



The Science Authority

Paleontology

Article by:

Brett, Carlton E. Department of Geological Sciences, University of Rochester, Rochester, New York.**Gould, Stephen J.** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

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The study of life history as recorded by fossil remains. The term fossil, from the Latin “*fossilis*” (digging; dug up), originally referred to a variety of objects dug from the Earth, some of which were believed to be supernatural substances imbued with mystical powers. However, in a modern context, fossils can be defined as recognizable remains or traces of activity of prehistoric life. This broad definition takes in a diversity of ancient remains, but specifically excludes inorganic, mineralized structures, even those that spuriously resemble life forms (for example, dendritic patterns of manganese crystals: dendrites), sometimes termed pseudofossils (false fossils). See also: [Fossil \(/content/fossil/270100\)](#)

The definition also makes several qualifying statements: Fossils must be recognizably tied to once-living organisms, excluding amorphous organic matter such as coal and petroleum (but see information on biomarkers below), although these are certainly derived from the products of organisms and sometimes referred to as “fossil fuels.” The definition also encompasses two broad categories of fossils: (a) remains that are primarily skeletal hard parts (body fossils) and (b) traces of activity that is evidence of behavior of living organisms (trace fossils). The latter can be broadly construed to include tracks, trails, burrows, borings, bite and gnaw marks, and even fecal remains (coprolites) and gizzard stones (gastroliths) polished in the digestive activity of dinosaurs. In addition, certain organisms, especially bacteria, archaea, algae, and vascular plants, produce distinctive and unique organic molecules, whose degraded remnants can be extracted from sediments and isolated. These biomarkers form a type of chemical fossil, whose potential for reconstruction of ancient life has only recently been realized. See also: [Paleobiochemistry \(/content/paleobiochemistry/483100\)](#)

The term prehistoric is also a key part of the definition of fossils: remains of recent animals and plants are not considered as fossils simply because they are not old enough; paleontologists commonly use, as an arbitrary definition of “prehistoric,” the approximate end of the last glacial advance, about 10,000 years before the present (BP). In some cases, ancient organism remains that are somewhat less than 10,000 years old are termed “subfossils.”

Artifacts made by people, however, are not termed fossils, for these constitute the data of the related science of archeology, the study of human civilizations. See also: [Archeology \(/content/archeology/047900\)](#)

The fossil record thus includes a very diverse class of objects ranging from molds of microscopic bacteria in rocks more than 3×10^9 years old to unaltered bones of fossil humans in ice-age gravel beds formed only a few thousand years ago. The

quality of preservation ranges from the occasional occurrence of soft parts (skin and feathers, for example) to barely decipherable impressions made by shells in soft mud that later hardened to rock.

The most common fossils are hard parts of various animal groups. Thus, the fossil record is not an accurate account of the complete spectrum of ancient life, but is biased in overrepresenting those forms with shells or skeletons. Fossilized worms are extremely rare, but it is not valid to make the supposition that worms were any less common in the geologic past than they are now.

Paleontology lies on the boundary between two disciplines, biology and geology. The field of paleontology has been subdivided in various ways. A distinction can be made between paleozoology (invertebrate and vertebrate paleontology) and paleobotany (study of fossil plants, algae, and bacteria). Micropaleontology deals with all of those fossils that must be studied with microscopes, including compound light and scanning electron microscopes (SEM). This field unites a highly varied series of fossil groups, including shelled protists such as radiolaria and foraminifera, tiny skeletons of planktonic diatoms, and coccoliths (the latter two sometimes referred to as nannofossils in recognition of their extremely small size), as well as conodonts (minute toothlike fossils that formed parts of the feeding apparatuses in early eel-like chordates). Because of their tiny size and great abundance in small samples, microfossils have traditionally been the most economically valuable fossils; many micropaleontologists have been employed by petroleum companies to aid in identification of particular stratigraphic levels, including those bearing petroleum. Most invertebrate paleontologists are employed in geology departments, where they are involved in a wide array of stratigraphic, paleobiological, and paleoenvironmental studies. Conversely, many vertebrate paleontologists are allied with biology or even medical departments because of their studies of vertebrate skeletal anatomy and evolution. Paleobotanists are traditionally plant anatomists, employed in botany departments. Palynology involves the study of organic-walled microfossils, such as pollen and spores, but also including enigmatic marine microfossils such as acritarchs (algal resting cysts of uncertain affinities) and chitinozoans (possible egg capsules of Paleozoic organisms). However, much modern paleontology defies simple categorization and is more commonly classified along lines reflecting application of fossil data in various disciplines; these include taxonomy/systematics, biostratigraphy, taphonomy, paleoecology/paleoenvironmental studies, biogeography, paleobiology, and evolutionary studies ([Fig. 1](#)). See also: [Biology \(/content/biology/083100\)](#); [Geology \(/content/geology/286600\)](#); [Micropaleontology \(/content/micropaleontology/423200\)](#); [Palynology \(/content/palynology/484800\)](#)

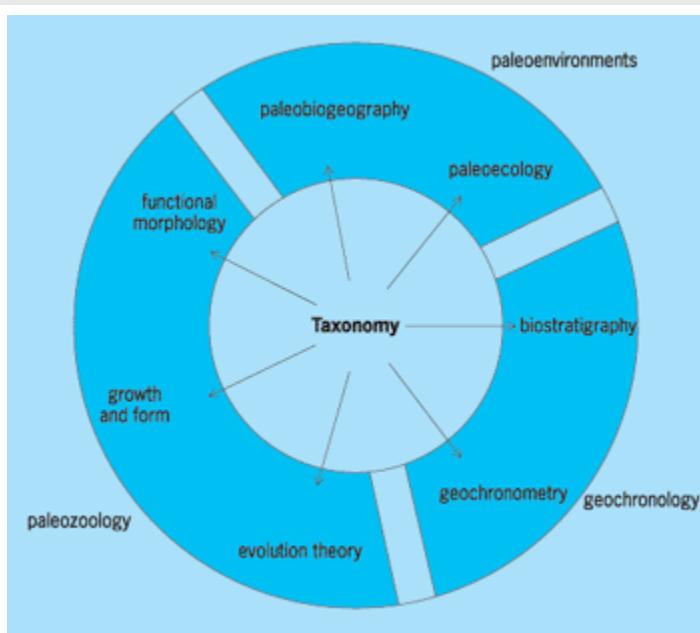


Fig. 1 Divisions of the field of paleontology. (Modified from Clarkson, 1993, with permission of Springer Science and Business Media)

Applications of Paleontology

Some of the key applications of paleontology are listed below.

