

Evolutionary trees are models that seek to reconstruct the evolutionary history of taxa—i.e., species or other groups of organisms, such as genera, families, or orders. The trees embrace two kinds of information related to evolutionary change, cladogenesis and anagenesis. The figure can be used to illustrate both kinds. The branching relationships of the trees reflect the relative relationships of ancestry, or cladogenesis. Thus, in the right side of the figure, humans and rhesus monkeys are seen to be more closely related to each other than either is to the horse. Stated another way, this tree shows that the last common ancestor to all three species lived in a more remote past than the last common ancestor to humans and monkeys.

Evolutionary trees may also indicate the changes that have occurred along each lineage, or anagenesis. Thus, in the evolution of cytochrome c since the last common ancestor of humans and rhesus monkeys, one amino acid changed in the lineage going to humans but none in the lineage going to rhesus monkeys. Similarly, the left side of the figure shows that three amino acid changes occurred in the lineage from B to C but only one in the lineage from B to D.

There exist several methods for constructing evolutionary trees. Some were developed for interpreting morphological data, others for interpreting molecular data; some can be used with either kind of data. The main methods currently in use are called distance, parsimony, and maximum likelihood.

Distance Methods

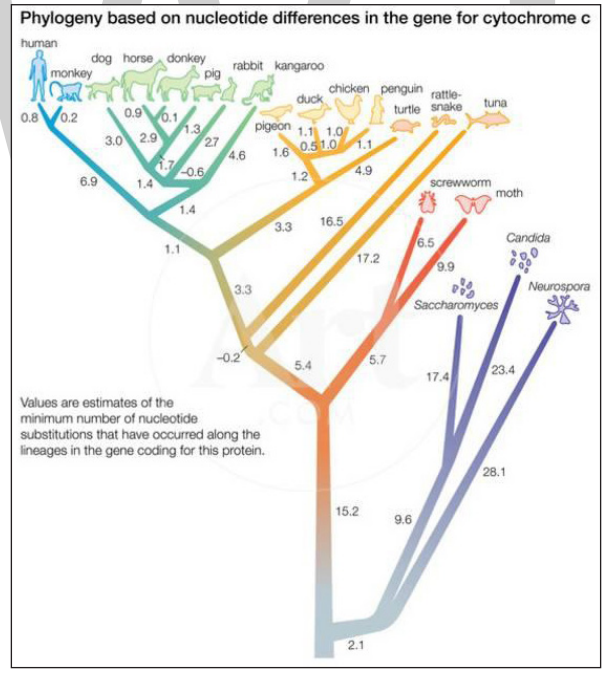
A "distance" is the number of differences between two taxa. The differences are measured with respect to certain traits (i.e., morphological data) or to certain macromolecules (primarily the sequence of amino acids in proteins or the sequence of nucleotides in DNA or RNA). The two trees illustrated in the figure were obtained by taking into account the distance, or number of amino acid differences, between three organisms with respect to a particular protein. The amino acid sequence of a protein contains more information than is reflected in the number of amino acid differences. This is because in some cases the replacement of one amino acid by another requires no more than one nucleotide substitution in the DNA that codes for the protein, whereas in other cases it requires at least two nucleotide changes. The table shows the minimum number of nucleotide differences in the genes of 20 separate species that are necessary to account for the amino acid differences in their cytochrome c. An evolutionary tree based on the data in the table, showing the minimum numbers of nucleotide changes in each branch, is illustrated in the complementary figure.

Minimum number of nucleotide differences in genes coding for cytochrome c in different organisms

Organism		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1.	Human	--	1	13	17	16	13	12	12	17	16	18	18	19	20	31	33	36	63	56	66
2.	Monkey			12	16	15	12	11	13	16	15	17	17	18	21	32	32	35	62	57	65
3.	Dog				10	8	4	6	7	12	12	14	14	13	30	29	24	28	64	61	66
4.	Horse					1	5	11	11	16	16	16	17	16	32	27	24	33	64	60	68
5.	Donkey						4	10	12	15	15	15	16	15	31	26	25	32	64	59	67
6.	Pig							6	7	13	13	13	14	13	30	25	26	31	64	59	67
7.	Rabbit								7	10	8	11	11	11	25	26	23	29	62	59	67
8.	Kangaroo									14	14	15	13	14	30	27	26	31	66	58	68
9.	Duck										3	3	3	7	24	26	25	29	61	62	66
10.	Pigeon											4	4	8	24	27	26	30	59	62	66
11.	Chicken												2	8	28	26	26	31	61	62	66
12.	Penguin													8	28	27	28	30	62	61	65
13.	Turtle														30	27	30	33	65	64	67
14.	Rattlesnake															38	40	41	61	61	69
15.	Tuna																34	41	72	66	69
16.	Screwworm																	16	58	63	65
17.	Moth																		59	60	61
18.	Neurospora (mold)																			57	61
19.	Saccharomyces (yeast)																				41

The relationships between species as shown in the figure correspond fairly well to the relationships determined from other sources, such as the fossil record. According to the figure, chickens are less closely related to ducks and pigeons than to penguins, and humans and monkeys diverged from the other mammals before the marsupial kangaroo separated from the nonprimate placentals. Although these examples are known to be erroneous relationships, the power of the method is apparent in that a single protein yields a fairly accurate reconstruction of the evolutionary history of 20 organisms that started to diverge more than one billion years ago.

Morphological data also can be used for constructing distance trees. The first step is to obtain a distance matrix based on a set of morphological comparisons between species or other taxa. For example, in some insects one can measure body length, wing length, wing width, number and length of wing veins, or another trait. The most common procedure to transform a distance matrix into a phylogeny is called cluster analysis. The distance matrix is scanned for the smallest distance element, and the two taxa involved (say, A and B) are joined at an internal node, or branching point. The matrix is scanned again for the next smallest distance, and the two new taxa (say, C and D) are clustered. The procedure is continued until all taxa have been joined. When a distance involves a taxon that is already part of a previous cluster (say, E and A), the average distance is obtained between the new taxon and the preexisting cluster (say, the average distance between E to A and E to B). This simple procedure, which can also be used with molecular data, assumes that the rate of evolution is uniform along all branches.



Phylogeny based on differences in the protein sequence of cytochrome c in organisms ranging from Neurospora mold to humans.

Other distance methods (including the one used to construct the tree in the figure of the 20-organism phylogeny) relax the condition of uniform rate and allow for unequal rates of evolution along the branches. One of the most extensively used methods of this kind is called neighbour-joining. The method starts, as before, by identifying the smallest distance in the matrix and linking the two taxa involved. The next step is to remove these two taxa and calculate a new matrix in which their

distances to other taxa are replaced by the distance between the node linking the two taxa and all other taxa. The smallest distance in this new matrix is used for making the next connection, which will be between two other taxa or between the previous node and a new taxon. The procedure is repeated until all taxa have been connected with one another by intervening nodes.

Maximum Parsimony Methods

Maximum parsimony methods seek to reconstruct the tree that requires the fewest (i.e., most parsimonious) number of changes summed along all branches. This is a reasonable assumption, because it usually will be the most likely. But evolution may not necessarily have occurred following a minimum path, because the same change instead may have occurred independently along different branches, and some changes may have involved intermediate steps. Consider three species—C, D, and E. If C and D differ by two amino acids in a certain protein and either one differs by three amino acids from E, parsimony will lead to a tree with the structure shown in the left side of the figure illustrating the two simple phylogenies. It may be the case, however, that in a certain position at which C and D both have amino acid g while E has h, the ancestral amino acid was g. Amino acid g did not change in the lineage going to C but changed to h in a lineage going to the ancestor of D and E and then changed again, back to g, in the lineage going to D. The correct phylogeny would lead then from the common ancestor of all three species to C in one branch (in which no amino acid changes occurred), and to the last common ancestor of D and E in the other branch (in which g changed to h) with one additional change (from h to g) occurring in the lineage from this ancestor to E.

Not all evolutionary changes, even those that involve a single step, may be equally probable. For example, among the four nucleotide bases in DNA, cytosine (C) and thymine (T) are members of a family of related molecules called pyrimidines; likewise, adenine (A) and guanine (G) belong to a family of molecules called purines. A change within a DNA sequence from one pyrimidine to another (C $\rightleftharpoons$ T) or from one purine to another (A $\rightleftharpoons$ G), called a transition, is more likely to occur than a change from a purine to a pyrimidine or the converse (G or A $\rightleftharpoons$ C or T), called a transversion. Parsimony methods take into account different probabilities of occurrence if they are known.

Maximum parsimony methods are related to cladistics, a very formalistic theory of taxonomic classification, extensively used with morphological and paleontological data. The critical feature in cladistics is the identification of derived shared traits, called synapomorphic traits. A synapomorphic trait is shared by some taxa but not others because the former inherited it from a common ancestor that acquired the trait after its lineage separated from the lineages going to the other taxa. In the evolution of carnivores, for example, domestic cats, tigers, and leopards are clustered together because of their possessing retractable claws, a trait acquired after their common ancestor branched off from the lineage leading to the dogs, wolves, and coyotes. It is important to ascertain that the shared traits are homologous rather than analogous. For example, mammals and birds, but not lizards, have a four-chambered heart. Yet birds are more closely related to lizards than to mammals; the four-chambered heart evolved independently in the bird and mammal lineages, by parallel evolution.

Maximum Likelihood Methods

Maximum likelihood methods seek to identify the most likely tree, given the available data. They require that an evolutionary model be identified, which would make it possible to estimate the

probability of each possible individual change. For example, transitions are more likely than transversions among DNA nucleotides, but a particular probability must be assigned to each. All possible trees are considered. The probabilities for each individual change are multiplied for each tree. The best tree is the one with the highest probability (or maximum likelihood) among all possible trees.

Maximum likelihood methods are computationally expensive when the number of taxa is large, because the number of possible trees (for each of which the probability must be calculated) grows factorially with the number of taxa. With 10 taxa, there are about 3.6 million possible trees; with 20 taxa, the number of possible trees is about 2 followed by 18 zeros (2 × 1018). Even with powerful computers, maximum likelihood methods can be prohibitive if the number of taxa is large. Heuristic methods exist in which only a subsample of all possible trees is examined and thus an exhaustive search is avoided.

Evaluation of Evolutionary Trees

The statistical degree of confidence of a tree can be estimated for distance and maximum likelihood trees. The most common method is called bootstrapping. It consists of taking samples of the data by removing at least one data point at random and then constructing a tree for the new data set. This random sampling process is repeated hundreds or thousands of times. The bootstrap value for each node is defined by the percentage of cases in which all species derived from that node appear together in the trees. Bootstrap values above 90 percent are regarded as statistically strongly reliable; those below 70 percent are considered unreliable.

Evolutionary Biology

Evolutionary biology is the discipline that describes the history of life and investigates the processes that account for this history.

Evolutionary biology has two encompassing goals:

- To discover the history of life on earth: that is, (1) to determine the ancestor-descendant relationships among all species that have ever lived—their phylogeny; (2) to determine the times at which they originated and became extinct; and (3) to determine the origin of and the rate and course of change in their characteristics.
- To understand the causal processes of evolution: that is, to understand (1) the origins of hereditary variations; (2) how various processes act to affect the fate of those variations; (3) the relative importance of the many co-acting processes of change; (4) how rapidly changes occur; (5) how processes such as mutation, natural selection, and genetic drift have given rise to the diverse molecular, anatomical, behavioral, and other characteristics of different organisms; and (6) how populations become different species. Virtually all of biology bears on this vast project of understanding the causes of evolution, and reciprocally, understanding the processes of evolution informs every area of biology.

Subdisciplines of Evolutionary Biology

Evolutionary biology includes numerous subdisciplines that differ in their subject matter and methods. Some of the major subdisciplines are:

- Behavioral evolution (also called behavioral ecology). Behavioral evolutionists study the evolution of adaptations such as mating systems, courtship behavior, foraging behavior, predator escape mechanisms, and cooperation. Behavioral characteristics evolve in much the same way as structural features. Changes in the neural, hormonal, and developmental mechanisms underlying behavior are also objects of evolutionary study, as are the adaptive differences among species in memory, patterns of learning, and other cognitive processes, some of which are reflected in differences in brain structure. Behavior, physiology, structure, and life history patterns often evolve in concert.

- Evolutionary developmental biology seeks to understand evolutionary changes in the processes that translate the genetic information contained in an organism's DNA (its genotype) into its anatomical and other characteristics (its phenotype). In part, it aims to describe how variation at the genetic level results in variation in the characteristics that affect survival and reproduction. Perhaps its greatest significance lies in its potential to reveal the extent to which developmental processes bias, constrain, or facilitate evolution of the phenotype.

- Evolutionary ecology looks at how the life histories, diets, and other ecological features of species evolve, how these processes affect the composition and properties of communities and ecosystems, and how species evolve in response to one another. Its salient questions include: How do we account for the evolution of short or long life spans? Why are some species broadly and others narrowly distributed? Do parasites (including microbial pathogens) evolve to be more benign or more virulent as time passes? How do evolutionary changes and evolutionary history affect the number of species in a community, such as a tropical forest or a temperate forest?

- Evolutionary genetics (which includes population genetics) is a central discipline in the study of evolutionary processes. It uses both molecular and classic genetic methods to understand the origin of variation by mutation and recombination. It describes patterns of genetic variation within and among populations and species, and employs both empirical study and mathematical theory to discover how this variation is affected by processes such as genetic drift, gene flow, and natural selection. The mathematical theory of evolutionary genetics is essential for interpreting genetic variation and for predicting evolutionary changes when many factors interact. It also provides a strong foundation for understanding the evolution of special classes of characteristics, such as genome structure and life histories.

- Evolutionary paleontology, often called paleobiology, addresses the large-scale evolutionary patterns of the fossil record. It examines the origins and fates of lineages and major groups, evolutionary trends and other changes in anatomy through time, and geographic and temporal variations in diversity throughout the geologic past. It also seeks to un-

derstand the physical and biological processes and the unique historical events that have shaped evolution. Paleontological data provide a window on deep time, and thus permit the direct study of problems ranging from the change in the form and distribution of species over millions of years to the evolutionary responses of major groups to both catastrophic and gradual environmental changes. These data also allow calibration of rates for such phenomena as mutations in nucleotide sequences.

- Evolutionary physiology and morphology looks at how the biochemical, physiological, and anatomical features of organisms provide adaptation to their environments and ways of life, and at the history of these adaptations. It is also beginning to define the limits to adaptation—for such limits may restrict a species' distribution or lead to its extinction. Among the questions studied in this field are: How do the form and the function of a feature change in relation to each other during evolution? How and why are some species tolerant of a broad range, and others of only a narrow range, of environmental factors such as temperature? Is there a diversity of mechanisms by which populations may adapt to a new environment?

- Human evolution is another sub-discipline**.** Many evolutionary biologists draw on the conceptual subdisciplines of evolutionary biology to study particular groups of organisms. Of these groups, one is especially notable: the genus Homo. The many anthropologists and biologists who take human evolution as their subject use principles, concepts, methods, and information from evolutionary systematics, paleontology, genetics, ecology, animal behavior—the full panoply of evolutionary disciplines. Other researchers study genetic variation and the processes that affect it in contemporary human populations (a subject intimately related to other areas of human genetics, such as medical genetics). Still others work in the controversial area of human behavior and psychology.

- Developing hand in hand with the spectacular advance of molecular biology, this field investigates the history and causes of evolutionary changes in the nucleotide sequences of genes (DNA), the structure and number of genes, their physical organization on chromosomes, and many other molecular phenomena. This field also provides tools for investigating numerous questions about the evolution of organisms, ranging from phylogenetic relationships among species to mating patterns within populations.

- Systematists distinguish and name species, infer phylogenetic relationships among species, and classify species on the basis of their evolutionary relationships. Systematists have contributed greatly to our understanding of variation and the nature of species. Their special knowledge of particular groups of organisms is indispensable both for inferring the history of evolution and for understanding the detailed workings of evolutionary processes, since each group of organisms presents special, fascinating, and often important questions. Moreover, systematists' knowledge often has unexpected uses. Knowledge of the systematics and biological characteristics of deer mice became invaluable when the novel hantavirus, harbored by these mice, caused fatalities in the United States. Likewise, plants that are related to a species in which a pharmacologically useful compound has been found are likely to contain similar compounds.

2
Types of Evolution

The change in heritable characteristics in successive generations of biological populations is known as evolution. Different types of evolution include the evolution of cell, evolution of sexual reproduction and the evolution of biological complexity. The aim of this chapter is to explore these types of evolution to provide an extensive understanding of the subject.

Evolution of Cells

Approximately 3.5 billion years ago, cellular life emerged on Earth in the form of primitive bacteria. Bacteria or "prokaryotes" organize their genes into a circular chromosome that lies exposed within the fluid environment of the cell. Within a billion years, bacterial cell types had flourished and diversified, evolving numerous ways of extracting energy from the environment. These types included first the fermenting anaerobic archaebacteria, then the oxygen-producing photosynthetic cyanobacteria, and finally respiring aerobic bacteria able to utilize the new oxygen-rich atmosphere. In addition some bacteria had become motile, such as the corkscrew-shaped wriggling spirochetes. All of these bacterial cell types have descendents living today.

Eukaryotes, whose deoxyribonucleic acid (DNA) is sequestered within a separate membrane-bound nucleus, first emerged perhaps 2 billion years ago. Eukaryotic cells also contain an extensive internal membrane system, a cytoskeleton, and different kinds of membrane-bound organelle, including mitochondria (the "power factories") and, in algae and plants, plastids (sites of photosynthesis). All multicellular life, including plants, animals, and fungi, are composed of eukaryotic cells; some microbes, such as unicellular algae and protozoa, are also eukaryotes.

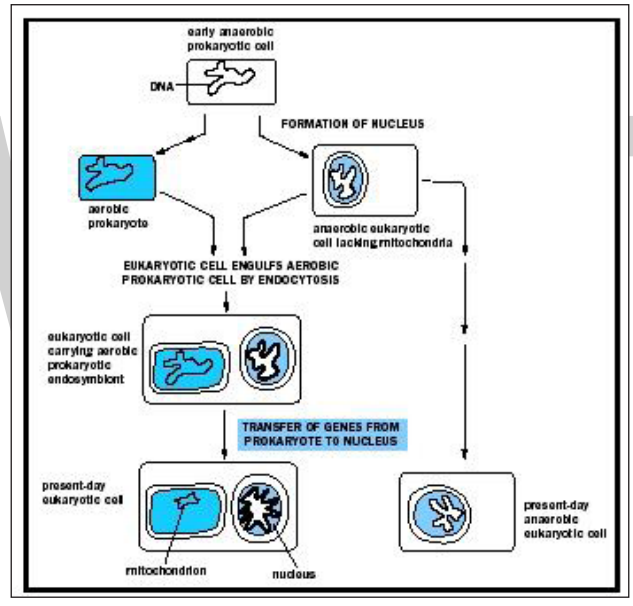
Serial Endosymbiosis

The most widely accepted theory of cell evolution is known as the Serial endosymbiosis theory (SET), articulated and championed by scientist Lynn Margulis. In 1905 Russian scientist Konstantin Merezhkovsky proposed that new organs or organisms could form through symbiosis ("the living together of different kinds of organisms"). In the 1920s researcher Ivan Wallin suggested that organelles such as chloroplasts and mitochondria originated as symbiotic bacteria. His theory was rejected by his colleagues, leading him to abandon his laboratory investigations.

However, in 1967 the theory was resuscitated by Margulis to explain observations by geneticists of "cytoplasmic genes," DNA found outside the nucleus. Margulis proposed that cytoplasmic

organelles with a bacterial origin were the source of the extranuclear genes. Margulis's SET begins with the merger of an archaebacterium, lacking a rigid cell wall, with motile spirochetes to form the first eukaryotic cell. The archeabacterium's flexible membrane pinched inwards to enclose the DNA within a double-membrane nucleus and the spirochetes provided cytoskeletal support, ultimately giving rise to motile structures known as microtubules.

This new cell type then engulfed an aerobic (needing oxygen) bacterium, which was retained within a membrane vesicle inside the host cell. Over many generations, this new cell component evolved into what scientists now call "mitochondrion" and allowed eukaryotes to thrive in an oxygen-rich environment by harnessing the metabolic capabilities of its newest partner. Over time, many of the proto-mitochondrion's genes were transferred to the host nucleus, making the mitochondrion dependent upon the host cell for its survival. In a similar fashion, some of these aerobic nucleated cells established symbiotic associations with intracellular cyanobacteria, leading to the evolution of photosynthetic eukaryotes.



Suggested evolutionary pathway for the origin of mitochondria.

The view that the eukaryotic cell evolved from an intimately associated consortium of bacteria initially met with sharp criticism. Some, including Margulis, argued that the discovery that both mitochondria and plastids contain bacteria-like circular chromosomes, the source of the "cytoplasmic genes," was evidence for the bacterial origins of these double-membrane-bound organelles. Others argued, however, that these organelles and their genes originated by pinching off from the nucleus.

Eventually researchers accumulated more and more supporting evidence for the main premise of SET: the symbiotic origin of mitochondria and plastids. The size, gene structure and sequences, biochemistry, and fission-style reproduction of these organelles all imply a closer evolutionary relationship to free-living aerobic bacteria and cyanobacteria than to the "host" archaebacteria-derived cell encoded by genes in the nucleus. The origin of microtubules from spirochete symbionts, however, is not as well supported and remains controversial. One of the reasons the theory met with such initial skepticism is that it challenged the prevailing ideas about how evolution occurs: that is, through slow accumulations of changes in vertically transmitted sets of genes, resulting in

speciation events in which branches of the tree of life are forever splitting, never joining. SET describes the wholesale fusion of two (three, four, or more) genomes, a process that joined previously diverging branches into one.

Evolution of Aging

Enquiry into the evolution of ageing aims to explain why survival, reproductive success, and functioning of almost all living organisms decline at old age. Leading hypothesessuggest that a combination of limited resources, and environmental causes determine an "optimal" level of repair regarding molecular and cellular level damage that accumulates over time. This process is known as self-maintenance.

An older gentleman sitting in a nursing home.

Theories and Hypotheses

August Weismann was responsible for interpreting and formalizing the mechanisms of Darwinianevolution in a modern theoretical framework. In 1889, he theorized that ageing was part of life's program to make room for the next generation in order to sustain the turnover that is necessary for evolution. The idea that the ageing characteristic was selected (an adaptation) because of its deleterious effect was largely discounted for much of the 20th century, but a theoretical model suggests that altruistic ageing could evolve if there is little migration among populations. Weismann later abandoned his theory and later followed up with his programmed death theory.

Mutation Accumulation

The first modern theory of mammal ageing was formulated by Peter Medawar in 1952. This theory formed in the previous decade with J. B. S. Haldane and his selection shadow concept. Their idea was that ageing was a matter of neglect, as nature is a highly competitive place. Almost all animals die in the wild from predators, disease, or accidents, which lowers the average age of death. Therefore, there is not much reason why the body should remain fit for the long haul because selection pressure is low for traits that would maintain viability past the time when most animals would have died anyway.

Medawar's theory is referred to as Mutation Accumulation. This theory is based on the idea that random, germline mutations occur that are detrimental to overall health and survival later in life. Overall, senescence would occur through a summation of deleterious genes, and would explain the overall phenotypic damage we associate with ageing.

Modern genetics science has disclosed a possible problem with the mutation accumulation concept with the knowledge of a mechanism that regulates genes.

Antagonistic Pleiotropy

Medawar's theory was critiqued and later further developed by George C. Williams in 1957. Williams noted that senescence may be causing many deaths even if animals are not 'dying of old age.' He began his hypothesis with the idea that ageing can cause earlier senescence due to the competitive nature of life. Even a small amount of ageing can be fatal; hence natural selection does indeed care and ageing is not cost-free.

Williams eventually proposed his own hypothesis called antagonistic *pleiotropy*. Pleiotropy, alone, means one mutation that cause multiple effects on phenotype. Antagonistic pleiotropy on the other hand deals with one gene that creates two traits with one being beneficial and the other being detrimental. In essence, this refers to genes that offer benefits early in life, but accumulate a cost later on.

Although antagonistic pleiotropy is a prevailing theory today, this is largely by default, and has not been well verified. Research has shown that this is not true for all genes and may be thought of as partial validation of the theory, but it cuts the core premise: that genetic trade-offs are the root cause of ageing.

In breeding experiments, Michael R. Rose selected fruit flies for long lifespan. Based on antagonistic pleiotropy, Rose expected that this would surely reduce their fertility. His team found that they were able to breed flies that lived more than twice as long as the flies they started with, but to their surprise, the long-lived, inbred flies actually laid more eggs than the short-lived flies. This was another setback for pleiotropy theory, though Rose maintains it may be an experimental artifact.

Disposable Soma Theory

A third mainstream theory of ageing, the ''Disposable soma *theory*, proposed in 1977 by Thomas Kirkwood, presumes that the body must budget the amount of energy available to it. The body uses food energy for metabolism, for reproduction, and for repair and maintenance, and the body must compromise when there is a finite supply of food. The theory states that this compromise causes the body to reallocate energy to the repair function that causes the body to gradually deteriorate with age.

A caveat to this theory suggests that this reallocation of energy is based on time instead of limiting resources. This concept focuses on the evolutionary pressure to reproduce in a set, optimal time period that is dictated by age and ecological niche. The way that this is successful is through the allocation of time and energy in damage repair at the cellular level resulting in an accumulation of damage and a decreased lifespan relative to organisms with longer gestation. This concept stems from a comparative analysis of genomic stability in mammalian cells.

One opposing argument is based on caloric restriction (CR) effect, which has demonstrated an increase in life. But dietary restriction has not been shown to increase lifetime reproductive success (fitness), because when food availability is lower, reproductive output is also lower. So CR does thus not completely dismiss disposable soma theory.

DNA Damage Theory

The DNA damage theory of aging postulates that DNA damage is ubiquitous in the biological world and is the primary cause of ageing. The theory is based off the idea that ageing occurs over time due to the damage of the DNA. As an example, studies of mammalian brain and muscle have shown that DNA repair capability is relatively high during early development when cells are dividing mitotically, but declines substantially as cells enter the post-mitotic state. The effect of reducing expression of DNA repair capability is increased accumulation of DNA damage. This impairs gene transcription and causes the progressive loss of cellular and tissue functions that define aging.

Programmed Maintenance Theories

Theories, such as Weismann's "programmed death" theory, suggest that deterioration and death due to ageing are a purposeful result of an organism's evolved design, and are referred to as theories of programmed ageing or adaptive ageing.

The programmed maintenance theory based on evolvability suggests that the repair mechanisms are controlled by a common control mechanism capable of sensing conditions, such as caloric restriction, and may be responsible for lifespan in particular species. In this theory, the survival techniques are based on control mechanisms instead of individual maintenance mechanism, which you see in the non-programmed theory of mammal ageing.

A non-programmed theory of mammal ageing states that different species possess different capabilities for maintenance and repair. Longer-lived species possess many mechanisms for offsetting damage due to causes such as oxidation, telomere shortening, and other deteriorative processes. Shorter-lived species, having earlier ages of sexual maturity, have less need for longevity and thus did not evolve or retain the more-effective repair mechanisms. Damage therefore accumulates more rapidly, resulting in earlier manifestations and shorter lifespan. Since there are a wide variety of ageing manifestations that appear to have very different causes, it is likely that there are many different maintenance and repair functions.

Natural Selection

Group Selection

Group selection is based on the idea that all members of a given group will either succeed or fail together depending on the circumstance. With this mechanism, genetic drift occurs collectively to all in the group and sets them apart from other groups of its own species. This is different than individual selection, as it focuses on the group rather than the individual.

Often also postreproductive individuals make intergenerational transfers: bottlenose dolphins and pilot whales guard their grandchildren; there is cooperative breeding in some mammals, many insects and about 200 species of birds; sex differences in the survival of anthropoid primates tend to correlate

with the care to offspring; or an Efe infant is often attended by more than 10 people. Lee developed a formal theory integrating selection due to transfers (at all ages) with selection due to fertility.

Evolvability

Evolvability is based on the idea that an organism adapts genetically to its present environment.

Goldsmith proposed that though increasing the generation rate and evolution rate is beneficial for a species, it is also important to limit lifespan so older individuals will not dominate the gene pool.

Skulachev has suggested that programmed ageing assists the evolution process by providing a gradually increasing challenge or obstacle to survival and reproduction, and therefore enhancing the selection of beneficial characteristics.

Yang's model is also based on the idea that ageing accelerates the accumulation of novel adaptive genes in local populations. However, Yang changed the terminology of "evolvability" into "genetic creativity" throughout his paper to facilitate the understanding of how ageing can have a shorter-term benefit than the word "evolvability" would imply.

Lenart and Vašku have also invoked evolvability as the main mechanism driving evolution of ageing. However, they proposed that even though the actual rate of aging can be an adaptation the aging itself is inevitable. In other words, evolution can change speed of aging but some ageing no matter how slow will always occur.

Mortality

There are two types of mortality: intrinsic and extrinsic mortality. Intrinsic mortality is thought to be a result of ageing from insider factors, whereas extrinsic is a direct result of environmental factors. An example would be that bats have fewer predators, and therefore have a low extrinsic mortality. Birds are warm-blooded and are similar in size to many small mammals, yet often live 5–10 times as long. They have less predation pressure than ground-dwelling mammals, and have a lower extrinsic mortality.

When examining the body-size vs. lifespan relationship, one also observes that predatory mammals tend to live longer than prey mammals in a controlled environment, such as a zoo or nature reserve. The explanation for the long lifespans of primates (such as humans, monkeys, and apes) relative to body size is that their intelligence, and they would have a lower intrinsic mortality.

Diseases

Progeria

Progeria is a single-gene genetic disease that cause acceleration of many or most symptoms of ageing during childhood Those who have this disease are known for failure to thrive and have a series of symptoms that cause abnormalities in the joints, hair, skin, eyes, and face.

Werner Syndrome

Werner syndrome is also a single-gene genetic disease. This syndrome starts to affect individuals during the teenage years, and prevents the teens from growing at puberty. Once the individual

reaches the twenties, there is generally a change in hair color, skin, and voice. This condition can also affect the weight distribution between the arms, legs, and torso.

Biogerontology

Theories of ageing affect efforts to understand and find treatments for age-related conditions:

- Those who believe in the idea that ageing is an unavoidable side effect of some necessary function (antagonistic pleiotropy or disposable soma theories) logically tend to believe that attempts to delay ageing would result in unacceptable side effects to the necessary functions. Altering ageing is therefore "impossible", and study of ageing mechanisms is of only academic interest.
- Those believing in default theories of multiple maintenance mechanisms tend to believe that ways might be found to enhance the operation of some of those mechanisms. Perhaps they can be assisted by anti-oxidants or other agents.
- Those who believe in programmed ageing suppose that ways might be found to interfere with the operation of the part of the ageing mechanism that appears to be common to multiple symptoms, essentially "slowing down the clock" and delaying multiple manifestations. Such effect might be obtained by fooling a sense function. One such effort is an attempt to find a "mimetic" that would "mime" the anti-ageing effect of calorie restriction without having to actually radically restrict diet.

Evolution of Sexual Reproduction

The evolution of sexual reproduction describes how sexually reproducing animals, plants, fungi and protistscould have evolved from a common ancestor that was a single celled eukaryotic species. There are a few species which have secondarily lost the ability to reproduce sexually, such as Bdelloidea, and some plants and animals that routinely reproduce asexually (by apomixis and parthenogenesis) without entirely losing sex. The evolution of sex contains two related, yet distinct, themes: its origin and its maintenance.

Ladybirds mating.

Pollen production is an essential step in sexual reproduction of seed plants.

The origin of sexual reproduction in prokaryotes is around 2 billion years ago (Gya) when bacteria started exchanging genes via the processes of conjugation, transformation, and transduction. In eukaryotes, it is thought to have arisen in the Last Common Eukaryotic Ancestor (LECA), possibly via several processes of varying success, and then to have persisted.

Since hypotheses for the origins of sex are difficult to verify experimentally (outside of evolutionary computation), most current work has focused on the maintenance of sexual reproduction. The maintenance of sexual reproduction - specifically, of its dioecious form - in a highly competitive world had long been one of the major mysteries of biology, as both other known mechanisms of reproduction - asexual reproduction and hermaphroditism - possess apparent advantages over it. Asexual reproduction can proceed by budding, fission, or spore formation not involving union of gametes, which results in a much faster rate compared to sexual reproduction, where 50% of offspring are males, unable to produce offspring themselves. In hermaphoditic reproduction each of the two parent organisms required for the formation of a zygote can provide either the male or the female gamete, which leads to advantages in both size and genetic variance of a population.

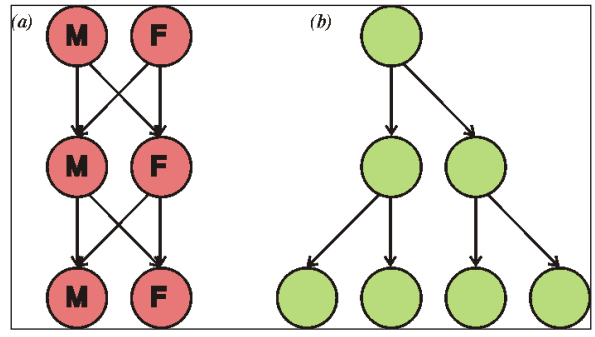
Sexual reproduction must offer significant fitness advantages to a species because despite the two-fold cost of sex, it dominates among multicellular forms of life, implying that the fitness of offspring produced outweighs the costs. Sexual reproduction derives from recombination, where parent genotypes are reorganized and shared with the offspring. This stands in contrast to single-parent asexual replication, where the offspring is identical to the parents. Recombination supplies two fault-tolerance mechanisms at the molecular level: recombinational DNA repair(promoted during meiosis because homologous chromosomes pair at that time) and complementation (also known as heterosis, hybrid vigor or masking of mutations).

Disadvantages of Sex and Sexual Reproduction

Population Expansion Cost of Sex

Among the most limiting disadvantages to the evolution of sexual reproduction by natural selection is that an asexual population can grow much more rapidly than a sexual one with each generation. Assume the entire population of some theoretical species has 100 total organisms consisting of two sexes (i.e. males and females) with 50:50 male-to-female representation, and only the females of this species can bear offspring. If all capable members of this population procreated once, a total of 50 offspring would be produced (the *F1* generation). Contrast this outcome with an

asexual species, where each member of the 100-organism population is capable of bearing young. If all capable members of this asexual population procreated once, a total of 100 offspring would be produced.



This diagram illustrates the *two-fold cost of sex*. If each individual were to contribute to the same number of offspring (two), *(a)*the sexual population remains the same size each generation, where the *(b)* asexual population doubles in size each generation.

This idea is sometimes referred to as the of sexual reproduction. It was first described mathematically by John Maynard Smith. In his manuscript Smith further speculated on the impact of an asexual mutant arising in a sexual population, which suppresses meiosis and allows eggs to develop by mitotic division into offspring genetically identical to the mother. The mutant-asexual lineage would double its representation in the population each generation, all else being equal.

Technically the problem above is not that of sexual reproduction but a problem of having a subset of organisms incapable of bearing offspring. Indeed some multicellular organisms (isogamous) engage in sexual reproduction but all members of the species are capable of bearing offspring. The two-fold reproductive disadvantage assumes that males contribute only genes to their offspring and sexual females waste half their reproductive potential on sons. Thus, in this formulation, the principal costs of sex is that males and females must successfully copulate (which almost always involves expending energy to come together through time and space).

Selfish Cytoplasmic Genes

Sexual reproduction implies that chromosomes and alleles segregate and recombine in every generation, but not all genes are transmitted together to the offspring. There is a chance of spreading mutants that cause unfair transmission at the expense of their non-mutant colleagues. These mutations are referred to as selfish because they promote their own spread at the cost of alternative alleles or host organism, these include; nuclear meiotic drivers and selfish cytoplasmic genes. Meiotic driver is defined as genes that distort meiosis to produce gametes containing themselves more than half the time and selfish cytoplasmic gene is a gene located in an organelle, plasmid, or intracellular parasite that modifies reproduction to cause its own increase at the expense of the cell or organism that carries it.

Genetic Heritability Cost of Sex

A sexually reproducing organism only passes on ~50% of its own genetic material to each L2 offspring. This is a consequence of the fact that gametes from sexually reproducing species

are haploid. Again however, this is not applicable to all sexual organisms. There are numerous species which are sexual but do not have a genetic-loss problem because they do not produce males or females. Yeast, for example, are isogamous sexual organisms which have two mating types which fuse and recombine their haploid genomes. Both sexes reproduce during the haploid and diploid stages of their life cycle and have a 100% chance of passing their genes into their offspring.

Some species avoid the cost of 50% of sexual reproduction, although they have "sex" (in the sense of genetic recombination). In these species (e.g., bacteria, ciliates, dinoflagellates and diatoms), "sex" and reproduction occurs separately.

Advantages of Sex and Sexual Reproduction

The concept of sex includes two fundamental phenomena: the sexual process (fusion of genetic information of two individuals) and sexual differentiation (separation of this information into two parts). Depending on the presence or absence of these phenomena, the existing ways of reproduction can be divided into asexual, hermaphrodite and dioecious forms. The sexual process and sexual differentiation are different phenomena, and, in essence, are diametrically opposed. The first creates (increases) diversity of genotypes, and the second decreases it by half.

Reproductive advantages of the asexual forms are in quantity of the progeny and the advantages of the hermaphrodite forms – in maximum diversity. Transition from the hermaphrodite to dioecious state leads to a loss of at least half of the diversity. So, the main question is to explain the advantages given by sexual differentiation, i.e. the benefits of two separate sexes compared to hermaphrodites rather than to explain benefits of sexual forms (hermaphrodite + dioecious) over asexual ones. It has already been understood that since sexual reproduction is not associated with any clear reproductive advantages, as compared with asexual, there should be some important advantages in evolution.

Advantages due to Genetic Variation

For the advantage due to genetic variation, there are three possible reasons this might happen. First, sexual reproduction can combine the effects of two beneficial mutations in the same individual (i.e. sex aids in the spread of advantageous traits). Also, the necessary mutations do not have to have occurred one after another in a single line of descendants. Second, sex acts to bring together currently deleterious mutations to create severely unfit individuals that are then eliminated from the population (i.e. sex aids in the removal of deleterious genes). However, in organisms containing only one set of chromosomes, deleterious mutations would be eliminated immediately, and therefore removal of harmful mutations is an unlikely benefit for sexual reproduction. Lastly, sex creates new gene combinations that may be more fit than previously existing ones, or may simply lead to reduced competition among relatives.

For the advantage due to DNA repair, there is an immediate large benefit of removing DNA damage by recombinational DNA repair during meiosis, since this removal allows greater survival of progeny with undamaged DNA. The advantage of complementation to each sexual partner is avoidance of the bad effects of their deleterious recessive genes in progeny by the masking effect of normal dominant genes contributed by the other partner.

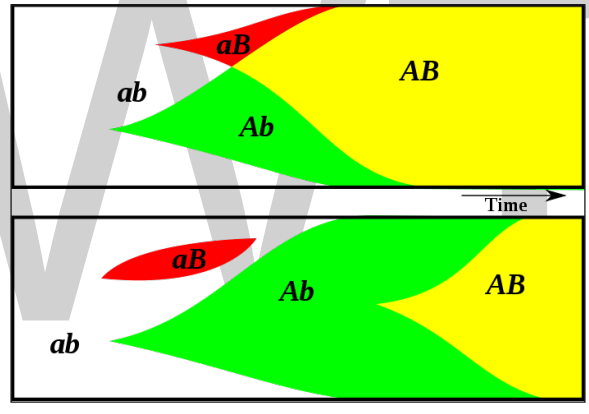
The classes of hypotheses based on the creation of variation are further broken down below. Any number of these hypotheses may be true in any given species (they are not mutually exclusive), and different hypotheses may apply in different species. However, a research framework based on creation of variation has yet to be found that allows one to determine whether the reason for sex is universal for all sexual species, and, if not, which mechanisms are acting in each species.

On the other hand, the maintenance of sex based on DNA repair and complementation applies widely to all sexual species.

Protection from Major Genetic Mutation

In contrast to the view that sex promotes genetic variation, Heng, and Gorelick and Hengreviewed evidence that sex actually acts as a constraint on genetic variation. They consider that sex acts as a coarse filter, weeding out major genetic changes, such as chromosomal rearrangements, but permitting minor variation, such as changes at the nucleotide or gene level (that are often neutral) to pass through the sexual sieve.

Novel Genotypes



This diagram illustrates how sex might create novel genotypes more rapidly. Two advantageous alleles *A* and *B* occur at random. The two alleles are recombined rapidly in a sexual population (top), but in an asexual population (bottom) the two alleles must independently arise because of clonal interference.

Sex could be a method by which novel genotypes are created. Because sex combines genes from two individuals, sexually reproducing populations can more easily combine advantageous genes than can asexual populations. If, in a sexual population, two different advantageous alleles arise at different loci on a chromosome in different members of the population, a chromosome containing the two advantageous alleles can be produced within a few generations by recombination. However, should the same two alleles arise in different members of an asexual population, the only way that one chromosome can develop the other allele is to independently gain the same mutation, which would take much longer. Several studies have addressed counterarguments, and the question of whether this model is sufficiently robust to explain the predominance of sexual versus asexual reproduction remains.

Ronald Fisher also suggested that sex might facilitate the spread of advantageous genes by allowing them to better escape their genetic surroundings, if they should arise on a chromosome with deleterious genes.

Supporters of these theories respond to the balance argument that the individuals produced by sexual and asexual reproduction may differ in other respects too – which may influence the persistence of sexuality. For example, in the heterogamous water fleas of the genus *Cladocera*, sexual offspring form eggs which are better able to survive the winter versus those the fleas produce asexually.

Increased Resistance to Parasites

One of the most widely discussed theories to explain the persistence of sex is that it is maintained to assist sexual individuals in resisting parasites, also known as the Red Queen Hypothesis.

When an environment changes, previously neutral or deleterious alleles can become favourable. If the environment changed sufficiently rapidly (i.e. between generations), these changes in the environment can make sex advantageous for the individual. Such rapid changes in environment are caused by the co-evolution between hosts and parasites.

Imagine, for example that there is one gene in parasites with two alleles *p* and *P* conferring two types of parasitic ability, and one gene in hosts with two alleles *h* and *H*, conferring two types of parasite resistance, such that parasites with allele *p* can attach themselves to hosts with the allele *h*, and *P* to *H*. Such a situation will lead to cyclic changes in allele frequency - as *p* increases in frequency, *h* will be disfavoured.

In reality, there will be several genes involved in the relationship between hosts and parasites. In an asexual population of hosts, offspring will only have the different parasitic resistance if a mutation arises. In a sexual population of hosts, however, offspring will have a new combination of parasitic resistance alleles.

In other words, like Lewis Carroll's Red Queen, sexual hosts are continually "running" (adapting) to "stay in one place" (resist parasites).

Evidence for this explanation for the evolution of sex is provided by comparison of the rate of molecular evolution of genes for kinases and immunoglobulins in the immune system with genes coding other proteins. The genes coding for immune system proteins evolve considerably faster.

Further evidence for the Red Queen hypothesis was provided by observing long-term dynamics and parasite coevolution in a "mixed" (sexual and asexual) population of snails (*Potamopyrgus antipodarum*). The number of sexuals, the number asexuals, and the rates of parasite infection for both were monitored. It was found that clones that were plentiful at the beginning of the study became more susceptible to parasites over time. As parasite infections increased, the once plentiful clones dwindled dramatically in number. Some clonal types disappeared entirely. Meanwhile, sexual snail populations remained much more stable over time.

However, Hanley et al. studied mite infestations of a parthenogenetic gecko species and its two related sexual ancestral species. Contrary to expectation based on the Red Queen hypothesis, they found that the prevalence, abundance and mean intensity of mites in sexual geckos was significantly higher than in asexuals sharing the same habitat.

In 2011, researchers used the microscopic roundworm *Caenorhabditis elegans* as a host and the pathogenic bacteria *Serratia marcescens* to generate a host-parasite coevolutionary system in a

controlled environment, allowing them to conduct more than 70 evolution experiments testing the Red Queen Hypothesis. They genetically manipulated the mating system of *C. elegans*, causing populations to mate either sexually, by self-fertilization, or a mixture of both within the same population. Then they exposed those populations to the *S. marcescens* parasite. It was found that the self-fertilizing populations of *C. elegans* were rapidly driven extinct by the coevolving parasites while sex allowed populations to keep pace with their parasites, a result consistent with the Red Queen Hypothesis. In natural populations of *C. elegans*, self-fertilization is the predominant mode of reproduction, but infrequent out-crossing events occur at a rate of about 1%.

Critics of the Red Queen hypothesis question whether the constantly changing environment of hosts and parasites is sufficiently common to explain the evolution of sex. In particular, Otto and Nuismer presented results showing that species interactions (e.g. host vs parasite interactions) typically select against sex. They concluded that, although the Red Queen hypothesis favors sex under certain circumstances, it alone does not account for the ubiquity of sex. Otto and Gerstein further stated that "it seems doubtful to us that strong selection per gene is sufficiently commonplace for the Red Queen hypothesis to explain the ubiquity of sex." Parker reviewed numerous genetic studies on plant disease resistance and failed to uncover a single example consistent with the assumptions of the Red Queen hypothesis.

DNA Repair and Complementation

Sexual reproduction is conventionally explained as an adaptation for producing genetic variation through allelic recombination. As acknowledged above, however, serious problems with this explanation have led many biologists to conclude that the benefit of sex is a major unsolved problem in evolutionary biology.

An alternative "informational" approach to this problem has led to the view that the two fundamental aspects of sex, genetic recombination and outcrossing, are adaptive responses to the two major sources of "noise" in transmitting genetic information. Genetic noise can occur as either physical damage to the genome (e.g. chemically altered bases of DNA or breaks in the chromosome) or replication errors (mutations) This alternative view is referred to as the repair and complementation hypothesis, to distinguish it from the traditional variation hypothesis.

The repair and complementation hypothesis assumes that genetic recombination is fundamentally a DNA repair process, and that when it occurs during meiosis it is an adaptation for repairing the genomic DNA which is passed on to progeny. Recombinational repair is the only repair process known which can accurately remove double-strand damages in DNA, and such damages are both common in nature and ordinarily lethal if not repaired. For instance, double-strand breaks in DNA occur about 50 times per cell cycle in human cells. Recombinational repair is prevalent from the simplest viruses to the most complex multicellular eukaryotes. It is effective against many different types of genomic damage, and in particular is highly efficient at overcoming double-strand damages. Studies of the mechanism of meiotic recombination indicate that meiosis is an adaptation for repairing DNA. These considerations form the basis for the first part of the repair and complementation hypothesis.

In some lines of descent from the earliest organisms, the diploid stage of the sexual cycle, which was at first transient, became the predominant stage, because it allowed complementation — the

masking of deleterious recessive mutations (i.e. hybrid vigor or heterosis). Outcrossing, the second fundamental aspect of sex, is maintained by the advantage of masking mutations and the disadvantage of inbreeding (mating with a close relative) which allows expression of recessive mutations (commonly observed as inbreeding depression). This is in accord with Charles Darwin,who concluded that the adaptive advantage of sex is hybrid vigor; or as he put it, "the offspring of two individuals, especially if their progenitors have been subjected to very different conditions, have a great advantage in height, weight, constitutional vigor and fertility over the self fertilised offspring from either one of the same parents".

However, outcrossing may be abandoned in favor of parthenogenesis or selfing (which retain the advantage of meiotic recombinational repair) under conditions in which the costs of mating are very high. For instance, costs of mating are high when individuals are rare in a geographic area, such as when there has been a forest fire and the individuals entering the burned area are the initial ones to arrive. At such times mates are hard to find, and this favors parthenogenic species.

In the view of the repair and complementation hypothesis, the removal of DNA damage by recombinational repair produces a new, less deleterious form of informational noise, allelic recombination, as a by-product. This lesser informational noise generates genetic variation, viewed by some as the major effect of sex.

Deleterious Mutation Clearance

Mutations can have many different effects upon an organism. It is generally believed that the majority of non-neutral mutations are deleterious, which means that they will cause a decrease in the organism's overall fitness. If a mutation has a deleterious effect, it will then usually be removed from the population by the process of natural selection. Sexual reproduction is believed to be more efficient than asexual reproduction in removing those mutations from the genome.

There are two main hypotheses which explain how sex may act to remove deleterious genes from the genome.

Evading Harmful Mutation Build-up

While DNA is able to recombine to modify alleles, DNA is also susceptible to mutations within the sequence that can affect an organism in a negative manner. Asexual organisms do not have the ability to recombine their genetic information to form new and differing alleles. Once a mutation occurs in the DNA or other genetic carrying sequence, there is no way for the mutation to be removed from the population until another mutation occurs that ultimately deletes the primary mutation. This is rare among organisms. Hermann Joseph Muller introduced the idea that mutations build up in asexual reproducing organisms. Muller described this occurrence by comparing the mutations that accumulate as a ratchet. Each mutation that arises in asexually reproducing organisms turns the ratchet once. The ratchet is unable to be rotated backwards, only forwards. The next mutation that occurs turns the ratchet once more. Additional mutations in a population continually turn the ratchet and the mutations, mostly deleterious, continually accumulate without recombination. These mutations are passed onto the next generation because the offspring are exact genetic clones of their parent. The genetic load of organisms and their populations will increase

due to the addition of multiple deleterious mutations and decrease the overall reproductive success and fitness.

For sexually reproducing populations, studies have shown that single-celled bottlenecks are beneficial for resisting mutation build-up. Passaging a population through a single-celled bottleneck involves the fertilization event occurring with haploid sets of DNA, forming one fertilized cell. For example, humans undergo a single-celled bottleneck in that the haploid sperm fertilizes the haploid egg, forming the diploid zygote, which is unicellular. This passage through a single cell is beneficial in that it lowers the chance of mutations from being passed on through multiple individuals. Further studies using Dictyostelium discoideum suggest that this unicellular initial stage is important for resisting mutations due to the importance of high relatedness. Highly related individuals are more closely related, and more clonal, whereas less related individuals are less so, increasing the likelihood that an individual in a population of low relatedness may have a detrimental mutation. Highly related populations also tend to thrive better than lowly related because the cost of sacrificing an individual is greatly offset by the benefit gained by its relatives and in turn, its genes, according to kin selection. The studies with D. discoideum showed that conditions of high relatedness resisted mutant individuals more effectively than those of low relatedness, suggesting the importance of high relatedness to resist mutations from proliferating.

Removal of Deleterious Genes

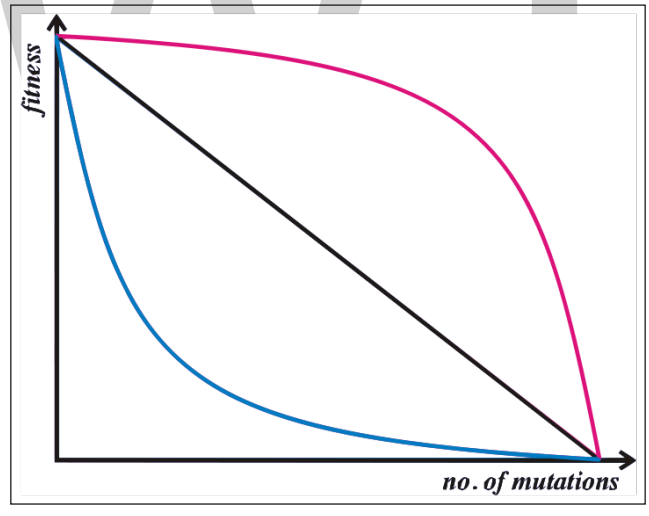


Diagram illustrating different relationships between numbers of mutations and fitness. Kondrashov's model requires *synergistic epistasis*, which is represented by the red line - each subsequent mutation has a disproportionately large effect on the organism's fitness.

This hypothesis was proposed by Alexey Kondrashov, and is sometimes known as the deterministic mutation hypothesis.It assumes that the majority of deleterious mutations are only slightly deleterious, and affect the individual such that the introduction of each additional mutation has an increasingly large effect on the fitness of the organism. This relationship between number of mutations and fitness is known as synergistic epistasis.

By way of analogy, think of a car with several minor faults. Each is not sufficient alone to prevent the car from running, but in combination, the faults combine to prevent the car from functioning.

Similarly, an organism may be able to cope with a few defects, but the presence of many mutations could overwhelm its backup mechanisms.

The slightly deleterious nature of mutations means that the population will tend to be composed of individuals with a small number of mutations. Sex will act to recombine these genotypes, creating some individuals with fewer deleterious mutations, and some with more. Because there is a major selective disadvantage to individuals with more mutations, these individuals die out. In essence, sex compartmentalises the deleterious mutations.

There has been much criticism of Kondrashov's theory, since it relies on two key restrictive conditions. The first requires that the rate of deleterious mutation should exceed one per genome per generation in order to provide a substantial advantage for sex. While there is some empirical evidence for it (for example in Drosophila and E. coli), there is also strong evidence against it. Thus, for instance, for the sexual species Saccharomyces cerevisiae (yeast) and Neurospora crassa(fungus), the mutation rate per genome per replication are 0.0027 and 0.0030 respectively. For the nematode worm Caenorhabditis elegans, the mutation rate per effective genome per sexual generation is 0.036. Secondly, there should be strong interactions among loci (synergistic epistasis), a mutation-fitness relation for which there is only limited evidence. Conversely, there is also the same amount of evidence that mutations show no epistasis (purely additive model) or antagonistic interactions (each additional mutation has a disproportionally small effect).

Geodakyan's Evolutionary Theory of Sex

Geodakyan suggested that sexual dimorphism provides a partitioning of a species' phenotypes into at least two functional partitions: a female partition that secures beneficial features of the species and a male partition that emerged in species with more variable and unpredictable environments. The male partition is suggested to be an "experimental" part of the species that allows the species to expand their ecological niche, and to have alternative configurations. This theory underlines the higher variability and higher mortality in males, in comparison to females. This functional partitioning also explains the higher susceptibility to disease in males, in comparison to females and therefore includes the idea of "protection against parasites" as another functionality of male sex. Geodakyan's evolutionary theory of sex was developed in Russia in 1960-80 and was not known to the West till the era of the Internet. Trofimova, who analysed psychological sex differences, hypothesised that the male sex might also provide a "redundancy pruning" function.

Speed of Evolution

Sex prevents rapid evolution. He suggests that recombination breaks up favourable gene combinations more often than it creates them, and sex is maintained because it ensures selection is longer-term than in asexual populations - so the population is less affected by short-term changes. This explanation is not widely accepted, as its assumptions are very restrictive.

It has been shown in experiments with Chlamydomonas algae that sex can remove the speed limit on evolution.

An information theoretic analysis using a simplified but useful model shows that in asexual reproduction, the information gain per generation of a species is limited to 1 bit per generation, while in

sexual reproduction, the information gain is bounded by $\sqrt{G}$, where G is the size of the genome in bits.

Libertine Bubble Theory

The evolution of sex can alternatively be described as a kind of gene exchange that is independent from reproduction. According to the Thierry Lodé's "libertine bubble theory", sex originated from an archaic gene transfer process among prebiotic bubbles. The contact among the pre-biotic bubbles could, through simple food or parasitic reactions, promote the transfer of genetic material from one bubble to another. That interactions between two organisms be in balance appear to be a sufficient condition to make these interactions evolutionarily efficient, i.e. to select bubbles that tolerate these interactions ("libertine" bubbles) through a blind evolutionary process of self-reinforcing gene correlations and compatibility.

The "libertine bubble theory" proposes that meiotic sex evolved in proto-eukaryotes to solve a problem that bacteria did not have, namely a large amount of DNA material, occurring in an archaic step of proto-cell formation and genetic exchanges. So that, rather than providing selective advantages through reproduction, sex could be thought of as a series of separate events which combines step-by-step some very weak benefits of recombination, meiosis, gametogenesis and syngamy. Therefore, current sexual species could be descendants of primitive organisms that practiced more stable exchanges in the long term, while asexual species have emerged, much more recently in evolutionary history, from the conflict of interest resulting from anisogamy.

Origin of Sexual Reproduction

Many protists reproduce sexually, as do the multicellular plants, animals, and fungi. In the eukaryotic fossil record, sexual reproduction first appeared by 1.2 billion years ago in the Proterozoic Eon. All sexually reproducing eukaryotic organisms likely derive from a single-celled common ancestor. It is probable that the evolution of sex was an integral part of the evolution of the first eukaryotic cell.There are a few species which have secondarily lost this feature, such as Bdelloidea and some parthenocarpic plants.

Diploidy

Organisms need to replicate their genetic material in an efficient and reliable manner. The necessity to repair genetic damage is one of the leading theories explaining the origin of sexual reproduction. Diploid individuals can repair a damaged section of their DNA via homologous recombination, since there are two copies of the gene in the cell and if one copy is damaged, the other copy is unlikely to be damaged at the same site.

A harmful mutation in a haploid individual, on the other hand, is more likely to become fixed (i.e. permanent), since any DNA repair mechanism would have no source to recover the original undamaged sequence from. The most primitive form of sex may have been one organism with damaged DNA replicating an undamaged strand from a similar organism in order to repair itself.

Meiosis

If, as evidence indicates, sexual reproduction arose very early in eukaryotic evolution, the essential features of meiosis may have already been present in the prokaryotic ancestors of eukaryotes.In extant organisms, proteins with central functions in meiosis are similar to key proteins in natural transformation in bacteria and DNA transfer in archaea. For example, recA recombinase, that catalyses the key functions of DNA homology search and strand exchange in the bacterial sexual process of transformation, has orthologs in eukaryotes that perform similar functions in meiotic recombination.

Natural transformation in bacteria, DNA transfer in archaea, and meiosis in eukaryotic microorganisms are induced by stressful circumstances such as overcrowding, resource depletion, and DNA damaging conditions. This suggests that these sexual processes are adaptations for dealing with stress, particularly stress that causes DNA damage. In bacteria, these stresses induce an altered physiologic state, termed competence, that allows active take-up of DNA from a donor bacterium and the integration of this DNA into the recipient genome allowing recombinational repair of the recipients' damaged DNA.

If environmental stresses leading to DNA damage were a persistent challenge to the survival of early microorganisms, then selection would likely have been continuous through the prokaryote to eukaryote transition, and adaptative adjustments would have followed a course in which bacterial transformation or archaeal DNA transfer naturally gave rise to sexual reproduction in eukaryotes.

Virus-like RNA-based Origin

Sex might also have been present even earlier, in the hypothesized RNA world that preceded DNA cellular life forms. One proposed origin of sex in the RNA world was based on the type of sexual interaction that is known to occur in extant single-stranded segmented RNA viruses, such as influenza virus, and in extant double-stranded segmented RNA viruses such as reovirus.

Exposure to conditions that cause RNA damage could have led to blockage of replication and death of these early RNA life forms. Sex would have allowed re-assortment of segments between two individuals with damaged RNA, permitting undamaged combinations of RNA segments to come together, thus allowing survival. Such a regeneration phenomenon, known as multiplicity reactivation, occurs in influenza virus and reovirus.

Parasitic DNA Elements

Another theory is that sexual reproduction originated from selfish parasitic genetic elements that exchange genetic material (that is: copies of their own genome) for their transmission and propagation. In some organisms, sexual reproduction has been shown to enhance the spread of parasitic genetic elements (e.g. yeast, filamentous fungi).

Bacterial conjugation is a form of genetic exchange that some sources describe as "sex", but technically is not a form of reproduction, even though it is a form of horizontal gene transfer. However, it does support the "selfish gene" part theory, since the gene itself is propagated through the F-plasmid.

A similar origin of sexual reproduction is proposed to have evolved in ancient haloarchaea as a combination of two independent processes: jumping genes and plasmid swapping.

Partial Predation

A third theory is that sex evolved as a form of cannibalism: One primitive organism ate another one, but instead of completely digesting it, some of the "eaten" organism's DNA was incorporated into the DNA of the "eater".

Vaccination-like Process

Sex may also be derived from another prokaryotic process. A comprehensive theory called "origin of sex as vaccination" proposes that eukaryan sex-as-syngamy (fusion sex) arose from prokaryan unilateral sex-as-infection, when infected hosts began swapping nuclearised genomes containing coevolved, vertically transmitted symbionts that provided protection against horizontal superinfection by other, more virulent symbionts.

Consequently, sex-as-meiosis (fission sex) would evolve as a host strategy for uncoupling from (and thereby render impotent) the acquired symbiotic/parasitic genes.

Mechanistic Origin of Sexual Reproduction

While theories positing fitness benefits that led to the origin of sex are often problematic, several theories addressing the emergence of the mechanisms of sexual reproduction have been proposed.

Viral Eukaryogenesis

The viral eukaryogenesis (VE) theory proposes that eukaryotic cells arose from a combination of a lysogenic virus, an archaean, and a bacterium. This model suggests that the nucleus originated when the lysogenic virus incorporated genetic material from the archaean and the bacterium and took over the role of information storage for the amalgam. The archaeal host transferred much of its functional genome to the virus during the evolution of cytoplasm, but retained the function of gene translation and general metabolism. The bacterium transferred most of its functional genome to the virus as it transitioned into a mitochondrion.

For these transformations to lead to the eukaryotic cell cycle, the VE hypothesis specifies a pox-like virus as the lysogenic virus. A pox-like virus is a likely ancestor because of its fundamental similarities with eukaryotic nuclei. These include a double stranded DNA genome, a linear chromosome with short telomeric repeats, a complex membrane bound capsid, the ability to produce capped mRNA, and the ability to export the capped mRNA across the viral membrane into the cytoplasm. The presence of a lysogenic pox-like virus ancestor explains the development of meiotic division, an essential component of sexual reproduction.

