

ENCYCLOPEDIA ARTICLE

Organic evolution

Organic, or biological, evolution is the modification of living organisms during their descent, generation by generation, from common ancestors. It is to be distinguished from other phenomena to which the term evolution is often applied, such as chemical evolution, cultural evolution, or the origin of life from nonliving matter. Organic evolution includes two major processes: anagenesis, the alteration of the genetic properties of a single lineage over time; and cladogenesis, or branching, whereby a single lineage splits into two or more distinct lineages that continue to change anagenetically.

Study of evolution

The subject matter of evolutionary biology may be roughly divided into the analysis of the history of evolutionary events and the analysis of the mechanisms, or processes, of evolutionary change. The study of evolutionary history attempts to determine the ancestry of and genealogical relationships among different kinds of organisms, the pathways by which their morphological, biochemical, and other features have become modified, the history by which they arrived at their present geographical distributions, and the changes in the diversity and number of species throughout geological time. The methods by which such inferences are made include analysis of the fossil record and the phylogenetic analysis of living taxa, many having an inadequate fossil record. Phylogenetic analysis, using data on the comparative anatomy, molecular characteristics [for example, protein and deoxyribonucleic acid (DNA) sequences], and geographical distributions of organisms, is part of the province of biological systematics.

The analysis of the mechanisms of evolutionary change addresses primarily the factors that cause changes in the genetic composition of populations and species, and those that influence diversification and extinction of species. The mathematical theory of population genetics is important to this enterprise. Experimental and observational testing of the theory includes molecular, genetic, and developmental analysis of genetic variation and the mechanisms by which it arises; ecological genetics, the study of the impact of ecological factors on genetic change of populations; studies in functional morphology, physiology, behavior, and ecology that address the adaptive value of genetically different traits; and taxonomic and phylogenetic analyses that shed light on processes such as cladogenesis. Thus the study of evolution embraces all of biology.

History

Although some ancient Greek philosophers had vague, often mythological, intimations of evolution, Platonic and Aristotelian philosophy, in which variation represented imperfect reflection of eternal, unchanging essences or "ideas," was antithetical to evolution. The adoption of this framework by Christian theology, and the literal interpretation of the first chapters of Genesis, led to the belief that all living things had been directly created in their current form (special creation) only a few thousand years ago. The first challenges to this view did not arise until the eighteenth century, when speculations on cosmic change, on the antiquity and dynamic nature of the Earth, and on human progress led naturally to the idea that living things might change as well. The French biologist G. de Buffon (1707–1788) was one of the first to hint at evolution, but his countryman J. de Lamarck (1744–1829) was the first to argue forcefully for evolution and to propose a mechanism by which it might occur. Lamarck supposed that new forms arise continually by spontaneous generation, and then progress toward greater complexity and perfection because of "powers conferred by the supreme author of all things" and because their behavioral responses to the environment cause changes in

their structure. Lamarckism was soon discredited by the implausibility and vagueness of the mechanisms he postulated, and by forceful arguments against evolution by leading French biologists of the day. Nevertheless, the idea of evolutionary change was "in the air" in the early nineteenth century.

Charles Darwin (1809–1882), son of an English physician, apparently came to think of the possibility of evolution toward the end of his 5-year (1831–1836) voyage as naturalist on the H.M.S. *Beagle*. He conceived of the theory of natural selection in 1838, and spent the next 20 years synthesizing and amassing evidence and refining his ideas until, faced with the possibility that the young naturalist Alfred Russel Wallace, who had independently thought of natural selection, might gain priority for the idea, he published an "abstract" of the massive book which he had been preparing. The "abstract" was a 490-page book, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, published on November 24, 1859. Darwin spent the rest of his life conducting research and writing books on an extraordinary range of subjects, from the power of movement in plants to the "descent of man," all of which are related directly or indirectly to the themes in his most famous book. But *The Origin of Species*, as it is generally known, is his triumph, one of the most important works in the history of western civilization.

The Origin of Species accomplishes two things. Darwin marshals evidence from every quarter of biology and geology that evolution has in fact occurred: that living things are descended with modification from common ancestors. Second, he presents an explicit, purely mechanistic theory of the causes of evolution. Every species, Darwin points out, has hereditary variation in numerous characteristics. Some variants will be better suited to the exigencies of life than others, and so will survive better or reproduce more prolifically than the inferior variants. Since descendants inherit their superior properties, the proportion of individuals in the population that bear superior characteristics will increase, and the proportion with inferior traits will decrease from generation to generation, until the species has been transformed. The new character itself is subject to further variation and to further alteration by this process of natural selection, so that in the vastness of time the feature comes to differ extremely from the original form—but it is a great change accomplished in small steps. Because different populations experience different environments and adapt to different resources, numerous forms may diverge from an original stock, each adapted to a different environment or way of life. This branching process, continued through the immensity of geological time, gives rise to the great "tree of life."

