Evolutionary history of life

"History of life" redirects here. For other uses, see Life history.
For a more concise outline of the evolution of life, see Timeline of evolutionary history of life.
"History of evolution" redirects here. It is not to be confused with History of evolutionary thought.

The **evolutionary history of life** on Earth traces the processes by which living and fossil organisms have evolved since life on the planet first originated until the present day. Earth formed about 4.5 Ga (billion years) ago and life appeared on its surface within 1 billion years. The similarities between all present-day organisms indicate the presence of a common ancestor from which all known species have diverged through the process of evolution.[1]

The earliest evidence for life on Earth is graphite found to be biogenic in 3.7 billion-year-old metasedimentary rocks discovered in Western Greenland[2] and microbial mat fossils found in 3.48 billion-year-old sandstone discovered in Western Australia.[3][4] Microbial mats of coexisting bacteria and archaea were the dominant form of life in the early Archean and many of the major steps in early evolution are thought to have taken place within them.[5] The evolution of oxygenic photosynthesis, around 3.5 Ga, eventually led to the oxygenation of the atmosphere, beginning around 2.4 Ga.[6] The earliest evidence of eukaryotes (complex cells with organelles) dates from 1.85 Ga,[7][8] and while they may have been present earlier, their diversification accelerated when they started using oxygen in their metabolism. Later, around 1.7 Ga, multicellular organisms began to appear, with differentiated cells performing specialised functions.[9] Bilateria, animals with a front and a back, appeared by 555 million years ago.[10]

The earliest land plants date back to around 450 Ma (million years ago),[11] although evidence suggests that microbes formed the earliest terrestrial ecosystems, at least 2.9 Ga ago.[12] Microbes are thought to have paved the way for the inception of land plants in the Phanerozoic. Land plants were so successful that they are thought to have contributed to the late Devonian extinction event.[13] Invertebrate animals appear during the Ediacaran period,[14] while vertebrates originated about 525 Ma during the Cambrian explosion.[15] During the Permian period, synapsids, including the ancestors of mammals, dominated the land,[16] but most of this group became extinct in the Permian–Triassic extinction event 252.17 Ma.[17] During the recovery from this catastrophe, archosaurs became the most abundant land vertebrates;[18] one archosaur group, the dinosaurs, dominated the Jurassic and Cretaceous periods.[19] After the Cretaceous–Paleogene extinction event 66 Ma killed off the dinosaurs,[20] mammals increased rapidly in size and diversity.[21] Such mass extinctions may have accelerated evolution by providing opportunities for new groups of organisms to diversify.[22]

1 Earliest history of Earth

History of Earth and its life
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Extinction of non-avian dinosaurs
Scale:
Ma (Millions of years)
Main article: History of the Earth

The oldest meteorite fragments found on Earth are about 4.54 billion years old; this, coupled primarily with the dating of ancient lead deposits, has put the estimated age of Earth at around that time.[24] The Moon has the same composition as Earth's crust but does not contain an iron-rich core like the Earth's. Many scientists think that about 40 million years later a body the size of Mars struck the Earth, throwing into orbit crust material that formed the Moon. Another hypothesis is that the Earth and Moon started to coalesce at the same time but the Earth, having much stronger gravity than the early Moon, attracted almost all the iron particles in the area.[25]

Until 2001, the oldest rocks found on Earth were about 3.8 Ga.[26] [27] [28] [29] leading scientists to believe that the Earth's surface had been molten until then. Accordingly, they named this part of Earth's history the Hadean eon, whose name means "hellish".[30] However analysis of zircons formed 4.4 billion years ago indicates that Earth's crust solidified about 100 Ma after the planet's formation and that the planet quickly acquired oceans and an atmosphere, which may have been capable of supporting life.[31] [32]

Evidence from the Moon indicates that from 4 billion to 3.8 billion years ago it suffered a Late Heavy Bombardment by debris that was left over from the formation of the Solar System, and the Earth should have experienced an even heavier bombardment due to its stronger gravity.[30][33] While there is no direct evidence of conditions on Earth 4 billion to 3.8 billion years ago, there is no reason to think that the Earth was not also affected by this late heavy bombardment.[34] This event may well have stripped away any previous atmosphere and oceans; in this case gases and water from comet impacts may have contributed to their replacement, although volcanic outgassing on Earth would have supplied at least half.[35] However, if subsurface microbial life had evolved by this point, it would have survived the bombardment.[36]

2 Earliest evidence for life on Earth

The earliest identified organisms were minute and relatively featureless, and their fossils look like small rods, which are very difficult to tell apart from structures that arise through abiotic physical processes. The oldest undisputed evidence of life on Earth, interpreted as fossilized bacteria, dates to 3 Ga.[37] Other finds in rocks dated to about 3.5 Ga have been interpreted as bacteria,[38] with geochemical evidence also seeming to show the presence of life 3.8 Ga.[39] However these analyses were closely scrutinized, and non-biological processes were found which could produce all of the "signatures of life" that had been reported.[40][41] While this does not prove that the structures found had a non-biological origin, they cannot be taken as clear evidence for the presence of life. Geochemical signatures from rocks deposited 3.4 Ga have been interpreted as evidence for life,[37][42] although these statements have not been thoroughly examined by critics.

3 Origins of life on Earth

Evolutionary tree showing the divergence of modern species from their common ancestor in the center.[1] The three domains are colored, with bacteria blue, archaea green, and eukaryotes red.

1. ^ Ciccarelli, F.D., Doerks, T., von Mering, C., Creevey, C.J. et al. (2006). "Toward automatic reconstruction of a highly resolved tree of life". *Science* **311** (5765): 1283–7. Bibcode:2006Sci...311.1283C. doi:10.1126/science.1123061. PMID 16513982.

