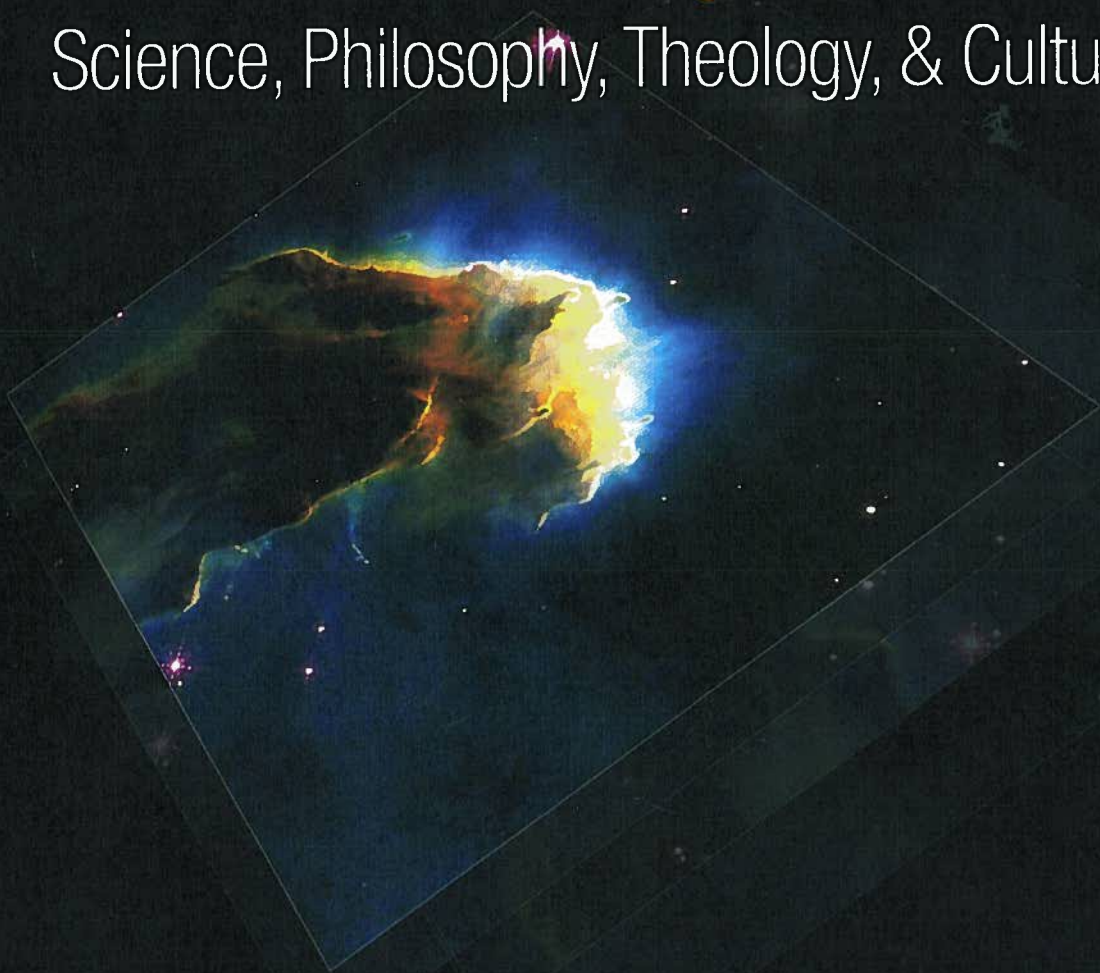


H. James Birx *Editor*

# ENCYCLOPEDIA OF TIME

Science, Philosophy, Theology, & Culture



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### Further Readings

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## EVOLUTION, ISSUES IN

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There is no shortage of issues in evolution. Some are highly contentious, others are benign. Evolution, by its very nature, is prone to controversy because it is largely a science of inference about a historical process, a process that takes place over time and space. Evolution involves unique events that can never be revisited in their entirety and can only be reconstructed through evidence associated with those events. In this way, reconstructing evolution is methodologically no different from a process of detective work that attempts to reconstruct a crime scene or any other event that has occurred only once. Because evolution is a historical process, its expression over time provides the focus for many of the uncertainties and questions in the science of evolution. These challenges may be relatively ephemeral as they are recognized and solved, or they may persist over longer periods before being solved or reformulated, or they may even emerge again under new scrutiny or with the discovery of new evidence. In evolutionary research, time is of the essence; it must always be addressed. This entry

illustrates some of the issues in evolution that focus on, or are derivative of, evolution in time.

### RNA or DNA?

A central dilemma for understanding the genetic origin of life is the identification of a stable, self-replicating genetic molecule that simultaneously carries the information necessary for copying itself and for catalyzing that replication process. Modern life relies on two complexly interrelated molecules for this process: DNA (deoxyribonucleic acid), as a carrier of information, and proteins, which perform chemical reactions. Proteins are involved in the formation and maintenance of DNA, and yet DNA is required for the protein formation instructions. This dual function raises the question of which process came first. One possibility is that a self-replicating peptide or other protein molecule evolved first, and DNA became possible as a result. The problem with this model is that it requires a random assembly of amino acids to form chainlike polymers rather than irregular clusters. A simultaneous evolution of proteins and DNA would require two improbable events. The evolution of a sequence of elements that replicates and also provides the template of replication represents another possibility, suggested by the role of RNA (ribonucleic acid) in living organisms.

