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A Detailed Study on Evolutionary Biology

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ABSTRACT: Evolutionary biology is the subfield of biology that studies the evolutionary processes (natural selection, common descent, speciation) that produced the diversity of life on Earth. It is also defined as the study of the history of life forms on Earth. Evolution holds that all species are related and gradually change over generations.[1] In a population, the genetic variations affect the phenotypes (physical characteristics) of an organism. These changes in the phenotypes will be an advantage to some organisms, which will then be passed onto their offspring. Some examples of evolution in species over many generations are the peppered moth and flightless birds. In the 1930s, the discipline of evolutionary biology emerged through what Julian Huxley called the modern synthesis of understanding, from previously unrelated fields of biological research, such as genetics and ecology, systematics, and paleontology.

KEYWORDS-evolutionar,biology, earth, phenotypes, discipline, research

I. EVOLUTIONARY BIOLOGY

The investigational range of current research has widened to encompass the genetic architecture of adaptation, molecular evolution, and the different forces that contribute to evolution, such as sexual selection, genetic drift, and biogeography. Moreover, the newer field of evolutionary developmental biology ("evo-devo") investigates how embryogenesis is controlled, thus yielding a wider synthesis that integrates developmental biology with the fields of study covered by the earlier evolutionary synthesis.[2]

Evolution is the central unifying concept in biology. Biology can be divided into various ways. One way is by the level of biological organization, from molecular to cell, organism to population. Another way is by perceived taxonomic group, with fields such as zoology, botany, and microbiology, reflecting what was once seen as the major divisions of life. A third way is by approaches, such as field biology, theoretical biology, experimental evolution, and paleontology. These alternative ways of dividing up the subject have been combined with evolutionary biology to create subfields like evolutionary ecology and evolutionary developmental biology.

More recently, the merge between biological science and applied sciences gave birth to new fields that are extensions of evolutionary biology, including evolutionary robotics, engineering,[3] algorithms,[4] economics,[5] and architecture.[6] The basic mechanisms of evolution are applied directly or indirectly to come up with novel designs or solve problems that are difficult to solve otherwise. The research generated in these applied fields, contribute towards progress, especially from work on evolution in computer science and engineering fields such as mechanical engineering.[7]

Different types of evolution

Adaptive evolution

Adaptive evolution[8] relates to evolutionary changes that happen due to the changes in the environment, this makes the organism suitable to its habitat. This change increases the chances of survival and reproduction of the organism (this can be referred to as an organism's fitness). For example, Darwin's Finches[9] on Galapagos island developed different shaped beaks in order to survive for a long time. Adaptive evolution can also be convergent evolution if two distantly related species live in similar environments facing similar pressures.

Convergent evolution

Convergent evolution is the process in which related or distantly related organisms evolve similar characteristics independently. This type of evolution creates analogous structures which have a similar function, structure, or form between the two species. For example, sharks and dolphins look alike but they are not related. Likewise, birds, flying insects, and bats all have the ability to fly, but they are not related to each other. These similar traits tend to evolve from having similar environmental pressures.

Divergent evolution

Divergent evolution is the process of speciation. This can happen in several ways:

- Allopatric speciation is when species are separated by a physical barrier that separates the population into two groups. evolutionary mechanisms such as genetic drift and natural selection can then act independently on each population.[10]

- Peripatric speciation is a type of allopatric speciation that occurs when one of the new populations is considerably smaller than the other initial population. This leads to the founder's effect and the population can have different allele frequencies and phenotypes than the original population. These small populations are also more likely to see effects from genetic drift.[10]

- Parapatric speciation is allopatric speciation but occurs when the species diverge without a physical barrier separating the population. This tends to occur when a population of a species is incredibly large and occupies a vast environment.[10]

- Sympatric speciation is when a new species or subspecies sprouts from the original population while still occupying the same small environment, and without any physical barriers separating them from members of their original population. There is scientific debate as to whether sympatric speciation actually exists.[10]

- Artificial speciation is when scientists purposefully cause new species to emerge to use in laboratory procedures.[10]

Coevolution

The influence of two closely associated species is known as coevolution.[11] When two or more species evolve in company with each other, one species adapts to changes in other species. This type of evolution often happens in species that have symbiotic relationships. For example, predator-prey coevolution, this is the most common type of co-evolution. In this, the predator must evolve to become a more effective hunter because there is a selective pressure on the prey to steer clear of capture. The prey in turn need to develop better survival strategies. The Red Queen hypothesis is an example of predator-prey interations. The relationship between pollinating insects like bees and flowering plants, herbivores and plants, are also some common examples of diffuse or guild coevolution.[12]

Mechanism: The process of evolution

The mechanisms of evolution focus mainly on mutation, genetic drift, gene flow, non-random mating, and natural selection.

Mutation: Mutation[13] is a change in the DNA sequence inside a gene or a chromosome of an organism. Most mutations are deleterious, or neutral; i.e. they can neither harm nor benefit, but can also be beneficial sometimes.

Genetic drift: Genetic drift[14] is a variational process, it happens as a result of the sampling errors from one generation to another generation where a random event that happens by chance in nature changes or influences allele frequency within a population. It has a much stronger effect on small populations than large ones.

Gene flow: Gene flow[15] is the transfer of genetic material from the gene pool of one population to another. In a population, migration occurs from one species to another, resulting in the change of allele frequency.

Natural selection: The survival and reproductive rate of a species depends on the adaptability of the species to their environment. This process is called natural selection.[16] Some species with certain traits in a population have higher survival and reproductive rate than others (fitness), and they pass on these genetic features to their offsprings.

Evolutionary developmental biology

In evolutionary developmental biology scientists look at how the different processes in development play a role in how a specific organism reaches its current body plan. The genetic regulation of ontogeny and the phylogenetic process is what allows for this kind of understanding of biology to be possible. By looking at different processes during development, and going through the evolutionary tree, one can determine at which point a specific structure came about. For example, the three germ layers can be observed to not be present in cnidarians and ctenophores, which instead present in worms, being more or less developed depending on the kind of worm itself. Other structures like the development of Hox genes and sensory organs such as eyes can also be traced with this practice.[17]

Phylogenetic Trees

The tree of life

Phylogenetic Trees are representations of genetic lineage. They are figures that show how related species are to one another. They formed by analyzing the physical traits as well as the similarities of the DNA between species. Then by using a molecular clock scientists can estimate when the species diverged. An example of a phylogeny would be the tree of life.

Homologs

Genes that have shared ancestry are homologs. If a speciation event occurs and one gene ends up in two different species the genes are now orthologous. If a gene is duplicated within the a singular species then it is a paralog. A molecular clock can be used to estimate when these events occurred.[18]

The idea of evolution by natural selection was proposed by Charles Darwin in 1859, but evolutionary biology, as an academic discipline in its own right, emerged during the period of the modern synthesis in the 1930s and 1940s.[19] It was not until the 1980s that many universities had departments of evolutionary biology. In the United States, many universities have created departments of *molecular and cell biology* or *ecology and evolutionary biology*, in place of the older departments of botany and zoology. Palaeontology is often grouped with earth science.

Microbiology too is becoming an evolutionary discipline now that microbial physiology and genomics are better understood. The quick generation time of bacteria and viruses such as bacteriophages makes it possible to explore evolutionary questions.

Many biologists have contributed to shaping the modern discipline of evolutionary biology. Theodosius Dobzhansky and E. B. Ford established an empirical research programme. Ronald Fisher, Sewall Wright, and J. B. S. Haldane created a sound theoretical framework. Ernst Mayr in systematics, George Gaylord Simpson in paleontology and G. Ledyard Stebbins in botany helped to form the modern synthesis. James Crow,[20] Richard Lewontin,[21] Dan Hartl,[22] Marcus Feldman,[23][24] and Brian Charlesworth[25] trained a generation of evolutionary biologists.

Current research topics

Current research in evolutionary biology covers diverse topics and incorporates ideas from diverse areas, such as molecular genetics and computer science.

First, some fields of evolutionary research try to explain phenomena that were poorly accounted for in the modern evolutionary synthesis. These include speciation,[26][27] the evolution of sexual reproduction,[28][29] the evolution of cooperation, the evolution of ageing,[30] and evolvability.[31]

Second, some evolutionary biologists ask the most straightforward evolutionary question: "what happened and when?". This includes fields such as paleobiology, where paleobiologists and evolutionary biologists, including Thomas Halliday and Anjali Goswami, studied the evolution of early mammals going far back in time during the Mesozoic and Cenozoic eras (between 299 million to 12,000 years ago).[32][33] Other fields related to generic exploration of evolution ("what happened and when?") include systematics and phylogenetics.

Third, the modern evolutionary synthesis was devised at a time when nobody understood the molecular basis of genes. Today, evolutionary biologists try to determine the genetic architecture of interesting evolutionary phenomena such as adaptation and speciation. They seek answers to questions such as how many genes are involved, how large are the effects of each gene, how interdependent are the effects of different genes, what do the genes do, and what changes happen to them (e.g., point mutations vs. gene duplication or even genome duplication). They try to reconcile the high heritability seen in twin studies with the difficulty in finding which genes are responsible for this heritability using genome-wide association studies.[34]

One challenge in studying genetic architecture is that the classical population genetics that catalysed the modern evolutionary synthesis must be updated to take into account modern molecular knowledge. This requires a great deal of mathematical development to relate DNA sequence data to evolutionary theory as part of a theory of molecular evolution. For example, biologists try to infer which genes have been under strong selection by detecting selective sweeps.[35]

Fourth, the modern evolutionary synthesis involved agreement about which forces contribute to evolution, but not about their relative importance.[36] Current research seeks to determine this. Evolutionary forces include natural selection, sexual selection, genetic drift, genetic draft, developmental constraints, mutation bias and biogeography.

This evolutionary approach is key to much current research in organismal biology and ecology, such as life history theory. Annotation of genes and their function relies heavily on comparative approaches. The field of evolutionary developmental biology ("evo-devo") investigates how developmental processes work, and compares them in different organisms to determine how they evolved.

Many physicians do not have enough background in evolutionary biology, making it difficult to use it in modern medicine.[37] However, there are efforts to gain a deeper understanding of disease through evolutionary medicine and to develop evolutionary therapies.

Drug resistance today

Evolution plays a role in resistance of drugs; for example, how HIV becomes resistant to medications and the body's immune system. The mutation of resistance of HIV is due to the natural selection of the survivors and their offspring. The few HIV that survive the immune system reproduced and had offspring that were also resistant to the immune system.[38] Drug resistance also causes many problems for patients such as a worsening sickness or the sickness can mutate into something that can no longer be cured with medication. Without the proper medicine, a sickness can be the death of a patient. If their body has resistance to a certain number of drugs, then the right medicine will be harder and harder to find. Not completing the prescribed full course of antibiotic is also an example of resistance that will cause the bacteria against which the antibiotic is being taken to evolve and continue to spread in the body.[39] When the full dosage of the medication does not enter the body and perform its proper job, the bacteria that survive the initial dosage will continue to reproduce. This can make for another bout of sickness later on that will be more difficult to cure because the bacteria involved will be resistant to the first medication used. Taking the full course of medicine that is prescribed is a vital step in avoiding antibiotic resistance.

Individuals with chronic illnesses, especially those that can recur throughout a lifetime, are at greater risk of antibiotic resistance than others.[40] This is because overuse of a drug or too high of a dosage can cause a patient's immune system to weaken and the illness will evolve and grow stronger. For example, cancer patients will need a stronger and stronger dosage of medication because of their low functioning immune system.[41]

Journals

Some scientific journals specialise exclusively in evolutionary biology as a whole, including the journals *Evolution*, *Journal of Evolutionary Biology*, and *BMC Evolutionary Biology*. Some journals cover sub-specialties within evolutionary biology, such as the journals *Systematic Biology*, *Molecular Biology and Evolution* and its sister journal *Genome Biology and Evolution*, and *Cladistics*.

Other journals combine aspects of evolutionary biology with other related fields. For example, *Molecular Ecology*, *Proceedings of the Royal Society of London Series B*, *The American Naturalist* and *Theoretical Population Biology* have overlap with ecology and other aspects of organismal biology. Overlap with ecology is also prominent in the review journals *Trends in Ecology and Evolution* and *Annual Review of Ecology, Evolution, and Systematics*. The journals *Genetics* and *PLoS Genetics* overlap with molecular genetics questions that are not obviously evolutionary in nature.

II. EVOLUTION AND GENETIC DRIFT

In biology, evolution is the change in heritable characteristics of biological populations over successive generations.[1][2] Evolution occurs when evolutionary processes such as natural selection (including sexual selection) and genetic drift act on genetic variation, resulting in certain characteristics becoming more or less common within a population over successive generations.[3] The process of evolution has given rise to biodiversity at every level of biological organisation.[4][5]

The theory of evolution by natural selection was conceived independently by Charles Darwin and Alfred Russel Wallace in the mid-19th century as an explanation for why organisms are adapted to their physical and biological environments. The theory was first set out in detail in Darwin's book *On the Origin of Species*.[6] Evolution by natural selection is established by observable facts about living organisms: (1) more offspring are often produced than can possibly survive; (2) traits vary among individuals with respect to their morphology, physiology, and behaviour; (3) different traits confer different rates of survival and reproduction (differential fitness); and (4) traits can be passed from generation to generation (heritability of fitness).[7] In successive generations, members of a population are therefore more likely to be replaced by the offspring of parents with favourable characteristics for that environment.

In the early 20th century, competing ideas of evolution were refuted and evolution was combined with Mendelian inheritance and population genetics to give rise to modern evolutionary theory.[8] In this synthesis the basis for heredity is in DNA molecules that pass information from generation to generation. The processes that change DNA in a population include natural selection, genetic drift, mutation, and gene flow.[3]

All life on Earth—including humanity—shares a last universal common ancestor (LUCA),[9][10][11] which lived approximately 3.5–3.8 billion years ago.[12] The fossil record includes a progression from early biogenic graphite[13] to microbial mat fossils[14][15][16] to fossilised multicellular organisms. Existing patterns of biodiversity have been shaped by repeated formations of new species (speciation), changes within species (anagenesis), and loss of species (extinction) throughout the evolutionary history of life on Earth.[17] Morphological and biochemical traits tend to be more similar among species that share a more recent common ancestor, which historically was used to reconstruct phylogenetic trees, although direct comparison of genetic sequences is a more common method today.[18][19]

Evolutionary biologists have continued to study various aspects of evolution by forming and testing hypotheses as well as constructing theories based on evidence from the field or laboratory and on data generated by the methods of mathematical and theoretical biology. Their discoveries have influenced not just the development of biology but also other fields including agriculture, medicine, and computer science.[20]

Evolution in organisms occurs through changes in heritable characteristics—the inherited 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.[21] Inherited traits are controlled by genes and the complete set of genes within an organism's genome (genetic material) is called its *genotype*.[22]

The complete set of observable traits that make up the structure and behaviour of an organism is called its *phenotype*. Some of these traits come from the interaction of its genotype with the environment while others are neutral.[23] Some observable characteristics 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. The phenotype is the ability of the skin to tan when exposed to sunlight. However, some people tan more easily than others, due to differences in genotypic variation; a striking example are people with the inherited trait of albinism, who do not tan at all and are very sensitive to sunburn.[24]

Heritable characteristics are passed from one generation to the next via DNA, a molecule that encodes genetic information.[22] DNA is a long biopolymer composed of four types of bases. The sequence of bases along a particular DNA molecule specifies 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, each long strand of DNA is called a chromosome. 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.[25] However, while this simple correspondence between an allele and a trait works in some cases, most traits are influenced by multiple genes in a quantitative or epistatic manner.[26][27]

Evolution can occur if there is genetic variation within a population. Variation comes from mutations in the genome, reshuffling of genes through sexual reproduction and migration between populations (gene flow). Despite the constant introduction of new variation through mutation and gene flow, most of the genome of a species is very similar among all individuals of that species.[28] However, discoveries in the field of evolutionary developmental biology have demonstrated that even relatively small differences in genotype can lead to dramatic differences in phenotype both within and between species.

An individual organism's phenotype results from both its genotype and the influence of the environment it has lived in.[27] The modern evolutionary synthesis defines evolution as the change over time in this genetic variation. The frequency of one particular allele will become more or less prevalent relative to other forms of that gene. Variation disappears when a new allele reaches the point of fixation—when it either disappears from the population or replaces the ancestral allele entirely.[29]

Mutations are changes in the DNA sequence of a cell's genome and are the ultimate source of genetic variation in all organisms.[30] When mutations occur, they may alter the product of a gene, or prevent the gene from functioning, or have no effect.

About half of the mutations in the coding regions of protein-coding genes are deleterious - the other half are neutral. A small percentage of the total mutations in this region confer a fitness benefit.[31] Some of the mutations in other parts of the genome are deleterious but the vast majority are neutral. A few are beneficial.

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.[32] Extra copies of genes are a major source of the raw material needed for new genes to evolve.[33] This is important because most new genes evolve within gene families from pre-existing genes that share common ancestors.[34] 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.[35]

New genes can be generated 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.[36][37] Other types of mutations can even generate entirely new genes from previously noncoding DNA, a phenomenon termed *de novo* gene birth.[38][39]

The generation 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 (exon shuffling).[40][41] When new genes are assembled from shuffling pre-existing parts, domains act as modules with simple independent functions, which can be mixed together to produce new combinations with new and complex functions.[42] For example, polyketide synthases are large enzymes that make antibiotics; they contain up to 100 independent domains that each catalyse one step in the overall process, like a step in an assembly line.[43]

One example of mutation is wild boar piglets. They are camouflage coloured and show a characteristic pattern of dark and light longitudinal stripes. However, mutations in *melanocortin 1 receptor* (*MC1R*) disrupt the pattern. The majority of pig breeds carry MC1R mutations disrupting wild-type colour and different mutations causing dominant black colouring.[44]

Sex and recombination

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.[45] 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.[46] Sex usually increases genetic variation and may increase the rate of evolution.[47][48]

The two-fold cost of sex was first described by John Maynard Smith.[49] The first cost is that in sexually dimorphic species only one of the two sexes can bear young. This cost does not apply to hermaphroditic species, like most plants and many invertebrates. The second cost is that any individual who reproduces sexually can only pass on 50% of its genes to any individual offspring, with even less passed on as each new generation passes.[50] Yet sexual reproduction is the more common means of reproduction among eukaryotes and multicellular organisms. The Red Queen hypothesis has been used to explain the significance of sexual reproduction as a means to enable continual evolution and adaptation in response to coevolution with other species in an ever-changing environment.[50][51][52][53] Another hypothesis is that sexual reproduction is primarily an adaptation for promoting accurate recombinational repair of damage in germline DNA, and that increased diversity is a byproduct of this process that may sometimes be adaptively beneficial.[54][55]

Gene flow

Gene flow is the exchange of genes between populations and between species.[56] It can therefore be a source of variation that is new to a population or to a species. Gene flow can be caused by the movement of individuals between separate populations of organisms, as might be caused by the movement of mice between inland and coastal populations, or the movement of pollen between heavy-metal-tolerant and heavy-metal-sensitive populations of grasses.