Meiotic division in the VE hypothesis arose because of the evolutionary pressures placed on the lysogenic virus as a result of its inability to enter into the lytic cycle. This selective pressure resulted in the development of processes allowing the viruses to spread horizontally throughout the population. The outcome of this selection was cell-to-cell fusion. (This is distinct from the conjugation methods used by bacterial plasmids under evolutionary pressure, with important consequences.)The possibility of this kind of fusion is supported by the presence of fusion proteins in the envelopes of the pox viruses that allow them to fuse with host membranes. These proteins could have been transferred to the cell membrane during viral reproduction, enabling cell-to-cell fusion

between the virus host and an uninfected cell. The theory proposes meiosis originated from the fusion between two cells infected with related but different viruses which recognised each other as uninfected. After the fusion of the two cells, incompatibilities between the two viruses result in a meiotic-like cell division.

The two viruses established in the cell would initiate replication in response to signals from the host cell. A mitosis-like cell cycle would proceed until the viral membranes dissolved, at which point linear chromosomes would be bound together with centromeres. The homologous nature of the two viral centromeres would incite the grouping of both sets into tetrads. It is speculated that this grouping may be the origin of crossing over, characteristic of the first division in modern meiosis. The partitioning apparatus of the mitotic-like cell cycle the cells used to replicate independently would then pull each set of chromosomes to one side of the cell, still bound by centromeres. These centromeres would prevent their replication in subsequent division, resulting in four daughter cells with one copy of one of the two original pox-like viruses. The process resulting from combination of two similar pox viruses within the same host closely mimics meiosis.

Neomuran Revolution

An alternative theory, proposed by Thomas Cavalier-Smith, was labeled the Neomuran revolution. The designation "Neomuran revolution" refers to the appearances of the common ancestors of eukaryotes and archaea. Cavalier-Smith proposes that the first neomurans emerged 850 million years ago. Other molecular biologists assume that this group appeared much earlier, but Cavalier-Smith dismisses these claims because they are based on the "theoretically and empirically" unsound model of molecular clocks. Cavalier-Smith's theory of the Neomuran revolution has implications for the evolutionary history of the cellular machinery for recombination and sex. It suggests that this machinery evolved in two distinct bouts separated by a long period of stasis; first the appearance of recombination machinery in a bacterial ancestor which was maintained for 3 Gy, until the neomuran revolution when the mechanics were adapted to the presence of nucleosomes. The archaeal products of the revolution maintained recombination machinery that was essentially bacterial, whereas the eukaryotic products broke with this bacterial continuity. They introduced cell fusion and ploidy cycles into cell life histories. Cavalier-Smith argues that both bouts of mechanical evolution were motivated by similar selective forces: the need for accurate DNA replication without loss of viability.

Evolution of Biological Complexity

The evolution of biological complexity is one important outcome of the process of evolution.Evolution has produced some remarkably complex organisms - although the actual level of complexity is very hard to define or measure accurately in biology, with properties such as gene content, the number of cell types or morphology all proposed as possible metrics.

Many biologists used to believe that evolution was progressive (orthogenesis) and had a direction that led towards so-called "higher organisms," despite a lack of evidence for this viewpoint. This idea of "progression" and "higher organisms" in evolution is now regarded as misleading, with

natural selection having no intrinsic direction and organisms selected for either increased or decreased complexity in response to local environmental conditions. Although there has been an increase in the maximum level of complexity over the history of life, there has always been a large majority of small and simple organisms and the most common level of complexity appears to have remained relatively constant.

Selection for Simplicity and Complexity

Usually organisms that have a higher rate of reproduction than their competitors have an evolutionary advantage. Consequently, organisms can evolve to become simpler and thus multiply faster and produce more offspring, as they require fewer resources to reproduce. A good example are parasites such as Plasmodium - the parasite responsible for malaria - and mycoplasma; these organisms often dispense with traits that are made unnecessary through parasitism on a host.

A lineage can also dispense with complexity when a particular complex trait merely provides no selective advantage in a particular environment. Loss of this trait need not necessarily confer a selective advantage, but may be lost due to the accumulation of mutations if its loss does not confer an immediate selective disadvantage. For example, a parasitic organism may dispense with the synthetic pathway of a metabolite where it can readily scavenge that metabolite from its host. Discarding this synthesis may not necessarily allow the parasite to conserve significant energy or resources and grow faster, but the loss may be fixed in the population through mutation accumulation if no disadvantage is incurred by loss of that pathway. Mutations causing loss of a complex trait occur more often than mutations causing gain of a complex trait.

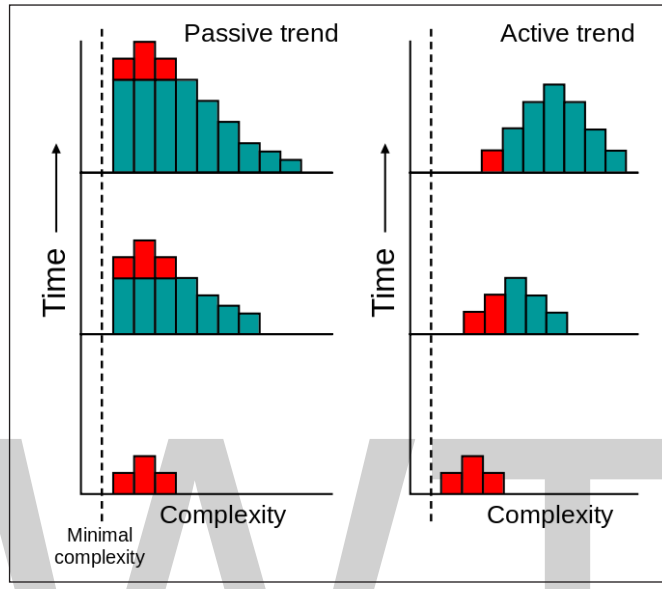
With selection, evolution can also produce more complex organisms. Complexity often arises in the co-evolution of hosts and pathogens, with each side developing ever more sophisticated adaptations, such as the immune system and the many techniques pathogens have developed to evade it. For example, the parasite *Trypanosoma brucei*, which causes sleeping sickness, has evolved so many copies of its major surface antigen that about 10% of its genome is devoted to different versions of this one gene. This tremendous complexity allows the parasite to constantly change its surface and thus evade the immune system through antigenic variation.

More generally, the growth of complexity may be driven by the co-evolution between an organism and the ecosystem of predators, prey and parasites to which it tries to stay adapted: as any of these become more complex in order to cope better with the diversity of threats offered by the ecosystem formed by the others, the others too will have to adapt by becoming more complex, thus triggering an ongoing evolutionary arms race towards more complexity. This trend may be reinforced by the fact that ecosystems themselves tend to become more complex over time, as species diversityincreases, together with the linkages or dependencies between species.

Types of Trends in Complexity

If evolution possessed an active trend toward complexity (orthogenesis), as was widely believed in the 19th century,then we would expect to see an active trend of increase over time in the most common value (the mode) of complexity among organisms.

However, an increase in complexity can also be explained through a passive process. Assuming unbiased random changes of complexity and the existence of a minimum complexity leads to an increase over time of the average complexity of the biosphere. This involves an increase in variance, but the mode does not change. The trend towards the creation of some organisms with higher complexity over time exists, but it involves increasingly small percentages of living things.



Passive versus active trends in complexity. Organisms at the beginning are red. Numbers are shown by height with time moving up in a series.

In this hypothesis, any appearance of evolution acting with an intrinsic direction towards increasingly complex organisms is a result of people concentrating on the small number of large, complex organisms that inhabit the right-hand tail of the complexity distribution and ignoring simpler and much more common organisms. This passive model predicts that the majority of species are microscopicprokaryotes, which is supported by estimates of 10^6 to 10^9 extant prokaryotes compared to diversity estimates of 10^6 to $3{\cdot}10^6$ for eukaryotes. Consequently, in this view, microscopic life dominates Earth, and large organisms only appear more diverse due to sampling bias.

Genome complexity has generally increased since the beginning of the life on Earth. Some computer models have suggested that the generation of complex organisms is an inescapable feature of evolution. Proteins tend to become more hydrophobic over time, and to have their hydrophobic amino acids more interspersed along the primary sequence. Increases in body size over time are sometimes seen in what is known as Cope's rule.

Constructive Neutral Evolution

Recently work in evolution theory has proposed that by relaxing selection pressure, which typically acts to streamline genomes, the complexity of an organism increases by a process called constructive neutral evolution. Since the effective population size in eukaryotes (especially multi-cellular organisms) is much smaller than in prokaryotes, they experience lower selection constraints.

According to this model, new genes are created by non-adaptive processes, such as by random gene duplication. These novel entities, although not required for viability, do give the organism

excess capacity that can facilitate the mutational decay of functional subunits. If this decay results in a situation where all of the genes are now required, the organism has been trapped in a new state where the number of genes has increased. This process has been sometimes described as a complexifying ratchet. These supplemental genes can then be co-opted by natural selection by a process called neofunctionalization. In other instances constructive neutral evolution does not promote the creation of new parts, but rather promotes novel interactions between existing players, which then take on new moonlighting roles.

Constructive neutral evolution has also been used to explain how ancient complexes, such as the spliceosome and the ribosome, have gained new subunits over time, how new alternative spliced isoforms of genes arise, how gene scrambling in ciliates evolved, and how pervasive pan-RNA editing may have arisen in Trypanosoma brucei.

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3

Fundamental Concepts of Evolutionary Biology

The fundamental concepts of evolutionary biology include genetic drift, natural selection, evolvability, modern synthesis, common descent and polyploidy. This chapter has been carefully written to provide an easy understanding of these concepts of evolutionary biology.

Common Descent

Common descent is a term within evolutionary biology which refers to the common ancestry of a particular group of organisms. The process of common decent involves the formation of new species from an ancestral population. When a recent common ancestor is shared between two organisms, they are said to be closely related. In contrast, common descent can also be traced back to a universal common ancestor of all living organisms using molecular genetic methods. Such evolution from a universal common ancestor is thought to have involved several speciation events as a result of natural selection and other processes, such as geographical separation.

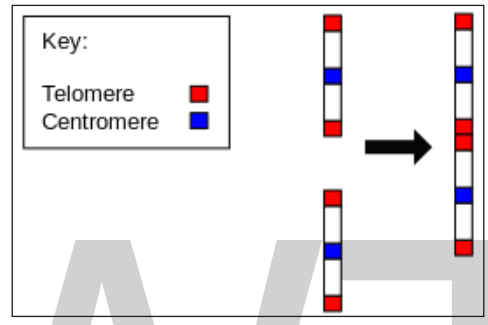
Theory of Common Descent

The theory of common descent states that all living organisms are descendants of a single ancestor. Thus, the Theory of Common Descent helps to explain why species living in different geographical regions exhibit different traits, some traits are highly conserved among broad animal classifications (e.g., vertebrates or tetrapods), seemly different species (e.g., birds and reptiles) share inherited physical and genetic traits, and successfully adapted organisms typically produce more offspring. While the Theory of Common Descent is primarily derived from the physical observation of various phenotypes (e.g., size, colour, beak shape, embryological development, etc.), modern advances in genetics and associated molecular techniques have been able to demonstrate that the process by which DNA is eventually translated into proteins is maintained among all lifeforms. Small changes in DNA between organisms have revealed a shared ancestry as well as insight into important changes that resulted in various speciation events. Phylogenetic trees and cladograms are often used to hypothesize the evolution of various organisms and shared common descent.

Examples of Common Descent

Human Chromosome 2

Compelling evidence of the shared common ancestry of humans with the great apes is the fusion event which occurred when two chromosomes common in apes fused to form chromosome 2 in humans. This resulted in humans having only 23 pairs of chromosomes, while all other hominidae have 24 pairs. The great apes (e.g., chimpanzees, gorillas, and orangutans) have two chromosomes with almost identical DNA sequences as that found in chromosome 2 of humans. Further evidence of such a fusion event is the residual presence of telomeres and a centromere, which indicate that the genetic information was historically found on two separate chromosomes.



Endogenous Retroviruses

Endogenous retroviruses are residual DNA sequences found in the genomes of virtually all living organisms as a result of ancient viral infections. Since the retroviral sequences are incorporated into the DNA of the host organism, such sequences are inherited in the offspring. Since such infections are random events, as is the location in which the viral genome is inserted within the genome, the identification of the same retroviral sequences in multiple species is indicative of a shared ancestry. Such analyses of endogenous retroviruses often reveal speciation events (e.g., feline endogenous retroviruses reveal the separation between large and small cat species) and how closely related two species may be, as observed in the shared endogenous retroviruses between humans and other primate species.

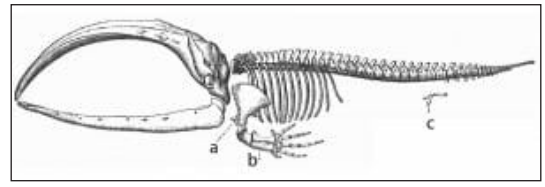
The Presence of Atavisms

Atavisms are the appearance of a lost trait observed in an ancestral species that is not observed in more recent ancestors. Atavisms are an example of common descent as they provide evidence of the phenotypical or vestigial features that are often retained throughout evolution. Some examples, include the appearance of hind limbs in whales as evidence of a terrestrial ancestor, teeth exhibited by chickens, additional toes observed in modern horse species, and the back flippers of bottlenose dolphins. Atavisms tend to arise because the ancestral genes are not deleted from the genome, but rather silenced and then reactivated in later offspring.

Vestigial Structures

Similar to atavisms, vestigial structures are structures that are homologous to those found in ancestral species, but have become underdeveloped, non-functional, or degenerated in more recently

evolved organisms. Such structures provide evidence of adaptations to a new environment, in which the ancestral organ or limb is no longer required, or has been modified to better suit a new purpose. There are an abundance of examples of vestigial structures observed in nature. Some examples include, the hind limbs and pelvic girdle observed in whales and snakes, non-functional wings exhibited by some insect species, non-functional wings of flightless bird species (e.g., ostriches), abdominal segments of barnacles, and the embryonic limb buds exhibited by several species lacking hind limbs (e.g., dolphins).



Pentadactyl Limbs

The presence of pentadactyl limbs is an example of a homologous trait exhibited by all tetrapods and is highly conserved throughout evolution, despite some modifications. Such limbs are first observed in the evolution from fishes to amphibians and consists of a single proximal, two distal, carpal, five metacarpal, and phalange bones. Although the overarching structure of the pentadactyl limbs is similar, various modifications have been made throughout evolution as adaptations to specific environments or lifestyles. Some examples include the modified pentadactyl wings of bats, the elongated forearms of primate species, the flippers of dolphin and whale species, and the modified digits of horses to form a hoof.

Fossil Evidence

The fossilized remains of various organisms combined with modern dating methods provides some of the most convincing evidence of common descent and evolutionary history. Fossilization occurs when the bones of a decaying animal become porous and the mineral salts in the surrounding earth infiltrate the bones, converting them to stone. Other methods include preservation in ice, imprinted remains (e.g., plants or footprints), tree resin, and peat. Since fossils are found in sedimentary rock, which is formed by layers of silt and mud, each layer corresponds to a specific geological period which can be dated. Thus, the extinction, evolution, and emergence of various species can be observed throughout history using the fossil record. Many extinct species are also observed in the fossil record, such as dinosaurs.

Biogeography

Biogeography presents compelling evidence of common descent by showcasing speciation and novel traits through adaptations to environmental pressures. One of the most famous examples is that of island biogeography and Charles Darwin's observations of the beaks of finches residing on the Galapagos Islands. In these finches, the beaks had been adapted for the specific vegetation found on the island, resulting in deviation from the ancestral finches found on the mainland. Long term effects of geographical separation are also observed with the evolution of new species that are not found elsewhere in the world. An example of this is the presence of marsupial species on the continent of Australia, and the emergence of polar bears as a result of geographical isolation in the arctic.

Evidence of Common Descent

Evidence of common descent of living organismshas been discovered by scientists researching in a variety of disciplines over many decades, demonstrating that all life on Earth comes from a single ancestor. This forms an important part of the evidenceon which evolutionary theory rests, demonstrates that evolution does occur, and illustrates the processes that created Earth's biodiversity. It supports the modern evolutionary synthesis—the current scientific theorythat explains how and why life changes over time. Evolutionary biologists document evidence of common descent, all the way back to the last universal common ancestor, by developing testable predictions, testing hypotheses, and constructing theories that illustrate and describe its causes.

Comparison of the DNA genetic sequences of organisms has revealed that organisms that are phylogenetically close have a higher degree of DNA sequence similarity than organisms that are phylogenetically distant. Genetic fragments such as pseudogenes, regions of DNA that are orthologous to a gene in a related organism, but are no longer active and appear to be undergoing a steady process of degeneration from cumulative mutations support common descent alongside the universal biochemical organization and molecular variance patterns found in all organisms. Additional genetic information conclusively supports the relatedness of life and has allowed scientists (since the discovery of DNA) to develop phylogenetic trees: a construction of organisms evolutionary relatedness. It has also led to the development of molecular clock techniques to date taxon divergence times and to calibrate these with the fossil record.

Fossils are important for estimating when various lineages developed in geologic time. As fossilization is an uncommon occurrence, usually requiring hard body parts and death near a site where sediments are being deposited, the fossil record only provides sparse and intermittent information about the evolution of life. Evidence of organisms prior to the development of hard body parts such as shells, bones and teeth is especially scarce, but exists in the form of ancient microfossils, as well as impressions of various soft-bodied organisms. The comparative study of the anatomy of groups of animals shows structural features that are fundamentally similar (homologous), demonstrating phylogenetic and ancestral relationships with other organisms, most especially when compared with fossils of ancient extinct organisms. Vestigial structures and comparisons in embryonic development are largely a contributing factor in anatomical resemblance in concordance with common descent. Since metabolic processes do not leave fossils, research into the evolution of the basic cellular processes is done largely by comparison of existing organisms' physiology and biochemistry. Many lineages diverged at different stages of development, so it is possible to determine when certain metabolic processes appeared by comparing the traits of the descendants of a common ancestor.

Evidence from animal coloration was gathered by some of Darwin's contemporaries; camouflage, mimicry, and warning coloration are all readily explained by natural selection. Special cases like the seasonal changes in the plumage of the ptarmigan, camouflaging it against snow in winter and against brown moorland in summer provide compelling evidence that selection is at work. Further evidence comes from the field of biogeography because evolution with common descent provides the best and most thorough explanation for a variety of facts concerning the geographical distribution of plants and animals across the world. This is especially obvious in the field of insular biogeography. Combined with the well-established geological theory of plate tectonics, common descent provides a way to combine facts about the current distribution of species with evidence

from the fossil record to provide a logically consistent explanation of how the distribution of living organisms has changed over time.

The development and spread of antibiotic resistant bacteria provides evidence that evolution due to natural selection is an ongoing process in the natural world. Alongside there are observed instances of the separation of populations of species into sets of new species (speciation). Speciation has been observed in the lab and in nature.

Evidence from Comparative Physiology and Biochemistry

Genetics

One of the strongest evidences for common descent comes from gene sequences. Comparative sequence analysis examines the relationship between the DNA sequences of different species,producing several lines of evidence that confirm Darwin's original hypothesis of common descent. If the hypothesis of common descent is true, then species that share a common ancestor inherited that ancestor's DNA sequence, as well as mutations unique to that ancestor. More closely related species have a greater fraction of identical sequence and shared substitutions compared to more distantly related species.

While on board HMS *Beagle*, Charles Darwin collected numerous specimens, many new to science, which supported his later theory of evolution by natural selection.

The simplest and most powerful evidence is provided by phylogenetic reconstruction. Such reconstructions, especially when done using slowly evolving protein sequences, are often quite robust and can be used to reconstruct a great deal of the evolutionary history of modern organisms (and even in some instances of the evolutionary history of extinct organisms, such as the recovered gene sequences of mammoths or Neanderthals). These reconstructed phylogenies recapitulate the relationships established through morphological and biochemical studies. The most detailed reconstructions have been performed on the basis of the mitochondrial genomes shared by all eukaryotic organisms, which are short and easy to sequence; the broadest reconstructions have been performed either using the sequences of a few very ancient proteins or by using ribosomal RNA sequence.

Phylogenetic relationships extend to a wide variety of nonfunctional sequence elements, including repeats, transposons, pseudogenes, and mutations in protein-coding sequences that do not change the amino-acid sequence. While a minority of these elements might later be found to harbor

function, in aggregate they demonstrate that identity must be the product of common descent rather than common function.

Universal Biochemical Organisation and Molecular Variance Patterns

All known extant (surviving) organisms are based on the same biochemical processes: genetic information encoded as nucleic acid (DNA, or RNA for many viruses), transcribed into RNA, then translated into proteins (that is, polymers of amino acids) by highly conserved ribosomes. Perhaps most tellingly, the Genetic Code (the "translation table" between DNA and amino acids) is the same for almost every organism, meaning that a piece of DNA in a bacterium codes for the same amino acid as in a human cell. ATP is used as energy currency by all extant life. A deeper understanding of developmental biology shows that common morphology is, in fact, the product of shared genetic elements. For example, although camera-like eyes are believed to have evolved independently on many separate occasions, they share a common set of light-sensing proteins (opsins), suggesting a common point of origin for all sighted creatures. Another example is the familiar vertebrate body plan, whose structure is controlled by the homeobox (Hox) family of genes.

DNA Sequencing

Comparison of DNA sequences allows organisms to be grouped by sequence similarity, and the resulting phylogenetic trees are typically congruent with traditional taxonomy, and are often used to strengthen or correct taxonomic classifications. Sequence comparison is considered a measure robust enough to correct erroneous assumptions in the phylogenetic tree in instances where other evidence is scarce. For example, neutral human DNA sequences are approximately 1.2% divergent (based on substitutions) from those of their nearest genetic relative, the chimpanzee, 1.6% from gorillas, and 6.6% from baboons. Genetic sequence evidence thus allows inference and quantification of genetic relatedness between humans and other apes. The sequence of the 16S ribosomal RNA gene, a vital gene encoding a part of the ribosome, was used to find the broad phylogenetic relationships between all extant life. The analysis by Carl Woese resulted in the three-domain system, arguing for two major splits in the early evolution of life. The first split led to modern Bacteria and the subsequent split led to modern Archaea and Eukaryotes.

Some DNA sequences are shared by very different organisms. It has been predicted by the theory of evolution that the differences in such DNA sequences between two organisms should roughly resemble both the biological difference between them according to their anatomy and the time that had passed since these two organisms have separated in the course of evolution, as seen in fossilevidence. The rate of accumulating such changes should be low for some sequences, namely those that code for critical RNA or proteins, and high for others that code for less critical RNA or proteins; but for every specific sequence, the rate of change should be roughly constant over time. These results have been experimentally confirmed. Two examples are DNA sequences coding for rRNA, which is highly conserved, and DNA sequences coding for fibrinopeptides (amino acid chains that are discarded during the formation of fibrin), which are highly non-conserved.

Proteins

Proteomic evidence also supports the universal ancestry of life. Vital proteins, such as the ribosome, DNA polymerase, and RNA polymerase, are found in everything from the most primitive bacteria

to the most complex mammals. The core part of the protein is conserved across all lineages of life, serving similar functions. Higher organisms have evolved additional protein subunits, largely affecting the regulation and protein-protein interaction of the core. Other overarching similarities between all lineages of extant organisms, such as DNA, RNA, amino acids, and the lipid bilayer, give support to the theory of common descent. Phylogenetic analyses of protein sequences from various organisms produce similar trees of relationship between all organisms. The chirality of DNA, RNA, and amino acids is conserved across all known life. As there is no functional advantage to right- or left-handed molecular chirality, the simplest hypothesis is that the choice was made randomly by early organisms and passed on to all extant life through common descent. Further evidence for reconstructing ancestral lineages comes from junk DNA such as pseudogenes, "dead" genes that steadily accumulate mutations.

Pseudogenes

Pseudogenes, also known as noncoding DNA, are extra DNA in a genome that do not get transcribed into RNA to synthesize proteins. Some of this noncoding DNA has known functions, but much of it has no known function and is called "Junk DNA". This is an example of a vestige since replicating these genes uses energy, making it a waste in many cases. A pseudogene can be produced when a coding gene accumulates mutations that prevent it from being transcribed, making it non-functional. But since it is not transcribed, it may disappear without affecting fitness, unless it has provided some beneficial function as non-coding DNA. Non-functional pseudogenes may be passed on to later species, thereby labeling the later species as descended from the earlier species.

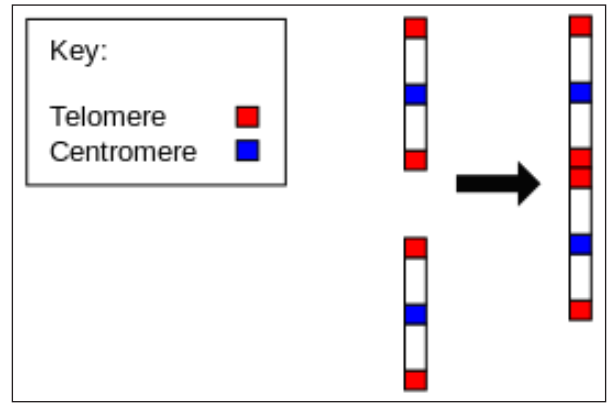
Other Mechanisms

A large body of molecular evidence supports a variety of mechanisms for large evolutionary changes, including: genome and gene duplication, which facilitates rapid evolution by providing substantial quantities of genetic material under weak or no selective constraints; horizontal gene transfer, the process of transferring genetic material to another cell that is not an organism's offspring, allowing for species to acquire beneficial genes from each other; and recombination, capable of reassorting large numbers of different alleles and of establishing reproductive isolation. The endosymbiotic theoryexplains the origin of mitochondria and plastids (including chloroplasts), which are organelles of eukaryotic cells, as the incorporation of an ancient prokaryotic cell into ancient eukaryotic cell. Rather than evolving eukaryotic organelles slowly, this theory offers a mechanism for a sudden evolutionary leap by incorporating the genetic material and biochemical composition of a separate species. Evidence supporting this mechanism has been found in the protist *Hatena*: as a predator it engulfs a green algal cell, which subsequently behaves as an endosymbiont, nourishing *Hatena*, which in turn loses its feeding apparatus and behaves as an autotroph.

Since metabolic processes do not leave fossils, research into the evolution of the basic cellular processes is done largely by comparison of existing organisms. Many lineages diverged when new metabolic processes appeared, and it is theoretically possible to determine when certain metabolic processes appeared by comparing the traits of the descendants of a common ancestor or by detecting their physical manifestations. As an example, the appearance of oxygen in the earth's atmosphere is linked to the evolution of photosynthesis.

Specific Examples from Comparative Physiology and Biochemistry

Chromosome 2 in Humans



Fusion of ancestral chromosomes left distinctive remnants of telomeres, and a vestigial centromere.

Evidence for the evolution of *Homo sapiens* from a common ancestor with chimpanzees is found in the number of chromosomes in humans as compared to all other members of Hominidae. All hominidae have 24 pairs of chromosomes, except humans, who have only 23 pairs. Human chromosome 2 is a result of an end-to-end fusion of two ancestral chromosomes.

The evidence for this includes:

- The correspondence of chromosome 2 to two ape chromosomes. The closest human relative, the common chimpanzee, has near-identical DNA sequences to human chromosome 2, but they are found in two separate chromosomes. The same is true of the more distant gorilla and orangutan.
- The presence of a vestigial centromere. Normally a chromosome has just one centromere, but in chromosome 2 there are remnants of a second centromere.
- The presence of vestigial telomeres. These are normally found only at the ends of a chromosome, but in chromosome 2 there are additional telomere sequences in the middle.

Chromosome 2 thus presents strong evidence in favour of the common descent of humans and other apes. According to J. W. Ijdo, "We conclude that the locus cloned in cosmids c8.1 and c29B is the relic of an ancient telomere-telomere fusion and marks the point at which two ancestral ape chromosomes fused to give rise to human chromosome 2."

Cytochrome c and b

A classic example of biochemical evidence for evolution is the variance of the ubiquitous (i.e. all living organisms have it, because it performs very basic life functions) protein Cytochrome c in living cells. The variance of cytochrome c of different organisms is measured in the number of differing amino acids, each differing amino acid being a result of a base pair substitution, a mutation. If each differing amino acid is assumed the result of one base pair substitution, it can be calculated how long ago the two species diverged by multiplying the number of base pair substitutions by the estimated time it takes for a substituted base pair of the cytochrome c gene to be successfully passed

on. For example, if the average time it takes for a base pair of the cytochrome c gene to mutate is N years, the number of amino acids making up the cytochrome c protein in monkeys differ by one from that of humans, this leads to the conclusion that the two species diverged N years ago.

The primary structure of cytochrome c consists of a chain of about 100 amino acids. Many higher order organisms possess a chain of 104 amino acids.

The cytochrome c molecule has been extensively studied for the glimpse it gives into evolutionary biology. Both chicken and turkeys have identical sequence homology (amino acid for amino acid), as do pigs, cows and sheep. Both humans and chimpanzees share the identical molecule, while rhesus monkeys share all but one of the amino acids: the 66th amino acid is isoleucine in the former and threonine in the latter.

What makes these homologous similarities particularly suggestive of common ancestry in the case of cytochrome c, in addition to the fact that the phylogenies derived from them match other phylogenies very well, is the high degree of functional redundancy of the cytochrome c molecule. The different existing configurations of amino acids do not significantly affect the functionality of the protein, which indicates that the base pair substitutions are not part of a directed design, but the result of random mutations that aren't subject to selection.

In addition, Cytochrome b is commonly used as a region of mitochondrial DNA to determine phylogenetic relationships between organisms due to its sequence variability. It is considered most useful in determining relationships within families and genera. Comparative studies involving cytochrome b have resulted in new classification schemes and have been used to assign newly described species to a genus, as well as deepen the understanding of evolutionary relationships.

Endogenous Retroviruses

Endogenous retroviruses (or ERVs) are remnant sequences in the genome left from ancient viral infections in an organism. The retroviruses (or virogenes) are always passed on to the next generation of that organism that received the infection. This leaves the virogene left in the genome. Because this event is rare and random, finding identical chromosomal positions of a virogene in two different species suggests common ancestry. Cats (Felidae) present a notable instance of virogene sequences demonstrating common descent. The standard phylogenetic tree for Felidae have smaller cats (*Felis chaus*, *Felis silvestris*, *Felis nigripes*, and *Felis catus*) diverging from larger cats such as the subfamily Pantherinae and other carnivores. The fact that small cats have an ERV where the larger cats do not suggests that the gene was inserted into the ancestor of the small cats after the larger cats had diverged. Another example of this is with humans and chimps. Humans contain numerous ERVs that comprise a considerable percentage of the genome. Sources vary, but 1% to 8% has been proposed. Humans and chimps share seven different occurrences of virogenes, while all primates share similar retroviruses congruent with phylogeny.

Recent African Origin of Modern Humans

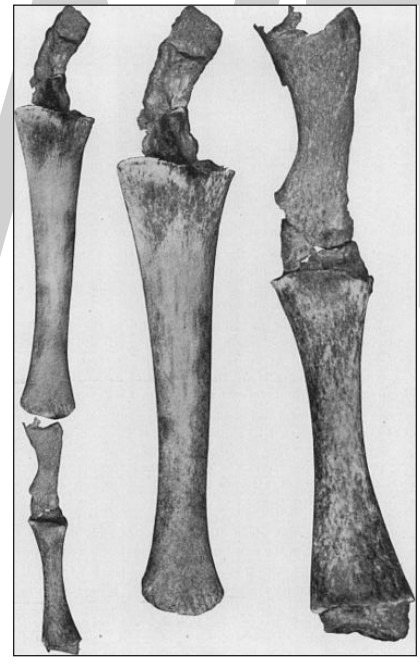
Mathematical models of evolution, pioneered by the likes of Sewall Wright, Ronald Fisher and J. B. S. Haldane and extended via diffusion theory by Motoo Kimura, allow predictions about the

genetic structure of evolving populations. Direct examination of the genetic structure of modern populations via DNA sequencing has allowed verification of many of these predictions. For example, the Out of Africa theory of human origins, which states that modern humans developed in Africa and a small sub-population migrated out (undergoing a population bottleneck), implies that modern populations should show the signatures of this migration pattern. Specifically, post-bottleneck populations (Europeans and Asians) should show lower overall genetic diversity and a more uniform distribution of allele frequencies compared to the African population. Both of these predictions are borne out by actual data from a number of studies.

Evidence from Comparative Anatomy

Comparative study of the anatomy of groups of animals or plants reveals that certain structural features are basically similar. For example, the basic structure of all flowers consists of sepals, petals, stigma, style and ovary; yet the size, colour, number of parts and specific structure are different for each individual species. The neural anatomy of fossilized remains may also be compared using advanced imaging techniques.

Atavisms



A humpback whale was caught by a ship operating out of Vancouver that had legs 4 ft 2 in (1.27 m) long.

Once thought of as a refutation to evolutionary theory, atavisms are "now seen as potent evidence of how much genetic potential is retained after a particular structure has disappeared from a species". "Atavisms are the reappearance of a lost character typical of remote ancestors and not seen in the parents or recent ancestors" and are an "[indication] of the developmental plasticity that exists within embryos" Atavisms occur because genes for previously existing phenotypical features are often preserved in DNA, even though the genes are not expressed in some or most of the organisms possessing them. Numerous examples have documented the occurrence of atavisms alongside experimental research triggering their formation. Due to the

complexity and interrelatedness of the factors involved in the development of atavisms, both biologists and medical professionals find it "difficult, if not impossible, to distinguish [them] from malformations."

Some examples of atavisms found in the scientific literature include:

- Hind limbs in whales.
- Reappearance of limbs in limbless vertebrates.
- Back pair of flippers on a bottlenose dolphin.
- Extra toes of the modern horse.
- Human tails (not pseudo-tails) and extra nipples in humans.
- Re-evolution of sexuality from parthenogenesis in orbitid mites.
- Teeth in chickens.
- Dewclaws in dogs.
- Reappearance of wings on wingless stick insects and earwigs.
- Atavistic muscles in several birds and mammals such as the beagle and the jerboa.
- Extra toes in guinea pigs.

Evolutionary Developmental Biology and Embryonic Development

Evolutionary developmental biology is the biological field that compares the developmental process of different organisms to determine ancestral relationships between species. A large variety of organism's genomes contain a small fraction of genes that control the organisms development. Hox genes are an example of these types of nearly universal genes in organisms pointing to an origin of common ancestry. Embryological evidence comes from the development of organisms at the embryological level with the comparison of different organisms embryos similarity. Remains of ancestral traits often appear and disappear in different stages of the embryological development process.

Some examples include:

- Hair growth and loss (lanugo) during human development.
- Development and degeneration of a yolk sac.
- Terrestrial frogs and salamanders passing through the larval stage within the egg—with features of typically aquatic larvae—but hatch ready for life on land.
- The appearance of gill-like structures (pharyngeal arch) in vertebrate embryo development. Note that in fish, the arches continue to develop as branchial arches while in humans, for example, they give rise to a variety of structures within the head and neck.

Homologous Structures and Divergent (Adaptive) Evolution

If widely separated groups of organisms are originated from a common ancestry, they are expected to have certain basic features in common. The degree of resemblance between two organisms should indicate how closely related they are in evolution:

- Groups with little in common are assumed to have diverged from a common ancestor much earlier in geological history than groups with a lot in common;
- In deciding how closely related two animals are, a comparative anatomist looks for structures that are fundamentally similar, even though they may serve different functions in the adult. Such structures are described as homologous and suggest a common origin.
- In cases where the similar structures serve different functions in adults, it may be necessary to trace their origin and embryonic development. A similar developmental origin suggests they are the same structure, and thus likely derived from a common ancestor.

When a group of organisms share a homologous structure that is specialized to perform a variety of functions to adapt different environmental conditions and modes of life, it is called adaptive radiation. The gradual spreading of organisms with adaptive radiation is known as divergent evolution.

Nested Hierarchies and Classification

Taxonomy is based on the fact that all organisms are related to each other in nested hierarchies based on shared characteristics. Most existing species can be organized rather easily in a nested hierarchical classification. This is evident from the Linnaean classification scheme. Based on shared derived characters, closely related organisms can be placed in one group (such as a genus), several genera can be grouped together into one family, several families can be grouped together into an order, etc. The existence of these nested hierarchies was recognized by many biologists before Darwin, but he showed that his theory of evolution with its branching pattern of common descent could explain them. Darwin described how common descent could provide a logical basis for classification:

> "All the foregoing rules and aids and difficulties in classification are explained, if I do not greatly deceive myself, on the view that the natural system is founded on descent with modification; that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, in so far, all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking."
>
> —Charles Darwin, On the Origin of Species

Evolutionary Trees

An evolutionary tree (of Amniota, for example, the last common ancestor of mammals and reptiles, and all its descendants) illustrates the initial conditions causing evolutionary patterns of similarity (e.g., all Amniotes produce an egg that possesses the amnios) and the patterns of

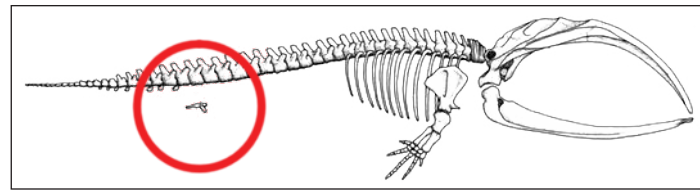
divergence amongst lineages (e.g., mammals and reptiles branching from the common ancestry in Amniota). Evolutionary trees provide conceptual models of evolving systems once thought limited in the domain of making predictions out of the theory. However, the method of phylogenetic bracketing is used to infer predictions with far greater probability than raw speculation. For example, paleontologists use this technique to make predictions about nonpreservable traits in fossil organisms, such as feathered dinosaurs, and molecular biologists use the technique to posit predictions about RNA metabolism and protein functions. Thus evolutionary trees are evolutionary hypotheses that refer to specific facts, such as the characteristics of organisms (e.g., scales, feathers, fur), providing evidence for the patterns of descent, and a causal explanation for modification (i.e., natural selection or neutral drift) in any given lineage (e.g., Amniota). Evolutionary biologists test evolutionary theory using phylogenetic systematic methods that measure how much the hypothesis (a particular branching pattern in an evolutionary tree) increases the likelihood of the evidence (the distribution of characters among lineages). The severity of tests for a theory increases if the predictions "are the least probable of being observed if the causal event did not occur." "Testability is a measure of how much the hypothesis increases the likelihood of the evidence."

Vestigial Structures

Evidence for common descent comes from the existence of vestigial structures. These rudimentary structures are often homologous to structures that correspond in related or ancestral species. A wide range of structures exist such as mutated and non-functioning genes, parts of a flower, muscles, organs, and even behaviors. This variety can be found across many different groups of species. In many cases they are degenerated or underdeveloped. The existence of vestigial organs can be explained in terms of changes in the environment or modes of life of the species. Those organs are typically functional in the ancestral species but are now either semi-functional, non-functional, or re-purposed.

Scientific literature concerning vestigial structures abounds. One study complied 64 examples of vestigial structures found in the literature across a wide range of disciplines within the 21st century. The following non-exhaustive list summarizes Senter et al. alongside various other examples:

- The presence of remnant mitochondria (mitosomes) that have lost the ability to synthesize ATP in Entamoeba histolytica, Trachipleistophora hominis, Cryptosporidium parvum, Blastocystis hominis, and Giardia intestinalis.
- Remnant chloroplast organelles (leucoplasts) in non-photosynthetic algae species (Plasmodium falciparum, Toxoplasma gondii, Aspasia longa, Anthophysa vegetans, Ciliophrys infusionum, Pteridomonas danica, Paraphysomonas, Spumella and Epifagus americana.
- Missing stamens (unvascularized staminodes) on Gilliesia and Gethyum flowers.
- Non-functioning androecium in female flowers and non-functioning gynoecium in male flowers of the cactus species Consolea spinosissima.
- Remnant stamens on female flowers of Fragaria virginiana; all species in the genus Schiedea; and on Penstemon centranthifolius, P. rostriflorus, P. ellipticus, and P. palmeri.
- Vestigial anthers on Nemophila menziesii.



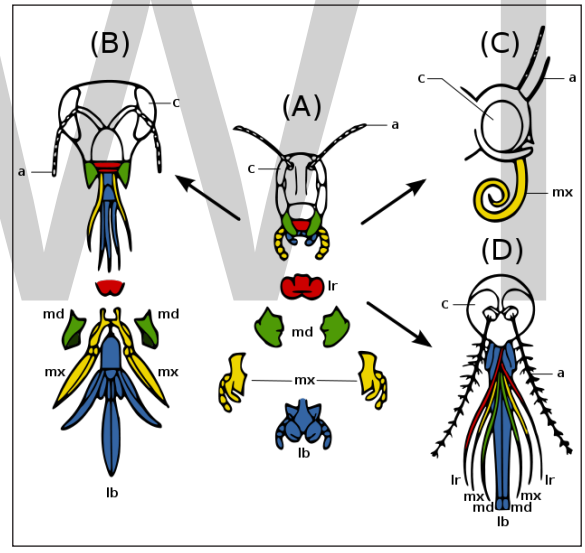
Skeleton of a baleen whale with the hind limb and pelvic bone structure circled in red. This bone structure stays internal during the entire life of the species:

- Reduced hindlimbs and pelvic girdleembedded in the muscles of extant whales.Occasionally, the genes that code for longer extremities cause a modern whale to develop legs. On 28 October 2006, a four-finned bottlenose dolphin was caught and studied due to its extra set of hind limbs. These legged Cetacea display an example of an atavism predicted from their common ancestry.
- Nonfunctional hind wings in *Carabus solieri* and other beetles.
- Remnant eyes (and eye structures) in animals that have lost sight such as blind cavefish (e.g. *Astyanax mexicanus*), mole rats, snakes, spiders, salamanders, shrimp, crayfish, and beetles.
- Vestigial eye in the extant *Rhineura floridana* and remnant jugal in the extinct *Rhineura hatchery*(reclassified as *Protorhineura hatcherii*).
- Functionless wings in flightless birds such as ostriches, kiwis, cassowaries, and emus.
- The presence of the plica semilunaris in the human eye—a vestigial remnant of the nictitating membrane.
- Harderian gland in primates.
- Reduced hind limbs and pelvic girdle structures in legless lizards, skinks, amphisbaenians, and some snakes.
- Reduced and missing olfactory apparatus in whales that still possess vestigial olfactory receptor subgenomes.
- Vestigial teeth in narwhal.
- Rudimentary digits of *Ateles geoffroyi*, *Colobus guereza*, and *Perodicticus potto*.
- Vestigial dental primordia in the embryonic tooth pattern in mice.
- Reduced or absent vomeronasal organ in humans and Old World monkeys.
- Presence of non-functional sinus hair muscles in humans used in whisker movement.
- Degenerating palmaris longus muscle in humans.
- Teleost fish, anthropoid primates (Simians), guinea pigs, some bat species, and some Passeriformes have lost the ability to synthesize vitamin C (ascorbic acid), yet still possess the

genes involved. This inability is due to mutations of the L-gulono-γ-lactone oxidase (*GLO*) gene— and in primates, teleost fish, and guinea pigs it is irreversible.

- Remnant abdominal segments in cirripedes (barnacles).
- Non-mammalian vertebrate embryos depend on nutrients from the yolk sac. Humans and other mammal genomes contain broken, non-functioning genes that code for the production of yolk. alongside the presence of an empty yolk sac with the embryo.
- Dolphin embryonic limb buds.
- Leaf formation in some cacti species.
- Presence of a vestigial endosymbiont *Lepidodinium viride* within the dinoflagellate *Gymnodinium chlorophorum*.
- The species *Dolabrifera dolabrifera* has an ink gland but is "incapable of producing ink or its associated anti-predator proteins".

Specific Examples from Comparative Anatomy



Adaptation of insect mouthparts: a, antennae; c, compound eye; lb, labrium; lr, labrum; md, mandibles; mx, maxillae:

- Primitive state — biting and chewing: *e.g*. grasshopper. Strong mandibles and maxillae for manipulating food.
- Ticking and biting: *e.g*. honey bee. Labium long to lap up nectar; mandibles chew pollen and mould wax.
- Sucking: *e.g*. butterfly. Labrum reduced; mandibles lost; maxillae long forming sucking tube.
- Piercing and sucking, *e.g*.. female mosquito. Labrum and maxillae form tube; mandibles form piercing stylets; labrum grooved to hold other parts.

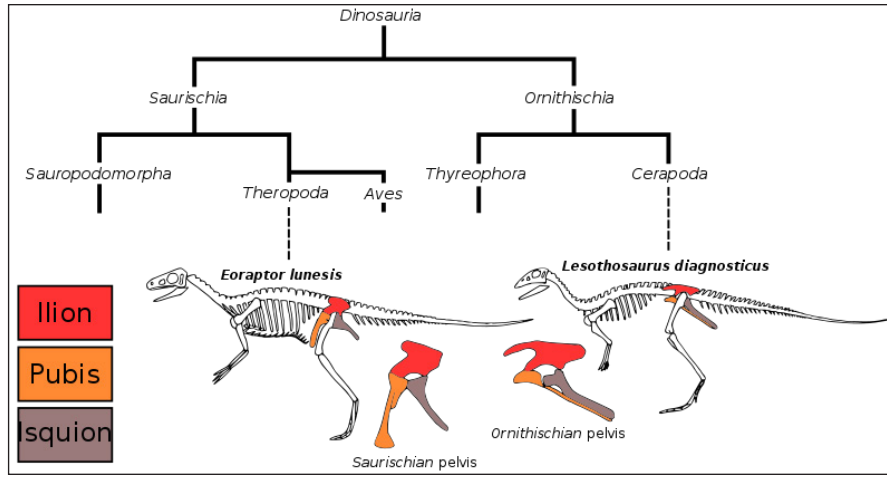
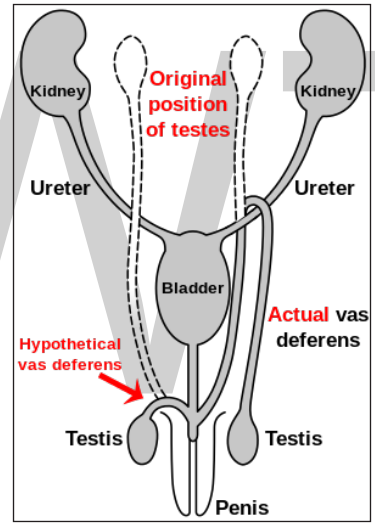


Illustration of the *Eoraptor lunensis* pelvis of the order Saurischia and the *Lesothosaurus diagnosticus* pelvis of the order Ornithischia in the clade Dinosauria. The parts of the pelvis show modification over time. The cladogram is shown to illustrate the distance of divergence between the two species.



Route of the vas deferens from the testis to the penis.

Insect Mouthparts and Appendages

Many different species of insects have mouthparts derived from the same embryonic structures, indicating that the mouthparts are modifications of a common ancestor's original features. These include a labrum (upper lip), a pair of mandibles, a hypopharynx(floor of mouth), a pair of maxillae, and a labium. Evolution has caused enlargement and modification of these structures in some species, while it has caused the reduction and loss of them in other species. The modifications enable the insects to exploit a variety of food materials.

Insect mouthparts and antennae are considered homologues of insect legs. Parallel developments are seen in some arachnids: The anterior pair of legs may be modified as analogues of antennae, particularly in whip scorpions, which walk on six legs. These developments provide support for the theory that complex modifications often arise by duplication of components, with the duplicates modified in different directions.

Pelvic Structure of Dinosaurs

Similar to the pentadactyl limb in mammals, the earliest dinosaurs split into two distinct orders—the *saurischia* and *ornithischia*. They are classified as one or the other in accordance with what the fossils demonstrate., shows that early *saurischians* resembled early *ornithischians*. The pattern of the pelvis in all species of dinosaurs is an example of homologous structures. Each order of dinosaur has slightly differing pelvis bones providing evidence of common descent. Additionally, modern birdsshow a similarity to ancient *saurischian* pelvic structures indicating the evolution of birds from dinosaurs.

Pentadactyl Limb

The pattern of limb bones called pentadactyl limb is an example of homologous structures. It is found in all classes of tetrapods (*i.e.* from amphibians to mammals). It can even be traced back to the fins of certain fossil fishesfrom which the first amphibians evolved such as tiktaalik. The limb has a single proximal bone (humerus), two distal bones (radius and ulna), a series of carpals (wrist bones), followed by five series of metacarpals (palm bones) and phalanges (digits). Throughout the tetrapods, the fundamental structures of pentadactyl limbs are the same, indicating that they originated from a common ancestor. But in the course of evolution, these fundamental structures have been modified. They have become superficially different and unrelated structures to serve different functions in adaptation to different environments and modes of life. This phenomenon is shown in the forelimbs of mammals. For example:

- In monkeys, the forelimbs are much elongated, forming a grasping hand used for climbing and swinging among trees.
- Pigs have lost their first digit, while the second and fifth digits are reduced. The remaining two digits are longer and stouter than the rest and bear a hoof for supporting the body.
- In horses, the forelimbs are highly adapted for strength and support. Fast and long-distance running is possible due to the extensive elongation of the third digit that bears a hoof.
- The mole has a pair of short, spade-like forelimbs for burrowing.
- Anteaters use their enlarged third digit for tearing into ant and termite nests.
- In cetaceans, the forelimbs become flippers for steering and maintaining equilibrium during swimming.
- In bats, the forelimbs have become highly modified and evolved into functioning wings. Four digits have become elongated, while the hook-like first digit remains free and is used to hang upside down.

Recurrent Laryngeal Nerve in Giraffes

The recurrent laryngeal nerve is a fourth branch of the vagus nerve, which is a cranial nerve. In mammals, its path is unusually long. As a part of the vagus nerve, it comes from the brain, passes through the neck down to heart, rounds the dorsal aorta and returns up to the larynx, again through the neck.

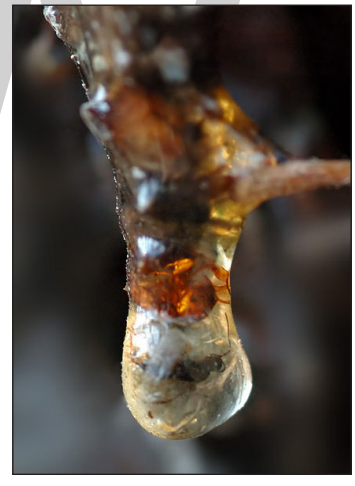
This path is suboptimal even for humans, but for giraffes it becomes even more suboptimal. Due to the lengths of their necks, the recurrent laryngeal nerve may be up to 4 m (13 ft) long, despite its optimal route being a distance of just several inches.

The indirect route of this nerve is the result of evolution of mammals from fish, which had no neck and had a relatively short nerve that innervated one gill slit and passed near the gill arch. Since then, the gill it innervated has become the larynx and the gill arch has become the dorsal aorta in mammals.

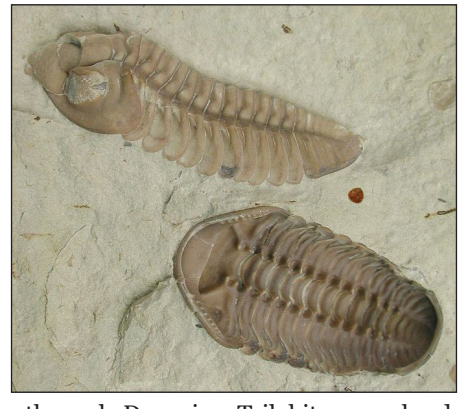
Route of the Vas Deferens

Similar to the laryngeal nerve in giraffes, the vas deferens is part of the male anatomy of many vertebrates; it transports sperm from the epididymis in anticipation of ejaculation. In humans, the vas deferens routes up from the testicle, looping over the ureter, and back down to the urethra and penis. It has been suggested that this is due to the descent of the testicles during the course of human evolution—likely associated with temperature. As the testicles descended, the vas deferens lengthened to accommodate the accidental "hook" over the ureter.

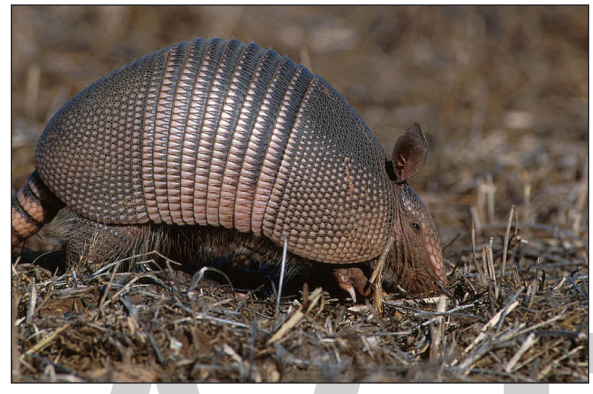
Evidence from Paleontology



An insect trapped in amber



Fossil trilobite, *Kainops invius*, from the early Devonian. Trilobites were hard-shelled arthropods, related to living horseshoe crabs and spiders, that first appeared in significant numbers around 540 mya, dying out 250 mya.



Charles Darwin collected, and found fragments of armor he thought were like giant versions of the scutes on the modern armadillos living nearby. The anatomist Richard Owenshowed him that the fragments were from the gigantic extinct *Glyptodon*, related to the armadillos. This was one of the patterns of distribution that helped Darwin to develop his theory.

When organisms die, they often decomposerapidly or are consumed by scavengers, leaving no permanent evidences of their existence. However, occasionally, some organisms are preserved. The remains or traces of organisms from a past geologic ageembedded in rocks by natural processes are called fossils. They are extremely important for understanding the evolutionary history of life on Earth, as they provide direct evidence of evolution and detailed information on the ancestry of organisms. Paleontology is the study of past life based on fossil records and their relations to different geologic time periods.

For fossilization to take place, the traces and remains of organisms must be quickly buried so that weathering and decomposition do not occur. Skeletal structures or other hard parts of the organisms are the most commonly occurring form of fossilized remains. There are also some trace "fossils" showing moulds, cast or imprints of some previous organisms.

As an animal dies, the organic materials gradually decay, such that the bones become porous. If the animal is subsequently buried in mud, mineral salts infiltrate into the bones and gradually fill up the pores. The bones harden into stones and are preserved as fossils. This process is known as petrification. If dead animals are covered by wind-blown sand, and if the sand is subsequently turned into mud by heavy rain or floods, the same process of mineral infiltration may occur. Apart from petrification, the dead bodies of organisms may be well preserved in ice, in hardened resin of coniferous trees, in tar, or in anaerobic, acidic peat. Fossilization can sometimes be a trace, an impression of a form. Examples include leaves and footprints, the fossils of which are made in layers that then harden.

Fossil Record

It is possible to decipher how a particular group of organisms evolved by arranging its fossil record in a chronological sequence. Such a sequence can be determined because fossils are mainly found in sedimentary rock. Sedimentary rock is formed by layers of silt or mud on top of each other; thus, the resulting rock contains a series of horizontal layers, or strata. Each layer contains fossils typical for a specific time period when they formed. The lowest strata contain the oldest rock and the earliest fossils, while the highest strata contain the youngest rock and more recent fossils.

A succession of animals and plants can also be seen from fossil discoveries. By studying the number and complexity of different fossils at different stratigraphic levels, it has been shown that older fossil-bearing rocks contain fewer types of fossilized organisms, and they all have a simpler structure, whereas younger rocks contain a greater variety of fossils, often with increasingly complex structures.

For many years, geologists could only roughly estimate the ages of various strata and the fossils found. They did so, for instance, by estimating the time for the formation of sedimentary rock layer by layer. Today, by measuring the proportions of radioactive and stable elements in a given rock, the ages of fossils can be more precisely dated by scientists. This technique is known as radiometric dating.

Throughout the fossil record, many species that appear at an early stratigraphic level disappear at a later level. This is interpreted in evolutionary terms as indicating the times when species originated and became extinct. Geographical regions and climatic conditions have varied throughout Earth's history. Since organisms are adapted to particular environments, the constantly changing conditions favoured species that adapted to new environments through the mechanism of natural selection.

Extent of the Fossil Record

Despite the relative rarity of suitable conditions for fossilization, an estimated 250,000 fossil species have been named. The number of individual fossils this represents varies greatly from species to species, but many millions of fossils have been recovered: for instance, more than three million fossils from the last ice age have been recovered from the La Brea Tar Pits in Los Angeles. Many more fossils are still in the ground, in various geological formations known to contain a high fossil density, allowing estimates of the total fossil content of the formation to be made. An example of this occurs in South Africa's Beaufort Formation (part of the Karoo Supergroup, which covers most of South Africa), which is rich in vertebrate fossils, including therapsids (reptile-mammal transitional forms). It has been estimated that this formation contains 800 billion vertebrate fossils. Palentologists have documented numerous transitional forms and have constructed "an astonishingly comprehensive record of the key transitions in animal evolution". Conducting a survey of the paleontological literature, one would find that there is "abundant evidence for how all the major groups of animals are related, much of it in the form of excellent transitional fossils".

Limitations

The fossil record is an important source for scientists when tracing the evolutionary history of organisms. However, because of limitations inherent in the record, there are not fine scales of

intermediate forms between related groups of species. This lack of continuous fossils in the record is a major limitation in tracing the descent of biological groups. When transitional fossils are found that show intermediate forms in what had previously been a gap in knowledge, they are often popularly referred to as "missing links".

There is a gap of about 100 million years between the beginning of the Cambrian period and the end of the Ordovician period. The early Cambrian period was the period from which numerous fossils of sponges, cnidarians (e.g., jellyfish), echinoderms (e.g., eocrinoids), molluscs (e.g., snails) and arthropods (e.g., trilobites) are found. The first animal that possessed the typical features of vertebrates, the Arandaspis, was dated to have existed in the later Ordovician period. Thus few, if any, fossils of an intermediate type between invertebrates and vertebrates have been found, although likely candidates include the Burgess Shale animal, Pikaia gracilens, and its Maotianshan shales relatives, Myllokunmingia, Yunnanozoon, Haikouella lanceolata, and Haikouichthys.

Some of the reasons for the incompleteness of fossil records are:

- In general, the probability that an organism becomes fossilized is very low.
- Some species or groups are less likely to become fossils because they are soft-bodied.
- Some species or groups are less likely to become fossils because they live (and die) in conditions that are not favourable for fossilization.
- Many fossils have been destroyed through erosion and tectonic movements.
- Most fossils are fragmentary.
- Some evolutionary change occurs in populations at the limits of a species' ecological range, and as these populations are likely small, the probability of fossilization is lower.
- Similarly, when environmental conditions change, the population of a species is likely to be greatly reduced, such that any evolutionary change induced by these new conditions is less likely to be fossilized.
- Most fossils convey information about external form, but little about how the organism functioned.
- Using present-day biodiversity as a guide, this suggests that the fossils unearthed represent only a small fraction of the large number of species of organisms that lived in the past.

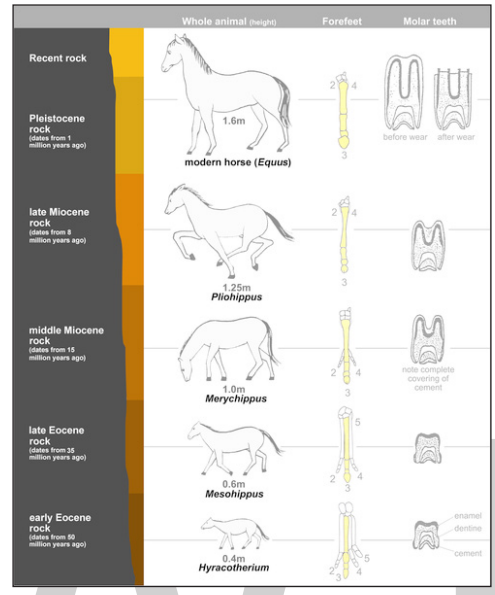
Specific Examples from Paleontology

Evolution of the Horse

Due to an almost-complete fossil record found in North American sedimentary deposits from the early Eocene to the present, the horse provides one of the best examples of evolutionary history (phylogeny).

This evolutionary sequence starts with a small animal called Hyracotherium(commonly referred to as Eohippus), which lived in North America about 54 million years ago then spread across to

Europeand Asia. Fossil remains of Hyracotherium show it to have differed from the modern horse in three important respects: it was a small animal (the size of a fox), lightly built and adapted for running; the limbs were short and slender, and the feet elongated so that the digits were almost vertical, with four digits in the forelimbs and three digits in the hindlimbs; and the incisors were small, the molars having low crowns with rounded cusps covered in enamel.



Evolution of the horse showing reconstruction of the fossil species obtained from successive rock strata. The foot diagrams are all front views of the left forefoot. The third metacarpal is shaded throughout. The teeth are shown in longitudinal section. The linear sequence is just one of many paths in the equine phylogenetic tree.

The probable course of development of horses from *Hyracotherium* to *Equus* (the modern horse) involved at least 12 genera and several hundred species. The major trends seen in the development of the horse to changing environmental conditions may be summarized as follows:

- Increase in size (from 0.4 m to 1.5 m — from 15 in to 60 in).
- Lengthening of limbs and feet.
- Reduction of lateral digits.
- Increase in length and thickness of the third digit.
- Increase in width of incisors.
- Replacement of premolars by molars.
- Increases in tooth length, crown height of molars.

Fossilized plants found in different strata show that the marshy, wooded country in which *Hyracotherium* lived became gradually drier. Survival now depended on the head being in an elevated position for gaining a good view of the surrounding countryside, and on a high turn of speed for escape from predators, hence the increase in size and the replacement of the splayed-out foot by the hoofed foot. The drier, harder ground would make the original splayed-out foot unnecessary for support. The changes in the teeth can be explained by assuming that the diet changed from soft

vegetation to grass. A dominant genus from each geological period has been selected to show the slow alteration of the horse lineage from its ancestral to its modern form.

Transition from Fish to Amphibians

Prior to 2004, paleontologists had found fossils of amphibians with necks, ears, and four legs, in rock no older than 365 million years old. In rocks more than 385 million years old they could only find fish, without these amphibian characteristics. Evolutionary theory predicted that since amphibians evolved from fish, an intermediate form should be found in rock dated between 365 and 385 million years ago. Such an intermediate form should have many fish-like characteristics, conserved from 385 million years ago or more, but also have many amphibian characteristics as well. In 2004, an expedition to islands in the Canadian arctic searching specifically for this fossil form in rocks that were 375 million years old discovered fossils of Tiktaalik. Some years later, however, scientists in Poland found evidence of fossilised tetrapod tracks predating *Tiktaalik*.