Systematics and taxonomy

The classification of fossil species into a hierarchical grouping of taxa is usually based on similarities in morphological characters. Many thousands of fossil species have been described and hundreds more are discovered and described each year; it has been estimated that the known fossil record comprises only 1–5% of the total number of easily preservable organisms that once lived on Earth. Beyond the very necessary, if mundane, description, illustration, and naming of new species lies the more challenging exercise of arranging these species into a classification that reflects evolutionary relationships or phylogeny. Several different approaches to classification have been used by paleontologists. Traditional classifications and most current ones use a modified Linnean classification, a hierarchy of nested categories beginning with the species, defined qualitatively based on overall similarities of body (or skeletal) morphology. Species in turn are grouped into related groups, genera; genera into families; families into orders; orders into classes; classes into phyla; and phyla into the very largest taxa, kingdoms: Archaea, Eubacteria, Plantae, Fungi, and Metazoa (Animalia). Additional categories are possible using prefixes sub-, super-, infra-, etc. (for example, subfamily). In phenetics, that is, numerical taxonomic procedures, taxa are grouped quantitatively, based upon overall similarity of measurable parameters (for example, length and width). Another approach, which has gained much momentum in recent years, is cladistics or phylogenetic systematics, which attempts to group taxa into dichotomous trees based upon shared possession of unique features. This cladistic approach has, in many ways, made the study of systematics more objective and rigorous. Such classifications take into account a number of characters to arrive at the most parsimonious or simplest trees of relationships between taxa and their sister taxa. See also: [Numerical taxonomy \(/content/numerical-taxonomy/461900\)](#); [Phylogeny \(/content/phylogeny/513300\)](#); [Systematics \(/content/systematics/036000\)](#); [Taxonomy \(/content/taxonomy/679400\)](#)

Evolutionary paleontology

Increasingly, systematic paleontologists are also interfacing their studies of phylogeny based on the morphology of ancient

organisms with supplemental techniques, based on the biochemistry of living organisms. For example, biologists have long examined the early development of organisms or embryology for clues as to deep relationships among groups of animals. Biologists have developed techniques to determine relationships among various living taxa based on similarities of portions of their DNA or complex molecules such as proteins and hemoglobin. Measures of molecular distance between any two living species can give a sense of how closely related the two are, independently of their external form or morphology. Using these techniques, together with cladistics, paleobiologists and molecular biologists have come to some radical new interpretations of the tree of life. For example, molecular studies have established that tiny, nonnucleated (prokaryotic) cells once assigned to bacteria actually belong to two different kingdoms: Eubacteria and Archaea. Molecular-cladistic studies have also revised our perceptions of the family tree of animals—for example, suggesting that annelid worms and mollusks are closely related, while the great phylum Arthropoda, once thought to be a sister group to annelids, may be more closely related to nematodes (roundworms). Moreover, molecular biologists have found evidence that the base pairs in some strands of DNA undergo mutations in a stochastic manner, somewhat akin to radioactive decay. On this basis, they postulate that changes in DNA structure occur in a regular clock-like, time-governed manner. If so, the total amount of difference between the DNA of any two related species or other taxa can be used to calculate the amount of time that has elapsed since the two taxa diverged from a common ancestor. Although this technique makes some major assumptions, it provides a method, independent of paleontology, for determining the timing of evolutionary branching. Moreover, while there are some significant discrepancies, many of the newer estimates in fact agree with the known fossil record.

Biostratigraphy

A major task of any historical science, such as geology, is to arrange events in a time sequence and to describe them as fully as possible. Arguably the most applied field of paleontology and its traditional linkage with geology is in the field of biostratigraphy. This field employs a principle established in the early 1800s by British engineer William Smith: the principle of “faunal and floral succession,” that is, suites of particular, unique fossil species are typical of successive time intervals. Geology, the study of Earth history, did not become a modern science until the nineteenth century, when a worldwide time scale based on fossils was established; Earth history could not be deciphered until events that occurred in different places were related to one another by their position in a standard time sequence ([Fig. 2](#)).

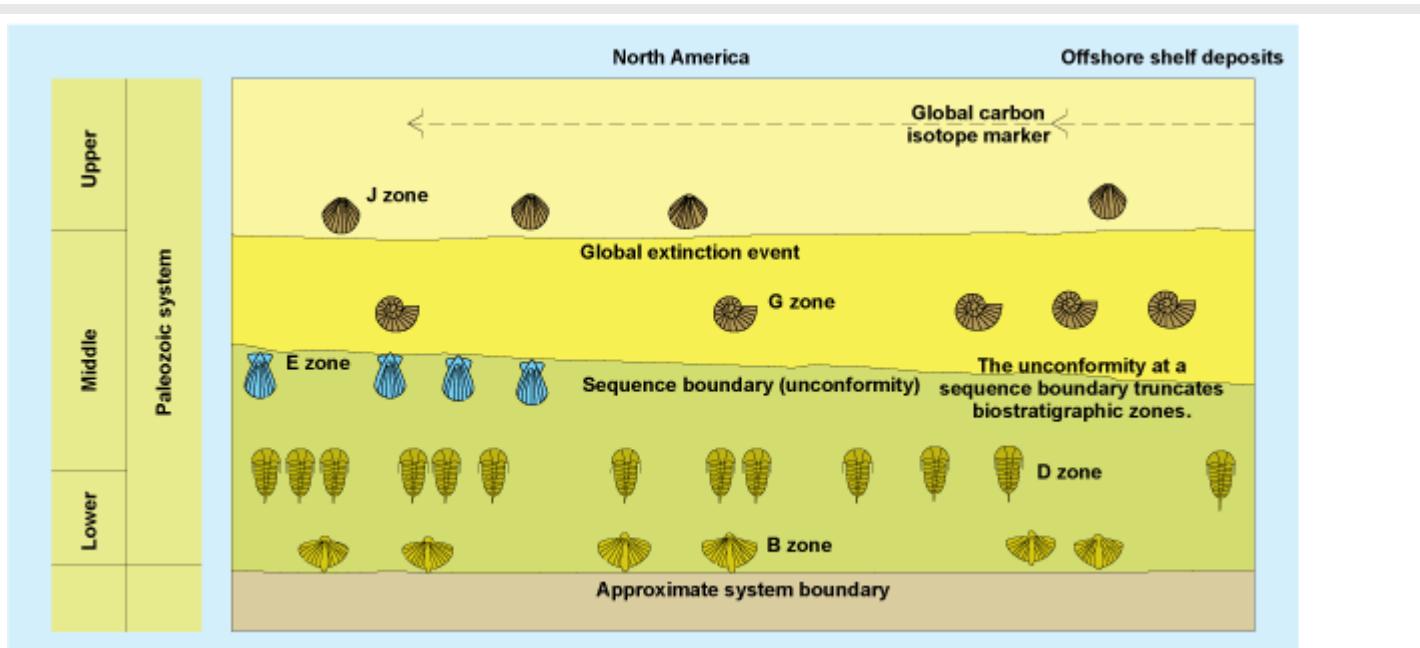


Fig. 2 Biostratigraphy, the use of fossils in identifying the age of particular stratigraphic levels. Note that certain types of fossils are characteristic of given levels that are assumed to be age-equivalent. (Adapted from Stanley, 2005)

Because of evolution, there is no recurrence of species in later rocks; hence fossils provide an arrow of time: unambiguous markers of increments of relative time known as biozones. Certain fossils are more useful in this pursuit than others and these form biostratigraphic guide or index fossils; these include groups that are abundant, geographically widespread, environmentally tolerant, and rapidly evolving. While few types of organisms share all of these traits, certain groups, such as free-swimming and planktonic organisms (for example, some foraminifera, graptolites, ammonoids, and conodonts), meet most criteria and are among the most widely used zonal fossils. The primary procedures of biostratigraphy involve establishing the ranges of species and using these index fossils to correlate rocks of similar age in different locations. In some cases, the precision of correlation can be improved by using overlapping ranges of several species, or assemblages of fossils. Correlations also can be improved by methods called graphic correlation in which the first and last appearances of many species in two or more sections are plotted against one another. Biostratigraphy is now commonly melded with other techniques for correlation, including studies of event beds and cycles, and geochemical stratigraphy, as in correlation of carbon-isotopic excursions (see below). See also: [Index fossil \(/content/index-fossil/340600\)](#); [Stratigraphy \(/content/stratigraphy/659000\)](#)

