Theories and Mechanisms of Evolution

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Chapter 1

Evolution

Evolution (also known as **biological** or **organic evolution**) is the change over time in one or more inherited traits found in populations of organisms. Inherited traits are particular distinguishing characteristics, including anatomical, biochemical or behavioural characteristics, that result from gene–environment interactions. Evolution may occur when there is variation of inherited traits within a population. The major sources of such variation are mutation, genetic recombination and gene flow. Evolution has led to the diversification of all living organisms, which are described by Charles Darwin as *endless forms most beautiful and most wonderful*.

Two processes are generally distinguished as common causes of evolution. One is natural selection, a process in which there is differential survival and/or reproduction of organisms that differ in one or more inherited traits. Another cause is genetic drift, a process in which there are random changes to the proportions of two or more inherited traits within a population.

In speciation, a single ancestral species splits into two or more different species. Speciation is visible in anatomical, genetic and other similarities between groups of organisms, geographical distribution of related species, the fossil record and the recorded genetic changes in living organisms over many generations. Speciation stretches back over 3.5 billion years during which life has existed on earth. It is thought to occur in multiple ways such as slowly, steadily and gradually over time or rapidly from one long static state to another.

The scientific study of evolution began in the mid-nineteenth century, when research into the fossil record and the diversity of living organisms convinced most scientists that species evolve. The mechanism driving these changes remained unclear until the theory of natural selection was independently proposed by Charles Darwin and Alfred Wallace in 1858. In the early 20th century, Darwinian theories of evolution were combined with genetics, palaeontology, and systematics, which culminated into a union of ideas known as the modern evolutionary synthesis. The synthesis became a major principle of biology as it provided a coherent and unifying explanation for the history and diversity of life on Earth.

Evolution is currently applied and studied in various areas within biology such as conservation biology, developmental biology, ecology, physiology, paleontology and medicine. Moreover, it has also made an impact on traditionally non-biological disciplines such as agriculture, anthropology, philosophy and psychology.

History of evolutionary thought

Jean-Baptiste Lamarck

The roots of naturalistic thinking in biology can be dated to at least the 6th century BCE, with the Greek philosopher Anaximander.

Early Christian Church Fathers and Medieval European scholars treated the Genesis creation narrative as allegory and believed that natural organisms were unstable and capricious, but the Protestant Reformation inspired Biblical literalism and a natural

theology in which the concept of species was essentialist, static and fixed. All entities within a species were seen as sharing a common essence.

As emerging science explored mechanical philosophy in the 18th century, proto-evolutionary ideas were set out by a few natural philosophers such as Pierre Maupertuis in 1745 and Erasmus Darwin in 1796.

The word *evolution* was first used in relation to development of species in 1762, when Charles Bonnet used it for his concept of "pre-formation", in which females carried a miniature form of all future generations. The term gradually gained a more general meaning of growth or progressive development. The first published modern use of the word has been attributed to the *Edinburgh New Philosophical Journal* in 1826, edited by Robert Jameson but arguably authored by Robert Edmond Grant.

The Bible-based Ussher chronology of the 1650s had calculated creation at 4004 BC, but by the 1780s geologists assumed a much older world. Wernerians thought strata were deposits from shrinking seas, but James Hutton proposed a self-maintaining infinite cycle. Georges Cuvier's paleontological work in the 1790s established the reality of extinction, which he explained by local catastrophes, followed by repopulation of the affected areas by other species. He held that species were fixed, and marginalised the ideas of the biologist Jean-Baptiste Lamarck about transmutation of species which were only taken up by radicals.

Geologists such as Adam Sedgwick adapted Cuvier's catastrophism to show repeated worldwide annihilation and creation of new fixed species adapted to a changed environment, identifying the most recent catastrophe as the biblical flood. In opposition to this view, Charles Lyell adapted Hutton's concept into a stricter uniformitarianism which strongly influenced the young geologist Charles Darwin during the *Beagle* expedition. Initially Darwin followed Lyell's idea of repeated "centres of creation" of fixed species, but questioned Lyell's views and in 1836, near the end of the voyage, he expressed doubts that species were fixed.

At this time, most natural historians conceived of "species" in terms of essences or ideals; actual individuals were either good or bad examples of the ideal. But natural scientists began to view regular patterns in nature statistically (that is, in terms of probabilities rather than determinism). Thomas Robert Malthus took this approach to human populations in An Essay on the Principle of Population that influenced Darwin. Beginning with Darwin, "species" were conceived in statistical terms; actual individuals were expected to be different, with most diverging from the average form, and species were viewed as variable and intergrading units.

Around 1854 Charles Darwin began writing out what became *On the Origin of Species*.

Darwin formulated his idea of natural selection in 1838 and was still developing his theory in 1858 when Alfred Russel Wallace sent him a similar theory, and both were presented to the Linnean Society of London in separate papers. At the end of 1859, Darwin's publication of *On the Origin of Species* explained natural selection in detail and presented evidence leading to increasingly wide acceptance of the occurrence of evolution. Thomas Henry Huxley applied Darwin's ideas to humans, using paleontology and comparative anatomy to provide strong evidence that humans and apes shared a common ancestry. This caused an uproar around the world since it implied that the creation myth in the Christian Bible was false, and humans did not have a special place in the universe.

Debate about the mechanisms of evolution continued, and Darwin could not explain the source of the heritable variations which would be acted on by natural selection. Like Lamarck, he still thought that parents passed on adaptations acquired during their lifetimes, a theory which was subsequently dubbed Lamarckism. In the 1880s, August Weismann's experiments indicated that changes from use and disuse were not heritable, and Lamarckism gradually fell from favour. More significantly, Darwin could not account for how traits were passed down from generation to generation. In 1865 Gregor Mendel found that traits were inherited in a predictable manner. When Mendel's work was rediscovered in the 1900s, disagreements over the rate of evolution predicted by early geneticists and biometricians led to a rift between the Mendelian and Darwinian models of evolution.

Hugo Marie de Vries was unaware of Gregor Mendel's work and rediscovered the laws of heredity in the 1890s. De Vries suggested the concept of genes as part of his mutation

theory of evolution. The rediscovery of Gregor Mendel's work provided a better understanding of how variation occurs in plant and animal traits. That variation is the main fuel used by natural selection to shape the wide variety of adaptive traits observed in organic life. Even though Hugo de Vries and other early geneticists rejected gradual natural selection, their rediscovery of and subsequent work on genetics eventually provided a solid basis on which the theory of evolution stood even more convincingly than when it was originally proposed. At the beginning of the 20th century, Thomas Hunt Morgan was able to demonstrate that genes are carried on chromosomes and are the mechanical basis of heredity. These discoveries formed the basis of the modern science of genetics.

The apparent contradiction between Darwin's theory of evolution by natural selection and Mendel's work was reconciled in the 1920s and 1930s by evolutionary biologists such as J.B.S. Haldane, Sewall Wright, and particularly Ronald Fisher, who set the foundations for the establishment of the field of population genetics. The end result was a combination of evolution by natural selection and Mendelian inheritance, the modern evolutionary synthesis. In the 1940s, the identification of DNA as the genetic material by Oswald Avery and colleagues and the subsequent publication of the structure of DNA by James Watson and Francis Crick in 1953, demonstrated the physical basis for inheritance. Since then, genetics and molecular biology have become core parts of evolutionary biology and have revolutionised the field of phylogenetics.

In its early history, evolutionary biology primarily drew in scientists from traditional taxonomically oriented disciplines, whose specialist training in particular organisms addressed general questions in evolution. As evolutionary biology expanded as an academic discipline, particularly after the development of the modern evolutionary synthesis, it began to draw more widely from the biological sciences. Currently the study of evolutionary biology involves scientists from fields as diverse as biochemistry, ecology, genetics and physiology, and evolutionary concepts are used in even more distant disciplines such as psychology, medicine, philosophy and computer science.

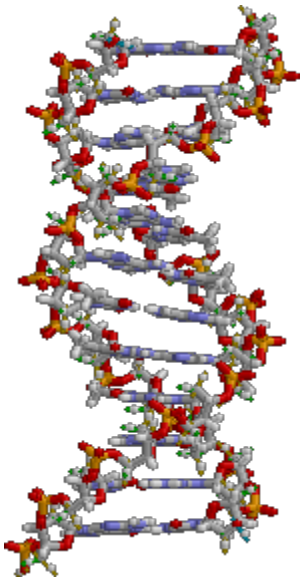
In the 1960s, scientists such as W. D. Hamilton and George C. Williams pioneered a gene-centered view of evolution, with concepts such as kin selection.

In 1975, E. O. Wilson's book *Sociobiology* established a significant place for evolutionary theory in psychology, giving rise to the field of evolutionary psychology. Critics argue that the hypotheses of evolutionary psychology are difficult or impossible to test, for example because many current traits probably evolved to serve different functions than they do now. While testing the hypotheses of evolutionary psychology is difficult, it is not impossible. Evolutionary Psychologists say that good evolutionary hypotheses can be corroborated or contradicted by data. The presence that evolutionary theory holds in psychology has been steadily increasing.

In the 21st century, current research in evolutionary biology deals with several areas where the modern evolutionary synthesis may need modification or extension, such as

assessing the relative importance of various ideas on the unit of selection and evolvability and how to fully incorporate the findings of evolutionary developmental biology.

Heredity



DNA structure. Bases are in the centre, surrounded by phosphate–sugar chains in a double helix.

Evolution in organisms occurs through changes in heritable traits – particular characteristics of an organism. In humans, for example, eye colour is an inherited characteristic and an individual might inherit the "brown-eye trait" from one of their parents. Inherited traits are controlled by genes and the complete set of genes within an organism's genome is called its genotype.

The complete set of observable traits that make up the structure and behaviour of an organism is called its phenotype. These traits come from the interaction of its genotype with the environment. As a result, many aspects of an organism's phenotype are not inherited. For example, suntanned skin comes from the interaction between a person's genotype and sunlight; thus, suntans are not passed on to people's children. However, some people tan more easily than others, due to differences in their genotype; a striking example are people with the inherited trait of albinism, who do not tan at all and are very sensitive to sunburn.

Heritable traits are known to be passed from one generation to the next via DNA, a molecule that encodes genetic information. DNA is a long polymer composed of four types of bases. The sequence of bases along a particular DNA molecule specify the genetic information, in a manner similar to a sequence of letters spelling out a sentence. Before a cell divides, the DNA is copied, so that each of the resulting two cells will inherit the DNA sequence. Portions of a DNA molecule that specify a single functional unit are called genes; different genes have different sequences of bases. Within cells, the long strands of DNA form condensed structures called chromosomes. The specific

location of a DNA sequence within a chromosome is known as a locus. If the DNA sequence at a locus varies between individuals, the different forms of this sequence are called alleles. DNA sequences can change through mutations, producing new alleles. If a mutation occurs within a gene, the new allele may affect the trait that the gene controls, altering the phenotype of the organism.

However, while this simple correspondence between an allele and a trait works in some cases, most traits are more complex and are controlled by multiple interacting genes. Developmental biologists suggest that complex interactions in genetic networks and communication among cells can lead to heritable variations that may underlay some of the mechanics in developmental plasticity and canalization.

Recent findings have confirmed important examples of heritable changes that cannot be explained by direct agency of the DNA molecule. These phenomena are classed as epigenetic inheritance systems that are causally or independently evolving over genes. Research into modes and mechanisms of epigenetic inheritance is still in its scientific infancy, however, this area of research has attracted much recent activity as it broadens the scope of heritability and evolutionary biology in general. DNA methylation marking chromatin, self-sustaining metabolic loops, gene silencing by RNA interference, and the three dimensional conformation of proteins (such as prions) are areas where epigenetic inheritance systems have been discovered at the organismic level. Heritability may also occur at even larger scales. For example, ecological inheritance through the process of niche construction is defined by the regular and repeated activities of organisms in their environment. This generates a legacy of effect that modifies and feeds back into the selection regime of subsequent generations. Descendants inherit genes plus environmental characteristics generated by the ecological actions of ancestors. Other examples of heritability in evolution that are not under the direct control of genes include the inheritance of cultural traits, group heritability, and symbiogenesis. These examples of heritability that operate above the gene are covered broadly under the title of multilevel or hierarchical selection, which has been a subject of intense debate in the history of evolutionary science.

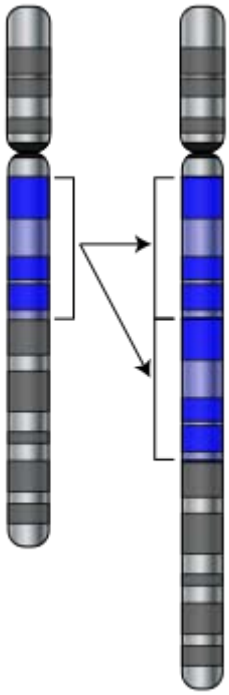
Variation

An individual organism's phenotype results from both its genotype and the influence from the environment it has lived in. A substantial part of the variation in phenotypes in a population is caused by the differences between their genotypes. The modern evolutionary synthesis defines evolution as the change over time in this genetic variation. The frequency of one particular allele will fluctuate, becoming more or less prevalent relative to other forms of that gene. Evolutionary forces act by driving these changes in allele frequency in one direction or another. Variation disappears when a new allele reaches the point of fixation — when it either disappears from the population or replaces the ancestral allele entirely.

Variation comes from mutations in genetic material, migration between populations (gene flow), and the reshuffling of genes through sexual reproduction. Variation also

comes from exchanges of genes between different species; for example, through horizontal gene transfer in bacteria, and hybridisation in plants. Despite the constant introduction of variation through these processes, most of the genome of a species is identical in all individuals of that species. However, even relatively small changes in genotype can lead to dramatic changes in phenotype: for example, chimpanzees and humans differ in only about 5% of their genomes.

Mutation



Duplication of part of a chromosome.

Random mutations constantly occur in the genomes of organisms; these mutations create genetic variation. 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. These mutations involve 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% 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 a chromosome becoming duplicated (usually by genetic recombination), which can introduce extra copies of a gene into a genome. Extra copies of genes are a major source of the raw material needed for new genes to evolve. This is important because most new genes evolve within gene families from pre-existing genes that share common ancestors. For example, the human eye uses four genes to make structures that sense light: three for colour vision and one for night vision; all four are descended from a single ancestral gene.

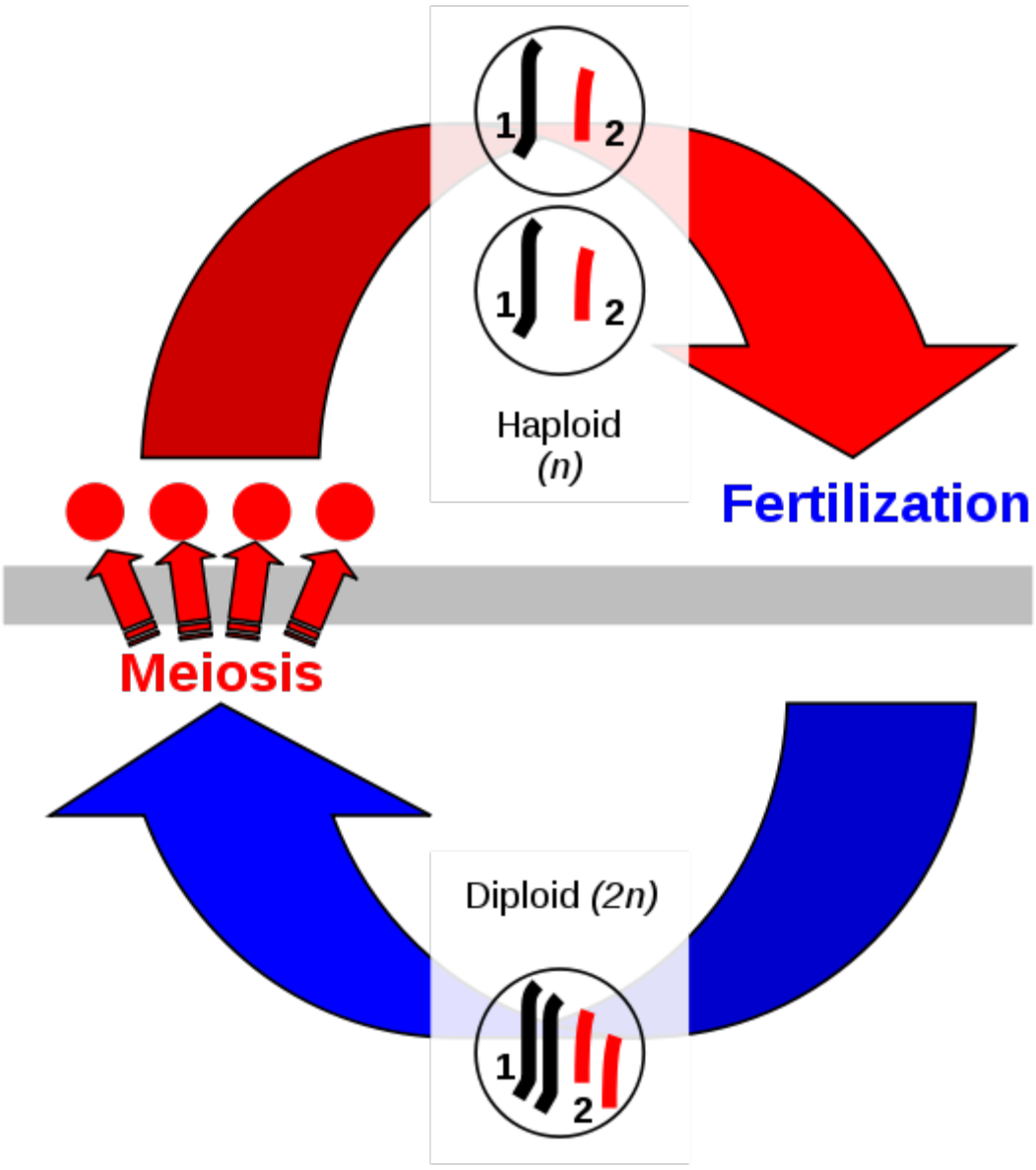
New genes can be created from an ancestral gene when a duplicate copy mutates and acquires a new function. This process is easier once a gene has been duplicated because it increases the redundancy of the system; one gene in the pair can acquire a new function while the other copy continues to perform its original function. Other types of mutation can even create entirely new genes from previously noncoding DNA.

The creation of new genes can also involve small parts of several genes being duplicated, with these fragments then recombining to form new combinations with new functions. When new genes are assembled from shuffling pre-existing parts, domains act as modules with simple independent functions, which can be mixed together creating new combinations with new and complex functions. For example, polyketide synthases are large enzymes that make antibiotics; they contain up to one hundred independent domains that each catalyze one step in the overall process, like a step in an assembly line.

Changes in chromosome number may involve even larger mutations, where segments of the DNA within chromosomes break and then rearrange. For example, two chromosomes in the *Homo* genus fused to produce human chromosome 2; this fusion did not occur in the lineage of the other apes, and they retain these separate chromosomes. In evolution, the most important role of such chromosomal rearrangements may be to accelerate the divergence of a population into new species by making populations less likely to interbreed, and thereby preserving genetic differences between these populations.

Sequences of DNA that can move about the genome, such as transposons, make up a major fraction of the genetic material of plants and animals, and may have been important in the evolution of genomes. For example, more than a million copies of the Alu sequence are present in the human genome, and these sequences have now been recruited to perform functions such as regulating gene expression. Another effect of these mobile DNA sequences is that when they move within a genome, they can mutate or delete existing genes and thereby produce genetic diversity.

Sex and recombination



In the first stage of sexual reproduction, "meiosis," the number of chromosomes is reduced from a diploid number (2n) to a haploid number (n). During "fertilization," haploid gametes come together to form a diploid zygote and the original number of chromosomes (2n) is restored.

In asexual organisms, genes are inherited together, or *linked*, as they cannot mix with genes of other organisms during reproduction. In contrast, the offspring of sexual organisms contain random mixtures of their parents' chromosomes that are produced through independent assortment. In a related process called homologous recombination, sexual organisms exchange DNA between two matching chromosomes. Recombination and reassortment do not alter allele frequencies, but instead change which alleles are

associated with each other, producing offspring with new combinations of alleles. Sex usually increases genetic variation and may increase the rate of evolution. However, asexuality is advantageous in some environments as it can evolve in previously sexual animals. Here, asexuality might allow the two sets of alleles in their genome to diverge and gain different functions.

Recombination allows even alleles that are close together in a strand of DNA to be inherited independently. However, the rate of recombination is low (approximately two events per chromosome per generation). As a result, genes close together on a chromosome may not always be shuffled away from each other, and genes that are close together tend to be inherited together, a phenomenon known as linkage. This tendency is measured by finding how often two alleles occur together on a single chromosome, which is called their linkage disequilibrium. A set of alleles that is usually inherited in a group is called a haplotype. This can be important when one allele in a particular haplotype is strongly beneficial: natural selection can drive a selective sweep that will also cause the other alleles in the haplotype to become more common in the population; this effect is called genetic hitchhiking.

When alleles cannot be separated by recombination – such as in mammalian Y chromosomes, which pass intact from fathers to sons – harmful mutations accumulate. By breaking up allele combinations, sexual reproduction allows the removal of harmful mutations and the retention of beneficial mutations. In addition, recombination and reassortment can produce individuals with new and advantageous gene combinations. These positive effects are balanced by the fact that sex reduces an organism's reproductive rate, can cause mutations and may separate beneficial combinations of genes. The reasons for the evolution of sexual reproduction are therefore unclear and this question is still an active area of research in evolutionary biology, that has prompted ideas such as the Red Queen hypothesis.

Population genetics

White peppered moth

Black morph in peppered moth evolution

From a genetic viewpoint, evolution is a *generation-to-generation change in the frequencies of alleles within a population that shares a common gene pool*. A population is a localised group of individuals belonging to the same species. For example, all of the moths of the same species living in an isolated forest represent a population. A single gene in this population may have several alternate forms, which account for variations between the phenotypes of the organisms. An example might be a gene for colouration in moths that has two alleles: black and white.

A gene pool is the complete set of alleles for a gene in a single population; the allele frequency measures the fraction of the gene pool composed of a single allele (for example, what fraction of moth colouration genes are the black allele). Evolution occurs when there are changes in the frequencies of alleles within a population of interbreeding organisms; for example, the allele for black colour in a population of moths becoming more common.

To understand the mechanisms that cause a population to evolve, it is useful to consider what conditions are required for a population not to evolve. The *Hardy-Weinberg principle* states that the frequencies of alleles (variations in a gene) in a sufficiently large population will remain constant if the only forces acting on that population are the random reshuffling of alleles during the formation of the sperm or egg, and the random combination of the alleles in these sex cells during fertilisation. Such a population is said to be in *Hardy-Weinberg equilibrium*; it is not evolving.

Gene flow

Gene flow is the exchange of genes between populations, and between species. Examples of gene flow within a species include the migration and then breeding of organisms and 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 introduce genetic variation in a population. Immigration may add genes to the gene pool while emigration may remove genes. 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.