Evidence from Biogeography

Data about the presence or absence of species on various continents and islands (biogeography) can provide evidence of common descent and shed light on patterns of speciation.

Continental Distribution

All organisms are adapted to their environment to a greater or lesser extent. If the abiotic and biotic factors within a habitat are capable of supporting a particular species in one geographic area, then one might assume that the same species would be found in a similar habitat in a similar geographic area, e.g. in Africa and South America. This is not the case. Plant and animal species are discontinuously distributed throughout the world:

- Africa has old world monkeys, apes, elephants, leopards, giraffes, and hornbills.
- South America has new world monkeys, cougars, jaguars, sloths, llamas, and toucans.
- Deserts in North and South America have native cacti, but deserts in Africa, Asia, and Australia have succulent (apart from *Rhipsalis baccifera*) which are native euphorbs that resemble cacti but are very different.

Even greater differences can be found if Australia is taken into consideration, though it occupies the same latitude as much of South America and Africa. Marsupials like kangaroos, bandicoots, and quolls make up about half of Australia's indigenous mammal species. By contrast, marsupials are today totally absent from Africa and form a smaller portion of the mammalian fauna of South America, where opossums, shrew opossums, and the monito del monte occur. The only living representatives of primitive egg-laying mammals (monotremes) are the echidnas and the platypus. The short-beaked echidna (*Tachyglossus aculeatus*) and its subspecies populate Australia, Tasmania, New Guinea, and Kangaroo Island while the long-beaked echidna (*Zaglossus bruijni*) lives only in New Guinea. The platypus lives in the waters of eastern Australia. They have been introduced to Tasmania, King Island, and Kangaroo Island. These Monotremes are totally absent in the rest of the world. On the other hand, Australia is missing many groups of placental mammals that are common on other continents (carnivorans, artiodactyls, shrews, squirrels, lagomorphs),

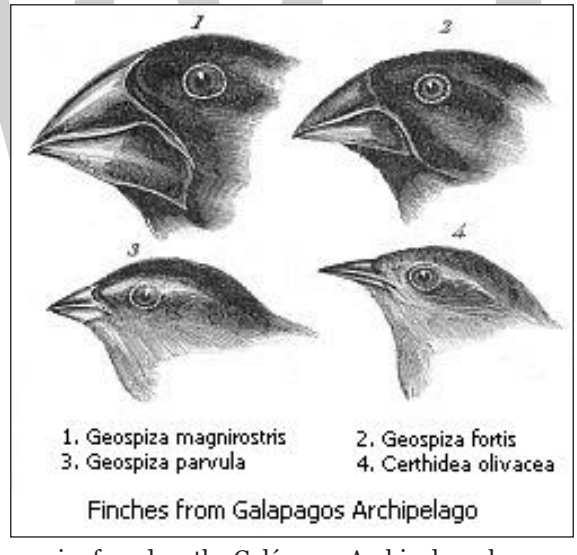
although it does have indigenous bats and murine rodents; many other placentals, such as rabbits and foxes, have been introduced there by humans.

Other animal distribution examples include bears, located on all continents excluding Africa, Australia and Antarctica, and the polar bear solely in the Arctic Circle and adjacent land masses. Penguinsare found only around the South Pole despite similar weather conditions at the North Pole. Families of sirenians are distributed around the earth's waters, where manatees are located in western Africa waters, northern South American waters, and West Indian waters only while the related family, the dugongs, are located only in Oceanic waters north of Australia, and the coasts surrounding the Indian Ocean. The now extinct Steller's sea cow resided in the Bering Sea.

The same kinds of fossils are found from areas known to be adjacent to one another in the past but that, through the process of continental drift, are now in widely divergent geographic locations. For example, fossils of the same types of ancient amphibians, arthropods and ferns are found in South America, Africa, India, Australia and Antarctica, which can be dated to the Paleozoic Era, when these regions were united as a single landmass called Gondwana. Sometimes the descendants of these organisms can be identified and show unmistakable similarity to each other, even though they now inhabit very different regions and climates.

Island Biogeography

Types of Species Found on Islands



Four of the 13 finch species found on the Galápagos Archipelago, have evolved by an adaptive radiation that diversified their beak shapes to adapt them to different food sources.

Evidence from island biogeography has played an important and historic role in the development of evolutionary biology. For purposes of biogeography, islands are divided into two classes. Continental islands are islands like Great Britain, and Japan that have at one time or another been part of a continent. Oceanic islands, like the Hawaiian islands, the Galápagos Islands and St. Helena, on the other hand are islands that have formed in the ocean and never been part of any continent. Oceanic islands have distributions of native plants and animals that are unbalanced in ways that make them distinct from the biotas found on continents or continental islands. Oceanic islands

do not have native terrestrial mammals (they do sometimes have bats and seals), amphibians, or fresh water fish. In some cases they have terrestrial reptiles (such as the iguanas and giant tortoises of the Galápagos Islands) but often (such as in Hawaii) they do not. This is despite the fact that when species such as rats, goats, pigs, cats, mice, and cane toads, are introduced to such islands by humans they often thrive. Starting with Charles Darwin, many scientists have conducted experiments and made observations that have shown that the types of animals and plants found, and not found, on such islands are consistent with the theory that these islands were colonized accidentally by plants and animals that were able to reach them. Such accidental colonization could occur by air, such as plant seeds carried by migratory birds, or bats and insects being blown out over the sea by the wind, or by floating from a continent or other island by sea (for example, by some kinds of plant seeds like coconuts that can survive immersion in salt water), and reptiles that can survive for extended periods on rafts of vegetation carried to sea by storms.

Endemism

Many of the species found on remote islands are endemic to a particular island or group of islands, meaning they are found nowhere else on earth. Examples of species endemic to islands include many flightless birds of New Zealand, lemurs of Madagascar, the Komodo dragon of Komodo,the dragon's blood tree of Socotra, Tuatara of New Zealand, and others. However, many such endemic species are related to species found on other nearby islands or continents; the relationship of the animals found on the Galápagos Islands to those found in South America is a well-known example. All of these facts, the types of plants and animals found on oceanic islands, the large number of endemic species found on oceanic islands, and the relationship of such species to those living on the nearest continents, are most easily explained if the islands were colonized by species from nearby continents that evolved into the endemic species now found there.

Other types of endemism do not have to include, in the strict sense, islands. Islands can mean isolated lakes or remote and isolated areas. Examples of these would include the highlands of Ethiopia, Lake Baikal, fynbos of South Africa, forests of New Caledonia, and others. Examples of endemic organisms living in isolated areas include the kagu of New Caledonia, cloud rats of the Luzon tropical pine forests of the Philippines, the boojum tree (*Fouquieria columnaris*) of the Baja California peninsula, the Baikal seal and the omul of Lake Baikal.

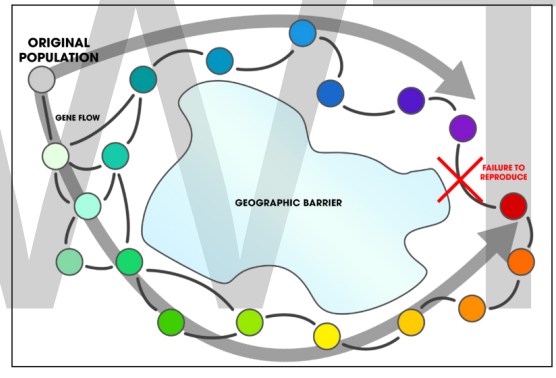
Adaptive Radiations

Oceanic islands are frequently inhabited by clusters of closely related species that fill a variety of ecological niches, often niches that are filled by very different species on continents. Such clusters, like the finches of the Galápagos, Hawaiian honeycreepers, members of the sunflower family on the Juan Fernandez Archipelago and wood weevils on St. Helena are called adaptive radiations because they are best explained by a single species colonizing an island (or group of islands) and then diversifying to fill available ecological niches. Such radiations can be spectacular; 800 species of the fruit fly family *Drosophila*, nearly half the world's total, are endemic to the Hawaiian islands. Another illustrative example from Hawaii is the silversword alliance, which is a group of thirty species found only on those islands. Members range from the silverswords that flower spectacularly on high volcanic slopes to trees, shrubs, vines and mats that occur at various elevations from mountain top to sea level, and in Hawaiian habitats that vary from deserts to rainforests. Their

closest relatives outside Hawaii, based on molecular studies, are tarweeds found on the west coast of North America. These tarweeds have sticky seeds that facilitate distribution by migrant birds. Additionally, nearly all of the species on the island can be crossed and the hybrids are often fertile, and they have been hybridized experimentally with two of the west coast tarweed species as well. Continental islands have less distinct biota, but those that have been long separated from any continent also have endemic species and adaptive radiations, such as the 75 lemur species of Madagascar, and the eleven extinct moa species of New Zealand.

Ring Species

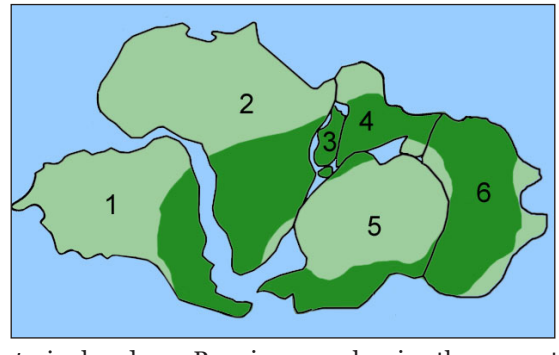
A ring species is a connected series of populations, each of which can interbreed with its neighbors, with at least two "end" populations which are too distantly related to interbreed, though with the potential for gene flow between all the populations. Ring species represent speciation and have been cited as evidence of evolution. They illustrate what happens over time as populations genetically diverge, specifically because they represent, in living populations, what normally happens over time between long deceased ancestor populations and living populations, in which the intermediates have become extinct. Richard Dawkins says that ring species "are only showing us in the spatial dimension something that must always happen in the time dimension".



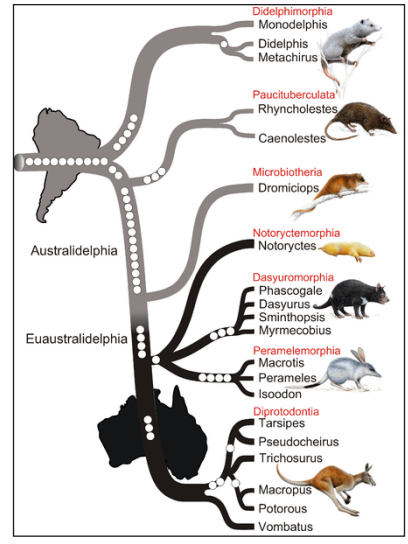
In a ring species, gene flow occurs between neighboring populations, but at the ends of the "ring", the populations cannot interbreed.

Specific Examples from Biogeography

Distribution of Glossopteris

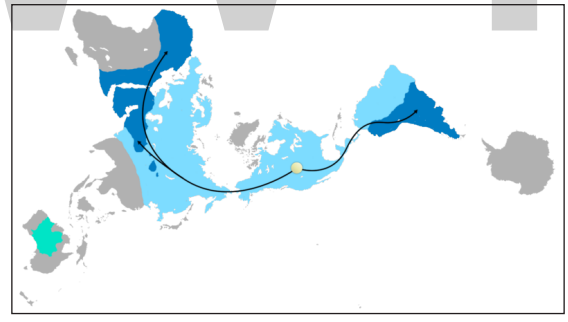


Current distribution of *Glossopteris* placed on a Permian map showing the connection of the continents. (1, South America; 2, Africa; 3, Madagascar; 4, India; 5, Antarctica; and 6, Australia). Note that the map is a rough approximation of which leaves out additional land masses such as the Eurasian and North American plates.



A simplified phylogenetic tree of marsupials showing which groups reside on each continent.

The combination of continental drift and evolution can sometimes be used to predict what will be found in the fossil record. *Glossopteris* is an extinct species of seed fernplants from the Permian. *Glossopteris* appears in the fossil record around the beginning of the Permian on the ancient continent of Gondwana. Continental drift explains the current biogeography of the tree. Present day *Glossopteris* fossils are found in Permian strata in southeast South America, southeast Africa, all of Madagascar, northern India, all of Australia, all of New Zealand, and scattered on the southern and northern edges of Antarctica. During the Permian, these continents were connected as Gondwana in agreement with magnetic striping, other fossil distributions, and glacial scratches pointing away from the temperate climate of the South Pole during the Permian.



A dymaxion map of the biogeographic distribution of Camelidae species. Light blue indicates the Tertiary distribution, dark blue indicates the present-day distributions, and green indicates the introduced (feral) distributions. The yellow dot is the origin of the family Camelidae and the black arrows are the historic migration routes that explain the present day distribution.

Metatherian Distribution

The history of metatherians (the clade containing marsupials and their extinct, primitive ancestors) provides an example of how evolutionary theory and the movement of continents can be combined to make predictions concerning fossil stratigraphy and distribution. The oldest metatherian fossils are found in present-day China. Metatherians spread westward into modern North America (still

attached to Eurasia) and then to South America, which was connected to North America until around 65 mya. Marsupials reached Australia via Antarctica about 50 mya, shortly after Australia had split off suggesting a single dispersion event of just one species.Evolutionary theory suggests that the Australian marsupials descended from the older ones found in the Americas. Geologic evidence suggests that between 30 and 40 million years ago South America and Australia were still part of the Southern Hemisphere super continent of Gondwana and that they were connected by land that is now part of Antarctica. Therefore, when combining the models, scientists could predict that marsupials migrated from what is now South America, through Antarctica, and then to present-day Australia between 40 and 30 million years ago. A first marsupial fossil of the extinct family Polydolopidae was found on Seymour Island on the Antarctic Peninsula in 1982. Further fossils have subsequently been found, including members of the marsupial orders Didelphimorphia (opossum) and Microbiotheria, as well as ungulates and a member of the enigmatic extinct order Gondwanatheria, possibly *Sudamerica ameghinoi*.

Migration, Isolation and Distribution of the Camel

The history of the camel provides an example of how fossil evidence can be used to reconstruct migration and subsequent evolution. The fossil record indicates that the evolution of camelids started in North America, from which, six million years ago, they migrated across the Bering Strait into Asia and then to Africa, and 3.5 million years ago through the Isthmus of Panama into South America. Once isolated, they evolved along their own lines, giving rise to the Bactrian cameland dromedary in Asia and Africa and the llama and its relatives in South America. Camelids then became extinct in North America at the end of the last ice age.

Evidence from Selection

Examples for the evidence for evolution often stem from direct observation of natural selection in the field and the laboratory.

Scientists have observed and documented a multitude of events where natural selection is in action. The most well known examples are antibiotic resistance in the medical field along with better-known laboratory experiments documenting evolution's occurrence. Natural selection is tantamount to common descent in that long-term occurrence and selection pressures can lead to the diversity of life on earth as found today. All adaptations—documented and undocumented changes concerned—are caused by natural selection (and a few other minor processes). It is well established that, "natural selection is a ubiquitous part of speciation", and is the primary driver of speciation;therefore, the following examples of natural selection *and* speciation will often interdepend or correspond with one another. The examples below are only a small fraction of the actual experiments and observations.

Artificial Selection and Experimental Evolution

Artificial selection demonstrates the diversity that can exist among organisms that share a relatively recent common ancestor. In artificial selection, one species is bred selectively at each generation, allowing only those organisms that exhibit desired characteristics to reproduce. These characteristics become increasingly well developed in successive generations. Artificial selection was successful long before science discovered the genetic basis. Examples of artificial selection

include dog breeding, genetically modified food, flower breeding, and the cultivation of foods such as wild cabbage, and others.

The Chihuahua mix and Great Dane illustrate the range of sizes among dog breeds.

Experimental evolution uses controlled experiments to test hypotheses and theories of evolution. In one early example, William Dallinger set up an experiment shortly before 1880, subjecting microbes to heat with the aim of forcing adaptive changes. His experiment ran for around seven years, and his published results were acclaimed, but he did not resume the experiment after the apparatus failed.

A large-scale example of experimental evolution is Richard Lenski's multi-generation experiment with *Escherichia coli*. Lenski observed that some strains of *E. coli* evolved a complex new ability, the ability to metabolize citrate, after tens of thousands of generations. The evolutionary biologist Jerry Coyne commented as a critique of creationism, saying, "the thing I like most is it says you can get these complex traits evolving by a combination of unlikely events. That's just what creationists say can't happen." In addition to the metabolic changes, the different bacterial populations were found to have diverged in respect to both morphology (the overall size of the cell) and fitness (of which was measured in competition with the ancestors). The *E. coli* long-term evolution experiment that began in 1988 is still in progress, and has shown adaptations including the evolution of a strain of *E. coli* that was able to grow on citric acid in the growth media—a trait absent in all other known forms of *E. coli*, including the initial strain.

Invertebrates

Lead Tolerance in Daphnia

A study of species of *Daphnia* and lead pollution in the 20th century predicted that an increase in lead pollution would lead to strong selection of lead tolerance. Researchers were able to use "resurrection ecology", hatching decades-old *Daphnia* eggs from the time when lakes were heavily polluted with lead. The hatchlings in the study were compared to current-day *Daphnia*, and demonstrated "dramatic fitness differences between old and modern phenotypes when confronted with a widespread historical environmental stressor". Essentially, the modern-day *Daphnia* were unable to resist or tolerate high levels of lead (this is due to the huge reduction of lead pollution in 21st century lakes). The old hatchlings, however, were able to tolerate high lead pollution. The authors concluded that "by employing the techniques of resurrection ecology, we were able to show clear phenotypic change over decades".

Peppered Moths

A classic example was the phenotypic change, light-to-dark color adaptation, in the peppered moth, due to pollution from the Industrial Revolution in England.

Microbes

Antimicrobial Resistance

The development and spread of antibiotic-resistant bacteria is evidence for the process of evolution of species. Thus the appearance of vancomycin-resistant *Staphylococcus aureus*, and the danger it poses to hospital patients, is a direct result of evolution through natural selection. The rise of *Shigella*strains resistant to the synthetic antibiotic class of sulfonamides also demonstrates the generation of new information as an evolutionary process. Similarly, the appearance of DDT resistance in various forms of *Anopheles* mosquitoes, and the appearance of myxomatosis resistance in breeding rabbit populations in Australia, are both evidence of the existence of evolution in situations of evolutionary selection pressure in species in which generations occur rapidly.

All classes of microbes develop resistance: including fungi (antifungal resistance), viruses (antiviralresistance), protozoa (antiprotozoal resistance), and bacteria (antibiotic resistance). This is to be expected when considering that all life exhibits universal genetic code and is therefore subject to the process of evolution through its various mechanisms.

Nylon-eating Bacteria

Another example of organisms adapting to human-caused conditions are Nylon-eating bacteria: a strain of *Flavobacterium* that are capable of digesting certain byproducts of nylon 6 manufacturing. There is scientific consensus that the capacity to synthesize nylonase most probably developed as a single-step mutation that survived because it improved the fitness of the bacteria possessing the mutation. This is seen as a good example of evolution through mutation and natural selection that has been observed as it occurs and could not have come about until the production of nylon by humans.

Plants and Fungi

Monkeyflower Radiation

Both subspecies Mimulus aurantiacus puniceus (red-flowered) and Mimulus aurantiacus australis(yellow-flowered) of monkeyflowers are isolated due to the preferences of their hummingbird and hawkmoth pollinators. The radiation of M. aurantiacus subspecies are mostly yellow colored; however, both M. a. ssp. puniceus and M. a. ssp. flemingii are red. Phylogenetic analysis suggests two independent origins of red-colored flowers that arose due to cis-regulatory mutations in the gene MaMyb2 that is present in all M. aurantiacus subspecies. Further research suggested that two independent mutations did not take place, but one MaMyb2 allele was transferred via introgressive hybridization. This study presents an example of the overlap of research in various disciplines. Gene isolation and cis-regulatory functions; phylogenetic analysis; geographic location and pollinator preference; and species hybridization and speciation are just some of the areas in which data can be obtained to document the occurrence of evolution.

Radiotrophic Fungi

Like the codfish, human-caused pollution can come in different forms. Radiotrophic fungi is a perfect example of natural selection taking place after a chemical accident. Radiotrophic fungi appears to use the pigment melanin to convert gamma radiation into chemical energy for growth and were first discovered in 2007 as black molds growing inside and around the Chernobyl Nuclear Power Plant. Research at the Albert Einstein College of Medicine showed that three melanin-containing fungi, *Cladosporium sphaerospermum*, *Wangiella dermatitidis*, and *Cryptococcus neoformans*, increased in biomass and accumulated acetate faster in an environment in which the radiation level was 500 times higher than in the normal environment.

Vertebrates

Guppies

While studying guppies (*Poecilia reticulata*) in Trinidad, biologist John Endler detected selection at work on the fish populations. To rule out alternative possibilities, Endler set up a highly controlled experiment to mimic the natural habitat by constructing ten ponds within a laboratory greenhouse at Princeton University. Each pond contained gravel to exactly match that of the natural ponds. After capturing a random sample of guppies from ponds in Trinidad, he raised and mixed them to create similar genetically diverse populations and measured each fish (spot length, spot height, spot area, relative spot length, relative spot height, total patch area, and standard body lengths). For the experiment he added *Crenicichla alta* (*P. reticulata*'s main predator) in four of the ponds, *Rivulushartii* (a non-predator fish) in four of the ponds, and left the remaining two ponds empty with only the guppies. After 10 generations, comparisons were made between each pond's guppy populations and measurements were taken again. Endler found that the populations had evolved dramatically different color patterns in the control and non-predator pools and drab color patterns in the predator pool. Predation pressure had caused a selection against standing out from background gravel.

Endler's Trinadadian guppies (*Poecilia reticulata*).

In parallel, during this experiment, Endler conducted a field experiment in Trinidad where he caught guppies from ponds where they had predators and relocated them to ponds upstream where the predators did not live. After 15 generations, Endler found that the relocated guppies had evolved dramatic and colorful patterns. Essentially, both experiments showed convergence due to similar selection pressures (i.e. predator selection against contrasting color patterns and sexual selection for contrasting color patterns).

In a later study by David Reznick, the field population was examined 11 years later after Endler relocated the guppies to high streams. The study found that the populations has evolved in a number of different ways: bright color patterns, late maturation, larger sizes, smaller litter sizes, and larger offspring within litters. Further studies of *P. reticulata* and their predators in the streams of Trinidad have indicated that varying modes of selection through predation have not only changed the guppies color patterns, sizes, and behaviors, but their life histories and life history patterns.

Humans

Natural selection is observed in contemporary human populations, with recent findings demonstrating that the population at risk of the severe debilitating disease kuru has significant overrepresentation of an immune variant of the prion protein gene G127V versus non-immune alleles. Scientists postulate one of the reasons for the rapid selection of this genetic variant is the lethality of the disease in non-immune persons. Other reported evolutionary trends in other populations include a lengthening of the reproductive period, reduction in cholesterol levels, blood glucose and blood pressure.

A well known example of selection occurring in human populations is lactose tolerance. Lactose intolerance is the inability to metabolize lactose, because of a lack of the required enzyme lactase in the digestive system. The normal mammalian condition is for the young of a species to experience reduced lactase production at the end of the weaning period (a species-specific length of time). In humans, in non-dairy consuming societies, lactase production usually drops about 90% during the first four years of life, although the exact drop over time varies widely. Lactase activity persistence in adults is associated with two polymorphisms: C/T 13910 and G/A 22018 located in the *MCM6* gene. This gene difference eliminates the shutdown in lactase production, making it possible for members of these populations to continue consumption of raw milk and other fresh and fermented dairy products throughout their lives without difficulty. This appears to be an evolutionarily recent (around 10,000 years ago and 7,500 years ago in Europe) adaptation to dairy consumption, and has occurred independently in both northern Europe and east Africa in populations with a historically pastoral lifestyle.

Italian Wall Lizards

In 1971, ten adult specimens of *Podarcis sicula* (the Italian wall lizard) were transported from the Croatian island of Pod Kopište to the island Pod Mrčaru (about 3.5 km to the east). Both islands lie in the Adriatic Sea near Lastovo, where the lizards founded a new bottlenecked population. The two islands have similar size, elevation, microclimate, and a general absence of terrestrial predators and the *P. sicula* expanded for decades without human interference, even out-competing the (now locally extinct) *Podarcis melisellensis* population.

In the 1990s, scientists returned to Pod Mrčaru and found that the lizards there differed greatly from those on Kopište. While mitochondrial DNA analyses have verified that *P. sicula* currently on Mrčaru are genetically very similar to the Kopište source population, the new Mrčaru population of *P. sicula* had a larger average size, shorter hind limbs, lower maximal sprint speed and altered response to simulated predatory attacks compared to the original Kopište population. These changes were attributed to “relaxed predation intensity” and greater protection from vegetation on Mrčaru.

In 2008, further analysis revealed that the Mrčaru population of *P. sicula* have significantly different head morphology (longer, wider, and taller heads) and increased bite force compared to the original Kopište population. This change in head shape corresponded with a shift in diet: Kopište *P. sicula*are primarily insectivorous, but those on Mrčaru eat substantially more plant matter. The changes in foraging style may have contributed to a greater population density and decreased territorial behavior of the Mrčaru population.

Another difference found between the two populations was the discovery, in the Mrčaru lizards, of cecal valves, which slow down food passage and provide fermenting chambers, allowing commensalmicroorganisms to convert cellulose to nutrients digestible by the lizards. Additionally, the researchers discovered that nematodes were common in the guts of Mrčaru lizards, but absent from Kopište *P. sicula*, which do not have cecal valves. The cecal valves, which occur in less than 1 percent of all known species of scaled reptiles, have been described as an "adaptive novelty, a brand new feature not present in the ancestral population and newly evolved in these lizards".

PAH Resistance in Killifish

A similar study was also done regarding the polycyclic aromatic hydrocarbons (PAHs) that pollute the waters of the Elizabeth River in Portsmouth, Virginia. This chemical is a product of creosote, a type of tar. The Atlantic killifish (*Fundulus heteroclitus*) has evolved a resistance to PAHs involving the AHR gene (the same gene involved in the tomcods). This particular study focused on the resistance to "acute toxicity and cardiac teratogenesis" caused by PAHs. that mutated within the tomcods in the Hudson River.

PCB Resistance in Codfish

An example involving the direct observation of gene modification due to selection pressures is the resistance to PCBs in codfish. After General Electric dumped polychlorinated biphenyls (PCBs) in the Hudson River from 1947 through 1976, tomcods (*Microgadus tomcod*) living in the river were found to have evolved an increased resistance to the compound's toxic effects. The tolerance to the toxins is due to a change in the coding section of specific gene. Genetic samples were taken from the cods from 8 different rivers in the New England region: The St. Lawrence River, Miramichi River, Margaree River, Squamscott River, Niantic River, the Shinnecock Basic, the Hudson River, and the Hackensack River. Genetic analysis found that in the population of tomcods in the four southernmost rivers, the gene AHR2 (aryl hydrocarbon receptor 2) was present as an allele with a difference of two amino acid deletions. This deletion conferred a resistance to PCB in the fish species and was found in 99% of Hudson River tomcods, 92% in the Hackensack River, 6% in the Niantic River, and 5% in Shinnecock Bay. This pattern along the sampled bodies of waters infers a direct correlation of selective pressures leading to the evolution of PCB resistance in Atlantic tomcod fish.

Urban Wildlife

Urban wildlife is a broad and easily observable case of human-caused selection pressure on wildlife. With the growth in human habitats, different animals have adapted to survive within these urban environments. These types of environments can exert selection pressures on organisms, often leading to new adaptations. For example, the weed *Crepis sancta*, found in France, has two

types of seed, heavy and fluffy. The heavy ones land nearby to the parent plant, whereas fluffy seeds float further away on the wind. In urban environments, seeds that float far often land on infertile concrete. Within about 5–12 generations, the weed evolves to produce significantly heavier seeds than its rural relatives. Other examples of urban wildlife are rock pigeons and species of crows adapting to city environments around the world; African penguins in Simon's Town; baboons in South Africa; and a variety of insects living in human habitations. Studies have been conducted and have found striking changes to animals' (more specifically mammals') behavior and physical brain size due to their interactions with human-created environments.

White Sands Lizards

H. M. Ruthveni, a White Sands ecotonal variant of Holbrookia maculata.

Animals that exhibit ecotonal variations allow for research concerning the mechanisms that maintain population differentiation. A wealth of information about natural selection, genotypic, and phenotypic variation;adaptation and ecomorphology; and social signalinghas been acquired from the studies of three species of lizards located in the White Sands desert of New Mexico. Holbrookia maculata, Aspidoscelis inornatus, and Sceloporus undulatus exhibit ecotonal populations that match both the dark soils and the white sands in the region. Research conducted on these species has found significant phenotypic and genotypic differences between the dark and light populations due to strong selection pressures. For example, H. maculataexhibits the strongest phenotypic difference (matches best with the substrate) of the light colored population coinciding with the least amount of gene flow between the populations and the highest genetic differences when compared to the other two lizard species.

New Mexico's White Sands are a recent geologic formation (approximately 6000 years old to possibly 2000 years old). This recent origin of these gypsum sand dunes suggests that species exhibiting lighter-colored variations have evolved in a relatively short time frame. The three lizard species previously mentioned have been found to display variable social signal coloration in coexistence with their ecotonal variants. Not only have the three species convergently evolved their lighter variants due to the selection pressures from the environment, they've also evolved ecomorphological differences: morphology, behavior (in is case, escape behavior), and performance (in this case, sprint speed) collectively. Roches' work found surprising results in the escape behavior of H. maculata and S. undulatus. When dark morphs were placed on white sands, their startle response was significantly diminished. This result could be due to varying factors relating to sand temperature or visual acuity; however, regardless of the cause, "failure of mismatched lizards to sprint could be maladaptive when faced with a predator".

Evidence from Speciation

Speciation is the evolutionary process by which new biological species arise. Biologists research species using different theoretical frameworks for what constitutes a species and there exists debate with regard to delineation. Nevertheless, much of the current research suggests that, "speciation is a process of emerging genealogical distinctness, rather than a discontinuity affecting all genes simultaneously" and, in allopatry (the most common form of speciation), "reproductive isolation is a byproduct of evolutionary change in isolated populations, and thus can be considered an evolutionary accident". Speciation occurs as the result of the latter (allopatry); however, a variety of differing agents have been documented and are often defined and classified in various forms (e.g. peripatric, parapatric, sympatric, polyploidization, hybridization, etc.). Instances of speciation have been observed in both nature and the laboratory. A.-B Florin and A. Ödeen note that, "strong laboratory evidence for allopatric speciation is lacking"; however, contrary to laboratory studies (focused specifically on models of allopatric speciation), "speciation most definitely occurs; and the vast amount of evidence from nature makes it unreasonable to argue otherwise". Coyne and Orr compiled a list of 19 laboratory experiments on *Drosophila* presenting examples of allopatric speciation by divergent selection concluding that, "reproductive isolation in allopatry can evolve as a byproduct of divergent selection".

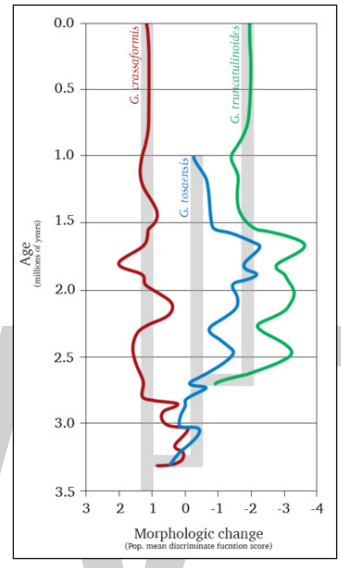
Research documenting speciation is abundant. Biologists have documented numerous examples of speciation in nature—with evolution having produced far more species than any observer would consider necessary. For example, there are well over 350,000 described species of beetles.Examples of speciation come from the observations of island biogeography and the process of adaptive radiation, both explained previously. Evidence of common descent can also be found through paleontological studies of speciation within geologic strata. The examples represent different modes of speciation and provide strong evidence for common descent. It is important to acknowledge that not all speciation research directly observes divergence from "start-to-finish". This is by virtue of research delimitation and definition ambiguity, and occasionally leads research towards historical reconstructions. In light of this, examples abound, and the following are by no means exhaustive—comprising only a small fraction of the instances observed. Once again, take note of the established fact that, "natural selection is a ubiquitous part of speciation", and is the primary driver of speciation, so; hereinafter, examples of speciation will often interdepend and correspond with selection.

Fossils

Limitations exist within the fossil record when considering the concept of what constitutes a species. Paleontologists largely rely on a different framework: the morphological species concept. Due to the absence of information such as reproductive behavior or genetic material in fossils, paleontologists distinguish species by their phenotypic differences. Extensive investigation of the fossil record has led to numerous theories concerning speciation (in the context of paleontology) with many of the studies suggesting that stasis, punctuation, and lineage branching are common. In 1995, D. H. Erwin, et al. published a major work—*New Approaches to Speciation in the Fossil Record*—which compiled 58 studies of fossil speciation (between 1972 and 1995) finding most of the examples suggesting stasis (involving anagenesis or punctuation) and 16 studies suggesting speciation. Despite stasis appearing to be the predominate conclusion at first glance, this particular meta-study investigated deeper, concluding that, "no single pattern appears dominate" with "the

preponderance of studies illustrating *both* stasis and gradualism in the history of a single lineage". Many of the studies conducted utilize seafloor sediments that can provide a significant amount of data concerning planktonic microfossils. The succession of fossils in stratigraphy can be used to determine evolutionary trends among fossil organisms. In addition, incidences of speciation can be interpreted from the data and numerous studies have been conducted documenting both morphological evolution and speciation.

Globorotalia



Morphologic change of Globorotalia crassaformis, G. tosaensis, and G. truncatulinoides over 3.5 Ma. Superimposed is a phylogenetic tree of the group.

Extensive research on the planktonic foraminifer *Globorotalia truncatulinoides* has provided insight into paleobiogeographical and paleoenvironmental studies alongside the relationship between the environment and evolution. In an extensive study of the paleobiogeography of *G. truncatulinoides*, researchers found evidence that suggested the formation of a new species (via the sympatric speciation framework). Cores taken of the sediment containing the three species *G. crassaformis*, *G. tosaensis*, and *G. truncatulinoides* found that before 2.7 Ma, only *G. crassaformis* and *G. tosaensis* existed. A speciation event occurred at that time, whereby intermediate forms existed for quite some time. Eventually *G. tosaensis* disappears from the record (suggesting extinction) but exists as an intermediate between the extant *G. crassaformis* and *G. truncatulinoides*. This record of the fossils also matched the already existing phylogeny constructed by morphological characters of the three species.

Radiolaria

In a large study of five species of radiolarians (*Calocycletta caepa*, *Pterocanium prismatium*, *Pseudoculous vema*, *Eucyrtidium calvertense*, and *Eucyrtidium matuyamai*), the researchers documented considerable evolutionary change in each lineage. Alongside this, trends with the closely related species *E. calvertense* and *E. matuyamai* showed that about 1.9 Mya *E. calvertense* invaded a new region of the Pacific, becoming isolated from the main population. The stratigraphy of this species clearly shows that this isolated population evolved into *E. Matuyamai*.

It then reinvaded the region of the still-existing and static *E. calvertense* population whereby a sudden decrease in body size occurred. Eventually the invader *E. matuyamai* disappeared from the stratum (presumably due to extinction) coinciding with a desistance of size reduction of the *E. calvertense* population. From that point on, the change in size leveled to a constant. The authors suggest competition-induced character displacement.

Rhizosolenia

Researchers conducted measurements on 5,000 *Rhizosolenia* (a planktonic diatom) specimens from eight sedimentary cores in the Pacific Ocean. The core samples spanned two million years and were chronologized using sedimentary magnetic field reversal measurements. All the core samples yielded a similar pattern of divergence: with a single lineage (*R. bergonii*) occurring before 3.1 Mya and two morphologically distinct lineages (daughter species: *R. praebergonii*) appearing after. The parameters used to measure the samples were consistent throughout each core. An additional study of the daughter species *R. praebergonii* found that, after the divergence, it invaded the Indian Ocean.

Turborotalia

A recent study was conducted involving the planktonic foraminifer Turborotalia. The authors extracted "51 stratigraphically ordered samples from a site within the oceanographically stable tropical North Pacific gyre". Two hundred individual species were examined using ten specific morphological traits (size, compression index, chamber aspect ratio, chamber inflation, aperture aspect ratio, test height, test expansion, umbilical angle, coiling direction, and the number of chambers in the final whorl). Utilizing multivariate statistical clustering methods, the study found that the species continued to evolve non-directionally within the Eocene from 45 Ma to about 36 Ma. However, from 36 Ma to approximately 34 Ma, the stratigraphic layers showed two distinct clusters with significantly defining characteristics distinguishing one another from a single species. The authors concluded that speciation must have occurred and that the two new species were ancestral to the prior species. Just as in most of evolutionary biology, this example represents the interdisciplinary nature of the field and the necessary collection of data from various fields (e.g. oceanography, paleontology) and the integration of mathematical analysis (e.g. biometry).

Vertebrates

There exists evidence for vertebrate speciation despite limitations imposed by the fossil record. Studies have been conducted documenting similar patterns seen in marine invertebrates. For example, extensive research documenting rates of morphological change, evolutionary trends, and speciation patterns in small mammals has significantly contributed to the scientific literature; once more, demonstrating that evolution (and speciation) occurred in the past and lends support common ancestry.

A study of four mammalian genera: *Hyopsodus*, *Pelycodus*, *Haplomylus* (three from the Eocene), and *Plesiadapis* (from the Paleocene) found that—through a large number of stratigraphic layers and specimen sampling—each group exhibited, "gradual phyletic evolution, overall size increase, iterative evolution of small species, and character divergence following the origin of each new lineage".The authors of this study concluded that speciation was discernible. In another study

concerning morphological trends and rates of evolution found that the European arvicolid rodent radiated into 52 distinct lineages over a time frame of 5 million years while documenting examples of phyletic gradualism, punctuation, and stasis.

Invertebrates

Drosophila Melanogaster

William R. Rice and George W. Salt found experimental evidence of sympatric speciation in the common fruit fly. They collected a population of *Drosophila melanogaster*from Davis, California and placed the pupae into a habitat maze. Newborn flies had to investigate the maze to find food. The flies had three choices to take in finding food. Light and dark (phototaxis), up and down (geotaxis), and the scent of acetaldehyde and the scent of ethanol (chemotaxis) were the three options. This eventually divided the flies into 42 spatio-temporal habitats.

A common fruit fly (Drosophila melanogaster).

They then cultured two strains that chose opposite habitats. One of the strains emerged early, immediately flying upward in the dark attracted to the acetaldehyde. The other strain emerged late and immediately flew downward, attracted to light and ethanol. Pupae from the two strains were then placed together in the maze and allowed to mate at the food site. They then were collected. A selective penalty was imposed on the female flies that switched habitats. This entailed that none of their gametes would pass on to the next generation. After 25 generations of this mating test, it showed reproductive isolation between the two strains. They repeated the experiment again without creating the penalty against habitat switching and the result was the same; reproductive isolation was produced.

Gall Wasps

A study of the gall-forming wasp species *Belonocnema treatae* found that populations inhabiting different host plants (*Quercus geminata* and *Q. Virginiana*) exhibited different body size and gallmorphology alongside a strong expression of sexual isolation. The study hypothesized that *B. treatae*populations inhabiting different host plants would show evidence of divergent selection promoting speciation. The researchers sampled gall wasp species and oak tree localities, measured body size (right hand tibia of each wasp), and counted gall chamber numbers. In

addition to measurements, they conducted mating assays and statistical analyses. Genetic analysis was also conducted on two mtDNA sites (416 base pairs from cytochrome C and 593 base pairs from cytochrome oxidase) to "control for the confounding effects of time since divergence among allopatric populations".

In an additional study, the researchers studied two gall wasp species *B. treatae* and *Disholcaspis quercusvirens* and found strong morphological and behavioral variation among host-associated populations. This study further confounded prerequisites to speciation.

Hawthorn Fly

One example of evolution at work is the case of the hawthorn fly, *Rhagoletis pomonella*, also known as the apple maggot fly, which 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 some time 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 the fact 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 speciation is occurring.

London Underground Mosquito

The London Underground mosquito is a species of mosquito in the genus *Culex* found in the London Underground. It evolved from the overground species *Culex pipiens*. This mosquito, although first discovered in the London Underground system, has been found in underground systems around the world. It is suggested that it may have adapted to human-made underground systems since the last century from local above-ground *Culex pipiens*, although more recent evidence suggests that it is a southern mosquito variety related to *Culex pipiens* that has adapted to the warm underground spaces of northern cities.

The two species have very different behaviours, are extremely difficult to mate, and with different allele frequency, consistent with genetic drift during a founder event. More specifically, this mosquito, *Culex pipiens molestus*, breeds all-year round, is cold intolerant, and bites rats, mice, and humans, in contrast to the above ground species *Culex pipiens* that is cold tolerant, hibernates in the winter, and bites only birds. When the two varieties were cross-bred the eggs were infertile suggesting reproductive isolation.

The genetic data indicates that the *molestus* form in the London Underground mosquito appears to have a common ancestry, rather than the population at each station being related to the nearest aboveground population (i.e. the *pipiens* form). Byrne and Nichols' working hypothesis was that adaptation to the underground environment had occurred locally in London only once. These widely separated populations are distinguished by very minor genetic differences, which suggest that the molestus form developed: a single mtDNA difference shared among the underground populations of ten Russian cities; a single fixed microsatellite difference in populations spanning Europe, Japan, Australia, the middle East and Atlantic islands.

Snapping Shrimp and the Isthmus of Panama

Debate exists determining when the isthmus of Panama closed. Much of the evidence supports a closure approximately 2.7 to 3.5 mya using "multiple lines of evidence and independent surveys". However, a recent study suggests an earlier, transient bridge existed 13 to 15 mya. Regardless of the 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." Studies of snapping shrimp in the genus *Alpheus* have provided direct evidence of allopatric speciation events, and contributed to the literature concerning rates of molecular evolution. Phylogenetic reconstructions using "multilocus datasets and coalescent-based analytical methods" support the relationships of the species in the group and molecular clock techniques support the separation of 15 pairs of *Alpheus* species between 3 and 15 million years ago.

Plants

The botanist Verne Grant pioneered the field of plant speciation with his research and major publications on the topic. As stated before, many biologists rely on the biological species concept, with some modern researchers utilizing the phylogenetic species concept. Debate exists in the field concerning which framework should be applied in the research. Regardless, reproductive isolation is the primary role in the process of speciation and has been studied extensively by biologists in their respective disciplines.

Both hybridization and polyploidy have also been found to be major contributors to plant speciation. With the advent of molecular markers, "hybridization is considerably more frequent than previously believed". In addition to these two modes leading to speciation, pollinator preference and isolation, chromosomal rearrangements, and divergent natural selection have become critical to the speciation of plants. Furthermore, recent research suggests that sexual selection, epigenetic drivers, and the creation of incompatible allele combinations caused by balancing selection also contribute to the formation of new species. Instances of these modes have been researched in both the laboratory and in nature. Studies have also suggested that, due to "the sessile nature of plants it increases the relative importance of ecological 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 a rare event. However, hybridization resulting in reproductive isolation is considered 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 *Heliconius* butterflies and sunflowers. Polyploid speciation, which involves changes in chromosome number, is a more common phenomenon, especially in plant species.

Polyploidy is a mechanism that has caused many rapid speciation events in sympatry because offspring of, for example, tetraploid x diploid matings often result in triploid sterile progeny. Not all polyploids are reproductively isolated from their parental plants, and gene flow may still occur for example through triploid hybrid x diploid matings that produce tetraploids, or matings between meiotically unreduced gametes from diploids and gametes from tetraploids. 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.

Researchers consider reproductive isolation as key to speciation. A major aspect of speciation research is to determine the nature of the barriers that inhibit reproduction. Botanists often consider the zoological classifications of prezygotic and postzygotic barriers as inadequate. The examples provided below give insight into the process of speciation.

Mimulus Peregrinus

The creation of a new allopolyploid species of monkeyflower (*Mimulus peregrinus*) was observed on the banks of the Shortcleuch Water—a river in Leadhills, South Lanarkshire, Scotland. Parented from the cross of the two species *Mimulus guttatus* (containing 14 pairs of chromosomes) and *Mimulus luteus* (containing 30-31 pairs from a chromosome duplication), *M. peregrinus* has six copies of its chromosomes (caused by the duplication of the sterile hybrid triploid). Due to the nature of these species, they have the ability to self-fertilize. Because of its number of chromosomes it is not able to pair with *M. guttatus*, *M. luteus*, or their sterile triploid offspring. *M. peregrinus* will either die, producing no offspring, or reproduce with itself effectively leading to a new species.

Raphanobrassica

Raphanobrassica includes all intergeneric hybrids between the genera *Raphanus* (radish) and *Brassica* (cabbages, etc.). The *Raphanobrassica* is an allopolyploid cross between the radish(*Raphanus sativus*) and cabbage (*Brassica oleracea*). Plants of this parentage are now known as radicole. Two other fertile forms of *Raphanobrassica* are known. Raparadish, an allopolyploid hybrid between *Raphanus sativus* and *Brassica rapa* is grown as a fodder crop. "Raphanofortii" is the allopolyploid hybrid between *Brassica tournefortii* and *Raphanus caudatus*. The *Raphanobrassica* is a fascinating plant, because (in spite of its hybrid nature), it is not sterile. This has led some botanists to propose that the accidental hybridization of a flower by pollen of another species in nature could be a mechanism of speciation common in higher plants.

Senecio (Groundsel)

The Welsh groundsel is an allopolyploid, a plant that contains sets of chromosomes originating from two different species. Its ancestor was *Senecio* × *baxteri*, an infertile hybrid that can arise spontaneously when the closely related groundsel (*Senecio vulgaris*) and Oxford ragwort (*Senecio squalidus*) grow alongside each other. Sometime in the early 20th century, an accidental doubling of the number of chromosomes in an *S.* × *baxteri* plant led to the formation of a new fertile species.

The York groundsel (*Senecio eboracensis*) is a hybrid species of the self-incompatible *Senecio squalidus* (also known as Oxford ragwort) and the self-compatible *Senecio vulgaris* (also known as common groundsel). Like *S. vulgaris*, *S. eboracensis* is self-compatible; however, it shows little or no natural crossing with its parent species, and is therefore reproductively isolated, indicating that strong breed barriers exist between this new hybrid and its parents. It resulted from a back-crossing of the F1 hybrid of its parents to *S. vulgaris*. *S. vulgaris* is native to Britain, while *S. squalidus* was introduced from Sicily in the early 18th century; therefore, *S. eboracensis* has speciated from those two species within the last 300 years.

Other hybrids descended from the same two parents are known. Some are infertile, such as *S.* x *baxteri*. Other fertile hybrids are also known, including *S. vulgaris* var. *hibernicus*, now common in Britain, and the allohexaploid *S. cambrensis*, which according to molecular evidence probably originated independently at least three times in different locations. Morphological and genetic evidence support the status of *S. eboracensis* as separate from other known hybrids.

Thale Cress

Arabidopsis thaliana (colloquially known as thale cress, mouse-ear cress or arabidopsis).

Kirsten Bomblies et al. discovered two genes in the thale cress plant, *Arabidopsis thaliana*. When both genes are inherited by an individual, it ignites a reaction in the hybrid plant that turns its own immune system against it. In the parents, the genes were not detrimental, but they evolved separately to react defectively when combined. To test this, Bomblies crossed 280 genetically different strains of *Arabidopsis* in 861 distinct ways and found that 2 percent of the resulting hybrids were necrotic. Along with allocating the same indicators, the 20 plants also shared a comparable collection of genetic activity in a group of 1,080 genes. In almost all of the cases, Bomblies discovered that only two genes were required to cause the autoimmune response. Bomblies looked at one hybrid in detail and found that one of the two genes belonged to the NB-LRR class, a common group of disease resistance genes involved in recognizing new infections. When Bomblies removed the problematic gene, the hybrids developed normally. Over successive generations, these incompatibilities could create divisions between different

plant strains, reducing their chances of successful mating and turning distinct strains into separate species.

Tragopogon (Salsify)

Purple salsify, *Tragopogon porrifolius*.

Tragopogon is one example where hybrid speciation has been observed. In the early 20th century, humans introduced three species of salsify into North America. These species, the western salsify (*Tragopogon dubius*), the meadow salsify (*Tragopogon pratensis*), and the oyster plant (*Tragopogon porrifolius*), are now common weeds in urban wastelands. In the 1950s, botanists found two new species in the regions of Idaho and Washington, where the three already known species overlapped. One new species, *Tragopogon miscellus*, is a tetraploid hybrid of *T. dubius* and *T. pratensis*. The other new species, *Tragopogon mirus*, is also an allopolyploid, but its ancestors were *T. dubius* and *T. porrifolius*. These new species are usually referred to as "the Ownbey hybrids" after the botanist who first described them. The *T. mirus* population grows mainly by reproduction of its own members, but additional episodes of hybridization continue to add to the *T. mirus*population.

T. dubius and *T. pratensis* mated in Europe but were never able to hybridize. A study published in March 2011 found that when these two plants were introduced to North America in the 1920s, they mated and doubled the number of chromosomes in there hybrid *Tragopogon miscellus* allowing for a "reset" of its genes, which in turn, allows for greater genetic variation. Professor Doug Soltis of the University of Florida said, "We caught evolution in the act New and diverse patterns of gene expression may allow the new species to rapidly adapt in new environments". This observable event of speciation through hybridization further advances the evidence for the common descent of organisms and the time frame in which the new species arose in its new environment. The hybridizations have been reproduced artificially in laboratories from 2004 to present day.

Vertebrates

Blackcap

The bird species, *Sylvia atricapilla*, commonly referred to as blackcaps, lives in Germany and flies southwest to Spain while a smaller group flies northwest to Great Britain during the winter.

Gregor Rolshausen from the University of Freiburg found that the genetic separation of the two populations is already in progress. The differences found have arisen in about 30 generations. With DNA sequencing, the individuals can be assigned to a correct group with an 85% accuracy. Stuart Bearhop from the University of Exeter reported that birds wintering in England tend to mate only among themselves, and not usually with those wintering in the Mediterranean. It is still inference to say that the populations will become two different species, but researchers expect it due to the continued genetic and geographic separation.

Mollies

The shortfin molly (*Poecilia mexicana*) is a small fish that lives in the Sulfur Caves of Mexico. Years of study on the species have found that two distinct populations of mollies—the dark interior fish and the bright surface water fish—are becoming more genetically divergent. The populations have no obvious barrier separating the two; however, it was found that the mollies are hunted by a large water bug (*Belostoma spp*). Tobler collected the bug and both types of mollies, placed them in large plastic bottles, and put them back in the cave. After a day, it was found that, in the light, the cave-adapted fish endured the most damage, with four out of every five stab-wounds from the water bugs sharp mouthparts. In the dark, the situation was the opposite. The mollies' senses can detect a predator's threat in their own habitats, but not in the other ones. Moving from one habitat to the other significantly increases the risk of dying. Tobler plans on further experiments, but believes that it is a good example of the rise of a new species.

Polar Bear

Natural selection, geographic isolation, and speciation in progress are illustrated by the relationship between the polar bear (*Ursus maritimus*) and the brown bear (*Ursus arctos*). Considered separate species throughout their ranges; however, it has been documented that they possess the capability to interbreed and produce fertile offspring. This introgressive hybridization has occurred both in the wild and in captivity and has been documented and verified with DNA testing. The oldest known fossil evidence of polar bears dates around 130,000 to 110,000 years ago;however, molecular data has revealed varying estimates of divergence time. Mitochondrial DNA analysis has given an estimate of 150,000 years ago while nuclear genome analysis has shown an approximate divergence of 603,000 years ago. Recent research using the complete genomes (rather than mtDNA or partial nuclear genomes) establishes the divergence of polar and brown bears between 479-343 thousand years ago. Despite the differences in divergence rates, molecular research suggests the sister species have undergone a highly complex process of speciation and admixture between the two.

Polar bears have acquired significant anatomical and physiological differences from the brown bear that allow it to comfortably survive in conditions that the brown bear likely could not. Notable examples include the ability to swim sixty miles or more at a time in freezing waters, fur that blends with the snow, and to stay warm in the arctic environment, an elongated neck that makes it easier to keep their heads above water while swimming, and oversized and heavy-matted webbed feet that act as paddles when swimming. It has also evolved small papillae and vacuole-like suction cups on the soles to make them less likely to slip on the ice, alongside smaller ears for a reduction of heat loss, eyelids that act like sunglasses, accommodations for their all-meat diet, a large stomach capacity to enable opportunistic feeding, and the ability to fast for up to nine months

while recycling their urea. This example presents a macro-evolutionary change involving an amalgamation of several fields of evolutionary biology, e.g. adaptation through natural selection, geographic isolation, speciation, and hybridization.

Evidence from Coloration

Animal coloration provided important early evidence for evolution by natural selection, at a time when little direct evidence was available. Three major functions of coloration were discovered in the second half of the 19th century, and subsequently used as evidence of selection: camouflage (protective coloration); mimicry, both Batesian and Müllerian; and aposematism. After the circumstantial evidence provided by Darwin in *On the Origin of Species*, and given the absence of mechanisms for genetic variation or heredity at that time, naturalists including Darwin's contemporaries, Henry Walter Bates and Fritz Müller sought evidence from what they could observe in the field.

Natural selection has driven the ptarmigan to change from snow camouflage in winter to disruptive coloration suiting moorland in summer.

Mimicry and Aposematism

Bates and Müller described forms of mimicry that now carry their names, based on their observations of tropical butterflies. These highly specific patterns of coloration are readily explained by natural selection, since predators such as birds which hunt by sight will more often catch and kill insects that are less good mimics of distasteful models than those that are better mimics; but the patterns are otherwise hard to explain. Darwinists such as Alfred Russel Wallace and Edward Bagnall Poulton, and in the 20th century Hugh Cott and Bernard Kettlewell, sought evidence that natural selection was taking place.

Camouflage

In 1889, Wallace noted that snow camouflage, especially plumage and pelage that changed with the seasons, suggested an obvious explanation as an adaptation for concealment. Poulton's 1890 book, *The Colours of Animals*, written during Darwinism's lowest ebb, used all the forms of coloration to argue the case for natural selection. Cott described many kinds of camouflage, mimicry and warning coloration in his 1940 book *Adaptive Coloration in Animals*, and in particular his

drawings of coincident disruptive coloration in frogs convinced other biologists that these deceptive markings were products of natural selection. Kettlewell experimented on peppered moth evolution, showing that the species had adapted as pollution changed the environment; this provided compelling evidence of Darwinian evolution.

Evidence from Mathematical Modeling

Computer science allows the iteration of self-changing complex systems to be studied, allowing a mathematical understanding of the nature of the processes behind evolution; providing evidence for the hidden causes of known evolutionary events. The evolution of specific cellular mechanisms like spliceosomes that can turn the cell's genome into a vast workshop of billions of interchangeable parts that can create tools that create us can be studied for the first time in an exact way.

"It has taken more than five decades, but the electronic computer is now powerful enough to simulate evolution", assisting bioinformatics in its attempt to solve biological problems.

Computational evolutionary biology has enabled researchers to trace the evolution of a large number of organisms by measuring changes in their DNA, rather than through physical taxonomy or physiological observations alone. It has compared entire genomes permitting the study of more complex evolutionary events, such as gene duplication, horizontal gene transfer, and the prediction of factors important in speciation. It has also helped build complex computational models of populations to predict the outcome of the system over time and track and share information on an increasingly large number of species and organisms.

Future endeavors are to reconstruct a now more complex tree of life.

Christoph Adami, a professor at the Keck Graduate Institute made this point in *Evolution of biological complexity*:

> "To make a case for or against a trend in the evolution of complexity in biological evolution, complexity must be both rigorously defined and measurable. A recent information-theoretic (but intuitively evident) definition identifies genomic complexity with the amount of information a sequence stores about its environment. We investigate the evolution of genomic complexity in populations of digital organisms and monitor in detail the evolutionary transitions that increase complexity. We show that, because natural selection forces genomes to behave as a natural "Maxwell Demon", within a fixed environment, genomic complexity is forced to increase."

David J. Earl and Michael W. Deem—professors at Rice University made this point in *Evolvability is a selectable trait*:

> "Not only has life evolved, but life has evolved to evolve. That is, correlations within protein structure have evolved, and mechanisms to manipulate these correlations have evolved in tandem. The rates at which the various events within the hierarchy of evolutionary moves occur are not random or arbitrary but are selected by Darwinian evolution. Sensibly, rapid or extreme environmental change leads to selection for greater evolvability. This selection is not forbidden by causality and is strongest on the largest-scale moves within the mutational hierarchy. Many observations within evolutionary biology, heretofore considered

evolutionary happenstance or accidents, are explained by selection for evolvability. For example, the vertebrate immune system shows that the variable environment of antigens has provided selective pressure for the use of adaptable codons and low-fidelity polymerases during somatic hypermutation. A similar driving force for biased codon usage as a result of productively high mutation rates is observed in the hemagglutinin protein of influenza A."

"Computer simulations of the evolution of linear sequences have demonstrated the importance of recombination of blocks of sequence rather than point mutagenesis alone. Repeated cycles of point mutagenesis, recombination, and selection should allow *in vitro* molecular evolution of complex sequences, such as proteins." Evolutionary molecular engineering, also called directed evolution or *in vitro* molecular evolution involves the iterated cycle of mutation, multiplication with recombination, and selection of the fittest of individual molecules (proteins, DNA, and RNA). Natural evolution can be relived showing us possible paths from catalytic cycles based on proteins to based on RNA to based on DNA.

Natural Selection

Natural selection is the differential survival and reproduction of individuals due to differences in phenotype. It is a key mechanism of evolution, the change in the heritable traits characteristic of a population over generations. Charles Darwinpopularised the term "natural selection", contrasting it with artificial selection, which in his view is intentional, whereas natural selection is not.

Variation exists within all populations of organisms. This occurs partly because random mutations arise in the genome of an individual organism, and offspringcan inherit such mutations. Throughout the lives of the individuals, their genomes interact with their environments to cause variations in traits. The environment of a genome includes the molecular biology in the cell, other cells, other individuals, populations, species, as well as the abiotic environment. Because individuals with certain variants of the trait tend to survive and reproduce more than individuals with other, less successful variants, the population evolves. Other factors affecting reproductive success include sexual selection (now often included in natural selection) and fecundity selection.

Natural selection acts on the phenotype, the characteristics of the organism which actually interact with the environment, but the genetic (heritable) basis of any phenotype that gives that phenotype a reproductive advantage may become more common in a population. Over time, this process can result in populations that specialise for particular ecological niches (microevolution) and may eventually result in speciation (the emergence of new species, macroevolution). In other words, natural selection is a key process in the evolution of a population.

Natural selection is a cornerstone of modern biology. The concept, published by Darwin and Alfred Russel Wallace in a joint presentation of papers in 1858, was elaborated in Darwin's influential 1859 book On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. He described natural selection as analogous to artificial selection, a process by which animals and plants with traits considered desirable by human breeders are systematically favoured for reproduction. The concept of natural selection originally developed in the absence of a valid theory of heredity; at the time of Darwin's writing, science had yet to develop

modern theories of genetics. The union of traditional Darwinian evolution with subsequent discoveries in classical genetics formed the modern synthesis of the mid-20th century. The addition of molecular geneticshas led to evolutionary developmental biology, which explains evolution at the molecular level. While genotypes can slowly change by random genetic drift, natural selection remains the primary explanation for adaptive evolution.

The term *natural selection* is most often defined to operate on heritable traits, because these directly participate in evolution. However, natural selection is "blind" in the sense that changes in phenotype can give a reproductive advantage regardless of whether or not the trait is heritable. Following Darwin's primary usage, the term is used to refer both to the evolutionary consequence of blind selection and to its mechanisms. It is sometimes helpful to explicitly distinguish between selection's mechanisms and its effects; when this distinction is important, scientists define "(phenotypic) natural selection" specifically as "those mechanisms that contribute to the selection of individuals that reproduce", without regard to whether the basis of the selection is heritable. Traits that cause greater reproductive success of an organism are said to be *selected for*, while those that reduce success are *selected against*.

Mechanism

Heritable Variation and Differential Reproduction

During the industrial revolution, pollution killed many lichens, leaving tree trunks dark. A dark (melanic) morph of the peppered mothlargely replaced the formerly usual light morph (both shown here). Since the moths are subject to predation by birds hunting by sight, the colour change offers better camouflage against the changed background, suggesting natural selection at work.

Natural variation occurs among the individuals of any population of organisms. Some differences may improve an individual's chances of surviving and reproducing such that its lifetime reproductive rate is increased, which means that it leaves more offspring. If the traits that give these individuals a reproductive advantage are also heritable, that is, passed from parent to offspring, then there will be differential reproduction, that is, a slightly higher proportion of fast rabbits or efficient algae in the next generation. Even if the reproductive advantage is very slight, over many generations any advantageous heritable trait becomes dominant in the population. In this way the natural environment of an organism "selects for" traits that confer a reproductive advantage, causing evolutionary change, as Darwin described. This gives the appearance of purpose, but in natural selection there is no intentional choice. Artificial selection is purposive where natural selection is not, though biologists often use teleological language to describe it.

The peppered moth exists in both light and dark colours in Great Britain, but during the industrial revolution, many of the trees on which the moths rested became blackened by soot, giving the dark-coloured moths an advantage in hiding from predators. This gave dark-coloured moths a better chance of surviving to produce dark-coloured offspring, and in just fifty years from the first dark moth being caught, nearly all of the moths in industrial Manchester were dark. The balance was reversed by the effect of the Clean Air Act 1956, and the dark moths became rare again, demonstrating the influence of natural selection on peppered moth evolution. A recent study, using image analysis and avian vision models, shows that pale individuals more closely match lichen backgrounds than dark morphs and for the first time quantifies the camouflage of moths to predation risk.