Darwin's ideas at first met with much opposition, but within 20 years after the *Origin* appeared, most scientists had been convinced of the reality of evolution, and many were stimulated to work in the areas of paleontology, comparative anatomy, and comparative embryology that provide evidence of the historical (phylogenetic) relationships among organisms. But Darwin's theory of the cause of evolution, natural selection, was not widely accepted for lack of sufficient evidence. It fell even deeper into disrepute in the early twentieth century, when the new science of genetics (developing after the rediscovery in 1900 of Mendel's work) seemed to provide alternative mechanisms for evolution, such as mutation.

Modern evolutionary theory began in the late 1920s and early 1930s, when naturalists and systematists amassed evidence on adaptive variation and the nature of species, and when the mathematical geneticists R. A. Fisher and J. B. S. Haldane in England and S. Wright in the United States developed equations showing that natural selection and mendelian genetics (including mutation) are not alternatives, but rather work in combination just as Darwin had proposed. Their theories, which include other causes of evolution in addition to the coaction of natural selection and mutation, are the foundation of mathematical population genetics. See also: Population genetics

During the 1930s through the early 1950s, the theory of population genetics, together with the ideas of

experimental workers and taxonomists concerned with evolution, congealed into the "modern synthesis" commonly known as neo-Darwinism. The experimental geneticists S. S. Chetverikov, Th. Dobzhansky, and E. B. Ford, the zoologists E. Mayr, B. Rensch, and J. S. Huxley, the paleontologist G. G. Simpson, and the botanist G. L. Stebbins, were among the chief figures who, together with Wright, Fisher, and Haldane, formulated a coherent, comprehensive theory of evolution and showed that it was consistent with data from diverse fields of study. Since the modern synthesis, new data and theories concerning especially evolution at the molecular level, evolution of behavior and of ecological interactions among species, and long-term patterns of evolution over geological time have been added to the neo-Darwinian framework, and some neo-Darwinian ideas have been called into question. Thus, although most of the neo-Darwinian theory is accepted by most evolutionary biologists, there remain controversies, as in any other field of science, about some aspects of the theory. There is no controversy, however, about the reality of evolution as a historical event. That organisms have descended from common ancestors is accepted by knowledgeable biologists as fact. Molecular and other similarities imply that all living things are related to each other by common ancestry.

Mechanisms of species transformation

Anagenesis consists of change in the genetic basis of the features of the organisms that constitute a single species. Populations in different geographic localities are commonly considered members of the same species if they exchange members at some rate and interbreed with each other (or are thought to be potentially able to interbreed); but unless the level of interchange (gene flow) is very high, some degree of genetic difference among different populations is likely to develop. The changes that transpire in a single population may be spread to other populations of the species by gene flow. See also: Species concept

Genetic variation

Almost every population harbors several different alleles (forms of a gene) at each of a great many of the gene loci; hence many characteristics of a species are genetically variable. This is evident by the existence of morphological and physiological variations that are shown to be inheritable, and by recent study of genes themselves (deoxyribonucleic acid, or DNA, sequences) and of their products (proteins). Studies of protein variation on *Drosophila*, humans, and numerous other species suggest that 40% or more of the gene loci may be variable within a population, and analyses of DNA suggest that almost all of a species' genes vary. Thus, to evolve in response to many environmental changes, a population need not wait for new mutations to occur; genetic variations that happen to be suitable for new conditions may already be present. For example, genes for insecticide resistance are present in low frequency in populations of insects that have never been exposed to insecticides.

Sources of genetic variation

All genetic variations ultimately arise by mutation of the genetic material. Broadly defined, mutations include changes in the number or structure of the chromosomes and changes in individual genes, including substitutions of individual nucleotide pairs, insertion and deletion of nucleotides, and duplication of genes. Many such mutations alter the properties of the gene products (RNA and proteins) or the timing or tissue localization of gene action, and consequently affect various aspects of the phenotype (that is, the morphological and physiological characteristics of an organism). Whether and how a mutation is phenotypically expressed often depends on developmental (epigenetic) events, some of which may "canalize" the phenotype to reduce phenotypic variability even if genetic variation exists. The phenotypic effect of mutations ranges from extremely subtle to drastic; many drastic mutations alter development so greatly that the organism's viability is severely reduced. However, some large mutations, as well as more subtle mutations which slightly change body size, the form of an appendage, the activity of an enzyme, or other features, are deleterious, neutral, or beneficial, depending on the organism's environment. Because a gene

typically affects several aspects of the phenotype, it may have both harmful and beneficial effects (pleiotropy), the relative magnitude of which determines the net effect of the mutation on survival and reproduction. Because different genes interact in determining phenotypes, the positive or negative value of a mutation may depend on which alleles are prevalent at other gene loci.