Further information: Evidence of common descent, Common descent and Homology (biology)

Biologists reason that all living organisms on Earth must share a single last universal ancestor, because it would be virtually impossible that two or more separate lineages could have independently developed the many complex biochemical mechanisms common to all living organisms.[43][44] As previously mentioned the earliest organisms for which fossil evidence is available are bacteria. The lack of fossil or geochemical evidence for earlier organisms has left plenty of scope for hypotheses, which fall into two main groups: 1) that life arose spontaneously on Earth or 2) that it was "seeded" from elsewhere in the Universe.[45]

3.1 Life "seeded" from elsewhere

Main article: Panspermia

The idea that life on Earth was "seeded" from elsewhere in the Universe dates back at least to the Greek philosopher Anaximander in the sixth century BCE.[46] In the twentieth century it was proposed by the physical chemist Svante Arrhenius,[47] by the astronomers Fred Hoyle and Chandra Wickramasinghe,[48] and by molecular biologist Francis Crick and chemist Leslie Orgel.[49] There are three main versions of the "seeded from elsewhere" hypothesis: from elsewhere in our Solar System via fragments knocked into space by a large meteor impact, in which case the most credible sources are Mars[50] and Venus;[51] by alien visitors, possibly as a result of accidental contamination by micro-organisms that they brought with them;[49] and from outside the Solar System but by natural means.[47][50] Experiments in low Earth orbit, such as EXOSTACK, demonstrated that some micro-organism spores can survive the shock of being catapulted into space and some can survive exposure to outer space radiation for at least 5.7 years.[52][53] Scientists are divided over the likelihood of life arising independently on Mars,[54] or on other planets in our galaxy.[50]

3.2 Independent emergence on Earth

Main article: Abiogenesis

Life on Earth is based on carbon and water. Carbon provides stable frameworks for complex chemicals and can be easily extracted from the environment, especially from carbon dioxide. The only other element with similar chemical properties, silicon, forms much less stable structures and, because most of its compounds are solids, would be more difficult for organisms to extract. Water is an excellent solvent and has two other useful properties: the fact that ice floats enables aquatic organisms to survive beneath it in winter; and its molecules have electrically negative and positive ends, which enables it to form a wider range of compounds than other solvents can. Other good solvents, such as ammonia, are liquid only at such low temperatures that chemical reactions may be too slow to sustain life, and lack water's other advantages.[55] Organisms based on alternative biochemistry may however be possible on other planets.[56]

Research on how life might have emerged from non-living chemicals focuses on three possible starting points: self-replication, an organism's ability to produce offspring that are very similar to itself; metabolism, its ability to feed and repair itself; and external cell membranes, which allow food to enter and waste products to leave, but exclude unwanted substances.[57] Research on abiogenesis still has a long way to go, since theoretical and empirical approaches are only beginning to make contact with each other.[58][59]

3.2.1 Replication first: RNA world

Main articles: Last universal ancestor and RNA world

Even the simplest members of the three modern domains of life use DNA to record their "recipes" and a complex array of RNA and protein molecules to “read” these instructions and use them for growth, maintenance and self-replication. The discovery that some RNA molecules can catalyze both their own replication and the construction of proteins led to the hypothesis of earlier life-forms based entirely on RNA.[60] These ribozymes could have formed an RNA world in which there were individuals but no species, as mutations and horizontal gene transfers would have meant that the offspring in each generation were quite likely to have different genomes from those that their parents started with.[61] RNA would later have been replaced by DNA, which is more stable and therefore can build longer genomes, expanding the range of capabilities a single organism can have.[61][62][63] Ribozymes remain as the main components of ribosomes, modern cells’ “protein factories”.[64]

Although short self-replicating RNA molecules have been artificially produced in laboratories,[65] doubts have been raised about where natural non-biological synthesis of RNA is possible.[66] The earliest “ribozymes” may have been formed of simpler nucleic acids such as PNA, TNA or GNA, which would have been replaced later by RNA.[67][68]

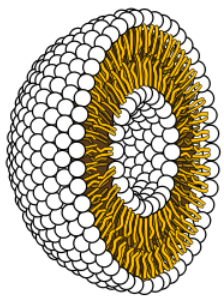
In 2003 it was proposed that porous metal sulfide precipitates would assist RNA synthesis at about 100 °C (212 °F) and ocean-bottom pressures near hydrothermal vents. Under this hypothesis, lipid membranes would be the last major cell components to appear and, until then, the protocells would be confined to the pores.[69]

3.2.2 Metabolism first: Iron–sulfur world

Main article: Iron–sulfur world theory

A series of experiments starting in 1997 showed that early stages in the formation of proteins from inorganic materials including carbon monoxide and hydrogen sulfide could be achieved by using iron sulfide and nickel sulfide as catalysts. Most of the steps required temperatures of about 100 °C (212 °F) and moderate pressures, although one stage required 250 °C (482 °F) and a pressure equivalent to that found under 7 kilometres (4.3 mi) of rock. Hence it was suggested that self-sustaining synthesis of proteins could have occurred near hydrothermal vents.[70]

3.2.3 Membranes first: Lipid world



= water-attracting heads of lipid molecules
= water-repellent tails
Cross-section through a liposome.

It has been suggested that double-walled “bubbles” of lipids like those that form the external membranes of cells may have been an essential first step.[71] Experiments that simulated the conditions of the early Earth have reported the formation of lipids, and these can spontaneously form liposomes, double-walled “bubbles”, and then reproduce themselves. Although they are not intrinsically information-carriers as nucleic acids are, they would be subject to natural selection for longevity and reproduction. Nucleic acids such as RNA might then have formed more easily within the liposomes than they would have outside.[72]

3.2.4 The clay theory

Main articles: Graham Cairns-Smith § Clay Theory and RNA world

RNA is complex and there are doubts about whether it can be produced non-biologically in the wild.[66] Some clays, notably montmorillonite, have properties that make them plausible accelerators for the emergence of an RNA world: they grow by self-replication of their crystalline pattern; they are subject to an analog of natural selection, as the clay "species" that grows fastest in a particular environment rapidly becomes dominant; and they can catalyze the formation of RNA molecules.[73] Although this idea has not become the scientific consensus, it still has active supporters.[74]

Research in 2003 reported that montmorillonite could also accelerate the conversion of fatty acids into "bubbles", and that the "bubbles" could encapsulate RNA attached to the clay. These "bubbles" can then grow by absorbing additional lipids and then divide. The formation of the earliest cells may have been aided by similar processes.[75]

A similar hypothesis presents self-replicating iron-rich clays as the progenitors of nucleotides, lipids and amino acids.[76]

4 Environmental and evolutionary impact of microbial mats

Main articles: Microbial mat and Oxygen catastrophe

Microbial mats are multi-layered, multi-species colonies of bacteria and other organisms that are generally only a few millimeters thick, but still contain a wide range of chemical environments, each of which favors a different set of micro-organisms.[77] To some extent each mat forms its own food chain, as the by-products of each group of micro-organisms generally serve as "food" for adjacent groups.[78]

Modern stromatolites in Shark Bay, Western Australia.