The single-stranded nucleic acid molecule known as RNA can function both as a carrier of information and as a catalyst promoting the self-replication. RNA also includes genes that accelerate biochemical reactions. RNA has the potential to make and maintain DNA as well as proteins. This RNA theory suggests that life may have first begun as an "RNA world" of organisms that preceded the evolution of DNA life. The RNA world theory suggests there was a time when RNA rather than DNA was the primary mechanism of storing genetic information, but when replication of genetic material already followed the same rules as modern DNA by matching the amino acid adenine with uracil (equivalent of the DNA thymine) and cytosine with guanine. This ancient, ancestral RNA is theorized to have played the same catalytic roles as modern protein enzymes where the first genetic life-form was simply a self-replicating strand of RNA that may have been enclosed within

a protective lipid membrane while modern metabolic processes, with an efficient replication process, emerged later.

If life and genetics are synonymous, the evolution of life through an RNA world may represent the beginnings of modern life. The possible antiquity of RNA implied by the RNA world model is emphasized in biochemical studies showing that RNA molecules play key structural roles in the formation of a variety of essential coenzymes that mediate manufacture of lipids and other biological molecules. RNA also includes genes that change shape when binding to specific cell molecules and regulates cell chemistry by turning genes on and off. There is widespread agreement that RNA represents a critical step in the origin of life, but after decades of chemical experiments, the emergence of a fully functional RNA world from earlier prebiotic chemical solution remains problematic.

The RNA theory provides no insight as to how life first made the transition from a prebiotic solution of biological molecules to those of DNA and cellular life. There may have been a critical transition stage, such as a metabolic system, that was followed by a genetic molecule that was structurally simpler and chemically more stable than RNA. Metabolism initially uses relatively simple molecules (carbon-oxygen-hydrogen and possibly sulfur), whereas RNA function relies on exact sequences of chemically complex nucleotides involving a carbon-oxygen-hydrogen-nitrogen-phosphorus system. Biologists are generally confident that there was a transition from an RNA world to the current DNA-protein genetic system, but how the prebiotic molecular world evolved the linkage between individual nucleotides comprising an RNA strand remains unsolved.

### Viruses as Life

Viruses cross the boundaries that are used to define the concept of life. In general, evolutionary biologists may not give due consideration to the role and contribution that viruses have made to the origin and evolution of life. This oversight may be due, in great part, to a widely held view that viruses do not represent living entities and do not, therefore, represent significant elements or contributors to the tree of life. But viruses can be

killed, can become extinct, and adhere to general rules of evolutionary biology, including the process of natural selection. And they do have a large impact on the survival and evolution of their hosts.

The determination of viruses as living or nonliving entities represents a persistent question since viruses were first identified. As in all other biological systems, viruses store, copy, and express information. In some respects they conform to qualities of organisms that are accepted as having a living state, but in other respects they do not. There is widespread agreement that life is bounded by birth and death for organisms that live with a degree of biochemical autonomy and have the metabolic ability to produce the molecules and energy necessary to maintain life. Viruses, on the other hand, lack biochemical autonomy because they lack the means to produce their own proteins and consequently rely totally on their symbiotic molecular parasitism of other living organisms. Because viruses are parasitic to support essentially all the biomolecular requirements, they may be viewed as nonliving parasites of living metabolic systems. In this context they can be described as metabolically active containers lacking the genetic potential to propagate without "borrowing" life from other living organisms. Viruses may be no more than environmental or chemical toxins that kill off some hosts.

The question of whether viruses are alive may be no more informative than the question of whether a gene or protein is alive. Individual subcellular constituents such as mitochondria, DNA, RNA, genes, enzymes, and cellular membranes all represent levels of chemical complexity equivalent to those of many viruses, and yet they are generally considered not to be living in the same way as cells or organisms are living. Unlike cellular organisms, some viruses can bring themselves back to an active or "living" state and some viruses can replicate in "dead" host cells such as those without nuclei. Where an individual cell is infected by more than one dead virus, the virus can become reactivated when the multiple viral genomes complement the damage and reassemble the "living" virus. This is the only known biological entity to have this capability.

A widely held view on the origin of cellular life is that it first evolved in oceans and that it was

preceded by a period of evolution involving precellular, chemical-replicating forms. These chemical entities were able to use themselves as a template for synthesis using existing molecules in the surrounding environment. Given the fact that all cellular life uses nucleic acid molecules as genetic information and relies on protein-based catalysis, the ancestral replicating systems may also be assumed to rely on nucleic acids or related molecules as information storage and biotic synthesis. As the main storage molecule of genetic information in living organisms, DNA is a comparatively chemically inert and stable molecule that cannot perform the catalytic process required for replication. In contrast, RNA is known to function as both genetic storage and as a catalyst of RNA, and autocatalytic RNA may have been the principal molecule used as both information storage and catalysis in the prebiotic world. RNA can break the molecular bonds of RNA, although it is comparatively inefficient in constructing new RNA molecules. If more efficient replicating systems did not exist in the prebiotic world, then this inefficient RNA-based process may have represented a viable system of replication. With the subsequent emergence of protein catalysis and faster replication processes, the prebiotic RNA replicators would have become extinct, with the possible exception of RNA viruses as the sole living descendants of the prebiotic world.

Viruses are obligate intracellular parasites. They cannot replicate outside cellular environments. This current condition may be seen to preclude the existence of viruses before the evolution of cellular life. If, however, viruses are recognized as molecular genetic parasites, they may be capable of parasitizing any replicating systems, including other viruses, and any prebiotic molecular systems. Any genetic replicators, including noncellular prebiotic replicators, would be susceptible to parasitic replicators or viruses, as are viruses parasitized by other viruses. These parasites of parasites could be anticipated to have also existed in the prebiotic world.

No fossil record of viruses has been discovered, so there is no external reference to calibrate the origin of various virus lineages. As prebiotic life forms, viruses would have to precede the first record of prokaryote cellular life (bacteria), about 4 billion years ago, and the cyanobacteria (blue-green algae), about 2.6 billion years ago. Each of

these groups has distinct and characteristic viruses, but they also share the presence of tailed viruses and this may be the result of this group of viruses evolving prior to their divergence. The earliest eukaryotes (unicellular algae) appear in the fossil record between 2.2 and 1.8 billion years ago, followed by relative evolutionary stasis until the Cambrian explosion with the appearance of numerous skeletal organisms. The evolution of these forms also is likely correlated with the emergence of many types of viruses.