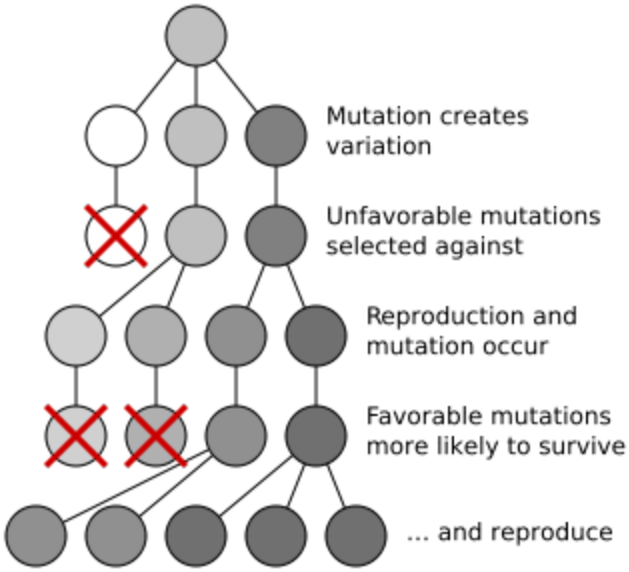
Horizontal gene transfer is the transfer of genetic material from one organism to another organism that is not its offspring; this is most common among bacteria. In medicine, this contributes to the spread of antibiotic resistance, as when one bacteria acquires resistance genes it can rapidly transfer 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 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.

Mechanisms

The two main mechanisms that produce evolution are natural selection and genetic drift. Natural selection is the process which favours genes that aid survival and reproduction. Genetic drift is the random change in the frequency of alleles, caused by the random sampling of a generation's genes during reproduction. The relative importance of natural selection and genetic drift in a population varies depending on the strength of the selection and the effective population size, which is the number of individuals capable of breeding. Natural selection usually predominates in large populations, whereas genetic drift dominates in small populations. The dominance of genetic drift in small populations can even lead to the fixation of slightly deleterious mutations. As a result, changing population size can dramatically influence the course of evolution. Population bottlenecks, where the population shrinks temporarily and therefore loses genetic variation, result in a more uniform population.

Natural selection



Natural selection of a population for dark colouration.

Evolution by means of natural selection is the process by which genetic mutations that enhance reproduction become, and remain, more common in successive generations of a population. It has often been called a "self-evident" mechanism because it necessarily follows from three simple facts:

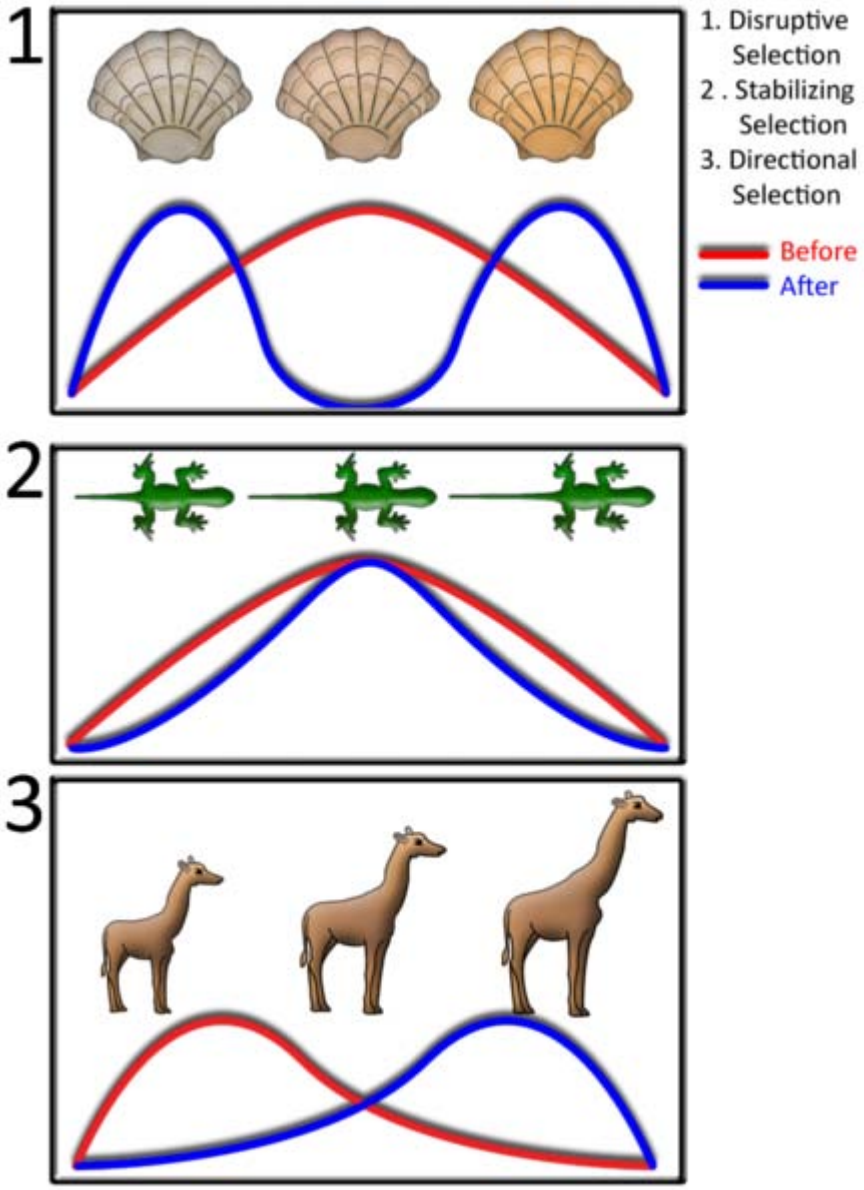
- Heritable variation exists within populations of organisms.
- Organisms produce more offspring than can survive.

- These offspring vary in their ability to survive and reproduce.

These conditions produce competition between organisms for survival and reproduction. Consequently, organisms with traits that give them an advantage over their competitors pass these advantageous traits on, while traits that do not confer an advantage are not passed on to the next generation.

The central concept of natural selection is the evolutionary fitness of an organism. Fitness is measured by an organism's ability to survive and reproduce, which determines the size of its genetic contribution to the next generation. However, fitness is not the same as the total number of offspring: instead fitness is indicated by the proportion of subsequent generations that carry an organism's genes. For example, if an organism could survive well and reproduce rapidly, but its offspring were all too small and weak to survive, this organism would make little genetic contribution to future generations and would thus have low fitness.

If an allele increases fitness more than the other alleles of that gene, then with each generation this allele will become more common within the population. These traits are said to be "selected *for*". Examples of traits that can increase fitness are enhanced survival, and increased fecundity. Conversely, the lower fitness caused by having a less beneficial or deleterious allele results in this allele becoming rarer — they are "selected *against*". Importantly, the fitness of an allele is not a fixed characteristic; if the environment changes, previously neutral or harmful traits may become beneficial and previously beneficial traits become harmful. However, even if the direction of selection does reverse in this way, traits that were lost in the past may not re-evolve in an identical form.



A chart showing three types of selection. 1.Disruptive selection 2.Stabilizing selection 3.Directional selection

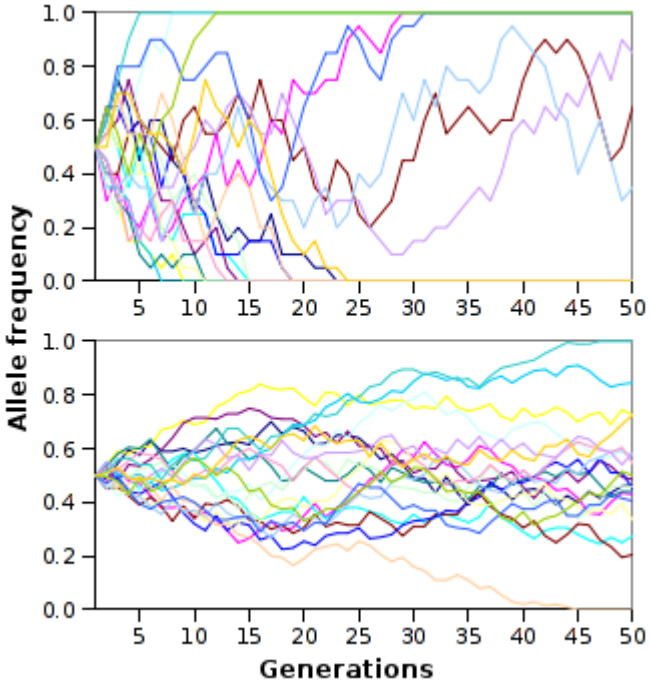
Natural selection within a population for a trait that can vary across a range of values, such as height, can be categorised into three different types. The first is directional selection, which is a shift in the average value of a trait over time — for example, organisms slowly getting taller. Secondly, disruptive selection is selection for extreme trait values and often results in two different values becoming most common, with selection against the average value. This would be when either short or tall organisms had an advantage, but not those of medium height. Finally, in stabilizing selection there is selection against extreme trait values on both ends, which causes a decrease in variance around the average value and less diversity. This would, for example, cause organisms to slowly become all the same height.

A special case of natural selection is sexual selection, which is selection for any trait that increases mating success by increasing the attractiveness of an organism to potential mates. Traits that evolved through sexual selection are particularly prominent in males of some animal species, despite traits such as cumbersome antlers, mating calls or bright colours that attract predators, decreasing the survival of individual males. This survival disadvantage is balanced by higher reproductive success in males that show these hard to fake, sexually selected traits.

Natural selection most generally makes nature the measure against which individuals, and individual traits, are more or less likely to survive. "Nature" in this sense refers to an ecosystem, that is, a system in which organisms interact with every other element, physical as well as biological, in their local environment. Eugene Odum, a founder of ecology, defined an ecosystem as: "Any unit that includes all of the organisms...in a given area interacting with the physical environment so that a flow of energy leads to clearly defined trophic structure, biotic diversity, and material cycles (ie: exchange of materials between living and nonliving parts) within the system." Each population within an ecosystem occupies a distinct niche, or position, with distinct relationships to other parts of the system. These relationships involve the life history of the organism, its position in the food chain, and its geographic range. This broad understanding of nature enables scientists to delineate specific forces which, together, comprise natural selection.

An active area of research is the unit of selection, with natural selection being proposed to work at the level of genes, cells, individual organisms, groups of organisms and species. None of these are mutually exclusive and selection can act on multiple levels simultaneously. An example of selection occurring below the level of the individual organism are genes called transposons, which can replicate and spread throughout a genome. Selection at a level above the individual, such as group selection, may allow the evolution of co-operation, as discussed below.

Genetic drift



Simulation of genetic drift of 20 unlinked alleles in populations of 10 (top) and 100 (bottom). Drift to fixation is more rapid in the smaller population.

Genetic drift is the change in allele frequency from one generation to the next that occurs because of the role that chance plays in determining whether a given individual will survive and reproduce. In mathematical terms, alleles are subject to sampling error. As a result, when selective forces are absent or relatively weak, allele frequencies tend to "drift" upward or downward randomly (in a random walk). This drift halts when an allele eventually becomes fixed, either by disappearing from the population, or replacing the other alleles entirely. Genetic drift may therefore eliminate some alleles from a population due to chance alone. Even in the absence of selective forces, genetic drift can cause two separate populations that began with the same genetic structure to drift apart into two divergent populations with different sets of alleles.

The time for an allele to become fixed by genetic drift depends on population size, with fixation occurring more rapidly in smaller populations. The precise measure of population that is important is called the effective population size. The effective population is always smaller than the total population since it takes into account factors such as the level of inbreeding, the number of animals that are too old or young to breed, and the lower probability of animals that live far apart managing to mate with each other.

An example of when genetic drift is probably of central importance in determining a trait is the loss of pigments from animals that live in caves, a change that produces no obvious advantage or disadvantage in complete darkness. However, it is usually difficult to

measure the relative importance of selection and drift, so the comparative importance of these two forces in driving evolutionary change is an area of current research. These investigations were prompted by the neutral theory of molecular evolution, which proposed that most evolutionary changes are the result of the fixation of neutral mutations that do not have any immediate effects on the fitness of an organism. Hence, in this model, most genetic changes in a population are the result of constant mutation pressure and genetic drift. This form of the neutral theory is now largely abandoned, since it does not seem to fit the genetic variation seen in nature. However, a more recent and better-supported version of this model is the nearly neutral theory, where most mutations only have small effects on fitness.

Outcomes

Evolution influences every aspect of the form and behaviour of organisms. Most prominent are the specific behavioural and physical adaptations that are the outcome of natural selection. These adaptations increase fitness by aiding activities such as finding food, avoiding predators or attracting mates. Organisms can also respond to selection by co-operating with each other, usually by aiding their relatives or engaging in mutually beneficial symbiosis. In the longer term, evolution produces new species through splitting ancestral populations of organisms into new groups that cannot or will not interbreed.

These outcomes of evolution are sometimes divided into macroevolution, which is evolution that occurs at or above the level of species, such as extinction and speciation, and microevolution, which is smaller evolutionary changes, such as adaptations, within a species or population. In general, macroevolution is regarded as the outcome of long periods of microevolution. Thus, the distinction between micro- and macroevolution is not a fundamental one – the difference is simply the time involved. However, in macroevolution, the traits of the entire species may be important. For instance, a large amount of variation among individuals allows a species to rapidly adapt to new habitats, lessening the chance of it going extinct, while a wide geographic range increases the chance of speciation, by making it more likely that part of the population will become isolated. In this sense, microevolution and macroevolution might involve selection at different levels – with microevolution acting on genes and organisms, versus macroevolutionary processes such as species selection acting on entire species and affecting their rates of speciation and extinction.

A common misconception is that evolution has goals or long-term plans; realistically however, evolution has no long-term goal and does not necessarily produce greater complexity. Although complex species have evolved, they occur as a side effect of the overall number of organisms increasing, and simple forms of life still remain more common in the biosphere. For example, the overwhelming majority of species are microscopic prokaryotes, which form about half the world's biomass despite their small size, and constitute the vast majority of Earth's biodiversity. Simple organisms have therefore been the dominant form of life on Earth throughout its history and continue to be the main form of life up to the present day, with complex life only appearing more diverse because it is more noticeable. Indeed, the evolution of microorganisms is

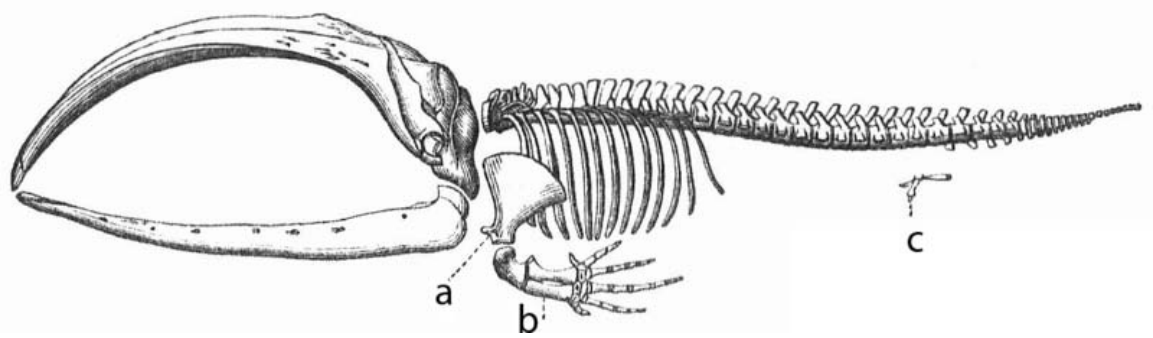
particularly important to modern evolutionary research, since their rapid reproduction allows the study of experimental evolution and the observation of evolution and adaptation in real time.

Adaptation

Adaptation is the process that makes organisms better suited to their habitat. Also, the term adaptation may refer to a trait that is important for an organism's survival. For example, the adaptation of horses' teeth to the grinding of grass. By using the term *adaptation* for the evolutionary process, and *adaptive trait* for the product (the bodily part or function), the two senses of the word may be distinguished. Adaptations are produced by natural selection. The following definitions are due to Theodosius Dobzhansky.

1. *Adaptation* is the evolutionary process whereby an organism becomes better able to live in its habitat or habitats.
2. *Adaptedness* is the state of being adapted: the degree to which an organism is able to live and reproduce in a given set of habitats.
3. An *adaptive trait* is an aspect of the developmental pattern of the organism which enables or enhances the probability of that organism surviving and reproducing.

Adaptation may cause either the gain of a new feature, or the loss of an ancestral feature. An example that shows both types of change is bacterial adaptation to antibiotic selection, with genetic changes causing antibiotic resistance by both modifying the target of the drug, or increasing the activity of transporters that pump the drug out of the cell. Other striking examples are the bacteria *Escherichia coli* evolving the ability to use citric acid as a nutrient in a long-term laboratory experiment, *Flavobacterium* evolving a novel enzyme that allows these bacteria to grow on the by-products of nylon manufacturing, and the soil bacterium *Sphingobium* evolving an entirely new metabolic pathway that degrades the synthetic pesticide pentachlorophenol. An interesting but still controversial idea is that some adaptations might increase the ability of organisms to generate genetic diversity and adapt by natural selection (increasing organisms' evolvability).



A baleen whale skeleton, *a* and *b* label flipper bones, which were adapted from front leg bones: while *c* indicates vestigial leg bones, suggesting an adaptation from land to sea.

Adaptation occurs through the gradual modification of existing structures. Consequently, structures with similar internal organisation may have different functions in related organisms. This is the result of a single ancestral structure being adapted to function in different ways. The bones within bat wings, for example, are very similar to those in mice feet and primate hands, due to the descent of all these structures from a common mammalian ancestor. However, since all living organisms are related to some extent, even organs that appear to have little or no structural similarity, such as arthropod, squid and vertebrate eyes, or the limbs and wings of arthropods and vertebrates, can depend on a common set of homologous genes that control their assembly and function; this is called deep homology.

During adaptation, some structures may lose their original function and become vestigial structures. Such structures may have little or no function in a current species, yet have a clear function in ancestral species, or other closely related species. Examples include pseudogenes, the non-functional remains of eyes in blind cave-dwelling fish, wings in flightless birds, and the presence of hip bones in whales and snakes. Examples of vestigial structures in humans include wisdom teeth, the coccyx, the vermiform appendix, and other behavioural vestiges such as goose bumps and primitive reflexes.

However, many traits that appear to be simple adaptations are in fact exaptations: structures originally adapted for one function, but which coincidentally became somewhat useful for some other function in the process. One example is the African lizard *Holaspis guentheri*, which developed an extremely flat head for hiding in crevices, as can be seen by looking at its near relatives. However, in this species, the head has become so flattened that it assists in gliding from tree to tree—an exaptation. Within cells, molecular machines such as the bacterial flagella and protein sorting machinery evolved by the recruitment of several pre-existing proteins that previously had different functions. Another example is the recruitment of enzymes from glycolysis and xenobiotic metabolism to serve as structural proteins called crystallins within the lenses of organisms' eyes.

A critical principle of ecology is that of competitive exclusion: no two species can occupy the same niche in the same environment for a long time. Consequently, natural selection will tend to force species to adapt to different ecological niches. This may mean that, for example, two species of cichlid fish adapt to live in different habitats, which will minimise the competition between them for food.

An area of current investigation in evolutionary developmental biology is the developmental basis of adaptations and exaptations. This research addresses the origin and evolution of embryonic development and how modifications of development and developmental processes produce novel features. These studies have shown that evolution can alter development to create new structures, such as embryonic bone structures that develop into the jaw in other animals instead forming part of the middle ear in mammals. It is also possible for structures that have been lost in evolution to reappear due to changes in developmental genes, such as a mutation in chickens causing

embryos to grow teeth similar to those of crocodiles. It is now becoming clear that most alterations in the form of organisms are due to changes in a small set of conserved genes.

Co-evolution

Common garter snake (*Thamnophis sirtalis sirtalis*) which has evolved resistance to tetrodotoxin in its amphibian prey.

Interactions between organisms can produce both conflict and co-operation. When the interaction is between pairs of species, such as a pathogen and a host, or a predator and its prey, these species can develop matched sets of adaptations. Here, the evolution of one species causes adaptations in a second species. These changes in the second species then, in turn, cause new adaptations in the first species. This cycle of selection and response is called co-evolution. An example is the production of tetrodotoxin in the rough-skinned newt and the evolution of tetrodotoxin resistance in its predator, the common garter snake. In this predator-prey pair, an evolutionary arms race has produced high levels of toxin in the newt and correspondingly high levels of toxin resistance in the snake.

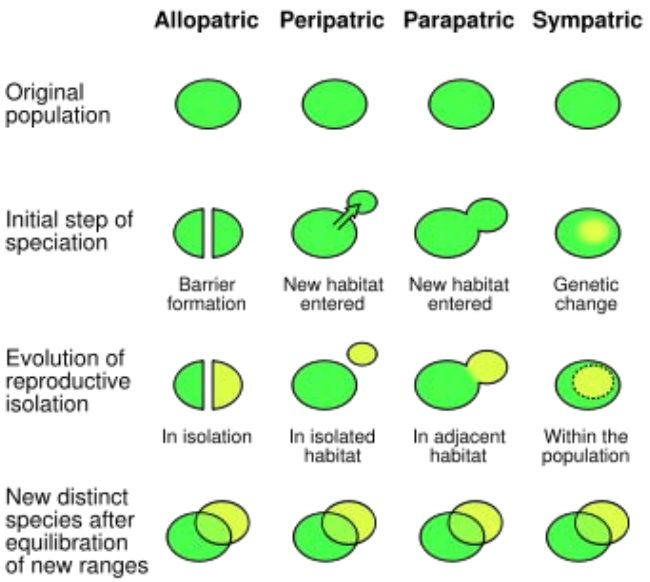
Co-operation

However, not all interactions between species involve conflict. Many cases of mutually beneficial interactions have evolved. For instance, an extreme cooperation exists between plants and the mycorrhizal fungi that grow on their roots and aid the plant in absorbing nutrients from the soil. This is a reciprocal relationship as the plants provide the fungi with sugars from photosynthesis. Here, the fungi actually grow inside plant cells, allowing them to exchange nutrients with their hosts, while sending signals that suppress the plant immune system.

Coalitions between organisms of the same species have also evolved. An extreme case is the eusociality found in social insects, such as bees, termites and ants, where sterile insects feed and guard the small number of organisms in a colony that are able to reproduce. On an even smaller scale, the somatic cells that make up the body of an animal limit their reproduction so they can maintain a stable organism, which then supports a small number of the animal's germ cells to produce offspring. Here, somatic cells respond to specific signals that instruct them whether to grow, remain as they are, or die. If cells ignore these signals and multiply inappropriately, their uncontrolled growth causes cancer.

Such cooperation within species may have evolved through the process of kin selection, which is where one organism acts to help raise a relative's offspring. This activity is selected for because if the *helping* individual contains alleles which promote the helping activity, it is likely that its kin will *also* contain these alleles and thus those alleles will be passed on. Other processes that may promote cooperation include group selection, where cooperation provides benefits to a group of organisms.

Speciation



The four mechanisms of speciation.

Speciation is the process where a species diverges into two or more descendant species.