Taphonomy

The field of taphonomy deals with the processes of fossil preservation both prior to (biostratinomy) or after burial (fossil diagenesis). Paleontologists pursuing studies of taphonomy may study the rates and processes of decay, disarticulation, breakage, abrasion, and disintegration of organisms and the compaction and mineralization of their remains. The objectives of taphonomy are twofold: First, by studying processes that affect potential fossil assemblages in modern times, it is possible to recognize the extent of biases of the fossil record in different environments. Second, fossils, as sedimentary particles, provide very important clues to many physical and chemical processes in ancient environments. For example, shallow-water, high-energy environments yield heavily fragmented and abraded skeletal remains, whereas muddy bottoms in deeper-water areas may preserve delicate shells and articulated crabs or sea urchins. See also: [Taphonomy \(/content/taphonomy/1677950\)](#)

Trace fossil studies (ichnology)

The realm of ichnology deals with trace fossils and their interpretation. This field together with taphonomy interfaces closely with sedimentology, as most trace fossils are in one sense literally a part of the sediments or organic sedimentary structures. Trace fossils have proven to be very useful as indicators of depositional environments. The size, depth, and diversity of traces may indicate the level of oxygen in marine bottom waters; the degree of deformation or sharpness of burrows is an indicator of sediment firmness and degree of compaction; and distinctive trace fossil assemblages may provide a proxy for water depth. In addition, of course, traces provide a direct record of the behavior of ancient organisms and may be useful in identifying patterns of locomotion, sediment feeding, and even predator-prey relationships. See also: [Trace fossils \(/content/trace-fossils/703400\)](#)

Paleoecology and paleoenvironmental analysis

Paleoecology is the ecology of ancient organisms: that is, their modes of life and interactions with physical and biotic environments. Modes of life of ancient organisms are reconstructed on the basis of biological information from closely related living analogs, functional morphology (function of skeletal parts inferred from detailed studies of their form) of the fossils themselves, and association with sediments or other fossils, which give environmental information ([Fig. 3](#)).

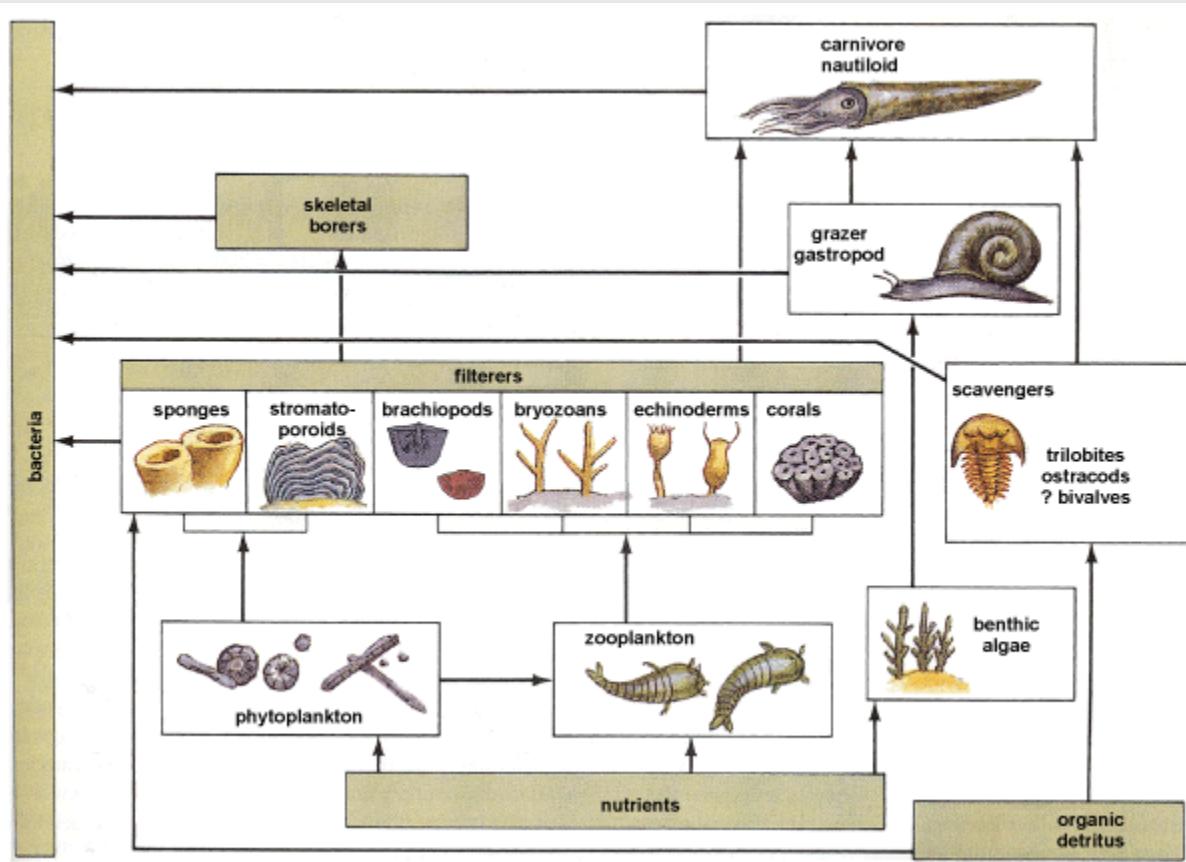


Fig. 3 Paleoecology of fossil organisms. A food web reconstructed for the Ordovician marine community showing inferred modes of life of various organisms found as fossils. (Adapted from Prothero and Dott, 2004)

Environments are reconstructed using multiple sources of data from sedimentary rocks including the sediments themselves (grain size, texture, color), sedimentary structures (for example, mud cracks, ripple marks), trace fossils, taphonomy of fossils, and geochemistry of sediments and fossils. In some instances, particularly with relatively recent fossils, knowledge of the environmental tolerances of modern species can be used to infer the environments of the same or closely related fossil species. Other, less direct applications of fossil data may be extremely useful in inferring ancient environmental parameters. For example, the forms of coral skeletons are commonly reflective of the energy of the environment in which they grew. See also: [Paleoecology \(/content/paleoecology/483700\)](#)

Paleoclimatology

Fossils provide very significant clues to ancient climates. The presence of growth rings in ancient woods, for example, provides evidence of seasonality, and the shapes of tree leaves prove to be a sensitive gauge of temperature. For reasons that are still unclear, leaves with smooth margins are typical of warmer climates, while those with ragged or serrated margins typify cooler temperatures. The ratio of the two leaf types can be used to hindcast ancient mean annual temperatures to within 1°C. In a similar way, the coiling directions, left-hand versus right-hand, in certain planktonic foraminifera (shelled protozoans) are temperature-dependent (more left-handed coiling in cooler temperatures) and the left-right ratio can be used to hindcast temperatures accurately, at least for the last few million years.