Viruses appear to have numerous evolutionary origins as indicated by the different specific genome replication processes of individual virus families, suggesting each virus family derived from a different ancestor. Other viral groups are so large and diverse that available sequence data currently do not support the view that even they evolved from a single common ancestor.

It is now widely thought that viral lineages are old, and they originated independently of the replication system in their hosts, and there are several independent origins for viruses.

### Origin of Complex Life

There is no objective demarcation between "complex" and "simple" life, but a major organizational difference separates unicellular and noncellular organisms from multicellular organisms (Metazoa) where specialized cell functions are present. Metazoan cells are interpreted as descendants of unicellular organisms that may also have a composite origin involving the combination of noncellular organisms resulting in the metazoan cell with a central membrane-bounded nucleus surrounded by cytoplasm with specialized organelles. The combination or incorporation of precellular organisms would explain the occurrence of nonnucleic DNA in organelles such as mitochondria and chloroplasts.

In the context of relative complexity, the combination of cells results in new features not present in unicellular organisms, such as extracellular matrix providing support for the cells and including gelatinous matrices infused with fibers such as collagen and other macromolecules. Metazoan cells comprising tissues are also connected to each other by molecules that form attachments and also

permit intercellular communication. Most tissues comprise sheets of cells that are usually interconnected and have apical and basal regions and are usually attached to a basal layer of extracellular matrix. Connective tissues are also embedded in extracellular matrix, but they are not as closely associated. Another major tissue category is nervous tissue, which forms the main integrating and coordinating system of the body and is present in almost all free living metazoans.

The Metazoa comprise a range of contrasting body structures that appear abruptly in the fossil record and lack intermediates. The Metazoa appear to be monophyletic (share a most recent common ancestor not shared by nonmetazoan life), but the arrangement of major lineages (phyla) is variable even though many researchers use the same information. In morphological studies, the Cnidaria (jellyfish and their relatives) are often represented as one of the earliest of living metazoan phyla. Even the Chordata, which mostly comprise the vertebrate groups (fish, amphibians, reptiles, birds, and mammals), are often treated as having originated near the beginning of metazoan life and are often linked with the invertebrate Echinodermata (starfishes). Molecular phylogenies have yielded some different results, some suggesting that cnidarians evolved independently of the remaining bilaterally organized metazoans.

Two main evolutionary issues concern when metazoan life evolved and in what sequence. The branching order of lineages may be theorized through phylogenetic analysis that predicts their evolutionary relationships. This order may be compared with their order of appearance in the fossil record, and where the two sources of evidence coincide, the sequence may be viewed as an accurate representation of metazoan evolutionary history. This approach is challenged by the uncertainties of fossilization, and soft-bodied organisms, particularly those that are unicellular, are rarely preserved as fossils. The definition and dating of the earliest geological formations in relation to the fossil record may also be problematic. The earliest rocks dating from about 600 million years ago (mya) comprise the Neoproterozoic era until the beginning of the Cambrian period about 543 mya. Metazoan fossils earlier than about 565 mya are limited to embryos, body fossils, and traces of metazoan activity and include the sponges as the

only living metazoan phyla represented, although Cnidaria (jellyfish) are thought likely present because they represent a basal or primitive lineage. Later Neoproterozoic fossils include small, shelled fossils. The first appearance of recognizable trace fossils (formed by disturbance of sediments by the activities of an organism) formed by a series of straight to curving segments mark the beginning of the Cambrian about 530 mya. The Cambrian fossil record includes the first appearance of 11 of the modern phyla, including mollusks, arthropods, starfish, and chordates. From the end of the Cambrian (490 mya) to the beginning of the Mesozoic (248 mya) only four additional metazoan phyla first appear, whereas most of the remaining phyla either have a post-Mesozoic (65 mya) fossil record or lack a fossil record altogether (14 soft-bodied phyla).

### Cambrian Explosion of Life

Fossils may raise as many problems as solutions for scientists who track the temporal origin and sequence of life in the fossil record. Fossils are informative in the sense that they provide empirical evidence for the existence of an organism at a particular place and time. But they are less informative about the evolutionary identity and the relationship of that past organism to modern life. This problem occurs at all levels, from identifying a species relationship for recent fossils (e.g., whether Neanderthals are a separate species or a variation within modern humans), to their placement at a higher taxonomic level such as a genus, family, order, class, or phylum. These problems may be compounded by the lack of preservation in fossils, particularly the general absence of information on soft-tissue organization. Even features that do fossilize may be only partially preserved.

Fossils also yield ambiguous information about the timing of evolutionary events. The oldest fossils represent forms that can be identified only at a high level of classification, that they represent, for example, a bacterium, a single-celled organism, an animal, or a plant (and even then, the identification may be uncertain). The oldest recognizable fossil for any particular group of organisms also cannot provide any temporal information other than the minimal age of fossilization of that group.

How much the origin of a group may precede the fossil record cannot be directly gleaned from the fossil itself. Given this limitation, the fossil record is presumed to give a reasonable indication of historical sequence as more derived groups (e.g., mammals) appear in the fossil record later than those that are more generalized (e.g., fish or invertebrates). When larger groups representing many species are absent from the fossil record, there may be greater confidence that they are either rare at that time or had not yet evolved. There may be a relatively high level of confidence in correlating fossil appearance with the timing of evolutionary origin when skeletonized organisms are involved, but in the absence of skeletons the lack of fossilization may represent the relative rarity of conditions for fossilization of soft tissues rather than an actual absence. In dealing with the origin and first appearance of skeletal life, this is a major constraint on scientists' efforts to identify the temporal origin of skeletonized organisms.