Stromatolites are stubby pillars built as microbes in mats slowly migrate upwards to avoid being smothered by sediment deposited on them by water.[77] There has been vigorous debate about the validity of alleged fossils from before 3 Ga,[79] with critics arguing that so-called stromatolites could have been formed by non-biological processes.[40] In 2006 another find of stromatolites was reported from the same part of Australia as previous ones, in rocks dated to 3.5 Ga.[80]

In modern underwater mats the top layer often consists of photosynthesizing cyanobacteria which create an oxygen-rich environment, while the bottom layer is oxygen-free and often dominated by hydrogen sulfide emitted by the organisms living there.[78] It is estimated that the appearance of oxygenic photosynthesis by bacteria in mats increased biological productivity by a factor of between 100 and 1,000. The reducing agent used by oxygenic photosynthesis is water, which is much more plentiful than the geologically produced reducing agents required by the earlier non-oxygenic photosynthesis.[81] From this point onwards life itself produced significantly more of the resources it needed than did geochemical processes.[82] Oxygen is toxic to organisms that are not adapted to it, but greatly increases the metabolic efficiency of oxygen-adapted organisms.[83][84] Oxygen became a significant component of Earth's atmosphere about 2.4 Ga.[85] Although eukaryotes may have been present much earlier,[86][87] the oxygenation of the atmosphere was a prerequisite for the evolution of the most complex eukaryotic cells, from which all multicellular organisms are built.[88] The boundary between oxygen-rich and oxygen-free layers in microbial mats would have moved upwards when photosynthesis shut down overnight, and then downwards as it resumed on the next day. This would have created selection pressure for organisms in this intermediate zone to acquire the ability to tolerate and then to use oxygen, possibly via endosymbiosis, where one organism lives inside another and both of them benefit from their association.[5]

Cyanobacteria have the most complete biochemical "toolkits" of all the mat-forming organisms. Hence they are the most self-sufficient of the mat organisms and were well-adapted to strike out on their own both as floating mats and as the first of the phytoplankton, providing the basis of most marine food chains.[5]

5 Diversification of eukaryotes

One possible family tree of eukaryotes.[89][90]
Main article: Eukaryote

5.1 Chromatin, nucleus, endomembrane system, and mitochondria

Eukaryotes may have been present long before the oxygenation of the atmosphere,[86] but most modern eukaryotes require oxygen, which their mitochondria use to fuel the production of ATP, the internal energy supply of all known cells.[88] In the 1970s it was proposed and, after much debate, widely accepted that eukaryotes emerged as a result of a sequence of endosymbioses between "prokaryotes". For example: a predatory micro-organism invaded a large prokaryote, probably an archaean, but the attack was neutralized, and the attacker took up residence and evolved into the first of the mitochondria; one of these chimeras later tried to swallow a photosynthesizing cyanobacterium, but the victim survived inside the attacker and the new combination became the ancestor of plants; and so on. After each endosymbiosis began, the partners would have eliminated unproductive duplication of genetic functions by re-arranging their genomes, a process which sometimes involved transfer of genes between them.[91][92][93] Another hypothesis proposes that mitochondria were originally sulfur- or hydrogen-metabolising endosymbionts, and became oxygen-consumers later.[94] On the other hand mitochondria might have been part of eukaryotes' original equipment.[95]

There is a debate about when eukaryotes first appeared: the presence of steranes in Australian shales may indicate that eukaryotes were present 2.7 Ga;[87] however an analysis in 2008 concluded that these chemicals infiltrated the rocks less than 2.2 Ga and prove nothing about the origins of eukaryotes.[96] Fossils of the alga *Grypania* have been reported in 1.85 Ga rocks (originally dated to 2.1 Ga but later revised[8]), and indicates that eukaryotes with organelles had already evolved.[97] A diverse collection of fossil algae were found in rocks dated between 1.5 and 1.4 Ga.[98] The earliest known fossils of fungi date from 1.43 Ga.[99]

5.2 Plastids

Plastids are thought to have originated from endosymbiotic cyanobacteria. The symbiosis evolved around 1500 million years ago and enabled eukaryotes to carry out oxygenic photosynthesis.[100] Three evolutionary lineages have since emerged in which the plastids are named differently: chloroplasts in green algae and plants, rhodoplasts in red algae and cyanelles in the glaucophytes.

6 Sexual reproduction and multicellular organisms

6.1 Evolution of sexual reproduction

Main articles: Evolution of sexual reproduction and Sexual reproduction

The defining characteristics of sexual reproduction in eukaryotes are meiosis and fertilization. There is much genetic recombination in this kind of reproduction, in which offspring receive 50% of their genes from each parent,[101] in contrast with asexual reproduction, in which there is no recombination. Bacteria also exchange DNA by bacterial conjugation, the benefits of which include resistance to antibiotics and other toxins, and the ability to utilize new metabolites.[102] However conjugation is not a means of reproduction, and is not limited to members of the same species – there are cases where bacteria transfer DNA to plants and animals.[103]

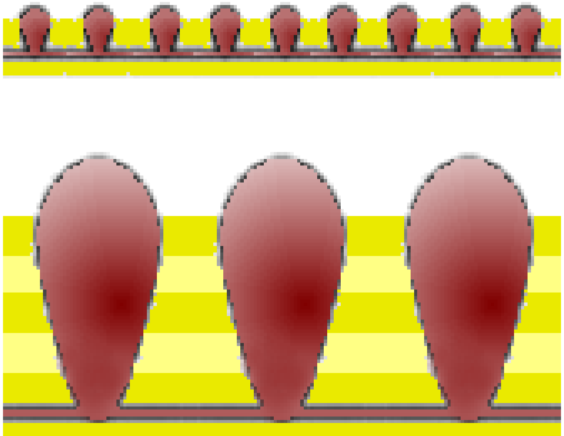
On the other hand, bacterial transformation is clearly an adaptation for transfer of DNA between bacteria of the same species. Bacterial transformation is a complex process involving the products of numerous bacterial genes and can be regarded as a bacterial form of sex.[104][105] This process occurs naturally in at least 67 prokaryotic species (in seven different phyla).[106] Sexual reproduction in eukaryotes may have evolved from bacterial transformation.[107] (Also see Evolution of sexual reproduction#Origin of sexual reproduction.)