The frequency with which a given gene mutates to a recognizably different allele is fairly low (often about 1 mutation per gene per 100,000 gametes), but can be considerably higher when mutation is caused by factors such as transposable segments of DNA that become inserted into a gene and affect its function. Although the mutation rate of any given gene is low, the total flux of mutations is appreciable (at least one new mutation somewhere in the genome of each gamete) because the number of genes is high. Mutation occurs spontaneously because of molecular "noise," but can be enhanced by factors such as heat, radiation, and chemical mutagens. See also: Mutation

Mutations are generally believed to occur at random, not in the sense that all genes mutate at the same rate or that all possible mutations of a gene are equally likely, but rather in the sense that the likelihood of a particular mutation is not influenced by whether it would be advantageous to the organism in its prevailing environment. Genes cannot respond to the environment by mutating in an appropriate direction; nor can the experiences of an individual organism enable it to change in an adaptive manner the genetic basis for the characteristics that the organism uses in its relations to the environment. This is the principal point of difference between the neo-Darwinian and the Lamarckian theories of evolution.

Recombination, arising from sexual reproduction and crossing-over, combines the mutant variants at various loci into a vast number of possible combinations; thus mutation and recombination together generate immense genetic variability among the members of a population. When, as is usually the case, many different loci each contribute to a particular trait such as body size, the result is "continuous" variation, often in the form of a bell-shaped (normal) distribution of the trait in the population. See also: Crossing-over (genetics); Distribution (probability)

Natural selection

The fundamental event in evolution is a change in the frequency of an allele in a population. In its full form, this entails the spread through a population of an allele that, having just come into existence by mutation, is very rare, but which ultimately comprises 100% of the gene copies at that locus (in a population of N diploid organisms, there are $2N$ gene copies at a locus that is not sex-linked). The allele is then said to have been fixed in the population. One of the factors that causes this process is natural selection.

Natural selection is a consistent difference in the average rate at which genetically different entities leave descendants to subsequent generations; such a difference arises from differences in fitness (that is, in the rate of survival, reproduction, or both). In fact, a good approximate measure of the strength of natural selection is the difference between two such entities in their per capita rate of increase r . The entities referred to are usually different alleles at a locus, or phenotypically different classes of individuals in the population that differ in genotype. Thus selection may occur at the level of the gene, as in the phenomenon of meiotic drive, whereby one allele predominates among the gametes produced by a heterozygote. Selection at the level of the individual organism, the more usual case, entails a difference in the survival and reproductive success of phenotypes that may differ (in body size, for instance) at one locus (for example, genotypes AA and aa differ in size) or at more than one locus (for example, $AABBCC$ versus $aabbcc$, where different letters denote different loci and upper- and lowercase letters denote different alleles at a locus). As a consequence of the difference in fitness, the proportion of one or the other allele increases in subsequent generations (**Fig. 1**). Numerous cases of such differences in fitness, often of very considerable magnitude,

have been documented in both laboratory-maintained and natural populations of many species. See also: Population ecology

The relative fitness of different genotypes usually depends on environmental conditions. Thus, for example, brown shell color in terrestrial snails is advantageous in forests, providing cryptic protection against predators, whereas yellow coloration is advantageous in open fields. Relative fitnesses of genotypes often switch as the environment changes from season to season or year to year, and the frequencies of genotypes often fluctuate in consequence. Thus changes in genetic composition are the passive consequence of changes in environment; a population cannot alter its genetic composition in anticipation of some future environmental change. This implies that populations cannot adapt so as to avoid future extinction. Natural selection does not act for the benefit of the species as a whole; it is a purely mechanical, mathematical phenomenon: the difference in reproductive success among individual members of the species.

Selection is sometimes directional, meaning that one extreme state of a phenotypic feature is most fit and ultimately becomes fixed if the environmental conditions to which it is adapted prevail long enough (**Fig. 2**). Often, however, selection is stabilizing, meaning that an intermediate phenotype is most fit. If this phenotype is produced by a heterozygote at a single locus, selection maintains both alleles in the population. Several cases of stabilizing selection are known in which the heterozygote is most fit. Genetic variation can also be maintained by diversifying selection, whereby several different phenotypes are favored. Diversifying (disruptive) selection includes the phenomenon of frequency-dependent selection: the rarer a genotype is, the higher its fitness becomes. This phenomenon often arises because of interactions among the members of a population, each of which constitutes part of the environment of every other member. For example, genotypes often differ in their relative ability to use one or another resource, such as different kinds of food. If there is competition for limited food, a rare genotype experiences less competition for its particular food type than the common genotype does for its particular food type; thus the per capita rate of increase of the rarer genotype is relatively greater. When it attains high frequency, the tables are turned, so an equilibrium is attained at which both genotypes persist.