The problem of correlating the first fossil appearance with evolutionary origin is exemplified by the various multicellular phyla that first make their appearance in the fossil record during the Cambrian period that began about 543 mya and lasted until 490 mya. The earliest Cambrian fossils indicate an increase in biological diversification and body size compared with Precambrian organisms. The earliest fossils are traces of movement or occupation of sediments by organisms and mineralized skeletons that increase in diversity during the first 15 million years of the early Cambrian. The traces are also larger and more diverse than Precambrian traces and include branching burrows and larger vertical burrows. Major locations recording diversification of Cambrian life include the Chengjiang fauna from Yunnan, China (Middle Cambrian), and the Burgess Shale formation, British Columbia, Canada (Middle Cambrian).

Precambrian fossils that may be recognized as members of living metazoan phyla are limited to sponges, although the soft-bodied Cnidaria (jellyfish) are presumed to be present. In the Early Cambrian, about 530 mya, fossil members of modern phyla that first appear include single- and double-shelled mollusks (snails and shellfish), echinoderms (starfish), annelids (worms), Cnidaria (jellyfish), chordates (precursor to vertebrates), a diverse array of arthropods (bodies with external,

jointed skeletons), many of which cannot be assigned to living arthropod classes, and forms that may represent primitive fish. It is the arthropod groups that show the most striking diversification of body structures, including many that are distinct from later arthropod groups, and others that look like members of the phylum Onychophora, a living group that may represent a transitional stage between soft-bodied annelids and the externally skeletonized arthropods.

Because these fossils appear over a geologically short period of time, their pattern of fossilization is characterized as the "Cambrian explosion." The appearance of these fossils would represent a comparatively rapid explosion of evolutionary diversification if the fossil record accurately represents their evolutionary origin. Because most of the diversity corresponds to organisms that have evolved durable, mineralized skeletons, their fossil appearance may be an artifact of fossil perseveration, representing an increase in the durability of skeletal structures rather than their first appearance. Evidence that may suggest the fossil record corresponds to a rapid diversification during the Early and Middle Cambrian is found in groups that appear to have required durable skeletons to function so their evolutionary origins may be no earlier than the origin of their durable skeletons. The large increase in trace fossil abundance and variety also began only shortly before the fossil explosion and may suggest that many of these groups may have first evolved around the time of their fossil appearance. There is also the possibility that the ancestral forms of the Cambrian phyla were present in the Precambrian, but rarely preserved, if at all. As with any fossil record, the absence of earlier fossils does not preclude an earlier origin, which may be corroborated only through later fossil discoveries.

### Origin of Sex

Sex involves the coming together of complementary cells, where the biological attraction is strong enough to recombine genes, with the result that the new organisms are genetically different from their parent cells. Understanding the evolutionary and temporal origins of sexual reproduction is linked to understanding the origin and evolutionary

relationships of organisms that may be classified into five main reproductive groups. Two groups are entirely or principally unicellular. The bacteria are single-celled organisms that lack nuclei. These organisms reproduce through binary fission, although bacteria may also incorporate genes from other bacteria or absorb genes that have been released into the surrounding water from dead bacteria. The protocists comprise cells with a nucleus (including algae, slime molds, and ciliates) that also often reproduce through binary fission, but also sometimes exhibit cellular fusion. Most protocists are single celled, but some form colonies of cells that adhere together.

The multicellular groups comprise the fungi, which reproduce through the production of spores, the plants that reproduce from both spores and the cellular unions that produce embryos, and the animals that develop from the union of egg and sperm. It is in plants and animals where sexual reproduction requires cellular fusion followed by the division of a fertilized egg that forms the embryo. This process requires an alternating halving and doubling of DNA in each generation and a correlated parental mortality.

The origin of multicellular organisms from unicellular ancestors appears to involve not only the adherence and intercommunication of individual cells but also novel combinations of unicellular organisms. Both animals and plants include organelles that have their own DNA (mitochondria in animals, chloroplasts in plants). Some comparative studies have resulted in the proposition that protocists first evolved through the integration of bacteria, and this process of symbiosis may also have significant implications for the origins of metazoan sex. Each generation of animals reverts to what is effectively a single-celled protocist-like stage, and the mammalian fertilized egg may resemble the ancestral protocists that evolved the first doubled chromosome complement. But instead of remaining a single-celled organism, the cells of this ancestor stayed together and formed an embryo with differentiated tissues and organs.

The origin of sex in plants and animals would appear to be contemporaneous with the evolution of multicellular organisms that develop from an embryo. The reproductive links may be indicated in some protocists where asexual and sexual reproduction is present along with multicellular

organization. Seaweeds comprise single algal cells that remain together, but they are not plants in the sense that they do not develop from an embryo. In some algal colonies any one cell may break away and start another colony, whereas others (e.g., *Volvox*) form small colonies within themselves that are later released when the gelatin holding the parent colony together dissolves. Some *Volvox* colonies will produce cells that function as ova and others that function as sperm that swim to and fertilize the ova. The fertilized ova forms a zygote within which meiosis will take place, and each resulting cell will begin a new colony.

The presence of sex within protocists suggests that sex may be as old as the protocists in general. There is no direct way of dating this origin. The earliest metazoans may extend back as far as 600 mya whereas the first protocist evolution may have taken place at any time earlier when life was first possible on the planet, perhaps 3.8 billion years ago. Even with such uncertainties, sex would seem to have a history as old as that of cellular life, and sexual reproduction through the formation of embryos may even have preceded the evolution of the multicellular organisms that comprise the plants and animals that dominate life's diversity in the present.