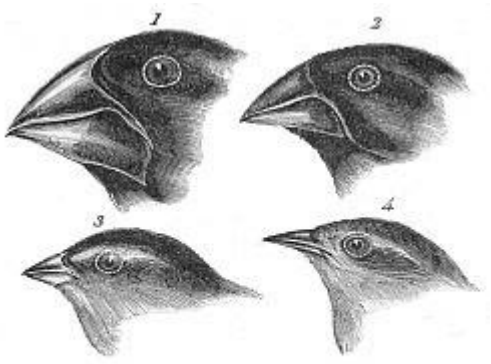
There are multiple ways to defining the species concept. The choice of which concept to use is dependent on the particularities of the species concerned. For example, some species concepts apply more readily toward sexually reproducing organisms while others lend themselves better toward asexual organisms. Despite the diversity of various species concepts, these various concepts can be placed into one of three broad philosophical approaches: interbreeding, ecological, and phylogenetic. The biological species concept (BSC) is a classic example of the interbreeding approach. Defined by Ernst Mayr in 1942, the BSC states that "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups"[:120]. Despite its wide and long-term use, the BSC like others is not without controversy, particularly in prokaryotes, and this is called the species problem. Some researchers have attempted a unifying monistic definition of species, while others adopt a pluralistic approach and suggest that there may be a different ways to logically interpret the definition of a species."

Barriers to reproduction between two diverging populations are required for the populations to become new species. Gene flow may slow this process by spreading the new genetic variants also to the other populations. 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. 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 hybridisation 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.

Speciation has been observed multiple times under both controlled laboratory conditions and in nature. In sexually reproducing organisms, speciation results from reproductive isolation followed by genealogical divergence. There are four mechanisms for speciation. The most common in animals is allopatric speciation, which occurs in populations initially isolated geographically, such as by habitat fragmentation or migration. Selection under these conditions can produce very rapid changes in the appearance and behaviour of organisms. As selection and drift act independently on populations isolated from the rest of their species, separation may eventually produce organisms that cannot interbreed.

The second mechanism of speciation is peripatric speciation, which occurs when small populations of organisms become isolated in a new environment. This differs from allopatric speciation in that the isolated populations are numerically much smaller than the parental population. Here, the founder effect causes rapid speciation through both rapid genetic drift and selection on a small gene pool.

The third mechanism of speciation is parapatric speciation. This is similar to peripatric speciation in that a small population enters a new habitat, but differs in that there is no physical separation between these two populations. Instead, speciation results from the evolution of mechanisms that reduce gene flow between the two populations. Generally this occurs when there has been a drastic change in the environment within the parental species' habitat. One example is the grass *Anthoxanthum odoratum*, which can undergo parapatric speciation in response to localised metal pollution from mines. Here, plants evolve that have resistance to high levels of metals in the soil. Selection against interbreeding with the metal-sensitive parental population produced a gradual change in the flowering time of the metal-resistant plants, which eventually produced complete reproductive isolation. Selection against hybrids between the two populations may cause *reinforcement*, which is the evolution of traits that promote mating within a species, as well as character displacement, which is when two species become more distinct in appearance.



Finches from Galapagos Archipelago

Geographical isolation of finches on the Galápagos Islands produced over a dozen new species.

Finally, in sympatric speciation species diverge without geographic isolation or changes in habitat. This form is rare since even a small amount of gene flow may remove genetic differences between parts of a population. Generally, sympatric speciation in animals requires the evolution of both genetic differences and non-random mating, to allow reproductive isolation to evolve.

One type of sympatric speciation involves cross-breeding of two related species to produce a new hybrid species. This is not common in animals as animal hybrids are usually sterile. This is because during meiosis the homologous chromosomes from each parent are from different species and cannot successfully pair. However, it is more common in plants because plants often double their number of chromosomes, to form polyploids. This allows the chromosomes from each parental species to form matching pairs during meiosis, since each parent's chromosomes are represented by a pair already. An example of such a speciation event is when the plant species *Arabidopsis thaliana* and *Arabidopsis arenosa* cross-bred to give the new species *Arabidopsis suecica*. This

happened about 20,000 years ago, and the speciation process has been repeated in the laboratory, which allows the study of the genetic mechanisms involved in this process. Indeed, chromosome doubling within a species may be a common cause of reproductive isolation, as half the doubled chromosomes will be unmatched when breeding with undoubled organisms.

Speciation events are important in the theory of punctuated equilibrium, which accounts for the pattern in the fossil record of short "bursts" of evolution interspersed with relatively long periods of stasis, where species remain relatively unchanged. In this theory, speciation and rapid evolution are linked, with natural selection and genetic drift acting most strongly on organisms undergoing speciation in novel habitats or small populations. As a result, the periods of stasis in the fossil record correspond to the parental population, and the organisms undergoing speciation and rapid evolution are found in small populations or geographically restricted habitats, and therefore rarely being preserved as fossils.

Extinction

Tyrannosaurus rex. Non-avian dinosaurs died out in the Cretaceous–Tertiary extinction event at the end of the Cretaceous period.

Extinction is the disappearance of an entire species. Extinction is not an unusual event, as species regularly appear through speciation, and disappear through extinction. Nearly all animal and plant species that have lived on Earth are now extinct, and extinction appears to be the ultimate fate of all species. These extinctions have happened continuously

throughout the history of life, although the rate of extinction spikes in occasional mass extinction events. The Cretaceous–Tertiary extinction event, during which the non-avian dinosaurs went extinct, is the most well-known, but the earlier Permian–Triassic extinction event was even more severe, with approximately 96% of species driven to extinction. The Holocene extinction event is an ongoing mass extinction associated with humanity's expansion across the globe over the past few thousand years. Present-day extinction rates are 100–1000 times greater than the background rate, and up to 30% of species may be extinct by the mid 21st century. Human activities are now the primary cause of the ongoing extinction event; global warming may further accelerate it in the future.

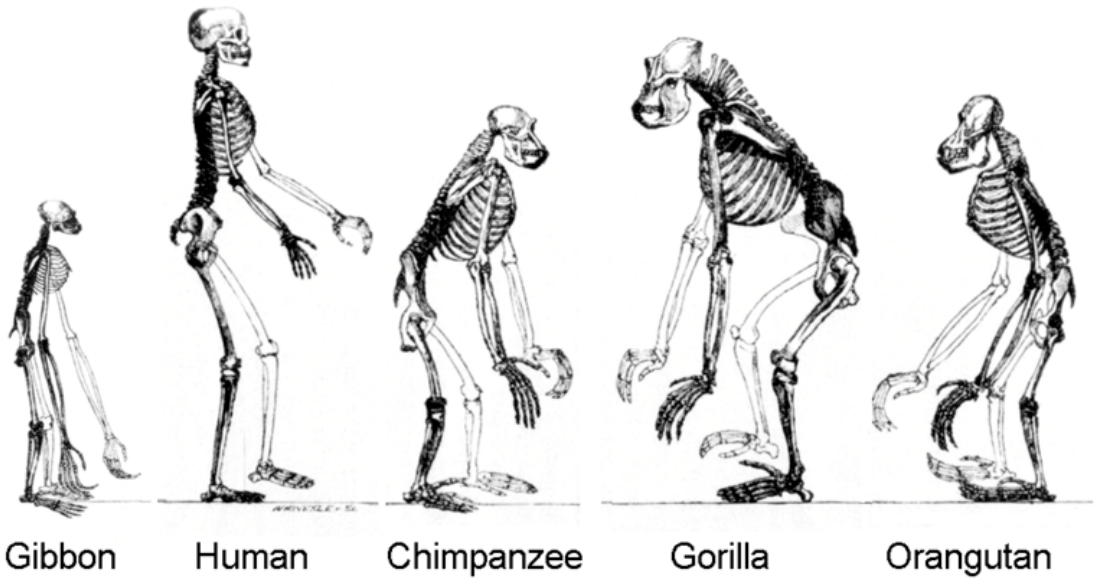
The role of extinction in evolution is not very well understood and may depend on which type of extinction is considered. The causes of the continuous "low-level" extinction events, which form the majority of extinctions, may be the result of competition between species for limited resources (competitive exclusion). If one species can out-compete another, this could produce species selection, with the fitter species surviving and the other species being driven to extinction. The intermittent mass extinctions are also important, but instead of acting as a selective force, they drastically reduce diversity in a nonspecific manner and promote bursts of rapid evolution and speciation in survivors.

Evolutionary history of life

Origin of life

Highly energetic chemistry is believed to have produced a self-replicating molecule around 4 billion years ago and half a billion years later the last common ancestor of all life existed. The current scientific consensus is that the complex biochemistry that makes up life came from simpler chemical reactions. The beginning of life may have included self-replicating molecules such as RNA, and the assembly of simple cells.

Common descent



The hominoids are descendants of a common ancestor.

All organisms on Earth are descended from a common ancestor or ancestral gene pool. Current species are a stage in the process of evolution, with their diversity the product of a long series of speciation and extinction events. The common descent of organisms was first deduced from four simple facts about organisms: First, they have geographic distributions that cannot be explained by local adaptation. Second, the diversity of life is not a set of completely unique organisms, but organisms that share morphological similarities. Third, vestigial traits with no clear purpose resemble functional ancestral traits, and finally, that organisms can be classified using these similarities into a hierarchy of nested groups – similar to a family tree. However, modern research has suggested that, due to horizontal gene transfer, this "tree of life" may be more complicated than a simple branching tree since some genes have spread independently between distantly related species.

Past species have also left records of their evolutionary history. Fossils, along with the comparative anatomy of present-day organisms, constitute the morphological, or anatomical, record. By comparing the anatomies of both modern and extinct species, paleontologists can infer the lineages of those species. However, this approach is most successful for organisms that had hard body parts, such as shells, bones or teeth. Further, as prokaryotes such as bacteria and archaea share a limited set of common morphologies, their fossils do not provide information on their ancestry.

More recently, evidence for common descent has come from the study of biochemical similarities between organisms. For example, all living cells use the same basic set of nucleotides and amino acids. The development of molecular genetics has revealed the

record of evolution left in organisms' genomes: dating when species diverged through the molecular clock produced by mutations. For example, these DNA sequence comparisons have revealed that humans and chimpanzees share 96% of their genomes and analyzing the few areas where they differ helps shed light on when the common ancestor of these species existed.

Evolution of life

Prokaryotes inhabited the Earth from approximately 3–4 billion years ago. No obvious changes in morphology or cellular organisation occurred in these organisms over the next few billion years.

The eukaryotic cells emerged between 1.6 – 2.7 billion years ago. The next major change in cell structure came when bacteria were engulfed by eukaryotic cells, in a cooperative association called endosymbiosis. The engulfed bacteria and the host cell then underwent co-evolution, with the bacteria evolving into either mitochondria or hydrogenosomes. Another engulfment of cyanobacterial-like organisms led to the formation of chloroplasts in algae and plants.

The history of life was that of the unicellular eukaryotes, prokaryotes, and archaea until about 610 million years ago when multicellular organisms began to appear in the oceans in the Ediacaran period. The evolution of multicellularity occurred in multiple independent events, in organisms as diverse as sponges, brown algae, cyanobacteria, slime moulds and myxobacteria.

Soon after the emergence of these first multicellular organisms, a remarkable amount of biological diversity appeared over approximately 10 million years, in an event called the Cambrian explosion. Here, the majority of types of modern animals appeared in the fossil record, as well as unique lineages that subsequently became extinct. Various triggers for the Cambrian explosion have been proposed, including the accumulation of oxygen in the atmosphere from photosynthesis.

About 500 million years ago, plants and fungi colonised the land, and were soon followed by arthropods and other animals. Insects were particularly successful and even today make up the majority of animal species. Amphibians first appeared around 300 million years ago, followed by early amniotes, then mammals around 200 million years ago and birds around 100 million years ago (both from "reptile"-like lineages). However, despite the evolution of these large animals, smaller organisms similar to the types that evolved early in this process continue to be highly successful and dominate the Earth, with the majority of both biomass and species being prokaryotes.

Applications

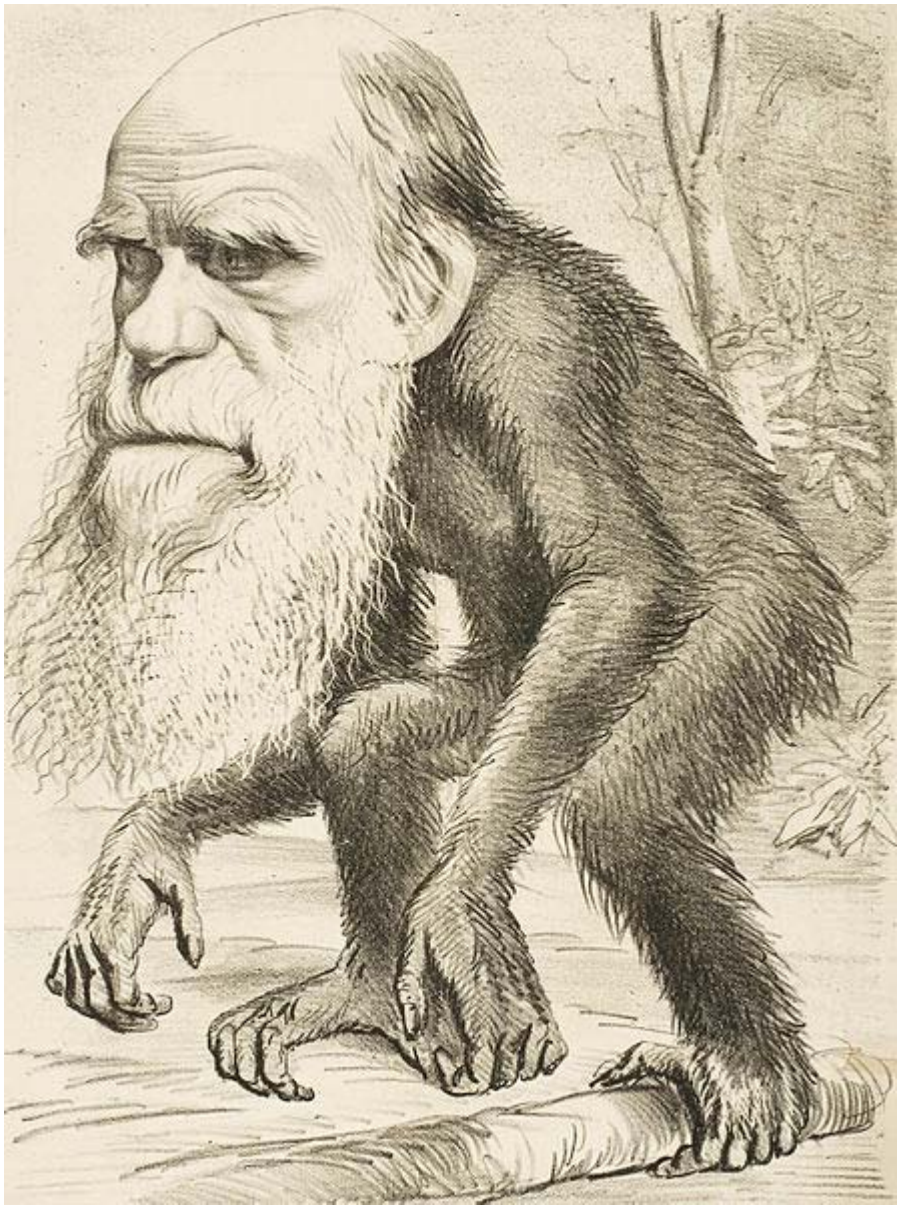
Concepts and models used in evolutionary biology, in particular natural selection, have many applications.

Artificial selection is the intentional selection of traits in a population of organisms. This has been used for thousands of years in the domestication of plants and animals. More recently, such selection has become a vital part of genetic engineering, with selectable markers such as antibiotic resistance genes being used to manipulate DNA. In repeated rounds of mutation and selection proteins with valuable properties have evolved, for example modified enzymes and new antibodies, in a process called directed evolution.

Understanding the changes that have occurred during organism's evolution can reveal the genes needed to construct parts of the body, genes which may be involved in human genetic disorders. For example, the mexican tetra is an albino cavefish that lost its eyesight during evolution. Breeding together different populations of this blind fish produced some offspring with functional eyes, since different mutations had occurred in the isolated populations that had evolved in different caves. This helped identify genes required for vision and pigmentation.

In computer science, simulations of evolution using evolutionary algorithms and artificial life started in the 1960s, and was extended with simulation of artificial selection. Artificial evolution became a widely recognised optimisation method as a result of the work of Ingo Rechenberg in the 1960s. He used evolution strategies to solve complex engineering problems. Genetic algorithms in particular became popular through the writing of John Holland. Practical applications also include automatic evolution of computer programs. Evolutionary algorithms are now used to solve multi-dimensional problems more efficiently than software produced by human designers, and also to optimise the design of systems.

Social and cultural responses



As evolution became widely accepted in the 1870s, caricatures of Charles Darwin with an ape or monkey body symbolised evolution.

In the 19th century, particularly after the publication of *On the Origin of Species* in 1859, the idea that life had evolved was an active source of academic debate centred on the philosophical, social and religious implications of evolution. Nowadays, the modern evolutionary synthesis is widely accepted by scientists. However, evolution remains a contentious concept for some theists.

While various religions and denominations have reconciled their beliefs with evolution through concepts such as theistic evolution, there are creationists who believe that

evolution is contradicted by the creation myths found in their respective religions and who raise various objections to evolution. As had been demonstrated by responses to the publication of *Vestiges of the Natural History of Creation* in 1844, the most controversial aspect of evolutionary biology is the implication of human evolution that humans share common ancestry with apes, and that the mental and moral faculties of humanity have the same types of natural causes as other inherited traits in animals. In some countries, notably the United States, these tensions between science and religion have fuelled the current creation-evolution controversy, a religious conflict focusing on politics and public education. While other scientific fields such as cosmology and Earth science also conflict with literal interpretations of many religious texts, evolutionary biology experiences significantly more opposition from religious literalists.

The teaching of evolution in American secondary school biology classes was uncommon in most of the first half of the 20th century. The Scopes Trial decision of 1925 caused the subject to become very rare in American secondary biology textbooks for a generation, but it was gradually re-introduced about a generation later and legally protected with the 1968 *Epperson v. Arkansas* decision. Since then, the competing religious belief of creationism was legally disallowed in secondary school curricula in various decisions in the 1970s and 1980s, but it returned in the form of intelligent design, to be excluded once again in the 2005 *Kitzmiller v. Dover Area School District* case.

Social Darwinism is ideas about "survival of the fittest" taken out of their biological context and applied to commerce and human societies as a whole, and misused to justify social inequality, sexism, racism and imperialism. The 19th century Malthusian theory developed by Whig philosopher Herbert Spencer is also seen as belonging to the social Darwinism movement.

Chapter 2

Evolution as Theory and Fact

The statement "evolution is both a theory and a fact" is often seen in biological literature. Evolution is a "theory" in the *scientific* sense of the term "theory"; it is an established scientific model of a portion of the universe that generates propositions with observational consequences. Such a model both helps generate new research and helps us understand observed phenomena.

When scientists say "evolution is a fact", they are using one of two meanings of the word "fact". One meaning is empirical: evolution can be observed through changes in allele frequencies or traits of a population over successive generations.

Another way "fact" is used is to refer to a certain kind of theory, one that has been so powerful and productive for such a long time that it is universally accepted by scientists. When scientists say evolution is a fact in *this* sense, they mean it is a fact that all living organisms have descended from a common ancestor (or ancestral gene pool) even though this cannot be directly observed. This implies more tangibly that it is a fact that humans share a common ancestor with other primates.

Evolution, fact and theory

Evolution has been described as "fact and theory", "fact not theory", and "only a theory, not a fact". This illustrates a confusion in terminology that hampers discussion. The meanings of the terms "evolution", "fact", and "theory" are described below.

Evolution

Evolution is usually defined simply as changes in trait or gene frequency in a population of organisms from one generation to the next. However, "evolution" is often used to include the following additional claims:

1. Differences in trait composition between isolated populations over many generations may result in the origin of new species.
2. All living organisms alive today have descended from a common ancestor (or ancestral gene pool).

According to Douglas Futuyma:

Biological evolution may be slight or substantial; it embraces everything from slight changes in the proportion of different alleles within a population (such as those determining blood types) to the successive alterations that led from the earliest proto-organism to snails, bees, giraffes, and dandelions.

The term "evolution", especially when referred to as a "theory", is also used more broadly to incorporate processes such as natural selection and genetic drift.

Fact

Fact is often used by scientists to refer to experimental or empirical data or objective verifiable observations. "Fact" is also used in a wider sense to mean any theory for which there is overwhelming evidence.

A fact is a hypothesis that is so firmly supported by evidence that we assume it is true, and act as if it were true. —Douglas Futyuma

Evolution is a fact in the sense that it is overwhelmingly validated by the evidence. Frequently, evolution is said to be a fact in the same way as the Earth revolving around the Sun is a fact. The following quotation from H. J. Muller, "One Hundred Years Without Darwin Are Enough" explains the point.

There is no sharp line between speculation, hypothesis, theory, principle, and fact, but only a difference along a sliding scale, in the degree of probability of the idea. When we say a thing is a fact, then, we only mean that its probability is an extremely high one: so high that we are not bothered by doubt about it and are ready to act accordingly. Now in this use of the term fact, the only proper one, evolution is a fact.

The National Academy of Science (U.S.) makes a similar point:

Scientists most often use the word "fact" to describe an observation. But scientists can also use fact to mean something that has been tested or observed so many times that there is no longer a compelling reason to keep testing or looking for examples. The occurrence of evolution in this sense is fact. Scientists no longer question whether descent with modification occurred because the evidence is so strong.

Philosophers of science argue that we do not know mind-independent empirical truths with absolute certainty: even direct observations may be "theory laden" and depend on

assumptions about our senses and the measuring instruments used. In this sense all facts are provisional.

Theory

A scientific theory is a well-supported body of interconnected statements that explains observations and can be used to make testable predictions. Scientific theories describe the coherent framework into which observable data fit. The "theory of evolution" is the framework that best explains observed changes of species over time and best predicts the new observations that continue to be made in evolutionary biology and related sciences.

The scientific definition of the word "theory" is different from the colloquial sense of the word. Colloquially, "theory" can mean a hypothesis, a conjecture, an opinion, or a speculation that does not have to be based on facts or make testable predictions. However, In science, the meaning of theory is more rigorous. A theory is hypothesis corroborated by observation of facts which makes testable predictions. In science, a current theory is a theory that has no equally acceptable or more acceptable alternative theory.

Evolution compared with gravity

The application of the terms "fact" and "theory" to evolution is similar to their use in describing gravity.

The most obvious *fact* of gravity is that objects in our everyday experience tend to fall downwards when not otherwise prevented from doing so. People throughout history have wondered what causes this effect. Many explanations have been proposed over the centuries. Aristotle, Galileo, Newton, and Einstein have all developed useful models of gravity, each of which constitutes a *theory of gravity*. (Newton, for example, realized that the fact of gravity can be extended to the tendency of any two masses to attract one another.) The word "gravity", therefore, can be used to refer to the observed facts (i.e., that masses attract one another) and the theory used to explain the facts (the *reason* why masses attract one another). In this way, gravity is both a theory and a fact.

In the study of biological species, the facts include the existence of many different species in existence today, some very similar to each other and some very dissimilar, the remains of extinct species in the fossil record, and so forth. In species that rapidly reproduce, for example fruit flies, the process of change from generation to generation — that is, evolutionary change — has been observed in the laboratory. The observation of fruit fly populations changing over time is also an example of a fact. So evolution is a fact just as the observations of gravity are a fact.