Furthermore, the geochemistry of fossil skeletons may encode information about paleotemperatures. For example, the oxygen isotopic ratios ($^{18}\text{O}/^{16}\text{O}$) of calcium carbonate (calcite or aragonite) of normal marine shells are dependent upon the temperature at which they were secreted. Thus, the $^{18}\text{O}/^{16}\text{O}$ ratio may be utilized indirectly to reconstruct the temperature of the water from which they were secreted. See also: [Paleoclimatology \(/content/paleoclimatology/483500\)](#)

Paleogeography

Fossils are indispensable guides for determining the positions of continents and seas in former times. Organisms isolated by barriers such as deep ocean basins evolve, although in some cases with parallel evolution to those in other areas, leading to geographically distinct provinces. The history of changing fossil assemblages provides evidence for the development and breakdown of barriers. The formation of the Isthmus of Panama can be dated, for example, by studying the distributions of marine and terrestrial fossils. Before North and South America were connected by this land bridge, Atlantic and Pacific marine faunas were very similar, but the mammals of the two continents were completely different. However, in South American rocks deposited after the Isthmus was formed, there are fossils of North American mammals, which had migrated over the newly formed land. Likewise, Atlantic and Pacific marine faunas, isolated from each other by the rise of the Isthmus, began to evolve in different directions; this increasing difference can be traced in the fossils of successively younger rocks. Fossils also provide evidence that continental drift has occurred. If South America and Africa were once united, their faunas should be similar during that time. As they drifted apart, there should be stronger and stronger faunal differences. See also:

Paleogeography (</content/paleogeography/483800>)

Biological Aspects

Some of the key biological aspects of paleontology are given below.

Evolutionary process and life history

The most fundamental fact of paleontology is that organisms have changed throughout the history of Earth and that each geological period has had its characteristic forms of life. When Charles Darwin published his theory of evolution in 1859, paleontological evidence for evolution was meager, but it began to accumulate quickly. The “feathered reptile” (*Archaeopteryx*), an almost perfect link between dinosaurs and birds, was discovered early in the 1860s and the first fossil humans were found a few years later. In the light of this evidence and the purview of a more scientific culture, evolution was accepted as the only reasonable explanation for change in the history of life. To a paleontologist, life's outstanding attribute is its evolution (**Fig. 4**).

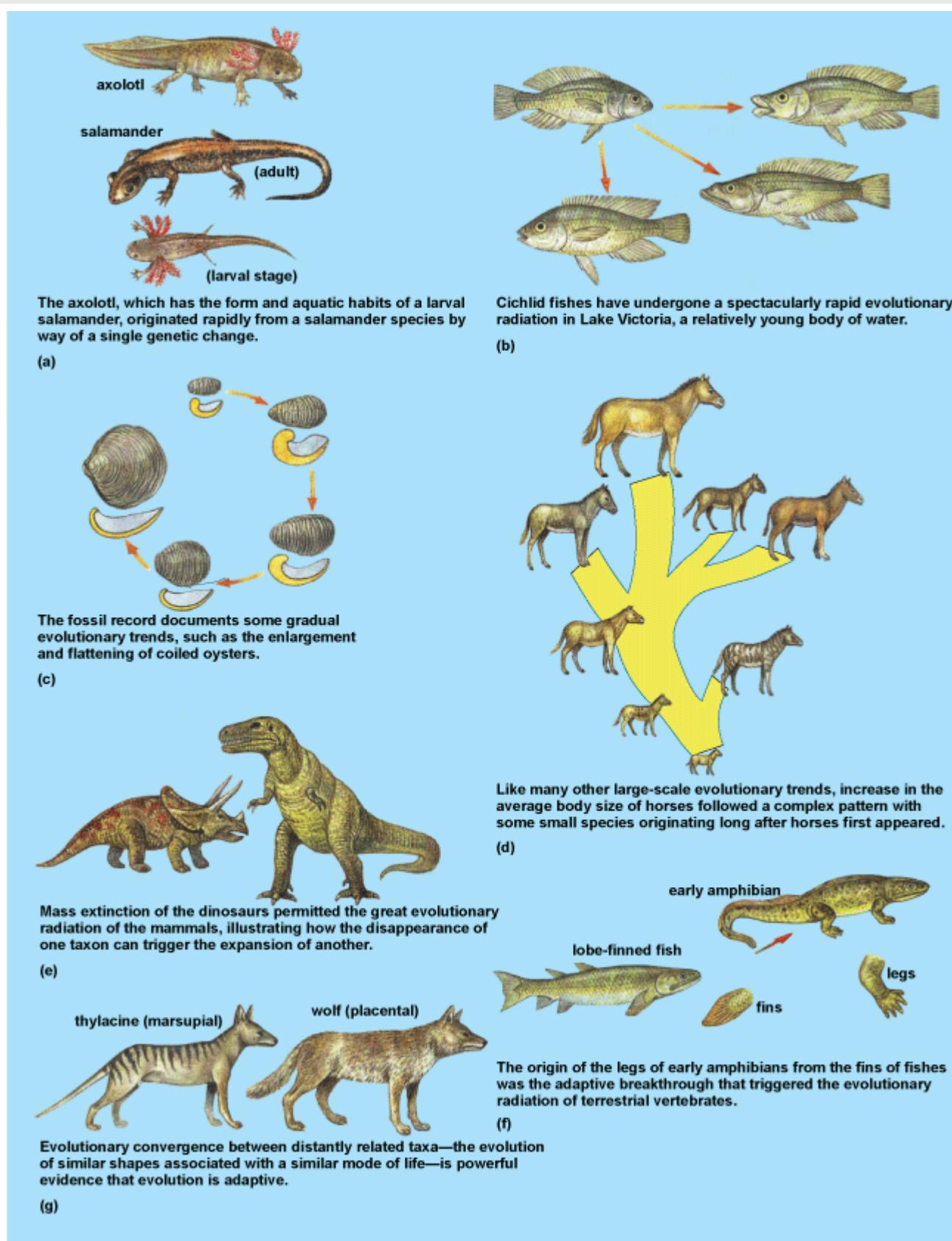


Fig. 4 Processes of evolution. (a) Heterochrony illustrated by the retention of larval features (neoteny) in evolution of the axolotl with adult gills from a normal salamander; (b) adaptive radiation of specialized descendants from a common ancestor; (c) gradual evolutionary trends in fossil oysters; (d) branching evolutionary patterns involving cladogenesis in horse evolution; note brushy rather than straight-line evolutionary patterns; (e) mass extinction illustrated by the Cretaceous/Tertiary boundary extinction; (f) adaptive transition involving modification (exaptation) of tetrapod limbs from lobed fins of fish; (g) evolutionary convergence (parallelism) in marsupial and placental mammals. (Adapted from Stanley, 2005)

An evolutionist has two major interests: first, to know how the process of evolution works, which is accomplished largely by

studying the genetics and population structure of modern organisms; second, to reconstruct the events produced by this process, that is, to trace the history of life. This is the paleontologist's exclusive domain. Any modern animal group is merely a stage, frozen at one moment in time, of a dynamic, evolving lineage. Fossils give the only direct evidence of previous stages in these lineages. Horses and rhinoceroses, for example, are very different animals today, but the fossil history of both groups is traced to a single ancestral species that lived early in the Cenozoic Era. From such evidence, a tree of life can be constructed whereby the relationships among organisms can be understood. See also: [**Organic evolution \(/content/organic-evolution/475150\)**](#)

Life properties

Evolution is responsible for life's outstanding properties: its diversity and its adaptation to environment.