### Punctuated Equilibrium?

A long-standing question is whether the rate of evolution is constant over time or whether it is variable with periods of rapid evolution and other periods when little or no evolution takes place (stasis). The concept of punctuated equilibrium represents a proposal in favor of evolution alternating between sometimes long periods of stasis punctuated by periods of rapid evolution during speciation. Punctuated equilibrium was popularized in the English-speaking world by Niles Eldredge of the American Museum of Natural History and Stephen Jay Gould of Harvard University. They introduced the concept of punctuated equilibrium in response to an incongruity between the fossil record and the popular version of evolution as a gradual process of evolutionary change over time.

Eldredge and Gould observed that Charles Darwin emphasized a process of gradual evolution,

but this theory was incongruent with the expectation that this gradual evolution would be observable by the prevalence of transitional forms between very similar stages in the fossil record. In reality, although a series of transitions in succeeding geological layers over time could sometimes be observed, in most cases there were gaps between the older and younger fossils. The lack of transitional forms was attributed by Darwin to the incomplete nature of the fossil record; transitional forms were missing because they were often not preserved. In this way, the fossil record was misleading about the process of evolution over time by giving the impression that evolution was a continually interrupted or punctuated process.

Not all evolutionists supported the theory of gradual evolution, and some proposed major evolutionary changes whereby new species or forms appeared without any identifiable intermediate form. These "saltationists" included Richard Goldschmidt, who proposed that species could give birth to entirely different forms that were anatomically different from their parents. As this process was not observed in the laboratory, it raised many questions about how such a novel form could survive and reproduce, and Goldschmidt's theory did not gain wide popularity among evolutionists.

Some fossil gaps may be apparent rather than real, where speciation occurred through dispersal to another locality where a new species evolved, and this did not overlap the related species until a later date when it would also fossilize in the same location and give the appearance of a gap. But that theoretical possibility notwithstanding, Eldredge and Gould argued that between the gaps in the fossil record were relatively long periods where a species persisted and that the problem with the fossil record was less that there were gaps than that there were these periods of stasis suggesting that evolution was not a gradual process.

As well as a description of the fossil record, punctuated equilibrium was also proposed as an evolutionary mechanism, based on conventional speciation theory and the notion of adaptive change through natural selection, which explained the origin of reproductively isolated communities over time. They argued that most anatomical change, whether or not it was adaptive, does not occur throughout the bulk of a species' history but during rare events when reproductively isolated species bud off from

parental species. Most species do not have a continuous distribution but comprise geographically isolated populations, and given physical isolation of relatively small populations on the edge of a species range, it was possible to get adaptive divergence taking place. This divergence was rapid over geological time although it was not ecologically instantaneous and may involve tens of thousands of years and may mostly involve small evolutionary changes.

As a pattern, punctuated equilibrium described the apparent stasis of species evolution interrupted by speciation taking place over relatively short time intervals. As a mechanism, punctuated equilibrium represents a theorized mechanism based on natural selection of isolated populations affected by changes in the environment. This mechanism may be problematic for many situations where related species are vicariant (replace each other in geographic space) and each occupies a relatively broad geographic distribution, which may suggest speciation involves multiple populations. New developments in developmental and molecular biology also suggest the possibility that the "sudden origin" of new species or morphological structure may take place without necessarily requiring natural selection as the driving force. This is particularly significant for the origin of species over broad geographic areas that span many different local environments and populations that may be broader than the effect of natural selection at the local level.

### Continuum

Evolution, by its very nature, is a theory about continuity. But in the present, life is full of discontinuities between those individual organisms that are involved in a close biological (usually reproductive) relationship and those that are not. The sense of discontinuity is also seen in the fossil record, where distinct species or other groups appear or disappear without apparent intermediate forms. The appearance of discontinuity is often seen as more of a problem for evolution than that of continuity and results in various theoretical solutions, ranging from that of punctuated equilibrium to proposed molecular and developmental transitions of entire organ or tissue systems rather than always through incremental and gradual evolution by many small steps.

Biological continuity may be seen in those individuals grouped into units called species. Most species are sufficiently distinct as to be almost self-evident, but limited cases involving various levels of hybridization and different modes of reproduction have led evolutionists to propose universal criteria for recognizing and distinguishing species. In most cases these attempts have focused on the creation of definitions that are true regardless of time and space. These definitions act as essential qualities or essences by which a species may be recognized and often center on reproductive relationships involving criteria such as a reproductive isolation (and its converse, mate recognition) with many, many scientific arguments about whether a species is a "true" species or not. All criteria of this kind are independent of a particular place and time and measure the status of a species solely on whether or not it conforms to the definition. In this approach, species are being defined according to an essential attribute (such as reproductive isolation) or essence.

The problem with essence as the attribute of a species is that essences do not evolve over time or space, but species do. Ancestral species diverge and become descendant species. For evolution to take place, species cannot exist as the expression of an essence because the essence precludes evolution. Recognition of this problem led to the formulation of species as historical entities or individuals that share a unique common history. At any one time and place, the biological limits of a species may be diagnosed with respect to those features of the organism and environment that are seen to identify the species boundaries. Such species diagnoses are valid in reference only to the specified place and time and do not, therefore, require a species to refer to an inner essence. In practice, species may be characterized by one or more particular features, including morphology or reproductive biology, but there is no absolute demarcation required to recognize these qualities independently of a particular spatial and temporal context.

As historical individuals, species may show evolutionary discontinuities where the biological features are spatially and temporally distinct and continuity where they are not. Evolutionary continuity may be seen over time as descendant species merge at their origin with the ancestor or over space where species may show local continuity in

biology or reproduction (e.g., breeding between adjacent populations) or discontinuity where more distant populations are spatially isolated so they never interbreed or are unable to produce viable offspring when brought into contact. Here discontinuity is a function of an overall biological continuity that separates out over time and space. In this context a species, like all other units of biological classification, represents a link in the chain of divergence and differentiation rather than a point of separation and isolation.