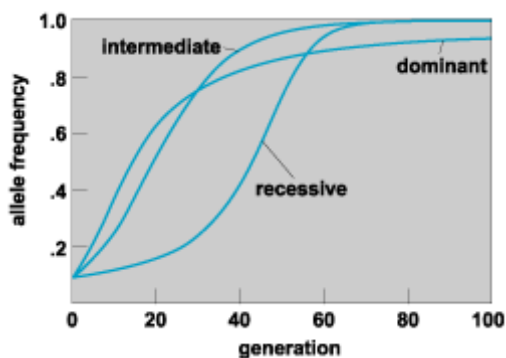


Fig. 1 Increase in the frequency of an advantageous allele within a population, from an initial frequency of 0.1. The fitness, or relative rate of increase, of the fittest genotype is 20% greater than that of the least fit genotype in each of three cases, in which the fittest genotype is dominant, recessive, or partially dominant (intermediate). (After D. J. Futuyma, *Evolutionary Biology*, Sinauer Associates, 1979)

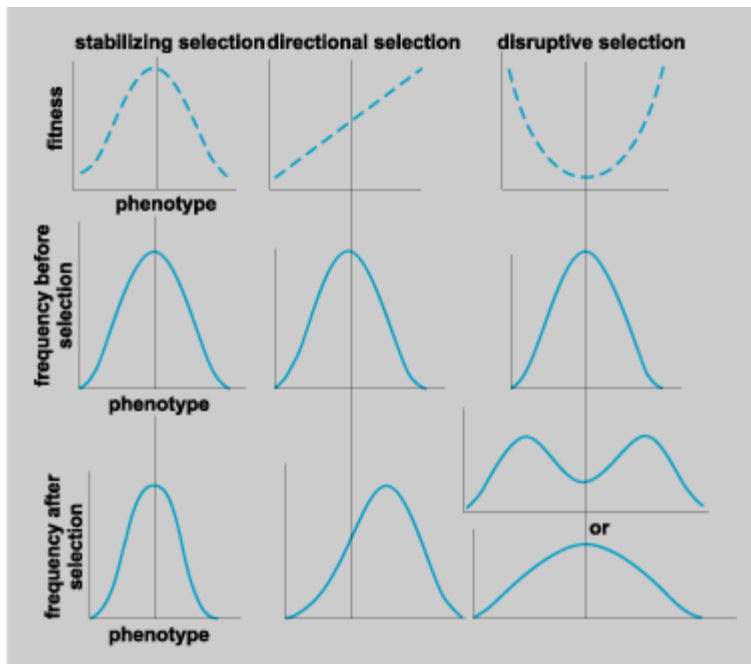


Fig. 2 Three modes of selection on a quantitatively varying phenotypic character. Because of the relation between fitness and phenotype, portrayed in the upper panels, the frequency distribution of the trait in the population changes during one generation of selection from the patterns shown in the middle to those shown in the lower panels. (After L. L. Cavalli-Sforza and W. F. Bodmer, *The Genetics of Human Populations*, W. H. Freeman, 1971)

Under directional selection, new mutations that enhance a particular trait may be consistently advantageous over the long run. For example, all other things being equal, greater height is advantageous for a tree because shorter trees are overtopped by their taller neighbors, and so do not receive as much light. But there is a limit to the height that natural selection favors, because countervailing selection pressures come into play: an excessively tall tree will be toppled by wind unless it has a sufficiently strong trunk and root system. Because wind conditions differ from one place to another, and the trunk and root structure differs among species, the relative strength of conflicting selection pressures differs among populations and species, which therefore evolve along divergent lines. In addition to divergent evolution, however, evolution is often convergent: different organisms sometimes experience similar selection pressures and so evolve at least superficially similar characteristics.

Random genetic drift

Different alleles of a gene that provides an important function do not necessarily differ in their effect on survival and reproduction; such alleles are said to be neutral. The proportion of two neutral alleles in a population fluctuates randomly from generation to generation by chance, because not all individuals in the population have the same number of surviving offspring. Random fluctuations of this kind are termed random genetic drift. If the process continues long enough in the absence of countervailing factors, one or another allele will ultimately fluctuate all the way to fixation, and the other alleles will be lost from the population by chance (**Fig. 3**). This process occurs more rapidly, the smaller the population. Many natural populations are quite small; in fact, their effective size, which can be thought of as the number of individuals that actually succeed in reproducing, is considerably smaller than the total number of individuals. Thus all populations are susceptible to genetic drift, and the process is likely to proceed quite rapidly in many species. Because the identity of the fixed allele is only a matter of chance, the allele that becomes fixed will differ from one population to another, so that the genetic composition of different populations or of different species diverges over time, at a rate inversely proportional to their effective population size. The theory of genetic drift has

been validated by laboratory experiments and by patterns of genetic difference among natural populations of species.