Diversity

A paleontologist studies diversity. Then, the number and geographic distribution of species in a more inclusive taxonomic group, such as vertebrates, can be tabulated for different periods of geologic history. When this is done for all major groups, very definite patterns emerge. Life history shows both periods of rapid diversification—evolutionary radiations—and brief intervals of rapid diversity decline—mass extinctions. At the close of the Permian and Cretaceous periods, for example, extensive extinction of species occurred in many major groups at about the same time ([**Fig. 5**](#)). These are major events in the history of life, and their causes have provided a major research agenda for paleontology. For example, the Cretaceous-Tertiary extinction has proven to be associated with abundant geochemical and sedimentary evidence for a major bolide (large meteor) impact on Earth, probably recorded in the Chixulub Crater in the Yucatan Peninsula. Many other causes have been invoked for various mass extinctions including rapid sea-level and climatic changes, low oxygen, and extensive volcanism. Evolutionary radiations may have resulted from new adaptive breakthroughs, such as the evolution of legs and lungs in lobe-finned fishes, environmental triggers such as increased levels of atmospheric oxygen, or the availability of adaptive “niche space” as occurred in the Cambrian or following mass extinctions. See also: [**Biodiversity \(/content/biodiversity/757491\)**](#)

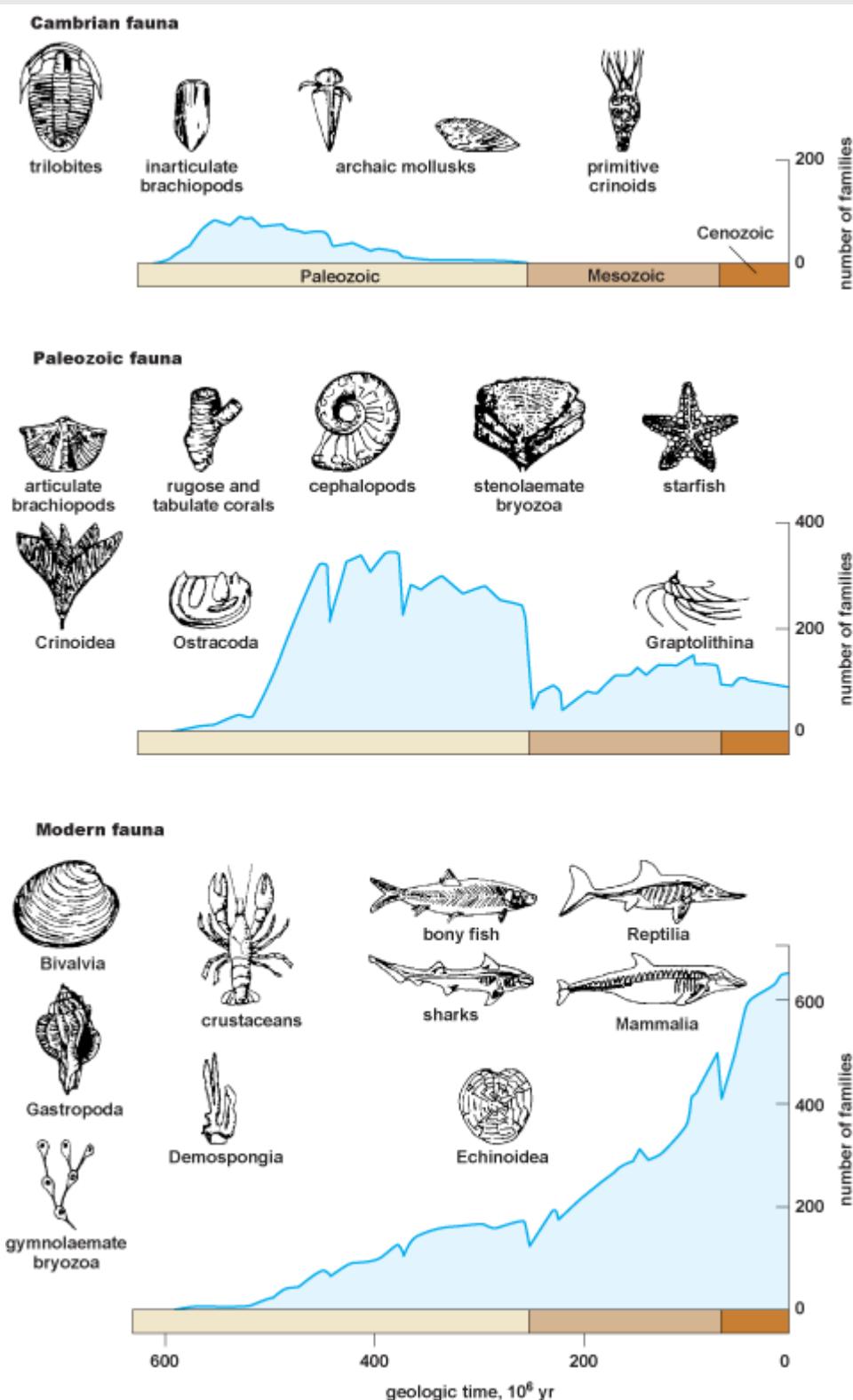


Fig. 5 Patterns of diversity of families of marine organisms through the Phanerozoic (last 543 million years). Note the major drops in diversity at the end of the Ordovician, Late Devonian, Permian/Triassic, Late Triassic, and Cretaceous that correspond to the major mass extinctions of Phanerozoic life history. The individual diagrams show patterns for the Cambrian fauna dominated by trilobites; the Paleozoic fauna dominated by brachiopods, bryozoans, crinoids, and rugose and tabulate corals; and the Modern fauna dominated by mollusks and crustaceans. (Adapted from Prothero and Dott, 2004)

Long-term rates of evolution

The fossil record provides information on the often linked rates of evolution and extinction of various large groups of organisms. Vertebrate paleontologist George Gaylord Simpson determined the average rates of taxonomic turnover of many

different taxonomic groups of animals and found that various taxa have characteristic rates of change and that certain groups evolve much more rapidly than others. Rapidly evolving taxa include mammals and ammonites; conversely, other groups such as horseshoe crabs and lingulid brachiopods evolve slowly and provide excellent examples of living fossils, extant organisms that have changed very little in millions of years. Many slowly evolving groups either have very generalized modes of life or live in protected environments, but just why different groups show such varying rates of change is one of the great mysteries of paleontology. See also: [Living fossils \(/content/living-fossils/387600\)](#)

Large-scale patterns and processes

Fossils also provide very important insights into large-scale evolutionary patterns that cannot be studied with modern organisms. New species may arise by one of two processes: (a) anagenesis, or gradual change within a lineage or evolving line of populations, such as the increase in size in successively younger populations of fossil oysters ([Fig. 4c](#)); or (b) cladogenesis (speciation), or splitting of a species into two or more distinct species, typically following geographic isolation ([Fig. 4d](#)). One of the most important observations about the fossil record is that, counter to the predictions of Darwin, many species arise geologically rapidly, probably during cladogenesis, but then show stasis—little or no change—for much of their history. This staccato pattern of evolution was referred to as punctuated equilibrium by paleontologists Niles Eldredge and Stephen Jay Gould. This pattern has proven to be very common, especially in many marine invertebrate animals, and it suggests that most evolutionary change occurs during short bursts associated with cladogenesis.

Long-term trends commonly observed in the fossil record include pattern convergence—the independent evolution of similar adaptations in distantly related groups of organisms.