### Extinctions

The history of evolution is the record of speciation and extinction, from the first appearance of life through to the present. The process of evolution is a complicating factor in understanding extinction. When speciation takes place, there is a transformation of the ancestor into descendants, and this transformation may be regarded as a form of extinction even though the lineage continues to exist. Species may also hybridize, causing the "extinction" of the original forms, at least with respect to their original spatial and temporal characteristics.

Extinction may be fast or slow, and its causes local or regional, and climatic or extraterrestrial in origin. The fact of extinction is not at issue, but the causes and extent of extinction are. Even in the present when the planet is faced with one of the most severe extinction rates over a geologically instantaneous moment of time, there is controversy over what, if anything, can be done about the global destruction of habitat and even climate through human modification and destruction of the environment.

Past extinctions on a similar scale have been referred to as "mass extinctions," when species diversity dropped dramatically and globally. Causes of such extinctions have been attributed to major planetary changes related to the balance of global temperature, the influence of massive regional volcanic eruptions, and climate altered through plate tectonics. Only over the more recent decades has greater attention been given to the extinction role of extraterrestrial objects such as asteroids and comets even though it has long been recognized that the earth has a history of many major meteorite impacts.

Periodic major extinctions became apparent to late-19th-century geologists, who delineated geological layers that could represent particular units of geological time. The sequential arrangement of these layers according to their relative age resulted in the formulation of a geologic timescale. The early geologists relied on fossils to correlate the geographically separate geological layers representing the same temporal units. Through their different fossil compositions, major geological layers could be recognized. The different fossil communities were at first attributed to the separate and sequential creations of life.

Evolutionary paleontologists later came to recognize that the contrasting fossil biotas in the major geological layers resulted from evolution and diversification following major extinctions of previously dominant forms. Several major episodes of global declines in species diversity have been identified over the last 550 million years of the earth's 4.6-billion-year history, beginning with a mass extinction inferred from geological evidence of a catastrophic climatic change to the most recent change characterized by the extinction of dinosaurs as the earth's dominant life form.

Extinction of dinosaurs at the end of the Cretaceous at 65 mya is widely attributed to the impact by a comet that caused a 30-fold increase in iridium deposits at the Cretaceous-Tertiary boundary. A major impact crater that also formed at this time in the Yucatán Peninsula of Mexico is widely believed to be involved with, or solely responsible for, the mass extinction of members of the dinosaur clade except the birds, and perhaps 79% of terrestrial plants and 47% of the marine genera, including most marine reptiles. The extinctions are attributed to the effect of the immediate impact as well as atmospheric dust, acid rain, and the elimination of sunlight sufficient for photosynthesis. The extent and persistence of these effects is, however, uncertain, as some studies suggest the dust may have been rapidly reduced through rainfall, and the correlation of many modern plant and animal distributions with Mesozoic tectonics suggests the widespread survival of many lineages, possibly including some modern bird and mammal groups that then diversified in the Tertiary.

The nature and causes of earlier mass extinctions becomes more difficult to assess. The end of

the Triassic at 199 mya is marked by the extinction of 53% of marine genera and 22% of marine families, and 12% of vertebrate families. It is after this extinction that dinosaurs became dominant on the land. The causes of this extinction remain unknown, but possibilities include rapid sea level rise and volcanic eruptions. Only 50 million years earlier was the largest recorded extinction, at the close of the Permian at 250 mya, reducing 57% of all families and perhaps 96% of all species in the sea. On the land there was a 77% reduction of tetrapod families (amphibians and reptiles). Among the marine extinctions, the tropical groups or members of the reef-building community were particularly affected. These relatively large estimates are problematic because there is a lack of complete terrestrial fossil layers from that time and errors in taxonomic classification as well as false extinctions where taxa disappear from the fossil record at the end of the Permian only to turn up again later in the Triassic. The extinctions coincide with the massive Siberian volcanic flood basalts, some degree of low oxygen and other changes in ocean chemistry, and a sudden spike in global temperatures. Explanations encompass a variety of terrestrial factors as well as the possibility of an extraterrestrial source.

In the late Devonian, at 376 mya, 57% of marine genera and 22% of marine families disappeared, including the trilobites. At the end of the Ordovician Period, at 439 mya, the second largest mass extinction induced the disappearance of the trilobite-dominated communities of the Cambrian. There was little life on land at this time, with the earliest fossil evidence of plants in the form of spores from the uppermost Ordovician. The extinction may have occurred through an alternation of cooling and warming over a short period of time, which eliminated 60% of marine genera and 26% of marine families. In the early Cambrian, at 512 mya, the elimination of about 50% of all marine species and geological evidence of sea-level glaciers near the equator at in the Precambrian at 600 to 700 mya have led to the Snowball Earth hypothesis, according to which the entire earth was ice-covered until terminated when carbon dioxide accumulation reversed the cooling. This event is inferred to have resulted in a major extinction of existing organisms, although this impact cannot be measured through the fossil record.

## Human Origins

The origin of humans begins at the time when the human lineage separated from the common ancestor shared with the nearest living great ape relative. It is at or after this point of separation that the human lineage (hominids) evolved a new skeletal structure that made bipedalism obligate and freed the forelimbs from necessarily assisting with terrestrial locomotion. In contrast, the nearest great ape relative is descended from a lineage that did not evolve these features even though it too is derived from the same common ancestor as humans.

The hominid fossil record currently extends back about 6 million years with fossils that are mostly assigned to the genus *Homo*, which includes humans (*Homo sapiens*) and the australopiths (*Australopithecus* and *Paranthropus*). There are also four other genera that have been proposed as hominids although the evidence for their being hominids is far more ambiguous as they comprise limited fragments and bipedalism extrapolated from indirect evidence (*Ardipithecus*, *Sahelanthropus*, *Kenyanthropus*) or partial direct evidence (*Orrorin*).