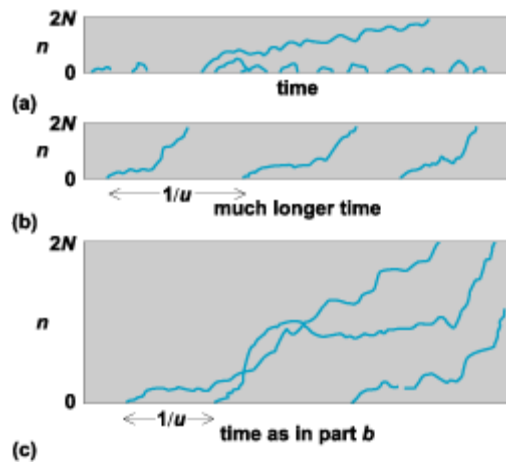


Fig. 3 Gene substitution by genetic drift. A population of N diploid individuals has $2N$ genes at any locus. The number of copies n of a mutation fluctuates by chance. (a) Numerous mutations arise, of which one is fixed while others increase and then decrease in frequency. (b, c) Only those mutations at various loci which are fixed are shown. The average number of generations between the origin of successive mutations that are ultimately fixed by genetic drift is $1/u$, where u is the mutation rate. In a large population, shown in c, several loci are polymorphic at any time, as it takes longer for mutations to reach fixation. (After J. F. Crow and M. Kimura, *An Introduction to Population Genetics Theory*, Burgess, 1970)

Drift versus selection

If different alleles do indeed differ in their effects on fitness, both genetic drift and natural selection operate simultaneously. The deterministic force of natural selection drives allele frequencies toward an equilibrium, while the stochastic (random) force of genetic drift brings them away from that equilibrium. The outcome for any given population depends on the relative strength of natural selection (the magnitude of differences in fitness) and of genetic drift (which depends on population size), just as the trajectory of a dust particle in still air depends on the relative power of gravitation and of brownian motion. Thus the fate of an allele that differs in fitness only slightly from other alleles may be dominated by selection if the population is large, but by genetic drift if the population is small.

The relative importance of genetic drift versus natural selection is the subject of considerable controversy and research, the chief focus of which is on genetic differences at the molecular level, such as different forms of an enzyme or slight differences in nucleotide sequences in DNA. There is reason to believe that many such differences have only a slight impact on fitness and that considerable evolution at the molecular level occurs primarily by genetic drift. The best evidence is provided by synonymous codons of DNA and by the nucleotide sequences of DNA that are not transcribed into RNA and protein. Many such changes at the DNA level are unlikely to affect the organism's fitness, yet comparison among species shows that these sequences have evolved at a high rate—higher than that of DNA sequences that are functional. Fixation of purely neutral alleles, according to mathematical theory, should occur at a constant rate per generation, and there is some evidence that the rate at which species have diverged at the molecular level has been moderately constant. Thus some evolutionary change has certainly transpired by genetic drift, although divergence in clearly adaptive features of morphology, physiology, and behavior has certainly come about primarily by natural selection.

In theory, genetic drift can act together with natural selection to enhance adaptation of a species to its environment. Often the pressure of natural selection can drive the population toward any one of several

different genetic constitutions: alternative genetic “solutions” to the same “problem” (**Fig. 4**). Which genetic constitution is achieved depends on which alleles happen to be most prevalent when the environmental challenge arises. The genetic “solution” actually achieved may be inferior to another genetic constitution that might have been achieved had the initial genetic composition of the population been different; yet the equations of gene frequency change show that natural selection alone cannot move the population from one stable genetic equilibrium to a different, superior, genetic equilibrium. If the population is small enough, however, genetic drift can destabilize the population, carrying the gene frequencies away from the inferior equilibrium enough for natural selection to bring them to a new, superior, genetic configuration. This theory is part of Sewall Wright's shifting-balance theory of genetic change.

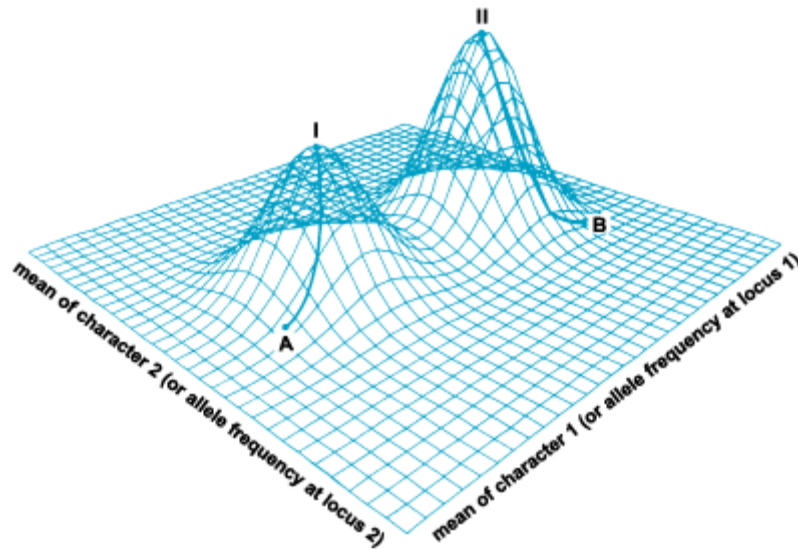


Fig. 4 Natural selection may drive a population to different genetic equilibria depending on initial allele frequencies. The elevation of a point on this landscape represents the mean fitness of a population that has a particular average value for each of two traits (or that has a particular gene frequency at each of two loci). Character combinations I or II represent high fitness, whereas intermediate phenotypes have low fitness. A population beginning with average phenotypes represented by point B will evolve to equilibrium II, whereas one beginning at point A will become stabilized by natural selection at equilibrium I, even though this represents an inferior condition relative to II. (After D. J. Futuyma and M. Slatkin, *Coevolution*, Sinauer Associates, 1983)