Gene transfer between species includes the formation of hybrid organisms and horizontal gene transfer. 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.[57] 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.[58] Horizontal transfer of genes from bacteria to eukaryotes such as the yeast *Saccharomyces cerevisiae* and the adzuki bean weevil *Callosobruchus chinensis* has occurred.[59][60] An example of larger-scale transfers are the eukaryotic bdelloid rotifers, which have received a range of genes from bacteria, fungi and plants.[61] Viruses can also carry DNA between organisms, allowing transfer of genes even across biological domains.[62]

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Large-scale gene transfer has also occurred between the ancestors of eukaryotic cells and bacteria, during the acquisition of chloroplasts and mitochondria. It is possible that eukaryotes themselves originated from horizontal gene transfers between bacteria and archaea.[63]

Epigenetics

Some heritable changes cannot be explained by changes to the sequence of nucleotides in the DNA. These phenomena are classed as epigenetic inheritance systems.[64] 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.[65] 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 canalisation.[66] 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 effects that modify and feed back into the selection regime of subsequent generations.[67] Other examples of heritability in evolution that are not under the direct control of genes include the inheritance of cultural traits and symbiogenesis.[68][69]

Evolutionary forces

From a neo-Darwinian perspective, evolution occurs when there are changes in the frequencies of alleles within a population of interbreeding organisms,[70] for example, the allele for black colour in a population of moths becoming more common. Mechanisms that can lead to changes in allele frequencies include natural selection, genetic drift, and mutation bias.

Natural selection

Evolution by natural selection is the process by which traits that enhance survival and reproduction become more common in successive generations of a population. It embodies three principles:[7]

- Variation exists within populations of organisms with respect to morphology, physiology and behaviour (phenotypic variation).
- Different traits confer different rates of survival and reproduction (differential fitness).
- These traits can be passed from generation to generation (heritability of fitness).

More offspring are produced than can possibly survive, and these conditions produce competition between organisms for survival and reproduction. Consequently, organisms with traits that give them an advantage over their competitors are more likely to pass on their traits to the next generation than those with traits that do not confer an advantage.[71] This teleonomy is the quality whereby the process of natural selection creates and preserves traits that are seemingly fitted for the functional roles they perform.[72] Consequences of selection include nonrandom mating[73] and genetic hitchhiking.

The central concept of natural selection is the evolutionary fitness of an organism.[74] Fitness is measured by an organism's ability to survive and reproduce, which determines the size of its genetic contribution to the next generation.[74] 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.[75] 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.[74]

If an allele increases fitness more than the other alleles of that gene, then with each generation this allele has a higher probability of becoming 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 likely becoming rarer—they are "selected *against*."[76]

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.[25] 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.[77][78] However, a re-activation of dormant genes, as long as they have not been eliminated from the genome and were only suppressed perhaps for hundreds of generations, can lead to the re-occurrence of traits thought to be lost like hindlegs in dolphins, teeth in chickens, wings in wingless stick insects, tails and additional nipples in humans etc. "Throwbacks" such as these are known as atavisms.[79]

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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.[80] 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 stabilising selection there is selection against extreme trait values on both ends, which causes a decrease in variance around the average value and less diversity.[71][81] This would, for example, cause organisms to eventually have a similar height.

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 (i.e., exchange of materials between living and nonliving parts) within the system...."[82] 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.

Natural selection can act at different levels of organisation, such as genes, cells, individual organisms, groups of organisms and species.[83][84][85] Selection can act at multiple levels simultaneously.[86] An example of selection occurring below the level of the individual organism are genes called transposons, which can replicate and spread throughout a genome.[87] Selection at a level above the individual, such as group selection, may allow the evolution of cooperation.[88]

Genetic drift

Genetic drift is the random fluctuation of allele frequencies within a population from one generation to the next.[89] When selective forces are absent or relatively weak, allele frequencies are equally likely to *drift* upward or downward in each successive generation because the alleles are subject to sampling error.[90] This drift halts when an allele eventually becomes fixed, either by disappearing from the population or by 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 begin with the same genetic structure to drift apart into two divergent populations with different sets of alleles.[91]

According to the neutral theory of molecular evolution most evolutionary changes are the result of the fixation of neutral mutations by genetic drift.[92] In this model, most genetic changes in a population are thus the result of constant mutation pressure and genetic drift.[93] This form of the neutral theory has been debated since it does not seem to fit some genetic variation seen in nature.[94][95] A better-supported version of this model is the nearly neutral theory, according to which a mutation that would be effectively neutral in a small population is not necessarily neutral in a large population.[71] Other theories propose that genetic drift is dwarfed by other stochastic forces in evolution, such as genetic hitchhiking, also known as genetic draft.[90][96][97] Another concept is constructive neutral evolution (CNE), which explains that complex systems can emerge and spread into a population through neutral transitions due to the principles of excess capacity, presuppression, and ratcheting,[98][99][100] and it has been applied in areas ranging from the origins of the spliceosome to the complex interdependence of microbial communities.[101][102][103]

The time it takes a neutral allele to become fixed by genetic drift depends on population size; fixation is more rapid in smaller populations.[104] The number of individuals in a population is not critical, but instead a measure known as the effective population size.[105] The effective population is usually smaller than the total population since it takes into account factors such as the level of inbreeding and the stage of the lifecycle in which the population is the smallest.[105] The effective population size may not be the same for every gene in the same population.[106]

It is usually difficult to measure the relative importance of selection and neutral processes, including drift.[107] The comparative importance of adaptive and non-adaptive forces in driving evolutionary change is an area of current research.[108]

Mutation bias

Mutation bias is usually conceived as a difference in expected rates for two different kinds of mutation, e.g., transition-transversion bias, GC-AT bias, deletion-insertion bias. This is related to the idea of developmental bias. Haldane[109] and Fisher[110] argued that, because mutation is a weak pressure easily overcome by selection, tendencies of mutation would be ineffectual except under conditions of neutral evolution or extraordinarily high mutation rates. This opposing-pressures argument was long used to dismiss the possibility of internal tendencies in evolution,[111] until the molecular era prompted renewed interest in neutral evolution.

Noboru Sueoka[112] and Ernst Freese[113] proposed that systematic biases in mutation might be responsible for systematic differences in genomic GC composition between species. The identification of a GC-biased *E. coli* mutator strain in 1967,[114] along with the proposal of the neutral theory, established the plausibility of mutational explanations for molecular patterns, which are now common in the molecular evolution literature.

For instance, mutation biases are frequently invoked in models of codon usage.[115] Such models also include effects of selection, following the mutation-selection-drift model,[116] which allows both for mutation biases and differential selection based on effects on translation. Hypotheses of mutation bias have played an important role in the development of thinking about the evolution of genome composition, including isochores.[117] Different insertion vs. deletion biases in different taxa can lead to the evolution of different genome sizes.[118][119] The hypothesis of Lynch regarding genome size relies on mutational biases toward increase or decrease in genome size.

However, mutational hypotheses for the evolution of composition suffered a reduction in scope when it was discovered that (1) GC-biased gene conversion makes an important contribution to composition in diploid organisms such as mammals[120] and (2) bacterial genomes frequently have AT-biased mutation.[121]

Contemporary thinking about the role of mutation biases reflects a different theory from that of Haldane and Fisher. More recent work[111] showed that the original "pressures" theory assumes that evolution is based on standing variation: when evolution depends on events of mutation that introduce new alleles, mutational and developmental biases in the introduction of variation (arrival biases) can impose biases on evolution without requiring neutral evolution or high mutation rates.[111][122] Several studies report that the mutations implicated in adaptation reflect common mutation biases[123][124][125] though others dispute this interpretation.[126]

Genetic hitchhiking

Recombination allows alleles on the same strand of DNA to become separated. 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.[127] This tendency is measured by finding how often two alleles occur together on a single chromosome compared to expectations, 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 or genetic draft.[128] Genetic draft caused by the fact that some neutral genes are genetically linked to others that are under selection can be partially captured by an appropriate effective population size.[96]

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.[130] Traits that evolved through sexual selection are particularly prominent among males of several animal species. Although sexually favoured, traits such as cumbersome antlers, mating calls, large body size and bright colours often attract predation, which compromises the survival of individual males.[131][132] This survival disadvantage is balanced by higher reproductive success in males that show these hard-to-fake, sexually selected traits.[133]

Natural outcomes

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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 cooperating 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 distinguished based on time scale as macroevolution versus microevolution. Macroevolution refers to evolution that occurs at or above the level of species, in particular speciation and extinction; whereas microevolution refers to smaller evolutionary changes within a species or population, in particular shifts in allele frequency and adaptation.[135] Macroevolution the outcome of long periods of microevolution.[136] Thus, the distinction between micro- and macroevolution is not a fundamental one—the difference is simply the time involved.[137] 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.[138][139][140]

A common misconception is that evolution has goals, long-term plans, or an innate tendency for "progress", as expressed in beliefs such as orthogenesis and evolutionism; realistically however, evolution has no long-term goal and does not necessarily produce greater complexity.[141][142][143] 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.[144] For example, the overwhelming majority of species are microscopic prokaryotes, which form about half the world's biomass despite their small size,[145] and constitute the vast majority of Earth's biodiversity.[146] 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.[147] Indeed, the evolution of microorganisms is particularly important to evolutionary research, since their rapid reproduction allows the study of experimental evolution and the observation of evolution and adaptation in real time.[148][149]

III. ADAPTATION

Adaptation is the process that makes organisms better suited to their habitat.[150][151] 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.[152] 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.[153]
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.[154]
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.[155]

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.[156] Other striking examples are the bacteria *Escherichia coli* evolving the ability to use citric acid as a nutrient in a long-term laboratory experiment,[157] *Flavobacterium* evolving a novel enzyme that allows these bacteria to grow on the by-products of nylon manufacturing,[158][159] and the soil bacterium *Sphingobium* evolving an entirely new metabolic pathway that degrades the synthetic pesticide pentachlorophenol.[160][161] 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).[162][163][164][165]

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.[167] However, since all living organisms are related to some extent,[168] 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.[169][170]

During evolution, some structures may lose their original function and become vestigial structures.[171] 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,[172] the non-functional remains of eyes in blind cave-dwelling fish,[173] wings in flightless birds,[174] the presence of hip bones in whales and snakes,[166] and sexual traits in organisms that reproduce via asexual reproduction.[175] Examples of vestigial structures in humans include wisdom teeth,[176] the coccyx,[171] the vermiform appendix,[171] and other behavioural vestiges such as goose bumps[177][178] and primitive reflexes.[179][180][181]

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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.[182] 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.[182] Within cells, molecular machines such as the bacterial flagella[183] and protein sorting machinery[184] evolved by the recruitment of several pre-existing proteins that previously had different functions.[135] 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.[185][186]

An area of current investigation in evolutionary developmental biology is the developmental basis of adaptations and exaptations.[187] This research addresses the origin and evolution of embryonic development and how modifications of development and developmental processes produce novel features.[188] These studies have shown that evolution can alter development to produce new structures, such as embryonic bone structures that develop into the jaw in other animals instead forming part of the middle ear in mammals.[189] 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.[190] It is now becoming clear that most alterations in the form of organisms are due to changes in a small set of conserved genes.[191]

Coevolution

Interactions between organisms can produce both conflict and cooperation. 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 coevolution.[192] 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.[193]

Cooperation

Not all co-evolved interactions between species involve conflict.[194] 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.[195] 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.[196]

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.[197]

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.[198] 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.[199] Other processes that may promote cooperation include group selection, where cooperation provides benefits to a group of organisms.[200]

Speciation

There are multiple ways to define the concept of "species." The choice of definition is dependent on the particularities of the species concerned.[202] 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.[203] The Biological Species Concept (BSC) is a classic example of the interbreeding approach. Defined by evolutionary biologist 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."[204] Despite its wide and long-term use, the BSC like other species concepts is not without controversy, for example, because genetic recombination among prokaryotes is not an intrinsic aspect of reproduction;[205] this is called the species problem.[202] Some researchers have attempted a unifying monistic definition of species, while others adopt a pluralistic approach and suggest that there may be different ways to logically interpret the definition of a species.[202][203]

Barriers to reproduction between two diverging sexual 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.[206] 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.[207] The importance of hybridisation in producing new species of animals is unclear, although cases have been seen in many types of animals,[208] with the gray tree frog being a particularly well-studied example.[209]

Speciation has been observed multiple times under both controlled laboratory conditions and in nature.[210] In sexually reproducing organisms, speciation results from reproductive isolation followed by genealogical divergence. There are four primary geographic modes of 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.[211][212] As selection and drift act independently on populations isolated from the rest of their species, separation may eventually produce organisms that cannot interbreed.[213]

The second mode 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 after an increase in inbreeding increases selection on homozygotes, leading to rapid genetic change.[214]

The third mode 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.[201] 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.[215] 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.[216]

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.[217] Generally, sympatric speciation in animals requires the evolution of both genetic differences and nonrandom mating, to allow reproductive isolation to evolve.[218]

One type of sympatric speciation involves crossbreeding 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.[219] 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.[220] An example of such a speciation event is when the plant species *Arabidopsis thaliana* and *Arabidopsis arenosa* crossbred to give the new species *Arabidopsis suecica*.[221] This happened about 20,000 years ago,[222] and the speciation process has been repeated in the laboratory, which allows the study of the genetic mechanisms involved in this process.[223] 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.[224]

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.[225] 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.[139]

Extinction

Extinction is the disappearance of an entire species. Extinction is not an unusual event, as species regularly appear through speciation and disappear through extinction.[226] Nearly all animal and plant species that have lived on Earth are now extinct,[227] and extinction appears to be the ultimate fate of all species.[228] These extinctions have happened continuously throughout the history of life, although the rate of extinction spikes in occasional mass extinction events.[229] The Cretaceous–Paleogene extinction event, during which the non-avian dinosaurs became extinct, is the most well-known, but the earlier Permian–Triassic extinction event was even more severe, with approximately 96% of all marine species driven to extinction.[229] 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 current species may be extinct by the mid 21st century.[230] Human activities are now the primary cause of the ongoing extinction event;[231][232] global warming may further accelerate it in the future.[233] Despite the estimated extinction of more than 99% of all species that ever lived on Earth,[234][235] about 1 trillion species are estimated to be on Earth currently with only one-thousandth of 1% described.[236]

The role of extinction in evolution is not very well understood and may depend on which type of extinction is considered.[229] 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 (the competitive exclusion principle).[237] 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.[84] 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.[238]

Applications

Concepts and models used in evolutionary biology, such as natural selection, have many applications.[239]

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.[240] 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. Proteins with valuable properties have evolved by repeated rounds of mutation and selection (for example modified enzymes and new antibodies) in a process called directed evolution.[241]

Understanding the changes that have occurred during an organism's evolution can reveal the genes needed to construct parts of the body, genes which may be involved in human genetic disorders.[242] 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.[243] This helped identify genes required for vision and pigmentation.[244]

Evolutionary theory has many applications in medicine. Many human diseases are not static phenomena, but capable of evolution. Viruses, bacteria, fungi and cancers evolve to be resistant to host immune defences, as well as to pharmaceutical drugs.[245][246][247] These same problems occur in agriculture with pesticide[248] and herbicide[249] resistance. It is possible that we are facing the end of the effective life of most of available antibiotics[250] and predicting the evolution and evolvability[251] of our pathogens and devising strategies to slow or circumvent it is requiring deeper knowledge of the complex forces driving evolution at the molecular level.[252]

In computer science, simulations of evolution using evolutionary algorithms and artificial life started in the 1960s and were extended with simulation of artificial selection.[253] 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.[254] Genetic algorithms in particular became popular through the writing of John Henry Holland.[255] Practical applications also include automatic evolution of computer programmes.[256] 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.[257]

Origin of life

The Earth is about 4.54 billion years old.[258][259][260] The earliest undisputed evidence of life on Earth dates from at least 3.5 billion years ago,[12][261] during the Eoarchean Era after a geological crust started to solidify following the earlier molten Hadean Eon. Microbial mat fossils have been found in 3.48 billion-year-old sandstone in Western Australia.[14][15][16] Other early physical evidence of a biogenic substance is graphite in 3.7 billion-year-old metasedimentary rocks discovered in Western Greenland[13] as well as "remains of biotic life" found in 4.1 billion-year-old rocks in Western Australia.[262][263] Commenting on the Australian findings, Stephen Blair Hedges wrote: "If life arose relatively quickly on Earth, then it could be common in the universe."[262][264] In July 2016, scientists reported identifying a set of 355 genes from the last universal common ancestor (LUCA) of all organisms living on Earth.[265]

More than 99% of all species, amounting to over five billion species,[266] that ever lived on Earth are estimated to be extinct.[234][235] Estimates on the number of Earth's current species range from 10 million to 14 million,[267][268] of which about 1.9 million are estimated to have been named[269] and 1.6 million documented in a central database to date,[270] leaving at least 80% not yet described.

Highly energetic chemistry is thought 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.[10] The current scientific consensus is that the complex biochemistry that makes up life came from simpler chemical reactions.[271][272] The beginning of life may have included self-replicating molecules such as RNA[273] and the assembly of simple cells.[274]

Common descent

All organisms on Earth are descended from a common ancestor or ancestral gene pool.[168][275] Current species are a stage in the process of evolution, with their diversity the product of a long series of speciation and extinction events.[276] 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. Fourth, organisms can be classified using these similarities into a hierarchy of nested groups, similar to a family tree.[277]

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.[278][279] To solve this problem and others, some authors prefer to use the "Coral of life" as a metaphor or a mathematical model to illustrate the evolution of life. This view dates back to an idea briefly mentioned by Darwin but later abandoned.[280]

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.[281] By comparing the anatomies of both modern and extinct species, palaeontologists 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.[282] 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.[283] For example, these DNA sequence comparisons have revealed that humans and chimpanzees share 98% of their genomes and analysing the few areas where they differ helps shed light on when the common ancestor of these species existed.[284]

Evolution of life

Prokaryotes inhabited the Earth from approximately 3–4 billion years ago.[286][287] No obvious changes in morphology or cellular organisation occurred in these organisms over the next few billion years.[288] The eukaryotic cells emerged between 1.6 and 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.[289][290] The engulfed bacteria and the host cell then underwent coevolution, with the bacteria evolving into either mitochondria or hydrogenosomes.[291] Another engulfment of cyanobacterial-like organisms led to the formation of chloroplasts in algae and plants.[292]

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.[286][293] The evolution of multicellularity occurred in multiple independent events, in organisms as diverse as sponges, brown algae, cyanobacteria, slime moulds and myxobacteria.[294] In January 2016, scientists reported that, about 800 million years ago, a minor genetic change in a single molecule called GK-PID may have allowed organisms to go from a single cell organism to one of many cells.[295]

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.[296] Various triggers for the Cambrian explosion have been proposed, including the accumulation of oxygen in the atmosphere from photosynthesis.[297]

About 500 million years ago, plants and fungi colonised the land and were soon followed by arthropods and other animals.[298] Insects were particularly successful and even today make up the majority of animal species.[299] Amphibians first appeared around 364 million years ago, followed by early amniotes and birds around 155 million years ago (both from "reptile"-like lineages), mammals around 129 million years ago, Homininae around 10 million years ago and modern humans around 250,000 years ago.[300][301][302] 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.[146]

History of evolutionary thought

Classical antiquity

The proposal that one type of organism could descend from another type goes back to some of the first pre-Socratic Greek philosophers, such as Anaximander and Empedocles.[304] Such proposals survived into Roman times. The poet and philosopher Lucretius followed Empedocles in his masterwork *De rerum natura* (*On the Nature of Things*).[305][306]

Middle Ages

In contrast to these materialistic views, Aristotelianism had considered all natural things as actualisations of fixed natural possibilities, known as forms.[307][308] This became part of a medieval teleological understanding of nature in which all things have an intended role to play in a divine cosmic order. Variations of this idea became the standard understanding of the Middle Ages and were integrated into Christian learning, but Aristotle did not demand that real types of organisms always correspond one-for-one with exact metaphysical forms and specifically gave examples of how new types of living things could come to be.[309]

A number of Arab Muslim scholars wrote about evolution, most notably Ibn Khaldun, who wrote the book *Muqaddimah* in 1377 AD, in which he asserted that humans developed from "the world of the monkeys", in a process by which "species become more numerous".[310]