There have been many attempts to explain these biological observations over the years. Lamarckism, transmutationism and orthogenesis were all non-Darwinian theories that attempted to explain the observations of species and fossils, as well as other evidence. However, the modern *theory of evolution* is the explanation for all relevant observations

regarding the development of life, based on a model that explains all the available data and observations (and provides testable predictions). Thus, evolution is not only a fact but also a theory, just as gravity is both a fact and a theory.

Evolution as theory and fact in the literature

The confusion over the word *evolution* and the distinction between "fact" and "theory" is largely due to authors using *evolution* to refer to three related yet distinct ideas: first, the changes that occur within species over generations; second, the mechanism thought to drive change; and third, the concept of common descent. However, among biologists there is a consensus that evolution is a fact:

- American zoologist and paleontologist George Simpson stated that *"Darwin... finally and definitely established evolution as a fact."*
- H. J. Muller wrote, *"If you like, then, I will grant you that in an absolute sense evolution is not a fact, or rather, that it is no more a fact than that you are hearing or reading these words."*
- Kenneth R. Miller writes, *"evolution is as much a fact as anything we know in science."*
- Ernst Mayr observed, *"The basic theory of evolution has been confirmed so completely that most modern biologists consider evolution simply a fact. How else except by the word evolution can we designate the sequence of faunas and floras in precisely dated geological strata? And evolutionary change is also simply a fact owing to the changes in the content of gene pools from generation to generation."*

Evolution as fact *and* theory

Commonly "fact" is used to refer to the observable changes in organisms' traits over generations while the word "theory" is reserved for the mechanisms that cause these changes:

- Paleontologist Stephen Jay Gould writes, *"Evolution is a theory. It is also a fact. And facts and theories are different things, not rungs in a hierarchy of increasing certainty. Facts are the world's data. Theories are structures of ideas that explain and interpret facts. Facts do not go away when scientists debate rival theories to explain them. Einstein's theory of gravitation replaced Newton's, but apples did not suspend themselves in mid-air, pending the outcome. And humans evolved from ape-like ancestors whether they did so by Darwin's proposed mechanism or by some other yet to be discovered."*
- Similarly, biologist Richard Lenski says, *"Scientific understanding requires both facts and theories that can explain those facts in a coherent manner. Evolution, in this context, is both a fact and a theory. It is an incontrovertible fact that organisms have changed, or evolved, during the history of life on Earth. And biologists have identified and investigated mechanisms that can explain the major patterns of change."*

- Biologist T. Ryan Gregory says, *"biologists rarely make reference to 'the theory of evolution,' referring instead simply to 'evolution' (i.e., the fact of descent with modification) or 'evolutionary theory' (i.e., the increasingly sophisticated body of explanations for the fact of evolution). That evolution is a theory in the proper scientific sense means that there is both a fact of evolution to be explained and a well-supported mechanistic framework to account for it."*

Evolution as fact *not* theory

Other commentators, focusing on the changes in species over generations and in some cases common ancestry have stressed that evolution is a fact to emphasize the weight of supporting evidence while denying it is helpful to use the term "theory":

- R. C. Lewontin wrote, *"It is time for students of the evolutionary process, especially those who have been misquoted and used by the creationists, to state clearly that evolution is a fact, not theory."*
- Douglas Futuyma writes in his *Evolutionary Biology* book, *"The statement that organisms have descended with modifications from common ancestors—the historical reality of evolution—is not a theory. It is a fact, as fully as the fact of the earth's revolution about the sun."*
- Richard Dawkins says, *"One thing all real scientists agree upon is the fact of evolution itself. It is a fact that we are cousins of gorillas, kangaroos, starfish, and bacteria. Evolution is as much a fact as the heat of the sun. It is not a theory, and for pity's sake, let's stop confusing the philosophically naive by calling it so. Evolution is a fact."*
- Neil Campbell wrote in his 1990 biology textbook, *"Today, nearly all biologists acknowledge that evolution is a fact. The term theory is no longer appropriate except when referring to the various models that attempt to explain how life evolves... it is important to understand that the current questions about how life evolves in no way implies any disagreement over the fact of evolution."*

Predictive power

A central tenet in science is that a scientific theory is supposed to have predictive power, and verification of predictions are seen as an important and necessary support for the theory. The theory of evolution has provided such predictions. Four examples are:

- Genetic information must be transmitted in a molecular way that will be almost exact but permit slight changes. Since this prediction was made, biologists have discovered the existence of DNA, which has a mutation rate of roughly 10^{-9} per nucleotide per cell division; this provides just such a mechanism.
- 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 fossil

evidence. 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.

- 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.
- Evolutionary theory predicts that novel inventions can arise, while creationists predict that new "information" cannot arise, and that the Second Law of Thermodynamics only allows for "information" to be lost. In an ongoing experiment, Richard Lenski observed that *E. coli* evolved the ability to metabolize citrate, which constitutes a novel invention, and an increase in the information of the DNA of the *E. coli*.

Related concepts and terminology

- Speculative or conjectural explanations are called hypotheses. Well-tested and corroborated (or validated) explanations are called *theories*.
- "Fact" does not mean "absolute certainty". In the words of Stephen J. Gould: *In science, "fact" can only mean "confirmed to such a degree that it would be perverse to withhold provisional assent."*
- "Proof" of a theory does not exist in natural sciences. Proof only exists in formal sciences, such as mathematics. Experimental observation of the predictions made by a hypothesis or theory is called *validation*.
- A *scientific law* is a concept related to a *scientific theory*. Very well-established "theories" that rely on a simple principle are often called scientific "laws". For example, it is common to encounter reference to "the law of gravity", "the law of natural selection", or the "laws of evolution."

Chapter 3

Fitness (Biology)

Fitness (often denoted *w* in population genetics models) is a central idea in evolutionary theory. It can be defined either with respect to a genotype or to a phenotype. In either case, it describes the ability to both survive and reproduce, and is equal to the average contribution to the gene pool of the next generation that is made by an average individual of the specified genotype or phenotype. If differences between alleles at a given gene affect fitness, then the frequencies of the alleles will change over generations; the alleles with higher fitness become more common. This process is called natural selection.

An individual's fitness is manifested through its phenotype. As phenotype is affected by both genes and environment, the fitnesses of different individuals with the same genotype are not necessarily equal, but depend on the environment in which the individuals live. However, since the fitness of the genotype is an averaged quantity, it will reflect the reproductive outcomes of all individuals with that genotype.

Inclusive fitness differs from individual fitness by including the ability of an allele in one individual to promote the survival and/or reproduction of other individuals that share that allele, in preference to individuals with a different allele. One mechanism of inclusive fitness is kin selection.

Measures of fitness

There are two commonly used measures of fitness; absolute fitness and relative fitness.

Absolute fitness

Absolute fitness (w_{abs}) of a genotype is defined as the ratio between the number of individuals with that genotype after selection to those before selection. It is calculated for a single generation and may be calculated from absolute numbers or from frequencies.

When the fitness is larger than 1.0, the genotype increases in frequency; a ratio smaller than 1.0 indicates a decrease in frequency.

$$w_{\mathrm{abs}} = \frac{N_{\mathrm{after}}}{N_{\mathrm{before}}}$$

Absolute fitness for a genotype can also be calculated as the product of the proportion survival times the average fecundity.

Relative fitness

Relative fitness is quantified as the average number of surviving progeny of a particular genotype compared with average number of surviving progeny of competing genotypes after a single generation, i.e. one genotype is normalized at $w = 1$ and the fitnesses of other genotypes are measured with respect to that genotype. Relative fitness can therefore take any nonnegative value, including 0.

While researchers can usually measure relative fitness, absolute fitness is more difficult. It is often difficult to determine how many individuals of a genotype there were immediately after reproduction.

The two concepts are related, and both of them are equivalent when they are divided by the mean fitness, which is weighted by genotype frequencies.

$$\frac{w_{abs}}{\overline{w}_{abs}} = \frac{w_{rel}}{\overline{w}_{rel}}$$

Because fitness is a coefficient, and a variable may be multiplied by it several times, biologists may work with "log fitness" (particularly so before the advent of computers). By taking the logarithm of fitness each term may be added rather than multiplied.

Maynard-Smith's Definition

As another example we may mention the definition of fitness given by Maynard Smith in the following way: "Fitness is a property, not of an individual, but of a class of individuals – for example homozygous for allele A at a particular locus. Thus the phrase ’expected number of offspring’ means the average number, not the number produced by some one individual. If the first human infant with a gene for levitation were struck by lightning in its pram, this would not prove the new genotype to have low fitness, but only that the particular child was unlucky."

Hartl's Definition

Yet another possible measure has been formulated: "The fitness of the individual - having an array x of phenotypes - is the probability, s(x), that the individual will be

included among the group selected as parents of the next generation." Then, the mean fitness may be determined as a mean over the set of individuals in a large population.

$$P(m) = \int s(x)N(m-x)\,dx$$

where N is the probability distribution function of phenotypes in the population, and m is its centre of gravity. This measure is a suitable basis of a model of an evolution selecting individuals. It may in principle take even the stroke of the lightning into consideration. In the case N is a Gaussian it is fairly easily proved that the average information (information entropy, disorder, diversity) of a large population may be maximized by Gaussian adaptation - keeping the mean fitness constant - in accordance with recapitulation, the central limit theorem, the Hardy-Weinberg law and the second law of thermodynamics. This is in contrast to Fisher's fundamental theorem of natural selection.

History

The British sociologist Herbert Spencer coined the phrase "survival of the fittest" (though originally, and perhaps more accurately, "survival of the best fitted") in his 1851 work *Social Statics* and later used it to characterise what Charles Darwin had called natural selection.

The British biologist J.B.S. Haldane was the first to quantify fitness, in terms of the modern evolutionary synthesis of Darwinism and Mendelian genetics starting with his 1924 paper *A Mathematical Theory of Natural and Artificial Selection*. The next further advance was the introduction of the concept of inclusive fitness by the British biologist W.D. Hamilton in 1964 in his paper on *The Evolution of Social Behavior*.

Fitness landscape

A fitness landscape, first conceptualized by Sewall Wright, is a way of visualising fitness in terms of a high-dimensional surface, in which height indicates fitness, and each of the other dimensions represents allele identity for a different gene. Peaks correspond to local fitness maxima; it is often said that natural selection always progresses uphill but can only do so locally. This can result in suboptimal local maxima becoming stable, because natural selection cannot return to the less-fit "valleys" of the landscape on the way to reach higher peaks.

Genetic load

Genetic load measures the average fitness of a population of individuals, relative to a hypothetical population in which the most fit genotype has become fixed.

Chapter 4

Natural Selection

Natural selection is the process by which traits become more or less common in a population due to consistent effects upon the survival or reproduction of their bearers. It is a key mechanism of evolution.

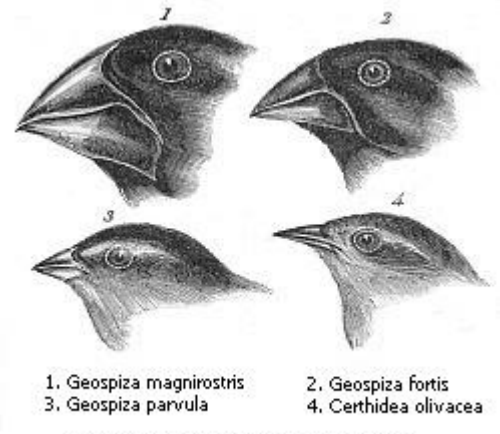
The natural genetic variation within a population of organisms may cause some individuals to survive and reproduce more successfully than others in their current environment. For example, the peppered moth exists in both light and dark colours in the United Kingdom, but during the industrial revolution many of the trees on which the moths rested became blackened by soot, giving the dark-colored moths an advantage in hiding from predators. This gave dark-colored moths a better chance of surviving to produce dark-colored offspring, and in just a few generations the majority of the moths were dark. 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 adaptations that specialize populations for particular ecological niches and may eventually result in the emergence of new species. In other words, natural selection is an important process (though not the only process) by which evolution takes place within a population of organisms. As opposed to artificial selection, in which humans favor specific traits, in natural selection the environment acts as a sieve through which only certain variations can pass.

Natural selection is one of the cornerstones of modern biology. The term was introduced by Darwin in his influential 1859 book *On the Origin of Species*, in which natural selection was described as analogous 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.

General principles



Finches from Galapagos Archipelago

Darwin's illustrations of beak variation in the finches of the Galápagos Islands, which hold 13 closely related species that differ most markedly in the shape of their beaks. The beak of each species is suited to its preferred food, suggesting that beak shapes evolved by natural selection.

Natural variation occurs among the individuals of any population of organisms. Many of these differences do not affect survival (such as differences in eye color in humans), but some differences may improve the chances of survival of a particular individual. A rabbit that runs faster than others may be more likely to escape from predators, and algae that are more efficient at extracting energy from sunlight will grow faster. Something that increases an animal's survival will often also include its reproductive rate; however, sometimes there is a trade-off between survival and current reproduction. Ultimately, what matters is total lifetime reproduction of the animal.

If the traits that give these individuals a reproductive advantage are also heritable, that is, passed from parent to child, then there will be a slightly higher proportion of fast rabbits or efficient algae in the next generation. This is known as *differential reproduction*. Even if the reproductive advantage is very slight, over many generations any heritable advantage will become dominant in the population. In this way the natural environment of an organism "selects" for traits that confer a reproductive advantage, causing gradual changes or evolution of life. This effect was first described and named by Charles Darwin.

The concept of natural selection predates the understanding of genetics, the mechanism of heredity for all known life forms. In modern terms, selection acts on an organism's phenotype, or observable characteristics, but it is the organism's genetic make-up or

genotype that is inherited. The phenotype is the result of the genotype and the environment in which the organism lives.

This is the link between natural selection and genetics, as described in the modern evolutionary synthesis. Although a complete theory of evolution also requires an account of how genetic variation arises in the first place (such as by mutation and sexual reproduction) and includes other evolutionary mechanisms (such as genetic drift and gene flow), natural selection appears to be the most important mechanism for creating complex adaptations in nature.

Nomenclature and usage

The term *natural selection* has slightly different definitions in different contexts. It is most often defined to operate on heritable traits, because these are the traits that directly participate in evolution. However, natural selection is "blind" in the sense that changes in phenotype (physical and behavioral characteristics) can give a reproductive advantage regardless of whether or not the trait is heritable (non heritable traits can be the result of environmental factors or the life experience of the organism).

Following Darwin's primary usage the term is often used to refer to both 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 "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. This is sometimes referred to as "phenotypic natural selection".

Traits that cause greater reproductive success of an organism are said to be selected for, whereas those that reduce success are selected against. Selection for a trait may also result in the selection of other correlated traits that do not themselves directly influence reproductive advantage. This may occur as a result of pleiotropy or gene linkage.

Fitness

The concept of fitness is central to natural selection. Broadly, individuals which are more "fit" have better potential for survival, as in the well-known phrase "survival of the fittest". However, as with natural selection above, the precise meaning of the term is much more subtle, and Richard Dawkins manages in his later books to avoid it entirely. (He devotes a chapter of his book, *The Extended Phenotype*, to discussing the various senses in which the term is used). 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 will 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. Very low-fitness genotypes cause their bearers to have few or no offspring on average; examples include many human genetic disorders like cystic fibrosis.

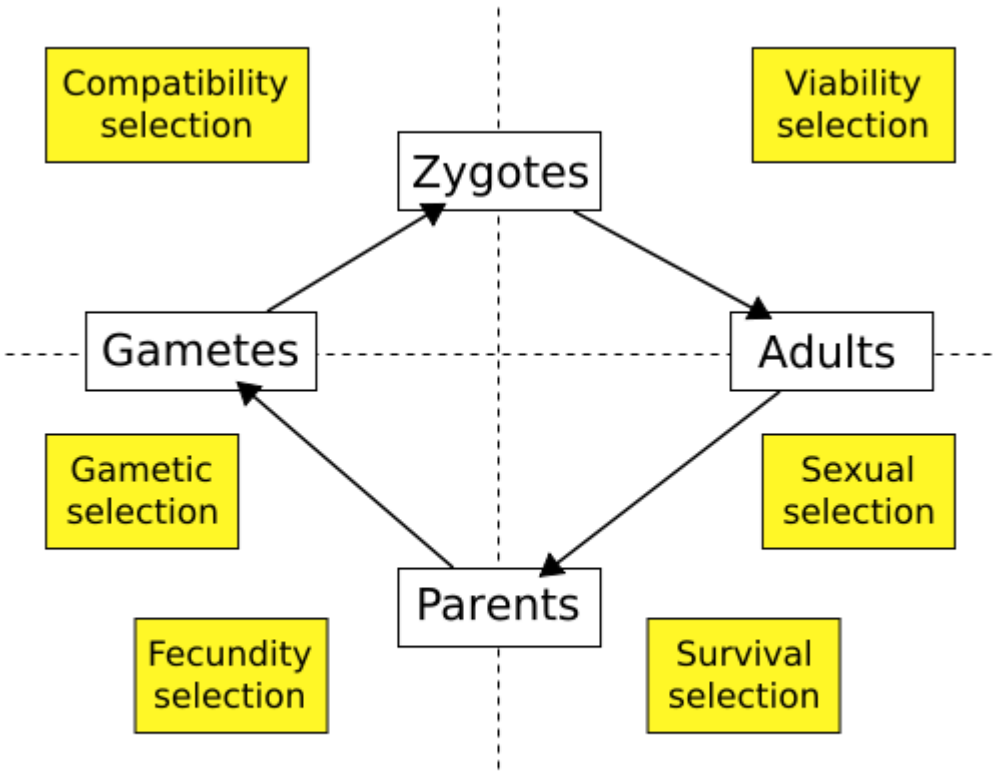
Since fitness is an averaged quantity, it is also possible that a favorable mutation arises in an individual that does not survive to adulthood for unrelated reasons. Fitness also depends crucially upon the environment. Conditions like sickle-cell anemia may have low fitness in the general human population, but because the sickle-cell trait confers immunity from malaria, it has high fitness value in populations which have high malaria infection rates.

Types of 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.

The unit of selection can be the individual or it can be another level within the hierarchy of biological organisation, such as genes, cells, and kin groups. There is still debate about whether natural selection acts at the level of groups or species to produce adaptations that benefit a larger, non-kin group. Likewise, there is debate as to whether selection at the molecular level prior to gene mutations and fertilization of the zygote should be ascribed to conventional natural selection because traditionally natural selection is an environmental and exterior force that acts upon a phenotype typically after birth. Some science journalists distinguish natural selection from gene selection by informally referencing selection of mutations as "pre-selection."

Selection at a different level such as the gene can result in an increase in fitness for that gene, while at the same time reducing the fitness of the individuals carrying that gene, in a process called intragenomic conflict. Overall, the combined effect of all selection pressures at various levels determines the overall fitness of an individual, and hence the outcome of natural selection.



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The life cycle of a sexually reproducing organism. Various components of natural selection are indicated for each life stage.

Natural selection occurs at every life stage of an individual. An individual organism must survive until adulthood before it can reproduce, and selection of those that reach this stage is called *viability selection*. In many species, adults must compete with each other for mates via sexual selection, and success in this competition determines who will parent the next generation. When individuals can reproduce more than once, a longer survival in the reproductive phase increases the number of offspring, called *survival selection*.

The fecundity of both females and males (for example, giant sperm in certain species of *Drosophila*) can be limited via "fecundity selection". The viability of produced gametes can differ, while intragenomic conflicts such as meiotic drive between the haploid gametes can result in gametic or "genic selection". Finally, the union of some combinations of eggs and sperm might be more compatible than others; this is termed *compatibility selection*.

Sexual selection

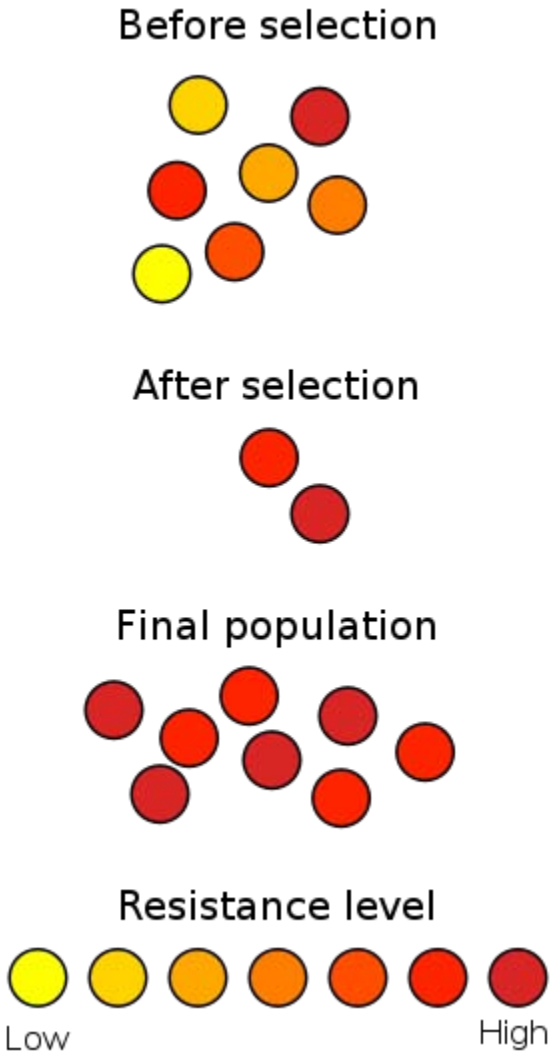
It is useful to distinguish between "ecological selection" and "sexual selection". Ecological selection covers any mechanism of selection as a result of the environment

(including relatives, e.g. kin selection, competition, and infanticide), while "sexual selection" refers specifically to competition for mates.

Sexual selection can be *intrasexual*, as in cases of competition among individuals of the same sex in a population, or *intersexual*, as in cases where one sex controls reproductive access by choosing among a population of available mates. Most commonly, intrasexual selection involves male–male competition and intersexual selection involves female choice of suitable males, due to the generally greater investment of resources for a female than a male in a single offspring. However, some species exhibit sex-role reversed behavior in which it is males that are most selective in mate choice; the best-known examples of this pattern occur in some fishes of the family *Syngnathidae*, though likely examples have also been found in amphibian and bird species.

Some features that are confined to one sex only of a particular species can be explained by selection exercised by the other sex in the choice of a mate, for example, the extravagant plumage of some male birds. Similarly, 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.

Examples of natural selection



Resistance to antibiotics is increased though the survival of individuals which are immune to the effects of the antibiotic, whose offspring then inherit the resistance, creating a new population of resistant bacteria.

A well-known example of natural selection in action is the development of antibiotic resistance in microorganisms. Since the discovery of penicillin in 1928 by Alexander Fleming, antibiotics have been used to fight bacterial diseases. Natural populations of bacteria contain, among their vast numbers of individual members, considerable variation in their genetic material, primarily as the result of mutations. When exposed to antibiotics, most bacteria die quickly, but some may have mutations that make them slightly less susceptible. If the exposure to antibiotics is short, these individuals will survive the treatment. This selective elimination of maladapted individuals from a population is natural selection.

These surviving bacteria will then reproduce again, producing the next generation. Due to the elimination of the maladapted individuals in the past generation, this population contains more bacteria that have some resistance against the antibiotic. At the same time, new mutations occur, contributing new genetic variation to the existing genetic variation. Spontaneous mutations are very rare, and advantageous mutations are even rarer. However, populations of bacteria are large enough that a few individuals will have beneficial mutations. If a new mutation reduces their susceptibility to an antibiotic, these individuals are more likely to survive when next confronted with that antibiotic.