Speciation and cladogenesis

The great diversity of organisms has come about because individual lineages (species) branch into separate species, which continue to diverge by the processes described above. This splitting process, speciation, occurs when genetic differences develop between two populations that prevent them from interbreeding and forming a common gene pool. The genetically based characteristics that cause such reproductive isolation are usually termed isolating mechanisms, but there is little reason to believe that they evolve specifically to prevent interbreeding, as the unfortunate term mechanism implies. Rather, reproductive isolation seems to develop usually as a fortuitous by-product of genetic divergence that occurs for other reasons (either by natural selection or by genetic drift).

The most common mode of speciation is undoubtedly genetic divergence among populations that are sufficiently spatially isolated that their gene pools are not homogenized by gene flow. This allopatric mode of speciation may occur when two widespread populations are separated by unsuitable habitat (for example, European and American populations), but is probably more frequent and more rapid when a population in a restricted locality is cut off (for example, by colonization across a habitat barrier) from the main body of the species, and undergoes rapid divergence because of genetic drift and different selection pressures. If

sufficient genetic divergence transpires before these populations expand and encounter each other, they will not exchange genes when they meet; if divergence has been insufficient, they interbreed and speciation has not been completed.

This genetic theory of speciation is well supported by evidence from taxonomists' analyses of the relationships among populations, which run the gamut from slight genetic differentiation to complete reproductive isolation. The genetic divergence that provides reproductive isolation sometimes consists of changes in chromosome structure that cause infertility of hybrids, or of genic alterations of development, especially in gametogenesis, that cause hybrids to be inviable or infertile. Hybrid inviability and infertility constitute postmating isolating mechanisms. Many species, however, are capable of forming fertile, viable hybrids, but do not do so in nature because they do not mate with each other; differences in time of reproduction, courtship behavior, or (in plants) flower form are among the premating isolating mechanisms that maintain the distinction between the species. Such differences can arise as pleiotropic by-products of the genetic changes that developed by genetic drift or as responses to different environmental factors. In many groups of animals, courtship signals and responses can diverge rapidly because of sexual selection, in which a characteristic (such as a peacock's train) becomes exaggerated to enable its bearer (often the male) to compete more successfully for mates. Analogous phenomena may occur in some plants, such as orchids. See also: Reproductive behavior

At least in plants, speciation can occur sympatrically, without initial geographic isolation, by polyploidy. Under special circumstances, sympatric speciation can theoretically also occur in animals, but the frequency with which this occurs is strongly debated. Ernst Mayr has developed cogent arguments for supposing that it is rare. See also: Speciation

Adaptations

A frequent consequence of natural selection is that a species comes to be dominated by individuals whose features equip them better for the environment or way of life of the species. Such features are termed adaptations. Thus in England in the nineteenth century, dark variants of the peppered moth (*Biston betularia*) replaced the light genotype because they were less evident to predatory birds; their dark coloration may be considered an adaptation to predation. It is sometimes difficult to determine the adaptive significance of a trait, or whether it is an adaptation at all. However, this can often be accomplished by experiment or observation. For example, it has been shown that the color patterns of certain butterflies that resemble distasteful species provide protection against predation, by experimentally altering their color patterns and finding that the altered individuals suffer greater predation. Convergent evolution is often evidence of adaptation: for example, leaflessness has evolved in many groups of desert plants as a mechanism of reducing water loss.

Most adaptive features benefit the individuals that bear them, rather than the population as a whole. Certain features, though, appear at first sight to be altruistic, such as the warning calls that some birds emit when they see a predator. Other members of the flock benefit from being alerted, but the call seems likely to place the warner in jeopardy, so that alleles for such behavior would appear unlikely to increase in the population. However, features like this can evolve because selection can act not only at the level of individual organisms but at other levels. One possibility, the prevalence of which is strongly disputed, is group selection, whereby the genetic composition of the species changes by the differential survival (or proliferation) of whole populations that differ in gene frequency. Thus populations that happen to have a high frequency of genes for warning behavior might survive best, so that these genes increase in the species as a whole, even if they are selected against within populations. A more likely explanation for apparently altruistic traits is a form of

selection at the level of the gene known as kin selection. In developing this theory, William Hamilton argued that because relatives share alleles by common descent, an allele may increase in frequency if it causes its bearer to help its relatives survive and reproduce, even if the fitness of the bearer suffers. Kin selection, the cornerstone of the study of sociobiology, is the most likely explanation for the sterility of workers in social insects, and for warning calls and many other aspects of social behavior. See also: Sociobiology

Although many features of organisms are adaptive, not all are, and it is a serious error to suppose that species are capable of attaining ideal states of adaptation. Some characteristics are likely to have developed by genetic drift rather than natural selection, and so are not adaptations; others are side effects of adaptive features, which exist because of pleiotropy or developmental correlations. The absence of appropriate genetic variations and the constraints imposed by processes of development limit the variety of adaptive responses of which a species is capable, so that the path of ideal adaptation may be closed to it. The phylogenetic history of a species determines its current state, and thus the kinds of variations that may be available to natural selection. Most species are not capable of adapting ideally to all environmental changes: more than 99% of all the species that have ever lived are extinct.