The disadvantages of sexual reproduction are well-known: the genetic reshuffle of recombination may break up favorable combinations of genes; and since males do not directly increase the number of offspring in the next generation, an asexual population can out-breed and displace in as little as 50 generations a sexual population that is equal in every other respect.[101] Nevertheless the great majority of animals, plants, fungi and protists reproduce sexually. There is strong evidence that sexual reproduction arose early in the history of eukaryotes and that the genes controlling it have changed very little since then.[108] How sexual reproduction evolved and survived is an unsolved puzzle.[109]

The Red Queen Hypothesis suggests that sexual reproduction provides protection against parasites, because it is easier for parasites to evolve means of overcoming the defenses of genetically identical clones than those of sexual species that present moving targets, and there is some experimental evidence for this. However there is still doubt about whether it would explain the survival of sexual species if multiple similar clone species were present, as one of the clones may survive the attacks of parasites for long enough to out-breed the sexual species.[101] Furthermore, 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.[110] In addition, 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 the host.[111]

The Mutation Deterministic Hypothesis assumes that each organism has more than one harmful mutation and the combined effects of these mutations are more harmful than the sum of the harm done by each individual mutation. If so, sexual recombination of genes will reduce the harm that bad mutations do to offspring and at the same time eliminate some bad mutations from the gene pool by isolating them in individuals that perish quickly because they have an above-average number of bad mutations. However the evidence suggests that the MDH's assumptions are shaky, because many species have on average less than one harmful mutation per individual and no species that has been investigated shows evidence of synergy between harmful mutations.[101] Further criticisms of this hypothesis are discussed in the article Evolution of sexual reproduction#Removal of deleterious genes

The random nature of recombination causes the relative abundance of alternative traits to vary from one generation to another. This genetic drift is insufficient on its own to make sexual reproduction advantageous, but a combination of genetic drift and natural selection may be sufficient. When chance produces combinations of good traits, natural selection gives a large advantage to lineages in which these traits become genetically linked. On the other hand, the benefits of good traits are neutralized if they appear along with bad traits. Sexual recombination gives good traits the opportunities to become linked with other good traits, and mathematical models suggest this may be more than enough to offset the disadvantages of sexual reproduction.[109] Other combinations of hypotheses that are inadequate on their own are also being examined.[101]



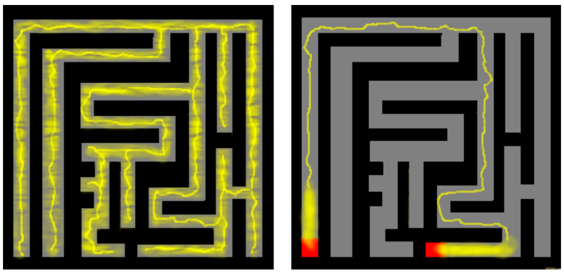
Horodyskia may have been an early metazoan,[8] or a colonial foraminiferan.[112] It apparently re-arranged itself into fewer but larger main masses as the sediment grew deeper round its base.[8]

The adaptive function of sex today remains a major unresolved issue in biology. The competing models to explain the adaptive function of sex were reviewed by Birdsell and Wills.[113] The hypotheses discussed above all depend on possible beneficial effects of random genetic variation produced by genetic recombination. An alternative view is that sex arose, and is maintained, as a process for repairing DNA damage, and that the genetic variation produced is an occasionally beneficial byproduct.[107][114]

6.2 Multicellularity

Main article: Multicellular organism

The simplest definitions of “multicellular”, for example “having multiple cells”, could include colonial cyanobacteria like Nostoc. Even a professional biologist’s definition such as “having the same genome but different types of cell” would still include some genera of the green alga Volvox, which have cells that specialize in reproduction.[115] Multicellularity evolved independently in organisms as diverse as sponges and other animals, fungi, plants, brown algae, cyanobacteria, slime moulds and myxobacteria.[8][116] For the sake of brevity this article focuses on the organisms that show the greatest specialization of cells and variety of cell types, although this approach to the evolution of complexity could be regarded as “rather anthropocentric".[117]



A slime mold solves a maze. The mold (yellow) explored and filled the maze (left). When the researchers placed sugar (red) at two separate points, the mold concentrated most of its mass there and left only the most efficient connection between the two points (right).[118]

The initial advantages of multicellularity may have included: more efficient sharing of nutrients that are digested outside the cell,[119] increased resistance to predators, many of which attacked by engulfing; the ability to resist currents by attaching to a firm surface; the ability to reach upwards to filter-feed or to obtain sunlight for photosynthesis;[120] the ability to create an internal environment that gives protection against the external one;[117] and even the opportunity for a group of cells to behave “intelligently” by sharing information.[118] These features would also have provided opportunities for other organisms to diversify, by creating more varied environments than flat microbial mats could.[120]

Multicellularity with differentiated cells is beneficial to the organism as a whole but disadvantageous from the point of view of individual cells, most of which lose the opportunity to reproduce themselves. In an asexual multicellular organism, rogue cells which retain the ability to reproduce may take over and reduce the organism to a mass of undifferentiated cells. Sexual reproduction eliminates such rogue cells from the next generation and therefore appears to be a prerequisite for complex multicellularity.[120]

The available evidence indicates that eukaryotes evolved much earlier but remained inconspicuous until a rapid diversification around 1 Ga. The only respect in which eukaryotes clearly surpass bacteria and archaea is their capacity for variety of forms, and sexual reproduction enabled eukaryotes to exploit that advantage by producing organisms with multiple cells that differed in form and function.[120]

6.3 Fossil evidence for multicellularity and sexual reproduction

The Francevillian Group Fossils, dated to 2.1 Ga, are the earliest known fossil organisms that are clearly multicellular.[23] They may have had differentiated cells.[121] Another early multicellular fossil, *Qingshania*,[note 1] dated to 1.7 Ga, appears to consist of virtually identical cells. The red alga called *Bangiomorpha*, dated at 1.2 Ga, is the earliest known organism that certainly has differentiated, specialized cells, and is also the oldest known sexually reproducing organism.[120] The 1.43 billion-year-old fossils interpreted as fungi appear to have been multicellular with differentiated cells.[99] The “string of beads” organism *Horodyskia*, found in rocks dated from 1.5 Ga to 900 Ma, may have been an early metazoan;[8] however it has also been interpreted as a colonial foraminiferan.[112]

7 Emergence of animals

Main articles: Animal, Ediacara biota, Cambrian Explosion, Burgess shale type fauna and Stem group
A family tree of the animals.[122]