Pre-Darwinian

The "New Science" of the 17th century rejected the Aristotelian approach. It sought to explain natural phenomena in terms of physical laws that were the same for all visible things and that did not require the existence of any fixed natural categories or divine cosmic order. However, this new approach was slow to take root in the biological sciences: the last bastion of the concept of fixed natural types. John Ray applied one of the previously more general terms for fixed natural types, "species", to plant and animal types, but he strictly identified each type of living thing as a species and proposed that each species could be defined by the features that perpetuated themselves generation after generation.[311] The biological classification introduced by Carl Linnaeus in 1735 explicitly recognised the hierarchical nature of species relationships, but still viewed species as fixed according to a divine plan.[312]

Other naturalists of this time speculated on the evolutionary change of species over time according to natural laws. In 1751, Pierre Louis Maupertuis wrote of natural modifications occurring during reproduction and accumulating over many generations to produce new species.[313] Georges-Louis Leclerc, Comte de Buffon, suggested that species could degenerate into different organisms, and Erasmus Darwin proposed that all warm-blooded animals could have descended from a single microorganism (or "filament").[314] The first full-fledged evolutionary scheme was Jean-Baptiste Lamarck's "transmutation" theory of 1809,[315] which envisaged spontaneous generation continually producing simple forms of life that developed greater complexity in parallel lineages with an inherent progressive tendency, and postulated that on a local level, these lineages adapted to the environment by inheriting changes caused by their use or disuse in parents.[316] (The latter process was later called Lamarckism.)[316][317][318] These ideas were condemned by established naturalists as speculation lacking empirical support. In particular, Georges Cuvier insisted that species were unrelated and fixed, their similarities reflecting divine design for functional needs. In the meantime, Ray's ideas of benevolent design had been developed by William Paley into the *Natural Theology or Evidences of the Existence and Attributes of the Deity* (1802), which proposed complex adaptations as evidence of divine design and which was admired by Charles Darwin.[319][320]

Darwinian revolution

The crucial break from the concept of constant typological classes or types in biology came with the theory of evolution through natural selection, which was formulated by Charles Darwin and Alfred Wallace in terms of variable populations. Darwin used the expression "descent with modification" rather than "evolution".[321] Partly influenced by *An Essay on the Principle of Population* (1798) by Thomas Robert Malthus, Darwin noted that population growth would lead to a "struggle for existence" in which favourable variations prevailed as others perished. In each generation, many offspring fail to survive to an age of reproduction because of limited resources. This could explain the diversity of plants and animals from a common ancestry through the working of natural laws in the same way for all types of organism.[322][323][324][325] Darwin developed his theory of "natural selection" from 1838 onwards and was writing up his "big book" on the subject when Alfred Russel Wallace sent him a version of virtually the same theory in 1858. Their separate papers were presented together at an 1858 meeting of the Linnean Society of London.[326] At the end of 1859, Darwin's publication of his "abstract" as *On the Origin of Species* explained natural selection in detail and in a way that led to an increasingly wide acceptance of Darwin's concepts of evolution at the expense of alternative theories. 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. Some were disturbed by this since it implied that humans did not have a special place in the universe.[327]

Pangenesis and heredity

The mechanisms of reproductive heritability and the origin of new traits remained a mystery. Towards this end, Darwin developed his provisional theory of pangenesis.[328] In 1865, Gregor Mendel reported that traits were inherited in a predictable manner through the independent assortment and segregation of elements (later known as genes). Mendel's laws of inheritance eventually supplanted most of Darwin's pangenesis theory.[329] August Weismann made the important distinction between germ cells that give rise to gametes (such as sperm and egg cells) and the somatic cells of the body, demonstrating that heredity passes through the germ line only. Hugo de Vries connected Darwin's pangenesis theory to Weismann's germ/soma cell distinction and proposed that Darwin's pangenes were concentrated in the cell nucleus and when expressed they could move into the cytoplasm to change the cell's structure. De Vries was also one of the researchers who made Mendel's work well known, believing that Mendelian traits corresponded to the transfer of heritable variations along the germline.[330] To explain how new variants originate, de Vries developed a mutation theory that led to a temporary rift between those who accepted Darwinian evolution and biometricians who allied with de Vries.[331][332] In the 1930s, pioneers in the field of population genetics, such as Ronald Fisher, Sewall Wright and J. B. S. Haldane set the foundations of evolution onto a robust statistical philosophy. The false contradiction between Darwin's theory, genetic mutations, and Mendelian inheritance was thus reconciled.[333]

The 'modern synthesis'

In the 1920s and 1930s, the modern synthesis connected natural selection and population genetics, based on Mendelian inheritance, into a unified theory that included random genetic drift, mutation, and gene flow. This new version of evolutionary theory focused on changes in allele frequencies in population. It explained patterns observed across species in populations, through fossil transitions in palaeontology.[333]

Further syntheses

Since then, further syntheses have extended evolution's explanatory power in the light of numerous discoveries, to cover biological phenomena across the whole of the biological hierarchy from genes to populations.[334]

The publication of the structure of DNA by James Watson and Francis Crick with contribution of Rosalind Franklin in 1953 demonstrated a physical mechanism for inheritance.[335] Molecular biology improved understanding of the relationship between genotype and phenotype. Advances were also made in phylogenetic systematics, mapping the transition of traits into a comparative and testable framework through the publication and use of evolutionary trees.[336] In 1973, evolutionary biologist Theodosius Dobzhansky penned that "nothing in biology makes sense except in the light of evolution," because it has brought to light the relations of what first seemed disjointed facts in natural history into a coherent explanatory body of knowledge that describes and predicts many observable facts about life on this planet.[337]

One extension, known as evolutionary developmental biology and informally called "evo-devo," emphasises how changes between generations (evolution) act on patterns of change within individual organisms (development).[237][338] Since the beginning of the 21st century, some biologists have argued for an extended evolutionary synthesis, which would account for the effects of non-genetic inheritance modes, such as epigenetics, parental effects, ecological inheritance and cultural inheritance, and evolvability.[339][340]

Social and cultural responses

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. Today, the modern evolutionary synthesis is accepted by a vast majority of scientists.[237] However, evolution remains a contentious concept for some theists.[342]

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 religions and who raise various objections to evolution.[135][343][344] 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.[345] 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.[346] While other scientific fields such as cosmology[347] and Earth science[348] 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 later and became 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 pseudoscientific form as intelligent design (ID), to be excluded once again in the 2005 *Kitzmiller v. Dover Area School District* case.[349] The debate over Darwin's ideas did not generate significant controversy in China.[350]

IV. GENETIC CHANGES AND MUTATIONS

In biology, evolution is the process of change in all forms of life over generations, and evolutionary biology is the study of how evolution occurs. Biological populations evolve through genetic changes that correspond to changes in the organisms' observable traits. Genetic changes include mutations, which are caused by damage or replication errors in organisms' DNA. As the genetic variation of a population drifts randomly over generations, natural selection gradually leads traits to become more or less common based on the relative reproductive success of organisms with those traits.

The age of the Earth is about 4.5 billion years.[1][2][3] The earliest undisputed evidence of life on Earth dates from at least 3.5 billion years ago.[4][5][6] Evolution does not attempt to explain the origin of life (covered instead by abiogenesis), but it does explain how early lifeforms evolved into the complex ecosystem that we see today.[7] Based on the similarities between all present-day organisms, all life on Earth is assumed to have originated through common descent from a last universal ancestor from which all known species have diverged through the process of evolution.[8]

All individuals have hereditary material in the form of genes received from their parents, which they pass on to any offspring. Among offspring there are variations of genes due to the introduction of new genes via random changes called mutations or via reshuffling of existing genes during sexual reproduction.[9][10] The offspring differs from the parent in minor random ways. If those differences are helpful, the offspring is more likely to survive and reproduce. This means that more offspring in the next generation will have that helpful difference and individuals will not have equal chances of reproductive success. In this way, traits that result in organisms being better adapted to their living conditions become more common in descendant populations.[9][10] These differences accumulate resulting in changes within the population. This process is responsible for the many diverse life forms in the world.

The modern understanding of evolution began with the 1859 publication of Charles Darwin's *On the Origin of Species*. In addition, Gregor Mendel's work with plants helped to explain the hereditary patterns of genetics.[11] Fossil discoveries in palaeontology, advances in population genetics and a global network of scientific research have provided further details into the mechanisms of evolution. Scientists now have a good understanding of the origin of new species (speciation) and have observed the speciation process in the laboratory and in the wild. Evolution is the principal scientific theory that biologists use to understand life and is used in many disciplines, including medicine, psychology, conservation biology, anthropology, forensics, agriculture and other social-cultural applications.

Simple overview

The main ideas of evolution may be summarised as follows:

- Life forms reproduce and therefore have a tendency to become more numerous.
- Factors such as predation and competition work against the survival of individuals.
- Each offspring differs from their parent(s) in minor, random ways.
- If these differences are beneficial, the offspring is more likely to survive and reproduce.

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- This makes it likely that more offspring in the next generation will have beneficial differences and fewer will have detrimental differences.
- These differences accumulate over generations, resulting in changes within the population.
- Over time, populations can split or branch off into new species.
- These processes, collectively known as evolution, are responsible for the many diverse life forms seen in the world.

Natural selection

In the 19th century, natural history collections and museums were popular. The European expansion and naval expeditions employed naturalists, while curators of grand museums showcased preserved and live specimens of the varieties of life. Charles Darwin was an English graduate educated and trained in the disciplines of natural history. Such natural historians would collect, catalogue, describe and study the vast collections of specimens stored and managed by curators at these museums. Darwin served as a ship's naturalist on board HMS *Beagle*, assigned to a five-year research expedition around the world. During his voyage, he observed and collected an abundance of organisms, being very interested in the diverse forms of life along the coasts of South America and the neighbouring Galápagos Islands.[12][13]

Darwin gained extensive experience as he collected and studied the natural history of life forms from distant places. Through his studies, he formulated the idea that each species had developed from ancestors with similar features. In 1838, he described how a process he called natural selection would make this happen.[14]

The size of a population depends on how much and how many resources are able to support it. For the population to remain the same size year after year, there must be an equilibrium or balance between the population size and available resources. Since organisms produce more offspring than their environment can support, not all individuals can survive out of each generation. There must be a competitive struggle for resources that aid in survival. As a result, Darwin realised that it was not chance alone that determined survival. Instead, survival of an organism depends on the differences of each individual organism, or "traits," that aid or hinder survival and reproduction. Well-adapted individuals are likely to leave more offspring than their less well-adapted competitors. Traits that hinder survival and reproduction would *disappear* over generations. Traits that help an organism survive and reproduce would *accumulate* over generations. Darwin realised that the unequal ability of individuals to survive and reproduce could cause gradual changes in the population and used the term *natural selection* to describe this process.[15][16]

Observations of variations in animals and plants formed the basis of the theory of natural selection. For example, Darwin observed that orchids and insects have a close relationship that allows the pollination of the plants. He noted that orchids have a variety of structures that attract insects, so that pollen from the flowers gets stuck to the insects' bodies. In this way, insects transport the pollen from a male to a female orchid. In spite of the elaborate appearance of orchids, these specialised parts are made from the same basic structures that make up other flowers. In his book, *Fertilisation of Orchids* (1862), Darwin proposed that the orchid flowers were adapted from pre-existing parts, through natural selection.[17]

Darwin was still researching and experimenting with his ideas on natural selection when he received a letter from Alfred Russel Wallace describing a theory very similar to his own. This led to an immediate joint publication of both theories. Both Wallace and Darwin saw the history of life like a family tree, with each fork in the tree's limbs being a common ancestor. The tips of the limbs represented modern species and the branches represented the common ancestors that are shared amongst many different species. To explain these relationships, Darwin said that all living things were related, and this meant that all life must be descended from a few forms, or even from a single common ancestor. He called this process *descent with modification*.[16]

Darwin published his theory of evolution by natural selection in *On the Origin of Species* in 1859.[18] His theory means that all life, including humanity, is a product of continuing natural processes. The implication that all life on Earth has a common ancestor has met with objections from some religious groups. Their objections are in contrast to the level of support for the theory by more than 99 percent of those within the scientific community today.[19]

Natural selection is commonly equated with *survival of the fittest*, but this expression originated in Herbert Spencer's *Principles of Biology* in 1864, five years after Charles Darwin published his original works. *Survival of the fittest* describes the process of natural selection incorrectly, because natural selection is not only about survival and it is not always the fittest that survives.[20]

Source of variation

Darwin's theory of natural selection laid the groundwork for modern evolutionary theory, and his experiments and observations showed that the organisms in populations varied from each other, that some of these variations were inherited, and that these differences could be acted on by natural selection. However, he could not explain the source of these variations. Like many of his predecessors, Darwin mistakenly thought that heritable traits were a product of use and disuse, and that features acquired during an organism's lifetime could be passed on to its offspring. He looked for examples, such as large ground feeding birds getting stronger legs through exercise, and weaker wings from not flying until, like the ostrich, they could not fly at all.[21] This misunderstanding was called the inheritance of acquired characters and was part of the theory of transmutation of species put forward in 1809 by Jean-Baptiste Lamarck. In the late 19th century this theory became known as Lamarckism. Darwin produced an unsuccessful theory he called pangenesis to try to explain how acquired characteristics could be inherited. In the 1880s August Weismann's experiments indicated that changes from use and disuse could not be inherited, and Lamarckism gradually fell from favour.[22]

The missing information needed to help explain how new features could pass from a parent to its offspring was provided by the pioneering genetics work of Gregor Mendel. Mendel's experiments with several generations of pea plants demonstrated that inheritance works by separating and reshuffling hereditary information during the formation of sex cells and recombining that information during fertilisation. This is like mixing different hands of playing cards, with an organism getting a random mix of half of the cards from one parent, and half of the cards from the other. Mendel called the information *factors*; however, they later became known as genes. Genes are the basic units of heredity in living organisms. They contain the information that directs the physical development and behaviour of organisms.

Genes are made of DNA. DNA is a long molecule made up of individual molecules called nucleotides. Genetic information is encoded in the sequence of nucleotides, that make up the DNA, just as the sequence of the letters in words carries information on a page. The genes are like short instructions built up of the "letters" of the DNA alphabet. Put together, the entire set of these genes gives enough information to serve as an "instruction manual" of how to build and run an organism. The instructions spelled out by this DNA alphabet can be changed, however, by mutations, and this may alter the instructions carried within the genes. Within the cell, the genes are carried in chromosomes, which are packages for carrying the DNA. It is the reshuffling of the chromosomes that results in unique combinations of genes in offspring. Since genes interact with one another during the development of an organism, novel combinations of genes produced by sexual reproduction can increase the genetic variability of the population even without new mutations.[23] The genetic variability of a population can also increase when members of that population interbreed with individuals from a different population causing gene flow between the populations. This can introduce genes into a population that were not present before.[24]

Evolution is not a random process. Although mutations in DNA are random, natural selection is not a process of chance: the environment determines the probability of reproductive success. Evolution is an inevitable result of imperfectly copying, self-replicating organisms reproducing over billions of years under the selective pressure of the environment. The outcome of evolution is not a perfectly designed organism. The end products of natural selection are organisms that are adapted to their present environments. Natural selection does not involve progress towards an ultimate goal. Evolution does not strive for more advanced, more intelligent, or more sophisticated life forms.[25] For example, fleas (wingless parasites) are descended from a winged, ancestral scorpionfly, and snakes are lizards that no longer require limbs—although pythons still grow tiny structures that are the remains of their ancestor's hind legs.[26][27] Organisms are merely the outcome of variations that succeed or fail, dependent upon the environmental conditions at the time.

Rapid environmental changes typically cause extinctions.[28] Of all species that have existed on Earth, 99.9 percent are now extinct.[29] Since life began on Earth, five major mass extinctions have led to large and sudden drops in the variety of species. The most recent, the Cretaceous–Paleogene extinction event, occurred 66 million years ago.[30]

Genetic drift

Genetic drift is a cause of allelic frequency change within populations of a species. Alleles are different variations of specific genes. They determine things like hair colour, skin tone, eye colour and blood type; in other words, all the genetic traits that vary between individuals. Genetic drift does not introduce new alleles to a population, but it can reduce variation within a population by removing an allele from the gene pool. Genetic drift is caused by random sampling of alleles. A truly random sample is a sample in which no outside forces affect what is selected. It is like pulling marbles of the same size and weight but of different colours from a brown paper bag. In any offspring, the alleles present are samples of the previous generations alleles, and chance plays a role in whether an individual survives to reproduce and to pass a sample of their generation onward to the next. The allelic frequency of a population is the ratio of the copies of one specific allele that share the same form compared to the number of all forms of the allele present in the population.[31]

Genetic drift affects smaller populations more than it affects larger populations.[32]

Hardy–Weinberg principle

The Hardy–Weinberg principle states that under certain idealised conditions, including the absence of selection pressures, a large population will have no change in the frequency of alleles as generations pass.[33] A population that satisfies these conditions is said to be in Hardy–Weinberg equilibrium. In particular, Hardy and Weinberg showed that dominant and recessive alleles do not automatically tend to become more and less frequent respectively, as had been thought previously.

The conditions for Hardy-Weinberg equilibrium include that there must be no mutations, immigration, or emigration, all of which can directly change allelic frequencies. Additionally, mating must be totally random, with all males (or females in some cases) being equally desirable mates. This ensures a true random mixing of alleles.[34] A population that is in Hardy–Weinberg equilibrium is analogous to a deck of cards; no matter how many times the deck is shuffled, no new cards are added and no old ones are taken away. Cards in the deck represent alleles in a population's gene pool.

In practice, no population can be in perfect Hardy-Weinberg equilibrium. The population's finite size, combined with natural selection and many other effects, cause the allelic frequencies to change over time.

Population bottleneck

A population bottleneck occurs when the population of a species is reduced drastically over a short period of time due to external forces.[35] In a true population bottleneck, the reduction does not favour any combination of alleles; it is totally random chance which individuals survive. A bottleneck can reduce or eliminate genetic variation from a population. Further drift events after the bottleneck event can also reduce the population's genetic diversity. The lack of diversity created can make the population at risk to other selective pressures.[36]

A common example of a population bottleneck is the Northern elephant seal. Due to excessive hunting throughout the 19th century, the population of the northern elephant seal was reduced to 30 individuals or less. They have made a full recovery, with the total number of individuals at around 100,000 and growing. The effects of the bottleneck are visible, however. The seals are more likely to have serious problems with disease or genetic disorders, because there is almost no diversity in the population.[37]

Founder effect

The founder effect occurs when a small group from one population splits off and forms a new population, often through geographic isolation. This new population's allelic frequency is probably different from the original population's, and will change how common certain alleles are in the populations. The founders of the population will determine the genetic makeup, and potentially the survival, of the new population for generations.[34]

One example of the founder effect is found in the Amish migration to Pennsylvania in 1744. Two of the founders of the colony in Pennsylvania carried the recessive allele for Ellis–van Creveld syndrome. Because the Amish tend to be religious isolates, they interbreed, and through generations of this practice the frequency of Ellis–van Creveld syndrome in the Amish people is much higher than the frequency in the general population.[38]

Modern synthesis

The modern evolutionary synthesis is based on the concept that populations of organisms have significant genetic variation caused by mutation and by the recombination of genes during sexual reproduction. It defines evolution as the change in allelic frequencies within a population caused by genetic drift, gene flow between sub populations, and natural selection. Natural selection is emphasised as the most important mechanism of evolution; large changes are the result of the gradual accumulation of small changes over long periods of time.[39][40]

The modern evolutionary synthesis is the outcome of a merger of several different scientific fields to produce a more cohesive understanding of evolutionary theory. In the 1920s, Ronald Fisher, J.B.S. Haldane and Sewall Wright combined Darwin's theory of natural selection with statistical models of Mendelian genetics, founding the discipline of population genetics. In the 1930s and 1940s, efforts were made to merge population genetics, the observations of field naturalists on the distribution of species and sub species, and analysis of the fossil record into a unified explanatory model.[41] The application of the principles of genetics to naturally occurring populations, by scientists such as Theodosius Dobzhansky and Ernst Mayr, advanced the understanding of the processes of evolution.