Fitness

The concept of fitness is central to natural selection. In broad terms, individuals that are more "fit" have better potential for survival, as in the well-known phrase "survival of the fittest", but the precise meaning of the term is much more subtle. Modern evolutionary theory defines fitness not by how long an organism lives, but by how successful it is at reproducing. If an organism lives half as long as others of its species, but has twice as many offspring surviving to adulthood, its genes become more common in the adult population of the next generation. Though natural selection acts on individuals, the effects of chance mean that fitness can only really be defined "on average" for the individuals within a population. The fitness of a particular genotype corresponds to the average effect on all individuals with that genotype. A distinction must be made between the concept of "survival of the fittest" and "improvement in fitness". "Survival of the fittest" does not give an "improvement in fitness", it only represents the removal of the less fit variants from a population. A mathematical example of "survival of the fittest" is given by Haldane in his paper "The Cost of Natural Selection". Haldane called this process "substitution" or more commonly in biology, this is called "fixation". This is correctly described by the differential survival and reproduction of individuals due to differences in phenotype. On the other hand, "improvement in fitness" is not dependent on the differential survival and reproduction of individuals due to differences in phenotype, it is dependent on the absolute survival of the particular variant. The probability of a beneficial mutation occurring on some member of a population depends on the total number of replications of that variant. The mathematics of "improvement in fitness was described by Kleinman. An empirical example of "improvement in fitness" is given by the Kishony Mega-plate experiment. In this experiment, "improvement in fitness" depends on the number of replications of the particular variant for a new variant to appear that is capable of growing in the next higher drug concentration region. Fixation or substitution is not required for this "improvement in fitness". On the other hand, "improvement in fitness" can occur in an environment where "survival of the fittest" is also acting. The classic Lenski "E. coli long-term evolution experiment" is an example of adaptation in a competitive environment, ("improvement in fitness" during "survival of the fittest"). The probability of a beneficial mutation occurring on some member of the lineage to give improved fitness is slowed by the competition. The variant which is a candidate for a beneficial mutation in this limited carrying capacity environment must first out-compete the "less fit" variants in order to accumulate the requisite number of replications for there to be a reasonable probability of that beneficial mutation occurring.

Competition

In biology, competition is an interaction between organisms in which the fitness of one is lowered by the presence of another. This may be because both rely on a limited supply of a resource such as food, water, or territory. Competition may be within or between species, and may be direct or indirect. Species less suited to compete should in theory either adapt or die out, since competition plays a powerful role in natural selection, but according to the "room to roam" theory it may be less important than expansion among larger clades.

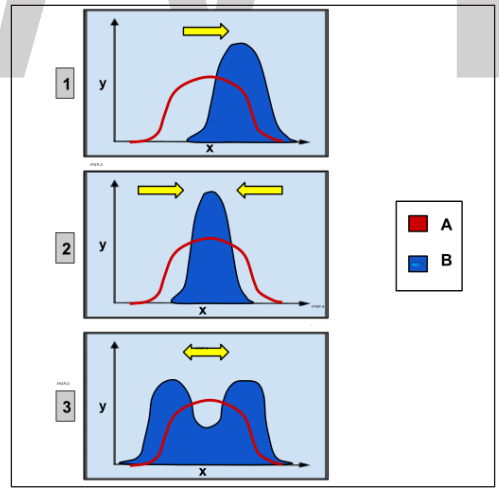
Competition is modelled by *r/K* selection theory, which is based on Robert MacArthur and E. O. Wilson's work on island biogeography. In this theory, selective pressures drive evolution in one of two stereotyped directions: *r*- or *K*-selection. These terms, *r* and *K*, can

be illustrated in a logistic model of population dynamics:

$$\frac{dN}{dt} = rN\left(-\frac{N}{K} \right)$$

where *r* is the growth rate of the population (*N*), and *K* is the carrying capacity of its local environmental setting. Typically, *r*-selected species exploit empty niches, and produce many offspring, each with a relatively low probability of surviving to adulthood. In contrast, *K*-selected species are strong competitors in crowded niches, and invest more heavily in much fewer offspring, each with a relatively high probability of surviving to adulthood.

Types of Selection



(1): directional selection: a single extreme phenotype favoured.; (2), stabilizing selection: intermediate favoured over extremes; (3): disruptive selection: extremes favoured over intermediate; X-axis: phenotypic trait; Y-axis: number of organisms; Group A: original population; Group B: after selection.

Natural selection can act on any heritable phenotypic trait, and selective pressure can be produced by any aspect of the environment, including sexual selection and competition with members of the same or other species. However, this does not imply that natural selection is always directional and results in adaptive evolution; natural selection often results in the maintenance of the status quo by eliminating less fit variants.

Selection can be classified in several different ways, such as by its effect on a trait, on genetic diversity, by the life cycle stage where it acts, by the unit of selection, or by the resource being competed for.

By Effect on a Trait

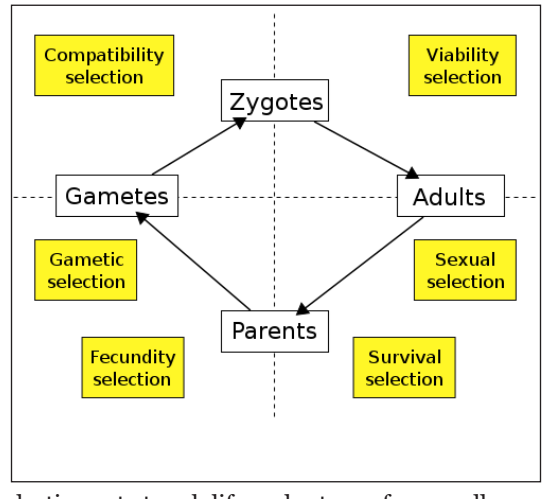
Selection has different effects on traits. Stabilizing selectionacts to hold a trait at a stable optimum, and in the simplest case all deviations from this optimum are selectively disadvantageous. Directional selection favours extreme values of a trait. The uncommon disruptive selection also acts during transition periods when the current mode is sub-optimal, but alters the trait in more than one direction. In particular, if the trait is quantitative and univariate then both higher and lower trait levels are favoured. Disruptive selection can be a precursor to speciation.

By Effect on Genetic Diversity

Alternatively, selection can be divided according to its effect on genetic diversity. Purifying or negative selection acts to remove genetic variation from the population (and is opposed by de novomutation, which introduces new variation. In contrast, balancing selection acts to maintain genetic variation in a population, even in the absence of de novo mutation, by negative frequency-dependent selection. One mechanism for this is heterozygote advantage, where individuals with two different alleles have a selective advantage over individuals with just one allele. The polymorphism at the human ABO blood group locus has been explained in this way.

By Life Cycle Stage

Another option is to classify selection by the life cyclestage at which it acts. Some biologists recognise just two types: viability (or survival) selection, which acts to increase an organism's probability of survival, and fecundity (or fertility or reproductive) selection, which acts to increase the rate of reproduction, given survival. Others split the life cycle into further components of selection. Thus viability and survival selection may be defined separately and respectively as acting to improve the probability of survival before and after reproductive age is reached, while fecundity selection may be split into additional sub-components including sexual selection, gametic selection, acting on gamete survival, and compatibility selection, acting on zygote formation.



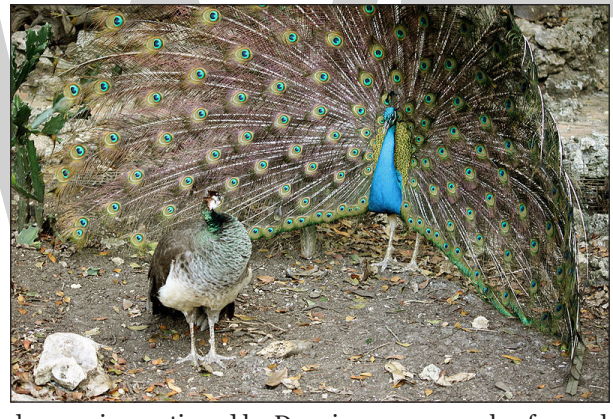
Different types of selection act at each life cycle stage of a sexually reproducing organism.

By Unit of Selection

Selection can also be classified by the level or unit of selection. Individual selection acts on the individual, in the sense that adaptations are "for" the benefit of the individual, and result from selection among individuals. Gene selection acts directly at the level of the gene. In kin selection and intragenomic conflict, gene-level selection provides a more apt explanation of the underlying process. Group selection, if it occurs, acts on groups of organisms, on the assumption that groups replicate and mutate in an analogous way to genes and individuals. There is an ongoing debate over the degree to which group selection occurs in nature.

By Resource being Competed for

Finally, selection can be classified according to the resource being competed for. Sexual selection results from competition for mates. Sexual selection typically proceeds via fecundity selection, sometimes at the expense of viability. Ecological selection is natural selection via any means other than sexual selection, such as kin selection, competition, and infanticide. Following Darwin, natural selection is sometimes defined as ecological selection, in which case sexual selection is considered a separate mechanism.



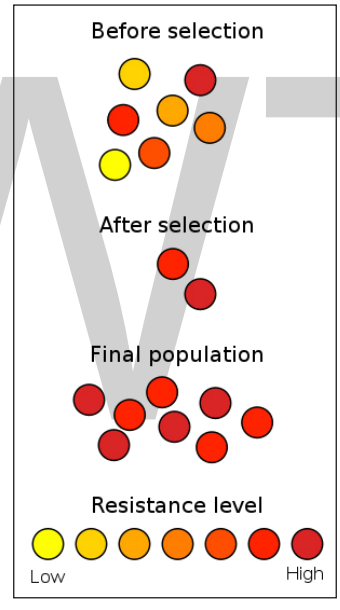
The peacock's elaborate plumage is mentioned by Darwin as an example of sexual selection, and is a classic example of Fisherian runaway, driven to its conspicuous size and coloration through mate choice by females over many generations.

Sexual selection as first articulated by Darwin (using the example of the peacock's tail) refers specifically to competition for mates, which can be intrasexual, between individuals of the same sex, that is male–male competition, or intersexual, where one gender chooses mates, most often with males displaying and females choosing. However, in some species, mate choice is primarily by males, as in some fishes of the family Syngnathidae.

Phenotypic traits can be displayed in one sex and desired in the other sex, causing a positive feedbackloop called a Fisherian runaway, for example, the extravagant plumage of some male birds such as the peacock. An alternate theory proposed by the same Ronald Fisher in 1930 is the sexy son hypothesis, that mothers want promiscuous sons to give them large numbers of grandchildren and so choose promiscuous fathers for their children. Aggression between members of the same sex is sometimes associated with very distinctive features, such as the antlers of stags, which are used in combat with other stags. More generally, intrasexual selection is often associated with sexual dimorphism, including differences in body size between males and females of a species.

Arms Races

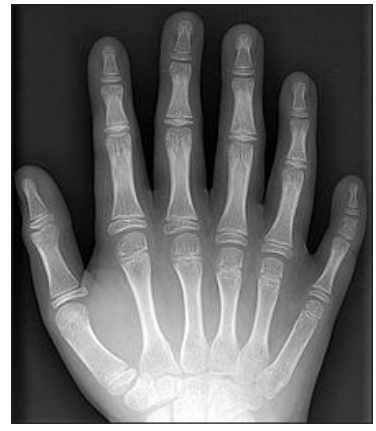
Natural selection is seen in action in the development of antibiotic resistance in microorganisms. Since the discovery of penicillin in 1928, antibiotics have been used to fight bacterial diseases. The widespread misuse of antibiotics has selected for microbial resistance to antibiotics in clinical use, to the point that the methicillin-resistant Staphylococcus aureus (MRSA) has been described as a “superbug” because of the threat it poses to health and its relative invulnerability to existing drugs. Response strategies typically include the use of different, stronger antibiotics; however, new strains of MRSA have recently emerged that are resistant even to these drugs. This is an evolutionary arms race, in which bacteria develop strains less susceptible to antibiotics, while medical researchers attempt to develop new antibiotics that can kill them. A similar situation occurs with pesticide resistance in plants and insects. Arms races are not necessarily induced by man; a well-documented example involves the spread of a gene in the butterfly Hypolimnas bolina suppressing male-killing activity by Wolbachiabacteria parasites on the island of Samoa, where the spread of the gene is known to have occurred over a period of just five years



Selection in action: resistance to antibiotics grows though the survival of individuals less affected by the antibiotic. Their offspring inherit the resistance.

Evolution by Means of Natural Selection

A prerequisite for natural selection to result in adaptive evolution, novel traits and speciation is the presence of heritable genetic variation that results in fitness differences. Genetic variation is the result of mutations, genetic recombinations and alterations in the karyotype (the number, shape, size and internal arrangement of the chromosomes). Any of these changes might have an effect that is highly advantageous or highly disadvantageous, but large effects are rare. In the past, most changes in the genetic material were considered neutral or close to neutral because they occurred in noncoding DNA or resulted in a synonymous substitution. However, many mutations in non-coding DNA have deleterious effects.Although both mutation rates and average fitness effects of mutations are dependent on the organism, a majority of mutations in humans are slightly deleterious.



X-ray of the left hand of a ten-year-old boy with polydactyly, caused by a mutant *Hox* gene.

Some mutations occur in "toolkit" or regulatory genes. Changes in these often have large effects on the phenotype of the individual because they regulate the function of many other genes. Most, but not all, mutations in regulatory genes result in non-viable embryos. Some nonlethal regulatory mutations occur in HOX genes in humans, which can result in a cervical rib or polydactyly, an increase in the number of fingers or toes. When such mutations result in a higher fitness, natural selection favours these phenotypes and the novel trait spreads in the population. Established traits are not immutable; traits that have high fitness in one environmental context may be much less fit if environmental conditions change. In the absence of natural selection to preserve such a trait, it becomes more variable and deteriorate over time, possibly resulting in a vestigial manifestation of the trait, also called evolutionary baggage. In many circumstances, the apparently vestigial structure may retain a limited functionality, or may be co-opted for other advantageous traits in a phenomenon known as preadaptation. A famous example of a vestigial structure, the eye of the blind mole-rat, is believed to retain function in photoperiod perception.

Speciation

Speciation requires a degree of reproductive isolation—that is, a reduction in gene flow. However, it is intrinsic to the concept of a species that hybrids are selected against, opposing the evolution of reproductive isolation, a problem that was recognised by Darwin. The problem does not occur in allopatric speciation with geographically separated populations, which can diverge with different sets of mutations. E. B. Poulton realized in 1903 that reproductive isolation could evolve through divergence, if each lineage acquired a different, incompatible allele of the same gene. Selection against the heterozygote would then directly create reproductive isolation, leading to the Bateson–Dobzhansky–Muller model, further elaborated by H. Allen Orr and Sergey Gavrilets. With reinforcement, however, natural selection can favor an increase in pre-zygotic isolation, influencing the process of speciation directly.

Genetic Basis

Genotype and Phenotype

Natural selection acts on an organism's phenotype, or physical characteristics. Phenotype is determined by an organism's genetic make-up (genotype) and the environment in which the organism

lives. When different organisms in a population possess different versions of a gene for a certain trait, each of these versions is known as an allele. It is this genetic variation that underlies differences in phenotype. An example is the ABO blood type antigens in humans, where three alleles govern the phenotype.

Some traits are governed by only a single gene, but most traits are influenced by the interactions of many genes. A variation in one of the many genes that contributes to a trait may have only a small effect on the phenotype; together, these genes can produce a continuum of possible phenotypic values.

Directionality of Selection

When some component of a trait is heritable, selection alters the frequencies of the different alleles, or variants of the gene that produces the variants of the trait. Selection can be divided into three classes, on the basis of its effect on allele frequencies: directional, stabilizing, and purifying selection. Directional selection occurs when an allele has a greater fitness than others, so that it increases in frequency, gaining an increasing share in the population. This process can continue until the allele is fixed and the entire population shares the fitter phenotype. Far more common is stabilizing selection, which lowers the frequency of alleles that have a deleterious effect on the phenotype—that is, produce organisms of lower fitness. This process can continue until the allele is eliminated from the population. Purifying selection conserves functional genetic features, such as protein-coding genes or regulatory sequences, over time by selective pressure against deleterious variants.

Some forms of balancing selection do not result in fixation, but maintain an allele at intermediate frequencies in a population. This can occur in diploid species (with pairs of chromosomes) when heterozygous individuals (with just one copy of the allele) have a higher fitness than homozygous individuals (with two copies). This is called heterozygote advantage or over-dominance, of which the best-known example is the resistance to malaria in humans heterozygous for sickle-cell anaemia. Maintenance of allelic variation can also occur through disruptive or diversifying selection, which favours genotypes that depart from the average in either direction (that is, the opposite of over-dominance), and can result in a bimodal distribution of trait values. Finally, balancing selection can occur through frequency-dependent selection, where the fitness of one particular phenotype depends on the distribution of other phenotypes in the population. The principles of game theory have been applied to understand the fitness distributions in these situations, particularly in the study of kin selection and the evolution of reciprocal altruism.

Selection, Genetic Variation and Drift

A portion of all genetic variation is functionally neutral, producing no phenotypic effect or significant difference in fitness. Motoo Kimura's neutral theory of molecular evolution by genetic drift proposes that this variation accounts for a large fraction of observed genetic diversity. Neutral events can radically reduce genetic variation through population bottlenecks. which among other things can cause the founder effect in initially small new populations. When genetic variation does not result in differences in fitness, selection cannot directly affect the frequency of such variation. As a result, the genetic variation at those sites is higher than at sites where variation does influence fitness.However, after a period with no new mutations, the genetic variation at these sites is

eliminated due to genetic drift. Natural selection reduces genetic variation by eliminating maladapted individuals, and consequently the mutations that caused the maladaptation. At the same time, new mutations occur, resulting in a mutation–selection balance. The exact outcome of the two processes depends both on the rate at which new mutations occur and on the strength of the natural selection, which is a function of how unfavourable the mutation proves to be.

Genetic linkage occurs when the loci of two alleles are in close proximity on a chromosome. During the formation of gametes, recombination reshuffles the alleles. The chance that such a reshuffle occurs between two alleles is inversely related to the distance between them. Selective sweepsoccur when an allele becomes more common in a population as a result of positive selection. As the prevalence of one allele increases, closely linked alleles can also become more common by "genetic hitchhiking", whether they are neutral or even slightly deleterious. A strong selective sweep results in a region of the genome where the positively selected haplotype (the allele and its neighbours) are in essence the only ones that exist in the population. Selective sweeps can be detected by measuring linkage disequilibrium, or whether a given haplotype is overrepresented in the population. Since a selective sweep also results in selection of neighbouring alleles, the presence of a block of strong linkage disequilibrium might indicate a 'recent' selective sweep near the centre of the block.

Background selection is the opposite of a selective sweep. If a specific site experiences strong and persistent purifying selection, linked variation tends to be weeded out along with it, producing a region in the genome of low overall variability. Because background selection is a result of deleterious new mutations, which can occur randomly in any haplotype, it does not produce clear blocks of linkage disequilibrium, although with low recombination it can still lead to slightly negative linkage disequilibrium overall.

Impact

Darwin's ideas, along with those of Adam Smith and Karl Marx, had a profound influence on 19th century thought, including his radical claim that "elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner" evolved from the simplest forms of life by a few simple principles. This inspired some of Darwin's most ardent supporters—and provoked the strongest opposition. Natural selection had the power, according to Stephen Jay Gould, to "dethrone some of the deepest and most traditional comforts of Western thought", such as the belief that humans have a special place in the world.

In the words of the philosopher Daniel Dennett, "Darwin's dangerous idea" of evolution by natural selection is a "universal acid," which cannot be kept restricted to any vessel or container, as it soon leaks out, working its way into ever-wider surroundings. Thus, in the last decades, the concept of natural selection has spread from evolutionary biology to other disciplines, including evolutionary computation, quantum Darwinism, evolutionary economics, evolutionary epistemology, evolutionary psychology, and cosmological natural selection. This unlimited applicability has been called universal Darwinism.

Origin of Life

How life originated from inorganic matter remains an unresolved problem in biology. One prominent hypothesis is that life first appeared in the form of short self-replicating RNA polymers. On

this view, life may have come into existence when RNA chains first experienced the basic conditions, as conceived by Charles Darwin, for natural selection to operate. These conditions are: heritability, variation of type, and competition for limited resources. The fitness of an early RNA replicator would likely have been a function of adaptive capacities that were intrinsic (i.e., determined by the nucleotide sequence) and the availability of resources. The three primary adaptive capacities could logically have been: (1) the capacity to replicate with moderate fidelity (giving rise to both heritability and variation of type), (2) the capacity to avoid decay, and (3) the capacity to acquire and process resources. These capacities would have been determined initially by the folded configurations (including those configurations with ribozyme activity) of the RNA replicators that, in turn, would have been encoded in their individual nucleotide sequences.

Cell and Molecular Biology

In 1881, the embryologist Wilhelm Roux published Der Kampf der Theile im Organismus (The Struggle of Parts in the Organism) in which he suggested that the development of an organism results from a Darwinian competition between the parts of the embryo, occurring at all levels, from molecules to organs. In recent years, a modern version of this theory has been proposed by Jean-Jacques Kupiec. According to this cellular Darwinism, random variation at the molecular level generates diversity in cell types whereas cell interactions impose a characteristic order on the developing embryo.

Social and Psychological Theory

The social implications of the theory of evolution by natural selection also became the source of continuing controversy. Friedrich Engels, a German political philosopher and co-originator of the ideology of communism, wrote in 1872 that "Darwin did not know what a bitter satire he wrote on mankind, and especially on his countrymen, when he showed that free competition, the struggle for existence, which the economists celebrate as the highest historical achievement, is the normal state of the animal kingdom." Herbert Spencer and the eugenics advocate Francis Galton's interpretation of natural selection as necessarily progressive, leading to supposed advances in intelligence and civilisation, became a justification for colonialism, eugenics, and social Darwinism. For example, in 1940, Konrad Lorenz, in writings that he subsequently disowned, used the theory as a justification for policies of the Nazi state. He wrote "selection for toughness, heroism, and social utility must be accomplished by some human institution, if mankind, in default of selective factors, is not to be ruined by domestication-induced degeneracy. The racial idea as the basis of our state has already accomplished much in this respect." Others have developed ideas that human societies and culture evolve by mechanisms analogous to those that apply to evolution of species.

More recently, work among anthropologists and psychologists has led to the development of sociobiology and later of evolutionary psychology, a field that attempts to explain features of human psychology in terms of adaptation to the ancestral environment. The most prominent example of evolutionary psychology, notably advanced in the early work of Noam Chomsky and later by Steven Pinker, is the hypothesis that the human brain has adapted to acquire the grammatical rules of natural language. Other aspects of human behaviour and social structures, from specific cultural norms such as incest avoidance to broader patterns such as gender roles, have been hypothesised to have similar origins as adaptations to the early environment in which modern humans evolved.

By analogy to the action of natural selection on genes, the concept of memes—"units of cultural transmission," or culture's equivalents of genes undergoing selection and recombination—has arisen, first described in this form by Richard Dawkins in 1976 and subsequently expanded upon by philosophers such as Daniel Dennett as explanations for complex cultural activities, including human consciousness.

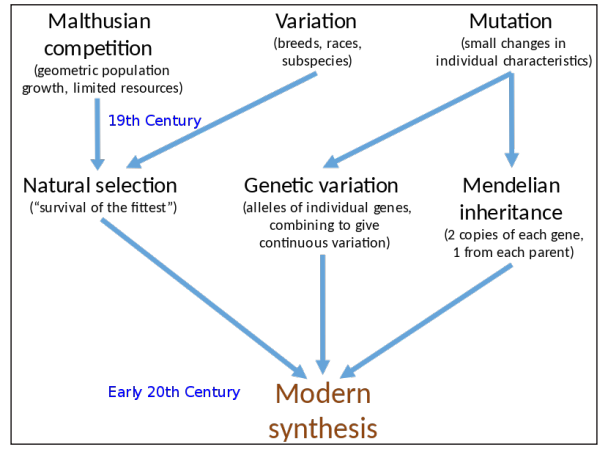
Information and Systems Theory

In 1922, Alfred J. Lotka proposed that natural selection might be understood as a physical principle that could be described in terms of the use of energy by a system, a concept later developed by Howard T. Odum as the maximum power principle in thermodynamics, whereby evolutionary systems with selective advantage maximise the rate of useful energy transformation.

The principles of natural selection have inspired a variety of computational techniques, such as "soft" artificial life, that simulate selective processes and can be highly efficient in 'adapting' entities to an environment defined by a specified fitness function. For example, a class of heuristic optimisationalgorithms known as genetic algorithms, pioneered by John Henry Holland in the 1970s and expanded upon by David E. Goldberg, identify optimal solutions by simulated reproduction and mutation of a population of solutions defined by an initial probability distribution. Such algorithms are particularly useful when applied to problems whose energy landscape is very rough or has many local minima.

Modern Synthesis

The modern synthesis was the early 20th-century synthesis reconciling Charles Darwin's theory of evolution and Gregor Mendel's ideas on heredity in a joint mathematical framework. Julian Huxley coined the term in his 1942 book, Evolution: The Modern Synthesis.



Several major ideas about evolution came together in the population genetics of the early 20th century to form the modern synthesis, including genetic variation, natural selection, and particulate (Mendelian) inheritance. This ended the eclipse of Darwinism and supplanted a variety of non-Darwinian theories of evolution.

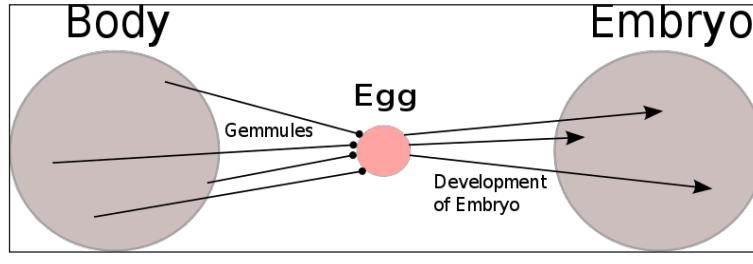
The 19th century ideas of natural selection and Mendelian geneticswere put together with population genetics, early in the twentieth century. The modern synthesis also addressed the relationship between the broad-scale changes of macroevolution seen by palaeontologists and the small-scale microevolution of local populations of living organisms. The synthesis was defined differently by its founders, with Ernst Mayrin 1959, G. Ledyard Stebbins in 1966 and Theodosius Dobzhansky in 1974 offering differing numbers of basic postulates, though they all included natural selection, working on heritable variation supplied by mutation. Other major figures in the synthesis included E. B. Ford, Bernhard Rensch, Ivan Schmalhausen, and George Gaylord Simpson. An early event in the modern synthesis was R. A. Fisher's 1918 paper on mathematical population genetics, but William Bateson, and separately Udny Yule, were already starting to show how Mendelian genetics could work in evolution in 1902.

Different syntheses followed, accompanying the gradual breakup of the early 20th century synthesis, including with social behaviour in E. O. Wilson's sociobiology in 1975, evolutionary developmental biology's integration of embryology with genetics and evolution, starting in 1977, and Massimo Pigliucci's proposed extended evolutionary synthesis of 2007. In the view of the evolutionary biologist Eugene Koonin in 2009, the modern synthesis will be replaced by a 'post-modern' synthesis that will include revolutionary changes in molecular biology, the study of prokaryotes and the resulting tree of life, and genomics.

Developments Leading up to the Synthesis

Darwin's Evolution by Natural Selection

Charles Darwin's 1859 book *On the Origin of Species* was successful in convincing most biologists that evolution had occurred, but was less successful in convincing them that natural selection was its primary mechanism. In the 19th and early 20th centuries, variations of Lamarckism (inheritance of acquired characteristics), orthogenesis(progressive evolution), saltationism (evolution by jumps) and mutationism (evolution driven by mutations) were discussed as alternatives. Alfred Russel Wallace advocated a selectionist version of evolution, and unlike Darwin completely rejected Lamarckism. In 1880, Wallace's view was labelled neo-Darwinism by Samuel Butler.

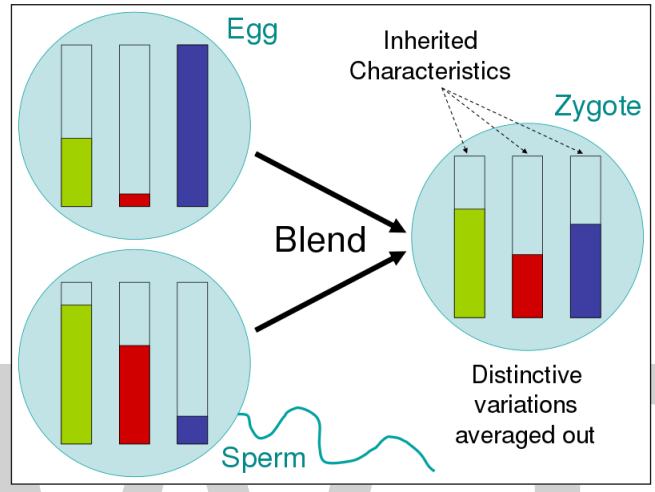


Darwin's pangenesis theory. Every part of the body emits tiny gemmules which migrate to the gonads and contribute to the next generation via the fertilised egg. Changes to the body during an organism's life would be inherited, as in Lamarckism.

The Eclipse of Darwinism

From the 1880s onwards, there was a widespread belief among biologists that Darwinian evolution was in deep trouble. This eclipse of Darwinism (in Julian Huxley's phrase) grew out of the weaknesses in Darwin's account, written with an incorrect view of inheritance. Darwin himself believed

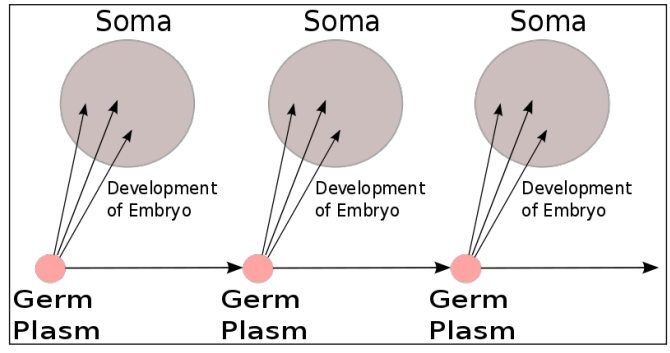
in blending inheritance, which implied that any new variation, even if beneficial, would be weakened by 50% at each generation, as the engineer Fleeming Jenkin correctly noted in 1868. This in turn meant that small variations would not survive long enough to be selected. Blending would therefore directly oppose natural selection. In addition, Darwin and others considered Lamarckian inheritance of acquired characteristics entirely possible, and Darwin's 1868 theory of pangenesis, with contributions to the next generation (gemmules) flowing from all parts of the body, actually implied Lamarckism as well as blending.



Blending inheritance, implied by pangenesis, causes the averaging out of every characteristic, which as the engineer Fleeming Jenkin pointed out, would make evolution by natural selection impossible.

Weismann's Germ Plasm

August Weismann's idea, set out in his 1892 book *Das Keimplasma: eine Theorie der Vererbung* (The Germ Plasm: a Theory of Inheritance), was that the hereditary material, which he called the germ plasm, and the rest of the body (the soma) had a one-way relationship: the germ-plasm formed the body, but the body did not influence the germ-plasm, except indirectly in its participation in a population subject to natural selection. If correct, this made Darwin's pangenesis wrong, and Lamarckian inheritance impossible. His experiment on mice, cutting off their tails and showing that their offspring had normal tails, demonstrated that inheritance was 'hard'. He argued strongly and dogmatically for Darwinism and against Lamarckism, polarising opinions among other scientists. This increased anti-Darwinian feeling, contributing to its eclipse.

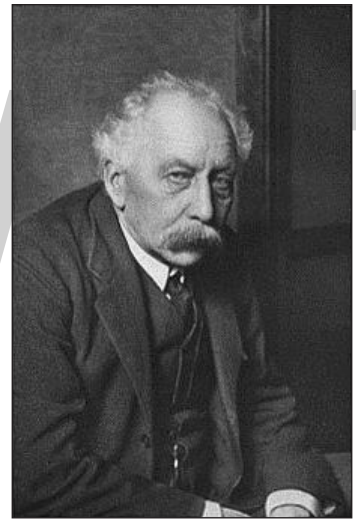


August Weismann's germ plasm theory. The hereditary material, the germ plasm, is confined to the gonads and the gametes. Somatic cells (of the body) develop afresh in each generation from the germ plasm.

Disputed Beginnings

Genetics, Mutationism and Biometrics

While carrying out breeding experiments to clarify the mechanism of inheritance in 1900, Hugo de Vries and Carl Correns independently rediscovered Gregor Mendel's work. News of this reached William Bateson in England, who reported on the paper during a presentation to the Royal Horticultural Society in May 1900. In Mendelian inheritance, the contributions of each parent retain their integrity rather than blending with the contribution of the other parent. In the case of a cross between two true-breeding varieties such as Mendel's round and wrinkled peas, the first-generation offspring are all alike, in this case all round. Allowing these to cross, the original characteristics reappear (segregation): about 3/4 of their offspring are round, 1/4 wrinkled. There is a discontinuity between the appearance of the offspring; de Vries coined the term allele for a variant form of an inherited characteristic. This reinforced a major division of thought, already present in the 1890s, between gradualists who followed Darwin, and saltationists such as Bateson.



William Bateson championed Mendelism.

The two schools were the Mendelians, such as Bateson and de Vries, who favoured mutationism, evolution driven by mutation, based on genes whose alleles segregated discretely like Mendel's peas; and the biometric school, led by Karl Pearson and Walter Weldon. The biometricians argued vigorously against mutationism, saying that empirical evidence indicated that variation was continuous in most organisms, not discrete as Mendelism seemed to predict; they wrongly believed that Mendelism inevitably implied evolution in discontinuous jumps.

A traditional view is that the biometricians and the Mendelians rejected natural selection and argued for their separate theories for 20 years, the debate only resolved by the development of population genetics. A more recent view is that Bateson, de Vries, Thomas Hunt Morgan and Reginald Punnett had by 1918 formed a synthesis of Mendelism and mutationism. The understanding achieved by these geneticists spanned the action of natural selection on alleles (alternative forms of a gene), the Hardy-Weinberg equilibrium, the evolution of continuously-varying traits (like height), and the probability that a new mutation will become fixed. In this view, the early geneticists accepted natural selection but rejected Darwin's non-Mendelian ideas about variation and

heredity, and the synthesis began soon after 1900. The traditional claim that Mendelians rejected the idea of continuous variation is false; as early as 1902, Bateson and Saunders wrote that "If there were even so few as, say, four or five pairs of possible allelomorphs, the various homo- and hetero-zygous combinations might, on seriation, give so near an approach to a continuous curve, that the purity of the elements would be unsuspected". Also in 1902, the statistician Udny Yule showed mathematically that given multiple factors, Mendel's theory enabled continuous variation. Yule criticised Bateson's approach as confrontational, but failed to prevent the Mendelians and the biometricians from falling out.

Karl Pearson led the biometric school.

Castle's Hooded Rats

Starting in 1906, William Castle carried out a long study of the effect of selection on coat colour in rats. The piebald or hooded pattern was recessive to the grey wild type. He crossed hooded rats with the black-backed Irish type, and then back-crossed the offspring with pure hooded rats. The dark stripe on the back was bigger. He then tried selecting different groups for bigger or smaller stripes for 5 generations, and found that it was possible to change the characteristics way beyond the initial range of variation. This effectively refuted de Vries's claim that continuous variation was caused by the environment and could not be inherited. By 1911 Castle noted that the results could be explained by Darwinian selection on heritable variation of a sufficient number of Mendelian genes.

Morgan's Fruit Flies

Thomas Hunt Morgan began his career in genetics as a saltationist, and started out trying to demonstrate that mutations could produce new species in fruit flies. However, the experimental work at his lab with the fruit fly, *Drosophila melanogaster* demonstrated that rather than creating new species in a single step, mutations increased the supply of genetic variation in the population. By 1912, after years of work on the genetics of fruit flies, Morgan showed that these insects had many small Mendelian factors (discovered as mutant flies) on which Darwinian evolution could work as if variation was fully continuous. The way was open for geneticists to conclude that Mendelism supported Darwinism.

An Obstruction: Woodger's Positivism

The theoretical biologist and philosopher of biology Joseph Henry Woodger led the introduction of positivism into biology with his 1929 book *Biological Principles*. He saw a mature science as being characterised by a framework of hypotheses that could be verified by facts established by experiments. He criticised the traditional natural history style of biology, including the study of evolution, as immature science, since it relied on narrative. Woodger set out to play for biology the role of Robert Boyle's 1661 *Sceptical Chymist*, intending to convert the subject into a formal, unified science, and ultimately, following the Vienna Circle of logical positivists like Otto Neurath and Rudolf Carnap, to reduce biology to physics and chemistry. His efforts stimulated the biologist J. B. S. Haldane to push for the axiomatisation of biology, and by influencing thinkers such as Huxley, helped to bring about the modern synthesis. The positivist climate made natural history unfashionable, and in America, research and university-level teaching on evolution declined almost to nothing by the late 1930s. The Harvard physiologist William John Crozier told his students that evolution was not even a science: "You can't experiment with two million years."

The tide of opinion turned with the adoption of mathematical modelling and controlled experimentation in population genetics, combining genetics, ecology and evolution in a framework acceptable to positivism.

Events in the Synthesis

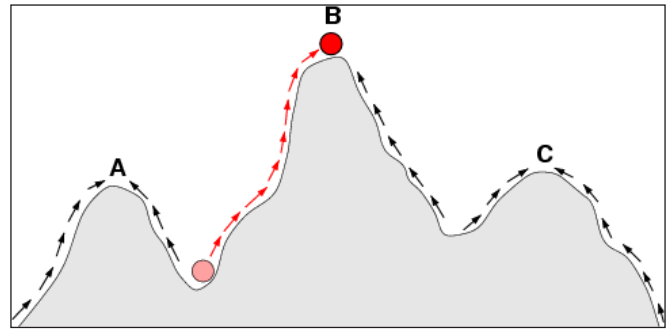
Fisher and Haldane's Mathematical Population Genetics

In 1918, R. A. Fisher wrote the paper "The Correlation between Relatives on the Supposition of Mendelian Inheritance," which showed mathematically how continuous variation could result from a number of discrete genetic loci. In this and subsequent papers culminating in his 1930 book *The Genetical Theory of Natural Selection*, Fisher showed how Mendelian genetics was consistent with the idea of evolution driven by natural selection.During the 1920s, a series of papers by J. B. S. Haldane applied mathematical analysis to real-world examples of natural selection, such as the evolution of industrial melanism in peppered moths.Haldane established that natural selection could work even faster than Fisher had assumed. Both workers, and others such as Dobzhansky and Wright, explicitly intended to bring biology up to the philosophical standard of the physical sciences, making it firmly based in mathematical modelling, its predictions confirmed by experiment. Natural selection, once considered hopelessly unverifiable speculation about history, was becoming predictable, measurable, and testable.

De Beer's Embryology

The traditional view is that developmental biology played little part in the modern synthesis, but in his 1930 book *Embryos and Ancestors*, the evolutionary embryologist Gavin de Beer anticipated evolutionary developmental biology by showing that evolution could occur by heterochrony,such as in the retention of juvenile features in the adult. This, de Beer argued, could cause apparently sudden changes in the fossil record, since embryos fossilise poorly. As the gaps in the fossil record had been used as an argument against Darwin's gradualist evolution, de Beer's explanation supported the Darwinian position. However, despite de Beer, the modern synthesis largely ignored

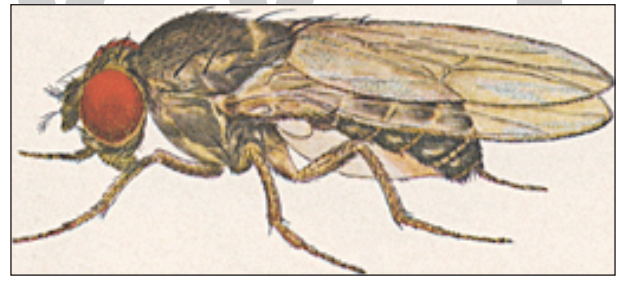
embryonic development to explain the form of organisms, since population genetics appeared to be an adequate explanation of how forms evolved.Wright's Adaptive Landscape



Sewall Wright introduced the idea of a fitness landscape with local optima.

The population geneticist Sewall Wright focused on combinations of genes that interacted as complexes, and the effects of inbreeding on small relatively isolated populations, which could be subject to genetic drift. In a 1932 paper, he introduced the concept of an adaptive landscape in which phenomena such as cross breeding and genetic drift in small populations could push them away from adaptive peaks, which would in turn allow natural selection to push them towards new adaptive peaks. Wright's model would appeal to field naturalists such as Theodosius Dobzhansky and Ernst Mayr who were becoming aware of the importance of geographical isolation in real world populations. The work of Fisher, Haldane and Wright helped to found the discipline of theoretical population genetics.

Dobzhansky's Evolutionary Genetics

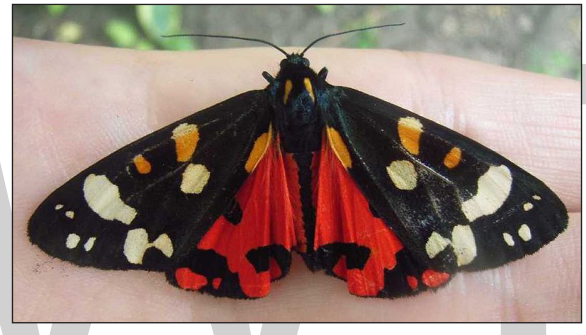


Drosophila pseudoobscura, the fruit fly which served as Theodosius Dobzhansky's model organism.

Theodosius Dobzhansky, an emigrant from the Soviet Unionto the United States, who had been a postdoctoral worker in Morgan's fruit fly lab, was one of the first to apply genetics to natural populations. He worked mostly with *Drosophila pseudoobscura*. He says pointedly: "Russia has a variety of climates from the Arctic to sub-tropical Exclusively laboratory workers who neither possess nor wish to have any knowledge of living beings in nature were and are in a minority." Not surprisingly, there were other Russiangeneticists with similar ideas, though for some time their work was known to only a few in the West. His 1937 work *Genetics and the Origin of Species* was a key step in bridging the gap between population geneticists and field naturalists. It presented the conclusions reached by Fisher, Haldane, and especially Wright in their highly mathematical papers in a form that was easily accessible to others. Further, Dobzhansky asserted that evolution was based on material genes, arranged in a string on physical hereditary structures, the chromosomes, and linked more or less strongly to each other according to their physical distances from each

other on the chromosomes. As with Haldane and Fisher, Dobzhansky's "evolutionary genetics" was a genuine science, now unifying cell biology, genetics, and both micro- and macroevolution. His work emphasized that real world populations had far more genetic variability than the early population geneticists had assumed in their models, and that genetically distinct sub-populations were important. Dobzhansky argued that natural selection worked to maintain genetic diversity as well as driving change. He was influenced by his exposure in the 1920s to the work of Sergei Chetverikov, who had looked at the role of recessive genes in maintaining a reservoir of genetic variability in a population before his work was shut down by the rise of Lysenkoism in the Soviet Union. By 1937, Dobzhansky was able to argue that mutations were the main source of evolutionary changes and variability, along with chromosome rearrangements, effects of genes on their neighbours during development, and polyploidy. Next, genetic drift, selection, migration, and geographical isolation could change gene frequencies. Thirdly, mechanisms like ecological or sexual isolation and hybrid sterility could fix the results of the earlier processes.

Ford's Ecological Genetics



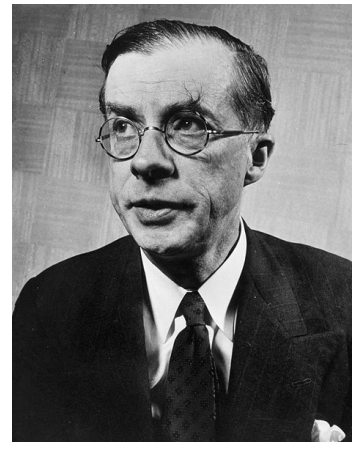
E. B. Ford studied polymorphism in the scarlet tiger moth for many years.

E. B. Ford was an experimental naturalist who wanted to test natural selection in nature, virtually inventing the field of ecological genetics. His work on natural selection in wild populations of butterflies and moths was the first to show that predictions made by R. A. Fisher were correct. In 1940, he was the first to describe and define genetic polymorphism, and to predict that human blood group polymorphisms might be maintained in the population by providing some protection against disease. His 1949 book *Mendelism and Evolution* helped to persuade Dobzhansky to change the emphasis in the third edition of his famous textbook *Genetics and the Origin of Species* from drift to selection.

Schmalhausen's Stabilizing Selection

Ivan Schmalhausen developed the theory of stabilizing selection, the idea that selection can preserve a trait at some value, publishing a paper in Russian titled "Stabilizing selection and its place among factors of evolution" in 1941 and a monograph *Factors of Evolution: The Theory of Stabilizing Selection* in 1945. He developed it from J. M. Baldwin's 1902 concept that changes induced by the environment will ultimately be replaced by hereditary changes (including the Baldwin effect on behaviour), following that theory's implications to their Darwinian conclusion, and bringing him into conflict with Lysenkoism. Schmalhausen observed that stabilizing selection would remove most variations from the norm, most mutations being harmful. Dobzhansky called the work "an important missing link in the modern view of evolution".

Huxley's Popularising Synthesis



Julian Huxley presented a serious but popularising version of the theory in his 1942 book *Evolution: The Modern Synthesis*.

In 1942, Julian Huxley's serious but popularising *Evolution: The Modern Synthesis* introduced a name for the synthesis and intentionally set out to promote a "synthetic point of view" on the evolutionary process. He imagined a wide synthesis of many sciences: genetics, developmental physiology, ecology, systematics, palaeontology, cytology, and mathematical analysis of biology, and assumed that evolution would proceed differently in different groups of organisms according to how their genetic material was organised and their strategies for reproduction, leading to progressive but varying evolutionary trends. His vision was of an "evolutionary humanism", with a system of ethics and a meaningful place for "Man" in the world grounded in a unified theory of evolution which would demonstrate progress leading to man at its summit. Natural selection was in his view a "fact of nature capable of verification by observation and experiment", while the "period of synthesis" of the 1920s and 1930s had formed a "more unified science", rivalling physics and enabling the "rebirth of Darwinism".

However, the book was not the research text that it appeared to be. In the view of the philosopher of science Michael Ruse, and in Huxley's own opinion, Huxley was "a generalist, a synthesizer of ideas, rather than a specialist". Ruse observes that Huxley wrote as if he were adding empirical evidence to the mathematical framework established by Fisher and the population geneticists, but that this was not so. Huxley avoided mathematics, for instance not even mentioning Fisher's fundamental theorem of natural selection. Instead, Huxley used a mass of examples to demonstrate that natural selection is powerful, and that it works on Mendelian genes. The book was successful in its goal of persuading readers of the reality of evolution, effectively illustrating topics such as island biogeography, speciation, and competition. Huxley further showed that the appearance of long-term orthogenetic trends – predictable directions for evolution – in the fossil record were readily explained as allometric growth (since parts are interconnected). All the same, Huxley did not reject orthogenesis out of hand, but maintained a belief in progress all his life, with *Homo sapiens* as the end point, and he had since 1912 been influenced by the vitalist philosopher Henri Bergson, though in public he maintained an atheistic position on evolution. Huxley's belief in progress within evolution and evolutionary humanism was shared in various forms by Dobzhansky, Mayr, Simpson and Stebbins, all of them writing about "the future of

Mankind". Both Huxley and Dobzhansky admired the palaeontologist priest Pierre Teilhard de Chardin, Huxley writing the introduction to Teilhard's 1955 book on orthogenesis, *The Phenomenon of Man*. This vision required evolution to be seen as the central and guiding principle of biology.

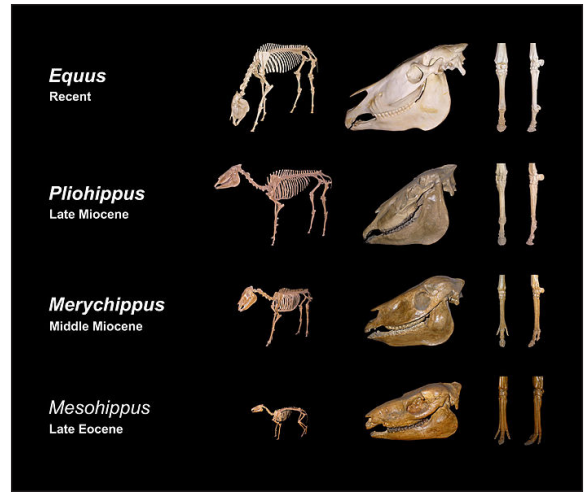
Mayr's Allopatric Speciation

Ernst Mayr argued that geographic isolation was needed to provide sufficient reproductive isolation for new species to form.

Ernst Mayr's key contribution to the synthesis was *Systematics and the Origin of Species*, published in 1942.It asserted the importance of and set out to explain population variation in evolutionary processes including speciation. He analysed in particular the effects of polytypic-species, geographic variation, and isolation by geographic and other means. Mayr emphasized the importance of allopatric speciation, where geographically isolated sub-populations diverge so far that reproductive isolation occurs. He was skeptical of the reality of sympatric speciationbelieving that geographical isolation was a prerequisite for building up intrinsic (reproductive) isolating mechanisms. Mayr also introduced the biological species concept that defined a species as a group of interbreeding or potentially interbreeding populations that were reproductively isolated from all other populations. Before he left Germany for the United States in 1930, Mayr had been influenced by the work of the German biologist Bernhard Rensch, who in the 1920s had analyzed the geographic distribution of polytypic species, paying particular attention to how variations between populations correlated with factors such as differences in climate.

Simpson's Palaeontology

George Gaylord Simpson was responsible for showing that the modern synthesis was compatible with palaeontology in his 1944 book *Tempo and Mode in Evolution*. Simpson's work was crucial because so many palaeontologists had disagreed, in some cases vigorously, with the idea that natural selection was the main mechanism of evolution. It showed that the trends of linear progression (in for example the evolution of the horse) that earlier palaeontologists had used as support for neo-Lamarckism and orthogenesis did not hold up under careful examination. Instead the fossil record was consistent with the irregular, branching, and non-directional pattern predicted by the modern synthesis.



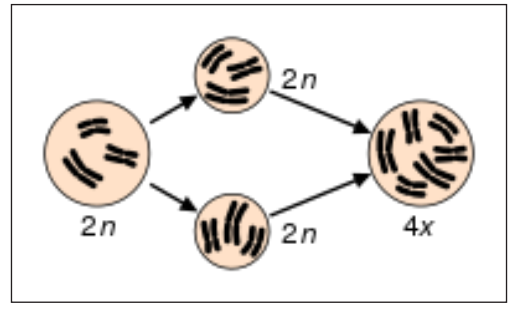
George Gaylord Simpson argued against the naive view that evolution such as of the horse took place in a "straight-line". He noted that any chosen line is one path in a complex branching tree, natural selection having no imposed direction.

The Society for the Study of Evolution

During the war, Mayr edited a series of bulletins of the Committee on Common Problems of Genetics, Paleontology, and Systematics, formed in 1943, reporting on discussions of a "synthetic attack" on the interdisciplinary problems of evolution. In 1946, the committee became the Society for the Study of Evolution, with Mayr, Dobzhansky and Sewall Wright the first of the signatories. Mayr became the editor of its journal, *Evolution*. From Mayr and Dobzhansky's point of view, suggests the historian of science Betty Smocovitis, Darwinism was reborn, evolutionary biology was legitimised, and genetics and evolution were synthesised into a newly unified science. Everything fitted in to the new framework, except "heretics" like Richard Goldschmidt who annoyed Mayr and Dobzhansky by insisting on the possibility of speciation by macromutation, creating "hopeful monsters". The result was "bitter controversy".

Stebbins's Botany

The botanist G. Ledyard Stebbins extended the synthesis to encompass botany. He described the important effects on speciation of hybridization and polyploidy in plants in his 1950 book *Variation and Evolution in Plants*. These permitted evolution to proceed rapidly at times, polyploidy in particular evidently being able to create new species effectively instantaneously.



Speciation via polyploidy: a diploidcell may fail to separate during meiosis, producing diploid gameteswhich self-fertilize to produce a fertile tetraploid zygote that cannot interbreed with its parent species.

Definitions by the Founders

The modern synthesis was defined differently by its various founders, with differing numbers of basic postulates, as shown in the table:

Definitions of the modern synthesis by its founders, as they numbered them			
Component	Mayr 1959	Stebbins, 1966	Dobzhansky, 1974
Mutation	(1) Randomness in all events that produce new genotypes, e.g. mutation.	(1) A source of variability, but not of direction.	(1) Yields genetic raw materials.
Recombination	(2) Randomness in recombination, fertilisation.	(2) A source of variability, but not of direction.	
Chromosomal organisation		(3) Affects genetic linkage, arranges variation in gene pool.	
Natural selection	(3) is only direction-giving factor, as seen in adaptations to physical and biotic environment.	(4) Guides changes to gene pool.	(2) Constructs evolutionary changes from genetic raw materials.
Reproductive isolation		(5) Limits direction in which selection can guide the population	(3) Makes divergence irreversible in sexual organisms.

After the Synthesis

After the synthesis, evolutionary biology continued to develop with major contributions from workers including W. D. Hamilton, George C. Williams, E. O. Wilson, Edward B. Lewis and others.

Hamilton's Inclusive Fitness

In 1964, W. D. Hamilton published two papers on "The Genetical Evolution of Social Behaviour". These defined inclusive fitness as the number of offspring equivalents an individual rears, rescues or otherwise supports through its behaviour. This was contrasted with personal reproductive fitness, the number of offspring that the individual directly begets. Hamilton, and others such as John Maynard Smith, argued that a gene's success consisted in maximising the number of copies of itself, either by begetting them or by indirectly encouraging begetting by related individuals who shared the gene, the theory of kin selection.

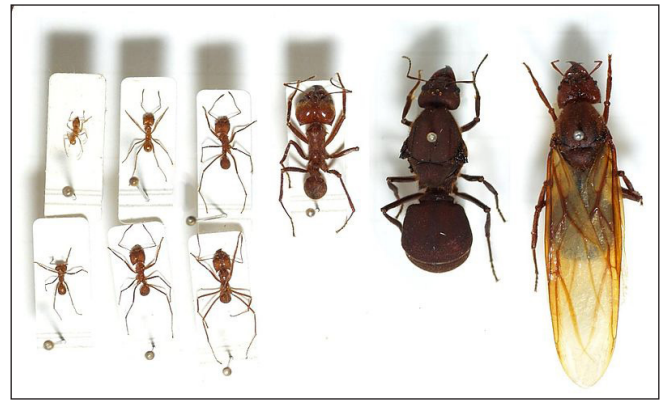
Williams's Gene-centred Evolution

In 1966, George C. Williams published *Adaptation and Natural Selection*, outlined a gene-centred view of evolution following Hamilton's concepts, disputing the idea of evolutionary progress, and attacking the then widespread theory of group selection. Williams argued that natural selection worked by changing the frequency of alleles, and could not work at the level of groups. Gene-centred evolution was popularised by Richard Dawkins in his 1976 book *The Selfish Gene* and developed in his more technical writings.

Wilson's Sociobiology

In 1975, E. O. Wilson published his controversial book *Sociobiology: The New Synthesis*, the subtitle alluding to the modern synthesis as he attempted to bring the study of animal society into

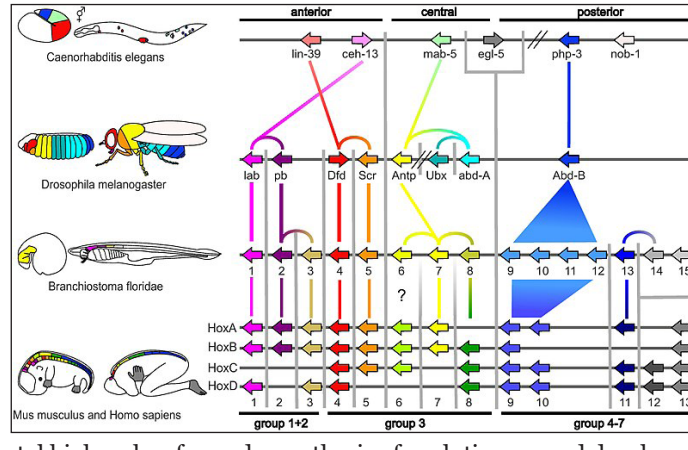
the evolutionary fold. This appeared radically new, although Wilson was following Darwin, Fisher, Dawkins and others. Critics such as Gerhard Lenskinoted that he was following Huxley, Simpson and Dobzhansky's approach, which Lenski considered needlessly reductive as far as human society was concerned. By 2000, the proposed discipline of sociobiology had morphed into the relatively well-accepted discipline of evolutionary psychology.



Ant societies have evolved elaborate caste structures, widely different in size and function.

Lewis's Homeotic Genes

In 1977, recombinant DNA technology enabled biologists to start to explore the genetic control of development. The growth of evolutionary developmental biology from 1978, when Edward B. Lewis discovered homeotic genes, showed that many so-called toolkit genes act to regulate development, influencing the expression of other genes. It also revealed that some of the regulatory genes are extremely ancient, so that animals as different as insects and mammals share control mechanisms; for example, the *Pax6* gene is involved in forming the eyes of mice and of fruit flies. Such deep homology provided strong evidence for evolution and indicated the paths that evolution had taken.



Evolutionary developmental biology has formed a synthesis of evolutionary and developmental biology, discovering deep homology between the embryogenesis of such different animals as insects and vertebrates.

Later Syntheses

In 1982, a historical note on a series of evolutionary biology books could state without qualification that evolution is the central organizing principle of biology. Smocovitis commented on this that

"What the architects of the synthesis had worked to construct had by 1982 become a matter of fact", adding in a footnote that "the centrality of evolution had thus been rendered tacit knowledge, part of the received wisdom of the profession".

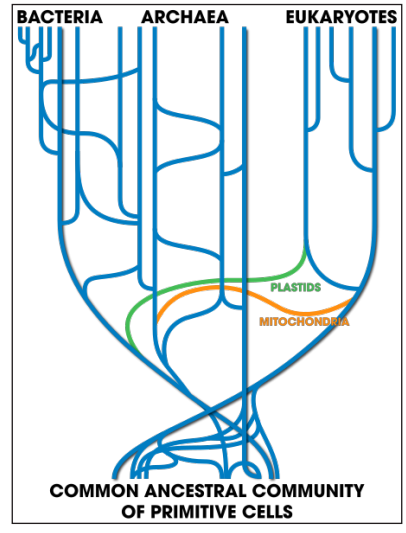
By the late 20th century, however, the modern synthesis was showing its age, and fresh syntheses to remedy its defects and fill in its gaps were proposed from different directions. These have included such diverse fields as the study of society, developmental biology, epigenetics, molecular biology, microbiology, genomics, symbiogenesis, and horizontal gene transfer. The physiologist Denis Noble argues that these additions render neo-Darwinism in the sense of the early 20th century's modern synthesis "at the least, incomplete as a theory of evolution", and one that has been falsified by later biological research.

Michael Rose and Todd Oakley note that evolutionary biology, formerly divided and "Balkanized", has been brought together by genomics. It has in their view discarded at least five common assumptions from the modern synthesis, namely that the genome is always a well-organised set of genes; that each gene has a single function; that species are well adapted biochemically to their ecological niches; that species are the durable units of evolution, and all levels from organism to organ, cell and molecule within the species are characteristic of it; and that the design of every organism and cell is efficient. They argue that the "new biology" integrates genomics, bioinformatics, and evolutionary genetics into a general-purpose toolkit for a "Postmodern Synthesis".

Pigliucci's Extended Evolutionary Synthesis

In 2007, more than half a century after the modern synthesis, Massimo Pigliucci called for an extended evolutionary synthesis to incorporate aspects of biology that had not been included or had not existed in the mid-20th century. It revisits the relative importance of different factors, challenges assumptions made in the modern synthesis, and adds new factors such as multilevel selection, transgenerational epigenetic inheritance, niche construction, and evolvability.

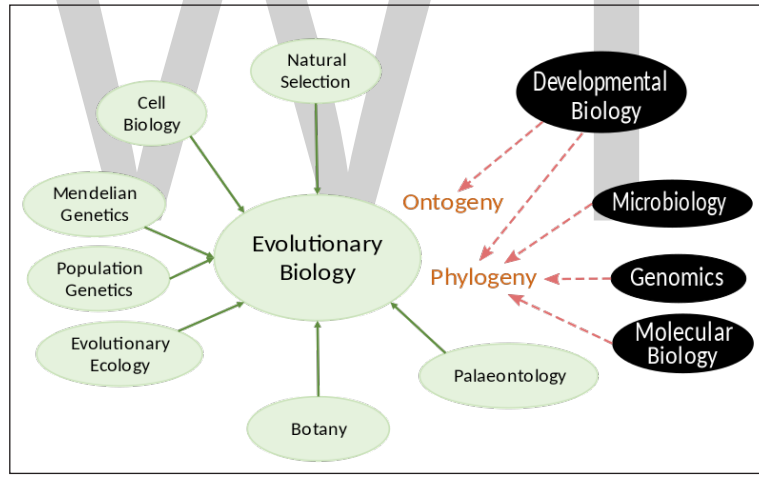
Koonin's 'Post-modern' Evolutionary Synthesis



A 21st century tree of life showing horizontal gene transfers among prokaryotes and the saltational endosymbiosis events that created the eukaryotes, neither fitting into the 20th century's modern synthesis.