Animals are multicellular eukaryotes,[note 2] and are distinguished from plants, algae, and fungi by lacking cell walls.[123] All animals are motile,[124] if only at certain life stages. All animals except sponges have bodies differentiated into separate tissues, including muscles, which move parts of the animal by contracting, and nerve tissue, which transmits and processes signals.[125]

The earliest widely accepted animal fossils are rather modern-looking cnidarians (the group that includes jellyfish, sea anemones and hydras), possibly from around 580 Ma, although fossils from the Doushantuo Formation can only be dated approximately. Their presence implies that the cnidarian and bilaterian lineages had already diverged.[126]

The Ediacara biota, which flourished for the last 40 Ma before the start of the Cambrian,[127] were the first animals more than a very few centimeters long. Many were flat and had a "quilted" appearance, and seemed so strange that there was a proposal to classify them as a separate kingdom, Vendozoa.[128] Others, however, been interpreted as early molluscs (*Kimberella*[129][130]), echinoderms (*Arkarua*[131]), and arthropods (*Spriggina*,[132] *Parvancorina*[133]). There is still debate about the classification of these specimens, mainly because the diagnostic features which allow taxonomists to classify more recent organisms, such as similarities to living organisms, are generally absent in the Ediacarans. However there seems little doubt that *Kimberella* was at least a triploblastic bilaterian animal, in other words significantly more complex than cnidarians.[134]

The small shelly fauna are a very mixed collection of fossils found between the Late Ediacaran and Mid Cambrian periods. The earliest, *Cloudina*, shows signs of successful defense against predation and may indicate the start of an evolutionary arms race. Some tiny Early Cambrian shells almost certainly belonged to molluscs, while the owners of some "armor plates", *Halkieria* and *Microdictyon*, were eventually identified when more complete specimens were found in Cambrian lagerstätten that preserved soft-bodied animals.[135]

Opabinia *made the largest single contribution to modern interest in the Cambrian explosion.[136]*

In the 1970s there was already a debate about whether the emergence of the modern phyla was "explosive" or gradual but hidden by the shortage of Pre-Cambrian animal fossils.[135] A re-analysis of fossils from the Burgess Shale lagerstätte increased interest in the issue when it revealed animals, such as *Opabinia*, which did not fit into any known phylum. At the time these were interpreted as evidence that the modern phyla had evolved very rapidly in the "Cambrian explosion" and that the Burgess Shale's "weird wonders" showed that the Early Cambrian was a uniquely experimental period of animal evolution.[137] Later discoveries of similar animals and the development of new theoretical approaches led to the conclusion that many of the "weird wonders" were evolutionary "aunts" or "cousins" of modern groups[138] – for example that *Opabinia* was a member of the lobopods, a group which includes the ancestors of the arthropods, and that it may have been closely related to the modern tardigrades.[139] Nevertheless there is still much debate about whether the Cambrian explosion was really explosive and, if so, how and why it happened and why it appears unique in the history of animals.[140]

7.1 Deuterostomes and the first vertebrates

Acanthodians were among the earliest vertebrates with jaws.[141]

Main articles: Chordate and Evolution of fish
See also: Chordate genomics

Most of the animals at the heart of the Cambrian explosion debate are protostomes, one of the two main groups of complex animals. The other major group, the deuterostomes, contains invertebrates such as sea stars and urchins (echinoderms), as well as chordates (see below). Many echinoderms have hard calcite "shells", which are fairly common from the Early Cambrian small shelly fauna onwards.[135] Other deuterostome groups are soft-bodied, and most of the significant Cambrian deuterostome fossils come from the Chengjiang fauna, a lagerstätte in China.[142] The chordates are another major deuterostome group: animals with a distinct dorsal nerve cord. Chordates include soft-bodied invertebrates such as tunicates as well as vertebrates- animals with a backbone. While tunicate fossils predate the Cambrian explosion,[143] the Chengjiang fossils *Haikouichthys* and *Myllokunmingia* appear to be true vertebrates,[144] and *Haikouichthys* had distinct vertebrae, which may have been slightly mineralized.[145] Vertebrates with jaws, such as the Acanthodians, first appeared in the Late Ordovician.[146]

8 Colonization of land

Adaptation to life on land is a major challenge: all land organisms need to avoid drying-out and all those above microscopic size must create special structures to withstand gravity; respiration and gas exchange systems have to change; reproductive systems cannot depend on water to carry eggs and sperm towards each other.[147][148] Although the earliest good evidence of land plants and animals dates back to the Ordovician Period (488 to 444 Ma), and a number of microorganism lineages made it onto land much earlier,[149] modern land ecosystems only appeared in the late Devonian, about 385 to 359 Ma.[150]

8.1 Evolution of terrestrial antioxidants

Oxygen is a potent oxidant whose accumulation in terrestrial atmosphere resulted from the development of photosynthesis over 3 Ga, in blue-green algae (cyanobacteria), which were the most primitive oxygenic photosynthetic organisms. Brown algae (seaweeds) accumulate inorganic mineral antioxidants such as rubidium, vanadium, zinc, iron, copper, molybdenum, selenium and iodine which is concentrated more than 30,000 times the concentration of this element in seawater. Protective endogenous antioxidant enzymes and exogenous dietary antioxidants helped to prevent oxidative damage. Most marine mineral antioxidants act in the cells as essential trace-elements in redox and antioxidant metallo-enzymes.

When plants and animals began to transfer from the sea to rivers and land about 500 Ma ago, environmental deficiency of these marine mineral antioxidants and iodine, was a challenge to the evolution of terrestrial life.[151][152] Terrestrial plants slowly optimized the production of "new" endogenous antioxidants such as ascorbic acid, polyphenols, flavonoids, tocopherols etc. A few of these appeared more recently, in last 200-50 Ma ago, in fruits and flowers of angiosperm plants.