Dobzhansky's 1937 work *Genetics and the Origin of Species* helped bridge the gap between genetics and field biology by presenting the mathematical work of the population geneticists in a form more useful to field biologists, and by showing that wild populations had much more genetic variability with geographically isolated subspecies and reservoirs of genetic diversity in recessive genes than the models of the early population geneticists had allowed for. Mayr, on the basis of an understanding of genes and direct observations of evolutionary processes from field research, introduced the biological species concept, which defined a species as a group of interbreeding or potentially interbreeding populations that are reproductively isolated from all other populations. Both Dobzhansky and Mayr emphasised the importance of subspecies reproductively isolated by geographical barriers in the emergence of new species. The palaeontologist George Gaylord Simpson helped to incorporate palaeontology with a statistical analysis of the fossil record that showed a pattern consistent with the branching and non-directional pathway of evolution of organisms predicted by the modern synthesis.[39]

Evidence for evolution

Fossil record

Research in the field of palaeontology, the study of fossils, supports the idea that all living organisms are related. Fossils provide evidence that accumulated changes in organisms over long periods of time have led to the diverse forms of life we see today. A fossil itself reveals the organism's structure and the relationships between present and extinct species, allowing palaeontologists to construct a family tree for all of the life forms on Earth.[42]

Modern palaeontology began with the work of Georges Cuvier. Cuvier noted that, in sedimentary rock, each layer contained a specific group of fossils. The deeper layers, which he proposed to be older, contained simpler life forms. He noted that many forms of life from the past are no longer present today. One of Cuvier's successful contributions to the understanding of the fossil record was establishing extinction as a fact. In an attempt to explain extinction, Cuvier proposed the idea of "revolutions" or catastrophism in which he speculated that geological catastrophes had occurred throughout the Earth's history, wiping out large numbers of species.[43] Cuvier's theory of revolutions was later replaced by uniformitarian theories, notably those of James Hutton and Charles Lyell who proposed that the Earth's geological changes were gradual and consistent.[44] However, current evidence in the fossil record supports the concept of mass extinctions. As a result, the general idea of catastrophism has re-emerged as a valid hypothesis for at least some of the rapid changes in life forms that appear in the fossil records.

A very large number of fossils have now been discovered and identified. These fossils serve as a chronological record of evolution. The fossil record provides examples of transitional species that demonstrate ancestral links between past and present life forms.[45] One such transitional fossil is *Archaeopteryx*, an ancient organism that had the distinct characteristics of a reptile (such as a long, bony tail and conical teeth) yet also had characteristics of birds (such as feathers and a wishbone). The implication from such a find is that modern reptiles and birds arose from a common ancestor.[46]

Comparative anatomy

The comparison of similarities between organisms of their form or appearance of parts, called their morphology, has long been a way to classify life into closely related groups. This can be done by comparing the structure of adult organisms in different species or by comparing the patterns of how cells grow, divide and even migrate during an organism's development.

Taxonomy

Taxonomy is the branch of biology that names and classifies all living things. Scientists use morphological and genetic similarities to assist them in categorising life forms based on ancestral relationships. For example, orangutans, gorillas, chimpanzees and humans all belong to the same taxonomic grouping referred to as a family—in this case the family called Hominidae. These animals are grouped together because of similarities in morphology that come from common ancestry (called *homology*).[47]

Strong evidence for evolution comes from the analysis of homologous structures: structures in different species that no longer perform the same task but which share a similar structure.[48] Such is the case of the forelimbs of mammals. The forelimbs of a human, cat, whale, and bat all have strikingly similar bone structures. However, each of these four species' forelimbs performs a different task. The same bones that construct a bat's wings, which are used for flight, also construct a whale's flippers, which are used for swimming. Such a "design" makes little sense if they are unrelated and uniquely constructed for their particular tasks. The theory of evolution explains these homologous structures: all four animals shared a common ancestor, and each has undergone change over many generations. These changes in structure have produced forelimbs adapted for different tasks.[49]

However, anatomical comparisons can be misleading, as not all anatomical similarities indicate a close relationship. Organisms that share similar environments will often develop similar physical features, a process known as *convergent evolution*. Both sharks and dolphins have similar body forms, yet are only distantly related—sharks are fish and dolphins are mammals. Such similarities are a result of both populations being exposed to the same selective pressures. Within both groups, changes that aid swimming have been favoured. Thus, over time, they developed similar appearances (morphology), even though they are not closely related.[50]

Embryology

In some cases, anatomical comparison of structures in the embryos of two or more species provides evidence for a shared ancestor that may not be obvious in the adult forms. As the embryo develops, these homologies can be lost to view, and the structures can take on different functions. Part of the basis of classifying the vertebrate group (which includes humans), is the presence of a tail (extending beyond the anus) and pharyngeal slits. Both structures appear during some stage of embryonic development but are not always obvious in the adult form.[51]

Because of the morphological similarities present in embryos of different species during development, it was once assumed that organisms re-enact their evolutionary history as an embryo. It was thought that human embryos passed through an amphibian then a reptilian stage before completing their development as mammals. Such a re-enactment, often called *recapitulation theory*, is not supported by scientific evidence. What does occur, however, is that the first stages of development are similar in broad groups of organisms.[52] At very early stages, for instance, all vertebrates appear extremely similar, but do not exactly resemble any ancestral species. As development continues, specific features emerge from this basic pattern.

Vestigial structures

Homology includes a unique group of shared structures referred to as *vestigial structures*. *Vestigial* refers to anatomical parts that are of minimal, if any, value to the organism that possesses them. These apparently illogical structures are remnants of organs that played an important role in ancestral forms. Such is the case in whales, which have small vestigial bones that appear to be remnants of the leg bones of their ancestors which walked on land.[53] Humans also have vestigial structures, including the ear muscles, the wisdom teeth, the appendix, the tail bone, body hair (including goose bumps), and the semilunar fold in the corner of the eye.[54]

Biogeography

Biogeography is the study of the geographical distribution of species. Evidence from biogeography, especially from the biogeography of oceanic islands, played a key role in convincing both Darwin and Alfred Russel Wallace that species evolved with a branching pattern of common descent.[55] Islands often contain endemic species, species not found anywhere else, but those species are often related to species found on the nearest continent. Furthermore, islands often contain clusters of closely related species that have very different ecological niches, that is have different ways of making a living in the environment. Such clusters form through a process of adaptive radiation where a single ancestral species colonises an island that has a variety of open ecological niches and then diversifies by evolving into different species adapted to fill those empty niches. Well-studied examples include Darwin's finches, a group of 13 finch species endemic to the Galápagos Islands, and the Hawaiian honeycreepers, a group of birds that once, before extinctions caused by humans, numbered 60 species filling diverse ecological roles, all descended from a single finch like ancestor that arrived on the Hawaiian Islands some 4 million years ago.[56] Another example is the Silversword alliance, a group of perennial plant species, also endemic to the Hawaiian Islands, that inhabit a variety of habitats and come in a variety of shapes and sizes that include trees, shrubs, and ground hugging mats, but which can be hybridised with one another and with certain tarweed species found on the west coast of North America; it appears that one of those tarweeds colonised Hawaii in the past, and gave rise to the entire Silversword alliance.[57]

Molecular biology

Every living organism (with the possible exception of RNA viruses) contains molecules of DNA, which carries genetic information. Genes are the pieces of DNA that carry this information, and they influence the properties of an organism. Genes determine an individual's general appearance and to some extent their behaviour. If two organisms are closely related, their DNA will be very similar.[58] On the other hand, the more distantly related two organisms are, the more differences they will have. For example, brothers are closely related and have very similar DNA, while cousins share a more distant relationship and have far more differences in their DNA. Similarities in DNA are used to determine the relationships between species in much the same manner as they are used to show relationships between individuals. For example, comparing chimpanzees with gorillas and humans shows that there is as much as a 96 percent similarity between the DNA of humans and chimps. Comparisons of DNA indicate that humans and chimpanzees are more closely related to each other than either species is to gorillas.[59][60][61]

The field of molecular systematics focuses on measuring the similarities in these molecules and using this information to work out how different types of organisms are related through evolution. These comparisons have allowed biologists to build a *relationship tree* of the evolution of life on Earth.[62] They have even allowed scientists to unravel the relationships between organisms whose common ancestors lived such a long time ago that no real similarities remain in the appearance of the organisms.

Artificial selection

Artificial selection is the controlled breeding of domestic plants and animals. Humans determine which animal or plant will reproduce and which of the offspring will survive; thus, they determine which genes will be passed on to future generations. The process of artificial selection has had a significant impact on the evolution of domestic animals. For example, people have produced different types of dogs by controlled breeding. The differences in size between the Chihuahua and the Great Dane are the result of artificial selection. Despite their dramatically different physical appearance, they and all other dogs evolved from a few wolves domesticated by humans in what is now China less than 15,000 years ago.[63]

Artificial selection has produced a wide variety of plants. In the case of maize (corn), recent genetic evidence suggests that domestication occurred 10,000 years ago in central Mexico.[64][Prior to domestication, the edible portion of the wild form was small and difficult to collect. Today *The Maize Genetics Cooperation • Stock Center* maintains a collection of more than 10,000 genetic variations of maize that have arisen by random mutations and chromosomal variations from the original wild type.[65]

In artificial selection the new breed or variety that emerges is the one with random mutations attractive to humans, while in natural selection the surviving species is the one with random mutations useful to it in its non-human environment. In both natural and artificial selection the variations are a result of random mutations, and the underlying genetic processes are essentially the same.[66] Darwin carefully observed the outcomes of artificial selection in animals and plants to form many of his arguments in support of natural selection.[67] Much of his book *On the Origin of Species* was based on these observations of the many varieties of domestic pigeons arising from artificial selection. Darwin proposed that if humans could achieve dramatic changes in domestic animals in short periods, then natural selection, given millions of years, could produce the differences seen in living things today.

Coevolution

Coevolution is a process in which two or more species influence the evolution of each other. All organisms are influenced by life around them; however, in coevolution there is evidence that genetically determined traits in each species directly resulted from the interaction between the two organisms.[58]

An extensively documented case of coevolution is the relationship between *Pseudomyrmex*, a type of ant, and the *acacia*, a plant that the ant uses for food and shelter. The relationship between the two is so intimate that it has led to the evolution of special structures and behaviours in both organisms. The ant defends the acacia against herbivores and clears the forest floor of the seeds from competing plants. In response, the plant has evolved swollen thorns that the ants use as shelter and special flower parts that the ants eat.[68] Such coevolution does not imply that the ants and the tree choose to behave in an altruistic manner. Rather, across a population small genetic changes in both ant and tree benefited each. The benefit gave a slightly higher chance of the characteristic being passed on to the next generation. Over time, successive mutations created the relationship we observe today.

Speciation

Given the right circumstances, and enough time, evolution leads to the emergence of new species. Scientists have struggled to find a precise and all-inclusive definition of *species*. Ernst Mayr defined a species as a population or group of populations whose members have the potential to interbreed naturally with one another to produce viable, fertile offspring. (The members of a species cannot produce viable, fertile offspring with members of *other* species).[69] Mayr's definition has gained wide acceptance among biologists, but does not apply to organisms such as bacteria, which reproduce asexually.

Speciation is the lineage-splitting event that results in two separate species forming from a single common ancestral population.[15] A widely accepted method of speciation is called *allopatric speciation*. Allopatric speciation begins when a population becomes geographically separated.[48] Geological processes, such as the emergence of mountain ranges, the formation of canyons, or the flooding of land bridges by changes in sea level may result in separate populations. For speciation to occur, separation must be substantial, so that genetic exchange between the two populations is completely disrupted. In their separate environments, the genetically isolated groups follow their own unique evolutionary pathways. Each group will accumulate different mutations as well as be subjected to different

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selective pressures. The accumulated genetic changes may result in separated populations that can no longer interbreed if they are reunited.[15] Barriers that prevent interbreeding are either *prezygotic* (prevent mating or fertilisation) or *postzygotic* (barriers that occur after fertilisation). If interbreeding is no longer possible, then they will be considered different species.[70] The result of four billion years of evolution is the diversity of life around us, with an estimated 1.75 million different species in existence today.[71][72]

Usually the process of speciation is slow, occurring over very long time spans; thus direct observations within human life-spans are rare. However speciation has been observed in present-day organisms, and past speciation events are recorded in fossils.[73][74][75] Scientists have documented the formation of five new species of cichlid fishes from a single common ancestor that was isolated fewer than 5,000 years ago from the parent stock in Lake Nagubago.[76] The evidence for speciation in this case was morphology (physical appearance) and lack of natural interbreeding. These fish have complex mating rituals and a variety of colorations; the slight modifications introduced in the new species have changed the mate selection process and the five forms that arose could not be convinced to interbreed.[77]

Mechanism

The theory of evolution is widely accepted among the scientific community, serving to link the diverse speciality areas of biology.[19] Evolution provides the field of biology with a solid scientific base. The significance of evolutionary theory is summarised by Theodosius Dobzhansky as "nothing in biology makes sense except in the light of evolution."[78][79] Nevertheless, the theory of evolution is not static. There is much discussion within the scientific community concerning the mechanisms behind the evolutionary process. For example, the rate at which evolution occurs is still under discussion. In addition, there are conflicting opinions as to which is the primary unit of evolutionary change—the organism or the gene.

Rate of change

Darwin and his contemporaries viewed evolution as a slow and gradual process. Evolutionary trees are based on the idea that profound differences in species are the result of many small changes that accumulate over long periods.

Gradualism had its basis in the works of the geologists James Hutton and Charles Lyell. Hutton's view suggests that profound geological change was the cumulative product of a relatively slow continuing operation of processes which can still be seen in operation today, as opposed to catastrophism which promoted the idea that sudden changes had causes which can no longer be seen at work. A uniformitarian perspective was adopted for biological changes. Such a view can seem to contradict the fossil record, which often shows evidence of new species appearing suddenly, then persisting in that form for long periods. In the 1970s palaeontologists Niles Eldredge and Stephen Jay Gould developed a theoretical model that suggests that evolution, although a slow process in human terms, undergoes periods of relatively rapid change (ranging between 50,000 and 100,000 years)[80] alternating with long periods of relative stability. Their theory is called *punctuated equilibrium* and explains the fossil record without contradicting Darwin's ideas.[81]

Unit of change

A common unit of selection in evolution is the organism. Natural selection occurs when the reproductive success of an individual is improved or reduced by an inherited characteristic, and reproductive success is measured by the number of an individual's surviving offspring. The organism view has been challenged by a variety of biologists as well as philosophers. Richard Dawkins proposes that much insight can be gained if we look at evolution from the gene's point of view; that is, that natural selection operates as an evolutionary mechanism on genes as well as organisms.[82] In his 1976 book, *The Selfish Gene*, he explains:

Individuals are not stable things, they are fleeting. Chromosomes too are shuffled to oblivion, like hands of cards soon after they are dealt. But the cards themselves survive the shuffling. The cards are the genes. The genes are not destroyed by crossing-over, they merely change partners and march on. Of course they march on. That is their business. They are the replicators and we are their survival machines. When we have served our purpose we are cast aside. But genes are denizens of geological time: genes are forever.[83]

Others view selection working on many levels, not just at a single level of organism or gene; for example, Stephen Jay Gould called for a hierarchical perspective on selection.[84]

V. DEVELOPMENTAL BIOLOGY AND EVOLUTION

Evolutionary developmental biology (informally, evo-devo) is a field of biological research that compares the developmental processes of different organisms to infer how developmental processes evolved.

The field grew from 19th-century beginnings, where embryology faced a mystery: zoologists did not know how embryonic development was controlled at the molecular level. Charles Darwin noted that having similar embryos implied common ancestry, but little progress was made until the 1970s. Then, recombinant DNA technology at last brought embryology together with molecular genetics. A key early discovery was of homeotic genes that regulate development in a wide range of eukaryotes.

The field is composed of multiple core evolutionary concepts. One is deep homology, the finding that dissimilar organs such as the eyes of insects, vertebrates and cephalopod molluscs, long thought to have evolved separately, are controlled by similar genes such as *pax-6*, from the evo-devo gene toolkit. These genes are ancient, being highly conserved among phyla; they generate the patterns in time and space which shape the embryo, and ultimately form the body plan of the organism. Another is that species do not differ much in their structural genes, such as those coding for enzymes; what does differ is the way that gene expression is regulated by the toolkit genes. These genes are reused, unchanged, many times in different parts of the embryo and at different stages of development, forming a complex cascade of control, switching other regulatory genes as well as structural genes on and off in a precise pattern. This multiple pleiotropic reuse explains why these genes are highly conserved, as any change would have many adverse consequences which natural selection would oppose.

New morphological features and ultimately new species are produced by variations in the toolkit, either when genes are expressed in a new pattern, or when toolkit genes acquire additional functions. Another possibility is the neo-Lamarckian theory that epigenetic changes are later consolidated at gene level, something that may have been important early in the history of multicellular life.