Given enough time, and repeated exposure to the antibiotic, a population of antibiotic-resistant bacteria will emerge. This new changed population of antibiotic-resistant bacteria is optimally adapted to the context it evolved in. At the same time, it is not necessarily optimally adapted any more to the old antibiotic free environment. The end result of natural selection is two populations that are both optimally adapted to their specific environment, while both perform substandard in the other environment.

The widespread use and misuse of antibiotics has resulted in increased 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 example of what is known as an evolutionary arms race, in which bacteria continue to develop strains that are less susceptible to antibiotics, while medical researchers continue 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 Wolbachia bacteria parasites on the island of Samoa, where the spread of the gene is known to have occurred over a period of just five years

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, 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 very 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, recent research suggests that many mutations in non-coding DNA do have slight deleterious effects. Although both mutation rates and average fitness effects of mutations are dependent on the organism, estimates from data in humans have found that a majority of mutations are slightly deleterious.

The exuberant tail of the peacock is thought to be the result of sexual selection by females. This peacock is an albino; selection against albinos in nature is intense because they are easily spotted by predators or are unsuccessful in competition for mates.

By the definition of fitness, individuals with greater fitness are more likely to contribute offspring to the next generation, while individuals with lesser fitness are more likely to die early or fail to reproduce. As a result, alleles which on average result in greater fitness become more abundant in the next generation, while alleles which generally reduce fitness become rarer. If the selection forces remain the same for many generations, beneficial alleles become more and more abundant, until they dominate the population, while alleles with a lesser fitness disappear. In every generation, new mutations and re-combinations arise spontaneously, producing a new spectrum of phenotypes. Therefore, each new generation will be enriched by the increasing abundance of alleles that contribute to those traits that were favored by selection, enhancing these traits over successive generations.

Some mutations occur in so-called regulatory genes. Changes in these can 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 zygotes. Examples of 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 will favor these phenotypes and the novel trait will spread in the population.

X-ray of the left hand of a ten year old boy with polydactyly.

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 will become 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 selective mating, which result in a reduced gene flow. Selective mating can be the result of 1. Geographic isolation, 2. Behavioral isolation, or 3. Temporal isolation. For example, a change in the physical environment (geographic isolation by an extrinsic barrier) would follow number 1, a change in camouflage for number 2 or a shift in mating times (i.e., one species of deer shifts location and therefore changes its "rut") for number 3.

Over time, these subgroups might diverge radically to become different species, either because of differences in selection pressures on the different subgroups, or because different mutations arise spontaneously in the different populations, or because of founder effects – some potentially beneficial alleles may, by chance, be present in only one or other of two subgroups when they first become separated. A lesser-known mechanism of speciation occurs via hybridization, well-documented in plants and occasionally observed in species-rich groups of animals such as cichlid fishes. Such mechanisms of rapid speciation can reflect a mechanism of evolutionary change known as punctuated equilibrium, which suggests that evolutionary change and particularly speciation typically happens quickly after interrupting long periods of stasis.

Genetic changes within groups result in increasing incompatibility between the genomes of the two subgroups, thus reducing gene flow between the groups. Gene flow will effectively cease when the distinctive mutations characterizing each subgroup become fixed. As few as two mutations can result in speciation: if each mutation has a neutral or positive effect on fitness when they occur separately, but a negative effect when they occur together, then fixation of these genes in the respective subgroups will lead to two reproductively isolated populations. According to the biological species concept, these will be two different species.

Historical development

The modern theory of natural selection derives from the work of Charles Darwin in the nineteenth century.

Pre-Darwinian theories

Several ancient philosophers expressed the idea that nature produces a huge variety of creatures, apparently randomly, and that only those creatures survive that manage to provide for themselves and reproduce successfully; well-known examples include Empedocles and his intellectual successor, Lucretius, while related ideas were later refined by Aristotle. The struggle for existence was later described by Al-Jahiz, who argued that environmental factors influence animals to develop new characteristics to ensure survival.

Abu Rayhan Biruni described the idea of artificial selection and argued that nature works in much the same way. Similar ideas were later expressed by Nasir al-Din Tusi and Ibn Khaldun. Such classical arguments were reintroduced in the 18th century by Pierre Louis Maupertuis and others, including Charles Darwin's grandfather Erasmus Darwin. While

these forerunners had an influence on Darwinism, they later had little influence on the trajectory of evolutionary thought after Charles Darwin.

Until the early 19th century, the prevailing view in Western societies was that differences between individuals of a species were uninteresting departures from their Platonic idealism (or typus) of created kinds. However, the theory of uniformitarianism in geology promoted the idea that simple, weak forces could act continuously over long periods of time to produce radical changes in the Earth's landscape. The success of this theory raised awareness of the vast scale of geological time and made plausible the idea that tiny, virtually imperceptible changes in successive generations could produce consequences on the scale of differences between species.

Early 19th century evolutionists such as Jean Baptiste Lamarck suggested the inheritance of acquired characteristics as a mechanism for evolutionary change; adaptive traits acquired by an organism during its lifetime could be inherited by that organism's progeny, eventually causing transmutation of species. This theory has come to be known as Lamarckism and was an influence on the anti-genetic ideas of the Stalinist Soviet biologist Trofim Lysenko.

Darwin's theory

In 1859, Charles Darwin set out his theory of evolution by natural selection as an explanation for adaptation and speciation. He defined natural selection as the "principle by which each slight variation [of a trait], if useful, is preserved". The concept was simple but powerful: individuals best adapted to their environments are more likely to survive and reproduce. As long as there is some variation between them, there will be an inevitable selection of individuals with the most advantageous variations. If the variations are inherited, then differential reproductive success will lead to a progressive evolution of particular populations of a species, and populations that evolve to be sufficiently different eventually become different species.

Darwin's ideas were inspired by the observations that he had made on the *Beagle* voyage, and by the work of a political economist, the Reverend Thomas Malthus, who in *An Essay on the Principle of Population*, noted that population (if unchecked) increases exponentially whereas the food supply grows only arithmetically; thus inevitable limitations of resources would have demographic implications, leading to a "struggle for existence". When Darwin read Malthus in 1838 he was already primed by his work as a naturalist to appreciate the "struggle for existence" in nature and it struck him that as population outgrew resources, "favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species."

Here is Darwin's own summary of the idea, which can be found in the fourth chapter of the *Origin*:

If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organisation, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection.

Once he had his theory "by which to work", Darwin was meticulous about gathering and refining evidence as his "prime hobby" before making his idea public. He was in the process of writing his "big book" to present his researches when the naturalist Alfred Russel Wallace independently conceived of the principle and described it in an essay he sent to Darwin to forward to Charles Lyell. Lyell and Joseph Dalton Hooker decided (without Wallace's knowledge) to present his essay together with unpublished writings which Darwin had sent to fellow naturalists, and *On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection* was read to the Linnean Society announcing co-discovery of the principle in July 1858. Darwin published a detailed account of his evidence and conclusions in *On the Origin of Species* in 1859. In the 3rd edition of 1861 Darwin acknowledged that others — notably William Charles Wells in 1813, and Patrick Matthew in 1831 — had proposed similar ideas, but had neither developed them nor presented them in notable scientific publications.

Darwin thought of natural selection by analogy to how farmers select crops or livestock for breeding, which he called "artificial selection"; in his early manuscripts he referred to a 'Nature' which would do the selection. At the time, other mechanisms of evolution such as evolution by genetic drift were not yet explicitly formulated, and Darwin believed that selection was likely only part of the story: "I am convinced that [it] has been the main, but not exclusive means of modification." In a letter to Charles Lyell in September 1860, Darwin regretted the use of the term "Natural Selection", preferring the term "Natural Preservation".

For Darwin and his contemporaries, natural selection was essentially synonymous with evolution by natural selection. After the publication of *On the Origin of Species*, educated people generally accepted that evolution had occurred in some form. However, natural selection remained controversial as a mechanism, partly because it was perceived to be too weak to explain the range of observed characteristics of living organisms, and partly because even supporters of evolution balked at its "unguided" and non-progressive nature, a response that has been characterized as the single most significant impediment to the idea's acceptance.

However, some thinkers enthusiastically embraced natural selection; after reading Darwin, Herbert Spencer introduced the term *survival of the fittest*, which became a popular summary of the theory. The fifth edition of *On the Origin of Species* published in 1869 included Spencer's phrase as an alternative to natural selection, with credit given: "But the expression often used by Mr. Herbert Spencer, of the Survival of the Fittest, is more accurate, and is sometimes equally convenient." Although the phrase is still often used by non-biologists, modern biologists avoid it because it is tautological if "fittest" is read to mean "functionally superior" and is applied to individuals rather than considered as an averaged quantity over populations.

Modern evolutionary synthesis

Natural selection relies crucially on the idea of heredity, but it was developed long before the basic concepts of genetics. Although the Austrian monk Gregor Mendel, the father of modern genetics, was a contemporary of Darwin's, his work would lie in obscurity until the early 20th century. Only after the integration of Darwin's theory of evolution with a complex statistical appreciation of Gregor Mendel's 're-discovered' laws of inheritance did natural selection become generally accepted by scientists.

The work of Ronald Fisher (who developed the required mathematical language and The Genetical Theory of Natural Selection), J.B.S. Haldane (who introduced the concept of the "cost" of natural selection), Sewall Wright (who elucidated the nature of selection and adaptation), Theodosius Dobzhansky (who established the idea that mutation, by creating genetic diversity, supplied the raw material for natural selection), William Hamilton (who conceived of kin selection), Ernst Mayr (who recognised the key importance of reproductive isolation for speciation) and many others formed the modern evolutionary synthesis. This synthesis cemented natural selection as the foundation of evolutionary theory, where it remains today.

Impact of the idea

Darwin's ideas, along with those of Adam Smith and Karl Marx, had a profound influence on 19th century thought. Perhaps the most radical claim of the theory of evolution through natural selection is 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 claim inspired some of Darwin's most ardent supporters—and provoked the most profound opposition. The radicalism of natural selection, according to Stephen Jay Gould, lay in its power to "dethrone some of the deepest and most traditional comforts of Western thought". In particular, it challenged long-standing beliefs in such concepts as a special and exalted place for humans in the natural world and a benevolent creator whose intentions were reflected in nature's order and design.

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 into virtually all disciplines, including evolutionary computation, quantum darwinism, evolutionary economics, evolutionary epistemology, evolutionary psychology and cosmological natural selection. This unlimited applicability has been called Universal Darwinism.

Cell and molecular biology

In the 19th century, Wilhelm Roux, a founder of modern embryology, wrote a book entitled « Der Kampf der Teile 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, stochasticity 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 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". Interpretation of natural selection as necessarily 'progressive', leading to increasing 'advances' in intelligence and civilisation, was used as a justification for colonialism and policies of eugenics, as well as broader sociopolitical positions now described as Social Darwinism. Konrad Lorenz won the Nobel Prize in Physiology or Medicine in 1973 for his analysis of animal behavior in terms of the role of natural selection (particularly group selection). However, in Germany in 1940, in writings that he subsequently disowned, he 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 that are 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 evolutionary psychology, a field that attempts to explain features of human psychology in terms of adaptation to the ancestral environment. The most prominent such example, notably advanced in the early work of Noam Chomsky and later by Steven Pinker, is the hypothesis that the human brain is adapted to acquire the grammatical rules of natural language. Other aspects of human behavior and social structures, from specific cultural norms such as incest avoidance to broader patterns such as gender roles, have been hypothesized 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 and subsequently expanded upon by philosophers such as Daniel Dennett as explanations for complex cultural activities, including human consciousness. Extensions of the theory of natural selection to such a wide range of cultural phenomena have been distinctly controversial and are not widely accepted.

Information and systems theory

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

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 optimization algorithms known as genetic algorithms, pioneered by John 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 solution landscape is very rough or has many local minima.

Genetic basis of natural selection

The idea of natural selection predates the understanding of genetics. We now have a much better idea of the biology underlying heritability, which is the basis of natural selection.

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. Often, natural selection acts on specific traits of an individual, and the terms phenotype and genotype are used narrowly to indicate these specific traits.

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 phenotypic traits. A typical example is that certain combinations of genes for eye color in humans which, for instance, give rise to the phenotype of blue eyes. (On the other hand, when all the organisms in a population share the same allele for a particular trait, and this state is stable over time, the allele is said to be *fixed* in that population.)

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 will alter 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 selection occurs when a certain allele has a greater fitness than others, resulting in an increase of its frequency. This process can continue until the allele is fixed and the entire population shares the fitter phenotype. It is directional selection that is illustrated in the antibiotic resistance example above.

Far more common is stabilizing selection (which is commonly **confused** with *purifying 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 results in functional genetic features, such as protein-coding genes or regulatory sequences, being conserved over time due to selective pressure against deleterious variants.

Finally, a number of forms of balancing selection exist, which do not result in fixation, but maintain an allele at intermediate frequencies in a population. This can occur in diploid species (that is, those that have two pairs of chromosomes) when heterozygote individuals, who have different alleles on each chromosome at a single genetic locus, have a higher fitness than homozygote individuals that have two of the same alleles. This is called heterozygote advantage or overdominance, of which the best-known example is the malarial resistance observed in heterozygous humans who carry only one copy of the gene for sickle cell anemia. Maintenance of allelic variation can also occur through disruptive or diversifying selection, which favors genotypes that depart from the average in either direction (that is, the opposite of overdominance), 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 and genetic variation

A portion of all genetic variation is functionally neutral in that it produces no phenotypic effect or significant difference in fitness; the hypothesis that this variation accounts for a large fraction of observed genetic diversity is known as the neutral theory of molecular evolution and was originated by Motoo Kimura. 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 will be higher than at sites where variation does influence fitness. However, after a period with no new mutation, the genetic variation at these sites will be eliminated due to genetic drift.

Mutation selection balance

Natural selection results in the reduction of genetic variation through the elimination of maladapted individuals and consequently of 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 unfavorable the mutation proves to be. Consequently, changes in the mutation rate or the selection pressure will result in a different mutation-selection balance.

Genetic linkage

Genetic linkage occurs when the loci of two alleles are *linked*, or in close proximity to each other on the chromosome. During the formation of gametes, recombination of the genetic material results in reshuffling of the alleles. However, the chance that such a reshuffle occurs between two alleles depends on the distance between those alleles; the closer the alleles are to each other, the less likely it is that such a reshuffle will occur. Consequently, when selection targets one allele, this automatically results in selection of the other allele as well; through this mechanism, selection can have a strong influence on patterns of variation in the genome.

Selective sweeps occur when an allele becomes more common in a population as a result of positive selection. As the prevalence of one allele increases, linked alleles can also become more common, whether they are neutral or even slightly deleterious. This is called *genetic hitchhiking*. A strong selective sweep results in a region of the genome where the positively selected haplotype (the allele and its neighbours) are essentially the only ones that exist in the population.

Whether a selective sweep has occurred or not can be investigated by measuring linkage disequilibrium, or whether a given haplotype is overrepresented in the population. Normally, genetic recombination results in a reshuffling of the different alleles within a haplotype, and none of the haplotypes will dominate the population. However, during a selective sweep, selection for a specific allele will also result in selection of neighbouring alleles. Therefore, the presence of a block of strong linkage disequilibrium might indicate that there has been a 'recent' selective sweep near the center of the block, and this can be used to identify sites recently under selection.

Background selection is the opposite of a selective sweep. If a specific site experiences strong and persistent purifying selection, linked variation will tend 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.

Chapter 5

Speciation

Speciation is the evolutionary process by which new biological species arise. The biologist Orator F. Cook seems to have been the first to coin the term 'speciation' for the splitting of lineages or 'cladogenesis,' as opposed to 'anagenesis' or 'phyletic evolution' occurring within lineages. Whether genetic drift is a minor or major contributor to speciation is the subject matter of much ongoing discussion.

There are four geographic modes of speciation in nature, based on the extent to which speciating populations are geographically isolated from one another: allopatric, peripatric, parapatric, and sympatric. Speciation may also be induced artificially, through animal husbandry or laboratory experiments. Observed examples of each kind of speciation are provided throughout.

Natural speciation

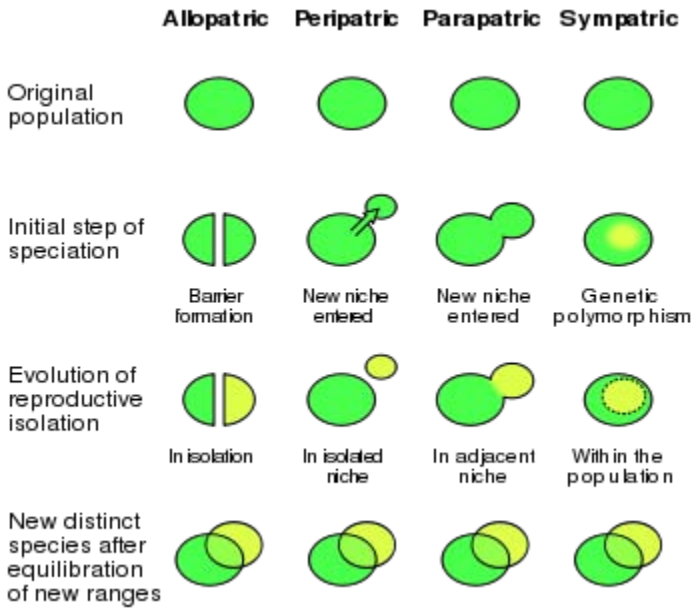
All forms of natural speciation have taken place over the course of evolution; however it still remains a subject of debate as to the relative importance of each mechanism in driving biodiversity.

The three-spined stickleback (*Gasterosteus aculeatus*)

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

There is debate as to the rate at which speciation events occur over geologic time. While some evolutionary biologists claim that speciation events have remained relatively constant over time, some palaeontologists such as Niles Eldredge and Stephen Jay Gould have argued that species usually remain unchanged over long stretches of time, and that speciation occurs only over relatively brief intervals, a view known as *punctuated equilibrium*.

Allopatric



Comparison of allopatric, peripatric, parapatric and sympatric speciation.

During allopatric speciation, a population splits into two geographically isolated populations (for example, by habitat fragmentation due to geographical change such as mountain building or social change such as emigration). The isolated populations then undergo genotypic and/or phenotypic divergence as: (a) they become subjected to dissimilar selective pressures; (b) they independently undergo genetic drift; (c) different mutations arise in the two populations. When the populations come back into contact, they have evolved such that they are reproductively isolated and are no longer capable of exchanging genes.

Observed instances

Island genetics, the tendency of small, isolated genetic pools to produce unusual traits, has been observed in many circumstances, including insular dwarfism and the radical changes among certain famous island chains, for example on Komodo. The Galápagos islands are particularly famous for their influence on Charles Darwin. During his five weeks there he heard that Galápagos tortoises could be identified by island, and noticed that Mockingbirds differed from one island to another, but it was only nine months later that he reflected that such facts could show that species were changeable. When he returned to England, his speculation on evolution deepened after experts informed him that these were separate species, not just varieties, and famously that other differing Galápagos birds were all species of finches. Though the finches were less important for Darwin, more recent research has shown the birds now known as Darwin's finches to be a classic case of adaptive evolutionary radiation.

Peripatric

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

Observed instances

- Mayr bird fauna
- The Australian bird *Petroica multicolor*
- Reproductive isolation occurs in populations of *Drosophila* subject to population bottlenecking

The London Underground mosquito is a variant of the mosquito *Culex pipiens* that entered in the London Underground in the nineteenth century. Evidence for its speciation include genetic divergence, behavioral differences, and difficulty in mating.

Parapatric

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

Ecologists refer to parapatric and peripatric speciation in terms of ecological niches. A niche must be available in order for a new species to be successful.

Observed instances

- Ring species
  - The *Larus* gulls form a ring species around the North Pole.
  - The *Ensatina* salamanders, which form a ring round the Central Valley in California.
  - The Greenish Warbler (*Phylloscopus trochiloides*), around the Himalayas.
- the grass *Anthoxanthum* has been known to undergo parapatric speciation in such cases as mine contamination of an area.

Sympatric

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

In sympatric speciation, species diverge while inhabiting the same place. Often-cited examples of sympatric speciation are found in insects that become dependent on different host plants in the same area. However, the existence of sympatric speciation as a mechanism of speciation is still hotly contested. People have argued that the evidences of sympatric speciation are in fact examples of micro-allopatric, or heteropatric speciation. The most widely accepted example of sympatric speciation is that of the cichlids of Lake Nabugabo in East Africa, which is thought to be due to **sexual selection**.

Until recently, there has a been a dearth of strong evidence that supports this form of speciation, with a general feeling that interbreeding would soon eliminate any genetic differences that might appear. But there has been at least one recent study that suggests that sympatric speciation has occurred in Tennessee cave salamanders.

The three-spined sticklebacks, freshwater fishes, that have been studied by Dolph Schluter (who received his Ph.D. for his work on Darwin's finches with Peter J. Grant) and his current colleagues in British Columbia, were once thought to provide an intriguing example best explained by sympatric speciation. Schluter and colleagues found:

- Two different species of three-spined sticklebacks in each of five different lakes
  - a large benthic species with a large mouth that feeds on large prey in the littoral zone
  - a smaller limnetic species — with a smaller mouth — that feeds on the small plankton in open water
- DNA analysis indicates that each lake was colonized independently, presumably by a marine ancestor, after the last ice age
- DNA analysis also shows that the two species in each lake are more closely related to each other than they are to any of the species in the other lakes
- The two species in each lake are reproductively isolated; neither mates with the other.

- However, aquarium tests showed:
    - the benthic species from one lake will spawn with the benthic species from the other lakes and
    - likewise the limnetic species from the different lakes will spawn with each other.
    - These benthic and limnetic species even display their mating preferences when presented with sticklebacks from Japanese lakes; that is, a Canadian benthic prefers a Japanese benthic over its close limnetic cousin from its own lake.
- Their conclusion: in each lake, what began as a single population faced such competition for limited resources that:
    - disruptive selection — competition favoring fishes at either extreme of body size and mouth size over those nearer the mean — coupled with:
    - assortative mating — each size preferred mates like it — favored a divergence into two subpopulations exploiting different food in different parts of the lake.
    - The fact that this pattern of speciation occurred the same way on three separate occasions suggests strongly that ecological factors in a sympatric population can cause speciation.

However, the DNA evidence cited above is from mitochondrial DNA (mtDNA), which can often move easily between closely related species ("introgression") when they hybridize. A more recent study, using genetic markers from the nuclear genome, shows that limnetic forms in different lakes are more closely related to each other (and to marine lineages) than to benthic forms in the same lake. The three-spine stickleback is now usually considered an example of "double invasion" (a form of allopatric speciation) in which repeated invasions of marine forms have subsequently differentiated into benthic and limnetic forms. The three-spine stickleback provides an example of how molecular biogeographic studies that rely solely on mtDNA can be misleading, and that consideration of the genealogical history of alleles from multiple unlinked markers (i.e. nuclear genes) is necessary to infer speciation histories.

Sympatric speciation driven by ecological factors may also account for the extraordinary diversity of crustaceans living in the depths of Siberia's Lake Baikal.

Speciation via polyploidization

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. However, 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.