In fact, angiosperms (the dominant type of plant today) and most of their antioxidant pigments evolved during the late Jurassic Period. Plants employ antioxidants to defend their structures against reactive oxygen species produced during photosynthesis. Animals are exposed to the same oxidants, and they have evolved endogenous enzymatic antioxidant systems.[153] Iodine is the most primitive and abundant electron-rich essential element in the diet of marine and terrestrial organisms, and as iodide acts as an electron-donor and has this ancestral antioxidant function in all iodide-concentrating cells from primitive marine algae to more recent terrestrial vertebrates.[154]

8.2 Evolution of soil

Before the colonization of land, soil, a combination of mineral particles and decomposed organic matter, did not exist. Land surfaces would have been either bare rock or unstable sand produced by weathering. Water and any nutrients in it would have drained away very quickly.[150]

Lichens growing on concrete

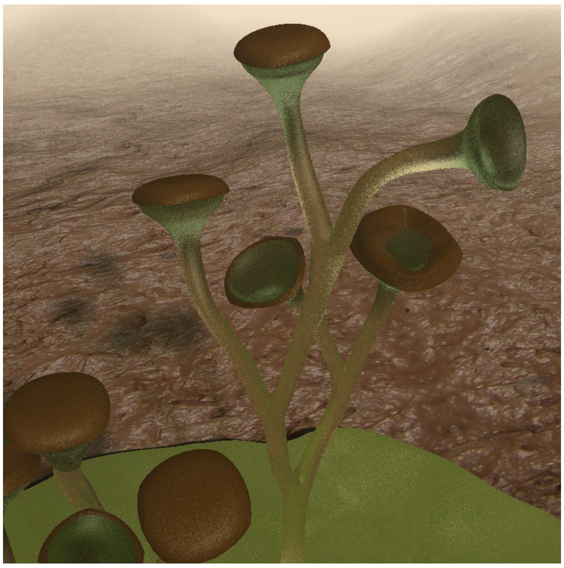
Films of cyanobacteria, which are not plants but use the same photosynthesis mechanisms, have been found in modern deserts, and only in areas that are unsuitable for vascular plants. This suggests that microbial mats may have been the first organisms to colonize dry land, possibly in the Precambrian. Mat-forming cyanobacteria could have gradually evolved resistance to desiccation as they spread from the seas to tidal zones and then to land.[150] Lichens, which are symbiotic combinations of a fungus (almost always an ascomycete) and one or more photosynthesizers (green algae or cyanobacteria),[155] are also important colonizers of lifeless environments,[150] and their ability to break down rocks contributes to soil formation in situations where plants cannot survive.[155] The earliest known ascomycete fossils date from 423 to 419 Ma in the Silurian.[150]

Soil formation would have been very slow until the appearance of burrowing animals, which mix the mineral and organic components of soil and whose feces are a major source of the organic components.[150] Burrows have been found in Ordovician sediments, and are attributed to annelids ("worms") or arthropods.[150][156]

8.3 Plants and the Late Devonian wood crisis

Main article: Evolutionary history of plants

In aquatic algae, almost all cells are capable of photosynthesis and are nearly independent. Life on land required plants to become internally more complex and specialized: photosynthesis was most efficient at the top; roots were required in order to extract water from the ground; the parts in between became supports and transport systems for water and nutrients.[147][157]



Reconstruction of Cooksonia*, a vascular plant from the Silurian*

Fossilized trees from the Mid-Devonian Gilboa fossil forest

Spores of land plants, possibly rather like liverworts, have been found in Mid Ordovician rocks dated to about 476 Ma. In Mid Silurian rocks 430 Ma there are fossils of actual plants including clubmosses such as *Baragwanathia*; most were under 10 centimetres (3.9 in) high, and some appear closely related to vascular plants, the group that includes trees.[157]

By the late Devonian 370 Ma, trees such as *Archaeopteris* were so abundant that they changed river systems from mostly braided to mostly meandering, because their roots bound the soil firmly.[158] In fact they caused a "Late Devonian wood crisis",[159] because:

- They removed more carbon dioxide from the atmosphere, reducing the greenhouse effect and thus causing an ice age in the Carboniferous period.[160] In later ecosystems the carbon dioxide "locked up" in wood is returned to the atmosphere by decomposition of dead wood. However, the earliest fossil evidence of fungi that can decompose wood also comes from the Late Devonian.[161]

- The increasing depth of plants' roots led to more washing of nutrients into rivers and seas by rain. This caused algal blooms whose high consumption of oxygen caused anoxic events in deeper waters, increasing the extinction rate among deep-water animals.[160]

8.4 Land invertebrates

Animals had to change their feeding and excretory systems, and most land animals developed internal fertilization of their eggs. The difference in refractive index between water and air required changes in their eyes. On the other hand, in some ways movement and breathing became easier, and the better transmission of high-frequency sounds in air encouraged the development of hearing.[148]

The oldest known air-breathing animal is *Pneumodesmus*, an archipolypodan millipede from the Mid Silurian, about 428 Ma.[162][163] Its air-breathing, terrestrial nature is evidenced by the presence of spiracles, the openings to tracheal systems.[164] However, some earlier trace fossils from the Cambrian-Ordovician boundary about 490 Ma are interpreted as the tracks of large amphibious arthropods on coastal sand dunes, and may have been made by euthycarcinoids,[165] which are thought to be evolutionary "aunts" of myriapods.[166] Other trace fossils from the Late Ordovician a little over 445 Ma probably represent land invertebrates, and there is clear evidence of numerous arthropods on coasts and alluvial plains shortly before the Silurian-Devonian boundary, about 415 Ma, including signs that some arthropods ate plants.[167] Arthropods were well pre-adapted to colonise land, because their existing jointed exoskeletons provided protection against desiccation, support against gravity and a means of locomotion that was not dependent on water.[168]

The fossil record of other major invertebrate groups on land is poor: none at all for non-parasitic flatworms, nematodes or nemerteans; some parasitic nematodes have been fossilized in amber; annelid worm fossils are known from the Carboniferous, but they may still have been aquatic animals; the earliest fossils of gastropods on land date from the Late Carboniferous, and this group may have had to wait until leaf litter became abundant enough to provide the moist conditions they need.[148]

The earliest confirmed fossils of flying insects date from the Late Carboniferous, but it is thought that insects developed the ability to fly in the Early Carboniferous or even Late Devonian. This gave them a wider range of ecological niches for feeding and breeding, and a means of escape from predators and from unfavorable changes in the environment.[169] About 99% of modern insect species fly or are descendants of flying species.[170]

8.5 Early land vertebrates

Main articles: Tetrapod and Evolution of tetrapods
Family tree of tetrapods[172]