Origin of higher taxa

Higher taxa are those above the species level, such as genera and families. A taxon such as a genus is typically a group of species, derived from a common ancestor, that share one or more features so distinctive that they merit recognition as a separate taxon. The degree of difference necessary for such recognition, however, is entirely arbitrary: there are often no sharp limits between related genera, families, or other higher taxa, and very often the diagnostic character exists in graded steps among a group of species that may be arbitrarily divided into different higher taxa. Moreover, a character that in some groups is used to distinguish higher taxa (such as the number of cotyledons, one of the features that divides flowering plants into Monocotyledonae and Dicotyledonae) sometimes varies among closely related species or even within species (as does the number of cotyledons in a few flowering plants). In addition, the fossil record of many groups shows that a trait that takes on very different forms in two living taxa has developed by intermediate steps along divergent lines from their common ancestor; thus the inner ear bones of mammals may be traced to jaw elements in reptiles that in turn are homologous to gill arch elements in Paleozoic fishes. Thus evolution of differences of great enough magnitude to define higher taxa appears to proceed usually by gradual incremental changes corresponding to the variations evident within species and among closely related species. However, it is possible that in some instances slight differences at the genetic level have altered developmental patterns so as to yield large discrete changes in a suite of developmentally correlated traits. Neoteny in salamanders, for example, whereby changes in hormone levels cause the retention of a complex of larval characteristics into the reproductive ages, appears to have a simple genetic (or in some cases a purely environmental) basis. The frequency with which such discontinuous, or saltational, changes in phenotype have occurred in evolution is a matter of some controversy. See also: Systematics; Macroevolution; Neoteny

Among the primary reasons for changes in the form of a structure is a change in its function. For example, the sting of a wasp is a morphologically and functionally altered ovipositor, the structure used by females of more primitive forms to insert eggs into the plants or animals in which the larvae develop. (Incidentally, this explains why male wasps and bees lack stings.) In many desert plants such as cacti, leaves or branches have taken on a defensive function and are modified into spines.

To a certain degree, simple evolutionary changes in structure or physiology can be reversed during evolution; but complex features, once lost or highly modified, are seldom regained in their original form, for natural

selection and genetic drift can act only on the variations of whatever “raw materials” are available. Thus numerous groups of plants, especially those that are wind-pollinated, have lost their petals; in some of these groups, insect pollination has secondarily evolved, but the structures that are colored and otherwise modified to attract insects are leaves, sepals, or other parts, the petals having been lost. See also: Phylogeny

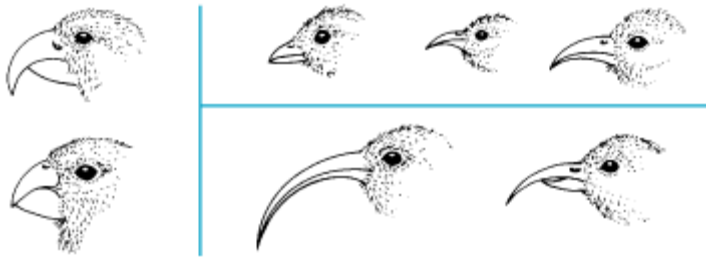


Fig. 5 Some members of an adaptive radiation, the Hawaiian honey-creepers. Although descended from finches, these birds have become adapted to a variety of ecological roles in the Hawaiian archipelago; some feed primarily on seeds (thick beaks), others on insects (short, thin beaks), others primarily on nectar (long, thin beaks). (After D. J. Futuyma, *Evolutionary Biology*, Sinauer Associates, 1979)

Rates of evolution

The characteristics of a species evolve individually or in concert with certain other traits that are developmentally or functionally correlated. Because of this mosaic pattern of evolution, it is meaningful to speak of the rate of evolution of characters, but not of species or lineages as total entities. Thus in some lineages, such as the so-called living fossils, many aspects of morphology have evolved slowly since the groups first came into existence, but evolution of their DNA and amino acid sequences has proceeded at much the same rate as in other lineages. Every species, including the living fossils, is a mixture of traits that have changed little since the species' remote ancestors, and traits that have undergone some evolutionary change in the recent past.