Early theories

Philosophers began to think about how animals acquired form in the womb in classical antiquity. Aristotle asserts in his *Physics* treatise that according to Empedocles, order "spontaneously" appears in the developing embryo. In his *The Parts of Animals* treatise, he argues that Empedocles' theory was wrong. In Aristotle's account, Empedocles stated that the vertebral column is divided into vertebrae because, as it happens, the embryo twists about and snaps the column into pieces. Aristotle argues instead that the process has a predefined goal: that the "seed" that develops into the embryo began with an inbuilt "potential" to become specific body parts, such as vertebrae. Further, each sort of animal gives rise to animals of its own kind: humans only have human babies.[1]

A recapitulation theory of evolutionary development was proposed by Étienne Serres in 1824–26, echoing the 1808 ideas of Johann Friedrich Meckel. They argued that the embryos of 'higher' animals went through or recapitulated a series of stages, each of which resembled an animal lower down the great chain of being. For example, the brain of a human embryo looked first like that of a fish, then in turn like that of a reptile, bird, and mammal before becoming clearly human. The embryologist Karl Ernst von Baer opposed this, arguing in 1828 that there was no linear sequence as in the great chain of being, based on a single body plan, but a process of epigenesis in which structures differentiate. Von Baer instead recognized four distinct animal body plans: radiate, like starfish; molluscan, like clams; articulate, like lobsters; and vertebrate, like fish. Zoologists then largely abandoned recapitulation, though Ernst Haeckel revived it in 1866.[3][4][5][6][7]

Evolutionary morphology

From the early 19th century through most of the 20th century, embryology faced a mystery. Animals were seen to develop into adults of widely differing body plan, often through similar stages, from the egg, but zoologists knew almost nothing about how embryonic development was controlled at the molecular level, and therefore equally little about how developmental processes had evolved.[8] Charles Darwin argued that a shared embryonic structure implied a common ancestor. For example, Darwin cited in his 1859 book *On the Origin of Species* the shrimp-like larva of the barnacle, whose sessile adults looked nothing like other arthropods; Linnaeus and Cuvier had classified them as molluscs.[9][10] Darwin also noted Alexander Kowalevsky's finding that the tunicate, too, was not a mollusc, but in its larval stage had a notochord and pharyngeal slits which developed from the same germ layers as the equivalent structures in vertebrates, and should therefore be grouped with them as chordates.[9][11]

19th century zoology thus converted embryology into an evolutionary science, connecting phylogeny with homologies between the germ layers of embryos. Zoologists including Fritz Müller proposed the use of embryology to discover phylogenetic relationships between taxa. Müller demonstrated that crustaceans shared the Nauplius larva, identifying several parasitic species that had not been recognized as crustaceans. Müller also recognized that natural selection must act on larvae, just as it does on adults, giving the lie to recapitulation, which would require larval forms to be shielded from natural selection.[9] Two of Haeckel's other ideas about the evolution of development have fared better than recapitulation: he argued in the 1870s that changes in the timing (heterochrony) and changes in the positioning within the body (heterotopy) of aspects of embryonic development would drive evolution by changing the shape of a descendant's body compared to an ancestor's. It took a century before these ideas were shown to be correct.[12][13][14]

In 1917, D'Arcy Thompson wrote a book on the shapes of animals, showing with simple mathematics how small changes to parameters, such as the angles of a gastropod's spiral shell, can radically alter an animal's form, though he preferred a mechanical to evolutionary explanation.[15][16] But without molecular evidence, progress stalled.[9]

In 1952, Alan Turing published his paper "The Chemical Basis of Morphogenesis", on the development of patterns in animals' bodies. He suggested that morphogenesis could be explained by a reaction–diffusion system, a system of reacting chemicals able to diffuse through the body.[17] He modelled catalysed chemical reactions using partial differential equations, showing that patterns emerged when the chemical reaction produced both a catalyst (A) and an inhibitor (B) that slowed down production of A. If A and B then diffused at different rates, A dominated in some places, and B in others. The Russian biochemist Boris Belousov had run experiments with similar results, but was unable to publish them because scientists thought at that time that creating visible order violated the second law of thermodynamics.[18]

The modern synthesis of the early 20th century

In the so-called modern synthesis of the early 20th century, between 1918 and 1930 Ronald Fisher brought together Darwin's theory of evolution, with its insistence on natural selection, heredity, and variation, and Gregor Mendel's laws of genetics into a coherent structure for evolutionary biology. Biologists assumed that an organism was a straightforward reflection of its component genes: the genes coded for proteins, which built the organism's body. Biochemical pathways (and, they supposed, new species) evolved through mutations in these genes. It was a simple, clear and nearly comprehensive picture: but it did not explain embryology.[9][19] Sean B. Carroll has commented that had evo-devo's insights been available, embryology would certainly have played a central role in the synthesis.[20]

The evolutionary embryologist Gavin de Beer anticipated evolutionary developmental biology in his 1930 book *Embryos and Ancestors*,[21] by showing that evolution could occur by heterochrony,[22] such as in the retention of juvenile features in the adult.[12] This, de Beer argued, could cause apparently sudden changes in the fossil record, since embryos fossilise poorly. As the gaps in the fossil record had been used as an argument against Darwin's gradualist evolution, de Beer's explanation supported the Darwinian position.[23] However, despite de Beer, the modern synthesis largely ignored embryonic development to explain the form of organisms, since population genetics appeared to be an adequate explanation of how forms evolved.[24][25][a]

The lac operon

In 1961, Jacques Monod, Jean-Pierre Changeux and François Jacob discovered the lac operon in the bacterium *Escherichia coli*. It was a cluster of genes, arranged in a feedback control loop so that its products would only be made when "switched on" by an environmental stimulus. One of these products was an enzyme that splits a sugar, lactose; and lactose itself was the stimulus that switched the genes on. This was a revelation, as it showed for the first time that genes, even in organisms as small as a bacterium, are subject to precise control. The implication was that many other genes were also elaborately regulated.[27]

The birth of evo-devo and a second synthesis

In 1977, a revolution in thinking about evolution and developmental biology began, with the arrival of recombinant DNA technology in genetics, the book *Ontogeny and Phylogeny* by Stephen J. Gould and the paper "Evolution and Tinkering"[28] by François Jacob. Gould laid to rest Haeckel's interpretation of evolutionary embryology, while Jacob set out an alternative theory.[9] This led to a second synthesis,[29][30] at last including embryology as well as molecular genetics, phylogeny, and evolutionary biology to form evo-devo.[31][32] In 1978, Edward B. Lewis discovered homeotic genes that regulate embryonic development in *Drosophila* fruit flies, which like all insects are arthropods, one of the major phyla of invertebrate animals.[33] Bill McGinnis quickly discovered homeotic gene sequences, homeoboxes, in animals in other phyla, in vertebrates such as frogs, birds, and mammals; they were later also found in fungi such as yeasts, and in plants.[34][35] There were evidently strong similarities in the genes that controlled development across all the eukaryotes.[36] In 1980, Christiane Nüsslein-Volhard and Eric Wieschaus described gap genes which help to create the segmentation pattern in fruit fly embryos;[37][38] they and Lewis won a Nobel Prize for their work in 1995.[34][39]

Later, more specific similarities were discovered: for example, the Distal-less gene was found in 1989 to be involved in the development of appendages or limbs in fruit flies,[40] the fins of fish, the wings of chickens, the parapodia of marine annelid worms, the ampullae and siphons of tunicates, and the tube feet of sea urchins. It was evident that the gene must be ancient, dating back to the last common ancestor of bilateral animals (before the Ediacaran Period, which

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began some 635 million years ago). Evo-devo had started to uncover the ways that all animal bodies were built during development.[41][42]

The control of body structure

Deep homology

Roughly spherical eggs of different animals give rise to unique morphologies, from jellyfish to lobsters, butterflies to elephants. Many of these organisms share the same structural genes for body-building proteins like collagen and enzymes, but biologists had expected that each group of animals would have its own rules of development. The surprise of evo-devo is that the shaping of bodies is controlled by a rather small percentage of genes, and that these regulatory genes are ancient, shared by all animals. The giraffe does not have a gene for a long neck, any more than the elephant has a gene for a big body. Their bodies are patterned by a system of switching which causes development of different features to begin earlier or later, to occur in this or that part of the embryo, and to continue for more or less time.[8]

The puzzle of how embryonic development was controlled began to be solved using the fruit fly *Drosophila melanogaster* as a model organism. The step-by-step control of its embryogenesis was visualized by attaching fluorescent dyes of different colours to specific types of protein made by genes expressed in the embryo.[8] A dye such as green fluorescent protein, originally from a jellyfish, was typically attached to an antibody specific to a fruit fly protein, forming a precise indicator of where and when that protein appeared in the living embryo.[43]

Using such a technique, in 1994 Walter Gehring found that the *pax-6* gene, vital for forming the eyes of fruit flies, exactly matches an eye-forming gene in mice and humans. The same gene was quickly found in many other groups of animals, such as squid, a cephalopod mollusc. Biologists including Ernst Mayr had believed that eyes had arisen in the animal kingdom at least 40 times, as the anatomy of different types of eye varies widely.[8] For example, the fruit fly's compound eye is made of hundreds of small lensed structures (ommatidia); the human eye has a blind spot where the optic nerve enters the eye, and the nerve fibres run over the surface of the retina, so light has to pass through a layer of nerve fibres before reaching the detector cells in the retina, so the structure is effectively "upside-down"; in contrast, the cephalopod eye has the retina, then a layer of nerve fibres, then the wall of the eye "the right way around".[44] The evidence of *pax-6*, however, was that the same genes controlled the development of the eyes of all these animals, suggesting that they all evolved from a common ancestor.[8] Ancient genes had been conserved through millions of years of evolution to create dissimilar structures for similar functions, demonstrating deep homology between structures once thought to be purely analogous.[45][46] This notion was later extended to the evolution of embryogenesis[47] and has caused a radical revision of the meaning of homology in evolutionary biology.[45][46][20]

Gene toolkit

A small fraction of the genes in an organism's genome control the organism's development. These genes are called the developmental-genetic toolkit. They are highly conserved among phyla, meaning that they are ancient and very similar in widely separated groups of animals. Differences in deployment of toolkit genes affect the body plan and the number, identity, and pattern of body parts. Most toolkit genes are parts of signalling pathways: they encode transcription factors, cell adhesion proteins, cell surface receptor proteins and signalling ligands that bind to them, and secreted morphogens that diffuse through the embryo. All of these help to define the fate of undifferentiated cells in the embryo. Together, they generate the patterns in time and space which shape the embryo, and ultimately form the body plan of the organism. Among the most important toolkit genes are the *Hox* genes. These transcription factors contain the homeobox protein-binding DNA motif, also found in other toolkit genes, and create the basic pattern of the body along its front-to-back axis.[20] Hox genes determine where repeating parts, such as the many vertebrae of snakes, will grow in a developing embryo or larva.[8] *Pax-6*, already mentioned, is a classic toolkit gene.[48] Although other toolkit genes are involved in establishing the plant bodyplan,[49] homeobox genes are also found in plants, implying they are common to all eukaryotes.[50][51][52]

The embryo's regulatory networks

The protein products of the regulatory toolkit are reused not by duplication and modification, but by a complex mosaic of pleiotropy, being applied unchanged in many independent developmental processes, giving pattern to many dissimilar body structures.[20] The loci of these pleiotropic toolkit genes have large, complicated and modular cis-regulatory elements. For example, while a non-pleiotropic rhodopsin gene in the fruit fly has a cis-regulatory element just a few hundred base pairs long, the pleiotropic eyeless cis-regulatory region contains 6 cis-regulatory elements in over 7000 base pairs.[20] The regulatory networks involved are often very large. Each regulatory protein controls "scores to hundreds" of cis-regulatory elements. For instance, 67 fruit fly transcription factors controlled on average 124 target genes each.[20] All this complexity enables genes involved in the development of the embryo to be switched on and off at exactly the right times and in exactly the right places. Some of these genes are structural, directly forming enzymes, tissues and organs of the embryo. But many others are themselves regulatory genes, so what is switched on is often a precisely-timed cascade of switching, involving turning on one developmental process after another in the developing embryo.[20]

Such a cascading regulatory network has been studied in detail in the development of the fruit fly embryo. The young embryo is oval in shape, like a rugby ball. A small number of genes produce messenger RNAs that set up concentration gradients along the long axis of the embryo. In the early embryo, the *bicoid* and *hunchback* genes are at high concentration near the anterior end, and give pattern to the future head and thorax; the *caudal* and *nanos* genes are at high concentration near the posterior end, and give pattern to the hindmost abdominal segments. The effects of these genes interact; for instance, the Bicoid protein blocks the translation of *caudal*'s messenger RNA, so the Caudal protein concentration becomes low at the anterior end. Caudal later switches on genes which create the fly's hindmost segments, but only at the posterior end where it is most concentrated.[53][54]

The Bicoid, Hunchback and Caudal proteins in turn regulate the transcription of gap genes such as *giant*, *knirps*, *Krüppel*, and *tailless* in a striped pattern, creating the first level of structures that will become segments.[37] The proteins from these in turn control the pair-rule genes, which in the next stage set up 7 bands across the embryo's long axis. Finally, the segment polarity genes such as *engrailed* split each of the 7 bands into two, creating 14 future segments.[53][54]

This process explains the accurate conservation of toolkit gene sequences, which has resulted in deep homology and functional equivalence of toolkit proteins in dissimilar animals (seen, for example, when a mouse protein controls fruit fly development). The interactions of transcription factors and cis-regulatory elements, or of signalling proteins and receptors, become locked in through multiple usages, making almost any mutation deleterious and hence eliminated by natural selection.[20]

The mechanism that sets up every animal's front-back axis is the same, implying a common ancestor. There is a similar mechanism for the back-belly axis for bilaterian animals, but it is reversed between arthropods and vertebrates.[55] Another process, gastrulation of the embryo, is driven by Myosin II molecular motors, which are not conserved across species. The process may have been started by movements of sea water in the environment, later replaced by the evolution of tissue movements in the embryo.[56][57]

The origins of novelty

Among the more surprising and, perhaps, counterintuitive (from a neo-Darwinian viewpoint) results of recent research in evolutionary developmental biology is that the diversity of body plans and morphology in organisms across many phyla are not necessarily reflected in diversity at the level of the sequences of genes, including those of the developmental genetic toolkit and other genes involved in development. Indeed, as John Gerhart and Marc Kirschner have noted, there is an apparent paradox: "where we most expect to find variation, we find conservation, a lack of change".[58] So, if the observed morphological novelty between different clades does not come from changes in gene sequences (such as by mutation), where does it come from? Novelty may arise by mutation-driven changes in gene regulation.[20][59][60][61]

Variations in the toolkit

Variations in the toolkit may have produced a large part of the morphological evolution of animals. The toolkit can drive evolution in two ways. A toolkit gene can be expressed in a different pattern, as when the beak of Darwin's large ground-finch was enlarged by the *BMP* gene,[62] or when snakes lost their legs as *distal-less* became under-expressed or not expressed at all in the places where other reptiles continued to form their limbs.[63] Or, a toolkit gene can acquire a new function, as seen in the many functions of that same gene, *distal-less*, which controls such diverse structures as the mandible in vertebrates,[64][65] legs and antennae in the fruit fly,[66] and eyespot pattern in butterfly wings.[67] Given that small changes in toolbox genes can cause significant changes in body structures, they have often enabled the same function convergently or in parallel. *distal-less* generates wing patterns in the butterflies *Heliconius erato* and *Heliconius melpomene*, which are Müllerian mimics. In so-called facilitated variation,[68] their wing patterns arose in different evolutionary events, but are controlled by the same genes.[69] Developmental changes can contribute directly to speciation.[70]

Consolidation of epigenetic changes

Evolutionary innovation may sometimes begin in Lamarckian style with epigenetic alterations of gene regulation or phenotype generation, subsequently consolidated by changes at the gene level. Epigenetic changes include modification of DNA by reversible methylation,[71] as well as nonprogrammed remoulding of the organism by physical and other environmental effects due to the inherent plasticity of developmental mechanisms.[72] The biologists Stuart A. Newman and Gerd B. Müller have suggested that organisms early in the history of multicellular life were more susceptible to this second category of epigenetic determination than are modern organisms, providing a basis for early macroevolutionary changes.[73]

Developmental bias

Development in specific lineages can be biased either positively, towards a given trajectory or phenotype,[b] or negatively, away from producing certain types of change; either may be absolute (the change is always or never produced) or relative. Evidence for any such direction in evolution is however hard to acquire and can also result from developmental constraints that limit diversification.[75] For example, in the gastropods, the snail-type shell is always built as a tube that grows both in length and in diameter; selection has created a wide variety of shell shapes such as flat spirals, cowries and tall turret spirals within these constraints. Among the centipedes, the Lithobiomorpha always have 15 trunk segments as adults, probably the result of a developmental bias towards an odd number of trunk segments. Another centipede order, the Geophilomorpha, the number of segments varies in different species between 27 and 191, but the number is always odd, making this an absolute constraint; almost all the odd numbers in that range are occupied by one or another species.[74][76][77]

Ecological evolutionary developmental biology

Ecological evolutionary developmental biology[c] integrates research from developmental biology and ecology to examine their relationship with evolutionary theory.[78] Researchers study concepts and mechanisms such as developmental plasticity, epigenetic inheritance, genetic assimilation, niche construction and symbiosis.[79][80]

V. ECOLOGY AND EVOLUTIONARY BIOLOGY

Ecology and evolutionary biology is an interdisciplinary field of study concerning interactions between organisms and their ever-changing environment, including perspectives from both evolutionary biology and ecology. This field of study includes topics such as the way organisms respond and evolve, as well as the relationships among animals, plants, and micro-organisms, when their habitats change.[1] Ecology and evolutionary biology is a broad field of study that covers various ranges of ages and scales, which can also help us to comprehend human impacts on the global ecosystem and find measures to achieve more sustainable development.

Examples of current research topics

Birdsong

There is a number of acoustic research about birds. Birds learn to sing in specific patterns because birdsong conveys information to select partners, which is a result of evolution. However, this evolution is also affected by ecological factors.[2] Research with recorded birdsong of male white-crowned sparrows from different regions found that the birdsongs from the same location have the same traits, while birdsongs from different locations are more likely to have different song types. Birdsongs from areas with dense vegetation tend to only have slow trilling sounds and low frequencies, while birdsongs from more open areas have fast trilling sounds and higher frequencies.[3] This is probably due to differences in the propagation of sound through vegetation. Low frequencies can be heard from further away when going through dense vegetation than high frequencies. For that reason it would be an advantage for birds who live in dense vegetation to sing at lower frequencies. That way, their songs can still be heard by competitors and potential mates far away.

Something similar was found in birds living on a mountain. The birds who lived higher up were singing at higher frequencies. This was probably due to the higher parts of the mountain being colder and therefore fewer other species living there. Other animals also make sounds with which the birds would have to compete, so when there are less species, there are less high frequency sounds to compete with.[4]

Snail colour

The colour and ornamentation of the snails' shells are almost entirely determined by their genes. One kind of land snail, *Cepaea nemoralis*, which is very common in Europe, has been studied and found to have a few different colours and a different amount of dark bands on their shells. In a large citizen science project 'the Evolution Mega-Lab', citizens of many different countries throughout Europe collected snails and counted how many snails of a certain colour/band pattern were present in a certain habitat.

Some colours can be seen better by birds, which is one way in which the best camouflaged snails are selected for. This also depends on the habitat in which the snails live. For instance yellow snails living in the dunes are better

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camouflaged than brown snails.[5] Another reason that one colour of shell might be better in a certain habitat is because of the temperature. It was found that darker shells absorb more heat, which can be a risk for overheating of the snail in certain habitats like dunes. In those places lighter coloured snails were found more often.[6]

Urban evolution

With fast growing cities and high rates of urbanization a whole new kind of environment has emerged. The urban ecosystem is a place of extremities and makes for fast evolution. Higher rates of phenotypic change have been observed in urban areas compared to natural and nonurban anthropogenic systems.[7] A field of study has emerged regarding urban evolution in which the adaptations of animals and plants to urban environments are studied.

In tropical regions a certain species of lizards, *Anolis cristatellus*, lives in both urban and natural areas. These lizards climb on tree trunks, fences and the walls of buildings. In urban areas more slippery and smooth surfaces are found than in natural areas. This creates a higher risk of falling and dying. The lizards in cities were found to have adapted to these slippery surfaces, by developing longer limbs and more lamellae under their feet that help them to run safely on these smooth surfaces.[8]

One of the differences between urban areas and natural areas is anthropogenic noise, such as traffic noise. The frequencies of these sounds overlap partly with the frequencies of bird songs. In cities, birds started to sing at higher frequencies than they do in natural areas, in order to still be heard by their conspecifics. Their songs were also found to be shorter.[9] This is a way in which the birds adapt to the new urban environment.

An example of urban evolution in plants was found in *Crepis sancta*. This plant makes seeds with pappus that can travel with the wind, for seed dispersal. In urban environments green patches are very rare and are also often very small and far apart. Due to this, the chances of the seeds landing on asphalt or stone and not being able to sprout are way higher than in open fields. *Crepis sancta* makes both light seeds with pappus as well as heavier seeds without pappus. In the city the plants were found to make more heavy seeds in comparison to the plants in nonurban areas.[10] This makes sense from an evolutionary perspective since heavy seeds fall very close to the mother-plant, probably in the same green patch, and therefore have a higher chance of sprouting.