Acanthostega *changed views about the early evolution of tetrapods.[171]*

Tetrapods, vertebrates with four limbs, evolved from other rhipidistian fish over a relatively short timespan during the Late Devonian (370 to 360 Ma).[173] The early groups are grouped together as Labyrinthodontia. They retained aquatic, fry-like tadpoles, a system still seen in modern amphibians. From the 1950s to the early 1980s it was thought that tetrapods evolved from fish that had already acquired the ability to crawl on land, possibly in order to go from a pool that was drying out to one that was deeper. However, in 1987, nearly complete fossils of *Acanthostega* from about 363 Ma showed that this Late Devonian transitional animal had legs and both lungs and gills, but could never have survived on land: its limbs and its wrist and ankle joints were too weak to bear its weight; its ribs were too short to prevent its lungs from being squeezed flat by its weight; its fish-like tail fin would have been damaged by dragging on the ground. The current hypothesis is that *Acanthostega*, which was about 1 metre (3.3 ft) long, was a wholly aquatic predator that hunted in shallow water. Its skeleton differed from that of most fish, in ways that enabled it to raise its head to breathe air while its body remained submerged, including: its jaws show modifications that would have enabled it to gulp air; the bones at the back of its skull are locked together, providing strong attachment points for muscles that raised its head; the head is not joined to the shoulder girdle and it has a distinct neck.[171]

The Devonian proliferation of land plants may help to explain why air breathing would have been an advantage: leaves falling into streams and rivers would have encouraged the growth of aquatic vegetation; this would have attracted grazing invertebrates and small fish that preyed on them; they would have been attractive prey but the environment was unsuitable for the big marine predatory fish; air-breathing would have been necessary because these waters would have been short of oxygen, since warm water holds less dissolved oxygen than cooler marine water and since the decomposition of vegetation would have used some of the oxygen.[171]

Later discoveries revealed earlier transitional forms between *Acanthostega* and completely fish-like animals.[174] Unfortunately there is then a gap (Romer's gap) of about 30 Ma between the fossils of ancestral tetrapods and Mid Carboniferous fossils of vertebrates that look well-adapted for life on land. Some of these look like early relatives of modern amphibians, most of which need to keep their skins moist and to lay their eggs in water, while others are accepted as early relatives of the amniotes, whose waterproof skin enables them to live and breed far from water.[172]

9 Dinosaurs, birds and mammals

Main articles: Dinosaur evolution, Origin of Birds and Evolution of mammals
Possible family tree of dinosaurs, birds and mammals[176][177]

Amniotes, whose eggs can survive in dry environments, probably evolved in the Late Carboniferous period (330 to 298.9 Ma). The earliest fossils of the two surviving amniote groups, synapsids and sauropsids, date from around 313 Ma.[176][177] The synapsid pelycosaurs and their descendants the therapsids are the most common land vertebrates in the best-known Permian (298.9 to 252.17 Ma) fossil beds. However at the time these were all in temperate zones at middle latitudes, and there is evidence that hotter, drier environments nearer the Equator were dominated by sauropsids and amphibians.[178]

The Permian-Triassic extinction wiped out almost all land vertebrates,[179] as well as the great majority of other life.[180] During the slow recovery from this catastrophe, estimated to have taken 30 million years,[181] a previously obscure sauropsid group became the most abundant and diverse terrestrial vertebrates: a few fossils of archosauriformes ("ruling lizard forms") have been found in Late Permian rocks,[182] but, by the Mid Triassic, archosaurs were the dominant land vertebrates. Dinosaurs distinguished themselves from other archosaurs in the Late Triassic, and became the dominant land vertebrates of the Jurassic and Cretaceous periods (201.3 to 66 Ma).[183]

During the Late Jurassic, birds evolved from small, predatory theropod dinosaurs.[184] The first birds inherited teeth and long, bony tails from their dinosaur ancestors,[184] but some had developed horny, toothless beaks by the very Late Jurassic[185] and short pygostyle tails by the Early Cretaceous.[186]

While the archosaurs and dinosaurs were becoming more dominant in the Triassic, the mammaliaform successors of the therapsids evolved into small, mainly nocturnal insectivores. This ecological role may have promoted the evolution of mammals, for example nocturnal life may have accelerated the development of endothermy ("warm-bloodedness") and hair or fur.[187] By 195 Ma in the Early Jurassic there were animals that were very like today's mammals in a number of respects.[188] Unfortunately there is a gap in the fossil record throughout the Mid Jurassic.[189] However fossil teeth discovered in Madagascar indicate that the split between the lineage leading to monotremes and the one leading to other living mammals had occurred by 167 Ma.[190] After dominating land vertebrate niches for about 150 Ma, the dinosaurs perished in the Cretaceous–Paleogene extinction (66 Ma) along with many other groups of organisms.[191] Mammals throughout the time of the dinosaurs had been restricted to a narrow range of taxa, sizes and shapes, but increased rapidly in size and diversity after the extinction,[192][193] with bats taking to the air within 13 Ma,[194] and cetaceans to the sea within 15 Ma.[195]

10 Flowering plants

Main articles: Flowering plant and Gymnosperm

The first flowering plants appeared around 130 million years ago.[198] The 250,000 to 400,000 species of flowering plants outnumber all other ground plants combined, and are the dominant vegetation in most terrestrial ecosystems. There is fossil evidence that flowering plants diversified rapidly in the Early Cretaceous, from 130 to 90 Ma,[196][197] and that their rise was associated with that of pollinating insects.[197] Among modern flowering plants Magnolias are thought to be close to the common ancestor of the group.[196] However paleontologists have not succeeded in identifying the earliest stages in the evolution of flowering plants.[196][197]

11 Social insects

These termite mounds have survived a bush fire.

Main article: Social insects

The social insects are remarkable because the great majority of individuals in each colony are sterile. This appears contrary to basic concepts of evolution such as natural selection and the selfish gene. In fact there are very few eusocial insect species: only 15 out of approximately 2,600 living families of insects contain eusocial species, and it seems that eusociality has evolved independently only 12 times among arthropods, although some eusocial lineages have diversified into several families. Nevertheless social insects have been spectacularly successful; for example although ants and termites account for only about 2% of known insect species, they form over 50% of the total mass of insects. Their ability to control a territory appears to be the foundation of their success.[199]

The sacrifice of breeding opportunities by most individuals has long been explained as a consequence of these species' unusual haplodiploid method of sex determination, which has the paradoxical consequence that two sterile worker daughters of the same queen share more genes with each other than they would with their offspring if they could breed.[200] However Wilson and Hölldobler argue that this explanation is faulty: for example, it is based on kin selection, but there is no evidence of nepotism in colonies that have multiple queens. Instead, they write, eusociality evolves only in species that are under strong pressure from predators and competitors, but in environments where it is possible to build "fortresses"; after colonies have established this security, they gain other advantages through co-operative foraging. In support of this explanation they cite the appearance of eusociality in bathyergid mole rats,[199] which are not haplodiploid.[201]