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 sympatric speciation is occurring. The emergence of the new hawthorn fly is an example of evolution in progress.

Speciation via hybrid formation

See Hybrid speciation section under the Genetics heading below.

Reinforcement (Wallace effect)

Reinforcement is the process by which natural selection increases reproductive isolation. It may occur after two populations of the same species are separated and then come back into contact. If their reproductive isolation was complete, then they will have already developed into two separate incompatible species. If their reproductive isolation is incomplete, then further mating between the populations will produce hybrids, which may or may not be fertile. If the hybrids are infertile, or fertile but less fit than their ancestors, then there will be no further reproductive isolation and speciation has essentially occurred (e.g., as in horses and donkeys.) The reasoning behind this is that if the parents of the hybrid offspring each have naturally selected traits for their own certain environments, the hybrid offspring will bear traits from both, therefore would not fit either ecological niche as well as either parent. The low fitness of the hybrids would cause selection to favor assortative mating, which would control hybridization. This is sometimes called the Wallace effect after the evolutionary biologist Alfred Russel Wallace who suggested in the late 19th century that it might be an important factor in speciation. If the hybrid offspring are more fit than their ancestors, then the populations will merge back into the same species within the area they are in contact.

Reinforcement is required for both parapatric and sympatric speciation. Without reinforcement, the geographic area of contact between different forms of the same species, called their "hybrid zone," will not develop into a boundary between the different species. Hybrid zones are regions where diverged populations meet and interbreed.

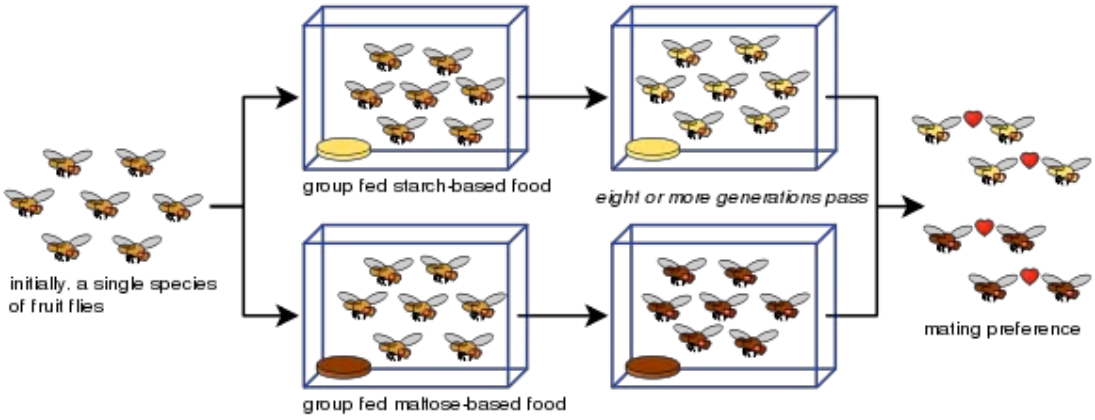
Hybrid offspring are very common in these regions, which are usually created by diverged species coming into secondary contact. Without reinforcement the two species would have uncontrollable inbreeding. Reinforcement may be induced in artificial selection experiments as described below.

Artificial speciation

New species have been created by domesticated animal husbandry, but the initial dates and methods of the initiation of such species are not clear. For example, domestic sheep were created by hybridisation, and no longer produce viable offspring with *Ovis orientalis*, one species from which they are descended. Domestic cattle, on the other hand, can be considered the same species as several varieties of wild ox, gaur, yak, etc., as they readily produce fertile offspring with them.

The best-documented creations of new species in the laboratory were performed in the late 1980s. William Rice and G.W. Salt bred fruit flies, *Drosophila melanogaster,* using a maze with three different choices of habitat such as light/dark and wet/dry. Each generation was placed into the maze, and the groups of flies that came out of two of the eight exits were set apart to breed with each other in their respective groups. After thirty-five generations, the two groups and their offspring were isolated reproductively because of their strong habitat preferences: they mated only within the areas they preferred, and so did not mate with flies that preferred the other areas. The history of such attempts is described in Rice and Hostert (1993).

Diane Dodd was also able to show how reproductive isolation can develop from mating preferences in *Drosophila pseudoobscura* fruit flies after only eight generations using different food types, starch and maltose.



Dodd's experiment has been easy for many others to replicate, including with other kinds of fruit flies and foods.

Genetics

Few speciation genes have been found. They usually involve the reinforcement process of late stages of speciation. In 2008 a speciation gene causing reproductive isolation was reported. It causes hybrid sterility between related subspecies.

Hybrid speciation

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

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

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

Gene transposition as a cause

Theodosius Dobzhansky, who studied fruit flies in the early days of genetic research in 1930s, speculated that parts of chromosomes that switch from one location to another might cause a species to split into two different species. He mapped out how it might be possible for sections of chromosomes to relocate themselves in a genome. Those mobile sections can cause sterility in inter-species hybrids, which can act as a speciation pressure. In theory, his idea was sound, but scientists long debated whether it actually happened in nature. Eventually a competing theory involving the gradual accumulation of mutations was shown to occur in nature so often that geneticists largely dismissed the moving gene hypothesis.

However, 2006 research shows that jumping of a gene from one chromosome to another can contribute to the birth of new species. This validates the reproductive isolation mechanism, a key component of speciation.

Interspersed repeats

Interspersed repetitive DNA sequences function as isolating mechanisms. These repeats protect newly evolving gene sequences from being overwritten by gene conversion, due to the creation of non-homologies between otherwise homologous DNA sequences. The non-homologies create barriers to gene conversion. This barrier allows nascent novel genes to evolve without being overwritten by the progenitors of these genes. This uncoupling allows the evolution of new genes, both within gene families and also allelic forms of a gene. The importance is that this allows the splitting of a gene pool without requiring physical isolation of the organisms harboring those gene sequences.

Human speciation

Humans have genetic similarities with chimpanzees and gorillas, suggesting common ancestors. Analysis of genetic drift and recombination using a Markov model suggests humans and chimpanzees speciated apart 4.1 million years ago.

Chapter 6

Lamarckism

Lamarckism (or **Lamarckian inheritance**) is the idea that an organism can pass on characteristics that it acquired during its lifetime to its offspring (also known as heritability of acquired characteristics or soft inheritance). It is named after the French biologist Jean-Baptiste Lamarck (1744–1829), who incorporated the action of soft inheritance into his evolutionary theories. He is often incorrectly cited as the founder of soft inheritance, which proposes that individual efforts during the lifetime of the organisms were the main mechanism driving species to adaptation, as they supposedly would acquire adaptive changes and pass them on to offspring.

After publication of Charles Darwin's theory of natural selection, the importance of individual efforts in the generation of adaptation was considerably diminished. Later, Mendelian genetics supplanted the notion of inheritance of acquired traits, eventually leading to the development of the modern evolutionary synthesis, and the general abandonment of the Lamarckian theory of evolution in biology. Despite this abandonment, interest in Lamarckism has recently increased, as several studies in the field of epigenetics have highlighted the possible inheritance of behavioral traits acquired by the previous generation. In a wider context, soft inheritance is of use when examining the evolution of cultures and ideas, and is related to the theory of Memetics.

History

Jean-Baptiste Lamarck

Between 1794 and 1796 Erasmus Darwin wrote *Zoönomia* suggesting "that all warm-blooded animals have arisen from one living filament... with the power of acquiring new parts" in response to stimuli, with each round of "improvements" being inherited by successive generations. Subsequently Jean-Baptiste Lamarck repeated in his *Philosophie Zoologique* of 1809 the folk wisdom that characteristics which were "needed" were acquired (or diminished) during the lifetime of an organism then passed on to the offspring. He incorporated this mechanism into his thoughts on evolution, seeing it as resulting in the adaptation of life to local environments.

Lamarck founded a school of French *Transformationism* which included Étienne Geoffroy Saint-Hilaire, and which corresponded with a radical British school of anatomy based in the extramural anatomy schools in Edinburgh which included the surgeon Robert Knox and the comparative anatomist Robert Edmund Grant. In addition, the Regius Professor of Natural History, Robert Jameson, was the probable author of an anonymous paper in 1826 praising "Mr. Lamarck" for explaining how the higher animals had "evolved" from the "simplest worms" – this was the first use of the word "evolved" in a modern sense. As a young student, Charles Darwin was tutored by Grant, and worked with him on marine creatures.

The *Vestiges of the Natural History of Creation*, authored by Robert Chambers in St Andrews and published anonymously in England in 1844, proposed a theory which combined radical phrenology with Lamarckism, causing political controversy for its radicalism and unorthodoxy, but exciting popular interest and preparing a huge and prosperous audience for Darwin.

Darwin's *Origin of Species* proposed natural selection as the main mechanism for development of species, but did not rule out a variant of Lamarckism as a supplementary mechanism. Darwin called his Lamarckian hypothesis Pangenesis, and explained it in the final chapter of his book *Variation in Plants and Animals under Domestication*, after describing numerous examples to demonstrate what he considered to be the inheritance of acquired characteristics. Pangenesis, which he emphasised was a hypothesis, was based on the idea that somatic cells would, in response to environmental stimulation (use and disuse), throw off 'gemmules' or 'pangenes' which travelled around the body (though not necessarily in the bloodstream). These pangenes were microscopic particles that supposedly contained information about the characteristics of their parent cell, and Darwin believed that they eventually accumulated in the germ cells where they could pass on to the next generation the newly acquired characteristics of the parents. Darwin's half-cousin, Francis Galton carried out experiments on rabbits, with Darwin's cooperation, in which he transfused the blood of one variety of rabbit into another variety in the expectation that its offspring would show some characteristics of the first. They did not, and Galton declared that he had disproved Darwin's hypothesis of Pangenesis, but Darwin objected, in a letter to *Nature*, that he had done nothing of the sort, since he had never mentioned blood in his writings. He pointed out that he regarded Pangenesis as occurring in Protozoa and plants, which have no blood. With the development of the modern synthesis of the theory of evolution and a lack of evidence for either a mechanism or even the heritability of acquired characteristics, Lamarckism largely fell from favor.

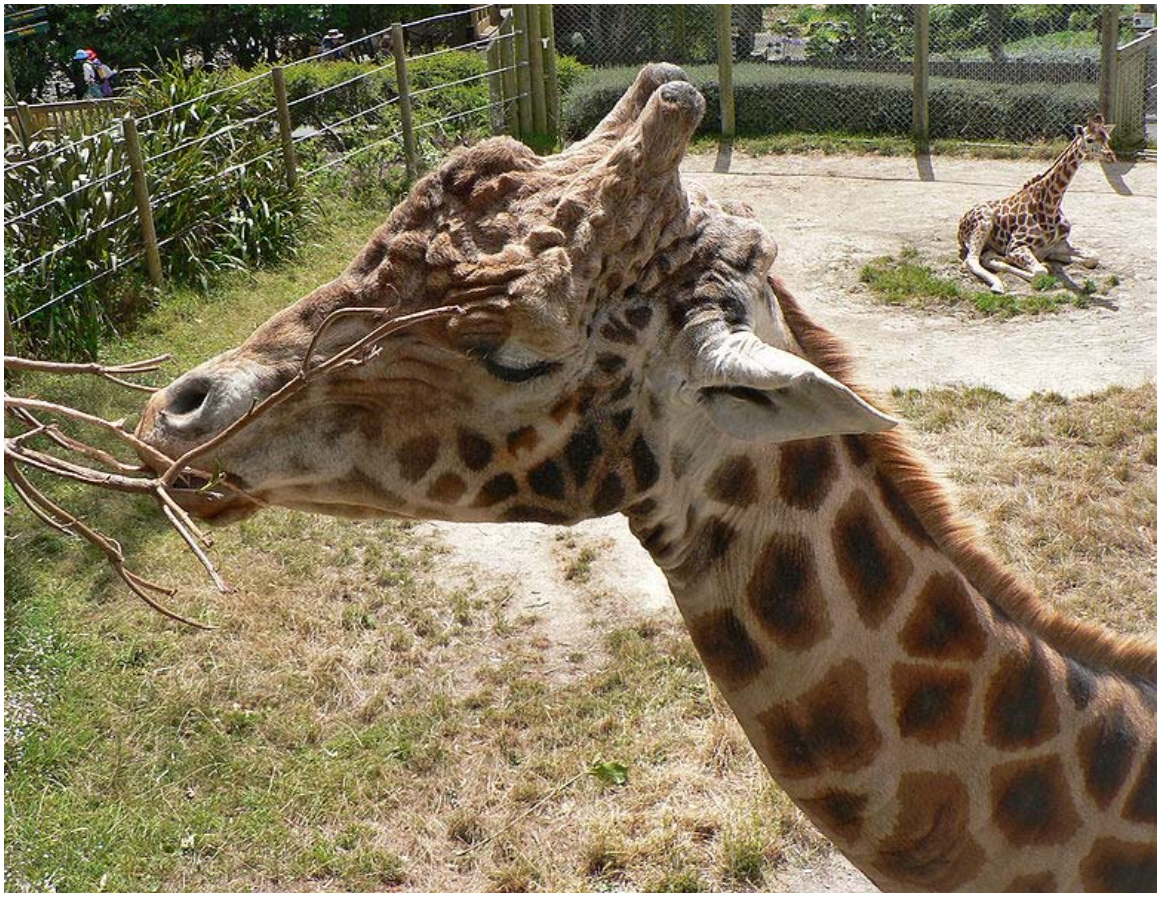
In the 1920s, experiments by Paul Kammerer on amphibians, particularly the midwife toad, appeared to find evidence supporting Lamarckism, but his specimens with supposedly-acquired black foot-pads were found to have been tampered with. In *The Case of the Midwife Toad* Arthur Koestler surmised that the specimens had been faked by a Nazi sympathiser to discredit Kammerer for his political views.

A form of Lamarckism was revived in the Soviet Union of the 1930s when Trofim Lysenko promoted Lysenkoism which suited the ideological opposition of Joseph Stalin to Genetics. This ideologically driven research influenced Soviet agricultural policy which in turn was later blamed for crop failures.

Since 1988 certain scientists have produced work proposing that Lamarckism could apply to single celled organisms. A version of Lamarckian acquisition in higher order animals is still posited in certain branches of psychology, as, for example, in the Jungian racial memory.

Neo-Lamarckism is a theory of inheritance based on a modification and extension of Lamarckism, essentially maintaining the principle that genetic changes can be influenced and directed by environmental factors.

Lamarck's theory



The evolution of necks is often used as the example in explanations of Lamarckism.

The identification of Lamarckism with the inheritance of acquired characteristics is regarded by some as an artifact of the subsequent history of evolutionary thought, repeated in textbooks without analysis. Stephen Jay Gould wrote that late 19th century evolutionists "*re-read Lamarck, cast aside the guts of it ... and elevated one aspect of the mechanics - inheritance of acquired characters - to a central focus it never had for Lamarck himself*." He argued that "*the restriction of "Lamarckism" to this relatively small and non-distinctive corner of Lamarck's thought must be labelled as more than a misnomer, and truly a discredit to the memory of a man and his much more comprehensive system*". Gould advocated defining "Lamarckism" more broadly, in line with Lamarck's overall evolutionary theory.

Lamarck incorporated two ideas into his theory of evolution, in his day considered to be generally true:

1. Use and disuse – Individuals lose characteristics they do not require (or use) and develop characteristics that are useful.
2. Inheritance of acquired traits – Individuals inherit the traits of their ancestors.

Examples of what is traditionally called "Lamarckism" would include:

- Giraffes stretching their necks to reach leaves high in trees (especially Acacias), strengthen and gradually lengthen their necks. These giraffes have offspring with slightly longer necks (also known as "soft inheritance").
- A blacksmith, through his work, strengthens the muscles in his arms. His sons will have similar muscular development when they mature.

With this in mind, Lamarck has been credited in some textbooks and popular culture with developing two laws:

1. *In every animal which has not passed the limit of its development, a more frequent and continuous use of any organ gradually strengthens, develops and enlarges that organ, and gives it a power proportional to the length of time it has been so used; while the permanent disuse of any organ imperceptibly weakens and deteriorates it, and progressively diminishes its functional capacity, until it finally disappears.*
2. *All the acquisitions or losses wrought by nature on individuals, through the influence of the environment in which their race has long been placed, and hence through the influence of the predominant use or permanent disuse of any organ; all these are preserved by reproduction to the new individuals which arise, provided that the acquired modifications are common to both sexes, or at least to the individuals which produce the young.*

In essence, a change in the environment brings about change in "needs" (*besoins*), resulting in change in behavior, bringing change in organ usage and development, bringing change in form over time — and thus the gradual transmutation of the species.

However, as historians of science such as Michael Ghiselin and Stephen Jay Gould have pointed out, none of these views were original to Lamarck. On the contrary, Lamarck's contribution was a systematic theoretical framework for understanding evolution. He saw evolution as comprising two processes;

1. *Le pouvoir de la vie (a complexifying force)* - in which the natural, alchemical movements of fluids would etch out organs from tissues, leading to ever more complex construction regardless of the organ's use or disuse. This would drive organisms from simple to complex forms.
2. *L'influence des circonstances (an adaptive force)* - in which the use and disuse of characters led organisms to become more adapted to their environment. This would take organisms sideways off the path from simple to complex, specialising them for their environment.

Current views

Interest in Lamarckism has recently increased, as several studies in the field of epigenetics have highlighted the possible inheritance of behavioral traits acquired by the

previous generation. A recent such study examined foraging behavior in chickens as a function of stress, concluding:

Our findings suggest that unpredictable food access caused seemingly adaptive responses in feeding behavior, which may have been transmitted to the offspring by means of epigenetic mechanisms, including regulation of immune genes. This may have prepared the offspring for coping with an unpredictable environment.... Transmissions of information across generations which does not involve traditional inheritance of DNA-sequence alleles is often referred to as soft inheritance or 'Lamarckian inheritance'.

The evolution of acquired characteristics has also been shown in human populations who have experienced starvation, resulting in altered gene function in both the starved population and their offspring. The process of DNA methylation is thought to be behind such changes.

In October 2010, further evidence linking food intake to traits inherited by the offspring were shown in a study of rats conducted by several Australian universities. The study strongly suggested that fathers can transfer a propensity for obesity to their daughters as a result of the fathers' food intake, **and not their genetics** (or specific genes), prior to the conception of the daughter. A "paternal high-fat diet" was shown to cause cell dysfunction in the daughter, which in turn led to obesity for the daughter.

Several historians have argued that Lamarck's name is linked somewhat unfairly to the theory that has come to bear his name, and that Lamarck deserves credit for being an influential early proponent of the *concept* of biological evolution, far more than for the *mechanism* of evolution, in which he simply followed the accepted wisdom of his time. Lamarck died 30 years before the first publication of Charles Darwin's *Origin of Species*. According to Stephen Jay Gould, if Lamarck had been aware of Darwin's proposed mechanism of natural selection, there is no reason to assume he would not have accepted it as a more likely alternative to his own mechanism. Note also that Darwin, like Lamarck, lacked a plausible alternative mechanism of inheritance - the particulate nature of inheritance was only observed by Gregor Mendel somewhat later, and published in 1866. Its full significance was not appreciated until the Modern evolutionary synthesis in the early 1920s. An important point in its favour at the time was that Lamarck's theory contained a mechanism describing how variation is maintained, which Darwin’s own theory lacked.

Several recent studies, one conducted by researchers at MIT and another by researchers at the Tufts University School of Medicine, have rekindled the debate once again. As reported in MIT's Technology Review in February 2009, "The effects of an animal's environment during adolescence can be passed down to future offspring ... The findings provide support for a 200-year-old theory of evolution that has been largely dismissed: Lamarckian evolution, which states that acquired characteristics can be passed on to offspring."

Neo-Lamarckism

Unlike neo-Darwinism, the term neo-Lamarckism refers more to a loose grouping of largely heterodox theories and mechanisms that emerged after Lamarck's time, than to any coherent body of theoretical work.

In the 1920s, Harvard University researcher William McDougall studied the abilities of rats to correctly solve mazes. He found that offspring of rats that had learned the maze were able to run it faster. The first rats would get it wrong 165 times before being able to run it perfectly each time, but after a few generations it was down to 20. McDougall attributed this to some sort of Lamarckian evolutionary process. Oscar Werner Tiegs and Wilfred Eade Agar later showed McDougall's results to be incorrect, caused by poor experimental controls.

At around the same time, Ivan Pavlov, who was also a Lamarckist, claimed to have observed a similar phenomenon in animals being subject to conditioned reflex experiments. He claimed that with each generation, the animals became easier to condition. However, Pavlov never suggested a mechanism to explain these observations.

Soma to germ-line feedback

In the 1970s the immunologist Ted Steele, formerly of the University of Wollongong, and colleagues, proposed a neo-Lamarckian mechanism to try to explain why homologous DNA sequences from the VDJ gene regions of parent mice were found in their germ cells and seemed to persist in the offspring for a few generations. The mechanism involved the somatic selection and clonal amplification of newly acquired antibody gene sequences that were generated via somatic hyper-mutation in B-cells. The mRNA products of these somatically novel genes were captured by retroviruses endogenous to the B-cells and were then transported through the blood stream where they could breach the soma-germ barrier and retrofect (reverse transcribe) the newly acquired genes into the cells of the germ line. Although Steele was advocating this theory for the better part of two decades, little more than indirect evidence was ever acquired to support it. An interesting attribute of this idea is that it strongly resembles Darwin's own theory of pangenesis, except in the soma to germ line feedback theory, pangenes are replaced with realistic retroviruses.

Science philosopher Ross Honeywill extended Steele's work by proposing Meta-Lamarckism, which he justifies as follows:

The real issue is whether a modern, well-supported Lamarckian theory can be devised, consistent with well-documented parts of modern molecular genetics, and be able to be articulated with a surviving core of Darwinian natural selection: a kind of Meta-Lamarckism that combines the best of both Darwin and Lamarck [...] Steele identified RNA as the critical transcription vehicle because unlike DNA, it was the medium that was out there in contact with what was going on in the body. It was the obedient servant that knew the secret language, the secret handshake. What a breakthrough it was to

discover from Lamarck via Steele that RNA could take vital changes back to the DNA for generational improvements. But imagine what it means if the RNA is capable of carrying its own information through generations; imagine the Meta-Lamarckian consequences and opportunities written all over these discoveries.

Epigenetic inheritance

Forms of 'soft' or epigenetic inheritance within organisms have been suggested as neo-Lamarckian in nature by such scientists as Eva Jablonka and Marion J. Lamb. In addition to 'hard' or genetic inheritance, involving the duplication of genetic material and its segregation during meiosis, there are other hereditary elements that pass into the germ cells also. These include things like methylation patterns in DNA and chromatin marks, both of which regulate the activity of genes. These are considered "Lamarckian" in the sense that they are responsive to environmental stimuli and can differentially affect gene expression adaptively, with phenotypic results that can persist for many generations in certain organisms. Although the reality of epigenetic inheritance is not doubted (as many experiments have validated it), its significance to the evolutionary process is uncertain. Most neo-Darwinians consider epigenetic inheritance mechanisms to be little more than a specialized form of phenotypic plasticity, with no potential to introduce evolutionary novelty into a species lineage.