Another characteristic of urban areas is light pollution. One of the well known consequences of light pollution is the attraction of insects. Before the presence of human light, the only source of light at night was the moon. Insects fly with a fixed angle to the moon to be able to fly in a straight line. Our light sources, however, are very close by. So if an insect flies with a fixed angle compared to a street light for instance, he starts flying in circles and eventually ends up circling the street light, which reduces his chances of finding food and a mating partner. Urban moths were found to have a reduced attraction to light sources, which directly impacts their chances for survival and mating by not wasting time close to a light source.[11]

Degrees in North America

Some North American universities are home to degree programs titled Ecology and Evolutionary Biology, offering integrated studies in the disciplines of ecology and evolutionary biology. The wording is intended as representing the alternative approach from the frequently used pairing of Cell and Molecular Biology, while being more inclusive than the terminology of Botany or Zoology. Recently, due to advances in the fields of genetics and molecular biology, research and education in ecology and evolutionary biology has integrated many molecular techniques.

A program that focuses on the relationships and interactions that range across levels of biological organization based on a scientific study is Ecology and Evolutionary Biology. The origins and history of ecosystems, species, genes and genomes, and organisms, and how these have changed over time is all part of the studies of how biodiversity has evolved and how it takes place. Ecology and Evolutionary biology in North America is based on research impact determined by the top 10% of ecology programs. The interactive web of organisms and environment are all part of what the field of Ecology explores. There have been studies in evolution that have worked to prove that "modern organisms have developed from ancestral ones." The reason that evolutionary biology is so interesting to learn about is because of the evolutionary processes that is the reason we have such a diversity of life on Earth.There are many processes that make up evolutionary biology that give great insight to how we came to be, some of which include natural selection, speciation, and common descent.

Evolutionary thought, the recognition that species change over time and the perceived understanding of how such processes work, has roots in antiquity—in the ideas of the ancient Greeks, Romans, Chinese, Church Fathers as well as in medieval Islamic science. With the beginnings of modern biological taxonomy in the late 17th century, two opposed ideas influenced Western biological thinking: essentialism, the belief that every species has essential characteristics that are unalterable, a concept which had developed from medieval Aristotelian metaphysics, and that fit well with natural theology; and the development of the new anti-Aristotelian approach to modern science: as the Enlightenment progressed, evolutionary cosmology and the mechanical philosophy spread from the physical sciences to natural history. Naturalists began to focus on the variability of species; the emergence of palaeontology with the concept of extinction further undermined static views of nature. In the early 19th century prior to Darwinism, Jean-Baptiste Lamarck (1744–1829) proposed his theory of the transmutation of species, the first fully formed theory of evolution.

In 1858 Charles Darwin and Alfred Russel Wallace published a new evolutionary theory, explained in detail in Darwin's *On the Origin of Species* (1859). Darwin's theory, originally called descent with modification is known contemporarily as Darwinism or Darwinian theory. Unlike Lamarck, Darwin proposed common descent and a branching tree of life, meaning that two very different species could share a common ancestor. Darwin based his theory on the idea of natural selection: it synthesized a broad range of evidence from animal husbandry, biogeography, geology, morphology, and embryology. Debate over Darwin's work led to the rapid acceptance of the general concept of evolution, but the specific mechanism he proposed, natural selection, was not widely accepted until it was revived by developments in biology that occurred during the 1920s through the 1940s. Before that time most biologists regarded other factors as responsible for evolution. Alternatives to natural selection suggested during "the eclipse of Darwinism" (c. 1880 to 1920) included inheritance of acquired characteristics (neo-Lamarckism), an innate drive for change (orthogenesis), and sudden large mutations (saltationism). Mendelian genetics, a series of 19th-century experiments with pea plant variations rediscovered in 1900, was integrated with natural selection by Ronald Fisher, J. B. S. Haldane, and Sewall Wright during the 1910s to 1930s, and resulted in the founding of the new discipline of population genetics. During the 1930s and 1940s population genetics became integrated with other biological fields, resulting in a widely applicable theory of evolution that encompassed much of biology—the modern synthesis.

Following the establishment of evolutionary biology, studies of mutation and genetic diversity in natural populations, combined with biogeography and systematics, led to sophisticated mathematical and causal models of evolution. Palaeontology and comparative anatomy allowed more detailed reconstructions of the evolutionary history of life. After the rise of molecular genetics in the 1950s, the field of molecular evolution developed, based on protein sequences and immunological tests, and later incorporating RNA and DNA studies. The gene-centred view of evolution rose to prominence in the 1960s, followed by the neutral theory of molecular evolution, sparking debates over adaptationism, the unit of selection, and the relative importance of genetic drift versus natural selection as causes of evolution.[2] In the late 20th-century, DNA sequencing led to molecular phylogenetics and the reorganization of the tree of life into the three-domain system by Carl Woese. In addition, the newly recognized factors of symbiogenesis and horizontal gene transfer introduced yet more complexity into evolutionary theory. Discoveries in evolutionary biology have made a significant impact not just within the traditional branches of biology, but also in other academic disciplines (for example: anthropology and psychology) and on society at large.[3]

Antiquity

Greeks

Proposals that one type of animal, even humans, could descend from other types of animals, are known to go back to the first pre-Socratic Greek philosophers. Anaximander of Miletus (c. 610 – c. 546 BC) proposed that the first animals lived in water, during a wet phase of the Earth's past, and that the first land-dwelling ancestors of mankind must have been born in water, and only spent part of their life on land. He also argued that the first human of the form known today must have been the child of a different type of animal (probably a fish), because man needs prolonged nursing to live.[5][6][4] In the late nineteenth century, Anaximander was hailed as the "first Darwinist", but this characterization is no longer commonly agreed.[7] Anaximander's hypothesis could be considered "evolution" in a sense, although not a Darwinian one.[7]

Empedocles (c. 490 – c. 430 BC), argued that what we call birth and death in animals are just the mingling and separations of elements which cause the countless "tribes of mortal things."[8] Specifically, the first animals and plants were like disjointed parts of the ones we see today, some of which survived by joining in different combinations, and then intermixing during the development of the embryo,[a] and where "everything turned out as it would have if it were on purpose, there the creatures survived, being accidentally compounded in a suitable way."[9] Other philosophers who became more influential at that time, including Plato (428/427—348/347 BC), Aristotle (384—322 BC), and members of the Stoic school of philosophy, believed that the types of all things, not only living things, were fixed by divine design.[10][11]

Plato was called by biologist Ernst Mayr "the great antihero of evolutionism,"[10] because he promoted belief in essentialism, which is also referred to as the theory of Forms. This theory holds that each natural type of object in the observed world is an imperfect manifestation of the ideal, form or "species" which defines that type. In his *Timaeus* for example, Plato has a character tell a story that the Demiurge created the cosmos and everything in it because, being good, and hence, "... free from jealousy, He desired that all things should be as like Himself as they could be." The creator created all conceivable forms of life, since "... without them the universe will be incomplete, for it will not contain every kind of animal which it ought to contain, if it is to be perfect." This "principle of plenitude"—the idea that all potential forms of life are essential to a perfect creation—greatly influenced Christian thought.[11] However some historians of science have questioned how much influence Plato's essentialism had on natural philosophy by stating that many philosophers after Plato believed that species might be capable of transformation and that the idea that biologic species were fixed and possessed unchangeable essential characteristics did not become important until the beginning of biological taxonomy in the 17th and 18th centuries.[12]

Aristotle, the most influential of the Greek philosophers in Europe, was a student of Plato and is also the earliest natural historian whose work has been preserved in any real detail. His writings on biology resulted from his research into natural history on and around the island of Lesbos, and have survived in the form of four books, usually known by their Latin names, *De anima* (*On the Soul*), *Historia animalium* (*History of Animals*), *De generatione animalium* (*Generation of Animals*), and *De partibus animalium* (*On the Parts of Animals*). Aristotle's works contain accurate observations, fitted into his own theories of the body's mechanisms.[13] However, for Charles Singer, "Nothing is more remarkable than [Aristotle's] efforts to [exhibit] the relationships of living things as a *scala naturae*."[13] This *scala naturae*, described in *Historia animalium*, classified organisms in relation to a hierarchical but static "Ladder of Life" or "great chain of being," placing them according to their complexity of structure and function, with organisms that showed greater vitality and ability to move described as "higher organisms."[11] Aristotle believed that features of living organisms showed clearly that they had what he called a final cause, that is to say that their form suited their function.[14] He explicitly rejected the view of Empedocles that living creatures might have originated by chance.[15]

Other Greek philosophers, such as Zeno of Citium (334—262 BC) the founder of the Stoic school of philosophy, agreed with Aristotle and other earlier philosophers that nature showed clear evidence of being designed for a purpose; this view is known as teleology.[16] The Roman Skeptic philosopher Cicero (106—43 BC) wrote that Zeno was known to have held the view, central to Stoic physics, that nature is primarily "directed and concentrated...to secure for the world...the structure best fitted for survival."[17]

Chinese

Ancient Chinese thinkers such as Zhuang Zhou (c. 369 – c. 286 BC), a Taoist philosopher, expressed ideas on changing biological species. According to Joseph Needham, Taoism explicitly denies the fixity of biological species and Taoist philosophers speculated that species had developed differing attributes in response to differing environments.[18] Taoism regards humans, nature and the heavens as existing in a state of "constant transformation" known as the *Tao*, in contrast with the more static view of nature typical of Western thought.[19]

Roman Empire

Lucretius' poem *De rerum natura* provides the best surviving explanation of the ideas of the Greek Epicurean philosophers. It describes the development of the cosmos, the Earth, living things, and human society through purely naturalistic mechanisms, without any reference to supernatural involvement. *De rerum natura* would influence the cosmological and evolutionary speculations of philosophers and scientists during and after the Renaissance.[20][21] This view was in strong contrast with the views of Roman philosophers of the Stoic school such as Seneca the Younger (c. 4 BC – AD 65), and Pliny the Elder (23—79 AD) who had a strongly teleological view of the natural world that influenced Christian theology.[16] Cicero reports that the peripatetic and Stoic view of nature as an agency concerned most basically with producing life "best fitted for survival" was taken for granted among the Hellenistic elite.[17]

Early Church Fathers

Origen of Alexandria

In line with earlier Greek thought, the third-century Christian philosopher and Church Father Origen of Alexandria argued that the creation story in the Book of Genesis should be interpreted as an allegory for the falling of human souls away from the glory of the divine, and not as a literal, historical account:[22][23]

For who that has understanding will suppose that the first, and second, and third day, and the evening and the morning, existed without a sun, and moon, and stars? And that the first day was, as it were, also without a sky? And who is so foolish as to suppose that God, after the manner of a husbandman, planted a paradise in Eden, towards the east, and placed in it a tree of life, visible and palpable, so that one tasting of the fruit by the bodily teeth obtained life? And again, that one was a partaker of good and evil by masticating what was taken from the tree? And if God is said to walk in the paradise in the evening, and Adam to hide himself under a tree, I do not suppose that anyone doubts that these things figuratively indicate certain mysteries, the history having taken place in appearance, and not literally.

—*Origen, On the First Principles IV.16*

Gregory of Nyssa

Gregory of Nyssa wrote:

Scripture informs us that the Deity proceeded by a sort of graduated and ordered advance to the creation of man. After the foundations of the universe were laid, as the history records, man did not appear on the earth at once, but the creation of the brutes preceded him, and the plants preceded them. Thereby Scripture shows that the vital forces blended with the world of matter according to a gradation; first it infused itself into insensate nature; and in continuation of this advanced into the sentient world; and then ascended to intelligent and rational beings (emphasis added).[9]

Henry Fairfield Osborn wrote in his work on the history of evolutionary thought, *From the Greeks to Darwin* (1894):

Among the Christian Fathers the movement towards a partly naturalistic interpretation of the order of Creation was made by Gregory of Nyssa in the fourth century, and was completed by Augustine in the fourth and fifth centuries. ...[Gregory of Nyssa] taught that Creation was potential. God imparted to matter its fundamental properties and laws. The objects and completed forms of the Universe developed gradually out of chaotic material. [24]

Augustine of Hippo

In the fourth century AD, the bishop and theologian Augustine of Hippo followed Origen in arguing that Christians should read the Genesis creation story allegorically. In his book *De Genesi ad Litteram* (*On the Literal Meaning of Genesis*) he prefaces his account

In all sacred books, we should consider the eternal truths that are taught, the facts that are narrated, the future events that are predicted, and the precepts or counsels that are given. In the case of a narrative of events, the question arises whether everything must be taken according to the figurative sense only, or whether it must be expounded and defended also as a faithful record of what happened. No Christian would dare say that the narrative must not be taken in a figurative sense. For St. Paul says: *Now all these things that happened to them were symbolic.* [1 Cor 10:11] And he explains the statement in Genesis, *And they shall be two in one flesh*, as a great mystery in reference to Christ and to the Church. [Eph 5:32][14]

Later he differentiates between the days of the Genesis 1 creation narrative and 24 hour days

But at least we know [the days of creation] are different from the ordinary day of which we are familiar[18]

He also talks about a form of theistic evolution

The things [God] had potentially created... [came] forth in the course of time on different days according to their different kinds... [and] the rest of the earth [was] filled with its various kinds of creatures, [which] produced their appropriate forms in due time.[20]

Which has led Francis Collins of Biologos to believe Augustine espoused a form of theistic evolution.[23]

Augustine deployed the concept of *rationes seminales* to blend the idea of divine creation with subsequent development.[26] This idea "that forms of life had been transformed 'slowly over time'" prompted Father Giuseppe Tanzella-Nitti, Professor of Theology at the Pontifical Santa Croce University in Rome, to claim that Augustine had suggested a form of evolution.[27][28]

Henry Fairfield Osborn wrote in *From the Greeks to Darwin* (1894):

If the orthodoxy of Augustine had remained the teaching of the Church, the final establishment of Evolution would have come far earlier than it did, certainly during the eighteenth instead of the nineteenth century, and the bitter controversy over this truth of Nature would never have arisen. ... Plainly as the direct or instantaneous Creation of animals and plants appeared to be taught in Genesis, Augustine read this in the light of primary causation and the gradual development from the imperfect to the perfect of Aristotle. This most influential teacher thus handed down to his followers opinions which closely conform to the progressive views of those theologians of the present day who have accepted the Evolution theory.[29]

In *A History of the Warfare of Science with Theology in Christendom* (1896), Andrew Dickson White wrote about Augustine's attempts to preserve the ancient evolutionary approach to the creation as follows:

For ages a widely accepted doctrine had been that water, filth, and carrion had received power from the Creator to generate worms, insects, and a multitude of the smaller animals; and this doctrine had been especially welcomed by St. Augustine and many of the fathers, since it relieved the Almighty of making, Adam of naming, and Noah of living in the ark with these innumerable despised species.[30]

In Augustine's *De Genesi contra Manichæos*, on Genesis he says: "To suppose that God formed man from the dust with bodily hands is very childish. ... God neither formed man with bodily hands nor did he breathe upon him with throat and lips." Augustine suggests in other work his theory of the later development of insects out of carrion, and the adoption of the old emanation or evolution theory, showing that "certain very small animals may not have been created on the fifth and sixth days, but may have originated later from putrefying matter." Concerning Augustine's *De Trinitate* (*On the Trinity*), White wrote that Augustine "...develops at length the view that in the creation of living beings there was something like a growth—that God is the ultimate author, but works through secondary causes; and finally argues that certain substances are endowed by God with the power of producing certain classes of plants and animals."[31]

Augustine implies that whatever science shows, the Bible must teach:

Usually, even a non-Christian knows something about the earth, the heavens, and the other elements of this world, about the motion and orbit of the stars ... Now, it is a disgraceful and dangerous thing for an infidel to hear a Christian, presumably giving the meaning of Holy Scripture, talking non-sense on these topics; and we should take all means to prevent such an embarrassing situation, in which people show up vast ignorance in a Christian and laugh it to scorn. The shame is not so much that an ignorant individual is derided, but that people outside the household of the faith think our sacred writers held such opinions, and, to the great loss of those for whose salvation we toil, the writers of our Scripture are criticized and rejected as unlearned men.[32]

Middle Ages

Islamic philosophy and the struggle for existence

Although Greek and Roman evolutionary ideas died out in Western Europe after the fall of the Roman Empire, they were not lost to Islamic philosophers and scientists (nor to the culturally Greek Byzantine Empire). In the Islamic Golden Age of the 8th to the 13th centuries, philosophers explored ideas about natural history. These ideas included transmutation from non-living to living: "from mineral to plant, from plant to animal, and from animal to man."[33]

In the medieval Islamic world, the scholar al-Jāḥiẓ (776 – c. 868) wrote his *Book of Animals* in the 9th century. Conway Zirkle, writing about the history of natural selection in 1941, said that an excerpt from this work was the only relevant passage he had found from an Arabian scholar. He provided a quotation describing the struggle for existence, citing a Spanish translation of this work: "Every weak animal devours those weaker than itself. Strong animals cannot escape being devoured by other animals stronger than they. And in this respect, men do not differ from animals, some with respect to others, although they do not arrive at the same extremes. In short, God has disposed some human beings as a cause of life for others, and likewise, he has disposed the latter as a cause of the death of the former."[34] Al-Jāḥiẓ also wrote descriptions of food chains.[35]

Some of Ibn Khaldūn's thoughts, according to some commentators, anticipate the biological theory of evolution.[36] In 1377, Ibn Khaldūn wrote the *Muqaddimah* in which he asserted that humans developed from "the world of the monkeys," in a process by which "species become more numerous".[36] In chapter 1 he writes: "This world with all the created things in it has a certain order and solid construction. It shows nexuses between causes and things caused, combinations of some parts of creation with others, and transformations of some existent things into others, in a pattern that is both remarkable and endless."[37]

The *Muqaddimah* also states in chapter 6:

We explained there that the whole of existence in (all) its simple and composite worlds is arranged in a natural order of ascent and descent, so that everything constitutes an uninterrupted continuum. The essences at the end of each particular stage of the worlds are by nature prepared to be transformed into the essence adjacent to them, either above or below them. This is the case with the simple material elements; it is the case with palms and vines, (which constitute) the last stage of plants, in their relation to snails and shellfish, (which constitute) the (lowest) stage of animals. It is also the case with monkeys, creatures combining in themselves cleverness and perception, in their relation to man, the being who has the ability to think and to reflect. The preparedness (for transformation) that exists on either side, at each stage of the worlds, is meant when (we speak about) their connection.[38]

Christian philosophy

Thomas Aquinas on creation and natural processes

While most Christian theologians held that the natural world was part of an unchanging designed hierarchy, some theologians speculated that the world might have developed through natural processes. Thomas Aquinas expounded on Augustine of Hippo's early idea of theistic evolution

On the day on which God created the heaven and the earth, He created also every plant of the field, not, indeed, actually, but 'before it sprung up in the earth,' that is, potentially... All things were not distinguished and adorned together, not from a want of power on God's part, as requiring time in which to work, but that due order might be observed in the instituting of the world.[33]

He saw that the autonomy of nature was a sign of God's goodness, and detected no conflict between a divinely created universe and the idea that the universe had developed over time through natural mechanisms.[39] However, Aquinas disputed the views of those (like the ancient Greek philosopher Empedocles) who held that such natural processes showed that the universe could have developed without an underlying purpose. Aquinas rather held that: "Hence, it is clear that nature is nothing but a certain kind of art, i.e., the divine art, impressed upon things, by which these things are moved to a determinate end. It is as if the shipbuilder were able to give to timbers that by which they would move themselves to take the form of a ship."[40]