In 2009, Darwin's 200th anniversary, the *Origin of Species*'150th, and the 200th of Lamarck's "early evolutionary synthesis", *Philosophie Zoologique*, the evolutionary biologist Eugene Koonin stated that while "the edifice of the [early 20th century] Modern Synthesis has crumbled, apparently, beyond repair", a new 21st century synthesis could be glimpsed. Three interlocking revolutions had, he argued, taken place in evolutionary biology: molecular, microbiological, and genomic. The molecular revolutionincluded the neutral theory, that most mutations are neutral and that purifying selection happens more often than the positive form, and that all current life evolved from a single common ancestor. In microbiology, the synthesis has expanded to cover the prokaryotes, using ribosomal RNA to form a tree of life. Finally, genomics brought together the molecular and microbiological syntheses, noting that a molecular view shows that the tree of life is problematic. In particular, horizontal gene transfer between bacteria means that prokaryotes freely share genes, challenging Mayr's foundational definition of species. Further, horizontal gene transfer, gene duplication, and "momentous events" like endosymbiosis enable evolution to proceed in sudden jumps, ending the old gradualist-saltationist debate by showing that on this point Darwin's gradualism was wrong. The idea of progress in biology, too, is seen to be wrong, along with the modern synthesis belief in pan-adaptationism, that everything is optimally adapted: genomes plainly are not. Many of these points had already been made by other researchers such as Ulrich Kutschera and Karl J. Niklas.

Towards a Replacement Synthesis



Inputs to the modern synthesis, with other topics (inverted colours) such as developmental biology that were not joined with evolutionary biology until the turn of the 21st century.

Biologists, alongside scholars of the history and philosophy of biology, have continued to debate the need for, and possible nature of, a replacement synthesis. For example, in 2017 Philippe Huneman and Denis M. Walsh stated in their book *Challenging the Modern Synthesis*that numerous theorists had pointed out that the disciplines of embryological developmental theory, morphology, and ecology had been omitted. They noted that all such arguments amounted to a continuing desire to replace the modern synthesis with one that united "all biological fields of research related to evolution, adaptation, and diversity in a single theoretical frame." They observed further that there are two groups of challenges to the way the modern synthesis viewed inheritance. The first is that other modes such as epigenetic inheritance, phenotypic plasticity, the Baldwin effect, and the maternal effect allow new characteristics to arise and be passed on, and for the genes to catch up with

the new adaptations later. The second is that all such mechanisms are part, not of an inheritance system, but a developmental system: the fundamental unit is not a discrete selfishly competing gene, but a collaborating system that works at all levels from genes and cells to organisms and cultures to guide evolution.

Evolvability

Evolvability is defined as the capacity of a system for adaptive evolution. Evolvability is the ability of a population of organisms to not merely generate genetic diversity, but to generate *adaptive* genetic diversity, and thereby evolve through natural selection.

In order for a biological organism to evolve by natural selection, there must be a certain minimum probability that new, heritable variants are beneficial. Random mutations, unless they occur in DNA sequences with no function, are expected to be mostly detrimental. Beneficial mutations are always rare, but if they are too rare, then adaptation cannot occur. Early failed efforts to evolve computer programs by random mutation and selection showed that evolvability is not a given, but depends on the representation of the program as a data structure, because this determines how changes in the program map to changes in its behavior. Analogously, the evolvability of organisms depends on their genotype–phenotype map. This means that genomes are structured in ways that make beneficial changes more likely. This has been taken as evidence that evolution has created not just fitter organisms, but populations of organisms that are better able to evolve.

Generating more Variation

More heritable phenotypic variation means more evolvability. While mutation is the ultimate source of heritable variation, its permutations and combinations also make a big difference. Sexual reproduction generates more variation (and thereby evolvability) relative to asexual reproduction. Evolvability is further increased by generating more variation when an organism is stressed, and thus likely to be less well adapted, but less variation when an organism is doing well. The amount of variation generated can be adjusted in many different ways, for example via the mutation rate, via the probability of sexual vs. asexual reproduction, via the probability of outcrossing vs. inbreeding, via dispersal, and via access to previously cryptic variants through the switching of an evolutionary capacitor. A large population size increases the influx of novel mutations each generation.

Enhancement of Selection

Rather than creating more phenotypic variation, some mechanisms increase the intensity and effectiveness with which selection acts on existing phenotypic variation. For example:

- Mating rituals that allow sexual selection on "good genes", and so intensify natural selection.
- Large effective population size increasing the threshold value of the selection coefficient above which selection becomes an important player. This could happen through an increase in the census population size, decreasing genetic drift, through an increase in the recombination rate, decreasing genetic draft, or through changes in the probability distribution of the numbers of offspring.

- Recombination decreasing the importance of the Hill-Robertson effect, where different genotypes contain different adaptive mutations. Recombination brings the two alleles together, creating a super-genotype in place of two competing lineages.
- Shorter generation time.

Robustness and Evolvability

The relationship between robustness and evolvability depends on whether recombination can be ignored. Recombination can generally be ignored in asexual populations and for traits affected by single genes.

Without Recombination

Robustness in the face of mutation does not increase evolvability in the first sense. In organisms with a high level of robustness, mutations have smaller phenotypic effects than in organisms with a low level of robustness. Thus, robustness reduces the amount of heritable genetic variation on which selection can act. However, robustness may allow exploration of large regions of genotype space, increasing evolvability according to the second sense. Even without genetic diversity, some genotypes have higher evolvability than others, and selection for robustness can increase the "neighborhood richness" of phenotypes that can be accessed from the same starting genotype by mutation. For example, one reason many proteins are less robust to mutation is that they have marginal thermodynamic stability, and most mutations reduce this stability further. Proteins that are more thermostable can tolerate a wider range of mutations and are more evolvable. For polygenic traits, neighborhood richness contributes more to evolvability than does genetic diversity or "spread" across genotype space.

With Recombination

Temporary robustness, or canalisation, may lead to the accumulation of significant quantities of cryptic genetic variation. In a new environment or genetic background, this variation may be revealedand sometimes be adaptive.

Factors affecting Evolvability via Robustness

Different genetic codes have the potential to change robustness and evolvability by changing the effect of single-base mutational changes.

Exploration Ahead of Time

When mutational robustness exists, many mutants will persist in a cryptic state. Mutations tend to fall into two categories, having either a very bad effect or very little effect: few mutations fall somewhere in between. Sometimes, these mutations will not be completely invisible, but still have rare effects, with very low penetrance. When this happens, natural selection weeds out the very bad mutations, while leaving the others relatively unaffected. While evolution has no "foresight" to know which environment will be encountered in the future, some mutations cause major disruption to a basic biological process, and will never be adaptive in any environment. Screening these out in advance leads to preadapted stocks of cryptic genetic variation.

Another way that phenotypes can be explored, prior to strong genetic commitment, is through learning. An organism that learns gets to "sample" several different phenotypes during its early development, and later sticks to whatever worked best. Later in evolution, the optimal phenotype can be genetically assimilated so it becomes the default behavior rather than a rare behavior. This is known as the Baldwin effect, and it can increase evolvability.

Learning biases phenotypes in a beneficial direction. But an exploratory flattening of the fitness landscape can also increase evolvability even when it has no direction, for example when the flattening is a result of random errors in molecular and developmental processes. This increase in evolvability can happen when evolution is faced with crossing a "valley" in an adaptive landscape. This means that two mutations exist that are deleterious by themselves, but beneficial in combination. These combinations can evolve more easily when the landscape is first flattened, and the discovered phenotype is then fixed by genetic assimilation.

Modularity

If every mutation affected every trait, then a mutation that was an improvement for one trait would be a disadvantage for other traits. This means that almost no mutations would be beneficial overall. But if pleiotropy is restricted to within functional modules, then mutations affect only one trait at a time, and adaptation is much less constrained. In a modular gene network, for example, a gene that induces a limited set of other genes that control a specific trait under selection may evolve more readily than one that also induces other gene pathways controlling traits not under selection.Individual genes also exhibit modularity. A mutation in one cis-regulatory element of a gene's promoter region may allow the expression of the gene to be altered only in specific tissues, developmental stages, or environmental conditions rather than changing gene activity in the entire organism simultaneously.

Evolution of Evolvability

While variation yielding high evolvability could be useful in the long term, in the short term most of that variation is likely to be a disadvantage. For example, naively it would seem that increasing the mutation rate via a mutator allele would increase evolvability. But as an extreme example, if the mutation rate is too high then all individuals will be dead or at least carry a heavy mutation load. Short-term selection for low variation most of the time is usually thought likely to be more powerful than long-term selection for evolvability, making it difficult for natural selection to cause the evolution of evolvability. Other forces of selection also affect the generation of variation; for example, mutation and recombination may in part be byproducts of mechanisms to cope with DNA damage.

When recombination is low, mutator alleles may still sometimes hitchhike on the success of adaptive mutations that they cause. In this case, selection can take place at the level of the lineage. This may explain why mutators are often seen during experimental evolution of microbes. Mutator alleles can also evolve more easily when they only increase mutation rates in nearby DNA sequences, not across the whole genome: this is known as a contingency locus.

The evolution of evolvability is less controversial if it occurs via the evolution of sexual reproduction, or via the tendency of variation-generating mechanisms to become more active when an organism is stressed. The yeast prion (PSI+) may also be an example of the evolution

of evolvability through evolutionary capacitance. An evolutionary capacitor is a switch that turns genetic variation on and off. This is very much like bet-hedging the risk that a future environment will be similar or different. Theoretical models also predict the evolution of evolvability via modularity. When the costs of evolvability are sufficiently short-lived, more evolvable lineages may be the most successful in the long-term. However, the hypothesis that evolvability is an adaptation is often rejected in favor of alternative hypotheses, e.g. minimization of costs.

Applications

Evolvability phenomena have practical applications. For protein engineering we wish to increase evolvability, and in medicine and agriculture we wish to decrease it. Protein evolvability is defined as the ability of the protein to acquire sequence diversity and conformational flexibility which can enable it to evolve toward a new function.

In protein engineering, both rational design and directed evolution approaches aim to create changes rapidly through mutations with large effects. Such mutations, however, commonly destroy enzyme function or at least reduce tolerance to further mutations. Identifying evolvable proteins and manipulating their evolvability is becoming increasingly necessary in order to achieve ever larger functional modification of enzymes. Proteins are also often studied as part of the basic science of evolvability, because the biophysical properties and chemical functions can be easily changed by a few mutations. More evolvable proteins can tolerate a broader range of amino acid changes and allow them to evolve toward new functions. The study of evolvability has fundamental importance for understanding very long term evolution of protein superfamilies.

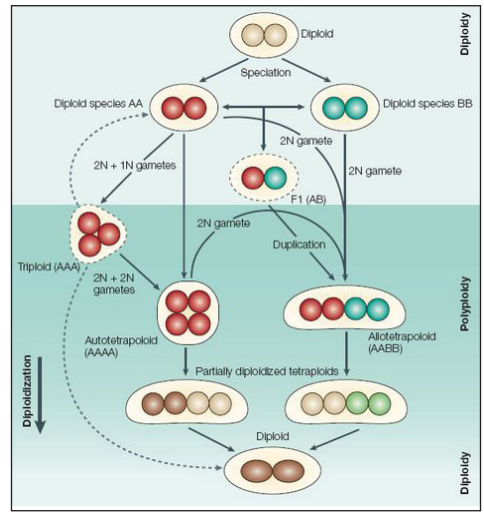
Many human diseases are capable of evolution. Viruses, bacteria, fungi and cancers evolve to be resistant to host immune defences, as well as pharmaceutical drugs. These same problems occur in agriculture with pesticide and herbicide resistance. It is possible that we are facing the end of the effective life of most of available antibiotics. Predicting the evolution and evolvabilityof our pathogens, and devising strategies to slow or circumvent the development of resistance, demands deeper knowledge of the complex forces driving evolution at the molecular level.

A better understanding of evolvability is proposed to be part of an Extended Evolutionary Synthesis.

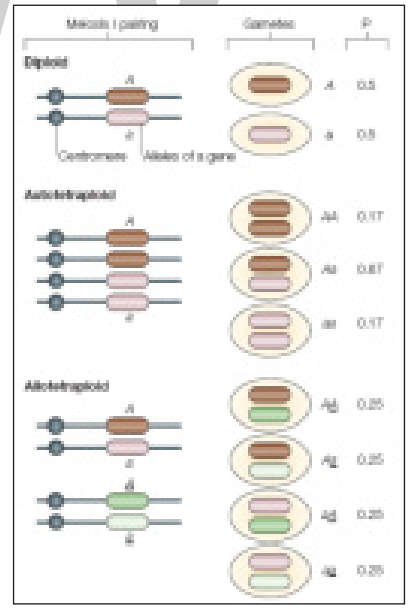
Polyploidy

Polyploidy is the heritable condition of possessing more than two complete sets of chromosomes. Polyploids are common among plants, as well as among certain groups of fish and amphibians. For instance, some salamanders, frogs, and leeches are polyploids. Many of these polyploid organisms are fit and well-adapted to their environments. In fact, recent findings in genome research indicate that many species that are currently diploid, including humans, were derived from polyploid . These species that have experienced ancient genome duplications and then genome reduction are referred to as paleopolyploids.

Mechanisms of Polyploidy



Polyploids arise when a rare mitotic or meiotic catastrophe, such as nondisjunction, causes the formation of gametes that have a complete set of duplicate chromosomes. Diploid gametes are frequently formed in this way. When a diploid gamete fuses with a haploid gamete, a triploid zygote forms, although these triploids are generally unstable and can often be sterile. If a diploid gamete fuses with another diploid gamete, however, this gives rise to a tetraploid zygote, which is potentially stable. Many types of polyploids are found in nature, including tetraploids (four sets of chromosomes), hexaploids (six sets of chromosomes), and other chromosome-pair multiples.

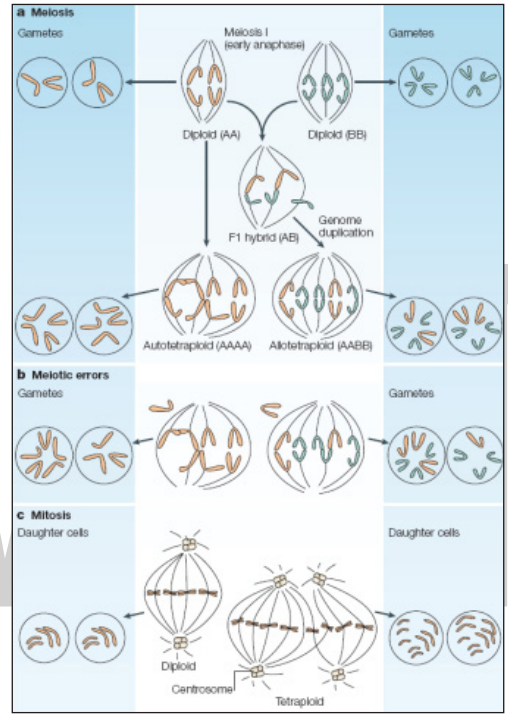


Researchers usually make a distinction between polyploids that arise within a species and those that arise due to the hybridization of two distinct species. The former are known as autopolyploids, while the latter are referred to as allopolyploids. Autopolyploids are essentially homozygous at every locus in the genome. However, allopolyploids may have varying degrees of heterozygosity depending on the divergence of the parental genomes. Heterozygosity is apparent in the gametes

that polyploids produce. Allopolyploids can generally be distinguished from autopolyploids because they produce a more diverse set of gametes.

Different species exhibit different levels of tolerance for polyploidy. For example, polyploids form at relatively high frequency in flowering plants (1 per 100,000 individuals), suggesting that plants have a remarkably high tolerance for polyploidy. This is also the case for some species of fish and frogs. However, higher vertebrates do not appear to tolerate polyploidy very well; in fact, it is believed that 10% of spontaneous abortions in humans are due to the formation of polyploid zygotes.

Advantages of Polyploidy



Polyploid formation and ensuing meiotic and mitotic irregularities.

The figure illustrates the chromosomal composition and behavior of diploids and derived polyploids at different developmental times in meiosis (a, b) and mitosis (c).

Due to the high incidence of polyploidy in some taxa, such as plants, fish, and frogs, there clearly must be some advantages to being polyploid. A common example in plants is the observation of hybrid vigor, or heterosis, whereby the polyploid offspring of two diploid progenitors is more vigorous and healthy than either of the two diploid parents. There are several possible explanations for this observation. One is that the enforced pairing of homologouschromosomes within an allotetraploid prevents recombination between the genomes of the original progenitors, effectively maintaining heterozygosity throughout generations. This heterozygosity prevents the accumulation of recessive mutations in the genomes of later generations, thereby maintaining hybrid vigor. Another important factor is gene redundancy. Because the polyploid offspring now have twice as many copies of any particular gene, the offspring are shielded from the deleterious effects of recessive mutations. This is particularly important during the gametophytelife stage. One might envision that, during the haploid stage of the life cycle, any allele that is recessive for a deleterious

mutation will not be masked by the presence of a dominant, normally functioning allele, allowing the mutation to cause developmental failure in the pollen or the egg sac. Conversely, a diploid gamete permits the masking of this deleterious allele by the presence of the dominant normal allele, thus protecting the pollen or egg sac from developmental dysfunction. This protective effect of polyploidy might be important when small, isolated populations are forced to inbreed.

Another advantage conferred by gene redundancy is the ability to diversify gene function over time. In other words, extra copies of genes that are not required for normal organism function might end up being used in new and entirely different ways, leading to new opportunities in evolutionary selection.

Interestingly, polyploidy can affect sexuality in ways that provide selective advantages. One way is by disrupting certain self-incompatibility systems, thereby allowing self-fertilization. This might be the result of the interactions between parental genomes in allopolyploids. Another way is by favoring the onset of asexual reproduction, which is associated with polyploidy in both plants and animals. This switch in reproductive strategies may improve fitness in static environments.

Disadvantages of Polyploidy

For all the advantages that polyploidy can confer to an organism, there are also a great number of disadvantages, both observed and hypothesized. One of these disadvantages relates to the relative changes between the size of the genome and the volume of the cell. Cell volume is proportional to the amount of DNA in the cell nucleus. For example, doubling a cell's genome is expected to double the volume of space occupied by the chromosomes in the nucleus, but it causes only a 1.6-fold increase in the surface area of the nuclear envelope. This can disrupt the balance of factors that normally mediate interactions between the chromosomes and nuclear components, including envelope-bound proteins. The peripheral positioning of telomeric and centromeric heterochromatin may be disturbed as well, because there is less relative surface space on the nuclear envelope to accommodate this positioning.

Polyploidy can also be problematic for the normal completion of mitosis and meiosis. For one, polyploidy increases the occurrence of spindle irregularities, which can lead to the chaotic segregation of chromatids and to the production of aneuploid cells in animals and yeast. Aneuploid cells, which have abnormal numbers of chromosomes, are more readily produced in meioses involving three or more sets of chromosomes than in diploid cells. Autopolyploids have the potential to form multiple arrangements of homologous chromosomes at meiotic metaphase I, which can result in abnormal segregation patterns, such as 3:1 or 2:1 plus one laggard. (Laggard chromosomes do not attach properly to the spindle apparatus and thus randomly segregate to daughter cells.) These abnormal segregation patterns cannot be resolved into balanced products, and random segregation of multiple chromosome types produces mostly aneuploid gametes. Chromosome pairing at meiosis I is more constrained in allopolyploids than in autopolyploids, but the stable maintenance of the two parental chromosomal complements also requires the formation of balanced gametes.

Another disadvantage of polyploidy includes potential changes in gene expression. It is generally assumed that an increase in the copy number of all chromosomes would affect all genes equally and should result in a uniform increase in gene expression. Possible exceptions would include genes that respond to regulating factors that do not change proportionally with ploidy. We now

have experimental evidence for such exceptions in several systems. In one interesting example, investigators compared the mRNA levels per genome for 18 genes in 1X, 2X, 3X, and 4X maize. While expression of most genes increased with ploidy, some genes demonstrated unexpected deviations from expected expression levels. For example, sucrose synthase showed the expected proportional expression in 2X and 4X tissues, but its expression was three and six times higher, respectively, in 1X and 3X tissues. Two other genes showed similar, if less extreme, trends. Altogether, about 10% of these genes demonstrated sensitivity to odd-numbered ploidy.

Epigenetic instability can pose yet another challenge for polyploids. Epigenetics refers to changes in phenotype and gene expression that are not caused by changes in DNA sequence. According to the genomic shock hypothesis, disturbances in the genome, such as polyploidization, may lead to widespread changes in epigenetic regulation. Although there are few instances of documented epigenetic instability in autopolyploids, there are a couple of intriguing examples worth mentioning. In one case, transgene silencing occurred more frequently in Arabidopsis thaliana tetraploids than in A. thaliana diploids, suggesting an effect of ploidy on chromosome remodeling. However, several factors cannot be ruled out in the observation of this phenomenon, including duplication of the strong 35S promoter from cauliflower mosaic virus in the transgene. In another case, the activation of a DNA transposon of the Spm/CACTA family was observed in autopolyploids. Unfortunately, the generality of this change could not be determined because multiple independent autopolyploids were not examined.

Conversely, extensive evidence for epigenetic remodeling is available in allopolyploids. Structural genomic changes, such as DNA methylation, and expression changes are reported to accompany the transition to alloploidy in several plant systems, including Arabidopsis and wheat. The most detailed information is available for the model system Arabidopsis. For instance, in a cross of A. thaliana and A. arenosa, epigenetically regulated genes were identified by comparing transcripts from the autotetraploid parents to transcripts from the neoallopolyploid progeny. A. thaliana genes affected by epigenetic regulation were defined as those that responded to the transition from autopolyploidy to allopolyploidy. Altogether, between 2% and 2.5% of A. thaliana genes were estimated to have undergone regulatory changes during the transition to allopolyploidy. A more detailed microarray study that examined the regulation of 26,000 genes in Arabidopsis neoallopolyploids detected a transcriptome divergence between the progenitors of more than 15%, due to genes that were highly expressed in A. thaliana and not in A. arenosa or vice versa. Significantly, expression of approximately 5% of the genes diverged from the mid-parent value in two independently derived allotetraploids, consistent with nonadditive gene regulation after hybridization. Taken together, these results suggest that the instability syndrome of neoallopolyploids may be attributed primarily to regulatory divergence between the parental species, leading to genomic incompatibilities in the allopolyploid offspring.

Aneuploidy might also be a factor in epigenetic remodeling in neoallopolyploids, either by altering the dosage of factors that are encoded by chromosomes that have greater or fewer than the expected number of copies leading to changes in imprinted loci, or by exposing unpaired chromatin regions to epigenetic remodeling mechanisms. In the latter case, this susceptibility of meiotically unpaired DNA to silencing was first reported for the fungus Neurospora crassa, but it appears to be

a general phenomenon. Therefore, some of the epigenetic instability that is observed in allopolyploids might result from aneuploidy.

Evolutionary Potential of Polyploid Organisms

At first sight, the epigenetic changes observed in polyploids would seem to be deleterious because of their disruptive effects on regulatory patterns established by selection. However, these epigenetic changes might instead increase diversity and plasticity by allowing for rapid adaptation in polyploids. One example may be the widespread dispersal of the invasive allopolyploid Spartina angelica. However, it is not clear whether the success of this species can be attributed to fixed heterosis or to the increased variability that results from epigenetic remodeling. Polyploidy is also believed to play a role in the rapid adaptation of some allopolyploid arctic flora, probably because their genomes confer hybrid vigor and buffer against the effects of inbreeding. However, fertility barriers between species often need to be overcome in order to form successful allopolyploids, and these barriers may have an epigenetic basis.

Genetic Drift

Genetic drift is change in allele frequencies in a population from generation to generation that occurs due to chance events. To be more exact, genetic drift is change due to "sampling error" in selecting the alleles for the next generation from the gene pool of the current generation. Although genetic drift happens in populations of all sizes, its effects tend to be stronger in small populations.

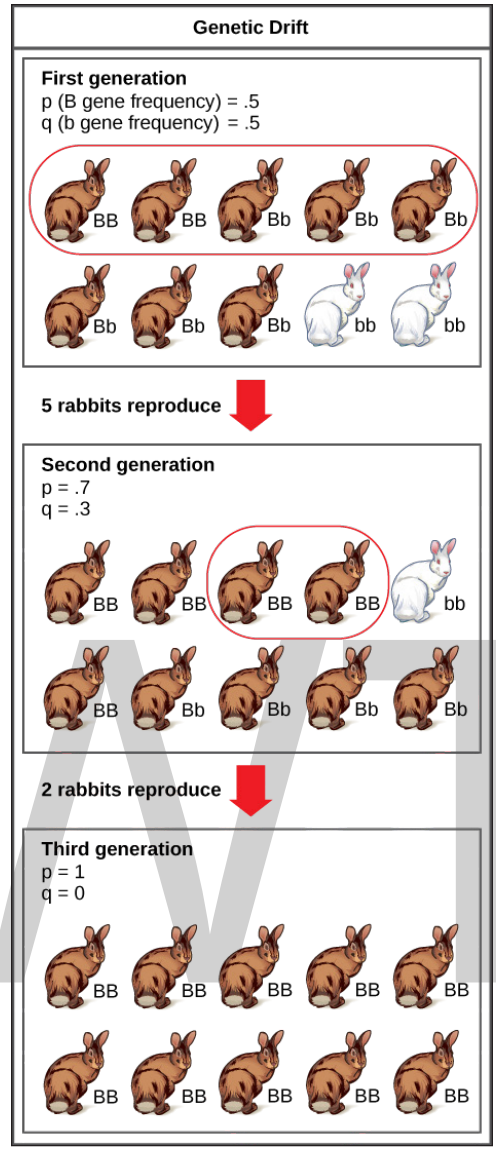
Example: Let's make the idea of drift more concrete by looking at an example. As shown in the diagram below, we have a very small rabbit population that's made up of 888 brown individuals (genotype BB or Bb) and 222 white individuals (genotype bb). Initially, the frequencies of the B and b alleles are equal.

Genetic drift at work in a small population of rabbits. By the third generation, the b allele has been lost from the population purely by chance.

What if, purely by chance, only the 555 circled individuals in the rabbit population reproduce? (Maybe the other rabbits died for reasons unrelated to their coat color, e.g., they happened to get caught in a hunter's snares.) In the surviving group, the frequency of the B allele is 0.70.70, point, 7, and the frequency of the b allele is 0.3.

In the example, the allele frequencies of the five lucky rabbits are perfectly represented in the second generation, as shown at right. Because the 5-rabbit "sample" in the previous generation had different allele frequencies than the population as a whole, frequencies of B and b in the population have shifted to 0.7and 0.3, respectively.

From this second generation, what if only two of the BB offspring survive and reproduce to yield the third generation? In this series of events, by the third generation, the b allele is completely lost from the population.



Population Size Matters

Larger populations are unlikely to change this quickly as a result of genetic drift. For instance, if we followed a population of 100010001000 rabbits (instead of 101010), it's much less likely that the b allele would be lost (and that the B allele would reach 100\%100%100, percent frequency, or fixation) after such a short period of time. If only half of the 100010001000-rabbit population survived to reproduce, as in the first generation of the example above, the surviving rabbits (500500500 of them) would tend to be a much more accurate representation of the allele frequencies of the original population – simply because the sample would be so much larger.

This is a lot like flipping a coin a small vs. a large number of times. If you flip a coin just a few times, you might easily get a heads-tails ratio that's different from 505050 - 505050. If you flip a coin a few hundred times, on the other hand, you had better get something quite close to 505050 - 505050 (or else you might suspect you have a doctored coin).

Allele Benefit or Harm doesn't Matter

Genetic drift, unlike natural selection, does not take into account an allele's benefit (or harm) to the individual that carries it. That is, a beneficial allele may be lost, or a slightly harmful allele may become fixed, purely by chance.

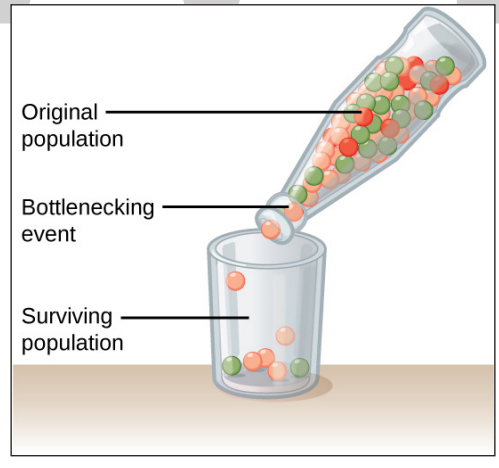
A beneficial or harmful allele would be subject to selection as well as drift, but strong drift (for example, in a very small population) might still cause fixation of a harmful allele or loss of a beneficial one.

The Bottleneck Effect

The bottleneck effect is an extreme example of genetic drift that happens when the size of a population is severely reduced. Events like natural disasters (earthquakes, floods, fires) can decimate a population, killing most indviduals and leaving behind a small, random assortment of survivors.

The allele frequencies in this group may be very different from those of the population prior to the event, and some alleles may be missing entirely. The smaller population will also be more susceptible to the effects of genetic drift for generations (until its numbers return to normal), potentially causing even more alleles to be lost.

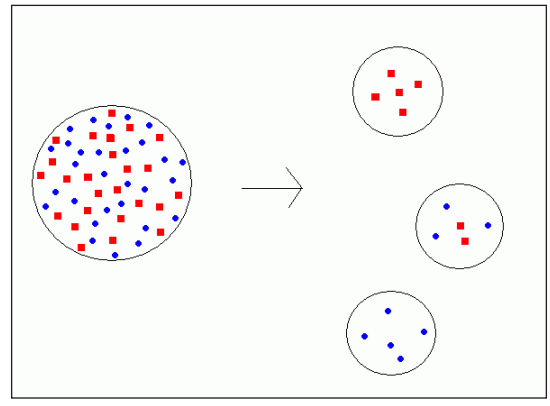
How can a bottleneck event reduce genetic diversity? Imagine a bottle filled with marbles, where the marbles represent the individuals in a population. If a bottleneck event occurs, a small, random assortment of individuals survive the event and pass through the bottleneck (and into the cup), while the vast majority of the population is killed off (remains in the bottle). The genetic composition of the random survivors is now the genetic composition of the entire population.



The Founder Effect

The founder effect is another extreme example of drift, one that occurs when a small group of individuals breaks off from a larger population to establish a colony. The new colony is isolated from the original population, and the founding individuals may not represent the full genetic diversity of the original population. That is, alleles in the founding population may be present at

different frequencies than in the original population, and some alleles may be missing altogether. The founder effect is similar in concept to the bottleneck effect, but it occurs via a different mechanism (colonization rather than catastrophe).



In the figure above, you can see a population made up of equal numbers of squares and circles. (Let's assume an individual's shape is determined by its alleles for a particular gene).

Random groups that depart to establish new colonies are likely to contain different frequencies of squares and circles than the original population. So, the allele frequencies in the colonies (small circles) may be different relative to the original population. Also, the small size of the new colonies means they will experience strong genetic drift for generations.

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4

Processes in Evolutionary Biology

There are numerous processes which are studied within the field of evolutionary biology. A few of them are co-operation, speciation, adaptation, adaptive radiation, parallel evolution, molecular evolution, coevolution, macroevolution, microevolution, etc. All these diverse processes have been carefully analyzed in this chapter.

Speciation

Speciation is a process within evolution that leads to the formation of new, distinct species that are reproductively isolated from one another.

Anagenesis, or 'phyletic evolution', occurs when evolution acts to create new species, which are distinct from their ancestors, along a single lineage, through gradual changes in physical or genetic traits. In this instance, there is no split in the phylogenetic tree. Conversely, 'speciation' or cladogenesis arises from a splitting event, where a parent species is split into two distinct species, often as the result of geographic isolation or another driving force involving the separation of populations.

The reproductive isolation that is integral to the process of speciation occurs due to reproductive barriers, which are formed as a consequence of genetic, behavioral or physical differences arising between the new species. These are either pre-zygotic (pre-mating) mechanisms, for example, differences in courtship rituals, non-compatible genitalia, or gametes, which are unable to fertilize between species. Alternatively, they are post-zygotic (post-mating), for example zygote mortality or the production of sterile offspring. Reproductive isolation leads to reinforcement of the distinction between species through natural selection and sexual selection.

Types of Speciation

Allopatric Speciation

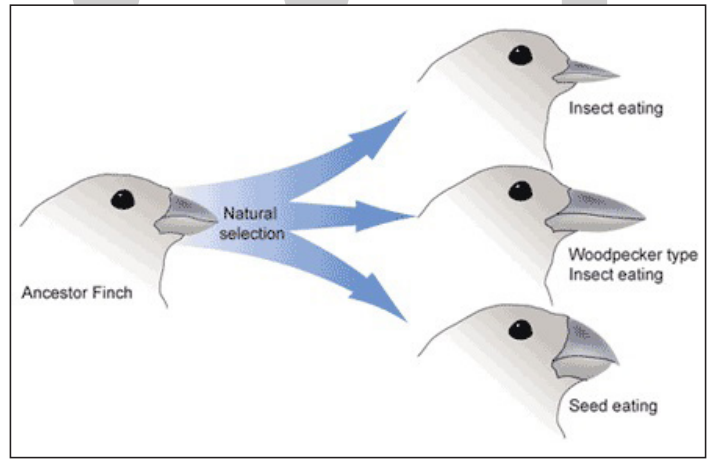
Allopatric speciation occurs when members of a population become geographically isolated from one another, to the extent that genetic exchange, through mating, is prevented or interfered with. This may be a result of geographical changes, such as the formation of a mountain by a volcano,

island formation, habitat separation by glaciers and rivers, or habitat fragmentation caused by human activity. Alternatively, species members may emigrate, resulting in population separation by dispersal; this is commonly known as vicariance.

The separated populations then undergo divergence in genotypic or phenotypic traits as a result of different selective pressures acting upon populations. This leads natural selection to cause genetic drift as mutations arise within populations. Over time, the separate populations may develop morphologically distinct features due to adaption to their new environment. The features may become so distinctively different that reproductive isolation occurs, preventing the inbreeding of populations and thus forming new species. If the populations become sufficiently different that they are classified as new species, but not distinct enough for reproductive isolation to occur, the species may come back into contact and mate, producing hybrids.

The extent of the effect that geographic barriers may have on a population often depends on the dispersal ability of the organism; for example, the new formation of a river in a landscape would create an impassable barrier for small terrestrial mammals, insects and reptiles. However, birds and larger mammals would likely disperse across the river with ease.

An elegant example of allopatric speciation, which first inspired Charles Darwin to develop the theory of evolution and natural selection, is the divergent populations of finches inhabiting the Galapagos Islands, and known as 'Darwin's finches'. Darwin noticed that each of the Galapagos Islands hosted a population of finches, which although relatively similar in morphology (compared with other bird species), exhibited slight differences in features such as body size, color and beak length or shape. He noted that there were different food sources available for the birds on each of the different islands, and came to the conclusion that the differences in beak shape were an adaption toward acquiring the particular food source.



Sympatric Speciation

Sympatric speciation is the evolutionary process whereby species are formed from a single ancestral species while inhabiting the same geographic area. In contrast to allopatric speciation, the distribution ranges of species which evolve through sympatry may be identical or they may only overlap. Rather than geographic distance prompting a reduction of gene flow between populations, sympatry occurs when members of one population make use of a new niche. This could occur, for

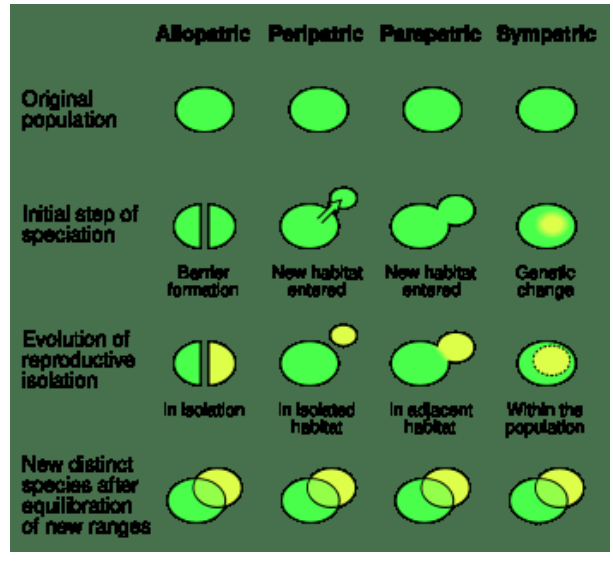
example, if a herbivorous insect begins to feed on a new or novel plant source with which it was not ancestrally associated, or if a new species of plant is introduced to the species' geographic range. As insects generally reproduce or lay eggs within the type of fruit that they were born in, over time, the individuals would specialize in feeding and mating on particular fruits. Consequently, gene flow between populations that specialize in different fruits will be reduced, leading to reproductive isolation of the populations. It is possible that the populations will also develop morphological differences as they adapt to most effectively exploit the new niche. Although sympatric speciation does sometimes occur, it is uncommon, especially within large, multicellular organisms.

Parapatric Speciation

Parapatric speciation is an extremely rare case of speciation that occurs when a population is continuously distributed within a geographic area without any specific barriers to gene flow. Nonetheless, the population does not mate randomly within the population, but rather individuals mate more commonly with their closest geographic neighbors, resulting in uneven gene flow. Non-random mating may increase the rate of dimorphism within populations, in which varied morphological forms of the same species are displayed. The result of parapatric speciation is one or more distinct sub-populations (known as 'sister species'), which have small, continuous overlaps in their biogeographic range and are genotypically dimorphic.

Peripatric Speciation

Peripatric speciation is a form of allopatric speciation that occurs when populations that have become isolated have very few individuals. Through this process, the population goes through a genetic bottleneck. Within the small sub-population, organisms which are able to survive within the new environment may carry genes that were rare within the main population but that cause a slight variation to behavior or morphology. Through repeated matings, the frequency of these, once rare, genes increases within the small population. This is known as the 'founder effect'. Over time, the characteristic that was determined by the gene becomes fixed within the population, leading to an isolated species that is evolutionarily distinct from the main population.

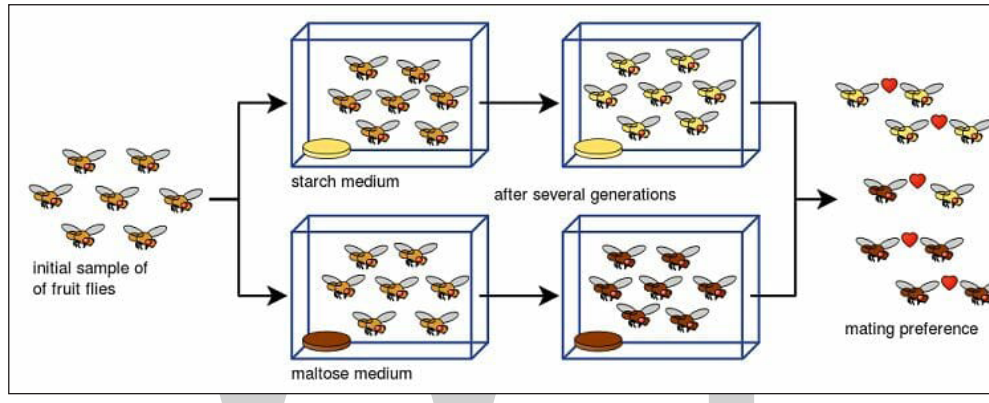


Speciation modes.

Artificial Speciation

Artificial speciation is the form of speciation that can be achieved by the input of human influence. By separating populations, and thereby preventing breeding, or by intentionally breeding individuals with desired morphological or genotypic traits, humans can create new, distinct species. This is also known as 'artificial selection'; most modern domesticated animals and plants have undergone artificial selection.

Although evolution of our modern crops and livestock has taken thousands of years, it is possible to visualize the process of artificial selection in species that have short life cycles. Artificial selection has been demonstrated most effectively in species of Fruit Fly (Drosophila melanogaster). Experiments in which flies are placed into environments which contain different resources or habitats show the changes that occur when the flies adapt to each environment. After several generations, the flies are removed from the experimental zone and are allowed to cohabitate, although the populations are unable to mate due to the reproductive isolation process that occurred while in isolation.



Drosophila speciation experiment.

Co-operation

In evolution, co-operation is the process where groups of organisms work or act together for common or mutual benefits. It is commonly defined as any adaptationthat has evolved, at least in part, to increase the reproductive success of the actor's social partners. For example, territorial choruses by male lionsdiscourage intruders and are likely to benefit all contributors.

This process contrasts with intragroup competition where individuals work against each other for selfish reasons. Cooperation exists not only in humans but in other animals as well. The diversity of taxa that exhibits cooperation is quite large, ranging from zebra herds to pied babblers to African elephants. Many animal and plant species cooperate with both members of their own species and with members of other species.

In Animals

Cooperation in animals appears to occur mostly for direct benefit or between relatives. Spending time and resources assisting a related individual may at first seem destructive to an organism's

chances of survival but is actually beneficial over the long-term. Since relatives share part of the helper's genetic make-up, enhancing each individual's chance of survival may actually increase the likelihood that the helper's genetic traits will be passed on to future generations.

However, some researchers, such as ecology professor Tim Clutton-Brock, assert that cooperation is a more complex process. They state that helpers may receive more direct, and less indirect, gains from assisting others than is commonly reported. These gains include protection from predation and increased reproductive fitness. Furthermore, they insist that cooperation may not solely be an interaction between two individuals but may be part of the broader goal of unifying populations.

Prominent biologists, such as Charles Darwin, E. O. Wilson, and W. D. Hamilton, have found the evolution of cooperationfascinating because natural selection favors those who achieve the greatest reproductive success while cooperative behavior often decreases the reproductive success of the actor (the individual performing the cooperative behavior). Hence, cooperation seemed to pose a challenging problem to the theory of natural selection, which rests on the assumption that individuals compete to survive and maximize their reproductive successes. Additionally, some species have been found to perform cooperative behaviors that may at first sight seem detrimental to their own evolutionary fitness. For example, when a ground squirrel sounds an alarm call to warn other group members of a nearby coyote, it draws attention to itself and increases its own odds of being eaten. There have been multiple hypotheses for the evolution of cooperation, all of which are rooted in Hamilton's models based on inclusive fitness. These models hypothesize that cooperation is favored by natural selection due to either direct fitness benefits (mutually beneficial cooperation) or indirect fitness benefits (altruistic cooperation). As explained below, direct benefits encompass by-product benefits and enforced reciprocity, while indirect benefits (kin selection) encompass limited dispersal, kin discrimination and the greenbeard effect.

Kin Selection

One specific form of cooperation in animals is kin selection, which involves animals promoting the reproductive success of their kin, thereby promoting their own fitness.

Different theories explaining kin selection have been proposed, including the "pay-to-stay" and "territory inheritance" hypotheses. The "pay-to-stay" theory suggests that individuals help others rear offspring in order to return the favor of the breeders allowing them to live on their land. The "territory inheritance" theory contends that individuals help in order to have improved access to breeding areas once the breeders depart.

Studies conducted on red wolves support previous researchers' contention that helpers obtain both immediate and long-term gains from cooperative breeding. Researchers evaluated the consequences of red wolves' decisions to stay with their packs for extended periods of time after birth. While delayed dispersal helped other wolves' offspring, studies also found that it extended male helper wolves' life spans. This suggests that kin selection may not only benefit an individual in the long-term through increased fitness but also in the short-term through increased survival chances.

Some research suggests that individuals provide more help to closer relatives. This phenomenon is known as kin discrimination. In their meta-analysis, researchers compiled data on kin selection as mediated by genetic relatedness in 18 species, including the western bluebird, pied kingfisher,

Australian magpie, and dwarf mongoose. They found that different species exhibited varying degrees of kin discrimination, with the largest frequencies occurring among those who have the most to gain from cooperative interactions.

In Plants

Cooperation exists not only in animals but also in plants. In a greenhouse experiment with *Ipomoea hederacea*, a climbing plant, results show that kin groups have higher efficiency rates in growth than non-kin groups do. This is expected to rise out of reduced competition within the kin groups.

Explanation

The inclusive fitness theory provides a good overview of possible solutions to the fundamental problem of cooperation. The theory is based on the hypothesis that cooperation helps in transmitting underlying genes to future generations either through increasing the reproductive successes of the individual (direct fitness) or of other individuals who carry the same genes (indirect fitness). Direct benefits can result from simple by-product of cooperation or enforcement mechanisms, while indirect benefits can result from cooperation with genetically similar individuals.

Direct Fitness Benefits

This is also called mutually beneficial cooperation as both actor and recipient depend on direct fitness benefits, which are broken down into two different types: by-product benefit and enforcement.

By-product benefit arises as a consequence of social partners having a shared interest in cooperation. For example, in meerkats, larger group size provides a benefit to all the members of that group by increasing survival rates, foraging success and conflict wins. This is because living in groups is better than living alone, and cooperation arises passively as a result of many animals doing the same thing. By-product benefit can also arise as a consequence of subordinate animals staying and helping a nest that is dominated by leaders who often suffer high mortality rates. It has been shown that cooperation would be most advantageous for the sex that is more likely to remain and breed in the natal group. This is because the subordinate will have a higher chance to become dominant in the group as time passes. Cooperation in this scenario is often seen between non-related members of the same species, such as the wasp *Polistes dominula*.

Prisoner's Delight, another term to describe by-product benefit, is a term coined by Kenneth Binmore in 2007 after he found that benefits can result as an automatic consequence of an otherwise "self-interested" act in cooperative hunting. He illustrated this with a scenario having two hunters, each hunter having the choice of hunting (cooperate) or not hunting (free-riding). Assuming that cooperative hunting results in greater rewards than just a one-player hunt, when hunting is not rare, both hunters and non-hunters benefit because either player is likely to be with other hunters, and thus likely to reap the rewards of a successful hunt. This situation demonstrates "Prisoner's Delight" because the food of a successful hunt is shared between the two players regardless of whether or not they participated.

It has been shown that free riding, or reaping the benefits without any effort, is often a problem in collective action. Examples of free riding would be if an employee in a labor union pays no dues, but still benefits from union representation. In a study published in 1995, scientists found that female lions showed individual differences in the extent to which they participated in group-territorial conflict. Some lions consistently 'cooperated' by approaching intruders, while others 'lagged' behind to avoid the risk of fighting. Although the lead female recognized the laggards, she failed to punish them, suggesting that cooperation is not maintained by reciprocity.

Cooperation is maintained in situations where free-riding is a problem through enforcement, which is the mechanism where the actor is rewarded for cooperating or punished for not cooperating. This happens when cooperation is favored in aiding those who have helped the actors in the past. Punishment for noncooperation has been documented in meerkats, where dominant females will attack and evict subordinate females who become pregnant. The pregnancy is seen as a failure to cooperate because only the dominant females are allowed to bear offspring. Dominant females will attack and kill the offspring of subordinate females if they evade eviction and eviction often leads to increased stress and decreased survival.

Enforcement can also be mutually beneficial, and is often called reciprocal cooperation because the act of cooperation is preferentially directed at individuals who have helped the actor in the past (directly), or helped those who have helped the actor in the past (indirectly).

Indirect Fitness Benefits

The second class of explanations for cooperation is indirect fitness benefits, or altruistic cooperation. There are three major mechanisms that generate this type of fitness benefit: Limited dispersal, kin discrimination and the green-beard effect.

Hamilton originally suggested that high relatedness could arise in two ways: Direct kin recognition between individuals or limited dispersal, or population viscosity, which can keep relatives together. The easiest way to generate relatedness between social partners is limited dispersal, a mechanism in which genetic similarity correlates with spatial proximity. If individuals do not move far, then kin usually surrounds them. Hence, any act of altruism would be directed primarily towards kin. This mechanism has been shown in *Pseudomonas aeruginosa* bacteria, where cooperation is disfavored when populations are well mixed, but favored when there is high local relatedness.

Kin discrimination also influences cooperation because the actor can give aid preferentially towards related partners. Since kin usually share common genes, it is thought that this nepotism can lead to genetic relatedness between the actor and the partner's offspring, which affects the cooperation an actor might give.

This mechanism is similar to what happens with the green-beard effect, but with the green-beard effect, the actor has to instead identify which of its social partners share the gene for cooperation. A green-beard system must always co-occur within individuals and alleles to produce a perceptible trait, recognition of this trait in others, and preferential treatment to those recognized. Examples of green-beard behavior have been found in hydrozoans, slime molds, yeast, and ants. An example is in side-blotch lizards, where blue-throated males preferentially establish territories next to each other. Results show that neighboring blue-throats are more successful at mate guarding. However, blue males next to larger, more aggressive orange males suffer a cost.

Multi-level Selection

Multi-level selection theory suggests that selection operates on more than one level: For example, it may operate at an atomic and molecular level in cells, at the level of cells in the body, and then again at the whole organism level, and the community level, and the species level. Any level which is not competitive with others of the same level will be eliminated, even if the level below is highly competitive. A classic example is that of genes which prevent cancer. Cancer cells divide uncontrollably, and at the cellular level, they are very successful, because they are (in the short term) reproducing very well and out competing other cells in the body. However, at the whole organism level, cancer is often fatal, and so may prevent reproduction. Therefore, changes to the genome which prevent cancer (for example, by causing damaged cells to act co-operatively by destroying themselves) are favoured. Multi-level selection theory contends that similar effects can occur, for example, to cause individuals to co-operate to avoid behaviours which favour themselves short-term, but destroy the community (and their descendants) long term.

Market Effect

One theory suggesting a mechanism that could lead to the evolution of co-operation is the "market effect" as suggested by Noe and Hammerstein. The mechanism relies on the fact that in many situations there exists a trade-off between efficiency obtaining a desired resource and the amount of resources one can actively obtain. In that case, each partner in a system could benefit from specializing in producing one specific resource and obtaining the other resource by trade. When only two partners exist, each can specialize in one resource, and trade for the other. Trading for the resource requires co-operation with the other partner and includes a process of bidding and bargaining.

This mechanism can be relied to both within a species or social group and within species systems. It can also be applied to a multi-partner system, in which the owner of a resource has the power to choose its co-operation partner. This model can be applied in natural systems (examples exist in the world of apes, cleaner fish, and more). Easy for exemplifying, though, are systems from international trading. Arabic countries control vast amounts of oil, but seek technologies from western countries. These in turn are in need of Arab oil. The solution is co-operation by trade.

Symbiosis

Symbiosis refers to two or more biological species that interact closely, often over a long period of time. Symbiosis includes three types of interactions—mutualism, commensalism, and parasitism—of which only mutualism can sometimes qualify as cooperation. Mutualism involves a close, mutually beneficial interaction between two different biological species, whereas "cooperation" is a more general term that can involve looser interactions and can be interspecific (between species) or intraspecific (within a species). In commensalism, one of the two participating species benefits, while the other is neither harmed nor benefitted. In parasitism, one of the two participating species benefits at the expense of the other.

Symbiosis may be obligate or facultative. In obligate symbiosis, one or both species depends on the other for survival. In facultative symbiosis, the symbiotic interaction is not necessary for the survival of either species.

Two special types of symbiosis include endosymbiosis, in which one species lives inside of another, and ectosymbiosis, in which one species lives on another.

Mutualism

Mutualism is a form of symbiosis in which both participating species benefit. A classic example of mutualism is the interaction between rhizobia soil bacteria and legumes (Fabaceae). In this interaction, rhizobia bacteria induce root nodule formation in legume plants via an exchange of molecular signals. Within the root nodules, rhizobia fix atmospheric nitrogen into ammonia using the nitrogenase enzyme. The legume benefits from a new supply of usable nitrogen from the rhizobia, and the rhizobia benefits from organic acid energy sources from the plant as well as the protection provided by the root nodule. Since the rhizobia live within the legume, this is an example of endosymbiosis, and since both the bacteria and the plant can survive independently, it is also an example of facultative symbiosis.

Rhizobia nodules on *Vigna unguiculata*.

Lichens are another example of mutualism. Lichens consist of a fungus (the mycobiont) and a photosynthetic partner (the photobiont), which is usually a green alga or a cyanobacteria. The mycobiont benefits from the sugar products of photosynthesisgenerated by the photobiont, and the photobiont benefits from the increased water retention and increased surface area to capture water and mineral nutrients conferred by the mycobiont. Many lichens are examples of obligate symbiosis. In fact, one-fifth of all known extant fungal species form obligate symbiotic associations with green algae, cyanobacteria or both.

Not all examples of mutualism are also examples of cooperation. Specifically, in by-product mutualism, both participants benefit, but cooperation is not involved. For example, when an elephant defecates, this is beneficial to the elephant as a way to empty waste, and it is also beneficial to a dung beetle that uses the elephant's dung. However, neither participant's behavior yields a benefit from the other, and thus cooperation is not taking place.

Hidden Benefits

Hidden benefits are benefits from cooperation that are not obvious because they are obscure or delayed. (For example, a hidden benefit would not involve an increase in the number of offspring or offspring viability.)

One example of a hidden benefit involves *Malarus cyaneus*, the superb fairy-wren. In *M. cyaneus*, the presence of helpers at the nest does not lead to an increase in chick mass. However, the presence of helpers does confer a hidden benefit: It increases the chance that a mother will survive to breed in the next year.

Another example of a hidden benefit is indirect reciprocity, in which a donor individual helps a beneficiary to increase the probability that observers will invest in the donor in the future, even when the donor will have no further interaction with the beneficiary.

In a study of 79 students, participants played a game in which they could repeatedly give money to others and receive from others. They were told that they would never interact with the same person in the reciprocal role. A player's history of donating was displayed at each anonymous interaction, and donations were significantly more frequent to receivers who had been generous to others in earlier interactions. Indirect reciprocity has only been shown to occur in humans.

Prisoner's Dilemma

Cooperative hunting by wolves allows them to tackle much larger and more nutritious prey than any individual wolf could handle. However, such cooperation could, potentially, be exploited by selfish individuals who do not expose themselves to the dangers of the hunt, but nevertheless share in the spoils.

Even if all members of a group benefit from cooperation, individual self-interest may not favor cooperation. The prisoner's dilemma codifies this problem and has been the subject of much research, both theoretical and experimental. 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

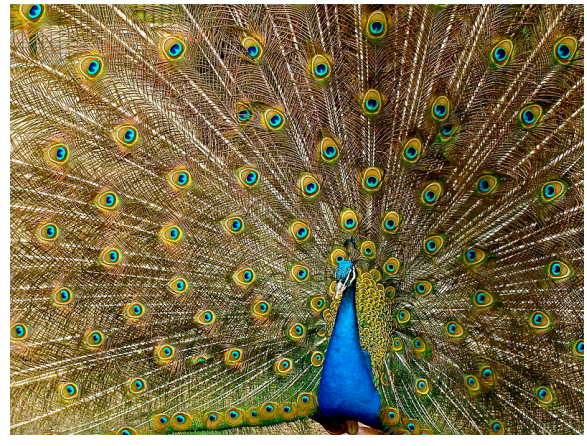
would be for both parties to order the cheapest items on the menu (mutual cooperation). But if one member of the party exploits the situation by ordering the most expensive items, then it is best for the other member to do likewise. In fact, if the fellow diner's personality is completely unknown, and 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 behavior: 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 (in the so-called iterated prisoner's dilemma game, IPD) then tit-for-tat (foreshadowed by Robert Trivers' 1971 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.

Results from experimental economics show, however, that humans often act more cooperatively than strict self-interest would dictate.

Evolutionary Mechanisms suggesting that reciprocity is the result, not the cause, of the evolution of cooperation

In the light of the iterated prisoner's dilemma game and the reciprocal altruism theory failing to provide full answers to the evolutionary stability of cooperation, several alternative explanations have been proposed.



A male peacock with its beautiful but clumsy, aerodynamically unsound erectile tail, which Amotz Zahavi believes is a handicap, comparable to a race horse's handicap. The larger the handicap the more intrinsically fit the individual.

The best horses in a handicap race carry the largest weights, so the size of the handicap is a measure of the animal's quality.

There are striking parallels between cooperative behavior and exaggerated sexual ornamentsdisplayed by some animals, particularly certain birds, 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 his increased access to females, which is as much of a fitness concern as is his health. A cooperative act is, by definition, similarly costly (e.g. helping raise the young at the nest of an unrelated pair of birds versus producing and raising one's own offspring). It would therefore also signal fitness, and is probably as attractive to females as a physical handicap. If this is the case, cooperation 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 probably 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-silent mutation 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 well adapted 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 least number of unusual or minority features. This will have the effect of a sexual population rapidly shedding peripheral phenotypic features, thereby canalizing the entire outward appearance and behavior of all of its members. They will all very quickly begin to look remarkably similar to one another 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 cooperative, altruistic and social interactions. Thus, in the example above 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 (koinophilia). 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.

An African pygmy kingfisher, showing details of appearance and coloration that are shared by all African pygmy kingfishers to a high degree of fidelity.

Adaptation

In evolutionary theory, adaptation is the biological mechanism by which organisms adjust to new environments or to changes in their current environment. Although scientists discussed adaptation prior to the 1800s, it was not until then that Charles Darwin and Alfred Russel Wallace developed the theory of natural selection.

Wallace believed that the evolution of organisms was connected in some way with adaptation of organisms to changing environmental conditions. In developing the theory of evolution by natural selection, Wallace and Darwin both went beyond simple adaptation by explaining how organisms adapt and evolve. The idea of natural selection is that traits that can be passed down allow organisms to adapt to the environment better than other organisms of the same species. This enables better survival and reproduction compared with other members of the species, leading to evolution.

Organisms can adapt to an environment in different ways. They can adapt biologically, meaning they alter body functions. An example of biological adaptation can be seen in the bodies of people

living at high altitudes, such as Tibet. Tibetans thrive at altitudes where oxygen levels are up to 40 percent lower than at sea level. Breathing air that thin would cause most people to get sick, but Tibetans' bodies have evolved changes in their body chemistry. Most people can survive at high altitudes for a short time because their bodies raise their levels of hemoglobin, a protein that transports oxygen in the blood. However, continuously high levels of hemoglobin are dangerous, so increased hemoglobin levels are not a good solution to high-altitude survival in the long term. Tibetans seemed to have evolved genetic mutations that allow them to use oxygen far more efficently without the need for extra hemoglobin.

Organisms can also exhibit behavioral adaptation. One example of behavioral adaptation is how emperor penguins in Antarctica crowd together to share their warmth in the middle of winter.

Scientists who studied adaptation prior to the development of evolutionary theory included Georges Louis Leclerc Comte de Buffon. He was a French mathematician who believed that organisms changed over time by adapting to the environments of their geographical locations. Another French thinker, Jean Baptiste Lamarck, proposed that animals could adapt, pass on their adaptations to their offspring, and therefore evolve. The example he gave stated the ancestors of giraffes might have adapted to a shortage of food from short trees by stretching their necks to reach higher branches. In Lamarck's thinking, the offspring of a giraffe that stretched its neck would then inherit a slightly longer neck. Lamarck theorized that behaviors aquired in a giraffe's lifetime would affect its offspring. However, it was Darwin's concept of natural selection, wherein favorable traits like a long neck in giraffes suvived not because of aquired skills, but because only giraffes that had long enough necks to feed themselves survived long enough to reproduce. Natural selection, then, provides a more compelling mechanism for adaptation and evolution than Lamarck's theories.

Seahorse. Some creatures, such as this leafy sea dragon fish (Phycodurus eques) have evolved adaptations that allow them to blend in with their environment (in this case, seaweed) to avoid the attention of hungry predators.

Types of Adaptation

Genetic Mutation and Recombination

Deoxyribonucleic acid, or DNA, is the molecule that carries the information necessary for creating and maintaining life. DNA is made from a series of nucleotides, 4 small chemicals which chain together. The sequence of these chemicals can be read by specialized enzymes and organelles

within cells to produce new proteins. These proteins have various functions, and determine how the cell functions within its environment.

Since the first proteins and cellular constituents aggregated to form the first self-replicating cell, the interaction between DNA and the environment has driven adaptation. Single-celled organisms rely solely on molecular adaptation, since their basic structure prohibits the complex nature of developing new limbs other structures. Instead, an adaptation in a prokaryote comes from advantageous mutations within their DNA which create new proteins or alter the effects of current proteins. The chemical reactions enabled by these proteins allow the organisms to more efficiently collect nutrients, grow, and divide. The adaptation will persist in the population as long as it increases fitness and reproduction.

In eukaryotes and multi-cellular species, the process of mutation also drives adaptation. As in prokaryotes, the DNA is controlled by a system of proteins which interacts with the environment, known as the epigenome. In eukaryotes, the complexity of this system has increased. An adaptation can affect the organism on any level, from creating a different way to replicate DNA to developing entirely new organelles and structures of the body. Studies have shown that mutations are often deleterious, or do not adapt the organism to the environment. These mutations are not typically considered adaptations because they do not persist in the population at high levels. However, as the environment changes mal-adapted traits may become beneficial and persist as an adaptation to a new scenario.

Changes in Environment

Changes in the environment are second major category of adaptation. In many cases the epigenome is as or more important that the DNA itself. Large environmental changes, such as a change in ocean temperature or acidity, can affect a great number of species. As the environment changes, the proteins of the organisms start to function differently. Changes to the DNA or to how the epigenome interacts with the new environment can lead to a novel adaptation. For instance, life on Earth currently depends on a system of oxygen and carbon dioxide, which its organisms use for energy and respiration. Scientists have estimated that this environment was not present until photosynthetic organisms started creating oxygen and depositing it into the atmosphere. The new chemicals in the atmosphere started a wave of adaptation which has led to the current biome we have now.

As more and more species became differentiated, their interactions with each other started to drive adaptation as much as the simple composition of the atmosphere. Vast food webs developed and fell apart over the billions of years of life. These events were driven in part by the ability of organisms to quickly form an adaptation to a situation and continue reproducing. However, during many of these events, as many as 90 percent of species didn't survive the abrupt change. While adaptation can make organisms more competitive in an environment, it can also make them less flexible to survive in a changing environment.