Lamarckism and single-celled organisms

While Lamarckism has been discredited as an evolutionary influence for larger lifeforms, some scientists controversially argue that it can be observed among microorganisms. Whether such mutations are directed or not also remains in contention.

In 1988, John Cairns at the Radcliffe Infirmary in Oxford, England, and a group of other scientists renewed the Lamarckian controversy (which at that point had been a dead debate for many years). The group took a mutated strain of *E. coli* that was unable to consume the sugar lactose and placed it in an environment where lactose was the only food source. They observed over time that mutations occurred within the colony at a rate that suggested the bacteria were overcoming their handicap by altering their own genes. Cairns, among others, dubbed the process adaptive mutation.

If bacteria that had overcome their own inability to consume lactose passed on this "learned" trait to future generations, it could be argued as a form of Lamarckism; though Cairns later chose to distance himself from such a position. More typically, it might be viewed as a form of ontogenic evolution.

There has been some research into Lamarckism and prions. A group of researchers, for example, discovered that in yeast cells containing a specific prion protein Sup35, the yeast were able to gain new genetic material, some of which gave them new abilities such as resistance to a particular herbicide. When the researchers crossed the yeast cells with cells not containing the prion, the trait reappeared in some of the resulting offspring, indicating that some information indeed was passed down, though whether or not the

information is genetic is debatable: trace prion amounts in the cells may be passed to their offspring, giving the appearance of a new genetic trait where there is none.

Finally, there is growing evidence that cells can activate low-fidelity DNA polymerases in times of stress to induce mutations. While this does not directly confer advantage to the organism on the organismal level, it makes sense at the gene-evolution level. While the acquisition of new genetic traits is random, and selection remains Darwinian, the active process of identifying the necessity to mutate is considered to be Lamarckian.

Lamarckism and societal change

Jean Molino (2000) has proposed that Lamarckian evolution may be accurately applied to cultural evolution. This was also previously suggested by Peter Medawar (1959) and Conrad Waddington (1961). K. N. Laland and colleagues have recently suggested that human culture can be looked upon as an ecological niche like phenomena, where the effects of cultural niche construction are transmissible from one generation to the next. One interpretation of the Meme theory is that memes are both Darwinian and Lamarckian in nature, as in addition to being subject to selection pressures based on their ability to differentially influence Human minds, memes can be modified and the effects of that modification passed on. Richard Dawkins notes (in Blackmore 2000: The Meme machine, page 13), that Memes can be copied in a Lamarckian way (copying of the product) or in a Weismann-type evolutionary way (copying of the instruction) which is much more resistant against changes.

Chapter 7

Orthogenesis

Orthogenesis, **orthogenetic evolution**, **progressive evolution** or **autogenesis**, is the hypothesis that life has an innate tendency to move in an unilinear fashion due to some internal or external "driving force". The hypothesis is based on essentialism and cosmic teleology and proposes an intrinsic drive which slowly transforms species. George Gaylord Simpson (1953) in an attack on orthogenesis called this mechanism "the mysterious inner force". Classic proponents of orthogenesis have rejected the theory of natural selection as the organising mechanism in evolution, and theories of speciation for a rectilinear model of guided evolution acting on discrete species with "essences". The term *orthogenesis* was popularised by Theodor Eimer, though many of the ideas are much older (Bateson 1909).

No Goal

Orthogenesis does not postulate a "goal" for evolution. Though it proceeds in a linear fashion driven by some internal mechanism, it does not have a goal.

Many sources mix this heterodox view of evolution with another—- that evolution is proceeding to some long term or ultimate goal; the result are definitions that state "orthogenesis proposes that evolution moves in a unilinear fashion towards a perfect goal". While it is true that early and famous examples of orthogenesis often conflated these two ideas (e.g. Jean-Baptiste Lamarck's theory of evolution), it is important to recognize that these are in fact two separate ideas that are rejected by mainstream science; the latter idea of goal-oriented evolution is better understood as a form of teleology.

The distinction can be seen when we recognize that orthogenesis is inherent in the theories of German biologist Ernst Haeckel and American paleontologist Richard Swann Lull. Both scientists proposed mechanisms whereby evolution proceeded in unilinear fashion, but neither saw goals (instead they made pseudo-scientific appeals to unknown genetic driving processes).

This is important because similar flaws occur recurrently at the fringes of science, typically taking the form of mysterious molecular drives that supposedly are pushing phenotypic evolution in certain directions or forcing the formation of new species.

Origins

The orthogenesis hypothesis had a significant following in the 19th century when a number of evolutionary mechanisms, such as Lamarckism, were being proposed. Jean-Baptiste Lamarck himself accepted the idea, and it had a central role in his theory of inheritance of acquired characteristics, the hypothesised mechanism of which resembled the "mysterious inner force" of orthogenesis. Other proponents of orthogenesis included Leo Berg, philosopher Henri Bergson and, for a time, the paleontologist Henry Fairfield Osborn. Orthogenesis was particularly accepted by paleontologists who saw in their fossils a directional change, and in invertebrate paleontology thought there was a gradual and constant directional change. Those who accepted orthogenesis in this way, however, did not necessarily accept that the mechanism that drove orthogenesis was teleological. In fact, Darwin himself rarely used the term "evolution" now so commonly used to describe his theory, because in Darwin's time, evolution usually was associated with some sort of progressive process like orthogenesis, and this had been common usage since at least 1647.

Comparison of Theories

Comparison of different theories of evolution

	Darwinism	**Orthogenesis**	**Lamarckism**
Mechanism	Short-sighted Natural Selection sorting random genetic variation, no other guidance or aim. Selected traits are adaptive, i.e. have some survival value.	Intrinsic drive towards perfection; natural selection unimportant. Characters produced may be totally *non-adaptive,* i.e. have no survival value.	Intrinsic drive towards perfection and inheritance of acquired characteristics (both are Lamarckian principles); natural selection adopted by some in latter years.
Common descent	Yes, new species coming into existence by speciation events.	No, speciation rejected or considered unimportant in long term trends; spontaneous generation of new species resulting in parallel evolution.	Depends upon source quoted. Signs that species shared a common ancestor were detected before Darwin, but in absence of a mechanism some still rejected the idea.
Status	Prevailing in modified	Refuted by Charles	Declined after the

	form as modern evolutionary synthesis.	Darwin's *Origin of Species* and the modern evolutionary synthesis.	*Origin*, though the mechanism was not refuted until the modern evolutionary synthesis in which it was established that the mechanism does not exist.

Collapse of the hypothesis

The orthogenesis hypothesis began to collapse when it became clear that it could not explain the patterns found by paleontologists in the fossil record, which was non-linear with many complications. The hypothesis was generally abandoned when no mechanism could be found that would account for the process, and the theory of evolution by natural selection became the prevailing theory of evolution. The modern evolutionary synthesis, in which the genetic mechanisms of evolution were discovered, refuted the hypothesis for good. As more was understood about these mechanisms it became obvious that there was no possible naturalistic way in which the newly discovered mechanism of heredity could be far-sighted or have a memory of past trends.

The orthogenetic hypothesis, however, died hard. Even Darwin was at first not opposed to orthogenic thinking, as this quote from the 1911 Encyclopedia Britannica demonstrates:

Darwin and his generation were deeply imbued with the Butlerian tradition, and regarded the organic world as almost a miracle of adaptation, of the minute dovetailing of structure, function and environment. Darwin certainly was impressed with the view that natural selection and variation together formed a mechanism, the central product of which was adaptation. From the Butlerian side, too, came the most urgent opposition to Darwinism. How is it possible, it was said, that fortuitous variations can furnish the material for the precise and balanced adaptations that all nature reveals? Selection cannot create the materials on which it is supposed to operate; the beginnings of new organs, the initial stages of new functions cannot be supposed to have been useful. Moreover, many naturalists, especially those concerned with palaeontology, pointed to the existence of orthogenetic series, of long lines of ancestry, which displayed not a sporadic differentiation. in every direction, but apparently a steady and progressive march in one direction.

Edward Drinker Cope put such a line of argument in the most cogent fashion; the course of evolution, both in the production of variations and their selection, seemed to him to imply the existence of an originative, conscious and directive force, for which he invented the term bathmism (Gr. βαθμ, a step or beginning). On the other hand, dislike of mystical interpretations of natural facts has driven many capable naturalists to another extreme and has led them to insist on the all-powerfulness of natural selection and on the complete indefiniteness of variation. The apparent opposition between the conflicting

schools is more acute than the facts justify.... there is no connection between the appearance of the variation and the use to which it may be put... in one sense it is a mere coincidence if a particular variation turn out to be useful. But there are several directions in which the field of variation appears to be not only limited but defined in a certain direction. Obviously variations depend on the constitution of the varying organism; a modification, whether it be large or small, is a modification of an already definite and limited structure.... A continuous environment both from the point of view of production of variation and selection of variation would appear necessarily to result in a series with the appearance of orthogenesis. The past history of the organic world displays many successful series and these, as they have survived, must inevitably display orthogenesis to some extent; but it also displays many failures which indeed may be regarded as showing that the limitation of variation has been such that the organisms have lost the possibility of successful response to a new environment.

A few hung on to the orthogenesis hypothesis as late as the 1950s by claiming that the processes of macroevolution, the long term trends in evolution, were distinct from the processes of microevolution (genetic variation and natural selection) which were by then well understood and it was known they could not behave in an orthogenetic manner. Teilhard de Chardin, a Jesuit paleontologist, in *The Phenomenon of Man* (a book influential among non-scientists that was published four years after his death in 1959) argued for evolution aiming for the "Omega Point", while putting man at the center of the universe and accounting for original sin (Dennett 1995, von Kitzing 1998). The term Chardin used for this was "directed additivity". This form of orthogenesis has now also been abandoned as more about evolutionary processes has been discovered (Wilkins 1997).

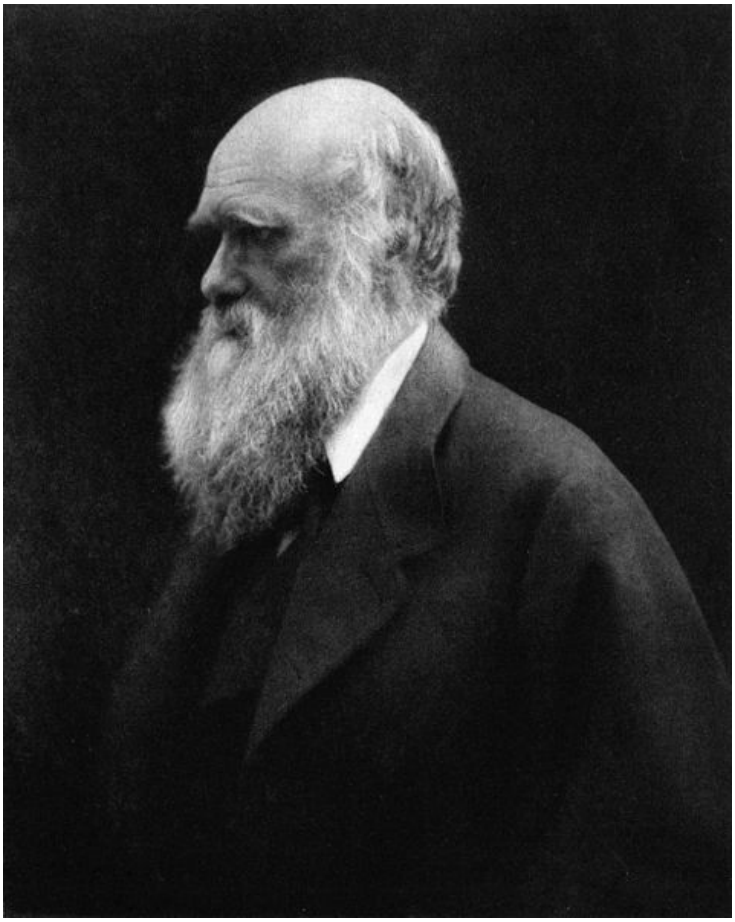
The refutation of orthogenesis had some ramifications in the field of philosophy, as it refuted the idea of teleology as first postulated by Aristotle and accepted by Immanuel Kant, who had greatly influenced many scientists. Before the scientific and philosophical revolution that began with Charles Darwin's ideas, the prevailing philosophy was that the world was teleological and purposeful, and that science was the study of God's creation. The refutation of these concepts have led to a shift in what science and scientists are perceived to be.

Modern co-opted usage

Though linear teleological evolution has been refuted, it is not true that evolution never proceeds in a linear way, reinforcing characteristics, in certain lineages at times, for example, during a period of slow, sustained environmental change, but such examples are entirely consistent with the modern neo-Darwinian theory of evolution. These examples have sometimes been referred to as orthogenetic (e.g. by Jacobs *et al.* 1995 & Woodley 2006) but are not strictly orthogenetic, and simply appear as linear and constant changes because of environmental and molecular constraints on the direction of change.

Chapter 8

Darwinism



Charles Darwin in 1868

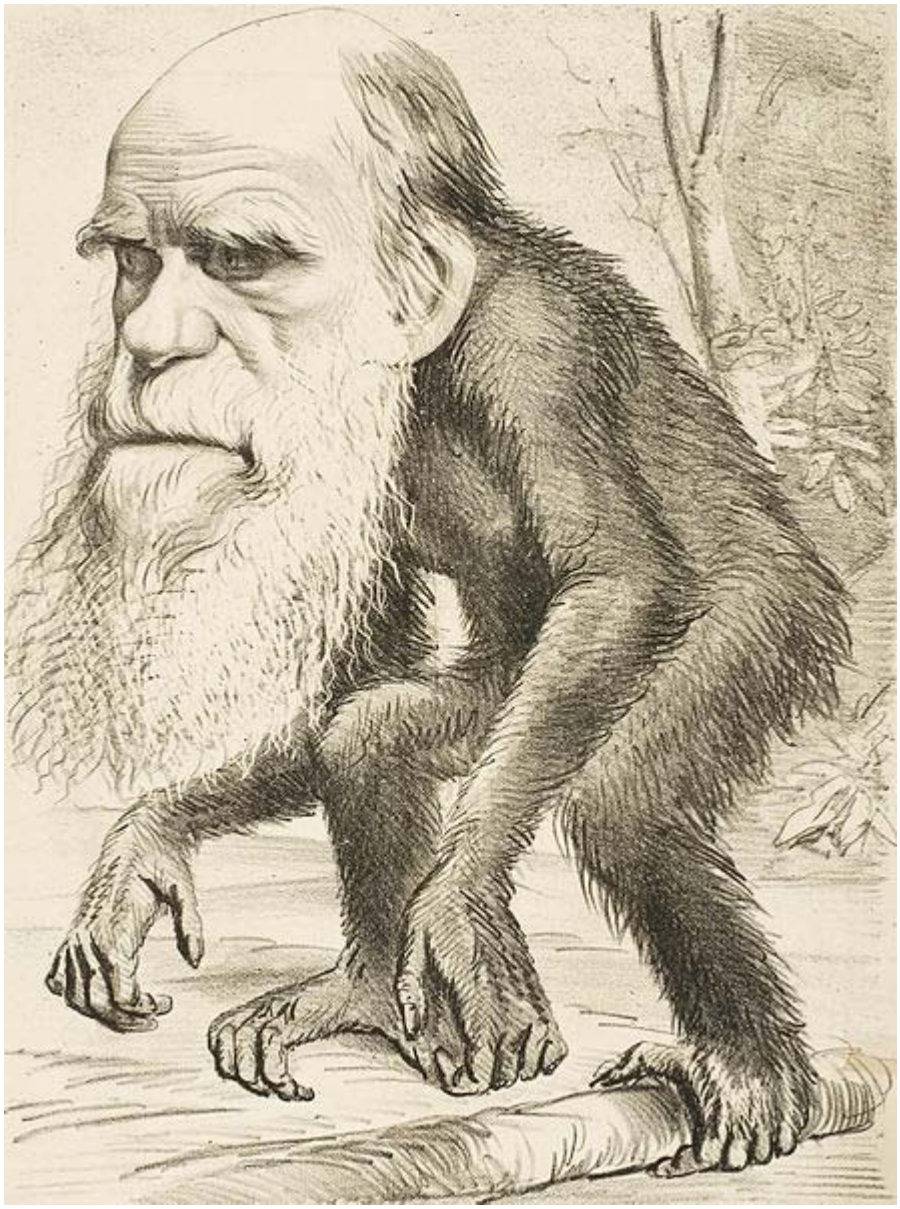
Darwinism is a set of movements and concepts related to ideas of transmutation of species or evolution, including ideas with *no* connection to the work of Charles Darwin. The meaning of "Darwinism" has changed over time, and varies depending on who is using the term. In the United States, the term "Darwinism" is often used by creationists as

a pejorative term, but in the United Kingdom the term has no negative connotations, being freely used as a short hand for evolutionary theory.

The term was coined by Thomas Henry Huxley in April 1860, and was used to describe evolutionary concepts, including earlier concepts such as Malthusianism and Spencerism. In the late 19th century it came to mean the concept that natural selection was the sole mechanism of evolution, in contrast to Lamarckism, then around 1900 it was eclipsed by Mendelism until the modern evolutionary synthesis unified Darwin's and Gregor Mendel's ideas. As modern evolutionary theory has developed, the term has been associated at times with specific ideas.

While the term has remained in use amongst scientific authors, it is increasingly regarded as an inappropriate description of modern evolutionary theory. For example, Darwin was unfamiliar with the work of Gregor Mendel, having as a result only a vague and inaccurate understanding of heredity, and knew nothing of genetic drift.

Conceptions of Darwinism



As "Darwinism" became widely accepted in the 1870s, caricatures of Charles Darwin with an ape or monkey body symbolised evolution.

While the term *Darwinism* had been used previously to refer to the work of Erasmus Darwin in the late 18th century, the term as understood today was introduced when Charles Darwin's 1859 book *On the Origin of Species* was reviewed by Thomas Henry Huxley in the April 1860 issue of the *Westminster Review*. Having hailed the book as, "a veritable Whitworth gun in the armoury of liberalism" promoting scientific naturalism over theology, and praising the usefulness of Darwin's ideas while expressing professional reservations about Darwin's gradualism and doubting if it could be proved

that natural selection could form new species, Huxley compared Darwin's achievement to that of Copernicus in explaining planetary motion:

What if the orbit of Darwinism should be a little too circular? What if species should offer residual phenomena, here and there, not explicable by natural selection? Twenty years hence naturalists may be in a position to say whether this is, or is not, the case; but in either event they will owe the author of "The Origin of Species" an immense debt of gratitude..... And viewed as a whole, we do not believe that, since the publication of Von Baer's "Researches on Development," thirty years ago, any work has appeared calculated to exert so large an influence, not only on the future of Biology, but in extending the domination of Science over regions of thought into which she has, as yet, hardly penetrated.

Another important evolutionariy theorist of the same period was Peter Kropotkin who, in his book *Mutual Aid: A Factor of Evolution*, advocated a conception of Darwinism counter to that of Huxley. His conception was centred around what he saw as the widespread use of cooperation as a survival mechanism in human societies and animals. He used biological and sociological arguments in an attempt to show that the main factor in facilitating evolution is cooperation between individuals in free-associated societies and groups. This was in order to counteract the conception of fierce competition as the core of evolution, which provided a rationalisation for the dominant political, economic and social theories of the time; and the prevalent interpretations of Darwinism, such as those by Huxley, who is targeted as an opponent by Kropotkin. Kropotkin's conception of Darwinism could be summed up by the following quote:

In the animal world we have seen that the vast majority of species live in societies, and that they find in association the best arms for the struggle for life: understood, of course, in its wide Darwinian sense – not as a struggle for the sheer means of existence, but as a struggle against all natural conditions unfavourable to the species. The animal species, in which individual struggle has been reduced to its narrowest limits, and the practice of mutual aid has attained the greatest development, are invariably the most numerous, the most prosperous, and the most open to further progress. The mutual protection which is obtained in this case, the possibility of attaining old age and of accumulating experience, the higher intellectual development, and the further growth of sociable habits, secure the maintenance of the species, its extension, and its further progressive evolution. The unsociable species, on the contrary, are doomed to decay.

19th Century usage

"Darwinism" soon came to stand for an entire range of evolutionary (and often revolutionary) philosophies about both biology and society. One of the more prominent approaches was that summed in the phrase "survival of the fittest" by the philosopher Herbert Spencer, which was later taken to be emblematic of Darwinism even though Spencer's own understanding of evolution was more similar to that of Jean-Baptiste Lamarck than to that of Darwin, and predated the publication of Darwin's theory. What is now called "Social Darwinism" was, in its day, synonymous with "Darwinism" — the

application of Darwinian principles of "struggle" to society, usually in support of anti-philanthropic political agendas. Another interpretation, one notably favoured by Darwin's half-cousin Francis Galton, was that Darwinism implied that because natural selection was apparently no longer working on "civilised" people it was possible for "inferior" strains of people (who would normally be filtered out of the gene pool) to overwhelm the "superior" strains, and voluntary corrective measures would be desirable—the foundation of eugenics.

> [Both] a Darwinian 'left' and a Darwinian 'right' were in place before most people had grasped the Darwinian middle, which was where the maker was.

In Darwin's day there was no rigid definition of the term "Darwinism", and it was used by opponents and proponents of Darwin's biological theory alike to mean whatever they wanted it to in a larger context. The ideas had international influence, and Ernst Haeckel developed what was known as *Darwinismus* in Germany, although, like Spencer Haeckel's "Darwinism" had only a rough resemblance to the theory of Charles Darwin, and was not centred on natural selection at all.

While the reaction against Darwin's ideas is nowadays often thought to have been widespread immediately, in 1886 Alfred Russel Wallace went on a lecture tour across the United States, starting in New York and going via Boston, Washington, Kansas, Iowa and Nebraska to California, lecturing on what he called Darwinism without any problems.

Other uses

The term *Darwinism* is often used in the United States by promoters of creationism, notably by leading members of the intelligent design movement, as an epithet to attack evolution as though it were an ideology (an "ism") of philosophical naturalism, or atheism. For example, Phillip E. Johnson makes this accusation of atheism with reference to Charles Hodge's book *What Is Darwinism?*. However, unlike Johnson, Hodge confined the term to exclude those like Asa Gray who combined Christian faith with support for Darwin's natural selection theory, before answering the question posed in the book's title by concluding: "It is Atheism." Creationists use the term *Darwinism*, often pejoratively,

to imply that the theory has been held as true only by Darwin and a core group of his followers, whom they cast as dogmatic and inflexible in their belief. Casting evolution as a doctrine or belief, as well as a pseudo-religious ideology like Marxism, bolsters religiously motivated political arguments to mandate equal time for the teaching of creationism in public schools.

However, *Darwinism* is also used neutrally within the scientific community to distinguish modern evolutionary theories from those first proposed by Darwin, as well as by historians to differentiate it from other evolutionary theories from around the same period. For example, *Darwinism* may be used to refer to Darwin's proposed mechanism of natural selection, in comparison to more recent mechanisms such as genetic drift and gene flow. It may also refer specifically to the role of Charles Darwin as opposed to others in the history of evolutionary thought — particularly contrasting Darwin's results with those of earlier theories such as Lamarckism or later ones such as the modern synthesis.

In the United Kingdom the term retains its positive sense as a reference to natural selection, and for example Richard Dawkins wrote in his collection of essays *A Devil's Chaplain*, published in 2003, that as a scientist he is a Darwinist.