The earliest fossils of insects have been found in Early Devonian rocks from about 400 Ma, which preserve only a few varieties of flightless insect. The Mazon Creek lagerstätten from the Late Carboniferous, about 300 Ma, include about 200 species, some gigantic by modern standards, and indicate that insects had occupied their main modern ecological niches as herbivores, detritivores and insectivores. Social termites and ants first appear in the Early Cretaceous, and advanced social bees have been found in Late Cretaceous rocks but did not become abundant until the Mid Cenozoic.[202]

12 Humans

Main article: Human evolution

The idea that, along with other life forms, modern-day humans evolved from an ancient, common ancestor was proposed by Robert Chambers in 1844 and taken up by Charles Darwin in 1871.[203] Modern humans evolved from a lineage of upright-walking apes that has been traced back over 6 Ma to *Sahelanthropus*.[204] The first known stone tools were made about 2.5 Ma, apparently by *Australopithecus garhi*, and were found near animal bones that bear scratches made by these tools.[205] The earliest hominines had chimp-sized brains, but there has been a fourfold increase in the last 3 Ma; a statistical analysis suggests that hominine brain sizes depend almost completely on the date of the fossils, while the species to which they are assigned has only slight influence.[206] There is a long-running debate about whether modern humans evolved all over the world simultaneously from existing advanced hominines or are descendants of a single small population in Africa, which then migrated all over the world less than 200,000 years ago and replaced previous hominine species.[207] There is also debate about whether anatomically modern humans had an intellectual, cultural and technological "Great Leap Forward" under 100,000 years ago and, if so, whether this was due to neurological changes that are not visible in fossils.[208]

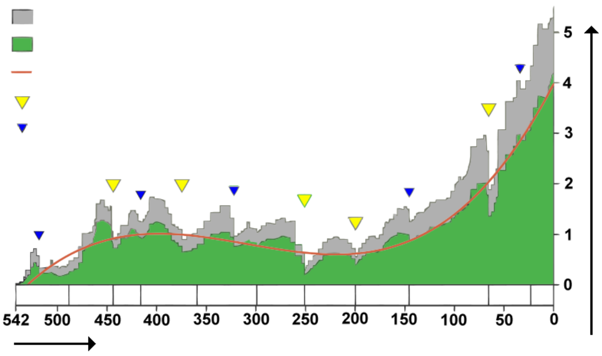
13 Mass extinctions

Main article: Mass extinction
Marine extinction intensity during the Phanerozoic eon
%
Millions of years ago
K–Pg
Tr–J
P–Tr
Late D
O–S
Apparent extinction intensity, i.e. the fraction of genera going extinct at any given time, as reconstructed from the fossil record. (Graph not meant to include recent epoch of Holocene extinction event)

Life on Earth has suffered occasional mass extinctions at least since 542 Ma. Although they were disasters at the time, mass extinctions have sometimes accelerated the evolution of life on Earth. When dominance of particular ecological niches passes from one group of organisms to another, it is rarely because the new dominant group is "superior" to the old and usually because an extinction event eliminates the old dominant group and makes way for the new one.[22][209]

The fossil record appears to show that the gaps between mass extinctions are becoming longer and the average and background rates of extinction are decreasing. Both of these phenomena could be explained in one or more ways:[210]

- The oceans may have become more hospitable to life over the last 500 Ma and less vulnerable to mass extinctions: dissolved oxygen became more widespread and penetrated to greater depths; the development of life on land reduced the run-off of nutrients and hence the risk of eutrophication and anoxic events; and marine ecosystems became more diversified so that food chains were less likely to be disrupted.[211][212]
- Reasonably complete fossils are very rare, most extinct organisms are represented only by partial fossils, and complete fossils are rarest in the oldest rocks. So paleontologists have mistakenly assigned parts of the same organism to different genera, which were often defined solely to accommodate these finds – the story of *Anomalocaris* is an example of this. The risk of this mistake is higher for older fossils because these are often unlike parts of any living organism. Many of the "superfluous" genera are represented by fragments which are not found again and the "superfluous" genera appear to become extinct very quickly.[210]



All genera
"Well-defined" genera
Trend line
"Big Five" mass extinctions
Other mass extinctions
Million years ago
Thousands of genera
Phanerozoic biodiversity as shown by the fossil record

Biodiversity in the fossil record, which is

> "the number of distinct genera alive at any given time; that is, those whose first occurrence predates and whose last occurrence postdates that time"[213]

shows a different trend: a fairly swift rise from 542 to 400 Ma; a slight decline from 400 to 200 Ma, in which the devastating Permian–Triassic extinction event is an important factor; and a swift rise from 200 Ma to the present.[213]

14 See also

- Constructal law
- Evolution
- Evolution of mammals
- Evolution of sexual reproduction
- Evolutionary history of plants
- Evolution of viruses
- History of evolutionary thought
- *On the Origin of Species*
- Speciation
- Taxonomy of commonly fossilised invertebrates
- Timeline of evolutionary history of life
- Treatise on Invertebrate Paleontology

15 Footnotes

[1] Name given as in Butterfield's paper "*Bangiomorpha pubescens* ..." (2000). A fossil fish, also from China, has also been named *Qingshania*. The name of one of these will have to change.

[2] Myxozoa were thought to be an exception, but are now thought to be heavily modified members of the Cnidaria: Jímenez-Guri, E., Philippe, H., Okamura, B. and Holland, P. W. H. (July 2007). "*Buddenbrockia* is a cnidarian worm". *Science* **317** (116): 116–118. Bibcode:2007Sci...317..116J. doi:10.1126/science.1142024. PMID 17615357. Retrieved 2008-09-03.

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17 Further reading

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18 External links

General information

- General information on evolution- Fossil Museum nav.
- Understanding Evolution from University of California, Berkeley
- National Academies Evolution Resources
- Evolution poster- PDF format "tree of life"
- Everything you wanted to know about evolution by *New Scientist*
- Howstuffworks.com — How Evolution Works
- Synthetic Theory Of Evolution: An Introduction to Modern Evolutionary Concepts and Theories

History of evolutionary thought

- The Complete Work of Charles Darwin Online
- Understanding Evolution: History, Theory, Evidence, and Implications

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19.1 Text

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