Rates of evolution are highly variable: whereas many characteristics have changed hardly at all for many millions of years in some lineages, others have responded rapidly to changes in selection pressures. For example, within decades, numerous species of insects have evolved resistance to insecticides, and some plants have become adapted to soils impregnated with toxic metals from mine works. Geographical variation in morphological traits has evolved within a century in house sparrows introduced into North America from Europe. Based on the geological history of their habitats, speciation in some groups of fresh-water fishes is believed to have transpired in less than 10,000 years, whereas in some groups of plants populations isolated for several million years have not become different species. In contrast to the highly variable rate of evolution of morphological and physiological characters, the rates at which nucleotide sequences of DNA and amino acid sequences of proteins have changed appears to be considerably more uniform; Motoo Kimura, Allan Wilson, and some other authors have in fact claimed that the rate of evolution at the molecular level is nearly constant, providing a “molecular clock” that may be used to estimate the time since species diverged from their common ancestors.

The fossil record of certain organisms, especially marine invertebrates, seems to indicate that species often change rather abruptly in morphology after being virtually static for up to a million years; the geological record, however, is usually so coarse that the “abrupt” changes may well have proceeded gradually over a period of many thousands of years. This pattern, of stasis punctuated by brief periods of change, has been termed punctuated equilibrium. Niles Eldredge, Stephen Gould, and Steven Stanley have suggested that the observed changes represent the origin of new species in localized populations, which become evident in the fossil record only after they expand from their site of origin. They also propose that after speciation the

species becomes incapable of substantial further change, so that evolutionary change is virtually restricted to divergence during speciation. There is little direct evidence for this notion of genetic paralysis, which is contested by most evolutionary geneticists. See also: Macroevolution

There is abundant evidence that rates of evolution are greatest when a lineage adapts to new ecological opportunities—to vacant ecological niches. Rapid divergent evolution is common, for example, when species colonize islands that harbor few competitors; similarly, the rate of evolution is high in lineages that have survived mass extinction events. The usual pattern in such instances is one of adaptive radiation: the origin, by speciation, of numerous descendant lineages that become adapted in different ways to a variety of available resources (**Fig. 5**). A famous example is the radiation of Darwin's finches in the Galápagos Islands, where related species have diverged in beak morphology and have become specialized for feeding on resources that on continents are typically preoccupied by unrelated families of birds. The major adaptive radiation of mammals occurred soon after the demise of the last dinosaurs, leading many authors to suspect that the mammalian radiation was possible only because competition had been alleviated. Thus extinction has played an important role in the history of life, making possible the subsequent diversification of groups that otherwise might not have flourished.

Evolutionary trends

The history of life is not one of progress in any one direction, but of adaptive radiation on a grand scale: the descendants of any one lineage diverge as they adapt to different resources, habitats, or ways of life, acquiring their own specialized features as they do so. There is no evidence that evolution has any goal, nor does the mechanistic theory of evolutionary processes admit of any way in which genetic change can have a goal or be directed toward the future.

Nevertheless, in examining the history of a major group of organisms, it is sometimes possible to discern in retrospect a trend in one or more characters. For example, in one group of horses that became increasingly adapted to grazing and running, body size, tooth size, and the number of the toes changed more or less monotonically (although not at a constant rate) during the Tertiary Period. Once embarked on a way of life, a lineage experiences selection for improvement in the features that adapt it to that particular way of life, and the more specialized such features become, the less capable they are of being modified in other directions. A very common trend, for example, is reduction and simplification of parts, as in the reduction of limbs, lungs, and other features of snakes, which are now so morphologically and developmentally committed to their ways of life that they would be incapable of reevolving the lizardlike form of their ancestors. But although such trends can be discerned retrospectively, no one can say that a group such as the snakes was destined from their beginning to take the evolutionary path that they in fact followed: other roads may have been open to them at one time, but are open no longer. All history, including evolutionary history, is contingent on antecedent events.

For particular groups, one can document trends of increasing reduction and simplification; of the converse, increasing structural or behavioral complexity; of increased ecological specialization; of its converse, increased homeostatic freedom from the environment; and of increased mechanical or functional efficiency of morphological and physiological features. Few such trends continue unabated throughout evolutionary time; most are terminated by complete extinction, the fate of most of the higher taxa of organisms that have ever existed.

For life taken as a whole, there is some very tentative evidence that species (at least of marine invertebrates) have on average become more resistant to extinction, so that Cenozoic species have persisted longer than Mesozoic or Paleozoic species; but any such trend has been interrupted repeatedly by mass

extinction events (the causes of which are actively disputed) that have eliminated much of the Earth's biota. The total number of species has increased after each such extinction event, and has been amplified in the last 100 million years or so by continental drift, which has accentuated differences in species composition in different parts of the world. More than 1½ million living species have been described (of the 5 to 10 million that probably exist); and even though many major taxa have become extinct, the diversity of species now and in the recent past is higher than ever before in Earth's history. For life taken as a whole, the only clearly discernible trend is toward ever-increasing diversity.

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