Adaptation and exaptation

The term adaptation refers to the way that organic form is fitted to function ([Fig. 4](#)). According to Darwinian evolution, this fit is shaped by natural selection, actually the elimination of suboptimal features and the accumulation, by default, of mutations or changes that promote survival or reproduction. Given the raw materials of life, an engineer could scarcely design a better flying machine than a bird, yet the bird evolved naturally from reptilian ancestors, which did not fly. As Darwin realized, however, it is the imperfections and oddities of nature that provide the best insights into evolution. Some features seen in fossil and living organisms are vestigial, such as the side splint bones in horses' hoofs, which as tracked through the fossil record are evidently remnants of once functional side toes. The sources of adaptive features are also varied, but constrained by evolutionary history. Many seemingly new features may appear abruptly simply by accelerating or slowing down development of existing features, a process referred to as heterochrony. For example, simple parasitic organisms may evolve by greatly accelerating their rates of reproductive maturation; alternatively, the proportions of the adult human cranium resemble those of juvenile great apes, suggesting that it may have evolved by retention of juvenile-like features into adulthood; both of these represent examples of paedomorphosis: adults of descendants are juvenile-like adults compared to their ancestors. See also: [Heterochrony \(/content/heterochrony/757301\)](#)

Other adaptations arise from preexisting structures that were present as nonfunctional side products of evolution or were initially adapted to other functions. For example, the bamboo stripping “thumbs” of pandas are actually a modified element of their wrist bones. Such exaptations are undoubtedly very common in evolution ([Fig. 4f](#)).

Paleontologists study the development of new adaptations by a variety of techniques. For example, consider the increase in brain-size between apelike ancestors and modern humans. To study this, a paleontologist employs the following: (1) studying the rocks in which fossil bones are found to look for signs of any environmental change that might have made increased brain-size advantageous; (2) determining the advantages of a larger brain, if possible; for example, it may, among other things, have conferred upon ancient humans the ability to learn to control fire for warmth and cooking (charred bones of

edible animals in caves inhabited by ancient humans could be used as evidence for such an assertion); and (3) applying mathematical techniques to obtain a precise measurement of the rate of evolution. See also: [Adaptation \(biology\) \(/content/adaptation-biology/009800\)](#); [Extinction \(biology\) \(/content/extinction-biology/249000\)](#); [Speciation \(/content/speciation/641200\)](#)

Sketch of life history

The range of life forms represented in the fossil record is extraordinarily broad from simple microbes and their biomarkers to complex vertebrates, but can be subdivided into realms: the marine and terrestrial ecosystems.

Marine ecosystem

Life on Earth probably originated in the early ocean, and possibly in mid-oceanic rifts, nearly 4 billion years ago ([Fig. 6](#)). The actual record of simple prokaryotic microbes including archaea and true bacteria such as photosynthetic cyanobacteria (blue-green bacteria) range back over 3.5 billion years. The record of these simple bacteria in the form of stromatolites—masses of layered sediments trapped on mucilaginous bacterial mats—is extensive throughout the Precambrian and later. Eukaryotes with nucleated cells and organelles evolved perhaps 2.5 billion years ago associated with elevated levels of atmospheric oxygen; their organelles may represent symbiotic bacteria. Unicellular and multicellular algae appeared by approximately 2.0 billion years ago ([Fig. 6](#)).

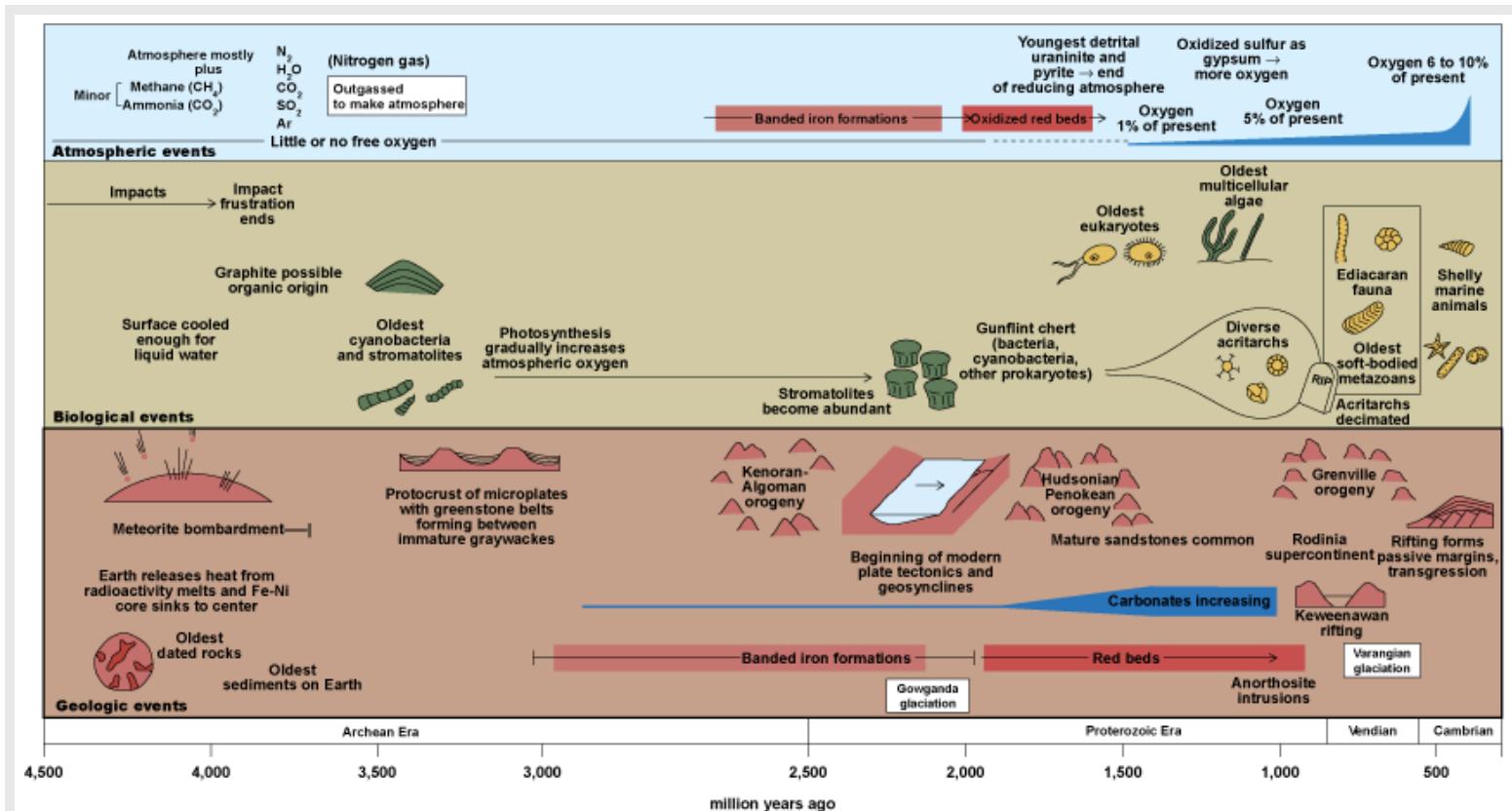


Fig. 6 Major evolutionary events in relation to physical events during the first 4 billion years (Precambrian interval) of Earth history. (Adapted from Prothero and Dott, 2004)

Single-celled animal-like protists (formerly, protozoans) are questionably represented by fossils, about 800 million years old from the Grand Canyon and elsewhere. Animal-like trace fossils include simple burrows that may extend back at least 600 million years; strings of fecal pellets preserved in ancient sediments indicate the presence of animals with guts.