The initial separation between humans and the nearest living great ape species was initially thought to have occurred much earlier, as another fossil thought to also be a hominid or close hominid relative dated to about 13 mya. This fossil, known as *Ramapithecus*, was represented by an apelike jaw with humanlike dentition. The fossil was fragmented at the midline of the palate, so the shape of the jaw was not known, but reconstructions suggested it was more like the squat, parabolic shape of humans than the U shape of apes. Paleontologists regarded *Ramapithecus* as a definitive hominid or at the very least a close hominid relative that showed the human lineage first diverged from the common great ape ancestor at least by this time.

An apparently contradictory perspective developed in the 1960s, as biologists started comparing protein molecules, and later, as they focused on DNA molecules. These studies at first pointed to African apes as being most closely related to humans, and subsequently this arrangement was replaced by a closer relationship between humans and chimpanzees because they showed the least amount of molecular differences in their DNA (although the contrast between humans and gorillas

and orangutans was also very small). Molecular systematists argued that differences in molecular similarity could also indicate the relative age of divergence between related groups. Where members of a group were equally different from another external group, their divergence was seen to occur at a steady, clock-like rate and this clock-like divergence could be used as a measure of evolutionary time. All that was needed was a calibration point to match divergence with absolute time, so that molecular ages could be given for those species lacking an adequate fossil record. By including species with an accepted fossil record, it was theoretically possible to date the divergence between humans and their nearest living great ape relative.

It is now almost universally accepted as a scientific fact that humans and chimpanzees diverged from a unique common ancestor and that even though chimpanzees are structurally more like gorillas, the latter resemblance is misleading. The oldest fossil members of the human lineage (hominids) date back to about 6 mya, but neither chimpanzees nor gorillas have a recognized fossil history beyond some very recent records. The molecular clock appeared to provide a solution, and calibrated molecular clocks predicted divergence dates of 5 to 8 mya for humans and chimpanzees. This was a much more recent date for hominid origins than suggested by the *Ramapithecus* fossil, but a later discovery of another fossil in the *Sivapithecus* group appeared to provide a solution. *Sivapithecus* was recognized as representing the same group as *Ramapithecus*, and because *Sivapithecus* was the older name, it took priority for naming this combined group that included the former *Ramapithecus*. As more complete fossils of *Sivapithecus* were found, it was apparent that these fossils were distinctly orangutan-like. This similarity was believed to preclude these fossils, including the original *Ramapithecus*, from representing a fossil hominid or even a close hominid relative because orangutans were not believed to be more closely related to humans than were the African apes. The alternative possibility, that orangutans were more closely related to humans than African apes, was not considered. Humans were now promoted as not only having diverged very recently from a common great ape ancestor with chimpanzees, but also having evolved a radically different biology resulting in very little, if

anything, that was structurally unique to humans and chimpanzees.

The absence of uniquely shared structures between humans and chimpanzees remained an evolutionary anomaly because the theory of evolutionary classification established over the past several decades is based on the principle that sister groups (those that share a unique common ancestor) also share one or more unique features inherited from that unique common ancestor. In the absence of any other theory of relationship, the lack of unique features shared by humans and chimpanzees could be disregarded, but in the early 1980s evidence for the existence of many features unique to humans and orangutans began to accumulate, and these structural characteristics support a closer relationship between humans and orangutans than humans and chimpanzees. As many as 40 unique features have been identified, and at least 30 are strongly documented comparative studies. If orangutans are more closely related to humans than are African apes, then so too are fossil orangutans relatives such as *Sivapithecus*, which is now dated to about 13 mya. This fossil record may suggest that the divergence of hominids from the nearest living great ape (the orangutan) occurred earlier than the time that the molecular clock theory predicts.

The structural evidence for the orangutan relationship with humans sharply contradicts the widely accepted theory that similarity of DNA molecules necessarily precludes any other pattern of relationship derived from nonmolecular evidence. Unlike the molecular evidence, which does not correspond to any comparable structural similarity between humans and chimpanzees, the orangutan evidence is congruent with the fact that the earliest accepted hominid fossils not only look more like orangutans than African apes, they also include several features that are otherwise unique to orangutans and their close fossil relatives.

The contradiction between the molecular and structural (anatomical, reproductive, physiological, behavioral) evidence for human origins represents one of the most controversial and profound challenges of modern biology. At the very least, the orangutan evidence raises critical questions over the validity of commonly accepted assumptions about molecular similarity and evolutionary relationships, and whether molecular clocks can necessarily

identify maximum divergence ages. And yet the orangutan theory of human origin has become one of the least recognized and debated issues in evolutionary biology today. There is an almost total silence on the subject within the scientific community. Such silence fails to apply the scientific method, according to which anomalous results demand further research and investigation. As long as this challenge to mediocrity remains unchallenged, the credibility of evolution as a science suffers. Here time is definitively of the essence.

### Teleology

Teleology is a temporal concept of causality by which a current structure or process originates in order to serve a future purpose or goal. In this concept it is the future that determines the past and the present. Teleology was the predominant mode of reasoning to explain the natural world dating from the time of Aristotle, who saw life as showing a trend toward perfection, and even after Darwin, who provided a mechanistic view of biology in his book *On the Origin of Species*. The theory of evolution was supposed to end teleology as an explanation of origin in terms of meeting a future goal or purpose because evolution was seen to be an interaction between random mutation and the process of natural selection favoring differential survival of those individuals with variations that resulted in increased reproductive fitness. In Darwin's theory the mechanism of evolution was seen not as a process having a demonstrable relationship to the future but rather as a consequence of past events and current relationships between the organism and the environment. This outlook does not preclude a philosophical or religious perspective that treats evolution as a teleological process, but such perspectives are not derived from scientific observations that are not informative about whether or not evolution, or the universe, has a purpose.