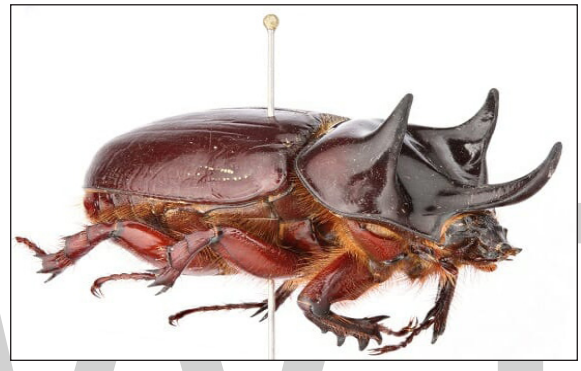
The complex interactions between animals have also led to diverse forms of selection which affect and form adaptation among the organisms involved. In sexual selection, for instance, differences and adaptation strategies between genders are not necessarily determined by the environment, but simply by the strange selection preferences of individuals trying to reproduce. Many birds

show highly colored males, selected for by the dull colored females. The adaptation of color in the males is a characteristic used to attract more females. The females' adaptation of dull color, on the other hand, is the result of a more directional selection of the predator prey relationship. Less colorful females are less likely to be spotted by predators. While these two adaptive traits contradict each other, they have persisted because they benefit the males and females in different ways.

Examples of Adaptation

Rhinocerous Beetle

If you've ever seen a Rhinoceros Beetle, you've probably wondered what it uses those huge horns for. Seen below is a male Rhino Beetle, with its distinctive headgear.



Like all arthropods, the beetle is divided into segments. These various sections are very responsive to adaptation. In the Rhino Beetle, the head section has developed these large thorns. The male beetles use these large obtrusions to fight each other, in competition for females. It is presumed that ancestral beetles had little to no horns. As the beetles competed for mates over many generations, mutations which created a better way to peel the opponent off his feet were rewarded. Over time, this adaptation of large horns emerged. Horns with the greatest ability of defeating opponents allow those males to reproduce more and the adaptation will persist within the population.

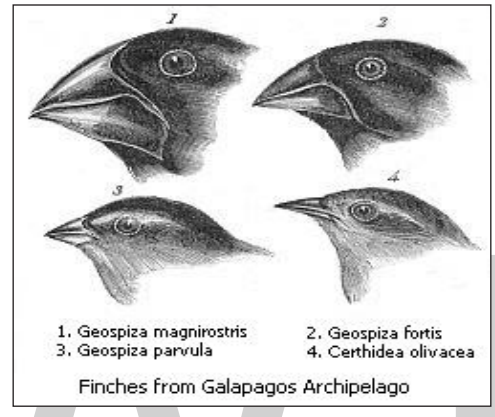
Digestive Tract in Mammals

If you were to dissect various mammals, you would find something very peculiar in the size and composition of their digestive tract. Carnivores, like wolves and cats, have very short and simple digestive tracts. In fact, the more carnivorous an animal, the shorter and simpler the digestive tract is. Meat and animal products are easily digested. The adaptation of a short gut allows these animals to quickly process the energy out of their meaty meal, before it starts to rot in their gut.

Herbivores, on the other hand, have a long and complex digestive system. Some mammals, the ruminants, have multiple stomachs to process the energy out of grasses and other tough plants. Non-ruminant herbivores have complex twists and turns in their guts which increases the surface area and the amount of time food spends in the digestive tract. This adaptation allows the animals to process all of the energy out of the plant material. Interestingly, humans have a vastly complex gut, an adaptation for herbivores. Part of the complex story behind diet, nutrition, and health probably arises from the fact that the Western diet focuses on meat, rather than the foods our body has adapted to eat.

Adaptive Radiation

In evolutionary biology, adaptive radiation is a process in which organisms diversify rapidly from an ancestral species into a multitude of new forms, particularly when a change in the environment makes new resources available, creates new challenges, or opens new environmental niches. Starting with a recent single ancestor, this process results in the speciation and phenotypic adaptation of an array of species exhibiting different morphological and physiological traits. The prototypical example of adaptive radiation is finch speciation on the Galapagos ("Darwin's finches"), but examples are known from around the world.



Four of the 14 finch species found in the Galápagos Archipelago, which are thought to have evolved via an adaptive radiation that diversified their beak shapes, enabling them to exploit different food sources.

Characteristics

Four features can be used to identify an adaptive radiation:

- A common ancestry of component species: Specifically a recent ancestry. Note that this is not the same as a monophyly in which all descendants of a common ancestor are included.
- A phenotype-environment correlation: A significant association between environments and the morphological and physiological traits used to exploit those environments.
- Trait utility: The performance or fitness advantages of trait values in their corresponding environments.
- Rapid speciation: Presence of one or more bursts in the emergence of new species around the time that ecological and phenotypic divergence is underway.

Conditions

Adaptive radiation tends to take place under the following conditions:

- A new habitat has opened up: A volcano, for example, can create new ground in the middle of the ocean. This is the case in places like Hawaii and the Galapagos. For aquatic species, the formation of a large new lake habitat could serve the same purpose; the tectonic movement that formed the East African Rift, ultimately leading to the creation of the Rift Valley

Lakes, is an example of this. An extinction event could effectively achieve this same result, opening up niches that were previously occupied by species that no longer exist.

- This new habitat is relatively isolated. When a volcano erupts on the mainland and destroys an adjacent forest, it is likely that the terrestrial plant and animal species that used to live in the destroyed region will recolonize without evolving greatly. However, if a newly formed habitat is isolated, the species that colonize it will likely be somewhat random and uncommon arrivals.
- The new habitat has a wide availability of niche space. The rare colonist can only adaptively radiate into as many forms as there are niches.

Examples

Darwin's Finches

Darwin's finches are an often-used textbook example of adaptive radiation. Today represented by approximately 15 species, Darwin's finches are Galapagos endemics famously adapted for a specialized feeding behavior (although one species, the Cocos finch (Pinaroloxias inornata), is not found in the Galapagos but on the island of Cocos south of Costa Rica). Darwin's finches are not actually finches in the true sense, but are members of the tanager family Thraupidae, and are derived from a single ancestor that arrived in the Galapagos from mainland South America perhaps just 3 million years ago. Excluding the Cocos finch, each species of Darwin's finch is generally widely distributed in the Galapagos and fills the same niche on each island. For the ground finches, this niche is a diet of seeds, and they have thick bills to facilitate the consumption of these hard materials. The ground finches are further specialized to eat seeds of a particular size: The large ground finch (Geospiza magnirostris) is the largest species of Darwin's finch and has the thickest beak for breaking open the toughest seeds, the small ground finch (Geospiza fuliginosa) has a smaller beak for eating smaller seeds, and the medium ground finch (Geospiza fortis) has a beak of intermediate size for optimal consumption of intermediately sized seeds (relative to G. magnirostris and G. fuliginosa). There is some overlap: For example, the most robust medium ground finches could have beaks larger than those of the smallest large ground finches. Because of this overlap, it can be difficult to tell the species apart by eye, though their songs differ. These three species often occur sympatrically, and during the rainy season in the Galapagos when food is plentiful, they specialize little and eat the same, easily accessible foods. It was not well-understood why their beaks were so adapted until Peter and Rosemary Grant studied their feeding behavior in the long dry season, and discovered that when food is scarce, the ground finches use their specialized beaks to eat the seeds that they are best suited to eat and thus avoid starvation.

The other finches in the Galapagos are similarly uniquely adapted for their particular niche. The cactus finches have somewhat longer beaks than the ground finches that serve the dual purpose of allowing them to feed on Opuntia cactus nectar and pollen while these plants are flowering, but on seeds during the rest of the year. The warbler-finches have short, pointed beaks for eating insects. The woodpecker finch (Camarhynchus pallidus) has a slender beak which it uses to pick at wood in search of insects; it also uses small sticks to reach insect prey inside the wood, making it one of the few animals that use tools.

The mechanism by which the finches initially diversified is still an area of active research. One proposition is that the finches were able to have a non-adaptive, allopatric speciation event on separate islands in the archipelago, such that when they reconverged on some islands, they were able to maintain reproductive isolation. Once they occurred in sympatry, niche specialization was favored so that the different species competed less directly for resources. This second, sympatric event was adaptive radiation.

Cichlids of the African Great Lakes

The haplochromine cichlid fishes in the Great Lakes of the East African Rift (particularly in Lake Tanganyika, Lake Malawi, and Lake Victoria) form the most speciose modern example of adaptive radiation. These lakes are believed to be home to about 2,000 different species of cichlid, spanning a wide range of ecological roles and morphological characteristics. Cichlids in these lakes fill nearly all of the roles typically filled by a large number of fish families, including those of predators, scavengers, and herbivores, with varying dentitions and head shapes to match their dietary habits. In each case, the radiation events are only a few million years old, making the very high level of speciation particularly remarkable. Several factors could be responsible for this diversity: The availability of a multitude of niches probably favored specialization, as few other fish taxa are present in the lakes (meaning that sympatric speciation was the most probable mechanism for initial specialization). Also, continual changes in the water level of the lakes during the Pleistocene (which often turned the largest lakes into several smaller ones) could have created the conditions for secondary allopatric speciation.

Tanganyika Cichlids

Lake Tanganyika is the site from which nearly all the cichlid lineages of East Africa (including both riverine and lake species) originated. Thus, the species in the lake constitute a single adaptive radiation event but do not form a single monophyletic clade. Lake Tanganyika is also the least speciose of the three largest African Great Lakes, with only around 200 species of cichlid; however, these cichlids are more morphologically divergent and ecologically distinct than their counterparts in lakes Malawi and Victoria, an artifact of Lake Tanganyika's older cichlid fauna. Lake Tanganyika itself is believed to have formed 9-12 million years ago, putting a recent cap on the age of the lake's cichlid fauna. Many of Tanganyika's cichlids live very specialized lifestyles. The giant or emperor cichlid (Boulengerochromis microlepis) is a piscivore often ranked the largest of all cichlids (though it competes for this title with South America's Cichla temensis, the speckled peacock bass). It is thought that giant cichlids spawn only a single time, breeding in their third year and defending their young until they reach a large size, before dying of starvation some time thereafter. The three species of Altolamprologus are also piscivores, but with laterally compressed bodies and thick scales enabling them to chase prey into thin cracks in rocks without damaging their skin.Plecodus straeleni has evolved large, strangely curved teeth that are designed to scrape scales off of the sides of other fish, scales being its main source of food. Gnathochromis permaxillaris possesses a large mouth with a protruding upper lip, and feeds by opening this mouth downward onto the sandy lake bottom, sucking in small invertebrates. A number of Tanganyika's cichlids are shell-brooders, meaning that mating pairs lay and fertilize their eggs inside of empty shells on the lake bottom. Lamprologus callipterus is the most unique egg-brooding species, with 15 cm-long males amassing collections of shells and guarding them in the hopes of attracting females (about 6 cm in length)

to lay eggs in these shells. These dominant males must defend their territories from three types of rival: (1) other dominant males looking to steal shells; (2) younger, "sneaker" males looking to fertilize eggs in a dominant male's territory; and (3) tiny, 2–4 cm "parasitic dwarf" males that also attempt to rush in and fertilize eggs in the dominant male's territory. These parasitic dwarf males never grow to the size of dominant males, and the male offspring of dominant and parasitic dwarf males grow with 100% fidelity into the form of their fathers. A number of other highly specialized Tanganyika cichlids exist aside from these examples, including those adapted for life in open lake water up to 200m deep.

Malawi Cichlids

The cichlids of Lake Malawi constitute a "species flock" of up to 1000 endemic species. Only seven cichlid species in Lake Malawi are not a part of the species flock: The Eastern happy (*Astatotilapia calliptera*), the sungwa (*Serranochromis robustus*), and five tilapia species (genera *Oreochromis* and *Coptodon*). All of the other cichlid species in the lake are descendants of a single original colonist species, which itself was descended from Tanganyikan ancestors. The common ancestor of Malawi's species flock is believed to have reached the lake 3.4 million years ago at the earliest, making Malawi cichlids' diversification into their present numbers particularly rapid. Malawi's cichlids span a similarly range of feeding behaviors to those of Tanganyika, but also show signs of a much more recent origin. For example, all members of the Malawi species flock are mouth-brooders, meaning the female keeps her eggs in her mouth until they hatch; in almost all species, the eggs are also fertilized in the female's mouth, and in a few species, the females continue to guard their fry in their mouth after they hatch. Males of most species display predominantly blue coloration when mating. However, a number of particularly divergent species are known from Malawi, including the piscivorous *Nimbochromis livingtonii*, which lies on its side in the substrate until small cichlids, perhaps drawn to its broken white patterning, come to inspect the predator - at which point they are swiftly eaten.

Victoria Cichlids

Lake Victoria's cichlids are also a species flock, once composed of some 500 or more species. The deliberate introduction of the Nile Perch (*Lates niloticus*) in the 1950s proved disastrous for Victoria cichlids, and the collective biomass of the Victoria cichlid species flock has decreased substantially and an unknown number of species have become extinct. However, the original range of morphological and behavioral diversity seen in the lake's cichlid fauna is still mostly present today, if endangered. These again include cichlids specialized for niches across the trophic spectrum, as in Tanganyika and Malawi, but again, there are standouts. Victoria is famously home to a large number of piscivorous cichlid species, some of which feed by sucking the contents out of mouth-brooding females' mouths. Victoria's cichlids constitute a far younger radiation than even that of Lake Malawi, with estimates of the age of the flock ranging from 200,000 years to as little as 14,000.

Adaptive Radiation in Hawaii

Hawaii has served as the site of a number of adaptive radiation events, owing to its isolation, recent origin, and large land area. The three most famous examples of these radiations are presented below, though insects like the Hawaiian drosophilid flies and Hyposmocoma moths have also undergone adaptive radiation.

An ʻiʻiwi (Drepanis coccinea). Note the long, curved beak for sipping nectar from tubular flowers.

Hawaiian Honeycreepers

The Hawaiian honeycreepers form a large, highly morphologically diverse species group that began radiating in the early days of the Hawaiian archipelago. While today only 17 species are known to persist in Hawaii (3 more may or may not be extinct), there were more than 50 species prior to Polynesian colonization of the archipelago (between 18 and 21 species have gone extinct since the discovery of the islands by westerners). The Hawaiian honeycreepers are known for their beaks, which are specialized to satisfy a wide range of dietary needs: For example, the beak of the ʻakiapōlāʻau (*Hemignathus wilsoni*) is characterized by a short, sharp lower mandible for scraping bark off of trees, and the much longer, curved upper mandible is used to probe the wood underneath for insects. Meanwhile, the ʻiʻiwi (*Drepanis coccinea*) has a very long curved beak for reaching nectar deep in *Lobelia* flowers. An entire clade of Hawaiian honeycreepers, the tribe Psittirostrini, is composed of thick-billed, mostly seed-eating birds, like the Laysan finch (*Telespiza cantans*). In at least some cases, similar morphologies and behaviors appear to have evolved convergently among the Hawaiian honeycreepers; for example, the short, pointed beaks of *Loxops* and *Oreomystis* evolved separately despite once forming the justification for lumping the two genera together. The Hawaiian honeycreepers are believed to have descended from a single common ancestor some 15 to 20 million years ago, though estimates range as low as 3.5 million years.

Hawaiian Silverswords

A mixture of blooming and non-blooming Haleakalā silverswords (*Argyroxiphium sandwicense macrocephalum*).

Adaptive radiation is not a strictly vertebrate phenomenon, and examples are also known from among plants. The most famous example of adaptive radiation in plants is quite possibly the Hawaiian silverswords, named for alpine desert-dwelling *Argyroxiphium* species with long, silvery leaves that live for up to 20 years before growing a single flowering stalk and then dying. The Hawaiian silversword alliance consists of twenty-eight species of Hawaiian plants which, aside from the namesake silverswords, includes trees, shrubs, vines, cushion plants, and more. The silversword alliance is believed to have originated in Hawaii no more than 6 million years ago, making this one of Hawaii's youngest adaptive radiation events. This means that the silverswords evolved on Hawaii's modern high islands, and descended from a single common ancestor that arrived on Kauai from western North America. The closest modern relatives of the silverswords today are California tarweeds of the family Asteraceae.

Hawaiian Lobelioids

Hawaii is also the site of a separate major floral adaptive radiation event: The Hawaiian lobelioids. The Hawaiian lobelioids are significantly more speciose than the silverswords, perhaps because they have been present in Hawaii for so much longer: They descended from a single common ancestor who arrived in the archipelago up to 15 million years ago. Today the Hawaiian lobelioids form a clade of over 125 species, including succulents, trees, shrubs, epiphytes, etc. A large number of species have been lost to extinction and many of the surviving species endangered.

Caribbean Anoles

Anole lizards are distributed broadly in the New World, from the Southeastern US to South America. With over 400 species currently recognized, often placed in a single genus (*Anolis*), they constitute one of the largest radiation events among all lizards. Anole radiation on the mainland has largely been a process of speciation, and is not adaptive to any great degree, but anoles on each of the Greater Antilles (Cuba, Hispaniola, Puerto Rico, and Jamaica) have adaptively radiated in separate, convergent ways. On each of these islands, anoles have evolved with such a consistent set of morphological adaptations that each species can be assigned to one of six "ecomorphs": Trunk–ground, trunk–crown, grass–bush, crown–giant, twig, and trunk. Take, for example, crown–giants from each of these islands: The Cuban *Anolis luteogularis*, Hispaniola's *Anolis ricordii*, Puerto Rico's *Anolis cuvieri*, and Jamaica's *Anolis garmani* (Cuba and Hispaniola are both home to more than one species of crown–giant). These anoles are all large, canopy-dwelling species with large heads and large lamellae (scales on the undersides of the fingers and toes that are important for traction in climbing), and yet none of these species are particularly closely related and appear to have evolved these similar traits independently. The same can be said of the other five ecomorphs across the Caribbean's four largest islands. Much like in the case of the cichlids of the three largest African Great Lakes, each of these islands is home to its own convergent *Anolis* adaptive radiation event.

Other Examples

Presented above are the most well-documented examples of modern adaptive radiation, but other examples are known. On Madagascar, birds of the family Vangidae are marked by very distinct beak shapes to suit their ecological roles. Madagascan mantellid frogs have radiated into forms that mirror other tropical frog faunas, with the brightly colored mantellas (Mantella) having evolved

convergently with the Neotropical poison dart frogs of Dendrobatidae, while the arboreal Boophis species are the Madagascan equivalent of tree frogs and glass frogs. The pseudoxyrhophiine snakes of Madagascar have evolved into fossorial, arboreal, terrestrial, and semi-aquatic forms that converge with the colubroid faunas in the rest of the world. These Madagascan examples are significantly older than most of the other examples presented here: Madagascar's fauna has been evolving in isolation since the island split from India some 88 million years ago, and the Mantellidae originated around 50 mya. Older examples are known: The K-Pg extinction event, which caused the disappearance of the dinosaurs and most other reptilian megafauna 65 million years ago, is seen as having triggered a global adaptive radiation event that created the mammal diversity that exists today.

Coevolution

In the context of evolutionary biology, coevolution refers to the evolution of at least two species, which occurs in a mutually dependent manner. Coevolution was first described in the context of insects and flowering plants, and has since been applied to major evolutionary events, including sexual reproduction, infectious disease, and ecological communities. Coevolution functions by reciprocal selective pressures on two or more species, analogous to an arms race in an attempt to outcompete each other. Classic examples include predator-prey, host-parasite, and other competitive relationships between species. While the process of coevolution generally only involves two species, multiple species can be involved. Moreover, coevolution also results in adaptations for mutual benefit. An example is the coevolution of flowering plants and associated pollinators (e.g., bees, birds, and other insect species).

Coevolution Examples

Predator-prey Coevolution

The predator-prey relationship is one of the most common examples of coevolution. In this respect, there is a selective pressure on the prey to avoid capture and thus, the predator must evolve to become more effective hunters. In this manner, predator-prey coevolution is analogous to an evolutionary arms race and the development of specific adaptations, especially in prey species, to avoid or discourage predation.

Herbivores and Plants

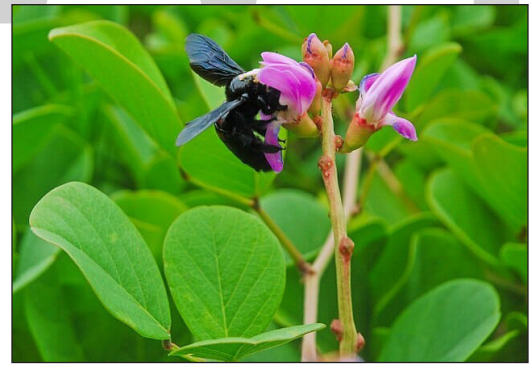
Similar to the predator-prey relationship, another common example of coevolution is the relationship between herbivore species and the plants that they consume. One example is that of the lodgepole pine seeds, which both red squirrels and crossbills eat in various regions of the Rocky Mountains. Both herbivores have different tactics for extracting the seeds from the lodgepole pine cone; the squirrels will simply gnaw through the pine cone, whereas the crossbills have specialized mandibles for extracting the seeds. Thus, in regions where red squirrels are more prevalent, the lodgepole pine cones are denser, contain fewer seeds, and have thinner scales to prevent the squirrels from obtaining the seeds. However, in regions where crossbills are more prevalent, the cones are lighter and contain thick scales, so as to prevent the crossbills from accessing the seeds. Thus, the lodgepole pine is concurrently coevolving with both of these herbivore species.

Acacia Ants and Acacias

An example of coevolution that is not characteristic of an arms race, but one which provides a mutual benefit to both a plant species and insect is that of the acacia ants and acacia plants. In this relationship, the plant and ants have coevolved to have a symbiotic relationship in which the ants provide the plant with protection against other potentially damaging insects, as well as other plants which may compete for nutrients and sunlight. In return, the plant provides the ants with shelter and essential nutrients for the ants and their growing larvae.

Flowering Plants and Pollinators

Another example of beneficial coevolution is the relationship between flowering plants and the respective insect and bird species that pollinate them. In this respect, flowering plants and pollinators have developed co-adaptations that allow flowers to attract pollinators, and insects and birds have developed specialized adaptations for extracting nectar and pollen from the plants.



Research indicates that there are at least three traits that flowering plants have evolved to attract pollinators:

- Distinct visual cues: Flowering plants have evolved bright colors, stripes, patterns, and colors specific to the pollinator. For example, flowering plants seeking to attract insect pollinators are typically blue an ultraviolet, whereas red and orange are designed to attract birds.
- Scent: Flowering plants use scents as a means of instructing insects as to their location. Since scents become stronger closer to the plant, the insect is able to hone-in and land on that plant to extract its nectar.

- Some flowers use chemical and tactile means to mimic female insect species to attract the male species. For example, orchids secrete a chemical that is the same as the pheromones of bee and wasp species. When the male insect lands on the flower and attempts to copulate, the pollen is transferred to him.

Hummingbirds are another type of pollinator that have coevolved for mutual benefit. The hummingbirds serve as pollinators and the flowers supply the birds with nutrient-rich nectar. The flowering plants attract the hummingbirds with certain colors, the shape of the flower accommodates the bird's bill, and such flowers tend to bloom when hummingbirds are breeding. Coevolution of such flowering plants with various hummingbird species is evident by the distinct shape and length of the flower's corolla tubes, which have adapted to the shape and length of the hummingbird bill that pollenates that plant. The shape of the flower has also adapted such that the pollen becomes attached to a particular region of the bird while it consumes the nectar from the flower.

Divergent Evolution

Divergent evolution or divergent selection is the accumulation of differences between closely related populations within a species, leading to speciation. Divergent evolution is typically exhibited when two populations become separated by a geographic barrier (such as in allopatric or peripatric speciation) and experience different selective pressures that drive adaptations to their new environment. After many generations and continual evolution, the populations become unable to interbreed with one another.The American naturalist J. T. Gulick (1832-1923) was the first to use the term "divergent evolution", with its use becoming widespread in modern evolutionary literature. Classic examples of divergence in nature are the adaptive radiation of the finches of the Galapagos or the coloration differences in populations of a species that live in different habitats such as with pocket mice and fence lizards.

The term can also be applied in molecular evolution, such as to proteins that derive from homologous genes. Both orthologous genes (resulting from a speciation event) and paralogous genes (resulting from gene duplication) can illustrate divergent evolution. Through gene duplication, it is possible for divergent evolution to occur between two genes within a species. Similarities between species that have diverged are due to their common origin, so such similarities are homologies. In contrast, convergent evolution arises when an adaptation has arisen independently, creating analogous structures such as the wings of birds and of insects.

Creation and Usage

The term divergent evolution is believed to have been first used by J. T. Gulick. Divergent evolution is commonly defined as what occurs when two groups of the same species evolve different traits within those groups in order to accommodate for differing environmental and social pressures. Various examples of such pressures can include predation, food supplies, and competition for mates. The tympanal ears of certain nocturnal insects are believed to be a result of needing the ultrasonic hearing that tympanal ears provide in order to hear predators in the dark. Non-nocturnal insects - that do not need to fear nocturnal predators - are often found to lack these tympanal ears.

Causes

Animals undergo divergent evolution for a number of reasons. Predators or their absence, changes in the environment, and the time at which certain animals are most active are chief among them.

Predators

A lack of predators – predatory birds and mammals - for cliff-side nest residing kittiwake caused that particular group of kittiwake to lose their ancestral mobbing behavior that had been exhibited up until that point for protecting young. The mobbing behavior normally displayed by the kittiwake is lost when the kittiwake take residence in this area with little threat from predators towards their young. The mobbing behavior was originally developed to protect ground-level nests containing young from various predators such as reptiles, mammals and other birds.

Environment

The cliff-side nesting area itself was similarly responsible for the kittiwakes losing their mobbing mentality – predatory mammals small enough to fit on the cliff edges along with the kittiwakes and their offspring would not be able to make the climb up while predatory birds would not be able to maneuver near the cliff face while also being afflicted by the weather conditions of the area.

Distinctions

Divergent evolution is always coupled with convergent evolution, as they are both similar and different in various facets such as whether something evolves, what evolves, and why it evolves. It is instructive to compare divergent evolution with both convergent and parallel evolution.

Divergent versus Convergent Evolution

Convergent evolution is defined as a similar trait evolution that occurs in two otherwise different species of animal as a result of those two species living in similar environments with similar environmental pressures like predators and food supply. It differs from divergent evolution in that the species involved are different while the traits they obtain do not differ from each other. An example of convergent evolution is the development of horns in various species for sparring over mates, resources, and territory.

Divergent versus Parallel Evolution

Parallel evolution is the development of a similar trait in species descending from the same ancestor. It is similar to divergent evolution in that the species descend from the same ancestor, but it differs in that the trait is the same while in divergent evolution the trait is not. An example of parallel evolution are certain arboreal frog species, 'flying' frogs, in both Old World families and New World families having developed the ability of gliding flight. They have "enlarged hands and feet, full webbing between all fingers and toes, lateral skin flaps on the arms and legs, and reduced weight per snout-vent length".

Darwin's Finches

One of the most famous examples of divergent evolution is the case of Darwin's Finches. During Darwin's travels to the Galápagos Islands he discovered several different species of finch that shared a common ancestor. They lived on varying diets and had beaks that differed in shape and size reflecting their diet. The change in beak shape and size was believed to be a result of the lengths the birds had to go to in order to support their change in diet. Some Galapagos finches have beaks that are larger and more powerful to crack nuts with. A different type allows the bird to use cactus spines to spear insects in the bark of trees.

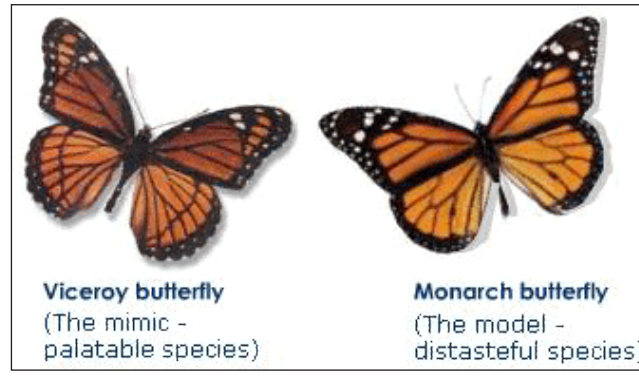
Divergent Evolution in Dogs

Another good example of divergent evolution is the origin of the domestic dog and the modern wolf. Dogs and wolves both diverged from a common ancestor. To further support divergent evolution of dogs and wolves, genomic research was conducted to compare mitochondrial DNA to indicate the presence of shared ancestry. Taking 162 wolves from various parts of the world as well as 140 dogs of 60 different breeds, it is found that dogs and wolves have shared ancestry by how similar their DNA sequences are. Comparison of the physical characteristics reveal that dogs and wolves have similar body shape, skull size, and limb formation, further supporting their close genetic makeup and thus shared ancestry. An example of this would be how physically and behaviorally similar malamutes and huskies are to wolves. Huskies and malamutes have very similar body size and skull shape. Huskies and wolves share similar coat patterns as well as tolerance to cold. In the hypothetical situations, mutations and breeding events were simulated to show the progression of the wolf behavior over ten generations. The results concluded that even though the last generation of the wolves were more docile and less aggressive, the temperament of the wolves fluctuated greatly from one generation to the next.

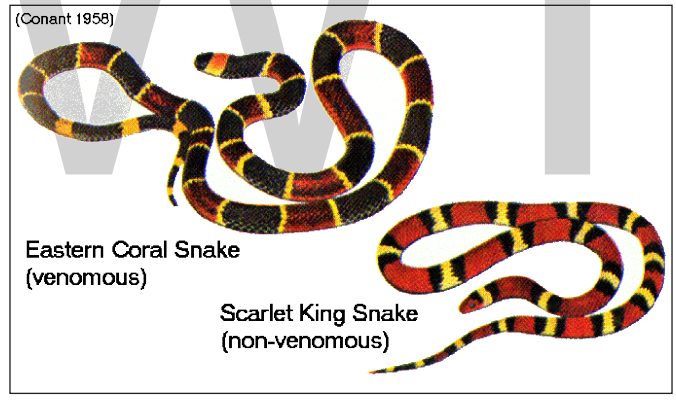
Convergent Evolution

Convergent evolution is the process by which unrelated or distantly related organisms evolve similar body forms, coloration, organs, and adaptations. Natural selection can result in evolutionary convergence under several different circumstances. Species can converge in sympatry, as in mimicry complexes among insects, especially butterflies (coral snakes and their mimics constitute another well-known example). Mimicry evolves after one species, the 'model' has become aposematic (warningly colored) because it is toxic or poisonous and therefore protected. Two distinct kinds of

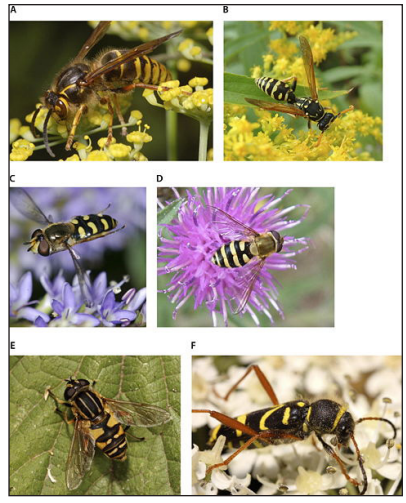
mimicry are recognized, Batesian and Müllerian. In Batesian mimicry, the mimic is palatable or unprotected, but gains from being mistaken for the model, which is unpalatable or protected. Two protected model species can also converge because of the advantage of being mistaken for each other (Müllerian mimicry).

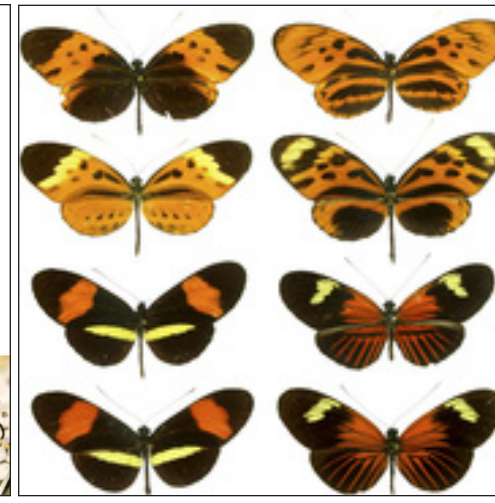


Mimicry is an interesting consequence of warning coloration that nicely demonstrates the power of natural selection. An organism that commonly occurs in a community along with a poisonous or distasteful species can benefit from a resemblance to the warningly colored species, even though the 'mimic' itself is nonpoisonous and quite palatable. Because predators that have experienced contacts with the model species, and have learned to avoid it, mistake the mimic species for the model and avoid it as well. Such false warning coloration is termed Batesian mimicry after its discoverer.



Many species of harmless snakes mimic poisonous snakes; in Central America, some harmless snakes are so similar to poisonous coral snakes that only an expert can distinguish the mimic from the 'model.' A few experts have even died as a result of a superficial misidentifications. Similarly, certain harmless flies and clearwing moths mimic bees and wasps, and palatable species of butterflies mimic distasteful species. Batesian mimicry is disadvantageous to the model species because some predators will encounter palatable or harmless mimics and thereby take longer to learn to avoid the model. The greater the proportion of mimics to models, the longer is the time required for predator learning and the greater the number of model casualties. In fact, if mimics became more abundant than models, predators might not learn to avoid the prey item at all but might actively search out model and mimic alike. For this reason Batesian mimics are usually much less abundant than their models; also, mimics of this sort are frequently polymorphic (often only females are mimics) and mimic several different model species.



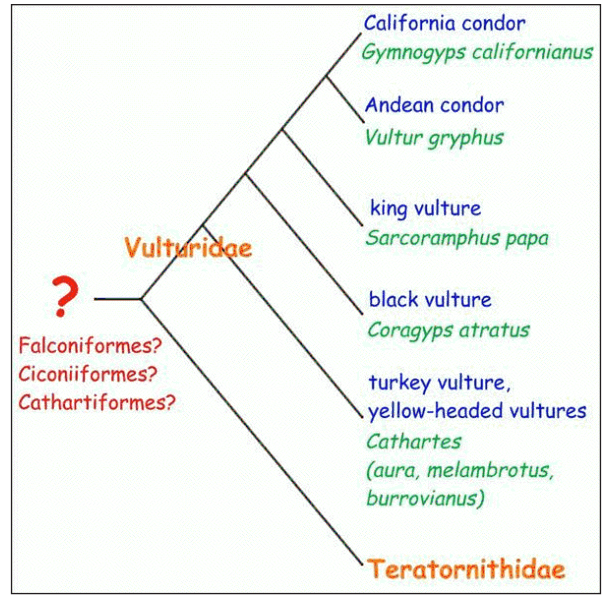


Müllerian mimicry is different, and occurs when two species, both distasteful or dangerous, mimic one another. Both bees and wasps, for example, are usually banded with yellows and blacks. Because potential predators encounter several species of Müllerian mimics more frequently than just a single species, they learn to avoid them faster, and the relationship is actually beneficial to both prey species. The resemblance need not be as precise as it must be under Batesian mimicry because neither species actually deceives the predator; rather, each only reminds the predator of its dangerous or distasteful properties. Müllerian mimicry is beneficial to all parties including the predator; mimics can be equally common and are rarely polymorphic.

Molecules can evolve convergently, especially when parasites mimic molecular messages that signal 'self' to immune responses of hosts, which allows the parasite to elude its host's defenses. Molecular convergence could also take place when a particular metabolic function requires similar or identical molecular structure. Some gene circuits and gene networks appear to have undergone convergent evolution by single-gene duplications in higher eukaryotes. Convergence in DNA nucleotide sequences would lead to erroneous phylogenetic conclusions, which would be problematical for molecular systematic studies.

Evolutionary convergence involving unrelated organisms living in similar environments but in different places (allopatry) can also occur in another way. This usually takes place in relatively simple communities in which biotic interactions are highly predictable and the resulting number of different ways of exploiting the environment are limited. Similar environments pose similar challenges to survival and reproduction, and those traits that enhance Darwinian fitness are selected for in each environment. Such organisms that fill similar ecological roles in different, independently-evolved, biotas are termed "ecological equivalents". Examples are legion.

Wings and wing-like structures have evolved independently several times, in insects, reptiles (pterosaurs and birds) and in mammals (bats). Flight first evolved in insects about 330 million years ago (mya), second in pterosaurs (about 225 mya), later in birds (about 150 mya), and still later in bats (50-60 mya). Some frogs, lizards, and mammals have also evolved the ability to glide, presumably a precursor to flight. In order to land safely, such hang gliders must time their stall precisely at the right moment and place.



For many years, avian systematists classified Old World and New World vultures as close relatives, both thought to be allied to raptors (hawks and owls). However, DNA hybridization suggested that, although Old World vultures are indeed related to raptors, New World vultures are not, but are descendents of common ancestors to storks and cranes (more recent studies are equivocal but still support independent evolution of the two clades). Morphological convergence was strong enough to actually mislead students of bird classification. Interestingly, a behavioral trait was conserved in the evolution of new world vultures: When heat stressed, storks defecate/urinate on their own legs to dissipate excess heat. New World vultures do this, whereas Old World vultures do not.

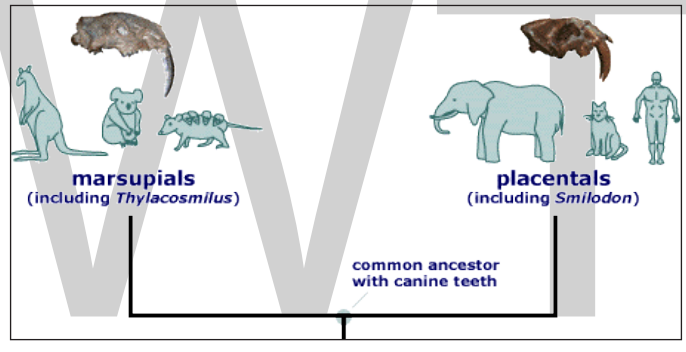
New World Cactus African Euphorb.

Arid regions of South Africa support a wide variety of euphorbeaceous plants, some of which are strikingly close to American cacti phenotypically. They are leafless stem succulents, protected by sharp spines, presumably adaptations to reduce water loss and predation in arid environments. Similarly, evergreen sclerophyll woody shrubs have evolved convergently under Mediterranean climates in several different regions.

African Macronix.

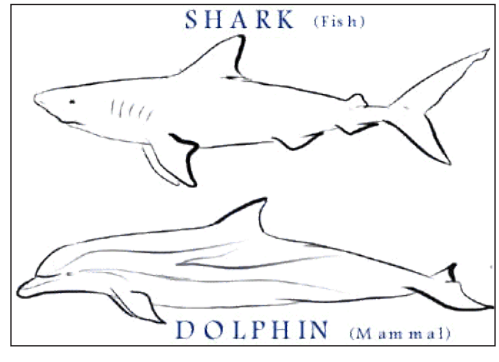
American Medolark.

A brown bird of some African prairies and grasslands, the African yellow-throated longclaw (Macronix croceus), a motacillid, has a yellow breast with a black chevron "V". This motacillid looks and acts so much like an American meadowlark (Sturnella magna), an icterid, that a competent bird watcher might mistake them for the same species, yet they belong to different avian families. Another example is the North American Little Auk and the Magellan Diving Petrel, two superficially very similar aquatic birds, which belong to different avian orders.

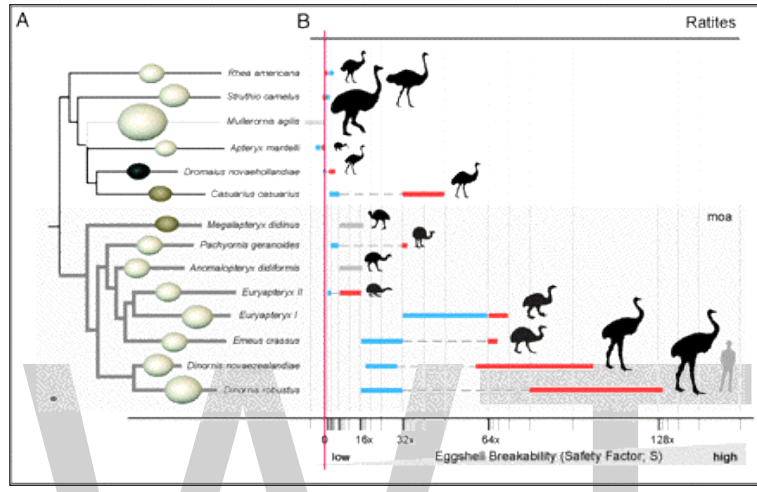


South American Thylacosmilus and North American Smilodon.

Convergence sometimes occurs under unusual conditions where selective forces for the achievement of a particular mode of existence are particularly strong. Presumably in response to thick-skinned prey, two fossil saber-tooth carnivores, the South American marsupial 'cat,' Thylacosmilus, and the North American placental saber-toothed tiger, Smilodon, evolved long knife-like canine teeth independently (but these were not contemporary). Many other marsupial mammals have undergone convergent evolution with placentals, including moles, mice, wombats (woodchucks), numbats (anteaters), quolls (cats), and thylacines (wolves).



Still another example of convergent evolution is seen in the similar shape and coloration of fish and cetaceans, both of which have adapted to the marine environment by developing a fusiform body and neutral buoyancy (an extinct group of marine reptiles known as ichthyosaurs evolved the same body plan). Sharks and dolphins are also countershaded, with a light underbelly and a darker upper surface, which makes them less visible from both below and above. However, countershading is actually the rule among both arthropods and vertebrates, so it is presumably an ancestral state that has been retained throughout the evolution of both groups.



Flightless birds such as the emu, ostrich, and rhea fill very similar ecological niches on different continents. If ratites evolved from a Gondwanan common ancestor, they would not represent evolutionary convergence but instead would constitute an example of a shared (and conserved) ancestral flightless state. Now thought to be convergent, DNA evidence suggests that these "ratites" do not share a common ancestry but have evolved independently.

Live bearing, or viviparity, has evolved over 100 times among squamate reptiles (lizards and snakes), usually in response to cold climates. The probable mechanism behind the evolution of viviparity is that, by holding her eggs, a gravid female can both protect them from predators and, by basking, warm them, which would increase rate of development. Eventually, such selective forces favoring egg retention could lead to eggs hatching within a mother and live birth. This has happened even in geckos, all of which lay eggs except for one genus in New Caledonia and several related cold temperate New Zealand forms, which bear their young alive. In some skinks and xantusiid lizards, embryos attach to their mother's oviducts and grow, gaining nutrients during development via placental arrangements reminiscent of those in mammals.


Thorny Devil Moloch horridus.

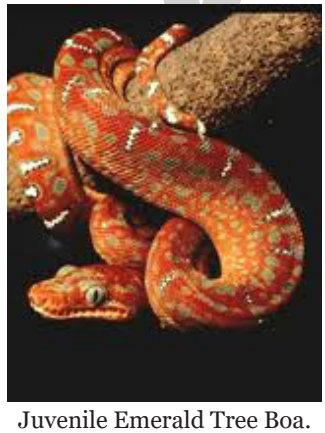

Horned Lizard Phrynosoma cornutum.

Convergent evolutionary responses of lizards to arid environments are evident between continents. For example, Australian and North American deserts both support a cryptically-colored and thornily-armored ant specialized species: The thorny devil, Moloch horridus, an agamid, exploits this ecological role in Australia, while its counterpart the desert horned lizard (Phrynosoma), an iguanid, occupies it in North America. No Kalahari lizard has adopted such a life style. Interestingly, morphometric analysis demonstrates that the thorny devil and desert horned lizard are actually anatomically closer to one another than either species is to another member of its own lizard fauna, which are much more closely related.

Emerald Tree Boa Corallus caninus.

Green tree python Chondropython viridis.

Emerald Tree Boas from South American Amazonian rainforests are strikingly convergent with Green Tree Pythons found halfway around the world in similar rainforests in Australia, a spectacular example of ecological equivalents. Both of these snakes live high up in the canopy and eat birds. Adults are green, cryptically colored, matching the colors of leaves. Juveniles of both species are bright yellow or orange.



Juvenile Emerald Tree Boa.

Juvenile Green Tree Python.

Colorful, blue, red and yellow tails have evolved repeatedly among distantly related lizards in many families (agamids, anguids, gymnopthlamids, lacerids, skinks, and teiids), presumably a ploy to attract a predator's attention away from the head to the tail, which can be broken off and regenerated should a predator attack it.

The New World iguanid Basiliscus, sometimes called 'Jesus lizards,' because they can run across the surface of water, have undergone convergent evolution with the Old World agamid Hydrosaurus. Both Basiliscus and Hydrosaurus have enlarged rectangular, plate-like, fringed scales on their toes, which allow these big lizards to run across water using surface tension for support.

Blue-tailed anguid from Mexico (Celestes).

A skink (Morethia butleri).

Open sandy deserts pose severe problems for their inhabitants: (1) windblown sands are always loose and provide little traction; (2) surface temperatures at midday rise to lethal levels; and (3) open sandy areas offer little food or shade or shelter for evading predators. Even so, natural selection over eons of time has enabled lizards to cope fairly well with such sandy desert conditions. Subterranean lizards simply bypass most problems by staying underground, and actually benefit from the loose sand since underground locomotion is facilitated. Burrowing is also made easier by evolution of a pointed, shovel-shaped head and a countersunk lower jaw, as well as by small appendages and muscular bodies and short tails. Such a reduced-limb adaptive suite associated with fossorial habits has evolved repeatedly among squamate reptiles in both lizards and snakes.

Meroles (Aporosaura) anchiete.

Toes of Uma scoparia.

Toes of Uma scopariaDuring the hours shortly after sunrise, but before sand temperatures climb too high, diurnal lizards scurry about above ground in sandy desert habitats. Sand specialized lizards provide one of the most striking examples of convergent evolution and ecological equivalence. Representatives of many different families of lizards scattered throughout the world's deserts have found a similar solution for getting better traction on loose sand: Enlarged scales on their toes, or lamellae, have evolved independently in six different families of lizards: Skinks, lacertids, iguanids, agamids, gerrhosaurids, and geckos. A skink, Scincus, appropriately dubbed the 'sand fish,' literally swims through sandy seas in search of insect food in the Sahara and other eastern deserts. These sandy desert regions also support lacertid lizards (Acanthodactylus) with fringed toes and shovel noses. Far away in the southern hemisphere, on the windblown dunes of the Namib desert of southwestern Africa, an independent lineage of lacertids, Meroles (formerly Aporosaura) anchietae, has evolved a similar life form. In North America, this body form has been adopted by

members of the iguanid genus Uma, which usually forage by waiting in the open and eat a fairly diverse diet of various insects, such as sand roaches, beetle larvae and other burrowing arthropods. They also listen intently for insects moving buried in the sand, and dig them up. Sometimes they dash, dig, and paw through a patch of sand and then watch the disturbed area for movements.

All of these lizards have flattened, duckbill-like, shovel-nosed snouts, which enable them to make remarkable 'dives' into the sand even while running at full speed. The lizards then wriggle along under the surface, sometimes for over a meter. One must see such a sand diving act to appreciate fully its effectiveness as a disappearing act. Some Namib desert lizards have discovered another solution to gain traction on powdery sands: Frog-like webbing between the toes as seen in the geckos Kaokogecko and Palmatogecko (now Pachydactylus).

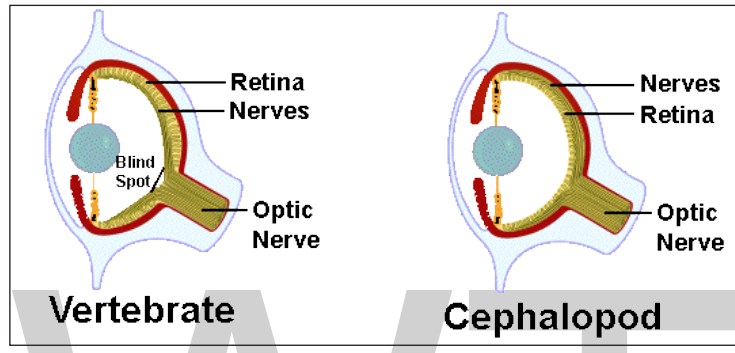
Pachydactylus (formerlyPalmatogecko) rangeri

Other lizards that have undergone convergent evolution include rock mimics such as the North American horned lizard Phrynosoma modestum, an iguanid, and the Australian agamid Tympanocryptis cephalus. New World teiids (Tupinambis) have converged on Old World varanids (Varanus): Members of both genera are large predatory lizards with forked tongues which they use as edge detectors to find scent trails and track down their prey (other vertebrates).

Rock Mimic Tympanocryptis cephalus.

Sometimes, roughly similar ecological systems support relatively few conspicuous ecological equivalents but instead are composed largely of distinctly different plant and animal types. For instance,

although bird species diversities of temperate forests in eastern North America and eastern Australia are similar, many avian niches appear to be fundamentally different on the two continents. Honeyeaters and parrots are conspicuous in Australia whereas hummingbirds and woodpeckers are entirely absent. Apparently different combinations of the various avian ecological activities are possible; thus, an Australian honeyeater might combine aspects of the food and place niches exploited in North America by both warblers and hummingbirds. An analogy can be made by comparing the 'total avian niche space' to a deck of cards. This niche space can be exploited in a limited number of ways, and each bird population or species has its own ways of doing things, or its own "hand of cards," determined in part by what other species in the community are doing.

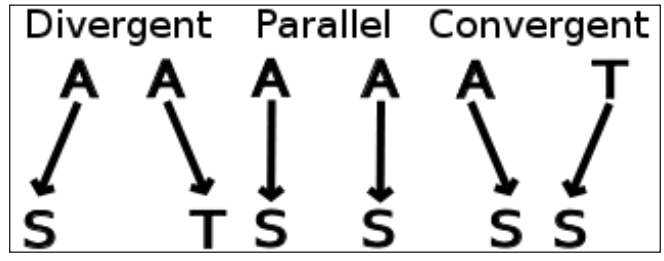


A very striking example of evolutionary convergence involves the eyes of vertebrates and cephalopod mollusks. Both have independently evolved complex camera-like eyes complete with an aperture, lens, and retina. Prominent anti-Darwinian Charles Hodges once suggested that the vertebrate eye was too complex to have evolved by natural selection and therefore must have been "designed." However, vertebrate eyes are poorly designed as compared to cephalopod eyes. In vertebrates, nerve fibers pass in front of the retina creating a blind spot, whereas nerves lie behind the retina in the superior cephalopod eye which does not have a blind spot.

Parallel Evolution

Parallel evolution is the similar development of a trait in distinct species that are not closely related, but share a similar original trait in response to similar evolutionary pressure.

Parallel vs. Convergent Evolution



Evolution at an amino acid position. In each case, the left-hand species changes from incorporating alanine (A) at a specific position within a protein in a hypothetical common ancestor deduced from

comparison of sequences of several species, and now incorporates serine (S) in its present-day form. The right-hand species may undergo divergent, parallel, or convergent evolutionat this amino acid position relative to that of the first species.

Given a particular trait that occurs in each of two lineages descended from a specified ancestor, it is possible in theory to define parallel and convergent evolutionary trends strictly, and distinguish them clearly from one another. However the criteria for defining convergent as opposed to parallel evolution often are unclear in practice, so that arbitrary diagnosis is common in some cases.

When two species are similar in a particular character, evolution is defined as parallel if the ancestors shared that similarity; if they did not, the evolution of that character in those species is defined as convergent. However, this distinction is not clear-cut. For one thing, the stated conditions are partly a matter of degree; all organisms share more or less recent common ancestors. In evolutionary biology the question of how far back to look for similar ancestors, and how similar those ancestors need be for one to consider parallel evolution to have taken place, cannot always be resolved. Some scientists accordingly have argued that parallel evolution and convergent evolution are more or less indistinguishable. Others insist that in practice we should not shy away from the gray area because many important distinctions between parallel and convergent evolution remain.

When the ancestral forms are unspecified or unknown, or the range of traits considered is not clearly specified, the distinction between parallel and convergent evolution becomes more subjective. For instance, Richard Dawkins in The Blind Watchmaker describes the striking similarity between placental and marsupial forms as the outcome of convergent evolution, because mammals on their respective ancestral continents had a long evolutionary history before the extinction of the dinosaurs. That period of separation would have permitted the accumulation of many relevant differences. Stephen Jay Gould differed; he described some of the same examples as having started from the common ancestor of all marsupials and placentals, and hence amounting to parallel evolution. And certainly, whenever similarities can be described in concept as having evolved from a common attribute deriving from a single remote ancestral line, that legitimately may be regarded as parallel evolution.

In contrast, where quite different structures clearly have been co-opted to a similar form and function, one must necessarily regard the evolution as convergent. For example, consider *Mixotricha paradoxa*, a eukaryotic microbe which has assembled a system of rows of apparent cilia and basal bodies closely resembling the system in ciliates. However, on inspection it turns out that in *Mixotricha paradoxa*, what appear to be cilia actually are smaller symbiont microorganisms; there is no question of parallel evolution in such a case. Again, the differently oriented tails of fish and whales derived at vastly different times from radically different ancestors and any similarity in the resultant descendants must therefore have evolved convergently; any case in which lineages do not evolve together at the same time in the same ecospace might be described as convergent evolution at some point in time.

The definition of a trait is crucial in deciding whether a change is seen as divergent, or as parallel or convergent. For example, the evolution of the sesamoid “thumb” of the giant panda certainly is not parallel to that of the thumbs of primates, particularly hominins, and it also differs morphologically from primate thumbs, but from some points of view it might be regarded as convergent in function and appearance.

Again, in the image above, note that since serine and threonine possess similar structures with an alcohol side chain, the example marked *"divergent"* would be termed *"parallel"* if the amino acids were grouped by similarity instead of being considered individually. As another example, if genes in two species independently become restricted to the same region of the animals through regulation by a certain transcription factor, this may be described as a case of parallel evolution - but examination of the actual DNA sequence will probably show only divergent changes in individual basepair positions, since a new transcription factor binding site can be added in a wide range of places within the gene with similar effect.

A similar situation occurs considering the homology of morphological structures. For example, many insects possess two pairs of flying wings. In beetles, the first pair of wings is hardened into elytra, wing covers with little role in flight, while in flies the second pair of wings is condensed into small halteres used for balance. If the two pairs of wings are considered as interchangeable, homologous structures, this may be described as a parallel reduction in the number of wings, but otherwise the two changes are each divergent changes in one pair of wings.

Similar to convergent evolution, evolutionary relay describes how independent species acquire similar characteristics through their evolution in similar ecosystems, but not at the same time, such as (dorsal fins of sharks, cetaceans and ichthyosaurs).

Examples:

- Colouration that serves as a warning to predators and for mating displays has evolved in many different species.
- In the plant kingdom, the most familiar examples of parallel evolution are the forms of leaves, where very similar patterns have appeared again and again in separate genera and families.
- In Arabidopsis thaliana it has been suggested that populations adapt to local climate through parallel evolution.
- In butterflies, many close similarities are found in the patterns of wing colouration, both within and among families.
- Old and New World porcupines shared a common ancestor, both evolved strikingly similar quill structures; this is also an example of convergent evolution as similar structures evolved in hedgehogs, echidnas and tenrecs.
- Some extinct archosaurs evolved an upright posture and likely were warm-blooded. These two characteristics are also found in most mammals. Modern crocodiles have a four chambered heart and a crurotarsal, the latter being also a characteristic of therian mammals.
- The extinct pterosaurs and the birds both evolved wings as well as a distinct beak, but not from a recent common ancestor.
- Internal fertilization has evolved independently in sharks, some amphibians and amniotes.

- The patagium is a fleshy membrane that is found in gliding mammals such as flying lemurs, flying squirrels, sugar gliders and the extinct Volaticotherium. These mammals all acquired the patagium independently.
- Pyrotherians evolved a body plan similar to proboscideans.
- The extinct South American litoptern ungulate Thoatherium had legs that are difficult to distinguish from those of horses.
- The eye of the octopus has the same complicated structure as the human eye. As a result, it is often substituted in studies of the eye when using a human eye would be inappropriate. As the two species diverged at the time animals evolved into vertebrates and invertebrates this is extraordinary.
- Certain arboreal frog species, 'flying' frogs, in both Old World families and New World families have developed the ability of gliding flight. They have "enlarged hands and feet, full webbing between all fingers and toes, lateral skin flaps on the arms and legs, and reduced weight per snout-vent length".
- The tree plant habit has evolved separately in unrelated classes of plants.

Parallel Evolution between Marsupials and Placentals

A number of examples of parallel evolution are provided by the two main branches of the mammals, the placentals and marsupials, which have followed independent evolutionary pathways following the break-up of land-masses such as Gondwanaland roughly 100 million years ago. In South America, marsupials and placentals shared the ecosystem (before the Great American Interchange); in Australia, marsupials prevailed; and in the Old World and North America the placentals won out. However, in all these localities mammals were small and filled only limited places in the ecosystem until the mass extinction of dinosaurs sixty-five million years ago. At this time, mammals on all three landmasses began to take on a much wider variety of forms and roles. While some forms were unique to each environment, surprisingly similar animals have often emerged in two or three of the separated continents. Examples of these include the placental sabre-toothed cats (Machairodontinae) and the South American marsupial sabre-tooth *(Thylacosmilus)*; the Tasmanian wolf and the European wolf; likewise marsupial and placental moles, flying squirrels, and (arguably) mice.

Molecular Evolution

Molecular evolution is the process of change in the sequence composition of cellular molecules such as DNA, RNA, and proteins across generations. The field of molecular evolution uses principles of evolutionary biology and population genetics to explain patterns in these changes. Major topics in molecular evolution concern the rates and impacts of single nucleotide changes, neutral evolution vs. natural selection, origins of new genes, the genetic nature of complex traits, the genetic basis of speciation, evolution of development, and ways that evolutionary forces influence genomic and phenotypic changes.

Forces in Molecular Evolution

The content and structure of a genome is the product of the molecular and population genetic forces which act upon that genome. Novel genetic variants will arise through mutation and will spread and be maintained in populations due to genetic driftor natural selection.

Mutation

This hedgehog has no pigmentation due to a mutation.

Mutations are permanent, transmissible changes to the genetic material (DNA or RNA) of a cellor virus. Mutations result from errors in DNA replication during cell division and by exposure to radiation, chemicals, and other environmental stressors, or viruses and transposable elements. Most mutations that occur are single nucleotide polymorphisms which modify single bases of the DNA sequence, resulting in point mutations. Other types of mutations modify larger segments of DNA and can cause duplications, insertions, deletions, inversions, and translocations.

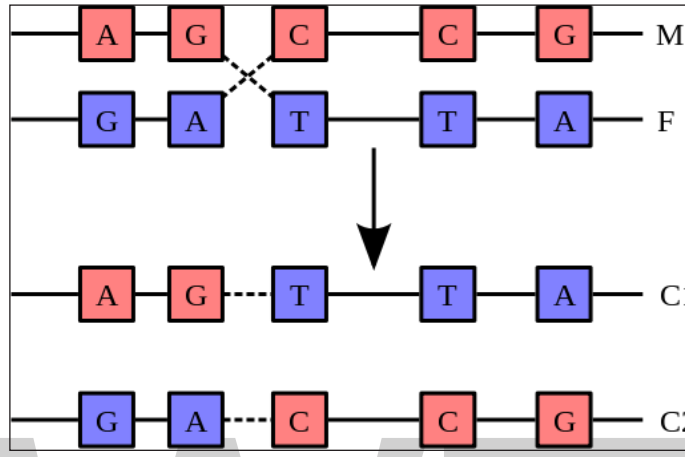
Most organisms display a strong bias in the types of mutations that occur with strong influence in GC-content. Transitions (A ↔ G or C ↔ T) are more common than transversions (purine(adenine or guanine)) ↔ pyrimidine (cytosine or thymine, or in RNA, uracil)) and are less likely to alter amino acid sequences of proteins.

Mutations are stochastic and typically occur randomly across genes. Mutation rates for single nucleotide sites for most organisms are very low, roughly 10^{-9} to 10^{-8} per site per generation, though some viruses have higher mutation rates on the order of 10^{-6} per site per generation. Among these mutations, some will be neutral or beneficial and will remain in the genome unless lost via genetic drift, and others will be detrimental and will be eliminated from the genome by natural selection.

Because mutations are extremely rare, they accumulate very slowly across generations. While the number of mutations which appears in any single generation may vary, over very long time periods

they will appear to accumulate at a regular pace. Using the mutation rate per generation and the number of nucleotide differences between two sequences, divergence times can be estimated effectively via the molecular clock.

Recombination



Recombination involves the breakage and rejoining of two chromosomes (M and F) to produce two re-arranged chromosomes (C1 and C2).

Recombination is a process that results in genetic exchange between chromosomes or chromosomal regions. Recombination counteracts physical linkage between adjacent genes, thereby reducing genetic hitchhiking. The resulting independent inheritance of genes results in more efficient selection, meaning that regions with higher recombination will harbor fewer detrimental mutations, more selectively favored variants, and fewer errors in replication and repair. Recombination can also generate particular types of mutations if chromosomes are misaligned.

Gene Conversion

Gene conversion is a type of recombination that is the product of DNA repair where nucleotide damage is corrected using an homologous genomic region as a template. Damaged bases are first excised, the damaged strand is then aligned with an undamaged homolog, and DNA synthesis repairs the excised region using the undamaged strand as a guide. Gene conversion is often responsible for homogenizing sequences of duplicate genes over long time periods, reducing nucleotide divergence.

Genetic Drift

Genetic drift is the change of allele frequencies from one generation to the next due to stochastic effects of random sampling in finite populations. Some existing variants have no effect on fitness and may increase or decrease in frequency simply due to chance. “Nearly neutral” variants whose selection coefficient is close to a threshold value of 1/the effective population size will also be affected by chance as well as by selection and mutation. Many genomic features have been ascribed to accumulation of nearly neutral detrimental mutations as a result of small effective population sizes. With a smaller effective population size, a larger variety of mutations will behave as if they are neutral due to inefficiency of selection.

Selection

Selection occurs when organisms with greater fitness, i.e. greater ability to survive or reproduce, are favored in subsequent generations, thereby increasing the instance of underlying genetic variants in a population. Selection can be the product of natural selection, artificial selection, or sexual selection. Natural selection is any selective process that occurs due to the fitness of an organism to its environment. In contrast sexual selection is a product of mate choice and can favor the spread of genetic variants which act counter to natural selection but increase desirability to the opposite sex or increase mating success. Artificial selection, also known as selective breeding, is imposed by an outside entity, typically humans, in order to increase the frequency of desired traits.