Extraordinary assemblages of large “leaflike” and radially symmetrical organisms occur as imprints in fine-grained marine

sandstones worldwide about 580–550 million years ago, the Ediacaran Period of the Neoproterozoic Era. The exact affinities of these Ediacaran organisms (“vendobionts” or “vendozoans”) have been the subject of debate, with some asserting that they represent early animals such as jellyfish, sea pens (colonial marine cnidarians that resemble a quill pen), and perhaps annelid worms; others have argued that the Ediacaran organisms represent a different type of life form, possibly simple, baglike mouthless organisms that died out without leaving descendants. Regardless of the affinities of the Ediacaran organisms, the extraordinary discovery in the late 1990s of fossil animal embryos in China provides ample evidence for simple animals such as sponges and relatives of jellyfish nearly 600 million years ago, in concert with some estimates from molecular clocks. See also: [**Ediacaran biota** \(/content/ediacaran-biota/213300\)](#)

The most dramatic recorded event in the history of animal life occurred about 543–530 million years ago (Early Cambrian Period): the so-called Cambrian Explosion ([**Fig. 7**](#)). Within less than 10 million years, nearly all of the major body plans of life, and perhaps others that are now extinct, appeared in the oceans. These include brachiopods, mollusks, arthropods (trilobites, crustaceans, and many others), echinoderms (simple early relatives of starfish), and the chordates. A further phase of diversification in the following Ordovician Period gave rise to a much larger number of class- and order-level groupings. For example, some 20 different classes of echinoderms existed at this time, including the ancestors of crinoids, starfish, and sea urchins that have persisted to the present day.

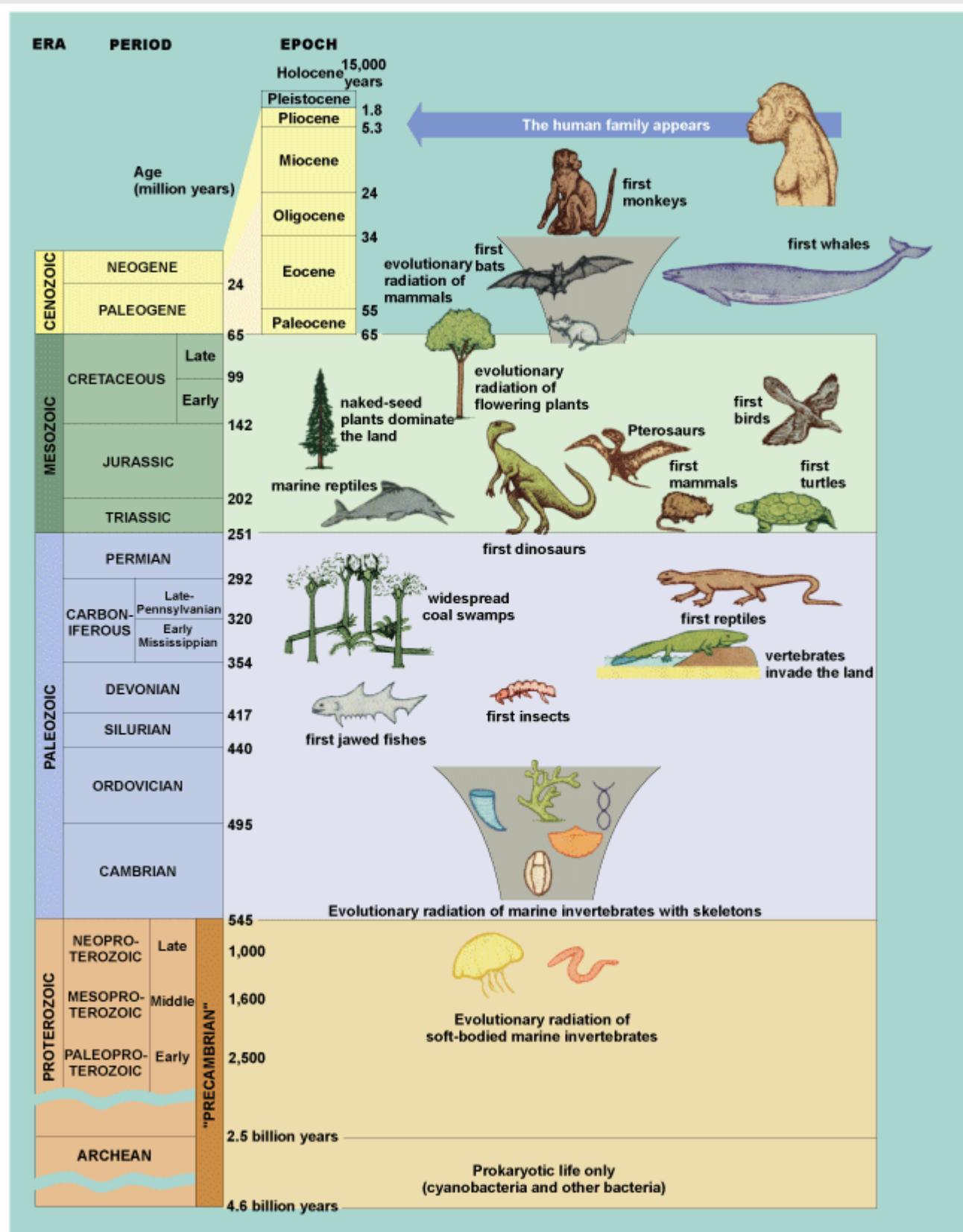


Fig. 7 Phanerozoic time scale with major evolutionary events of both marine and terrestrial life. (Adapted from Stanley, 2005)

Vertebrates (animals with backbones) are now known from fossils to range back nearly as far as most invertebrates. Recent discoveries from China indicate that early vertebrates, simple jawless fishes, had evolved at least 530 million years ago. Conodont animals represent an early, eel-like vertebrate group that flourished for over 300 million years before going extinct in the Triassic Period. Armored jawless fishes (ostracoderms) and the first jawed fishes appeared early in the Ordovician Period, with jaws evolving from gill bars. The Devonian Period (417–365 million years ago) is often termed the “Age of

Fishes" because of the rapid diversification of a large number of jawed fish groups: placoderms (which diversified and then went extinct within the period), sharks, bony ray-finned fishes, and lobe-finned fishes including lungfish and crossopterygians.

As more complex relationships evolved, organisms began to partition the environment by growing at different heights or "tiers" within and below the sediment: from a few centimeters to well over a meter above the substrate and by burrowing more deeply into the sediment. Such fractionation of the environment may represent a response to competition.

Different groups of invertebrate animals formed reef structures at various times: spongelike archeocyathans in the Early Cambrian, stromatoporoid sponges and tabulate corals in the Silurian-Devonian, peculiar coral-like rudistid bivalves in the Cretaceous, and stony hexacorals in the Cenozoic Era, including the modern Great Barrier Reef of Australia.

Predator-prey interactions in the marine ecosystem also intensified in two pulses. The middle Paleozoic showed rapid diversification of jawed fish predators and animals with the ability to crush and bore into shells. Potential prey organisms show a variety of probable responses including increased shell thickness and spinosity.