Renaissance and Enlightenment

In the first half of the 17th century, René Descartes' mechanical philosophy encouraged the use of the metaphor of the universe as a machine, a concept that would come to characterise the scientific revolution.[41] Between 1650 and 1800, some naturalists, such as Benoît de Maillet, produced theories that maintained that the universe, the Earth, and life, had developed mechanically, without divine guidance.[42] In contrast, most contemporary theories of evolution, such of those of Gottfried Leibniz and Johann Gottfried Herder, regarded evolution as a fundamentally *spiritual* process.[43] In 1751, Pierre Louis Maupertuis veered toward more materialist ground. He wrote of natural modifications occurring during reproduction and accumulating over the course of many generations, producing races and even new species, a description that anticipated in general terms the concept of natural selection.[44]

Maupertuis' ideas were in opposition to the influence of early taxonomists like John Ray. In the late 17th century, Ray had given the first formal definition of a biological species, which he described as being characterized by essential unchanging features, and stated the seed of one species could never give rise to another.[12] The ideas of Ray and other 17th-century taxonomists were influenced by natural theology and the argument from design.[45]

The word *evolution* (from the Latin *evolutio*, meaning "to unroll like a scroll") was initially used to refer to embryological development; its first use in relation to development of species came 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.[46]

Later in the 18th century, the French philosopher Georges-Louis Leclerc, Comte de Buffon, one of the leading naturalists of the time, suggested that what most people referred to as species were really just well-marked varieties, modified from an original form by environmental factors. For example, he believed that lions, tigers, leopards, and house cats might all have a common ancestor. He further speculated that the 200 or so species of mammals then known might have descended from as few as 38 original animal forms. Buffon's evolutionary ideas were limited; he believed each of the original forms had arisen through spontaneous generation and that each was shaped by "internal moulds" that limited the amount of change. Buffon's works, *Histoire naturelle* (1749–1789) and *Époques de la nature* (1778), containing well-developed theories about a completely materialistic origin for the Earth and his ideas questioning the fixity of species, were extremely influential.[47][48] Another French philosopher, Denis Diderot, also wrote that living things might have first arisen through spontaneous generation, and that species were always changing through a constant process of experiment where new forms arose and survived or not based on trial and error; an idea that can be considered a partial anticipation of natural selection.[49] Between 1767 and 1792, James Burnett, Lord Monboddo, included in his writings not only the concept that man had descended from primates, but also that, in response to the environment, creatures had found methods of transforming their characteristics over long time intervals.[50] Charles Darwin's grandfather, Erasmus Darwin, published *Zoonomia* (1794–1796) which suggested that "all warm-blooded animals have arisen from one living filament."[51] In his poem *Temple of Nature* (1803), he described the rise of life from minute organisms living in mud to all of its modern diversity.[52]

Early 19th century

Paleontology and geology

In 1796, Georges Cuvier published his findings on the differences between living elephants and those found in the fossil record. His analysis identified mammoths and mastodons as distinct species, different from any living animal, and effectively ended a long-running debate over whether a species could become extinct.[54] In 1788, James Hutton described gradual geological processes operating continuously over deep time.[55] In the 1790s, William Smith began the process of ordering rock strata by examining fossils in the layers while he worked on his geologic map of England. Independently, in 1811, Cuvier and Alexandre Brongniart published an influential study of the geologic history of the region around Paris, based on the stratigraphic succession of rock layers. These works helped establish the antiquity of the Earth.[56] Cuvier advocated catastrophism to explain the patterns of extinction and faunal succession revealed by the fossil record.

Knowledge of the fossil record continued to advance rapidly during the first few decades of the 19th century. By the 1840s, the outlines of the geologic timescale were becoming clear, and in 1841 John Phillips named three major eras, based on the predominant fauna of each: the Paleozoic, dominated by marine invertebrates and fish, the Mesozoic, the age of reptiles, and the current Cenozoic age of mammals. This progressive picture of the history of life was accepted even by conservative English geologists like Adam Sedgwick and William Buckland; however, like Cuvier, they attributed the progression to repeated catastrophic episodes of extinction followed by new episodes of creation.[57] Unlike Cuvier, Buckland and some other advocates of natural theology among British geologists made efforts to explicitly link the last catastrophic episode proposed by Cuvier to the biblical flood.[58][59]

From 1830 to 1833, geologist Charles Lyell published his multi-volume work *Principles of Geology*, which, building on Hutton's ideas, advocated a uniformitarian alternative to the catastrophic theory of geology. Lyell claimed that, rather than being the products of cataclysmic (and possibly supernatural) events, the geologic features of the Earth are better explained as the result of the same gradual geologic forces observable in the present day—but acting over immensely long periods of time. Although Lyell opposed evolutionary ideas (even questioning the consensus that the fossil record demonstrates a true progression), his concept that the Earth was shaped by forces working gradually over an extended period, and the immense age of the Earth assumed by his theories, would strongly influence future evolutionary thinkers such as Charles Darwin.[60]

Transmutation of species

Jean-Baptiste Lamarck proposed, in his *Philosophie zoologique* of 1809, a theory of the transmutation of species (*transformisme*). Lamarck did not believe that all living things shared a common ancestor but rather that simple forms of life were created continuously by spontaneous generation. He also believed that an innate life force drove species to become more complex over time, advancing up a linear ladder of complexity that was related to the great chain of being. Lamarck recognized that species adapted to their environment. He explained this by saying that the same innate force driving increasing complexity caused the organs of an animal (or a plant) to change based on the use or disuse of those organs, just as exercise affects muscles. He argued that these changes would be inherited by the next generation and produce slow adaptation to the environment. It was this secondary mechanism of adaptation through the inheritance of acquired characteristics that would become known as Lamarckism and would influence discussions of evolution into the 20th century.[62][63]

A radical British school of comparative anatomy that included the anatomist Robert Edmond Grant was closely in touch with Lamarck's French school of *Transformationism*. One of the French scientists who influenced Grant was the anatomist Étienne Geoffroy Saint-Hilaire, whose ideas on the unity of various animal body plans and the homology of certain anatomical structures would be widely influential and lead to intense debate with his colleague Georges Cuvier. Grant became an authority on the anatomy and reproduction of marine invertebrates. He developed Lamarck's and Erasmus Darwin's ideas of transmutation and evolutionism, and investigated homology, even proposing that plants and animals had a common evolutionary starting point. As a young student, Charles Darwin joined Grant in investigations of the life cycle of marine animals. In 1826, an anonymous paper, probably written by Robert Jameson, praised Lamarck for explaining how higher animals had "evolved" from the simplest worms; this was the first use of the word "evolved" in a modern sense.[64][65]

In 1844, the Scottish publisher Robert Chambers anonymously published an extremely controversial but widely read book entitled *Vestiges of the Natural History of Creation*. This book proposed an evolutionary scenario for the origins of the Solar System and of life on Earth. It claimed that the fossil record showed a progressive ascent of animals, with current animals branching off a main line that leads progressively to humanity. It implied that the transmutations lead to the unfolding of a preordained plan that had been woven into the laws that governed the universe. In this sense it was less completely materialistic than the ideas of radicals like Grant, but its implication that humans were only the last step in the ascent of animal life incensed many conservative thinkers. The high profile of the public debate over *Vestiges*, with its depiction of evolution as a progressive process, would greatly influence the perception of Darwin's theory a decade later.[66][67]

Ideas about the transmutation of species were associated with the radical materialism of the Enlightenment and were attacked by more conservative thinkers. Cuvier attacked the ideas of Lamarck and Geoffroy, agreeing with Aristotle that species were immutable. Cuvier believed that the individual parts of an animal were too closely correlated with one another to allow for one part of the anatomy to change in isolation from the others, and argued that the fossil record showed patterns of catastrophic extinctions followed by repopulation, rather than gradual change over time. He also noted that drawings of animals and animal mummies from Egypt, which were thousands of years old, showed no signs of change when compared with modern animals. The strength of Cuvier's arguments and his scientific reputation helped keep transmutational ideas out of the mainstream for decades.[68]

In Great Britain, the philosophy of natural theology remained influential. William Paley's 1802 book *Natural Theology* with its famous watchmaker analogy had been written at least in part as a response to the transmutational ideas of Erasmus Darwin.[70] Geologists influenced by natural theology, such as Buckland and Sedgwick, made a regular practice of attacking the evolutionary ideas of Lamarck, Grant, and *Vestiges*.[71][72] Although Charles Lyell opposed scriptural geology, he also believed in the immutability of species, and in his *Principles of Geology*, he criticized Lamarck's theories of development.[60] Idealists such as Louis Agassiz and Richard Owen believed that each species was fixed and unchangeable because it represented an idea in the mind of the creator. They believed that relationships between species could be discerned from developmental patterns in embryology, as well as in the fossil record, but that these relationships represented an underlying pattern of divine thought, with progressive creation leading to increasing complexity and culminating in humanity. Owen developed the idea of "archetypes" in the Divine mind that would produce a sequence of species related by anatomical homologies, such as vertebrate limbs. Owen led a public campaign that successfully marginalized Grant in the scientific community. Darwin would make good use of the homologies analyzed by Owen in his own theory, but the harsh treatment of Grant, and the controversy surrounding *Vestiges*, showed him the need to ensure that his own ideas were scientifically sound.[65][73][74]

Anticipations of natural selection

It is possible to look through the history of biology from the ancient Greeks onwards and discover anticipations of almost all of Charles Darwin's key ideas. As an example, Loren Eiseley has found isolated passages written by Buffon suggesting he was almost ready to piece together a theory of natural selection, but states that such anticipations should not be taken out of the full context of the writings or of cultural values of the time which made Darwinian ideas of evolution unthinkable.[75]

When Darwin was developing his theory, he investigated selective breeding and was impressed[76] by John Sebright's observation that "A severe winter, or a scarcity of food, by destroying the weak and the unhealthy, has all the good effects of the most skilful selection" so that "the weak and the unhealthy do not live to propagate their infirmities."[77] Darwin was influenced by Charles Lyell's ideas of environmental change causing ecological shifts, leading to what Augustin de Candolle had called a war between competing plant species, competition well described by the botanist William Herbert. Darwin was struck by Thomas Robert Malthus' phrase "struggle for existence" used of warring human tribes.[78][79]

Several writers anticipated evolutionary aspects of Darwin's theory, and in the third edition of *On the Origin of Species* published in 1861 Darwin named those he knew about in an introductory appendix, *An Historical Sketch of the Recent Progress of Opinion on the Origin of Species*, which he expanded in later editions.[80]

In 1813, William Charles Wells read before the Royal Society essays assuming that there had been evolution of humans, and recognising the principle of natural selection. Darwin and Alfred Russel Wallace were unaware of this work when they jointly published the theory in 1858, but Darwin later acknowledged that Wells had recognised the principle before them, writing that the paper "An Account of a White Female, part of whose Skin resembles that of a Negro" was published in 1818, and "he distinctly recognises the principle of natural selection, and this is the first recognition which has been indicated; but he applies it only to the races of man, and to certain characters alone."[81]

Patrick Matthew wrote in his book *On Naval Timber and Arboriculture* (1831) of "continual balancing of life to circumstance. ... [The] progeny of the same parents, under great differences of circumstance, might, in several generations, even become distinct species, incapable of co-reproduction."[82] Darwin implies that he discovered this work after the initial publication of the *Origin*. In the brief historical sketch that Darwin included in the third edition he says "Unfortunately the view was given by Mr. Matthew very briefly in scattered passages in an Appendix to a work on a different subject ... He clearly saw, however, the full force of the principle of natural selection."[83]

However, as historian of science Peter J. Bowler says, "Through a combination of bold theorizing and comprehensive evaluation, Darwin came up with a concept of evolution that was unique for the time." Bowler goes on to say that simple priority alone is not enough to secure a place in the history of science; someone has to develop an idea and convince others of its importance to have a real impact.[84] Thomas Henry Huxley said in his essay on the reception of *On the Origin of Species*:

The suggestion that new species may result from the selective action of external conditions upon the variations from their specific type which individuals present—and which we call "spontaneous," because we are ignorant of their causation—is as wholly unknown to the historian of scientific ideas as it was to biological specialists before 1858. But that suggestion is the central idea of the 'Origin of Species,' and contains the quintessence of Darwinism.[85]

Natural selection

The biogeographical patterns Charles Darwin observed in places such as the Galápagos Islands during the second voyage of HMS *Beagle* caused him to doubt the fixity of species, and in 1837 Darwin started the first of a series of secret notebooks on transmutation. Darwin's observations led him to view transmutation as a process of divergence and branching, rather than the ladder-like progression envisioned by Jean-Baptiste Lamarck and others. In 1838 he read the new sixth edition of *An Essay on the Principle of Population*, written in the late 18th century by Thomas Robert Malthus. Malthus' idea of population growth leading to a struggle for survival combined with Darwin's knowledge on how breeders selected traits, led to the inception of Darwin's theory of natural selection. Darwin did not publish his ideas on evolution for 20 years. However, he did share them with certain other naturalists and friends, starting with Joseph Dalton Hooker, with whom he discussed his unpublished 1844 essay on natural selection. During this period he used the time he could spare from his other scientific work to slowly refine his ideas and, aware of the intense controversy around transmutation, amass evidence to support them. In September 1854 he began full-time work on writing his book on natural selection.[74][86][87]

Unlike Darwin, Alfred Russel Wallace, influenced by the book *Vestiges of the Natural History of Creation*, already suspected that transmutation of species occurred when he began his career as a naturalist. By 1855, his biogeographical observations during his field work in South America and the Malay Archipelago made him confident enough in a branching pattern of evolution to publish a paper stating that every species originated in close proximity to an already existing closely allied species. Like Darwin, it was Wallace's consideration of how the ideas of Malthus might apply to animal populations that led him to conclusions very similar to those reached by Darwin about the role of natural selection. In February 1858, Wallace, unaware of Darwin's unpublished ideas, composed his thoughts into an essay and mailed them to Darwin, asking for his opinion. The result was the joint publication in July of an extract from Darwin's 1844 essay along with Wallace's letter. Darwin also began work on a short abstract summarising his theory, which he would publish in 1859 as *On the Origin of Species*.[88]

1859–1930s: Darwin and his legacy

By the 1850s, whether or not species evolved was a subject of intense debate, with prominent scientists arguing both sides of the issue.[90] The publication of Charles Darwin's *On the Origin of Species* fundamentally transformed the discussion over biological origins.[91] Darwin argued that his branching version of evolution explained a wealth of facts in biogeography, anatomy, embryology, and other fields of biology. He also provided the first cogent mechanism by which evolutionary change could persist: his theory of natural selection.[92]

One of the first and most important naturalists to be convinced by *Origin* of the reality of evolution was the British anatomist Thomas Henry Huxley. Huxley recognized that unlike the earlier transmutational ideas of Jean-Baptiste Lamarck and *Vestiges of the Natural History of Creation*, Darwin's theory provided a mechanism for evolution without supernatural involvement, even if Huxley himself was not completely convinced that natural selection was the key evolutionary mechanism. Huxley would make advocacy of evolution a cornerstone of the program of the X Club to reform and professionalise science by displacing natural theology with naturalism and to end the domination of British natural science by the clergy. By the early 1870s in English-speaking countries, thanks partly to these efforts, evolution had become the mainstream scientific explanation for the origin of species.[92] In his campaign for public and scientific acceptance of Darwin's theory, Huxley made extensive use of new evidence for evolution from paleontology. This included evidence that birds had evolved from reptiles, including the discovery of *Archaeopteryx* in Europe, and a number of fossils of primitive birds with teeth found in North America. Another important line of evidence was the finding of fossils that helped trace the evolution of the horse from its small five-toed ancestors.[93] However, acceptance of evolution among scientists in non-English speaking nations such as France, and the countries of southern Europe and Latin America was slower. An exception to this was Germany, where both August Weismann and Ernst Haeckel championed this idea: Haeckel used evolution to challenge the established tradition of metaphysical idealism in German biology, much as Huxley used it to challenge natural theology in Britain.[94] Haeckel and other German scientists would take the lead in launching an ambitious programme to reconstruct the evolutionary history of life based on morphology and embryology.[95]

Darwin's theory succeeded in profoundly altering scientific opinion regarding the development of life and in producing a small philosophical revolution.[96] However, this theory could not explain several critical components of the evolutionary process. Specifically, Darwin was unable to explain the source of variation in traits within a species, and could not identify a mechanism that could pass traits faithfully from one generation to the next. Darwin's hypothesis of pangenesis, while relying in part on the inheritance of acquired characteristics, proved to be useful for statistical models of evolution that were developed by his cousin Francis Galton and the "biometric" school of evolutionary thought. However, this idea proved to be of little use to other biologists.[97]

Application to humans

Charles Darwin was aware of the severe reaction in some parts of the scientific community against the suggestion made in *Vestiges of the Natural History of Creation* that humans had arisen from animals by a process of transmutation. Therefore, he almost completely ignored the topic of human evolution in *On the Origin of Species*. Despite this precaution, the issue featured prominently in the debate that followed the book's publication. For most of the first half of the 19th century, the scientific community believed that, although geology had shown that the Earth and life were very old, human beings had appeared suddenly just a few thousand years before the present. However, a series of archaeological discoveries in the 1840s and 1850s showed stone tools associated with the remains of extinct animals. By the early 1860s, as summarized in Charles Lyell's 1863 book *Geological Evidences of the Antiquity of Man*, it had become widely accepted that humans had existed during a prehistoric period—which stretched many thousands of years before the start of written history. This view of human history was more compatible with an evolutionary origin for humanity than was the older view. On the other hand, at that time there was no fossil evidence to demonstrate human evolution. The only human fossils found before the discovery of Java Man in the 1890s were either of anatomically modern humans or of Neanderthals that were too close, especially in the critical characteristic of cranial capacity, to modern humans for them to be convincing intermediates between humans and other primates.[100]

Therefore, the debate that immediately followed the publication of *On the Origin of Species* centered on the similarities and differences between humans and modern apes. Carolus Linnaeus had been criticised in the 18th century for grouping humans and apes together as primates in his ground breaking classification system.[101] Richard Owen vigorously defended the classification suggested by Georges Cuvier and Johann Friedrich Blumenbach that placed humans in a separate order from any of the other mammals, which by the early 19th century had become the orthodox view. On the other hand, Thomas Henry Huxley sought to demonstrate a close anatomical relationship between humans and apes. In one famous incident, which became known as the Great Hippocampus Question, Huxley showed that Owen was mistaken in claiming that the brains of gorillas lacked a structure present in human brains. Huxley summarized his argument in his highly influential 1863 book *Evidence as to Man's Place in Nature*. Another viewpoint was advocated by Lyell and Alfred Russel Wallace. They agreed that humans shared a common ancestor with apes, but questioned whether any purely materialistic mechanism could account for all the differences between humans and apes, especially some aspects of the human mind.[100]

In 1871, Darwin published *The Descent of Man, and Selection in Relation to Sex*, which contained his views on human evolution. Darwin argued that the differences between the human mind and the minds of the higher animals were a matter of degree rather than of kind. For example, he viewed morality as a natural outgrowth of instincts that were beneficial to animals living in social groups. He argued that all the differences between humans and apes were explained by a combination of the selective pressures that came from our ancestors moving from the trees to the plains, and sexual selection. The debate over human origins, and over the degree of human uniqueness continued well into the 20th century.[100]

Alternatives to natural selection

The concept of evolution was widely accepted in scientific circles within a few years of the publication of *Origin*, but the acceptance of natural selection as its driving mechanism was much less widespread. The four major alternatives to natural selection in the late 19th century were theistic evolution, neo-Lamarckism, orthogenesis, and saltationism. Alternatives supported by biologists at other times included structuralism, Georges Cuvier's teleological but non-evolutionary functionalism, and vitalism.