The principles of population genetics apply similarly to all types of selection, though in fact each may produce distinct effects due to clustering of genes with different functions in different parts of the genome, or due to different properties of genes in particular functional classes. For instance, sexual selection could be more likely to affect molecular evolution of the sex chromosomes due to clustering of sex specific genes on the X, Y, Z or W.

Intragenomic Conflict

Selection can operate at the gene level at the expense of organismal fitness, resulting in a selective advantage for selfish genetic elements in spite of a host cost. Examples of such selfish elements include transposable elements, meiotic drivers, killer X chromosomes, selfish mitochondria, and self-propagating introns.

Genome Architecture

Genome Size

Genome size is influenced by the amount of repetitive DNA as well as number of genes in an organism. The C-value paradoxrefers to the lack of correlation between organism 'complexity' and genome size. Explanations for the so-called paradox are two-fold. First, repetitive genetic elements can comprise large portions of the genome for many organisms, thereby inflating DNA content of the haploid genome. Secondly, the number of genes is not necessarily indicative of the number of developmental stages or tissue types in an organism. An organism with few developmental stages or tissue types may have large numbers of genes that influence non-developmental phenotypes, inflating gene content relative to developmental gene families.

Neutral explanations for genome size suggest that when population sizes are small, many mutations become nearly neutral. Hence, in small populations repetitive content and other 'junk' DNA can accumulate without placing the organism at a competitive disadvantage. There is little evidence to suggest that genome size is under strong widespread selection in multicellular eukaryotes. Genome size, independent of gene content, correlates poorly with most physiological traits and many eukaryotes, including mammals, harbor very large amounts of repetitive DNA.

However, birds likely have experienced strong selection for reduced genome size, in response to changing energetic needs for flight. Birds, unlike humans, produce nucleated red blood cells, and larger nuclei lead to lower levels of oxygen transport. Bird metabolism is far higher than that of mammals, due largely to flight, and oxygen needs are high. Hence, most birds have small, compact

genomes with few repetitive elements. Indirect evidence suggests that non-avian theropod dinosaur ancestors of modern birds also had reduced genome sizes, consistent with endothermy and high energetic needs for running speed. Many bacteria have also experienced selection for small genome size, as time of replication and energy consumption are so tightly correlated with fitness.

Repetitive Elements

Transposable elements are self-replicating, selfish genetic elements which are capable of proliferating within host genomes. Many transposable elements are related to viruses, and share several proteins in common.

Chromosome Number and Organization

The number of chromosomes in an organism's genome also does not necessarily correlate with the amount of DNA in its genome. The ant Myrmecia pilosula has only a single pair of chromosomes whereas the Adders-tongue fern Ophioglossumreticulatum has up to 1260 chromosomes. Cilliate genomes house each gene in individual chromosomes, resulting in a genome which is not physically linked. Reduced linkage through creation of additional chromosomes should effectively increase the efficiency of selection.

Changes in chromosome number can play a key role in speciation, as differing chromosome numbers can serve as a barrier to reproduction in hybrids. Human chromosome 2 was created from a fusion of two chimpanzee chromosomes and still contains central telomeres as well as a vestigial second centromere. Polyploidy, especially allopolyploidy, which occurs often in plants, can also result in reproductive incompatibilities with parental species. Agrodiatus blue butterflies have diverse chromosome numbers ranging from n=10 to n=134 and additionally have one of the highest rates of speciation identified to date.

Gene Content and Distribution

Different organisms house different numbers of genes within their genomes as well as different patterns in the distribution of genes throughout the genome. Some organisms, such as most bacteria, Drosophila, and Arabidopsis have particularly compact genomes with little repetitive content or non-coding DNA. Other organisms, like mammals or maize, have large amounts of repetitive DNA, long introns, and substantial spacing between different genes. The content and distribution of genes within the genome can influence the rate at which certain types of mutations occur and can influence the subsequent evolution of different species. Genes with longer introns are more likely to recombine due to increased physical distance over the coding sequence. As such, long introns may facilitate ectopic recombination, and result in higher rates of new gene formation.

Organelles

In addition to the nuclear genome, endosymbiont organelles contain their own genetic material typically as circular plasmids. Mitochondrial and chloroplast DNA varies across taxa, but membrane-bound proteins, especially electron transport chain constituents are most often encoded in the organelle. Chloroplasts and mitochondria are maternally inherited in most species, as the

organelles must pass through the egg. In a rare departure, some species of mussels are known to inherit mitochondria from father to son.

Origins of New Genes

New genes arise from several different genetic mechanisms including gene duplication, de novo origination, retrotransposition, chimeric gene formation, recruitment of non-coding sequence, and gene truncation.

Gene duplication initially leads to redundancy. However, duplicated gene sequences can mutate to develop new functions or specialize so that the new gene performs a subset of the original ancestral functions. In addition to duplicating whole genes, sometimes only a domain or part of a protein is duplicated so that the resulting gene is an elongated version of the parental gene.

Retrotransposition creates new genes by copying mRNA to DNA and inserting it into the genome. Retrogenes often insert into new genomic locations, and often develop new expression patterns and functions.

Chimeric genes form when duplication, deletion, or incomplete retrotransposition combine portions of two different coding sequences to produce a novel gene sequence. Chimeras often cause regulatory changes and can shuffle protein domains to produce novel adaptive functions.

De novo gene birth can also give rise to new genes from previously non-coding DNA. For instance, Levine and colleagues reported the origin of five new genes in the *D. melanogaster* genome from noncoding DNA. Similar de novo origin of genes has been also shown in other organisms such as yeast, rice and humans. De novo genes may evolve from transcripts that are already expressed at low levels. Mutation of a stop codon to a regular codon or a frameshift may cause an extended protein that includes a previously non-coding sequence. The formation of novel genes from scratch typically can not occur within genomic regions of high gene density. The essential events for de novo formation of genes is recombination/mutation which includes insertions, deletions, and inversions. These events are tolerated if the consequence of these genetic events does not interfere in cellular activities. Most genomes comprise prophages wherein genetic modifications do not, in general, affect the host genome propagation. Hence, there is higher probability of genetic modifications, in regions such as prophages, which is proportional to the probability of de novo formation of genes.

De novo evolution of genes can also be simulated in the laboratory. For example, semi-random gene sequences can be selected for specific functions. More specifically, they selected sequences from a library that could complement a gene deletion in *E. coli*. The deleted gene encodes ferric enterobactin esterase (Fes), which releases iron from an iron chelator, enterobactin. While Fes is a 400 amino acid protein, the newly selected gene was only 100 amino acids in length and unrelated in sequence to Fes.

In Vitro Molecular Evolution Experiments

Principles of molecular evolution have also been discovered, and others elucidated and tested using experimentation involving amplification, variation and selection of rapidly proliferating and genetically varying molecular species outside cells. Since the pioneering work of Sol Spiegelmann

in 1967, involving RNA that replicates itself with the aid of an enzyme extracted from the Qß virus, several groups (such as Kramers and Biebricher/Luce/Eigen) studied mini and micro variants of this RNA in the 1970s and 1980s that replicate on the timescale of seconds to a minute, allowing hundreds of generations with large population sizes (e.g. 10^14 sequences) to be followed in a single day of experimentation. The chemical kinetic elucidation of the detailed mechanism of replication meant that this type of system was the first molecular evolution system that could be fully characterised on the basis of physical chemical kinetics, later allowing the first models of the genotype to phenotype map based on sequence dependent RNA folding and refolding to be produced. Subject to maintaining the function of the multicomponent Qß enzyme, chemical conditions could be varied significantly, in order to study the influence of changing environments and selection pressures. Experiments with in vitro RNA quasi species included the characterisation of the error threshold for information in molecular evolution, the discovery of de novo evolution leading to diverse replicating RNA species and the discovery of spatial travelling waves as ideal molecular evolution reactors. Later experiments employed novel combinations of enzymes to elucidate novel aspects of interacting molecular evolution involving population dependent fitness, including work with artificially designed molecular predator prey and cooperative systems of multiple RNA and DNA. Special evolution reactors were designed for these studies, starting with serial transfer machines, flow reactors such as cell-stat machines, capillary reactors, and microreactors including line flow reactors and gel slice reactors. These studies were accompanied by theoretical developments and simulations involving RNA folding and replication kinetics that elucidated the importance of the correlation structure between distance in sequence space and fitness changes, including the role of neutral networks and structural ensembles in evolutionary optimisation.

Molecular Phylogenetics

Molecular systematics is the product of the traditional fields of systematics and molecular genetics. It uses DNA, RNA, or protein sequences to resolve questions in systematics, i.e. about their correct scientific classification or taxonomy from the point of view of evolutionary biology.

Molecular systematics has been made possible by the availability of techniques for DNA sequencing, which allow the determination of the exact sequence of nucleotides or *bases* in either DNA or RNA. At present it is still a long and expensive process to sequence the entire genome of an organism, and this has been done for only a few species. However, it is quite feasible to determine the sequence of a defined area of a particular chromosome. Typical molecular systematic analyses require the sequencing of around 1000 base pairs.

The Driving Forces of Evolution

Depending on the relative importance assigned to the various forces of evolution, three perspectives provide evolutionary explanations for molecular evolution.

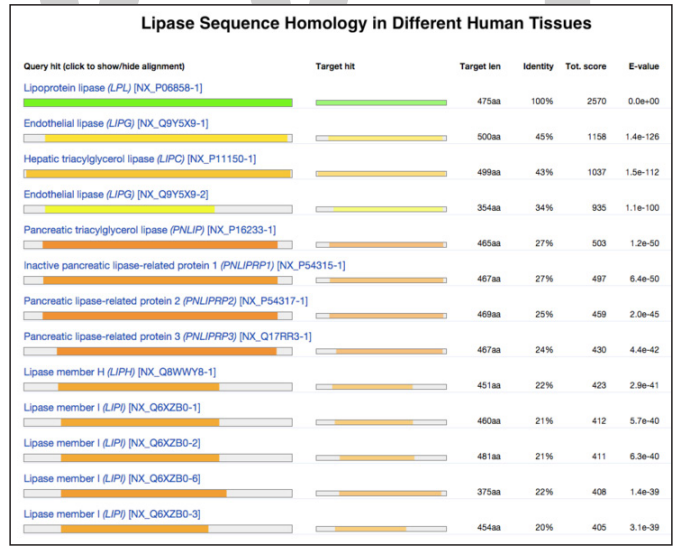
Selectionist hypotheses argue that selection is the driving force of molecular evolution. While acknowledging that many mutations are neutral, selectionists attribute changes in the frequencies of neutral alleles to linkage disequilibrium with other loci that are under selection, rather than to random genetic drift. Biases in codon usage are usually explained with reference to the ability of even weak selection to shape molecular evolution.

Neutralist hypotheses emphasize the importance of mutation, purifying selection, and random genetic drift. The introduction of the neutral theory by Kimura, quickly followed by King and Jukes' own findings, led to a fierce debate about the relevance of neodarwinism at the molecular level. The Neutral theory of molecular evolution proposes that most mutations in DNA are at locations not important to function or fitness. These neutral changes drift towards fixation within a population. Positive changes will be very rare, and so will not greatly contribute to DNA polymorphisms. Deleterious mutations do not contribute much to DNA diversity because they negatively affect fitness and so are removed from the gene pool before long.This theory provides a framework for the molecular clock. The fate of neutral mutations are governed by genetic drift, and contribute to both nucleotide polymorphism and fixed differences between species.

In the strictest sense, the neutral theory is not accurate. Subtle changes in DNA very often have effects, but sometimes these effects are too small for natural selection to act on. Even synonymous mutations are not necessarily neutral because there is not a uniform amount of each codon. The nearly neutral theory expanded the neutralist perspective, suggesting that several mutations are nearly neutral, which means both random drift and natural selection is relevant to their dynamics. The main difference between the neutral theory and nearly neutral theory is that the latter focuses on weak selection, not strictly neutral.

Mutationists hypotheses emphasize random drift and biases in mutation patterns. Sueoka was the first to propose a modern mutationist view. He proposed that the variation in GC content was not the result of positive selection, but a consequence of the GC mutational pressure.

Protein Evolution



This chart compares the sequence identity of different lipase proteins throughout the human body. It demonstrates how proteins evolve, keeping some regions conserved while others change dramatically.

Evolution of proteins is studied by comparing the sequences and structures of proteins from many organisms representing distinct evolutionary clades. If the sequences/structures of two proteins

are similar indicating that the proteins diverged from a common origin, these proteins are called as homologous proteins. More specifically, homologous proteins that exist in two distinct species are called as orthologs. Whereas, homologous proteins encoded by the genome of a single species are called paralogs.

The phylogenetic relationships of proteins are examined by multiple sequence comparisons. Phylogenetic trees of proteins can be established by the comparison of sequence identities among proteins. Such phylogenetic trees have established that the sequence similarities among proteins reflect closely the evolutionary relationships among organisms.

Protein evolution describes the changes over time in protein shape, function, and composition. Through quantitative analysis and experimentation, scientists have strived to understand the rate and causes of protein evolution. Using the amino acid sequences of hemoglobin and cytochrome c from multiple species, scientists were able to derive estimations of protein evolution rates. What they found was that the rates were not the same among proteins. Each protein has its own rate, and that rate is constant across phylogenies (i.e., hemoglobin does not evolve at the same rate as cytochrome c, but hemoglobins from humans, mice, etc. do have comparable rates of evolution.). Not all regions within a protein mutate at the same rate; functionally important areas mutate more slowly and amino acid substitutions involving similar amino acids occurs more often than dissimilar substitutions. Overall, the level of polymorphisms in proteins seems to be fairly constant. Several species (including humans, fruit flies, and mice) have similar levels of protein polymorphism.

Relation to Nucleic Acid Evolution

Protein evolution is inescapably tied to changes and selection of DNA polymorphisms and mutations because protein sequences change in response to alterations in the DNA sequence. Amino acid sequences and nucleic acid sequences do not mutate at the same rate. Due to the degenerate nature of DNA, bases can change without affecting the amino acid sequence. For example, there are six codons that code for leucine. Thus, despite the difference in mutation rates, it is essential to incorporate nucleic acid evolution into the discussion of protein evolution. At the end of the 1960s, two groups of scientists—Kimura (1968) and King and Jukes (1969)—independently proposed that a majority of the evolutionary changes observed in proteins were neutral.Since then, the neutral theory has been expanded upon and debated.

Discordance with Morphological Evolution

There are sometimes discordances between molecular and morphological evolution, which are reflected in molecular and morphological systematic studies, especially of bacteria, archaea and eukaryotic microbes. These discordances can be categorized as two types: (i) one morphology, multiple lineages (e.g. morphological convergence, cryptic species) and (ii) one lineage, multiple morphologies (e.g. phenotypic plasticity, multiple life-cycle stages). Neutral evolution possibly could explain the incongruences in some cases.

Gene Duplication

Gene duplication (or chromosomal duplication or gene amplification) is a major mechanism through which new genetic material is generated during molecular evolution. It can be defined as

any duplication of a region of DNA that contains a gene. Gene duplications can arise as products of several types of errors in DNA replication and repair machinery as well as through fortuitous capture by selfish genetic elements. Common sources of gene duplications include ectopic recombination,retrotransposition event, aneuploidy, polyploidy, and replication slippage.

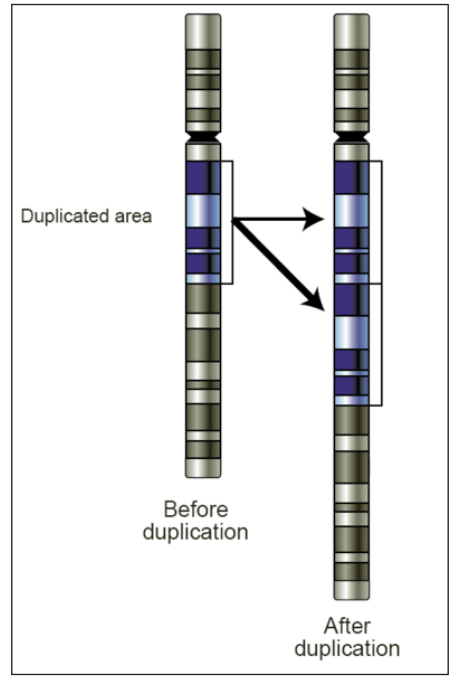
Mechanisms of Duplication

Ectopic Recombination

Duplications arise from an event termed unequal crossing-over that occurs during meiosis between misaligned homologous chromosomes.The chance of this happening is a function of the degree of sharing of repetitive elements between two chromosomes. The products of this recombination are a duplication at the site of the exchange and a reciprocal deletion. Ectopic recombination is typically mediated by sequence similarity at the duplicate breakpoints, which form direct repeats. Repetitive genetic elements such as transposable elements offer one source of repetitive DNA that can facilitate recombination, and they are often found at duplication breakpoints in plants and mammals.

Replication Slippage

Replication slippage is an error in DNA replication that can produce duplications of short genetic sequences. During replication DNA polymerase begins to copy the DNA. At some point during the replication process, the polymerase dissociates from the DNA and replication stalls. When the polymerase reattaches to the DNA strand, it aligns the replicating strand to an incorrect position and incidentally copies the same section more than once. Replication slippage is also often facilitated by repetitive sequences, but requires only a few bases of similarity.



Schematic of a region of a chromosome before and after a duplication event.

Retrotransposition

During the cellular invasion by a replicating retroelement or retrovirus, viral proteins copy their genome by reverse transcribing RNA to DNA. If viral proteins aberrantly attach to cellular mRNA, they can reverse transcribe copies of genes to create retrogenes. Retrogenes usually lack intronic sequences and often contain poly, sequences that are also integrated into the genome. Many retrogenes display changes in gene regulation in comparison to their parental gene sequences, which sometimes results in novel functions.

Aneuploidy

Aneuploidy occurs when nondisjunction at a single chromosome results in an abnormal number of chromosomes. Aneuploidy is often harmful and in mammals regularly leads to spontaneous abortions (miscarriages). Some aneuploid individuals are viable, for example trisomy 21 in humans, which leads to Down syndrome. Aneuploidy often alters gene dosage in ways that are detrimental to the organism; therefore, it is unlikely to spread through populations.

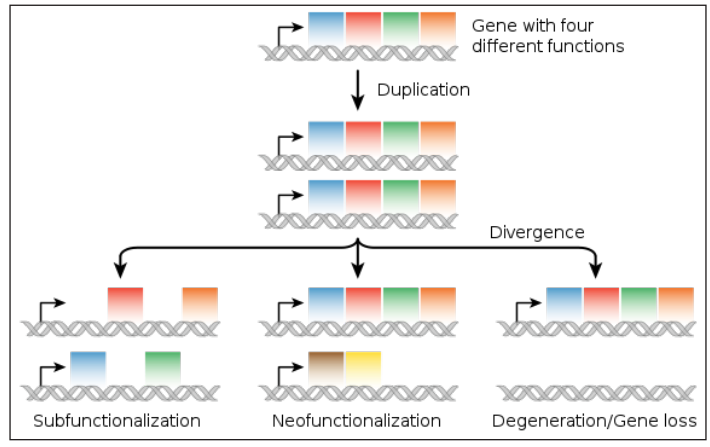
Whole Genome Duplication

Whole genome duplication, or polyploidy, is a product of nondisjunction during meiosis which results in additional copies of the entire genome. Polyploidy is common in plants, but historically has also occurred in animals, with two rounds of whole genome duplication in the vertebrate lineage leading to humans. After whole genome duplications many sets of additional genes are eventually lost, returning to singleton state. However, retention of many genes, most notably Hox genes, has led to adaptive innovation.

Polyploidy is also a well known source of speciation, as offspring, which have different numbers of chromosomes compared to parent species, are often unable to interbreed with non-polyploid organisms. Whole genome duplications are thought to be less detrimental than aneuploidy as the relative dosage of individual genes should be the same.

As an Evolutionary Event

Rate of Gene Duplication



Evolutionary fate of duplicate genes.

Comparisons of genomes demonstrate that gene duplications are common in most species investigated. This is indicated by variable copy numbers (copy number variation) in the genome of humans or fruit flies. However, it has been difficult to measure the rate at which such duplications occur. Recent studies yielded a first direct estimate of the genome-wide rate of gene duplication in *C. elegans*, the first multicellular eukaryote for which such as estimate became available. The gene duplication rate in *C. elegans* is on the order of 10^{-7}duplications/gene/generation, that is, in a population of 10 million worms, one will have a gene duplication per generation. This rate is two orders of magnitude greater than the spontaneous rate of point mutation per nucleotide site in this species. Older (indirect) studies reported locus-specific duplication rates in bacteria, *Drosophila*, and humans ranging from 10^{-3} to 10^{-7}/gene/generation.

Neofunctionalization

Gene duplications are an essential source of genetic novelty that can lead to evolutionary innovation. Duplication creates genetic redundancy, where the second copy of the gene is often free from selective pressure—that is, mutations of it have no deleterious effects to its host organism. If one copy of a gene experiences a mutation that affects its original function, the second copy can serve as a 'spare part' and continue to function correctly. Thus, duplicate genes accumulate mutations faster than a functional single-copy gene, over generations of organisms, and it is possible for one of the two copies to develop a new and different function. Some examples of such neofunctionalization is the apparent mutation of a duplicated digestive gene in a family of ice fish into an antifreeze gene and duplication leading to a novel snake venom gene and the synthesis of 1 beta-hydroxytestosterone in pigs.

Gene duplication is believed to play a major role in evolution; this stance has been held by members of the scientific community for over 100 years. Susumu Ohno was one of the most famous developers of this theory in his classic book *Evolution by gene duplication* (1970). Ohno argued that gene duplication is the most important evolutionary force since the emergence of the universal common ancestor. Major genome duplication events can be quite common. It is believed that the entire yeastgenome underwent duplication about 100 million years ago. Plants are the most prolific genome duplicators. For example, wheat is hexaploid (a kind of polyploid), meaning that it has six copies of its genome.

Subfunctionalization

Another possible fate for duplicate genes is that both copies are equally free to accumulate degenerative mutations, so long as any defects are complemented by the other copy. This leads to a neutral "subfunctionalization" or DDC (duplication-degeneration-complementation) model, in which the functionality of the original gene is distributed among the two copies. Neither gene can be lost, as both now perform important non-redundant functions, but ultimately neither is able to achieve novel functionality.

Subfunctionalization can occur through neutral processes in which mutations accumulate with no detrimental or beneficial effects. However, in some cases subfunctionalization can occur with clear adaptive benefits. If an ancestral gene is pleiotropicand performs two functions, often neither one of these two functions can be changed without affecting the other function. In this way, partitioning the ancestral functions into two separate genes can allow for adaptive specialization of subfunctions, thereby providing an adaptive benefit.

Loss

Often the resulting genomic variation leads to gene dosage dependent neurological disorders such as Rett-like syndrome and Pelizaeus–Merzbacher disease. Such detrimental mutations are likely to be lost from the population and will not be preserved or develop novel functions. However, many duplications are, in fact, not detrimental or beneficial, and these neutral sequences may be lost or may spread through the population through random fluctuations via genetic drift.

Identifying Duplications in Sequenced Genomes

Criteria and Single Genome Scans

The two genes that exist after a gene duplication event are called paralogs and usually code for proteins with a similar function and structure. By contrast, orthologous genes present in different species which are each originally derived from the same ancestral sequence.

It is important (but often difficult) to differentiate between paralogs and orthologs in biological research. Experiments on human gene function can often be carried out on other species if a homolog to a human gene can be found in the genome of that species, but only if the homolog is orthologous. If they are paralogs and resulted from a gene duplication event, their functions are likely to be too different. One or more copies of duplicated genes that constitute a gene family may be affected by insertion of transposable elements that causes significant variation between them in their sequence and finally may become responsible for divergent evolution. This may also render the chances and the rate of gene conversion between the homologs of gene duplicates due to less or no similarity in their sequences.

Paralogs can be identified in single genomes through a sequence comparison of all annotated gene models to one another. Such a comparison can be performed on translated amino acid sequences (e.g. BLASTp, tBLASTx) to identify ancient duplications or on DNA nucleotide sequences (e.g. BLASTn, megablast) to identify more recent duplications. Most studies to identify gene duplications require reciprocal-best-hits or fuzzy reciprocal-best-hits, where each paralog must be the other's single best match in a sequence comparison.

Most gene duplications exist as low copy repeats (LCRs), rather highly repetitive sequences like transposable elements. They are mostly found in pericentronomic, subtelomeric and interstitial regions of a chromosome. Many LCRs, due to their size (>1Kb), similarity, and orientation, are highly susceptible to duplications and deletions.

Genomic Microarrays Detect Duplications

Technologies such as genomic microarrays, also called array comparative genomic hybridization (array CGH), are used to detect chromosomal abnormalities, such as microduplications, in a high throughput fashion from genomic DNA samples. In particular, DNA microarray technology can simultaneously monitor the expression levels of thousands of genes across many treatments or experimental conditions, greatly facilitating the evolutionary studies of gene regulation after gene duplication or speciation.

Next Generation Sequencing

Gene duplications can also be identified through the use of next-generation sequencing platforms. The simplest means to identify duplications in genomic resequencing data is through the use of paired-end sequencing reads. Tandem duplications are indicated by sequencing read pairs which map in abnormal orientations. Through a combination of increased sequence coverage and abnormal mapping orientation, it is possible to identify duplications in genomic sequencing data.

As Amplification

Gene duplication does not necessarily constitute a lasting change in a species' genome. In fact, such changes often don't last past the initial host organism. From the perspective of molecular genetics, amplification is one of many ways in which a genecan be overexpressed. Genetic amplification can occur artificially, as with the use of the polymerase chain reaction technique to amplify short strands of DNA *in vitro* using enzymes, or it can occur naturally. If it's a natural duplication, it can still take place in a somatic cell, rather than a germline cell (which would be necessary for a lasting evolutionary change).

Role in Cancer

Duplications of oncogenes are a common cause of many types of cancer. In such cases the genetic duplication occurs in a somatic cell and affects only the genome of the cancer cells themselves, not the entire organism, much less any subsequent offspring.

Macroevolution

Macroevolution is evolution on a scale at or above the level of species, in contrast with microevolution, which refers to smaller evolutionary changes of allele frequencies within a species or population. Macroevolution and microevolution describe fundamentally identical processes on different scales.

The process of speciation may fall within the purview of either, depending on the forces thought to drive it. Paleontology, evolutionary developmental biology, comparative genomics and genomic phylostratigraphy contribute most of the evidence for macroevolution's patterns and processes.

Macroevolution and the Modern Synthesis

Within the modern synthesis of the early 20th century, macroevolution is thought of as the compounded effects of microevolution. Thus, the distinction between micro- and macroevolution is not a fundamental one – the only difference between them is of time and scale. As Ernst W. Mayr observes, "transspecific evolution is nothing but an extrapolation and magnification of the events that take place within populations and species it is misleading to make a distinction between the causes of micro- and macroevolution". However, time is not a necessary distinguishing factor – macroevolution can happen without gradual compounding of small changes; whole-genome duplication can result in speciation occurring over a single generation – this is especially common in plants.

Changes in the genes regulating development have also been proposed as being important in producing speciation through large and relatively sudden changes in animals morphology.

Types of Macroevolution

There are many ways to view macroevolution, for example, by observing changes in the genetics, morphology, taxonomy, ecology, and behavior of organisms, though these are interrelated. Sahney et al. stated the connection as "As taxonomic diversity has increased, there have been incentives for tetrapods to move into new modes of life, where initially resources may seem unlimited, there are few competitors and possible refuge from danger. And as ecological diversity increases, taxa diversify from their ancestors at a much greater rate among faunas with more superior, innovative or more flexible adaptations."

Early cetaceans like *Ambulocetus natans* possessed hindlimbs, derived from their walking ancestors, but no longer useful in their marine environment.

Molecular evolution occurs through small changes in the molecular or cellular level. Over a long period of time, this can cause big effects on the genetics of organisms. Taxonomic evolution occurs through small changes between populations and then species. Over a long period of time, this can cause big effects on the taxonomy of organisms, with the growth of whole new clades above the species level. Morphological evolution occurs through small changes in the morphology of an organism. Over a long period of time, this can cause big effects on the morphology of major clades. This can be clearly seen in the Cetacea, where throughout the group's early evolution, hindlimbswere still present. However over millions of years the hindlimbs regressed and became internal.

Abrupt transformations from one biologic system to another, for example the passing of life from water into land or the transition from invertebrates to vertebrates, are rare. Few major biological types have emerged during the evolutionary history of life. When lifeforms take such giant leaps, they meet little to no competition and are able to exploit many available niches, following an adaptive radiation. This can lead to convergent evolution as the empty niches are filled by whichever lifeform encounters them.

Subjects studied within macroevolution include:

- Adaptive radiations such as the Cambrian Explosion.

- Changes in biodiversity through time.
- Genome evolution, like horizontal gene transfer, genome fusions in endosymbioses, and adaptive changes in genome size.
- Mass extinctions.
- Estimating diversification rates, including rates of speciation and extinction.
- The debate between punctuated equilibrium and gradualism.
- The role of development in shaping evolution, particularly such topics as heterochrony and phenotypic plasticity.

Microevolution

Microevolution is the change in allele frequencies that occurs over time within a population. This change is due to four different processes: Mutation, selection (natural and artificial), gene flow and genetic drift. This change happens over a relatively short (in evolutionary terms) amount of time compared to the changes termed macroevolution which is where greater differences in the population occur.

Population genetics is the branch of biology that provides the mathematical structure for the study of the process of microevolution. Ecological geneticsconcerns itself with observing microevolution in the wild. Typically, observable instances of evolution are examples of microevolution; for example, bacterialstrains that have antibiotic resistance.

Microevolution over time leads to speciation or the appearance of novel structure, sometimes classified as macroevolution. Macro and microevolution describe fundamentally identical processes on different scales.

Difference from Macroevolution

Macroevolution and microevolution describe fundamentally identical processes on different time scales. Microevolution refers to small evolutionary changes (typically described as changes in allele frequencies) within a species or population. while macroevolution is evolution on a scale of separated gene pools. Macroevolutionary studies focus on change that occurs at or above the level of species.

Four Processes

Mutation

Mutations are changes in the DNA sequence of a cell's genome and are caused by radiation, viruses, transposons and mutagenic chemicals, as well as errors that occur during meiosis or DNA replication. Errors are introduced particularly often in the process of DNA replication, in the polymerization of the second strand. These errors can also be induced by the organism itself, by

cellular processes such as hypermutation. Mutations can affect the phenotype of an organism, especially if they occur within the protein coding sequence of a gene. Error rates are usually very low—1 error in every 10–100 million bases—due to the proofreading ability of DNA polymerases. (Without proofreading error rates are a thousandfold higher; because many viruses rely on DNA and RNA polymerases that lack proofreading ability, they experience higher mutation rates.) Processes that increase the rate of changes in DNA are called mutagenic: Mutagenic chemicals promote errors in DNA replication, often by interfering with the structure of base-pairing, while UV radiation induces mutations by causing damage to the DNA structure. Chemical damage to DNA occurs naturally as well, and cells use DNA repair mechanisms to repair mismatches and breaks in DNA—nevertheless, the repair sometimes fails to return the DNA to its original sequence.

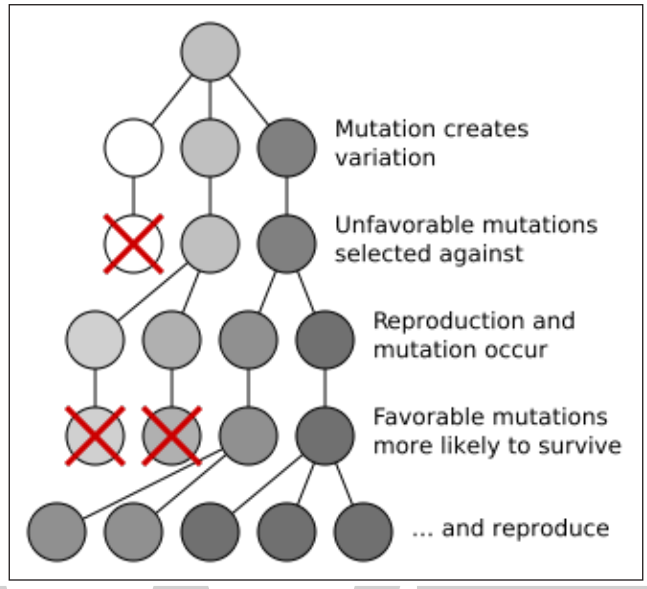
In organisms that use chromosomal crossover to exchange DNA and recombine genes, errors in alignment during meiosis can also cause mutations. Errors in crossover are especially likely when similar sequences cause partner chromosomes to adopt a mistaken alignment making some regions in genomes more prone to mutating in this way. These errors create large structural changes in DNA sequence—duplications, inversions or deletions of entire regions, or the accidental exchanging of whole parts between different chromosomes (called translocation).

Mutation can result in several different types of change in DNA sequences; these can either 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. Due to the damaging effects that mutations can have on cells, organisms have evolved mechanisms such as DNA repair to remove mutations. Therefore, the optimal mutation rate for a species is a trade-off between costs of a high mutation rate, such as deleterious mutations, and the metabolic costs of maintaining systems to reduce the mutation rate, such as DNA repair enzymes. Viruses that use RNA as their genetic material have rapid mutation rates, which can be an advantage since these viruses will evolve constantly and rapidly, and thus evade the defensive responses of e.g. the human immune system.

Mutations can involve large sections of DNA becoming duplicated, usually through genetic recombination. These duplications are a major source of raw material for evolving new genes, with tens to hundreds of genes duplicated in animal genomes every million years. Most genes belong to larger families of genes of shared ancestry. Novel genes are produced by several methods, commonly through the duplication and mutation of an ancestral gene, or by recombining parts of different genes to form new combinations with new functions.

Here, domains act as modules, each with a particular and independent function, that can be mixed together to produce genes encoding new proteins with novel properties. For example, the human eye uses four genes to make structures that sense light: Three for color vision and one for night vision; all four arose from a single ancestral gene. Another advantage of duplicating a gene (or even an entire genome) is that this increases redundancy; this allows one gene in the pair to acquire a new function while the other copy performs the original function. Other types of mutation occasionally create new genes from previously noncoding DNA.

Selection



Natural selection of a population for dark coloration.

Selection is the process by which heritable traits that make it more likely for an organism to survive and successfully reproducebecome more common in a population over successive generations.

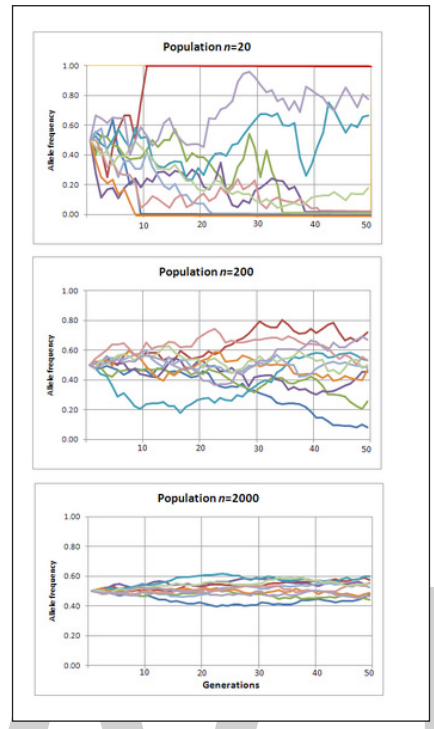
It is sometimes valuable to distinguish between naturally occurring selection, natural selection, and selection that is a manifestation of choices made by humans, artificial selection. This distinction is rather diffuse. Natural selection is nevertheless the dominant part of selection.

The natural genetic variation within a population of organisms means that some individuals will survive more successfully than others in their current environment. Factors which affect reproductive success are also important, an issue which Charles Darwin developed in his ideas on sexual selection.

Natural selection acts on the phenotype, or the observable characteristics of an organism, but the genetic (heritable) basis of any phenotype which gives a reproductive advantage will become more common in a population. Over time, this process can result in adaptationsthat specialize organisms for particular ecological niches and may eventually result in the speciation (the emergence of new species).

Natural selection is one of the cornerstones of modern biology. The term was introduced by Darwin in his groundbreaking 1859 book On the Origin of Species, in which natural selection was described by analogy to artificial selection, a process by which animals and plants with traits considered desirable by human breeders are systematically favored for reproduction. The concept of natural selection was originally developed in the absence of a valid theory of heredity; at the time of Darwin's writing, nothing was known of modern genetics. The union of traditional Darwinian evolution with subsequent discoveries in classical and molecular genetics is termed the modern evolutionary synthesis. Natural selection remains the primary explanation for adaptive evolution.

Genetic Drift



Ten simulations of random genetic drift of a single given allele with an initial frequency distribution 0.5 measured over the course of 50 generations, repeated in three reproductively synchronous populations of different sizes. In general, alleles drift to loss or fixation (frequency of 0.0 or 1.0) significantly faster in smaller populations.

Genetic drift is the change in the relative frequency in which a gene variant (allele) occurs in a population due to random sampling. That is, the alleles in the offspring in the population are a random sample of those in the parents. And chance has a role in determining whether a given individual survives and reproduces. A population's allele frequency is the fraction or percentage of its gene copies compared to the total number of gene alleles that share a particular form.

Genetic drift is an evolutionary process which leads to changes in allele frequencies over time. It 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 may be beneficial, neutral, or detrimental to reproductive success.

The effect of genetic drift is larger in small populations, and smaller in large populations. Vigorous debates wage among scientists over the relative importance of genetic drift compared with natural selection. 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. In Motoo Kimura rekindled the debate with his neutral theory of molecular evolution which claims that most of the changes in the genetic material are caused by genetic drift. The predictions of neutral theory, based on genetic drift, do not fit recent data on whole genomes well: These data suggest that the frequencies of neutral alleles change primarily due to selection at linked sites, rather than due to genetic drift by means of sampling error.

Gene Flow

Gene flow is the exchange of genes between populations, which are usually of the same species. 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.

Migration into or out of a population can change allele frequencies, as well as introducing genetic variation into a population. Immigration may add new genetic material to the established gene pool of a population. Conversely, emigration may remove genetic material. As barriers to reproduction between two diverging populations are required for the populations to become new species, gene flow may slow this process by spreading genetic differences between the populations. 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.

Depending on how far two species have diverged since their most recent common ancestor, it may still be possible for them to produce offspring, as with horses and donkeys mating to produce mules. Such hybrids are generally infertile, due to the two different sets of chromosomes being unable to pair up during meiosis. In this case, closely related species may regularly interbreed, but hybrids will be selected against and the species will remain distinct. However, viable hybrids are occasionally formed and these new species can either have properties intermediate between their parent species, or possess a totally new phenotype. The importance of hybridization in creating new species of animals is unclear, although cases have been seen in many types of animals, with the gray tree frog being a particularly well-studied example.

Hybridization is, however, 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.Polyploid hybrids also have more genetic diversity, which allows them to avoid inbreeding depression in small populations.

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 bacteria. In medicine, this contributes to the spread of antibiotic resistance, as when one bacteria 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.

Gene flow is the transfer of alleles from one population to another. Migration into or out of a population may be responsible for a marked change in allele frequencies. Immigration may also result in the addition of new genetic variants to the established gene pool of a particular species or population.

There are a number of factors that affect the rate of gene flow between different populations. One of the most significant factors is mobility, as greater mobility of an individual tends to give it greater migratory potential. Animals tend to be more mobile than plants, although pollen and seeds may be carried great distances by animals or wind.

Maintained gene flow between two populations can also lead to a combination of the two gene pools, reducing the genetic variation between the two groups. It is for this reason that gene flow strongly acts against speciation, by recombining the gene pools of the groups, and thus, repairing the developing differences in genetic variation that would have led to full speciation and creation of daughter species.

For example, if a species of grass grows on both sides of a highway, pollen is likely to be transported from one side to the other and vice versa. If this pollen is able to fertilise the plant where it ends up and produce viable offspring, then the alleles in the pollen have effectively been able to move from the population on one side of the highway to the other.

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5

Fields Related to Evolutionary Biology

Evolutionary physiology, experimental evolution, population genetics, paleontology, phylogenetics are some of the fields that are studied in association with evolutionary biology. All these diverse fields related to evolutionary biology have been carefully analyzed in this chapter.

Population Genetics

Population genetics is a field of biology that studies the genetic composition of biological populations, and the changes in genetic composition that result from the operation of various factors, including natural selection. Population geneticists pursue their goals by developing abstract mathematical models of gene frequency dynamics, trying to extract conclusions from those models about the likely patterns of genetic variation in actual populations, and testing the conclusions against empirical data.

Population genetics is intimately bound up with the study of evolution and natural selection, and is often regarded as the theoretical cornerstone of modern Darwinism. This is because natural selection is one of the most important factors that can affect a population's genetic composition. Natural selection occurs when some variants in a population out-reproduce other variants as a result of being better adapted to the environment, or 'fitter'. Presuming the fitness differences are at least partly due to genetic differences, this will cause the population's genetic makeup to be altered over time. By studying formal models of gene frequency change, population geneticists therefore hope to shed light on the evolutionary process, and to permit the consequences of different evolutionary hypotheses to be explored in a quantitatively precise way.

The Hardy-Weinberg Principle

The Hardy-Weinberg principle, discovered independently by G.H. Hardy and W. Weinberg in 1908, is one of the simplest and most important principles in population genetics. To illustrate the principle, consider a large population of sexually reproducing organisms. The organisms are assumed to be diploids, meaning that they contain two copies of each chromosome, one received from each parent. The gametes they produce are haploid, meaning that they contain only one

of each chromosome pair. During sexual fusion, two haploid gametes fuse to form a diploid zygote, which then grows and develops into an adult organism. Most multi-celled animals, and many plants, have a lifecycle of this sort.

Suppose that at a given locus, or chromosomal 'slot', there are two possible alleles, A_1 and A_2 the locus is assumed to be on an autosome, not a sex chromosome. With respect to the locus in question, there are three possible genotypes in the population, A_1A_1, A_1A_2 and A_2A_2 (just as in Mendel's pea plant example). Organisms with the A_1A_1 and A_2A_2 genotypes are called homozygotes; those with the A_1A_2 genotype are heterozygotes. The proportions, or relative frequencies, of the three genotypes in the overall population may be denoted $f(A_1A_1), f(A_1A_2)$ and $f(A_2A_2)$ respectively, where $f(A_1A_1) + f(A_1A_2) + f(A_2A_2) = 1$. It is assumed that these genotypic frequencies are the same for both males and females. The relative frequencies of the A and B alleles in the population may be denoted p and q, where $p + q = 1$.

The Hardy-Weinberg principle is about the relation between the allelic and the genotypic frequencies. It states that if mating is random in the population, and if the evolutionary forces of natural selection, mutation, migration and drift are absent, then in the offspring generation the genotypic and allelic frequencies will be related by the following simple equations:

$$f(A_1A_1) = p^2,\ f(A_1A_2) = 2pq,\ \ f(A_2A_2) = q^2$$

Random mating means the absence of a genotypic correlation between mating partners, i.e. the probability that a given organism mates with an A_1A_1 partner, for example, does not depend on the organism's own genotype, and similarly for the probability of mating with a partner of one of the other two types.

That random mating will lead the genotypes to be in the above proportions (so-called Hardy-Weinberg proportions) is a consequence of Mendel's law of segregation. To see this, note that random mating is in effect equivalent to offspring being formed by randomly picking pairs of gametes from a large 'gamete pool' and fusing them into a zygote. The gamete pool contains all the successful gametes of the parent organisms. Since we are assuming the absence of selection, all parents contribute equal numbers of gametes to the pool. By the law of segregation, an A_1A_2 heterozygote produces gametes bearing the A_1 and A_2 alleles in equal proportion. Therefore, the relative frequencies of the A and B alleles in the gamete pool will be the same as in the parental population, namely p and q respectively. Given that the gamete pool is very large, when we pick pairs of gametes from the pool at random, we will get the ordered genotypic pairs $\{A_1A_1\}, \{A_1A_2\}, \{A_2A_1\}, \{A_2A_2$ in the proportions $p^2 : pq : qp : q^2$. But order does not matter, so we can regard the $\{A_1A_2\}$ and $\{A_2A_1\}$ pairs as equivalent, giving the Hardy-Weinberg proportions for the unordered offspring genotypes.

This simple derivation of the Hardy-Weinberg principle deals with two alleles at a single locus, but can easily be extended to multiple alleles. For the multi-allelic case, suppose there are n alleles at the locus, $A_1 \ldots A_n$ with relative frequencies of $p_1 \ldots p_n$ respectively, where $p_1 + p_2 + \ \ldots \ + p_n = 1$. Assuming again that the population is large, mating is random, evolutionary forces are absent, and Mendel's law of segregation holds, then in the offspring generation the frequency of the A_iA_i genotype will be p_i^2, and the frequency of the (unordered) A_iA_j genotype $(i \neq j)$ will be $2p_ip_j$. It is easy to see that the two allele case above is a special case of this generalized principle.

Importantly, whatever the initial genotypic proportions are, random mating will automatically produce offspring in Hardy-Weinberg proportions (for one-locus genotypes). So if generations are non-overlapping, i.e. parents die as soon as they have reproduced, just one round of random mating is needed to bring about Hardy-Weinberg proportions in the whole population; if generations overlap, more than one round of random mating is needed. Once Hardy-Weinberg proportions have been achieved, they will be maintained in subsequent generations so long as the population continues to mate at random and is unaffected by evolutionary forces such as selection, mutation etc. The population is then said to be in Hardy-Weinberg equilibrium—meaning that the genotypic proportions are constant from generation to generation.

The importance of the Hardy-Weinberg principle lies in the fact that it contains the solution to the problem of blending that troubled Darwin. As we saw, Jenkins argued that with sexual reproduction, the variation in the population would be exhausted very rapidly. But the Hardy-Weinberg principle teaches us that this is not so. Sexual reproduction has no inherent tendency to destroy the genotypic variation present in the population, for the genotypic proportions remain constant over generations, given the assumptions noted above. It is true that natural selection often tends to destroy variation, and is thus a homogenizing force; but this is a quite different matter. The 'blending' objection was that sexual mixing itself would produce homogeneity, even in the absence of selection, and the Hardy-Weinberg principle shows that this is untrue.

Another benefit of the Hardy-Weinberg principle is that it greatly simplifies the task of modelling evolutionary change. When a population is in Hardy-Weinberg equilibrium, it is possible to track the genotypic composition of the population by directly tracking the allelic frequencies (or gametic frequencies). That this is so is clear—for if we know the relative frequencies of all the alleles (at a single locus), and know that the population is in Hardy-Weinberg equilibrium, the entire genotype frequency distribution can be easily computed. Were the population not in Hardy-Weinberg equilibrium, we would need to explicitly track the genotype frequencies themselves, which is more complicated.

Primarily for this reason, many population-genetic models assume that Hardy-Weinberg equilibrium obtains; as we have seen, this is tantamount to assuming that mating is random with respect to genotype. But is this assumption empirically plausible? The answer is sometimes but not always. In the human population, for example, mating is close to random with respect to ABO blood group, so the genotype that determines blood group is found in approximately Hardy-Weinberg proportions in many populations. But mating is not random with respect to height; on the contrary, people tend to choose mates similar in height to themselves. So if we consider a genotype that influences height, mating will not be random with respect to this genotype.

The geneticist W.J. Ewens has written of the Hardy-Weinberg principle, 'it does not often happen that the most important theorem in any subject is the easiest and most readily derived theorem for that subject'. The main importance of the principle, as Ewens stresses, is not the gain in mathematical simplicity that it permits, which is simply a beneficial side effect, but rather what it teaches us about the preservation of genetic variation in a sexually reproducing population.

Population-genetic Models of Evolution

Population geneticists usually define 'evolution' as any change in a population's genetic composition over time. The four factors that can bring about such a change are: natural selection, mutation,

random genetic drift, and migration into or out of the population. (A fifth factor—changes to the mating pattern—can change the genotype but not the allele frequencies; many theorists would not count this as an evolutionary change.)

Selection at One Locus

Natural selection occurs when some genotypic variants in a population enjoy a survival or reproduction advantage over others. The simplest population-genetic model of natural selection assumes one autosomal locus with two alleles, A_1 and A_2, as above. The three diploid genotypes A_1A_1, A_1A_2 and A_2A_2 have different fitnesses, denoted by w_{11}, w_{12} and w_{22} respectively. These fitnesses are assumed to be constant across generations. A genotype's fitness may be defined, in this context, as the average number of successful gametes that an organism of that genotype contributes to the next generation—which depends on how well the organism survives, how many matings it achieves, and how fertile it is. Unless w_{11}, w_{12} and w_{22} are all equal, then natural selection will occur, possibly leading the genetic composition of the population to change.

Suppose that initially, i.e. before selection has operated, the zygote genotypes are in Hardy-Weinberg proportions and the frequencies of the A_1 and A_2 alleles are p and q respectively, where $p + q = 1$. The zygotes then grow to adulthood and reproduce, giving rise to a new generation of offspring zygotes. Our task is to compute the frequencies of A_1 and A_2 in the second generation; let us denote these by p' and q' respectively, where $p' + q' = 1$. (Note that in both generations, we consider gene frequencies at the zygotic stage; these may differ from the adult gene frequencies if there is differential survivorship.)

In the first generation, the genotypic frequencies at the zygotic stage are p^2, $2pq$ and q^2 for A_1A_1, A_1A_2, A_2A_2 respectively, by the Hardy-Weinberg law. The three genotypes produce successful gametes in proportion to their fitnesses, i.e. in the ratio $w_{11} : w_{12} : w_{22}$. The average fitness in the population is $\bar{w} = p^2 w_{11} + 2pq w_{12} + q^2 w_{22}$, so the total number of successful gametes produced is $N\bar{w}$ where N is population size. Assuming there is no mutation, and that Mendel's law of segregation holds, then an A_1A_1 organism will produce only A_1 gametes, an A_2A_2 organism will produce only A_2 gametes, and an A_1A_2 organism will produce A_1 and A_2 gametes in equal proportion. Therefore, the proportion of A_1 gametes, and thus the frequency of the A_1 allele in the second generation at the zygotic stage, is:

$$\begin{aligned} p' &= \left[N p^2 w_{11} + \tfrac{1}{2} \left(N 2pq w_{12} \right) \right] / N\bar{w} \\ &= \left(p^2 w_{11} + pq w_{12} \right) / \bar{w} \end{aligned}$$

Equation above is known as a 'recurrence' equation—it expresses the frequency of the A_1 allele in the second generation in terms of its frequency in the first generation. The change in frequency between generations can then be written as:

$$\begin{aligned} \Delta p &= p' - p \\ &= \left(p^2 w_{11} + pq w_{12} \right) / \bar{w} - p \\ &= pq \left[p\left(w_{11} - w_{12} \right) + q\left(w_{12} - w_{22} \right) \right] / \bar{w} \end{aligned}$$

If $\Delta p > 0$, then natural selection has led the A_1 allele to increase in frequency; if $\Delta p < 0$ then selection has led the allele to increase in frequency. If $\Delta p = 0$ then no gene frequency change has

occurred, i.e. the system is in allelic equilibrium. (Note, however, that the condition $\Delta p = 0$ does not imply that no natural selection has occurred; the condition for that is $w_{11} = w_{12} = w_{22}$. It is possible for natural selection to occur but to have no effect on gene frequencies.)

Equations ($p' = \ldots \left(p^2 w_{11} + pq w_{12} \right) / \overline{w}$) and the one above, show, in precise terms, how fitness differences between genotypes will lead to evolutionary change. This enables us to explore the consequences of various different selective regimes.

Suppose firstly that $w_{11} > w_{12} > w_{22}$ i.e. the A_1A_1 homozygote is fitter than the A_1A_2 heterozygote, which in turn is fitter than the A_2A_2 homozygote. By inspection of the equation above, we can see that Δp must be positive (so long as neither p nor q is zero, in which case $\Delta p = 0$). So in each generation, the frequency of the A_1 allele will be greater than in the previous generation, until it eventually reaches fixation and the A_2 allele is eliminated from the population. Once the A_1 allele reaches fixation, i.e. $p = 1$ and $q = 0$, no further evolutionary change will occur, for if $p = 1$ then $\Delta p = 0$. This makes good sense inutitively: since the A_1 allele confers a fitness advantage on organisms that carry it, its relative frequency in the population will increase from generation to generation until it is fixed.

It is obvious that analogous reasoning applies in the case where $w_{22} > w_{12} > w_{11}$. Equation

($\Delta p = \ldots = pq\left[p\left(w_{11} - w_{12} \right) + q\left(w_{12} - w_{22} \right) \right] / w$) tells us that Δp must then be negative, so long as neither p nor q is zero, so the A2 allele will sweep to fixation, eliminating the A_1 allele.

A more interesting situation arises when the heterozygote is superior in fitness to both of the homozygotes, i.e. $w_{12} > w_{11}$ and $w_{12} > w_{22}$—a phenomenon known as heterosis. Intuitively it is clear what should happen in this situation: an equilibrium situation should be reached in which both alleles are present in the population. Equation ($\Delta p = \ldots = pq\left[p\left(w_{11} - w_{12} \right) + q\left(w_{12} - w_{22} \right) \right] / \overline{w}$) confirms this intuition. It is easy to see that $\Delta p = 0$ if either allele has gone to fixation (i.e. if $p = 0$ or $q = 0$), or, thirdly, if the following condition obtains:

$$p(w_{11} - w_{12}) + q(w_{12} - w_{22}) = 0$$

which reduces to,

$$p = p^* = (w_{12} - w_{22}) / (w_{12} - w_{22}) + (w_{12} - w_{11})$$

(The asterisk indicates that this is an equilibrium condition.) Since p must be non-negative, this condition can only be satisfied if there is heterozygote superiority or heterozygote inferiority; it represents an equilibrium state of the population in which both alleles are present. This equilibrium is known as polymorphic, by contrast with the monomorphic equilibria that arise when either of the alleles has gone to fixation. The possibility of polymorphic equilibrium is quite significant. It teaches us that natural selection will not always produce genetic homogeneity; in some cases, selection preserves the genetic variation found in a population.

Numerous further questions about natural selection can be addressed using a simple population-genetic model. For example, by incorporating a parameter which measures the fitness differences between genotypes, we can study the rate of evolutionary change, permitting us to ask questions such as: how many generations are needed for selection to increase the frequency of the A_1 allele from 0.1 to 0.9? If a given deleterious allele is recessive, how much longer will it take to eliminate it from the population than if it were dominant? By permitting questions such as these to be formulated and answered, population geneticists have brought mathematical rigour to the theory of evolution, to an extent that would have seemed unimaginable in Darwin's day.

Of course, the one-locus model is too simple to apply to many real-life populations, for it incorporates simplifying assumptions that are unlikely to hold true. Selection is rarely the only evolutionary force in operation, genotypic fitnesses are unlikely to be constant across generations, Mendelian segregation does not always hold exactly, and so-on. Much research in population genetics consists in devising more realistic evolutionary models, which rely on fewer simplifying assumptions and are thus more complicated. But the one-locus model illustrates the essence of population-genetic reasoning, and the attendant clarification of the evolutionary process that it brings.

Selection-mutation Balance

Mutation is the ultimate source of genetic variation, preventing populations from becoming genetically homogeneous in situations where they otherwise would. Once mutation is taken into account, the conclusions drawn need to be modified. Even if one allele is selectively superior to all others at a given locus, it will not become fixed in the population; recurrent mutation will ensure that other alleles are present at low frequency, thus maintaining a degree of polymorphism. Population geneticists have long been interested in exploring what happens when selection and mutation act simultaneously.

Continuing with our one-locus, two allele model, let us suppose that the A_1 allele is selectively superior to A_2, but recurrent mutation from A_1 to A_2 prevents A_1 from spreading to fixation. The rate of mutation from A_2 to A_1 per generation, i.e. the proportion of A_1 alleles that mutate every generation, is denoted *u*. (Empirical estimates of mutation rates are typically in the region of 10-6.) Back mutation from A_2 to A_1 can be ignored, because we are assuming that the A_2 allele is at a very low frequency in the population, thanks to natural selection. What happens to the gene frequency dynamics under these assumptions? Recall equation ($p' = ...\left(p^2 w_{11} + pq\, w_{12}\right) / \overline{w}$) above, which expresses the frequency of the A_1 allele in terms of its frequency in the previous generation. Since a certain fraction (*u*) of the A_1 alleles will have mutated to A_2, this recurrence equation must be modified to:

$$p' = (p^2 w_{11} + pq\, w_{12})\ (1 - u) / \overline{w}$$

to take account of mutation. As before, equilibrium is reached when $p' = p$, i.e. $\Delta p = 0$. The condition for equilibrium is therefore:

$$p = p^* = (p^2 w_{11} + pq\, w_{12})\ (1 - u) / \overline{w}$$

A useful simplification of above equation can be achieved by making some assumptions about the genotype fitnesses, and adopting a new notation. Let us suppose that the A_2 allele is completely recessive (as is often the case for deleterious mutants). This means that the A_1A_1 and A_1A_2 genotypes have identical fitness. Therefore, genotypic fitnesses can be written $w_{11} = 1, w_{12} = 1, w_{22} = 1 - s$, where s denotes the difference in fitness of the A_2A_2 homozygote from that of the other two genotypes. (s is known as the selection co-efficient against A_2A_2). Since we are assuming that the A_2 allele is deleterious, it follows that $s > 0$. Substituting these genotype fitnesses in above equation yields:

$$p^* = p\ (1-u) / p^2 + 2pq + q^2(1-s)$$

which reduces to:

$$p^* = 1 - (u / s)^{½}$$

or equivalently (since $p + q = 1$):

$$q^* = (u / s)^{½}$$

Equation above gives the equilibrium frequency of the A_2 allele, under the assumption that it is completely recessive. Note that as u increases, q^* increases too. This is highly intuitive: the greater the mutation rate from A_2A_2 A_1 to A_2, the greater the frequency of A_2 that can be maintained at equilibrium, for a given value of s. Conversely, as s increases, q*decreases. This is also intuitive: the stronger the selection against the A_2A_2 homozygote, the lower the equilibrium frequency of A_2, for a given value of *u*.

It is easy to see why equation above is said to describe selection-mutation balance—natural selection is continually removing A_2 alleles from the population, while mutation is continually re-creating them. Equation above tells us the equilibrium frequency of A_2 that will be maintained, as a function of the rate of mutation from A_2A_2 to A_2 and the magnitude of the selective disadvantage suffered by the A2A2 homozygote. Importantly, equation above was derived under the assumption that the A_2 allele is completely recessive, i.e. that the A_1A_2 heterozygote is phenotypically identical to the A_1A_1 homozygote. However, it is straightforward to derive similar equations for the cases where the A_2 allele is dominant, or partially dominant. If A_2 is dominant, or partially dominant, its equilibrium frequency will be lower than if it is completely recessive; for selection is more efficient at removing it from the population. A deleterious allele that is recessive can 'hide' in heterozygotes, and thus escape the purging power of selection, but a dominant allele cannot.

The discussion has focused exclusively on deleterious mutations, i.e. ones which reduce the fitness of their host organism. This may seem odd, given that beneficial mutations play so crucial a role in the evolutionary process. The reason is that in population genetics, a major concern is to understand the causes of the genetic variability found in biological populations. If a gene is beneficial, natural selection is likely to be the major determinant of its equilibrium frequency; the rate of sporadic mutation to that gene will play at most a minor role. It is only where a gene is deleterious that mutation plays a major role in maintaining it in a population.

Random Drift

Random genetic drift refers to the chance fluctuations in gene frequency that arise in finite populations; it can be thought of as a type of 'sampling error'. In many evolutionary models, the population is assumed to be infinite, or very large, precisely in order to abstract away from chance fluctuations. But though mathematically convenient, this assumption is often unrealistic. In real life, chance factors will invariably play a role, particularly in small populations. The term 'random drift' is sometimes used in broad sense, to refer to any stochastic factors that affect gene frequencies in a population, including for example chance fluctuations in survival and mating success; and sometimes in a narrower sense, to refer to the random sampling of gametes to form the offspring generation (which arises because organisms produce many more gametes than will ever make it into a fertilized zygote). The broader sense is used here.

To understand the nature of random drift, consider a simple example. A population contains just ten organisms, five of type A and five of type B; the organisms reproduce asexually and beget offspring of the same type. Suppose that neither type is selectively superior to the other—both are equally well-adapted to the environment. However, this does not imply that the two types will produce identical numbers of offspring, for chance factors may play a role. For example, it is possible that all the type Bs might die by accident before reproducing; in which case the frequency of B in the second generation will fall to zero. If so, then the decline of the B type (and thus the spread of the A type) is the result of random drift. Evolutionists are often interested in knowing whether a given gene frequency change is the result of drift, selection, or some combination of the two.

The label 'random drift' is slightly misleading. In saying that the spread of the A type is due to random drift, or chance, we do not mean that no cause can be found of its spread. In theory, we could presumably discover the complete causal story about why each organism in the population left exactly the number of offspring that it did. In ascribing the evolutionary change to random drift, we are not denying that there is such a causal story to be told. Rather, we mean that the spread of the A type was not due to its adaptive superiority over the B type. Put differently, the A and the B types had the same expected number of offspring, so were equally fit; but the A types had a greater actual number of offspring. In a finite population, actual reproductive output will almost always deviate from expectation, leading to evolutionary change.

An analogy with coin tossing can illuminate random drift. Suppose a fair coin is tossed ten times. The probability of heads on any one toss is ½, and so the expected frequency of heads in the sequence of ten is 50%. But the probability of actually getting half heads and half tails is only 242/1024, or approximately 23.6%. So even though the coin is fair, we are unlikely to get equal proportions of heads and tails in a sequence of ten tosses; some deviation from expectation is more probable than not. In just the same way, it is likely that some evolutionary change will occur. This analogy also illustrates the role of population size. If we tossed the coin a hundred times rather than ten, the proportion of heads would probably be very close to ½. In just the same way, the larger the population, the less important the effect of random drift on gene frequencies; in the infinite limit, drift has no effect.