Evolutionary explanations based on teleological language continue to abound in modern biology in publications ranging from professional research to popular media. This teleological language explains the origin of a particular structure, behavior, or other adaptation as having occurred "in order to" serve its current function—where *function* refers

to the contribution a structure gives to the survival of an organism or a species. This function cannot empirically exist without the structure that makes the function possible, and yet the origin of the structure is attributed to that future function. In this context, evolutionary theory uses teleology to explain the origin of biological structure (whether anatomical, physiological, or behavioral) as meeting the requirements of future functions that confer increased survival on the species.

The prominent American Darwinian evolutionist Ernst Mayr claimed that there is now complete consensus among biologists that teleological statements do not imply any conflict with physical or chemical actuality, and the problem of teleology is reduced to the distinction between which teleological statements are legitimate and which are not. It may be argued that teleological language may not require a teleological meaning if it does not endorse unverifiable theological or metaphysical doctrines, attribute physical and chemical properties to biology that are not also applicable to inanimate objects, accept future goals as the cause of current events, or apply human qualities such as intent, purpose, planning, or deliberation to organic structures. Because biological systems behave as if they were teleological (e.g., the maintenance of homeostasis by physiological processes of the cell), teleological language may be unavoidable. It may also be argued that evolutionary biologists are irreducibly involved with teleology because they are in the practice of trying to understand the world with reference to the future when addressing the evolutionary significance of biological structures in terms of their functions.

The principal teleological expression in modern evolutionary biology is the explanation of a structure in terms of its function. This expression is usually in the form of a structure evolving in order to serve or achieve a particular function. For example, feathers evolved as an adaptation for flight. But when it became evident that feathers preceded flight, feathers were understood as an adaptation for some other preexisting function that was later co-opted into a new function. This resulted in evolutionists trying to guess whether an adaptation existed for the existing function or an imagined preexisting function, or whether there is ever any function in the original appearance of the structure or during its subsequent evolution.

Evolutionary history becomes a field of imagination where any manner of functions may be invented and somehow explain the origin of the structure, even though such temporal and goal-directed explanations say nothing about the nature of the structure itself.

In preevolutionary biology, natural theology provided a supernatural explanation for teleology. Darwin's argument for natural selection suggested that evolution was a mechanical or physical process that is not organized to meet future goals or purposes. Many early evolutionists, however, continued to view evolution as a teleological process such as the *scala naturae* or "chain of being" where a steady advance was seen to occur through a supernatural force or internal drive toward perfection. This teleological philosophy was also applied to non-Darwinian alternatives to natural selection such as *orthogenesis*, a term used in 1893 by the German evolutionist William Hacke, who recognized that there were evolutionary sequences in complexity in which reversals either did not occur or were rare. As an example, a penguin may become a marine animal, but it remains a bird and does not become a fish. Hacke argued that if any kind of variation could occur, such reversals should be frequent due to those variations being advantageous as some stage. That this was not the case suggested that evolutionary changes may take place that did not owe their origin to environmental selection.

The orthogenetic theory recognized that evolutionary changes were limited to those that were made possible by existing biological structures. This view was supported by a minority of early evolutionary biologists, and it was most explicitly developed and supported as an alternative to Darwinism in the panbiogeographic synthesis of Léon Croizat. In the absence of a biological mechanism for explaining how new mutations may not be random, orthogenesis was characterized by Darwinian evolutionists as mystical and teleological. The teleological restriction for orthogenesis was also seen to be evident in examples from the fossil record that were supposed to demonstrate a linear direction to evolution, with the reduction of toes in horses from the ancestral five to the current single toe as the classic example. This linear concept was contrasted to phylogenetic evidence that evolution was not linear but rather involved a

process of diversification or branching. Falsification of linear evolution was consequently a falsification of orthogenesis. This rejection mistakenly conflated two distinct concepts: that of linear evolution and that of orthogenesis. In his original formulation of orthogenesis, Hacke cited the reduction of horse toes from five to one as an illustration of a biologically driven trend, but he did not confine the process to that of a linear or purposeful evolution. Whether or not the historical sequence of horse evolution was "linear" or a branching "bush," there was a reduction of toes that took place over space and time resulting in the single-toed horse of today. Croizat resolved the apparent contradiction between diversification through speciation and the apparent linear sequence implied by orthogenetic sequences by proposing a vicariant form-making model by which characters are heterogeneously distributed over a widespread ancestral range and these geographic variations provide spatially different starting points for subsequent differentiation and speciation. In recent decades new molecular genetic discoveries have also drawn attention to patterns of "concerted evolution" and biological mechanisms of molecular drive, such as biased gene conversion, that result in evolutionary novelty without requiring improved reproductive fitness as a necessary result.

It may be argued that resorting to teleological explanations for the origin of structures in terms of their future function obfuscates the evolutionary process by avoiding the need for causal explanation and a deeper understanding of biological structure. For example, the teleological explanation for the evolution of the leaf as an adaptation for photosynthesis, or the evolution of a feather as an adaptation to flight or insulation, provides no information about the evolutionary origin and structure of the organs themselves. Adaptive, teleological explanations contain no greater information content than purely teleological creationist explanations.

As an empirical science, evolutionary theory can only be neutral about whether or not there is an underlying teleology in the universe and its evolution. Such possibilities are broached from theological or philosophical perspectives but not from science. Teleology remains the most troubling presence of nonscientific thought in modern

evolutionary biology that obscures any distinction between a supposedly empirical science of evolution and teleological theories of existence such as intelligent design.

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See also Dinosaurs; DNA; Evidence of Human Evolution, Interpreting; Evolution, Organic; Extinction and Evolution; Extinctions, Mass; Fossils, Living; Hominid-Pongid Split; Life, Origin of; Pilttdown Man Hoax; Saltationism and Gradualism; Teleology

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