Theistic evolution was the idea that God intervened in the process of evolution, to guide it in such a way that the living world could still be considered to be designed. The term was promoted by Charles Darwin's greatest American advocate Asa Gray. However, this idea gradually fell out of favor among scientists, as they became more and more committed to the idea of methodological naturalism and came to believe that direct appeals to supernatural involvement were scientifically unproductive. By 1900, theistic evolution had largely disappeared from professional scientific discussions, although it retained a strong popular following.[103][104]

In the late 19th century, the term neo-Lamarckism came to be associated with the position of naturalists who viewed the inheritance of acquired characteristics as the most important evolutionary mechanism. Advocates of this position included the British writer and Darwin critic Samuel Butler, the German biologist Ernst Haeckel, and the American paleontologist Edward Drinker Cope. They considered Lamarckism to be philosophically superior to Darwin's idea of selection acting on random variation. Cope looked for, and thought he found, patterns of linear progression in the fossil record. Inheritance of acquired characteristics was part of Haeckel's recapitulation theory of evolution, which held that the embryological development of an organism repeats its evolutionary history.[103][104] Critics of neo-Lamarckism, such as the German biologist August Weismann and Alfred Russel Wallace, pointed out that no one had ever produced solid evidence for the inheritance of acquired characteristics. Despite these criticisms, neo-Lamarckism remained the most popular alternative to natural selection at the end of the 19th century, and would remain the position of some naturalists well into the 20th century.[103][104]

Orthogenesis was the hypothesis that life has an innate tendency to change, in a unilinear fashion, towards ever-greater perfection. It had a significant following in the 19th century, and its proponents included the Russian biologist Leo S. Berg and the American paleontologist Henry Fairfield Osborn. Orthogenesis was popular among some paleontologists, who believed that the fossil record showed a gradual and constant unidirectional change.

Saltationism was the idea that new species arise as a result of large mutations. It was seen as a much faster alternative to the Darwinian concept of a gradual process of small random variations being acted on by natural selection, and was popular with early geneticists such as Hugo de Vries, William Bateson, and early in his career, Thomas Hunt Morgan. It became the basis of the mutation theory of evolution.[103][104]

Mendelian genetics, biometrics, and mutation

The rediscovery of Gregor Mendel's laws of inheritance in 1900 ignited a fierce debate between two camps of biologists. In one camp were the Mendelians, who were focused on discrete variations and the laws of inheritance. They were led by William Bateson (who coined the word *genetics*) and Hugo de Vries (who coined the word *mutation*). Their opponents were the biometricians, who were interested in the continuous variation of characteristics within populations. Their leaders, Karl Pearson and Walter Frank Raphael Weldon, followed in the tradition of Francis Galton, who had focused on measurement and statistical analysis of variation within a population. The biometricians rejected Mendelian genetics on the basis that discrete units of heredity, such as genes, could not explain the continuous range of variation seen in real populations. Weldon's work with crabs and snails provided evidence that selection pressure from the environment could shift the range of variation in wild populations, but the Mendelians maintained that the variations measured by biometricians were too insignificant to account for the evolution of new species.[105][106]

When Thomas Hunt Morgan began experimenting with breeding the fruit fly *Drosophila melanogaster*, he was a saltationist who hoped to demonstrate that a new species could be created in the lab by mutation alone. Instead, the work at his lab between 1910 and 1915 reconfirmed Mendelian genetics and provided solid experimental evidence linking it to chromosomal inheritance. His work also demonstrated that most mutations had relatively small effects, such as a change in eye color, and that rather than creating a new species in a single step, mutations served to increase variation within the existing population.[105][106]

1920s–1940s

Population genetics

The Mendelian and biometrician models were eventually reconciled with the development of population genetics. A key step was the work of the British biologist and statistician Ronald Fisher. In a series of papers starting in 1918 and culminating in his 1930 book *The Genetical Theory of Natural Selection*, Fisher showed that the continuous variation measured by the biometricians could be produced by the combined action of many discrete genes, and that natural selection could change gene frequencies in a population, resulting in evolution. In a series of papers beginning in 1924, another British geneticist, J. B. S. Haldane, applied statistical analysis to real-world examples of natural selection, such as the evolution of industrial melanism in peppered moths, and showed that natural selection worked at an even faster rate than Fisher assumed.[107][108]

The American biologist Sewall Wright, who had a background in animal breeding experiments, focused on combinations of interacting genes, and the effects of inbreeding on small, relatively isolated populations that exhibited genetic drift. In 1932, Wright introduced the concept of an adaptive landscape and argued that genetic drift and inbreeding could drive a small, isolated sub-population away from an adaptive peak, allowing natural selection to drive it towards different adaptive peaks. The work of Fisher, Haldane and Wright founded the discipline of population genetics. This integrated natural selection with Mendelian genetics, which was the critical first step in developing a unified theory of how evolution worked.[107][108]

Modern synthesis

In the first few decades of the 20th century, most field naturalists continued to believe that alternative mechanisms of evolution such as Lamarckism and orthogenesis provided the best explanation for the complexity they observed in the living world. But as the field of genetics continued to develop, those views became less tenable.[109] Theodosius Dobzhansky, a postdoctoral worker in Thomas Hunt Morgan's lab, had been influenced by the work on genetic diversity by Russian geneticists such as Sergei Chetverikov. He helped to bridge the divide between the foundations of microevolution developed by the population geneticists and the patterns of macroevolution observed by field biologists, with his 1937 book *Genetics and the Origin of Species*. Dobzhansky examined the genetic diversity of wild populations and showed that, contrary to the assumptions of the population geneticists, these populations had large amounts of genetic diversity, with marked differences between sub-populations. The book also took the highly mathematical work of the population geneticists and put it into a more accessible form. In Britain, E. B. Ford, the pioneer of ecological genetics, continued throughout the 1930s and 1940s to demonstrate the power of selection due to ecological factors including the ability to maintain genetic diversity through genetic polymorphisms such as human blood types. Ford's work would contribute to a shift in emphasis during the course of the modern synthesis towards natural selection over genetic drift.[107][108][110][111]

The evolutionary biologist Ernst Mayr was influenced by the work of the German biologist Bernhard Rensch showing the influence of local environmental factors on the geographic distribution of sub-species and closely related species. Mayr followed up on Dobzhansky's work with the 1942 book *Systematics and the Origin of Species*, which emphasized the importance of allopatric speciation in the formation of new species. This form of speciation occurs when the geographical isolation of a sub-population is followed by the development of mechanisms for reproductive isolation. Mayr also formulated 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.[107][108][112]

In the 1944 book *Tempo and Mode in Evolution*, George Gaylord Simpson showed that the fossil record was consistent with the irregular non-directional pattern predicted by the developing evolutionary synthesis, and that the linear trends that earlier paleontologists had claimed supported orthogenesis and neo-Lamarckism did not hold up to closer examination. In 1950, G. Ledyard Stebbins published *Variation and Evolution in Plants*, which helped to integrate botany into the synthesis. The emerging cross-disciplinary consensus on the workings of evolution would be known as the modern synthesis. It received its name from the 1942 book *Evolution: The Modern Synthesis* by Julian Huxley.[107][108]

The modern synthesis provided a conceptual core—in particular, natural selection and Mendelian population genetics—that tied together many, but not all, biological disciplines: developmental biology was one of the omissions. It helped establish the legitimacy of evolutionary biology, a primarily historical science, in a scientific climate that favored experimental methods over historical ones.[113] The synthesis also resulted in a considerable narrowing of the range of mainstream evolutionary thought (what Stephen Jay Gould called the "hardening of the synthesis"): by the 1950s, natural selection acting on genetic variation was virtually the only acceptable mechanism of evolutionary change (panselectionism), and macroevolution was simply considered the result of extensive microevolution.[114][115]

1940s–1960s: Molecular biology and evolution

The middle decades of the 20th century saw the rise of molecular biology, and with it an understanding of the chemical nature of genes as sequences of DNA and of their relationship—through the genetic code—to protein sequences. At the same time, increasingly powerful techniques for analyzing proteins, such as protein electrophoresis and sequencing, brought biochemical phenomena into the realm of the synthetic theory of evolution. In the early 1960s, biochemists Linus Pauling and Emile Zuckerkandl proposed the molecular clock hypothesis (MCH): that sequence differences between homologous proteins could be used to calculate the time since two species diverged. By 1969, Motoo Kimura and others provided a theoretical basis for the molecular clock, arguing that—at the molecular level at least—most genetic mutations are neither harmful nor helpful and that mutation and genetic drift (rather than natural selection) cause a large portion of genetic change: the neutral theory of molecular evolution.[116] Studies of protein differences *within* species also brought molecular data to bear on population genetics by providing estimates of the level of heterozygosity in natural populations.[117]

From the early 1960s, molecular biology was increasingly seen as a threat to the traditional core of evolutionary biology. Established evolutionary biologists—particularly Ernst Mayr, Theodosius Dobzhansky, and George Gaylord

Simpson, three of the architects of the modern synthesis—were extremely skeptical of molecular approaches, especially when it came to the connection (or lack thereof) to natural selection. The molecular-clock hypothesis and the neutral theory were particularly controversial, spawning the neutralist-selectionist debate over the relative importance of mutation, drift and selection, which continued into the 1980s without a clear resolution.[118][119]

Late 20th century

Gene-centered view

In the mid-1960s, George C. Williams strongly critiqued explanations of adaptations worded in terms of "survival of the species" (group selection arguments). Such explanations were largely replaced by a gene-centered view of evolution, epitomized by the kin selection arguments of W. D. Hamilton, George R. Price and John Maynard Smith.[120] This viewpoint would be summarized and popularized in the influential 1976 book *The Selfish Gene* by Richard Dawkins.[121] Models of the period seemed to show that group selection was severely limited in its strength; though newer models do admit the possibility of significant multi-level selection.[122]

In 1973, Leigh Van Valen proposed the term "Red Queen," which he took from *Through the Looking-Glass* by Lewis Carroll, to describe a scenario where a species involved in one or more evolutionary arms races would have to constantly change just to keep pace with the species with which it was co-evolving. Hamilton, Williams and others suggested that this idea might explain the evolution of sexual reproduction: the increased genetic diversity caused by sexual reproduction would help maintain resistance against rapidly evolving parasites, thus making sexual reproduction common, despite the tremendous cost from the gene-centric point of view of a system where only half of an organism's genome is passed on during reproduction.[123][124]

However, contrary to the expectations of the Red Queen hypothesis, Hanley *et al.* found that the prevalence, abundance and mean intensity of mites was significantly higher in sexual geckos than in asexuals sharing the same habitat.[125] Furthermore, Parker, after reviewing numerous genetic studies on plant disease resistance, failed to find a single example consistent with the concept that pathogens are the primary selective agent responsible for sexual reproduction in their host.[126] At an even more fundamental level, Heng[127] and Gorelick and Heng[128] reviewed evidence that sex, rather than enhancing diversity, acts as a constraint on genetic diversity. They considered that sex acts as a coarse filter, weeding out major genetic changes, such as chromosomal rearrangements, but permitting minor variation, such as changes at the nucleotide or gene level (that are often neutral) to pass through the sexual sieve. The adaptive function of sex remains a major unresolved issue in biology. The competing models to explain the adaptive function of sex were reviewed by Birdsell and Wills.[129] A principal alternative view to the Red Queen hypothesis is that sex arose, and is maintained, as a process for repairing DNA damage, and that genetic variation is produced as a byproduct.[130][131]

The gene-centric view has also led to an increased interest in Charles Darwin's old idea of sexual selection,[132] and more recently in topics such as sexual conflict and intragenomic conflict.

Sociobiology

W. D. Hamilton's work on kin selection contributed to the emergence of the discipline of sociobiology. The existence of altruistic behaviors has been a difficult problem for evolutionary theorists from the beginning.[133] Significant progress was made in 1964 when Hamilton formulated the inequality in kin selection known as Hamilton's rule, which showed how eusociality in insects (the existence of sterile worker classes) and many other examples of altruistic behavior could have evolved through kin selection. Other theories followed, some derived from game theory, such as reciprocal altruism.[134] In 1975, E. O. Wilson published the influential and highly controversial book *Sociobiology: The New Synthesis* which claimed evolutionary theory could help explain many aspects of animal, including human, behavior. Critics of sociobiology, including Stephen Jay Gould and Richard Lewontin, claimed that sociobiology greatly overstated the degree to which complex human behaviors could be determined by genetic factors. They also claimed that the theories of sociobiologists often reflected their own ideological biases. Despite these criticisms, work has continued in sociobiology and the related discipline of evolutionary psychology, including work on other aspects of the altruism problem.[135][136]

Evolutionary paths and processes

One of the most prominent debates arising during the 1970s was over the theory of punctuated equilibrium. Niles Eldredge and Stephen Jay Gould proposed that there was a pattern of fossil species that remained largely unchanged for long periods (what they termed *stasis*), interspersed with relatively brief periods of rapid change during speciation.[137][138] Improvements in sequencing methods resulted in a large increase of sequenced genomes, allowing the testing and refining of evolutionary theories using this huge amount of genome data.[139] Comparisons between these genomes provide insights into the molecular mechanisms of speciation and adaptation.[140][141] These genomic analyses have produced fundamental changes in the understanding of the evolutionary history of life, such as the proposal of the three-domain system by Carl Woese.[142] Advances in computational hardware and software allow the testing and extrapolation of increasingly advanced evolutionary models and the development of the field of systems biology.[143] One of the results has been an exchange of ideas between theories of biological evolution and the field of computer science known as evolutionary computation, which attempts to mimic biological evolution for the purpose of developing new computer algorithms. Discoveries in biotechnology now allow the modification of entire genomes, advancing evolutionary studies to the level where future experiments may involve the creation of entirely synthetic organisms.[144]

Microbiology, horizontal gene transfer, and endosymbiosis

Microbiology was largely ignored by early evolutionary theory. This was due to the paucity of morphological traits and the lack of a species concept in microbiology, particularly amongst prokaryotes.[145] Now, evolutionary researchers are taking advantage of their improved understanding of microbial physiology and ecology, produced by the comparative ease of microbial genomics, to explore the taxonomy and evolution of these organisms.[146] These studies are revealing unanticipated levels of diversity amongst microbes.[147][148]

One important development in the study of microbial evolution came with the discovery in Japan in 1959 of horizontal gene transfer.[149] This transfer of genetic material between different species of bacteria came to the attention of scientists because it played a major role in the spread of antibiotic resistance.[150] More recently, as knowledge of genomes has continued to expand, it has been suggested that lateral transfer of genetic material has played an important role in the evolution of all organisms.[151] These high levels of horizontal gene transfer have led to suggestions that the family tree of today's organisms, the so-called "tree of life," is more similar to an interconnected web or net.[152][153]

Indeed, the endosymbiotic theory for the origin of organelles sees a form of horizontal gene transfer as a critical step in the evolution of eukaryotes such as fungi, plants, and animals.[154][155] The endosymbiotic theory holds that organelles within the cells of eukorytes such as mitochondria and chloroplasts, had descended from independent bacteria that came to live symbiotically within other cells. It had been suggested in the late 19th century when similarities between mitochondria and bacteria were noted, but largely dismissed until it was revived and championed by Lynn Margulis in the 1960s and 1970s; Margulis was able to make use of new evidence that such organelles had their own DNA that was inherited independently from that in the cell's nucleus.[156]

From spandrels to evolutionary developmental biology

In the 1980s and 1990s, the tenets of the modern evolutionary synthesis came under increasing scrutiny. There was a renewal of structuralist themes in evolutionary biology in the work of biologists such as Brian Goodwin and Stuart Kauffman,[157] which incorporated ideas from cybernetics and systems theory, and emphasized the self-organizing processes of development as factors directing the course of evolution. The evolutionary biologist Stephen Jay Gould revived earlier ideas of heterochrony, alterations in the relative rates of developmental processes over the course of evolution, to account for the generation of novel forms, and, with the evolutionary biologist Richard Lewontin, wrote an influential paper in 1979 suggesting that a change in one biological structure, or even a structural novelty, could arise incidentally as an accidental result of selection on another structure, rather than through direct selection for that particular adaptation. They called such incidental structural changes "spandrels" after an architectural feature.[158] Later, Gould and Elisabeth Vrba discussed the acquisition of new functions by novel structures arising in this fashion, calling them "exaptations."[159]

Molecular data regarding the mechanisms underlying development accumulated rapidly during the 1980s and 1990s. It became clear that the diversity of animal morphology was not the result of different sets of proteins regulating the development of different animals, but from changes in the deployment of a small set of proteins that were common to all animals.[160] These proteins became known as the "developmental-genetic toolkit."[161] Such perspectives influenced the disciplines of phylogenetics, paleontology and comparative developmental biology, and spawned the new discipline of evolutionary developmental biology also known as evo-devo.[162]

21st century

Macroevolution and microevolution

One of the tenets of population genetics since its inception has been that macroevolution (the evolution of phylogenic clades at the species level and above) was solely the result of the mechanisms of microevolution (changes in gene frequency within populations) operating over an extended period of time. During the last decades of the 20th century some paleontologists raised questions about whether other factors, such as punctuated equilibrium and group selection operating on the level of entire species and even higher level phylogenic clades, needed to be considered to explain patterns in evolution revealed by statistical analysis of the fossil record. Near the end of the 20th century some researchers in evolutionary developmental biology suggested that interactions between the environment and the developmental process might have been the source of some of the structural innovations seen in macroevolution, but other evo-devo researchers maintained that genetic mechanisms visible at the population level are fully sufficient to explain all macroevolution.[163][164][165]

Epigenetic inheritance

Epigenetics is the study of heritable changes in gene expression or cellular phenotype caused by mechanisms other than changes in the underlying DNA sequence. By the first decade of the 21st century it had become accepted that epigenetic mechanisms were a necessary part of the evolutionary origin of cellular differentiation.[166] Although epigenetics in multicellular organisms is generally thought to be a mechanism involved in differentiation, with epigenetic patterns "reset" when organisms reproduce, there have been some observations of transgenerational epigenetic inheritance. This shows that in some cases nongenetic changes to an organism can be inherited and it has been suggested that such inheritance can help with adaptation to local conditions and affect evolution.[167] Some have suggested that in certain cases a form of Lamarckian evolution may occur.[168]

Extended evolutionary syntheses

The idea of an extended evolutionary synthesis is to extend the 20th century modern synthesis to include concepts and mechanisms such as multilevel selection theory, transgenerational epigenetic inheritance, niche construction and evolvability—though several different such syntheses have been proposed, with no agreement on what exactly would be included.[169][170][171][172]

Unconventional evolutionary theory

Omega Point

Pierre Teilhard de Chardin's metaphysical Omega Point theory, found in his book *The Phenomenon of Man* (1955),[173] describes the gradual development of the universe from subatomic particles to human society, which he viewed as its final stage and goal, a form of orthogenesis.[174]

Gaia hypothesis

The Gaia hypothesis proposed by James Lovelock holds that the living and nonliving parts of Earth can be viewed as a complex interacting system with similarities to a single organism,[175] as being connected to Lovelock's ideas.[176] The Gaia hypothesis has also been viewed by Lynn Margulis[177] and others as an extension of endosymbiosis and exosymbiosis.[178] This modified hypothesis postulates that all living things have a regulatory effect on the Earth's environment that promotes life overall.

Self-organization

The mathematical biologist Stuart Kauffman has suggested that self-organization may play roles alongside natural selection in three areas of evolutionary biology, namely population dynamics, molecular evolution, and morphogenesis.[157] However, Kauffman does not take into account the essential role of energy (for example, using pyrophosphate) in driving biochemical reactions in cells, as proposed by Christian de Duve and modelled mathematically by Richard Bagley and Walter Fontana. Their systems are self-catalyzing but not simply self-organizing as they are thermodynamically open systems relying on a continuous input of energy.[179]

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