During the Jurassic and Cretaceous, the marine ecosystem appears to have become increasingly "high energy," possibly owing to an increased nutrient runoff fostered by angiosperm plant weathering of soils. The planktonic ecosystem experienced dramatic evolution: diatoms and coccoliths both became exceptionally common and formed large amounts of sediment. Radiolarians flourished in offshore settings and planktonic foraminifera appeared for the first time in the Cretaceous. This rise of primary and secondary producers was matched by unprecedented evolution of the predatory consumer guilds. A second and perhaps more intense phase of predator-prey interaction termed the "Mesozoic marine revolution" yielded highly complex predator-prey interactions involving a host of new predators. Teleost fishes, some of them huge, shared the key advance of a swim bladder for buoyancy regulation and increased maneuverability. A host of more efficient predatory sharks appeared, and these were matched by an unprecedented number of large predatory marine reptiles. Ichthyosaurs, plesiosaurs, and sea-going crocodilians flourished in the middle-to-late Mesozoic Era and mosasaurs, giant swimming relatives of the monitor lizards, diversified in the Cretaceous. With the exception of sharks and bony fishes, most of the large predators died out near or at the end of the Cretaceous. The niches left vacant from these large reptiles were later partially filled by predaceous whales beginning in the Eocene. However, the slightly later occurring baleen whales, the most gigantic animals on Earth, feed directly on plankton, which they sieve from the water. See also: [Marine ecology](#) ([/content/marine-ecology/405800](#)); [Predator-prey interactions](#) ([/content/predator-prey-interactions/757602](#))

Terrestrial ecosystem

The terrestrial ecosystem evolved late relative to the marine. Spore-bearing land plants such as mosses and lichens may have invaded rocky coastlines as far back as the Proterozoic; however, vascular land plants, tiny psilophytes, did not appear until the Late Ordovician or Silurian periods about 440 million years ago. These plants possessed the key adaptive breakthrough of tracheids to allow conduction of fluids up the stem, but they lacked both roots and leaves. The first land invertebrate animals, probably relatives of the millipedes, appeared at about the same time, as evidenced by trace fossils in paleosols (ancient soil deposits) from the Ordovician of Pennsylvania. Many new plant groups, including lycopods, sphenopsids ("horsetails"), ferns, and the ancestors of gymnosperms, evolved during a very critical time in land plant evolution in the Devonian Period (about 416–359 million years ago). The oldest known fossil forests, supporting trees up to 15 m (50 ft) high, are known from stumps preserved in place in paleosols in eastern New York. Late in the Devonian (~365 million years ago), one group of trees also evolved the first seeds, a reproductive breakthrough that permitted invasion of drier, upland areas.

Associated with the radiating land plants in the Devonian were some of the first spiders and insects. Also, at about this time, the first semiterrestrial vertebrates, the early tetrapods, ancestors of modern amphibians, evolved apparently from lobe-finned

fishes or crossopterygians. These animals possessed several key adaptive breakthroughs, including fully developed lungs and tetrapod limbs with digits, effective for walking on land.

During the succeeding Carboniferous Period, coal swamps flourished in coastal wetlands fringing the rising Appalachian Mountains (now in the eastern United States) and the corresponding Hercynian Mountains in ancestral Europe. Coals, typically overlying heavily leached soils or underclays, were formed largely of primitive plants such as lycopods and seed-ferns. Casts of stumps of these plants at Joggins, Nova Scotia, have yielded skeletons of some of the oldest animals assignable to the reptiles. These animals possessed another key evolutionary breakthrough, amniotic eggs, with protective membranes and a shell to prevent desiccation of embryos, making reptiles the first fully terrestrial animals. Drying of coal swamps during the following Permian Period led to a shift toward drier, upland vegetation, including conifers. Also, new groups of reptiles appeared, including the mammal-like reptiles, a precursor of which were the pelycosaurs. Some, such as *Dimetrodon*, possessed specialized vertebral "sails," which possibly aided in thermal regulation. The so-called mammal-like reptiles or therapsids also flourished in the Late Paleozoic. Both groups underwent extinction at the end of the Paleozoic Era.

Also during the Carboniferous Period, primitive insects that were flightless evolved both wings and wing-folding ability, enabling a more fully aerial mode of life.

During the Late Triassic Period, about 220 million years ago, the dinosaurs appeared. These animals dominated Mesozoic terrestrial faunas, but they coexisted with small, furry, and warm-blooded mammals, which also evolved in the Late Triassic from therapsid ancestors. In terms of plant life, the Triassic was an age of ferns and early conifers, but the succeeding Jurassic Period is sometimes called the "Age of Cycads," a group of related gymnosperms with short, stocky trunks and palmate leaves. Such gymnospermous plants no doubt provided a food source for the dinosaurs that included the vast sauropods, the largest land animals that ever lived, weighing in excess of 100 tons (90,000 kg) and perhaps standing 15 m (50 ft) high. Flight evolved twice among the archosaurs: First, the pterosaurs, batlike reptiles that are a sister group to the dinosaurs, appeared in the Triassic, and by the Cretaceous evolved into the largest flying animals ever, with wingspans exceeding 15 m (50 ft). Second, remains of the first birds, including imprints of feathers, are found in fine-grained Solnhofen Limestone also of Jurassic age from Bavaria, Germany. These animals apparently evolved from small, feathered theropod dinosaurs, relatives of the large predatory tyrannosaurids.

A very important new group of seed-bearing plants, the angiosperms or flowering plants, appeared midway through the Cretaceous Period (**Fig. 7**); their key breakthrough, double fertilization, led to accelerated reproduction. These plants coevolved with new groups of pollinating insects such as the butterflies and moths. Dinosaurs continued to flourish during the Cretaceous and included the largest terrestrial carnivores of all time, such as *Tyrannosaurus*, which may have weighed 6 tons (5500 kg). In response to these predators, herbivorous dinosaurs evolved varied defenses including armor in ankylosaurs and horns in the ceratopsians, such as *Triceratops*, the youngest known dinosaur. Dinosaurs, pterosaurs, and many marine animals such as swimming reptiles, ammonoids, and others became extinct at the end of the Cretaceous Period. A great debacle in the form of an asteroid impact occurred at this time, as evidenced by enrichment of iridium and shocked quartz in Cretaceous-Tertiary boundary clays about 65 million years ago and no doubt contributed to the demise of these organisms.

The demise of dinosaurs in terrestrial ecosystems may have opened ecological space and cleared the way for an extremely rapid adaptive radiation of mammals during the Cenozoic Era, often called the "Age of Mammals." However, this era could equally be called the "Age of Angiosperms," the "Age of Frogs," the "Age of Snakes," or the "Age of Songbirds," as all of these groups also evolved and radiated during the Cenozoic. The evolution of C-4 plants, with their more efficient photosynthetic pathways, including the constantly growing grasses, was closely tied to the rise of ungulates, that is, hoofed, grazing mammals, during the mid-Cenozoic. These included cloven-hoofed, even-toed ungulates (pigs, camels, cattle), as well as rhinos and horses, a group of odd-toed ungulates, whose evolution of long legs, reduced side toes, and abrasion-resistant

high-crowned teeth is well documented.

Finally, about 6 million years ago, the hominid family evolved in Africa. Fossils document the early members of the genus *Australopithecus*, which gave rise to the larger brained genus *Homo* about 2 million years ago. Subsequently, *Homo sapiens* evolved about 100,000 years ago also in Africa, and then spread across the Old World and eventually across the Bering land bridge into North America. This immigration may have ultimately led to a wave of extinction, especially of large mammals such as mammoths and mastodons, perhaps as a result of overhunting by the one species (humans) whose activities continue to alter the terrestrial ecosystem in many ways. See also: [Geologic time scale \(/content/geologic-time-scale/286500\)](#); [Terrestrial ecosystem \(/content/terrestrial-ecosystem/685500\)](#)

Carlton E. Brett

Stephen Jay Gould

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