Drift greatly complicates the task facing the population geneticist. It is obviously impossible to deduce the composition of the population in the second generation from its composition in the first generation; at most, we can hope to deduce the probability distribution over all the possible

compositions. So once drift is taken into account, no simple recurrence relation for gene frequencies, of the sort expressed in equation $p' = ... = \left(p^2 w_{11} + pq w_{12} \right) / \overline{w}$ above, can be derived.

One important effect of random drift is to decrease the degree of heterozygosity in a population over time. This happens because, given enough time, any finite population will eventually become homozygous through drift (though if the population is large, the approach to homozygosity will be slow.) It is easy to see why this is—for gene frequencies of 0 and 1 are 'absorbing boundaries', meaning that once the boundary is reached, there is no way back from it (apart from mutation). So eventually, a given allele will eventually become fixed in a population, or go extinct, the latter being the more likely fate. Indeed mathematical models show that a neutral allele arising by mutation has a very low probability of becoming fixed in a population; the larger the population, the lower the probability of fixation.

Another important effect of random drift is to cause the different subpopulations of a species to diverge genetically from each other, as the chance accumulation of alleles will probably proceed differently in each, particularly if the alleles confer little selective advantage or disadvantage. By chance, one population may become fixed for allele A_1, while a second population becomes fixed for another allele A_2. This possibility is an important one, for if we ignore it, we may mistakenly conclude that the A_1 allele must have been advantageous in the environment of the first population, the A_2 allele in the environment of the second, i.e. that selection was responsible for the genetic differentiation. Such an explanation might be right, but it is not the only one—random drift provides an alternative.

The question of whether drift or selection plays a more important role in molecular evolution was much debated in the 1960s and 1970s; it lay at the heart of the heated controversy between 'selectionists' and 'neutralists'. The neutralist camp, headed by M. Kimura, argued that most molecular variants had no effect on phenotype, so were not subject to natural selection; random drift was the major determinant of their fate. Kimura argued that the apparently constant rate at which the amino acid sequences of proteins evolved, and the extent of genetic polymorphism observed in natural populations, could best be explained by the neutralist hypothesis. Selectionists countered that natural selection was also capable of explaining the molecular data. In recent years, the controversy has subsided somewhat, without a clear victory for either side. Most biologists believe that some molecular variants are indeed neutral, though fewer than were claimed by the original neutralists.

Migration

Migration into or out of a population is the fourth and final factor that can affect its genetic composition. Obviously, if immigrants are genetically different from the population they are entering, this will cause the population's genetic composition to be altered. The evolutionary importance of migration stems from the fact that many species are composed of a number of distinct subpopulations, largely isolated from each other but connected by occasional migration. (For an extreme example of population subdivision, think of ant colonies.) Migration between subpopulations gives rise to gene flow, which acts as a sort of 'glue', limiting the extent to which subpopulations can diverge from each other genetically.

The simplest model for analysing migration assumes that a given population receives a number of migrants each generation, but sends out no emigrants. Suppose the frequency of the A_1 allele

in the resident population is p, and the frequency of the A_1 allele among the migrants arriving in the population is pm. The proportion of migrants coming into the population each generation is m (i.e. as a proportion of the resident population). So post-migration, the frequency of the A_1 allele in the population is:

$$p' = (1 - m)\, p + m p_m$$

The change in gene frequency across generations is therefore:

$$\begin{aligned} \Delta p &= p' - p \\ &= -m\left(p - p_m\right) \end{aligned}$$

Therefore, migration will increase the frequency of the A_1 allele if $p_m > p$, decrease its frequency if $p > p_m$, and leave its frequency unchanged if $p = p_m$. It is then a straightforward matter to derive an equation giving the gene frequency in generation t as a function of its initial frequency and the rate of migration. The equation is:

$$p_t = p_m + (p_0 - p_m)(1 - m)^t$$

Where p_0 is the initial frequency of the A_1 allele in the population, i.e. before any migration has taken place. Since the expression $(1 - m)^t$ tends towards zero as t grows large, it is easy to see that equilibrium is reached when $p_t = p_m$, i.e. when the gene frequency of the migrants equals the gene frequency of the resident population.

This simple model assumes that migration is the only factor affecting gene frequency at the locus, but this is unlikely to be the case. So it is necessary to consider how migration will interact with selection, drift and mutation. A balance between migration and selection can lead to the maintenance of a deleterious allele in a population, in a manner closely analogous to mutation-selection balance. The interaction between migration and drift is especially interesting. We have seen that drift can lead the separate subpopulations of a species to diverge genetically. Migration opposes this trend—it is a homogenising force that tends to make subpopulations more alike. Mathematical models suggest that that even a fairly small rate of migration will be sufficient to prevent the subpopulations of a species from diverging genetically. Some theorists have used this to argue against the evolutionary importance of group selection, on the grounds that genetic differences between groups, which are essential for group selection to operate, are unlikely to persist in the face of migration.

Non-random Mating

Recall that the Hardy-Weinberg law, the starting point for most population-genetic analysis, was derived under the assumption of random mating. But departures from random mating are actually quite common. Organisms may tend to choose mates who are similar to them phenotypically or genotypically—a mating system known as 'positive assortment'. Alternatively, organisms may choose mates dissimilar to them—'negative assortment'. Another type of departure from random mating is inbreeding, or preferentially mating with relatives.

Analysing the consequences of non-random mating is quite complicated, but some conclusions are fairly easily seen. Firstly and most importantly, non-random mating does not in itself affect gene frequencies (so is not an evolutionary 'force' on a par with selection, mutation, migration and

drift); rather, it affects genotype frequencies. To appreciate this point, note that the gene frequency of a population, at the zygotic stage, is equal to the gene frequency in the pool of successful gametes from which the zygotes are formed. The pattern of mating simply determines the way in which haploid gametes are 'packaged' into diploid zygotes. Thus if a random mating population suddenly starts to mate non-randomly, this will have no effect on gene frequencies.

Secondly, positive assortative mating will tend to decrease the proportion of heterozygotes in the population, thus increasing the genotypic variance. To see this, consider again a single locus with two alleles, A_1 and A_2, with frequencies p and q in a given population. Initially the population is at Hardy-Weinberg equilibrium, so the proportion of A_1A_2 heterozygotes is $2pq$. If the population then starts to mate completely assortatively, i.e. mating only occurs between organisms of identical genotype, it is obvious that the proportion of heterozygotes must decline. For $A_1A_1 \times A_1A_1$ and $A_2A_2 \times A_2A_2$ matings will produce no heterozygotes; and only half the progeny of $A_1A_2 \times A_1A_2$ matings will be heterozygotic. So the proportion of heterozygotes in the second generation must be less than $2pq$. Conversely, negative assortment will tend to increase the proportion of heterozygotes from what it would be under Hardy-Weinberg equilibrium.

What about inbreeding? In general, inbreeding will tend to increase the homozygosity of a population, like positive assortment. The reason for this is obvious—relatives tend to be more genotypically similar than randomly chosen members of the population. In the majority of species, including the human species, inbreeding has negative effects on organismic fitness—a phenomenon known as 'inbreeding depression'. The explanation for this is that deleterious alleles often tend to be recessive, so have no phenotypic effect when found in heterozygotes. Inbreeding reduces the proportion of heterozygotes, making recessive alleles more likely to be found in homozygotes where their negative phenotypic effects become apparent. The converse phenomenon—'hybrid vigour' resulting from outbreeding—is widely utilised by animal and plant breeders.

Two-locus Models and Linkage

So far, our exposition has dealt with gene frequency change at a single locus, which is the simplest sort of population-genetic analysis. However, in practice it is unlikely that an organism's fitness will depend on its single-locus genotype, so there is a limit on the extent to which single-locus models can illuminate the evolutionary process. The aim of two-locus (and more generally, multi-locus) models is to track changes in gene frequency at more than one locus simultaneously. Such models are invariably more complicated that their single-locus counterparts, but achieve greater realism.

The simplest two-locus model assumes two autosomal loci, A and B, each with two alleles, A_1 and A_2, B_1 and B_2 respectively. Thus there are four types of haploid gamete in the population—A_1B_1, A_1B_2, A_2B_1—whose frequencies we will denote by x_1, x_2, x_3 and x_4 respectively. (Note that the x_i are not allele frequencies; in the two-locus case, we cannot equate 'gamete frequency' with 'allelic frequency', as is possible for a single locus.) Diploid organisms are formed by the fusion of two gametes, as before. Thus there are ten possible diploid genotypes in the population—found by taking each gamete type in combination with every other.

In the one-locus case, we saw that in a large randomly mating population, there is a simple relationship between the frequencies of the gamete types and of the zygotic genotypes that they

form. In the two-locus case, the same relationship holds. Thus for example, the frequency of the A_1B_1 / A_1B_1 genotype will be $(x_1)^2$; the frequency of the A_1B_1 / A_2B_1 genotype will be $2x_1x_3$, and so-on. (This can be established rigorously with an argument based on random sampling of gametes, analogous to the argument used in the one-locus case.) The first aspect of the Hardy-Weinberg law—genotypic frequencies given by the square of the array of gametic frequencies—therefore transposes neatly to the two-locus case. However, the second aspect of the Hardy-Weinberg law—stable genotypic frequencies after one round of random mating—does not generally apply in the two-locus case.

A key concept in two-locus population genetics is that of linkage, or lack of independence between the two loci. To understand linkage, consider the set of gametes produced by an organism of the A_1B_1 / A_2B_2 genotype, i.e. a double heterozygote. If the two loci are unlinked, then the composition of this set will be $\{¼A_1B_1, ¼A_1B_2, ¼A_2B_1, ¼A_2B_2\}$ i.e. all four gamete types will be equally represented. (We are presuming that Mendel's first law holds at both loci.) So unlinked loci are independent—which allele a gamete has at the A locus tells us nothing about which allele it has at the B locus. The opposite extreme is perfect linkage. If the two loci are perfectly linked, then the set of gametes produced by the A_1B_1 / A_2B_2 double heterozygote has the composition $\{½A_1B_1, ½A_2B_2\}$; this means that if a gamete receives the A_1 allele at the A locus, it necessarily receives the B_1 allele at the B locus and vice versa.

In physical terms, perfect linkage means that the A and B loci are located close together on the same chromosome; the alleles at the two loci are thus inherited as a single unit. Unlinked loci are either on different chromosomes, or on the same chromosome but separated by a considerable distance, hence likely to be broken up by recombination. Where the loci are on the same chromosome, perfect linkage and complete lack of linkage are two ends of a continuum. The degree of linkage is measured by the recombination fraction r, where $0 \le r \le ½$. The composition of the set of gametes produced by an organism of the A_1B_1 / A_2B_2 genotype can be written in terms of r, as follows:

$$\begin{aligned} A_1B_1 &\quad ½\ (1-r) \\ A_1B_2 &\quad ½r \\ A_2B_1 &\quad ½r \\ A_2B_2 &\quad ½\ (1-r) \end{aligned}$$

It is easy to see that $r = ½$ means that the loci are unlinked, so all four gamete types are produced in equal proportion, while r = 0 means that they are perfectly linked.

In a two-locus model, the gametic (and therefore genotypic) frequencies need not be constant across generations, even in the absence of selection, mutation, migration and drift, unlike in the one-locus case. (Though allelic frequencies will of course be constant, in the absence of any evolutionary forces.) It is possible to write recurrence equations for the gamete frequencies, as a function of their frequencies in the previous generation plus the recombination fraction. The equations are:

$$\begin{aligned} x_1' &= x_1 + r(x_2x_3 - x_1x_4) \\ x_2' &= x_2 + r(x_2x_3 - x_1x_4) \\ x_3' &= x_3 + r(x_2x_3 - x_1x_4) \\ x_4' &= x_4 + r(x_2x_3 - x_1x_4) \end{aligned}$$

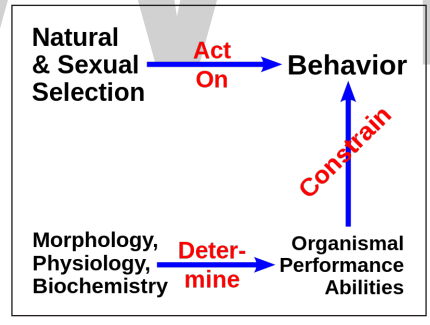
From the recurrence equations, it is easy to see that gametic (and thus genotypic) frequencies will be stable across generations, i.e. $x_i' = x_i$ for each i, under either of two conditions: (i) $r = 0$ or (ii) $x_2x_3 - x_1x_4 = 0$. Condition (i) means that the two loci are perfectly linked, and thus in effect behaving as one locus; condition (ii) means that the two loci are in 'linkage equilibrium', which means that the alleles at the A-locus are in random association with the alleles at the B-locus. More precisely, linkage equilibrium means that the population-wide frequency of the A_iB_i gamete is equal to the frequency of the A_i allele multiplied by the frequency of the Bi allele.

An important result in two-locus theory shows that, given random mating, the quantity $(x_2x_3 - x_1x_4)$ will decrease every generation until it reaches zero—at which point the genotype frequencies will be in equilibrium. So a population initially in linkage disequilibrium will approach linkage equilibrium over a number of generations. The rate of approach depends on the value of r, the recombination fraction. Note the contrast with the one-locus case, where just one round of random mating is sufficient to bring the genotype frequencies into equilibrium.

Evolutionary Physiology

Evolutionary physiology is the study of physiological evolution, which is to say, the manner in which the functional characteristics of individuals in a population of organismshave responded to selection across multiple generations during the history of the population.

It is a subdiscipline of both physiology and evolutionary biology. Practitioners in this field come from a variety of backgrounds, including physiology, evolutionary biology, ecologyand genetics.



Accordingly, the range of phenotypes studied by evolutionary physiologists is broad, including life history, behavior, whole-organism performance, functional morphology, biomechanics, anatomy, classical physiology, endocrinology, biochemistry, and molecular evolution. It is closely related to comparative physiology and environmental physiology, and its findings are a major concern of evolutionary medicine. One definition that has been offered is "the study of the physiological basis of fitness, namely, correlated evolution (including constraints and trade-offs) of physiological form and function associated with the environment, diet, homeostasis, energy management, longevity, and mortality and life history characteristics".

Natural and sexual selection are often presumed to act most directly on behavior (e.g., what an animal chooses to do when confronted by a predator), which is expressed within limits set by whole-organism performance abilities(e.g., how fast it can run) that are determined by subordinate

traits (e.g., muscle fiber-type composition). A weakness of this conceptual and operational model is the absence of an explicit recognition of the place of life history traits.

Important areas of current research include:

- Organismal performance as a central phenotype (e.g., measures of speed or stamina in animal locomotion).
- Role of behavior in physiological evolution.
- Physiological and endocrinological basis of variation in life history traits (e.g., clutch size).
- Functional significance of molecular evolution.
- Extent to which species differences are adaptive.
- Physiological underpinnings of limits to geographic ranges.
- Geographic variation in physiology.
- Role of sexual selection in shaping physiological evolution.
- Magnitude of "phylogenetic signal" in physiological traits.
- Role of pathogens and parasites in physiological evolution and immunity.
- Application of optimality modeling to elucidate the degree of adaptation.
- Role of phenotypic plasticity in accounting for individual, population, and species differences.
- Mechanistic basis of trade-offs and constraints on evolution (e.g., putative Carrier's constraint on running and breathing).
- Limits on sustained metabolic rate.
- Origin of allometric scaling relations or allometric laws (and the so-called metabolic theory of ecology).
- Individual variation.
- Functional significance of biochemical polymorphisms.
- Analysis of physiological variation via quantitative genetics.
- Paleophysiology and the evolution of endothermy.
- Human adaptational physiology.
- Darwinian medicine.
- Evolution of dietary antioxidants.
- Emergent properties.

As a hybrid scientific discipline, evolutionary physiology provides some unique perspectives. For example, an understanding of physiological mechanisms can help in determining whether a particular pattern of phenotypic variation or covariation (such as an allometric relationship) represents what could possibly exist or just what selection has allowed. Similarly, a thorough knowledge of physiological mechanisms can greatly enhance understanding of possible reasons for evolutionary correlations and constraints than is possible for many of the traits typically studied by evolutionary biologists (such as morphology).

Techniques

- Artificial selection and experimental evolution mouse wheel running video.
- Genetic analyses and manipulations.
- Measurement of selection in the wild.
- Phenotypic plasticity and manipulation.
- Phylogenetically based comparisons.
- Doubly labeled water measurements of free-living energy demands of animals.

Experimental Evolution

Experimental evolution is the use of laboratory experiments or controlled field manipulations to explore evolutionary dynamics. Evolution may be observed in the laboratory as individuals/populations adapt to new environmental conditions by natural selection. There are two different ways in which adaptation can arise in experimental evolution. One is via an individual organism gaining a novel beneficial mutation. The other is from allele frequency change in standing genetic variation already present in a population of organisms. Other evolutionary forces outside of mutation and natural selection can also play a role or be incorporated into experimental evolution studies, such as genetic drift and gene flow. The organism used is decided by the experimenter, based on whether the hypothesis to be tested involves adaptation through mutation or allele frequency change. A large number of generations are required for adaptive mutation to occur, and experimental evolution via mutation is carried out in viruses or unicellular organisms with rapid generation times, such as bacteria and asexual clonal yeast. Polymorphic populations of asexual or sexual yeast, and multicellular eukaryotes like Drosophila, can adapt to new environments through allele frequency change in standing genetic variation. Organisms with longer generations times, although costly, can be used in experimental evolution. Laboratory studies with foxes and with rodents have shown that notable adaptations can occur within as few as 10–20 generations and experiments with wild guppies have observed adaptations within comparable numbers of generations. More recently, experimentally evolved individuals or populations are often analyzed using whole genome sequencing, an approach known as Evolve and Resequence (E&R). E&R can identify mutations that lead to adaptation in clonal individuals or identify alleles that changed in frequency in polymorphic populations, by comparing the sequences of individuals/populations before and after adaptation.

The sequence data makes it possible to pinpoint the site in a DNA sequence that a mutation/allele frequency change occurred to bring about adaptation. The nature of the adaptation and functional follow up studies can shed insight into what effect the mutation/allele has on phenotype.

Domestication and Breeding

This Chihuahua mix and Great Dane show the wide range of dog breed sizes created using artificial selection.

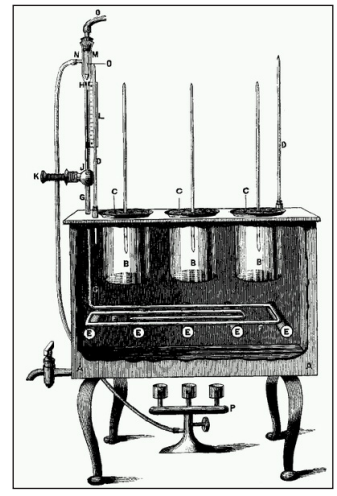
Unwittingly, humans have carried out evolution experiments for as long as they have been domesticating plants and animals. Selective breeding of plants and animals has led to varieties that differ dramatically from their original wild-type ancestors. Examples are the cabbage varieties, maize, or the large number of different dog breeds. The power of human breeding to create varieties with extreme differences from a single species was already recognized by Charles Darwin. In fact, he started out his book *The Origin of Species* with a chapter on variation in domestic animals. In this chapter, Darwin discussed in particular the pigeon.

> "Altogether at least a score of pigeons might be chosen, which if shown to an ornithologist, and he were told that they were wild birds, would certainly, I think, be ranked by him as well-defined species. Moreover, I do not believe that any ornithologist would place the English carrier, the short-faced tumbler, the runt, the barb, pouter, and fantail in the same genus; more especially as in each of these breeds several truly-inherited sub-breeds, or species as he might have called them, could be shown him. I am fully convinced that the common opinion of naturalists is correct, namely, that all have descended from the rock-pigeon (Columba livia), including under this term several geographical races or sub-species, which differ from each other in the most trifling respects."

— Charles Darwin, The Origin of Species

One of the first to carry out a controlled evolution experiment was William Dallinger. In the late 19th century, he cultivated small unicellular organisms in a custom-built incubator over a time period of seven years. Dallinger slowly increased the temperature of the incubator from an initial 60 °F up to 158 °F. The early cultures had shown clear signs of distress at a temperature of 73 °F, and were certainly not capable of surviving at 158 °F. The organisms Dallinger had in his incubator at the end of the experiment, on the other hand, were perfectly fine at 158 °F. However, these organisms would no longer grow at the initial 60 °F. Dallinger concluded that he had found

evidence for Darwinian adaptation in his incubator, and that the organisms had adapted to live in a high-temperature environment. Dallinger's incubator was accidentally destroyed in 1886, and Dallinger could not continue this line of research.



Drawing of the incubator used by Dallinger in his evolution experiments.

From the 1880s to 1980, experimental evolution was intermittently practiced by a variety of evolutionary biologists, including the highly influential Theodosius Dobzhansky. Like other experimental research in evolutionary biology during this period, much of this work lacked extensive replication and was carried out only for relatively short periods of evolutionary time.

Experimental evolution has been used in various formats to understand underlying evolutionary processes in a controlled system. Experimental evolution has been performed on multicellular and unicellular eukaryotes, prokaryotes, and viruses. Similar works have also been performed by directed evolution of individual enzyme, ribozyme and replicator genes.

Aphids

In the 1950s, the Soviet biologist Georgy Shaposhnikov conducted experiments on aphids of the Dysaphis genus. By transferring them to plants normally nearly or completely unsuitable for them, he had forced populations of parthenogenetic descendants to adapt to the new food source to the point of reproductive isolation from the regular populations of the same species.

Fruit Flies

One of the first of a new wave of experiments using this strategy was the laboratory "evolutionary radiation" of Drosophila melanogaster populations that Michael R. Rose started in February, 1980. This system started with ten populations, five cultured at later ages, and five cultured at early ages. Since then more than 200 different populations have been created in this laboratory radiation, with selection targeting multiple characters. Some of these highly differentiated populations have also been selected "backward" or "in reverse," by returning experimental populations to their ancestral culture regime. Hundreds of people have worked with these populations over the better part of three decades. Much of this work is summarized in the papers collected in the book Methuselah Flies.

The early experiments in flies were limited to studying phenotypes but the molecular mechanisms, i.e., changes in DNA that facilitated such changes, could not be identified. This changed with genomics technology. Subsequently, Thomas Turner coined the term Evolve and Resequence (E&R) and several studies used E&R approach with mixed success. One of the more interesting experimental evolution studies was conducted by Gabriel Haddad's group at UC San Diego, where Haddad and colleagues evolved flies to adapt to low oxygen environments, also known as hypoxia. After 200 generations, they used E&R approach to identify genomic regions that were selected by natural selection in the hypoxia adapted flies. More recent experiments are following up E&R predictions with RNAseq and genetic crosses. Such efforts in combining E&R with experimental validations should be powerful in identifying genes that regulate adaptation in flies.

Bacteria

Bacteria have short generation times, easily sequenced genomes, and well-understood biology. They are therefore commonly used for experimental evolution studies.

Lenski's E. coli Experiment

One of the most widely known examples of laboratory bacterial evolution is the long-term *E.coli* experiment of Richard Lenski. On February 24, 1988, Lenski started growing twelve lineages of *E. coli* under identical growth conditions. When one of the populations evolved the ability to aerobically metabolize citrate from the growth medium and showed greatly increased growth, this provided a dramatic observation of evolution in action. The experiment continues to this day, and is now the longest-running (in terms of generations) controlled evolution experiment ever undertaken. Since the inception of the experiment, the bacteria have grown for more than 60,000 generations. Lenski and colleagues regularly publish updates on the status of the experiments.

Laboratory Mice

Mouse from the Garland selection experiment with attached running wheel and its rotation counter.

In 1998, Theodore Garland, Jr. and colleagues started a long-term experiment that involves selective breeding of mice for high voluntary activity levels on running wheels. This experiment also continues to this day (> 65 generations). Mice from the four replicate "High Runner" lines evolved to run almost three times as many running-wheel revolutions per day compared with the four unselected control lines of mice, mainly by running faster than the control mice rather than running for more minutes/day.

Female mouse with her litter, from the Garland selection experiment.

The HR mice exhibit an elevated maximal aerobic capacity when tested on a motorized treadmill. They also exhibit alterations in motivation and the reward system of the brain. Pharmacological studies point to alterations in dopamine function and the endocannabinoid system. The High Runner lines have been proposed as a model to study human attention-deficit hyperactivity disorder (ADHD), and administration of Ritalin reduces their wheel running approximately to the levels of control mice.

Other Examples

Stickleback fish have both marine and freshwater species, the freshwater species evolving since the last ice age. Freshwater species can survive colder temperatures. Scientists tested to see if they could reproduce this evolution of cold-tolerance by keeping marine sticklebacks in cold freshwater. It took the marine sticklebacks only three generations to evolve to match the 2.5 degree Celsius improvement in cold-tolerance found in wild freshwater sticklebacks. Microbial cells and recently mammalian cells are evolved under nutrient limiting conditions to study their metabolic response and engineer cells for better characteristics.

Because of their rapid generation times microbes offer an opportunity to study microevolution in the classroom. A number of exercises involving bacteria and yeast teach concepts ranging from the evolution of resistance to the evolution of multicellularity. With the advent of next-generation sequencing technology it has become possible for students to conduct an evolutionary experiment, sequence the evolved genomes, and to analyze and interpret the results.

Paleontology

Paleontology, sometimes spelled palaeontology is the scientific study of life that existed prior to, and sometimes including, the start of the Holocene Epoch (roughly 11,700 years before present). It includes the study of fossils to determine organisms' evolution and interactions with each other and their environments (their paleoecology). Paleontological observations have been documented as far back as the 5th century BC. The science became established in the 18th century as a result of Georges Cuvier's work on comparative anatomy, and developed rapidly in the 19th century.

A paleontologist at work.

Paleontology lies on the border between biology and geology, but differs from archaeology in that it excludes the study of anatomically modern humans. It now uses techniques drawn from a wide range of sciences, including biochemistry, mathematics, and engineering. Use of all these techniques has enabled paleontologists to discover much of the evolutionary history of life, almost all the way back to when Earth became capable of supporting life, about 3.8 billion years ago. As knowledge has increased, paleontology has developed specialised sub-divisions, some of which focus on different types of fossil organisms while others study ecology and environmental history, such as ancient climates.

Body fossils and trace fossils are the principal types of evidence about ancient life, and geochemical evidence has helped to decipher the evolution of life before there were organisms large enough to leave body fossils. Estimating the dates of these remains is essential but difficult: sometimes adjacent rock layers allow radiometric dating, which provides absolute dates that are accurate to within 0.5%, but more often paleontologists have to rely on relative dating by solving the "jigsaw puzzles" of biostratigraphy(arrangement of rock layers from youngest to oldest). Classifying ancient organisms is also difficult, as many do not fit well into the Linnaean taxonomy classifying living organisms, and paleontologists more often use cladistics to draw up evolutionary "family trees". The final quarter of the 20th century saw the development of molecular phylogenetics, which investigates how closely organisms are related by measuring the similarity of the DNA in their genomes. Molecular phylogenetics has also been used to estimate the dates when species diverged, but there is controversy about the reliability of the molecular clock on which such estimates depend.

The simplest definition of paleontology is "the study of ancient life". The field seeks information about several aspects of past organisms: "their identity and origin, their environment and evolution, and what they can tell us about the Earth's organic and inorganic past".

A Historical Science

The preparation of the fossilised bones of *Europasaurus holgeri*.

Paleontology is one of the historical sciences, along with archaeology, geology, astronomy, cosmology, philology and history itself: it aims to describe phenomena of the past and reconstruct their causes. Hence it has three main elements: description of past phenomena; developing a general theory about the causes of various types of change; and applying those theories to specific facts. When trying to explain the past, paleontologists and other historical scientists often construct a set of hypotheses about the causes and then look for a *smoking gun*, a piece of evidence that strongly accords with one hypothesis over the others. Sometimes the smoking gun is discovered by a fortunate accident during other research. For example, the discovery by Luis and Walter Alvarez of iridium, a mainly extraterrestrial metal, in the Cretaceous–Tertiary boundary layer made asteroid impact the most favored explanation for the Cretaceous–Paleogene extinction event, although the contribution of volcanism continues to be debated.

The other main type of science is experimental science, which is often said to work by conducting experiments to *disprove*hypotheses about the workings and causes of natural phenomena. This approach cannot prove a hypothesis, since some later experiment may disprove it, but the accumulation of failures to disprove is often compelling evidence in favor. However, when confronted with totally unexpected phenomena, such as the first evidence for invisible radiation, experimental scientists often use the same approach as historical scientists: construct a set of hypotheses about the causes and then look for a "smoking gun".

Related Sciences

Paleontology lies between biology and geology since it focuses on the record of past life, but its main source of evidence is fossils in rocks. For historical reasons, paleontology is part of the geology department at many universities: in the 19th and early 20th centuries, geology departments found fossil evidence important for dating rocks, while biology departments showed little interest.

Paleontology also has some overlap with archaeology, which primarily works with objects made by humans and with human remains, while paleontologists are interested in the characteristics and evolution of humans as a species. When dealing with evidence about humans, archaeologists and paleontologists may work together – for example paleontologists might identify animal or plant fossils around an archaeological site, to discover what the people who lived there ate; or they might analyze the climate at the time of habitation.

In addition, paleontology often borrows techniques from other sciences, including biology, osteology, ecology, chemistry, physics and mathematics.For example, geochemical signatures from rocks may help to discover when life first arose on Earth, and analyses of carbon isotope ratios may help to identify climate changes and even to explain major transitions such as the Permian–Triassic extinction event. A relatively recent discipline, molecular phylogenetics, compares the DNA and RNA of modern organisms to re-construct the "family trees" of their evolutionary ancestors. It has also been used to estimate the dates of important evolutionary developments, although this approach is controversial because of doubts about the reliability of the "molecular clock". Techniques from engineering have been used to analyse how the bodies of ancient organisms might have worked, for example the running speed and bite strength of *Tyrannosaurus,* or the flight mechanics of *Microraptor*. It is relatively commonplace to study the internal details of fossils using X-ray microtomography. Paleontology, biology, archaeology, and paleoneurobiology combine to study endocranial casts (endocasts) of species related to humans to clarify the evolution of the human brain.

Paleontology even contributes to astrobiology, the investigation of possible life on other planets, by developing models of how life may have arisen and by providing techniques for detecting evidence of life.

Subdivisions

As knowledge has increased, paleontology has developed specialised subdivisions. Vertebrate paleontology concentrates on fossils from the earliest fish to the immediate ancestors of modern mammals. Invertebrate paleontology deals with fossils such as molluscs, arthropods, annelid worms and echinoderms. Paleobotany studies fossil plants, algae, and fungi. Palynology, the study of pollen and spores produced by land plants and protists, straddles paleontology and botany, as it deals with both living and fossil organisms. Micropaleontology deals with microscopic fossil organisms of all kinds.

Analyses using engineering techniques show that *Tyrannosaurus*had a devastating bite, but raise doubts about its running ability.

Instead of focusing on individual organisms, paleoecology examines the interactions between different ancient organisms, such as their food chains, and the two-way interactions with their environments. For example, the development of oxygenic photosynthesis by bacteria caused the oxygenation of the atmosphere and hugely increased the productivity and diversity of ecosystems. Together, these led to the evolution of complex eukaryotic cells, from which all multicellular organisms are built.

Paleoclimatology, although sometimes treated as part of paleoecology, focuses more on the history of Earth's climate and the mechanisms that have changed it – which have sometimes included evolutionary developments, for example the rapid expansion of land plants in the Devonian period removed more carbon dioxide from the atmosphere, reducing the greenhouse effect and thus helping to cause an ice age in the Carboniferous period.

Biostratigraphy, the use of fossils to work out the chronological order in which rocks were formed, is useful to both paleontologists and geologists. Biogeography studies the spatial distribution of organisms, and is also linked to geology, which explains how Earth's geography has changed over time.

Body Fossils

This *Marrella* specimen illustrates how clear and detailed the fossils from the Burgess Shale lagerstätte are.

Fossils of organisms' bodies are usually the most informative type of evidence. The most common types are wood, bones, and shells. Fossilisation is a rare event, and most fossils are destroyed by erosion or metamorphism before they can be observed. Hence the fossil record is very incomplete, increasingly so further back in time. Despite this, it is often adequate to illustrate the broader patterns of life's history. There are also biases in the fossil record: different environments are more favorable to the preservation of different types of organism or parts of organisms. Further, only the parts of organisms that were already mineralised are usually preserved, such as the shells of molluscs. Since most animal species are soft-bodied, they decay before they can become fossilised. As a result, although there are 30-plus phyla of living animals, two-thirds have never been found as fossils.

Occasionally, unusual environments may preserve soft tissues. These lagerstätten allow paleontologists to examine the internal anatomy of animals that in other sediments are represented only by shells, spines, claws, etc. – if they are preserved at all. However, even lagerstätten present an incomplete picture of life at the time. The majority of organisms living at the time are probably not represented because lagerstätten are restricted to a narrow range of environments, e.g. where soft-bodied organisms can be preserved very quickly by events such as mudslides; and the exceptional events that cause quick burial make it difficult to study the normal environments of the animals. The sparseness of the fossil record means that organisms are expected to exist long before and after they are found in the fossil record – this is known as the Signor–Lipps effect.

Trace Fossils

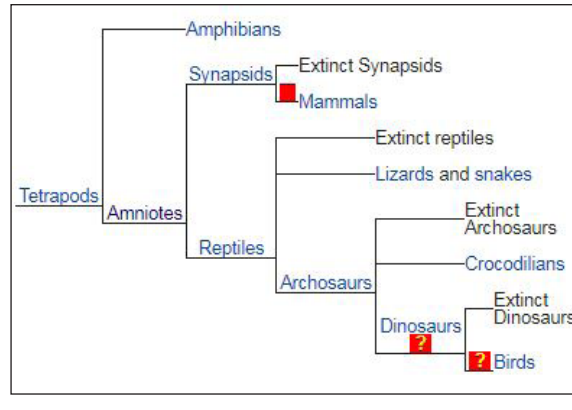
Cambrian trace fossils including *Rusophycus*, made by a trilobite.

Trace fossils consist mainly of tracks and burrows, but also include coprolites (fossil feces) and marks left by feeding. Trace fossils are particularly significant because they represent a data source that is not limited to animals with easily fossilised hard parts, and they reflect organisms' behaviours. Also many traces date from significantly earlier than the body fossils of animals that are thought to have been capable of making them. Whilst exact assignment of trace fossils to their makers is generally impossible, traces may for example provide the earliest physical evidence of the appearance of moderately complex animals (comparable to earthworms).

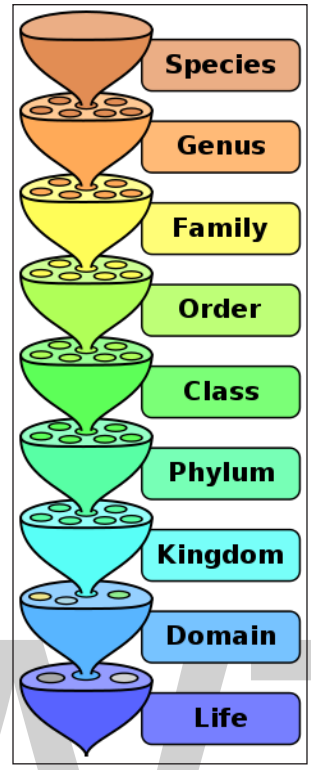
Geochemical Observations

Geochemical observations may help to deduce the global level of biological activity at a certain period, or the affinity of certain fossils. For example, geochemical features of rocks may reveal when life first arose on Earth, and may provide evidence of the presence of eukaryotic cells, the type from which all multicellular organisms are built. Analyses of carbon isotope ratiosmay help to explain major transitions such as the Permian–Triassic extinction event.

Classifying Ancient Organisms



Simple example cladogram Warm-bloodedness evolved somewhere in the synapsid–mammal transition. ? Warm-bloodedness must also have evolved at one of these points – an example of convergent evolution.



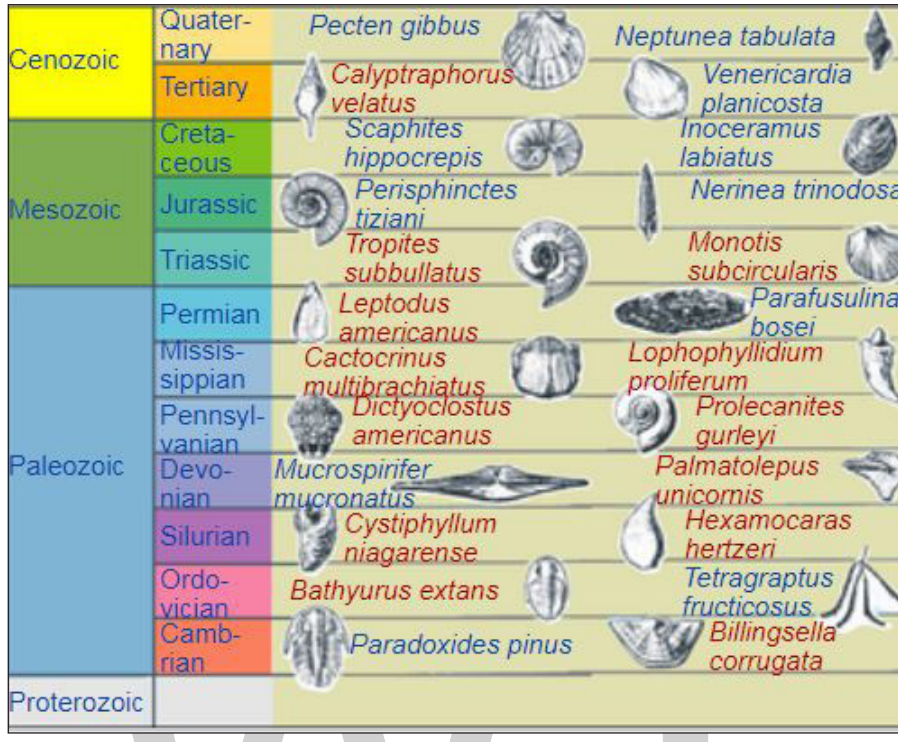
Levels in the Linnaean taxonomy.

Naming groups of organisms in a way that is clear and widely agreed is important, as some disputes in paleontology have been based just on misunderstandings over names.Linnaean taxonomy is commonly used for classifying living organisms, but runs into difficulties when dealing with newly discovered organisms that are significantly different from known ones. For example: it is hard to decide at what level to place a new higher-level grouping, e.g. genus or family or order; this is important since the Linnaean rules for naming groups are tied to their levels, and hence if a group is moved to a different level it must be renamed.

Paleontologists generally use approaches based on cladistics, a technique for working out the evolutionary "family tree" of a set of organisms. It works by the logic that, if groups B and C have more similarities to each other than either has to group A, then B and C are more closely related to each other than either is to A. Characters that are compared may be anatomical, such as the presence of a notochord, or molecular, by comparing sequences of DNA or proteins. The result of a successful analysis is a hierarchy of clades – groups that share a common ancestor. Ideally the "family tree" has only two branches leading from each node ("junction"), but sometimes there is too little information to achieve this and paleontologists have to make do with junctions that have several branches. The cladistic technique is sometimes fallible, as some features, such as wings or camera eyes, evolved more than once, convergently – this must be taken into account in analyses.

Evolutionary developmental biology, commonly abbreviated to "Evo Devo", also helps paleontologists to produce "family trees", and understand fossils. For example, the embryological development of some modern brachiopods suggests that brachiopods may be descendants of the halkieriids, which became extinct in the Cambrian period.

Estimating the Dates of Organisms



Common index fossils used to date rocks.

Paleontology seeks to map out how living things have changed through time. A substantial hurdle to this aim is the difficulty of working out how old fossils are. Beds that preserve fossils typically lack the radioactive elements needed for radiometric dating. This technique is our only means of giving rocks greater than about 50 million years old an absolute age, and can be accurate to within 0.5% or better. Although radiometric dating requires very careful laboratory work, its basic principle is simple: the rates at which various radioactive elements decay are known, and so the ratio of the radioactive element to the element into which it decays shows how long ago the radioactive element was incorporated into the rock. Radioactive elements are common only in rocks with a volcanic origin, and so the only fossil-bearing rocks that can be dated radiometrically are a few volcanic ash layers.

Consequently, paleontologists must usually rely on stratigraphy to date fossils. Stratigraphy is the science of deciphering the "layer-cake" that is the sedimentary record, and has been compared to a jigsaw puzzle. Rocks normally form relatively horizontal layers, with each layer younger than the one underneath it. If a fossil is found between two layers whose ages are known, the fossil's age must lie between the two known ages. Because rock sequences are not continuous, but may be broken up by faults or periods of erosion, it is very difficult to match up rock beds that are not directly next to one another. However, fossils of species that survived for a relatively short time can be used to link up isolated rocks: this technique is called *biostratigraphy*. For instance, the conodont *Eoplacognathus pseudoplanus* has a short range in the Middle Ordovician period. If rocks of unknown age are found to have traces of *E. pseudoplanus*, they must have a mid-Ordovician age. Such index fossils must be distinctive, be globally distributed and have a short time range to be useful. However, misleading results are produced if the index fossils turn out to have longer fossil ranges than first thought. Stratigraphy and biostratigraphy can in general provide only relative dating (*A* was before

B), which is often sufficient for studying evolution. However, this is difficult for some time periods, because of the problems involved in matching up rocks of the same age across different continents.

Family-tree relationships may also help to narrow down the date when lineages first appeared. For instance, if fossils of B or C date to X million years ago and the calculated "family tree" says A was an ancestor of B and C, then A must have evolved more than X million years ago.

It is also possible to estimate how long ago two living clades diverged – i.e. approximately how long ago their last common ancestor must have lived – by assuming that DNA mutations accumulate at a constant rate. These "molecular clocks", however, are fallible, and provide only a very approximate timing: for example, they are not sufficiently precise and reliable for estimating when the groups that feature in the Cambrian explosion first evolved, and estimates produced by different techniques may vary by a factor of two.

History of Life

This wrinkled "elephant skin" texture is a trace fossil of a non-stromatolite microbial mat. The image shows the location, in the Burgsvik beds of Sweden, where the texture was first identified as evidence of a microbial mat.

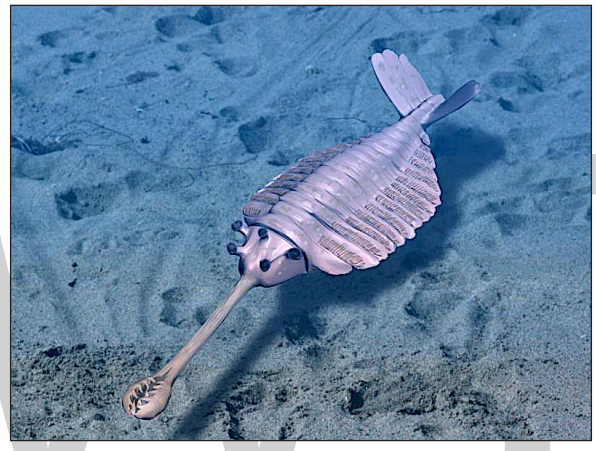
Earth formed about 4,570 million years ago and, after a collision that formed the Moonabout 40 million years later, may have cooled quickly enough to have oceans and an atmosphere about 4,440 million years ago. There is evidence on the Moon of a Late Heavy Bombardment by asteroids from 4,000 to 3,800 million years ago. If, as seems likely, such a bombardment struck Earth at the same time, the first atmosphere and oceans may have been stripped away.

Paleontology traces the evolutionary history of life back to over 3,000 million years ago, possibly as far as 3,800 million years ago. The oldest clear evidence of life on Earth dates to 3,000 million years ago, although there have been reports, often disputed, of fossil bacteria from 3,400 million years ago and of geochemical evidence for the presence of life 3,800 million years ago. Some scientists have proposed that life on Earth was "seeded" from elsewhere, but most research concentrates on various explanations of how life could have arisen independently on Earth.

For about 2,000 million years microbial mats, multi-layered colonies of different bacteria, were the dominant life on Earth. The evolution of oxygenic photosynthesis enabled them to play the major role in the oxygenation of the atmosphere from about 2,400 million years ago. This change in the

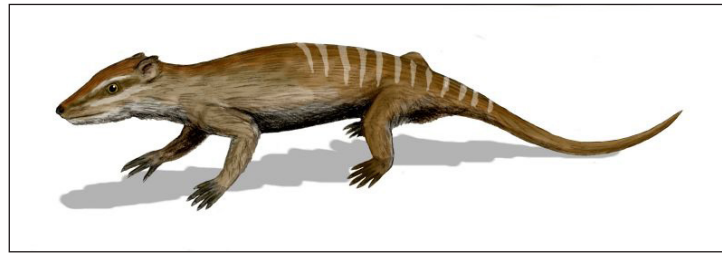
atmosphere increased their effectiveness as nurseries of evolution. While eukaryotes, cells with complex internal structures, may have been present earlier, their evolution speeded up when they acquired the ability to transform oxygen from a poison to a powerful source of metabolic energy. This innovation may have come from primitive eukaryotes capturing oxygen-powered bacteria as endosymbionts and transforming them into organelles called mitochondria. The earliest evidence of complex eukaryotes with organelles (such as mitochondria) dates from 1,850 million years ago.

Multicellular life is composed only of eukaryotic cells, and the earliest evidence for it is the Francevillian Group Fossils from 2,100 million years ago, although specialisation of cells for different functions first appears between 1,430 million years ago (a possible fungus) and 1,200 million years ago (a probable red alga). Sexual reproduction may be a prerequisite for specialisation of cells, as an asexual multicellular organism might be at risk of being taken over by rogue cells that retain the ability to reproduce.



Opabinia sparked modern interest in the Cambrian explosion.

The earliest known animals are cnidarians from about 580 million years ago, but these are so modern-looking that must be descendants of earlier animals. Early fossils of animals are rare because they had not developed mineralised, easily fossilized hard parts until about 548 million years ago. The earliest modern-looking bilaterianananimals appear in the Early Cambrian, along with several "weird wonders" that bear little obvious resemblance to any modern animals. There is a long-running debate about whether this Cambrian explosion was truly a very rapid period of evolutionary experimentation; alternative views are that modern-looking animals began evolving earlier but fossils of their precursors have not yet been found, or that the "weird wonders" are evolutionary "aunts" and "cousins" of modern groups. Vertebrates remained a minor group until the first jawed fish appeared in the Late Ordovician.



At about 13 centimetres (5.1 in) the Early Cretaceous *Yanoconodon* was longer than the average mammal of the time.

The spread of life from water to land required organisms to solve several problems, including protection against drying out and supporting themselves against gravity. The earliest evidence of land plants and land invertebrates date back to about 476 million years ago and 490 million years ago respectively. The lineage that produced land vertebrates evolved later but very rapidly between 370 million years ago and 360 million years ago; recent discoveries have overturned earlier ideas about the history and driving forces behind their evolution. Land plants were so successful that their detritus caused an ecological crisis in the Late Devonian, until the evolution of fungi that could digest dead wood.

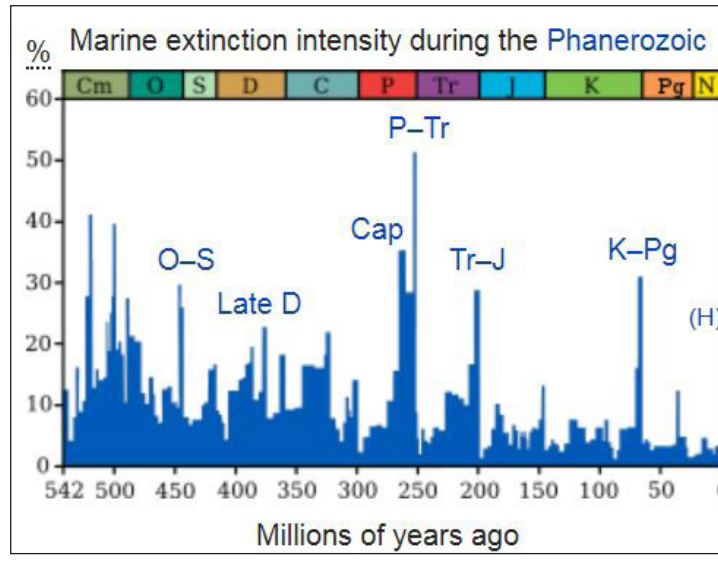
Birds are the only surviving dinosaurs.

During the Permian period, synapsids, including the ancestors of mammals, may have dominated land environments, but this ended with the Permian–Triassic extinction event 251 million years ago, which came very close to wiping out all complex life.The extinctions were apparently fairly sudden, at least among vertebrates. During the slow recovery from this catastrophe a previously obscure group, archosaurs, became the most abundant and diverse terrestrial vertebrates. One archosaur group, the dinosaurs, were the dominant land vertebrates for the rest of the Mesozoic, and birdsevolved from one group of dinosaurs. During this time mammals' ancestors survived only as small, mainly nocturnal insectivores, which may have accelerated the development of mammalian traits such as endothermy and hair. After the Cretaceous–Paleogene extinction event 66 million years ago killed off all the dinosaurs except the birds, mammals increased rapidly in size and diversity, and some took to the air and the sea.

Fossil evidence indicates that flowering plants appeared and rapidly diversified in the Early Cretaceous between 130 million years ago and 90 million years ago. Their rapid rise to dominance of terrestrial ecosystems is thought to have been propelled by coevolution with pollinating insects. Social insects appeared around the same time and, although they account for only small parts of the insect "family tree", now form over 50% of the total mass of all insects.

Humans evolved from a lineage of upright-walking apes whose earliest fossils date from over 6 million years ago. Although early members of this lineage had chimp-sized brains, about 25% as big as modern humans', there are signs of a steady increase in brain size after about 3 million years ago. There is a long-running debate about whether *modern* humans are descendants of a single small population in Africa, which then migrated all over the world less than 200,000 years ago and replaced previous hominine species, or arose worldwide at the same time as a result of interbreeding.

Mass Extinctions



Apparent extinction intensity, i.e. the fraction of generagoing extinct at any given time, as reconstructed from the fossil record (graph not meant to include recent epoch of Holocene extinction event).

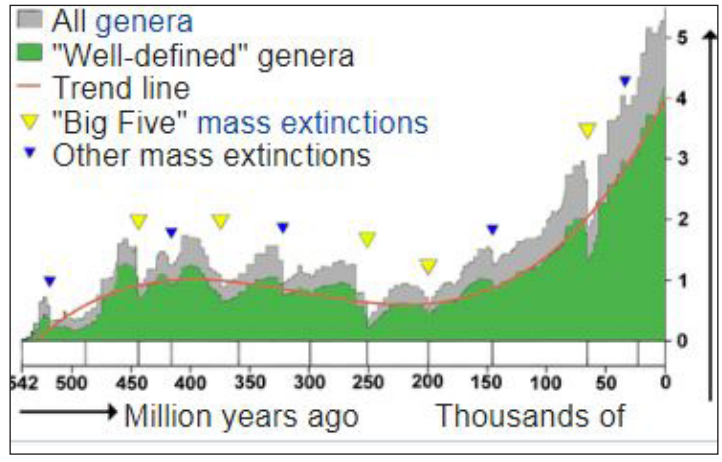
Life on earth has suffered occasional mass extinctions at least since 542 million years ago. Despite their distrous effects, mass extinctions have sometimes accelerated the evolution of life on earth. When dominance of an ecological niche passes from one group of organisms to another, this is rarely because the new dominant group outcompetes the old, but usually because an extinction event allows new group to outlive the old and move into its niche.

The fossil record appears to show that the rate of extinction is slowing down, with both the gaps between mass extinctions becoming longer and the average and background rates of extinction decreasing. However, it is not certain whether the actual rate of extinction has altered, since both of these observations could be explained in several ways:

- The oceans may have become more hospitable to life over the last 500 million years and less vulnerable to mass extinctions: dissolved oxygen became more widespread and penetrated to greater depths; the development of life on land reduced the run-off of nutrients and hence the risk of eutrophication and anoxic events; marine ecosystems became more diversified so that food chains were less likely to be disrupted.
- Reasonably complete fossils are very rare, most extinct organisms are represented only by partial fossils, and complete fossils are rarest in the oldest rocks. So paleontologists have mistakenly assigned parts of the same organism to different genera, which were often defined solely to accommodate these finds – the story of Anomalocaris is an example of this. The risk of this mistake is higher for older fossils because these are often unlike parts of any living organism. Many "superfluous" genera are represented by fragments that are not found again, and these "superfluous" genera are interpreted as becoming extinct very quickly.

Biodiversity in the fossil record, which is "the number of distinct genera alive at any given time; that is, those whose first occurrence predates and whose last occurrence postdates that time" shows

a different trend: a fairly swift rise from 542 to 400 million years ago, a slight decline from 400 to 200 million years ago, in which the devastating Permian–Triassic extinction event is an important factor, and a swift rise from 200 million years ago to the present.



Phanerozoic biodiversity as shown by the fossil record.

Phylogenetics

In biology, phylogenetics is the study of the evolutionary history and relationships among individuals or groups of organisms (e.g. species, or populations). These relationships are discovered through phylogenetic inference methods that evaluate observed heritable traits, such as DNA sequences or morphology under a model of evolution of these traits. The result of these analyses is a phylogeny (also known as a phylogenetic tree) – a diagrammatic hypothesis about the history of the evolutionary relationships of a group of organisms. The tips of a phylogenetic tree can be living organisms or fossils, and represent the "end", or the present, in an evolutionary lineage. A phylogenetic tree can be rooted or unrooted. A rooted tree indicates the common ancestor, or ancestral lineage, of the tree. An unrooted tree makes no assumption about the ancestral line, and does not show the origin or "root" of the gene or organism in question. Phylogenetic analyses have become central to understanding biodiversity, evolution, ecology, and genomes.

Taxonomy is the identification, naming and classification of organisms. It is usually richly informed by phylogenetics, but remains a methodologically and logically distinct discipline. The degree to which taxonomies depend on phylogenies (or classification depends on evolutionary development) differs depending on the school of taxonomy: phenetics ignores phylogeny altogether, trying to represent the similarity between organisms instead; cladistics (phylogenetic systematics) tries to reproduce phylogeny in its classification without loss of information; evolutionary taxonomy tries to find a compromise between them.

Construction of a Phylogenetic Tree

Usual methods of phylogenetic inference involve computational approaches implementing the optimality criteria and methods of parsimony, maximum likelihood (ML), and MCMC-based

Bayesian inference. All these depend upon an implicit or explicit mathematical modeldescribing the evolution of characters observed.

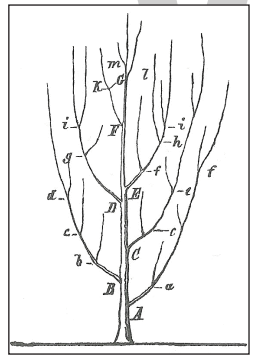
Phenetics, popular in the mid-20th century but now largely obsolete, used distance matrix-based methods to construct trees based on overall similarity in morphology or similar observable traits (i.e. in the phenotype or the overall similarity of DNA, not the DNA sequence), which was often assumed to approximate phylogenetic relationships.

Prior to 1950, phylogenetic inferences were generally presented as narrative scenarios. Such methods are often ambiguous and lack explicit criteria for evaluating alternative hypotheses.

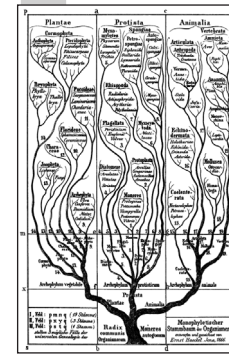
Ernst Haeckel's Recapitulation Theory

During the late 19th century, Ernst Haeckel's recapitulation theory, or "biogenetic fundamental law", was widely accepted. It was often expressed as "ontogeny recapitulates phylogeny", i.e. the development of a single organism during its lifetime, from germ to adult, successively mirrors the adult stages of successive ancestors of the species to which it belongs. But this theory has long been rejected. Instead, ontogeny evolves – the phylogenetic history of a species cannot be read directly from its ontogeny, as Haeckel thought would be possible, but characters from ontogeny can be (and have been) used as data for phylogenetic analyses; the more closely related two species are, the more apomorphies their embryos share.

Timeline of Key Events



Branching tree diagram from Heinrich Georg Bronn's work.



Phylogenetic tree suggested by Haeckel.

- 14th century, lex parsimoniae (parsimony principle), William of Ockam, English philosopher, theologian, and Franciscan friar, but the idea actually goes back to Aristotle, precursor concept.
- 1763, Bayesian probability, Rev. Thomas Bayes, precursor concept.
- 18th century, Pierre Simon (Marquis de Laplace), perhaps first to use ML (maximum likelihood), precursor concept.
- 1809, evolutionary theory, Philosophie Zoologique, Jean-Baptiste de Lamarck, precursor concept, foreshadowed in the 17th century and 18th century by Voltaire, Descartes, and

Leibniz, with Leibniz even proposing evolutionary changes to account for observed gaps suggesting that many species had become extinct, others transformed, and different species that share common traits may have at one time been a single race, also foreshadowed by some early Greek philosophers such as Anaximander in the 6th century BC and the atomists of the 5th century BC, who proposed rudimentary theories of evolution.

- 1837, Darwin's notebooks show an evolutionary tree.
- 1843, distinction between homology and analogy (the latter now referred to as homoplasy), Richard Owen, precursor concept.
- 1858, Paleontologist Heinrich Georg Bronn published a hypothetical tree to illustrating the paleontological "arrival" of new, similar species following the extinction of an older species. Bronn did not propose a mechanism responsible for such phenomena, precursor concept.
- 1858, elaboration of evolutionary theory, Darwin and Wallace, also in Origin of Species by Darwin the following year, precursor concept.
- 1866, Ernst Haeckel, first publishes his phylogeny-based evolutionary tree, precursor concept.
- 1893, Dollo's Law of Character State Irreversibility, precursor concept.
- 1912, ML recommended, analyzed, and popularized by Ronald Fisher, precursor concept.
- 1921, Tillyard uses term "phylogenetic" and distinguishes between archaic and specialized characters in his classification system.
- 1940, term "clade" coined by Lucien Cuénot.
- 1949, Jackknife resampling, Maurice Quenouille (foreshadowed in '46 by Mahalanobis and extended in '58 by Tukey), precursor concept.
- 1950, Willi Hennig's classic formalization.
- 1952, William Wagner's groundplan divergence method.
- 1953, "cladogenesis" coined.
- 1960, "cladistic" coined by Cain and Harrison.
- 1963, first attempt to use ML (maximum likelihood) for phylogenetics, Edwards and Cavalli-Sforza.
- 1965:
  - Camin-Sokal parsimony, first parsimony (optimization) criterion and first computer program/algorithm for cladistic analysis both by Camin and Sokal.
  - character compatibility method, also called clique analysis, introduced independently by Camin and Sokal (loc. cit.) and E. O. Wilson.
- 1966:
  - English translation of Hennig.

- "cladistics" and "cladogram" coined (Webster's, loc. cit.).

- 1969:
  - Dynamic and successive weighting, James Farris.
  - Wagner parsimony, Kluge and Farris.
  - CI (consistency index), Kluge and Farris.
  - Introduction of pairwise compatibility for clique analysis, Le Quesne.
- 1970, Wagner parsimony generalized by Farris.
- 1971:
  - First successful application of ML to phylogenetics (for protein sequences), Neyman.
  - Fitch parsimony, Fitch.
  - NNI (nearest neighbour interchange), first branch-swapping search strategy, developed independently by Robinsonand Moore et al.
  - ME (minimum evolution), Kidd and Sgaramella-Zonta (it is unclear if this is the pairwise distance method or related to ML as Edwards and Cavalli-Sforza call ML "minimum evolution").
- 1972, Adams consensus, Adams.
- 1976, prefix system for ranks, Farris.
- 1977, Dollo parsimony, Farris.
- 1979:
  - Nelson consensus, Nelson.
  - MAST (maximum agreement subtree)((GAS)greatest agreement subtree), a consensus method, Gordon.
  - bootstrap, Bradley Efron, precursor concept.
- 1980, PHYLIP, first software package for phylogenetic analysis, Felsenstein.
- 1981:
  - Majority consensus, Margush and MacMorris.
  - Strict consensus, Sokal and Rohlf.
  - First computationally efficient ML algorithm, Felsenstein.
- 1982:
  - PHYSIS, Mikevich and Farris.

- Branch and bound, Hendy and Penny.

- 1985:
  - First cladistic analysis of eukaryotes based on combined phenotypic and genotypic evidence Diana Lipscomb.
  - First issue of *Cladistics*.
  - First phylogenetic application of bootstrap, Felsenstein.
  - First phylogenetic application of jackknife, Scott Lanyon.
- 1986, MacClade, Maddison and Maddison.
- 1987, neighbor-joining method Saitou and Nei.
- 1988, Hennig86 (version 1.5), Farris.
  - Bremer support (decay index), Bremer.
- 1989:
  - RI (retention index), RCI (rescaled consistency index), Farris.
  - HER (homoplasy excess ratio), Archie.
- 1990:
  - Combinable components (semi-strict) consensus, Bremer.
  - SPR (subtree pruning and regrafting), TBR (tree bisection and reconnection), Swofford and Olsen.
- 1991:
  - DDI (data decisiveness index), Goloboff.
  - First cladistic analysis of eukaryotes based only on phenotypic evidence, Lipscomb.
- 1993, implied weighting Goloboff.
- 1994, reduced consensus: RCC (reduced cladistic consensus) for rooted trees, Wilkinson.
- 1995, reduced consensus RPC (reduced partition consensus) for unrooted trees, Wilkinson.
- 1996, first working methods for BI (Bayesian Inference)independently developed by Li, Mau, and Rannala and Yangand all using MCMC (Markov chain-Monte Carlo).
- 1998, TNT (Tree Analysis Using New Technology), Goloboff, Farris, and Nixon.
- 1999, Winclada, Nixon.
- 2003, symmetrical resampling, Goloboff.

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