Chapter 9

Modern Evolutionary Synthesis

The **modern evolutionary synthesis** is a union of ideas from several biological specialties which provides a widely accepted account of evolution. It is also referred to as the *new synthesis*, the *modern synthesis*, the *evolutionary synthesis*, *millennium synthesis* and the *neo-darwinian synthesis*.

The synthesis, produced between 1936 and 1947, reflects the current consensus. The previous development of population genetics, between 1918 and 1932, was a stimulus, as it showed that Mendelian genetics was consistent with natural selection and gradual evolution. The synthesis is still, to a large extent, the current paradigm in evolutionary biology.

The modern synthesis solved difficulties and confusions caused by the specialisation and poor communication between biologists in the early years of the 20th century. At its heart was the question of whether Mendelian genetics could be reconciled with gradual evolution by means of natural selection. A second issue was whether the broad-scale changes (macroevolution) seen by palaeontologists could be explained by changes seen in local populations (microevolution).

The synthesis included evidence from biologists, trained in genetics, who studied populations in the field and in the laboratory. These studies were crucial to evolutionary theory. The synthesis drew together ideas from several branches of biology which had become separated, particularly genetics, cytology, systematics, botany, morphology, ecology and paleontology.

Julian Huxley invented the term, when he produced his book, *Evolution: The Modern Synthesis* (1942). Other major figures in the modern synthesis include R. A. Fisher, Theodosius Dobzhansky, J.B.S. Haldane, Sewall Wright, E.B. Ford, Ernst Mayr, Bernhard Rensch, Sergei Chetverikov, George Gaylord Simpson, and G. Ledyard Stebbins.

Summary of the modern synthesis

The modern synthesis bridged the gap between experimental geneticists and naturalists, and between palaeontologists. It states that:

1. All evolutionary phenomena can be explained in a way consistent with known genetic mechanisms and the observational evidence of naturalists.
2. Evolution is gradual: small genetic changes, recombination ordered by natural selection. Discontinuities amongst species (or other taxa) are explained as originating gradually through geographical separation and extinction (not saltation).
3. Natural selection is by far the main mechanism of change; even slight advantages are important when continued. The object of selection is the phenotype in its surrounding environment.
4. The role of genetic drift is equivocal. Though strongly supported initially by Dobzhansky, it was downgraded later as results from ecological genetics were obtained.
5. Thinking in terms of populations, rather than individuals, is primary: the genetic diversity existing in natural populations is a key factor in evolution. The strength of natural selection in the wild is greater than previously expected; the effect of ecological factors such as niche occupation and the significance of barriers to gene flow are all important.
6. In palaeontology, the ability to explain historical observations by extrapolation from microevolution to macroevolution is proposed. Historical contingency means explanations at different levels may exist. Gradualism does not mean constant rate of change.

The idea that speciation occurs after populations are reproductively isolated has been much debated. In plants, polyploidy must be included in any view of speciation. Formulations such as 'evolution consists primarily of changes in the frequencies of alleles between one generation and another' were proposed rather later. The traditional view is that developmental biology ('evo-devo') played little part in the synthesis, but an account of Gavin de Beer's work by Stephen J. Gould suggests he may be an exception.

Developments leading up to the synthesis

1859–1899

Charles Darwin's *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, orthogenesis ('progressive' evolution), and saltationism (evolution by jumps) were discussed as alternatives. Also, Darwin did not offer a precise explanation of how new species arise. As part of the disagreement about whether natural selection alone was sufficient to explain speciation, George Romanes coined the term neo-Darwinism to refer to the version of evolution advocated by Alfred Russel Wallace and August

Weismann with its heavy dependence on natural selection. Weismann and Wallace rejected the Lamarckian idea of inheritance of acquired characteristics, something that Darwin had not ruled out.

Weismann's idea was that the relationship between the hereditary material, which he called the germ plasm (de: *Keimplasma*), and the rest of the body (the soma) was 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. Weismann was translated into English, and though he was influential, it took many years for the full significance of his work to be appreciated. Later, after the completion of the modern synthesis, the term neo-Darwinism came to be associated with its core concept: evolution, driven by natural selection acting on variation produced by genetic mutation, and genetic recombination (chromosomal crossovers).

1900–1915

Gregor Mendel's work was re-discovered by Hugo de Vries and Carl Correns in 1900. News of this reached William Bateson in England, who reported on the paper during a presentation to the Royal Horticultural Society in May 1900. It showed that the contributions of each parent retained their integrity rather than blending with the contribution of the other parent. This reinforced a division of thought, which was already present in the 1890s. The two schools were:

- Saltationism (large mutations or jumps), favored by early Mendelians who viewed hard inheritance as incompatible with natural selection
- Biometric school: led by Karl Pearson and Walter Weldon, argued vigorously against it, saying that empirical evidence indicated that variation was continuous in most organisms, not discrete as Mendelism predicted.

The relevance of Mendelism to evolution was unclear and hotly debated, especially by Bateson, who opposed the biometric ideas of his former teacher Weldon. Many scientists believed the two theories substantially contradicted each other. This debate between the biometricians and the Mendelians continued for some 20 years and was only solved by the development of population genetics.

T. H. 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 *Drosophila melanogaster*, which helped establish the link between Mendelian genetics and the chromosomal theory of inheritance, demonstrated that rather than creating new species in a single step, mutations increased the genetic variation in the population.

The foundation of population genetics

The first step towards the synthesis was the development of population genetics. R.A. Fisher, J.B.S. Haldane, and Sewall Wright provided critical contributions. In 1918, Fisher

produced the paper "The Correlation Between Relatives on the Supposition of Mendelian Inheritance", which showed how the continuous variation measured by the biometricians could be the result of the action of many discrete genetic loci. In this and subsequent papers culminating in his 1930 book *The Genetical Theory of Natural Selection*, Fisher was able to show how Mendelian genetics was, contrary to the thinking of many early geneticists, completely 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 in the real world at a faster rate than even Fisher had assumed.

Sewall Wright focused on combinations of genes that interacted as complexes, and the effects of inbreeding on small relatively isolated populations, which could exhibit 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 founded the discipline of population genetics. This is the precursor of the modern synthesis, which is an even broader coalition of ideas.

The modern synthesis

Theodosius Dobzhansky, a Ukrainian emigrant, 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 Russian geneticists 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. It also 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. Dobzhansky had been influenced by his exposure in the 1920s to the work of a Russian geneticist named 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.

Edmund Brisco Ford's work complemented that of Dobzhansky. It was as a result of Ford's work, as well as his own, that Dobzhansky changed the emphasis in the third edition of his famous text from drift to selection. Ford was an experimental naturalist

who wanted to test natural selection in nature. He virtually invented the field of research known as 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. 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.

Ernst Mayr's key contribution to the synthesis was *Systematics and the Origin of Species*, published in 1942. Mayr emphasized the importance of allopatric speciation, where geographically isolated sub-populations diverge so far that reproductive isolation occurs. He was sceptical of the reality of sympatric speciation believing 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 German biologist Bernhard Rensch. In the 1920s Rensch, who like Mayr did field work in Indonesia, analyzed the geographic distribution of polytypic species and complexes of closely related species paying particular attention to how variations between different populations correlated with local environmental factors such as differences in climate. In 1947, Rensch published *Neuere Probleme der Abstammungslehre: die Transspezifische Evolution* (English translation 1959: *Evolution above the Species level*). This looked at how the same evolutionary mechanisms involved in speciation might be extended to explain the origins of the differences between the higher level taxa. His writings contributed to the rapid acceptance of the synthesis in Germany.

George Gaylord Simpson was responsible for showing that the modern synthesis was compatible with paleontology in his book *Tempo and Mode in Evolution* published in 1944. Simpson's work was crucial because so many paleontologists 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 paleontologists 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.

The botanist G. Ledyard Stebbins was another major contributor to the synthesis. His major work, *Variation and Evolution in Plants*, was published in 1950. It extended the synthesis to encompass botany including the important effects of hybridization and polyploidy in some kinds of plants.

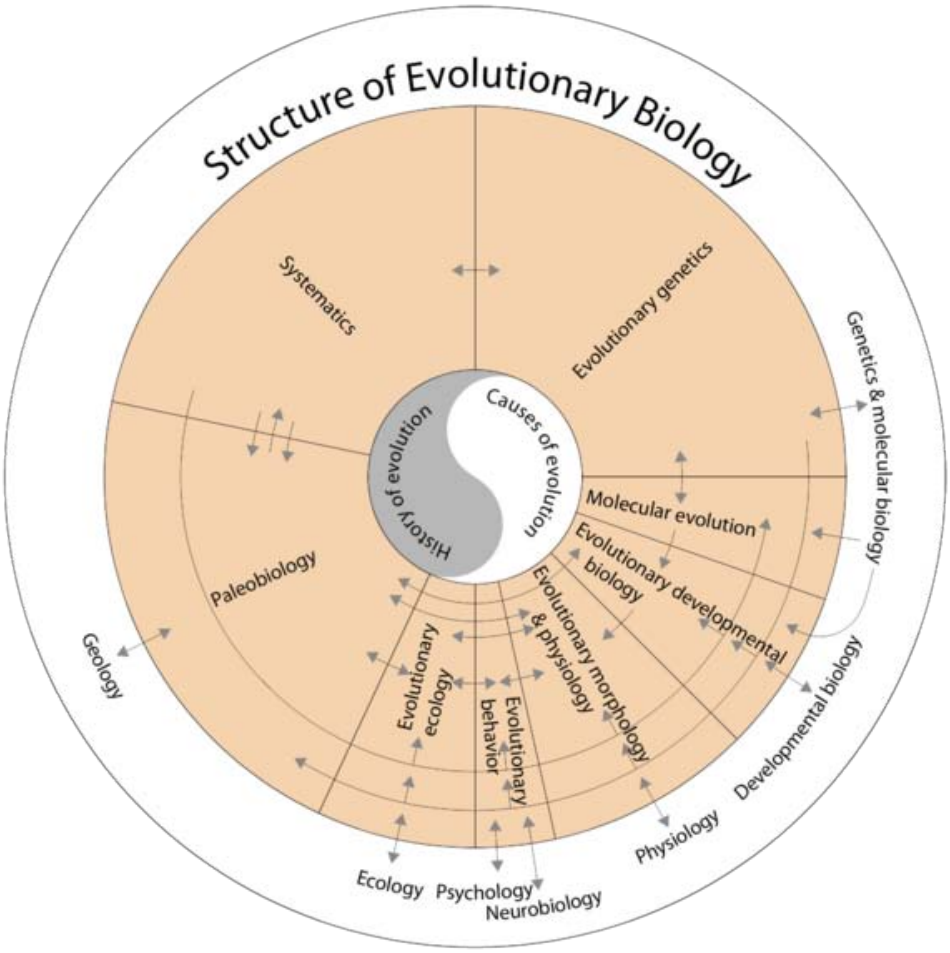
Further advances

The modern evolutionary synthesis continued to be developed and refined after the initial establishment in the 1930s and 1940s. The work of W. D. Hamilton, George C. Williams, John Maynard Smith and others led to the development of a gene-centric view of

evolution in the 1960s. The synthesis as it exists now has extended the scope of the Darwinian idea of natural selection to include subsequent scientific discoveries and concepts unknown to Darwin, such as DNA and genetics, which allow rigorous, in many cases mathematical, analyses of phenomena such as kin selection, altruism, and speciation.

A particular interpretation most commonly associated with Richard Dawkins, author of *The Selfish Gene*, asserts that the gene is the only true unit of selection. Dawkins further extended the Darwinian idea to include non-biological systems exhibiting the same type of selective behavior of the 'fittest' such as memes in culture. The synthesis continues to undergo regular review.

After the synthesis



The structure of evolutionary biology.
The history and causes of evolution (center) are subject to various subdisciplines of evolutionary biology. The areas of segments give an impression of the contributions of subdisciplines to the literature of evolutionary biology.

There are a number of discoveries in earth sciences and biology which have arisen since the synthesis. Listed here are some of those topics which are relevant to the evolutionary synthesis, and which seem soundly based.

Understanding of Earth history

The Earth is the stage on which the evolutionary play is performed. Darwin studied evolution in the context of Charles Lyell's geology, but our present understanding of Earth history includes some critical advances made during the last half-century.

- The age of the Earth has been revised upwards. It is now estimated at 4.56 billion years, about one-third of the age of the universe. It is worth noting that the Phanerozoic only occupies the last 1/9th of this period of time.

- The triumph of Alfred Wegener's idea of continental drift came around 1960. The key principle of plate tectonics is that the lithosphere exists as separate and distinct tectonic plates, which ride on the fluid-like (visco-elastic solid) asthenosphere. This discovery provides a unifying theory for geology, linking phenomena such as volcanos, earthquakes, orogeny, and providing data for many paleogeographical questions. One major question is still unclear: when did plate tectonics begin?

- Our understanding of the evolution of the Earth's atmosphere has progressed. The substitution of oxygen for carbon dioxide in the atmosphere, which occurred in the Proterozoic, caused probably by cyanobacteria in the form of stromatolites, caused changes leading to the evolution of aerobic organisms.

- The identification of the first generally accepted fossils of microbial life was made by geologists. These rocks have been dated as about 3.465 billion years ago. Walcott was the first geologist to identify pre-Cambrian fossil bacteria from microscopic examination of thin rock slices. He also thought stromatolites were organic in origin. His ideas were not accepted at the time, but may now be appreciated as great discoveries.

- Information about paleoclimates is increasingly available, and being used in paleontology. One example: the discovery of massive ice ages in the Proterozoic, following the great reduction of CO_2 in the atmosphere. These ice ages were immensely long, and led to a crash in microflora.

- Catastrophism and mass extinctions. A partial reintegration of catastrophism has occurred, and the importance of mass extinctions in large-scale evolution is now apparent. Extinction events disturb relationships between many forms of life and may remove dominant forms and release a flow of adaptive radiation amongst groups that remain. Causes include meteorite strikes (K–T junction; Upper Devonian); flood basalt provinces (Deccan traps at K/T junction; Siberian traps at P–T junction); and other less dramatic processes.

Conclusion: Our present knowledge of earth history strongly suggests that large-scale geophysical events influenced macroevolution and megaevolution. These terms refer to evolution above the species level, including such events as mass extinctions, adaptive radiation, and the major transitions in evolution.

Symbiotic origin of eukaryotic cell structures

Once symbiosis was discovered in lichen and in plant roots (rhizobia in root nodules) in the 19th century, the idea arose that the process might have occurred more widely, and might be important in evolution. Anton de Bary invented the concept of *symbiosis*; several Russian biologists promoted the idea; Edwin Wilson mentioned it in his epic text *The Cell*; as did Ivan Emmanuel Wallin in his *Symbionticism and the origin of species*; and there was a brief mention by Julian Huxley in 1930; all in vain because sufficient evidence was lacking. Symbiosis as a major evolutionary force was not discussed at all in the evolutionary synthesis.

The role of symbiosis in cell evolution was revived partly by Joshua Lederberg, and finally brought to light by Lynn Margulis in a series of papers and books. It turns out that some cell organelles are of microbial origin: mitochondria and chloroplasts definitely, cilia, flagella and centrioles possibly, and perhaps the nuclear membrane and much of the chromosome structure as well. What is now clear is that the evolution of eukaryote cells is either caused by, or at least profoundly influenced by, symbiosis with bacterial and archaean cells in the Proterozoic.

The origin of the eukaryote cell by symbiosis in several stages was not part of the evolutionary synthesis. It is, at least on first sight, an example of megaevolution by big jumps. However, what symbiosis provided was a copious supply of heritable variation from microorganisms, which was fine-tuned over a long period to produce the cell structure we see today. This part of the process is consistent with evolution by natural selection.

Trees of life

The ability to analyse sequence in macromolecules (protein, DNA, RNA) provides evidence of descent, and permits us to work out genealogical trees covering the whole of life, since now there are data on every major group of living organisms. This project, begun in a tentative way in the 1960s, has become a search for the universal tree or the universal ancestor, a phrase of Carl Woese. The tree that results has some unusual features, especially in its roots. There are two domains of prokaryotes: bacteria and archaea, both of which contributed genetic material to the eukaryotes, mainly by means of symbiosis. Also, since bacteria can pass genetic material to other bacteria, their relationships look more like a web than a tree. Once eukaryotes were established, their sexual reproduction produced the traditional branching tree-like pattern, the only diagram Darwin put in the *Origin*. The last universal ancestor (LUA) would be a prokaryotic cell before the split between the bacteria and archaea. LUA is defined as most recent

organism from which all organisms now living on Earth descend (some 3.5 to 3.8 billion years ago, in the Archean era).

This technique may be used to clarify relationships within any group of related organisms. It is now a standard procedure, and examples are published regularly. April 2009 sees the publication of a tree covering all the animal phyla, derived from sequences from 150 genes in 77 taxa.

Early attempts to identify relationships between major groups were made in the 19th century by Ernst Haeckel, and by comparative anatomists such as Thomas Henry Huxley and E. Ray Lankester. Enthusiasm waned: it was often difficult to find evidence to adjudicate between different opinions. Perhaps for that reason, the evolutionary synthesis paid surprisingly little attention to this activity. It is certainly a lively field of research today.

Evo-devo

What once was called embryology played a modest role in the evolutionary synthesis, mostly about evolution by changes in developmental timing (allometry and heterochrony). Man himself was, according to Bolk, a typical case of evolution by retention of juvenile characteristics (neoteny). He listed many characters where "Man, in his bodily development, is a primate foetus that has become sexually mature". Unfortunately, his interpretation of these ideas was non-Darwinian, but his list of characters is both interesting and convincing.

Modern interest in Evo-devo springs from clear proof that development is closely controlled by special genetic systems, and the hope that comparison of these systems will tell us much about the evolutionary history of different groups. In a series of experiments with the fruit-fly *Drosophila*, Edward B. Lewis was able to identify a complex of genes whose proteins bind to the cis-regulatory regions of target genes. The latter then activate or repress systems of cellular processes that accomplish the final development of the organism. Furthermore, the sequence of these control genes show *co-linearity*: the order of the loci in the chromosome parallels the order in which the loci are expressed along the anterior-posterior axis of the body. Not only that, but this cluster of master control genes programs the development of all higher organisms. Each of the genes contains a homeobox, a remarkably conserved DNA sequence. This suggests the complex itself arose by gene duplication. In his Nobel lecture, Lewis said "Ultimately, comparisons of the [control complexes] throughout the animal kingdom should provide a picture of how the organisms, as well as the [control genes] have evolved".

The term *deep homology* was coined to describe the common origin of genetic regulatory apparatus used to build morphologically and phylogenetically disparate animal features. It applies when a complex genetic regulatory system is inherited from a common ancestor, as it is in the evolution of vertebrate and invertebrate eyes. The phenomenon is implicated in many cases of parallel evolution.

A great deal of evolution may take place by changes in the control of development. This may be relevant to punctuated equilibrium theory, for in development a few changes to the control system could make a significant difference to the adult organism. An example is the giant panda, whose place in the Carnivora was long uncertain. Apparently, the giant panda's evolution required the change of only a few genetic messages (5 or 6 perhaps), yet the phenotypic and lifestyle change from a standard bear is considerable. The transition could therefore be effected relatively swiftly.

Fossil discoveries

In the past thirty or so years there have been excavations in parts of the world which had scarcely been investigated before. Also, there is fresh appreciation of fossils discovered in the 19th century, but then denied or deprecated: the classic example is the Ediacaran biota from the immediate pre-Cambrian, after the Cryogenian period. These soft-bodied fossils are the first record of multicellular life. The interpretation of this fauna is still in flux.

Many outstanding discoveries have been made, and some of these have implications for evolutionary theory. The discovery of feathered dinosaurs and early birds from the Lower Cretaceous of Liaoning, N.E. China have convinced most students that birds did evolve from coelurosaurian theropod dinosaurs. Less well known, but perhaps of equal evolutionary significance, are the studies on early insect flight, on stem tetrapods from the Upper Devonian, and the early stages of whale evolution.

Recent work has shed light on the evolution of flatfish (pleuronectiformes), such as plaice, sole, turbot and halibut. Flatfish are interesting because they are one of the few vertebrate groups with external asymmetry. Their young are perfectly symmetrical, but the head is remodelled during a metamorphosis, which entails the migration of one eye to the other side, close to the other eye. Some species have both eyes on the left (turbot), some on the right (halibut, sole); all living and fossil flatfish to date show an 'eyed' side and a 'blind' side. The lack of an intermediate condition in living and fossil flatfish species had led to debate about the origin of such a striking adaptation. The case was considered by Lamark, who thought flatfish precursors would have lived in shallow water for a long period, and by Darwin, who predicted a gradual migration of the eye, mirroring the metamorphosis of the living forms. Darwin's long-time critic St. George Mivart thought that the intermediate stages could have no selective value, and in the 6th edition of the *Origin*, Darwin made a concession to the possibility of acquired traits. Many years later the geneticist Richard Goldschmidt put the case forward as an example of evolution by saltation, bypassing intermediate forms.

A recent examination of two fossil species from the Eocene has provided the first clear picture of flatfish evolution. The discovery of stem flatfish with incomplete orbital migration refutes Goldschmidt's ideas, and demonstrates that "the assembly of the flatfish bodyplan occurred in a gradual, stepwise fashion". There are no grounds for thinking that incomplete orbital migration was maladaptive, because stem forms with this condition ranged over two geological stages, and are found in localities which also yield flatfish

with the full cranial asymmetry. The evolution of flatfish falls squarely within the evolutionary synthesis.

Horizontal gene transfer

Horizontal gene transfer (HGT) (or *Lateral gene transfer*) is any process in which an organism gets genetic material from another organism without being the offspring of that organism.

Most thinking in genetics has focused on vertical transfer, but there is a growing awareness that horizontal gene transfer is a significant phenomenon. Amongst single-celled organisms it may be the dominant form of genetic transfer. Artificial horizontal gene transfer is a form of genetic engineering.

Richardson and Palmer (2007) state: "Horizontal gene transfer (HGT) has played a major role in bacterial evolution and is fairly common in certain unicellular eukaryotes. However, the prevalence and importance of HGT in the evolution of multicellular eukaryotes remain unclear".

The bacterial means of HGT are:

- Transformation, the genetic alteration of a cell resulting from the introduction, uptake and expression of foreign genetic material (DNA or RNA).
- Transduction, the process in which bacterial DNA is moved from one bacterium to another by a bacterial virus (a bacteriophage, or 'phage').
- Bacterial conjugation, a process in which a bacterial cell transfers genetic material to another cell by cell-to-cell contact.
- Gene transfer agent or 'GTA' is a virus-like element which contains random pieces of the host chromosome. They are found in most members of the alphaproteobacteria order Rhodobacterales. They are encoded by the host genome. GTAs transfer DNA so frequently that they may have an important role in evolution.
  A 2010 report found that genes for antibiotic resistance could be transferred by engineering GTAs in the laboratory.

Some examples of HGT in metazoa are now known. Genes in bdelloid rotifers have been found which appear to have originated in bacteria, fungi, and plants. This suggests they arrived by horizontal gene transfer. The capture and use of exogenous (~foreign) genes may represent an important force in bdelloid evolution. The team led by Matthew S. Meselson at Harvard University has also shown that, despite the lack of sexual reproduction, bdelloid rotifers do engage in genetic (DNA) transfer within a species or clade. The method used is not known at present.