M. Feldm

Evolution and Extinction

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I. THE BIG QUESTIONS AND OUR PRESENT WORLD PICTURE

The most fundamental question ever asked by humans relates to our origin and place in the universe. This question has been answered in a multidisciplinary way by all sciences in the all-embracing theory of Cosmic Evolution, comprising physical, chemical, biological, and human interlinked stages of evolution. The major feature of the universe and life is that they are critically explorable by humans: mind reflecting on its own evolution from lifeless to living matter, from featureless simplicity to increasing complexity. The universe is not static, small, and young, as conceived in the prescientific world belief. By contrast, science indicates that it is a large, old, evolving, ever-dynamic universe. The major discovery of humans is that the universe and its components, that is, time, space, matter, galaxies, stars, planets, life, and humans themselves, are interrelated historical entities that are constantly evolving. Many gaps and puzzles exist in our knowledge and major mysteries still remain, such as the origin of galaxies, life, and consciousness. Thus, a healthy degree of skepticism is in order, for we are using scanty evidence to draw a grand world picture.

The basic features of nature comprise change and evolution from simple physical and biological entities to complex derivatives, climaxing, on our planet, into astounding biodiversity and the extraordinary complexity of the human brain. Remarkably, this cosmic evolution, whose physical and chemical foundations are the cradle of all life, is explicable by materialistic, explorable, lawful patterns and processes. The evolutionary theory of the universe relates time, space, energy, matter, and life into a consistent, comprehensive, theoretical, and lawful framework beginning with the astronomical Big Bang explosion 15±4 billion years ago (Ba) and culminating, from our local planetary perspective, in life and humans. A grand holistic

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continuum of cosmic evolution emerges, leading from lifeless matter to life and mind.

I will first briefy set the cosmic stage and then give an overview of the evolutionary patterns and processes of life on our planet, including biological diversification and extinction.

II. ORIGIN, STRUCTURE, AND EVOLUTION OF THE UNIVERSE

According to the general theory of relativity, there must have been a universal state of infinite density about 15±4 Ba, at the Big Bang, which would have been an effective beginning of time of our present universe. By combining quantum mechanics with general relativity, space and time together might form a finite four-dimensional space without singularities and boundaries. This idea could explain the large-scale uniformity of the universe and the smaller-scale departure from it resulting in galaxies, stars, planets, life, and humans. The standard Big Bang model is the best current cosmology explaining the origin and evolution of the universe. It assumes that our universe is expanding according to Hubble's law and the dynamics of the expansion is described by Einstein's general relativity theory. Theories of the expanding universe are rapidly converging with unified theories of force and matter at the level of subatomic particles.

In a tiny fraction of a second after the Big Bang, the universe expanded dramatically by a factor of 10^{30}, or more, and is still inflating and forming cosmic structure involving clusters and superclusters of hundreds of billions of galaxies in the visible universe. Our own Milky Way galaxy alone contains more than 100 billion suns, many of which apparently have planetary systems. However, there are many billions of similar galaxies throughout the observable universe and billions of galaxies lie beyond our cosmic horizon.

The early universe was very hot, dense, and perhaps also irregular. The irregularity gradually decayed. Within minutes after the Big Bang, some nuclear reactions occurred. All the helium in the universe was then synthesized. The cosmic background radiation discovered in 1964 is apparently a residual vestige of the Primeval Fireball of this early era, filling all space. During the expansion of the universe it cooled, eventually condensing into galaxies and quasars and showing cosmic evolution. The galaxies clustered and fragmented into stars. As the first generation of stars were born and died, heavy elements, such as carbon, oxygen, silicon, and iron, were gradually evolving through nucleosynthesis. As stars evolved into red giants they ejected matter that condensed into dust grains. New stars formed from clouds of gas and dust. In at least one such nebula, the cold dust collapsed into a thin disc surrounding the star. Dust grains accumulated into larger bodies that grew in size by their gravitational attraction, forming the diverse array of bodies, from asteroids to giant planets, that constitute our solar system. On the size-fitting planet Earth, both appropriate hydrosphere and atmosphere set the stage for the evolution of life and humans. We are children of the stars.

The Big Bang model for the expanding universe yielded a set of interpretations and successful predictions with no well-established empirical contradictions. It is reasonable to conclude that this standard cosmology has developed into a mature and believable model providing the physical and chemical theater for the evolution of life on Earth.

Evolutionary biology is the science studying the history of life on our planet. Two major ideas unify life and humans with nature: the ideas of biological and molecular evolution. [*See* MOLECULAR EVOLUTION.]

III. BIOLOGICAL EVOLUTION

The idea of biological evolution was substantiated by Charles Darwin (1859) and his followers. Life and humans were not created. They originated ultimately, given the proper environment, from inanimate matter, and evolved gradually from a primitive common ancestor throughout 4 billion years of chemical and biological evolution, generating all biodiversity and, of course, humans (Fig. 1). The evolutionary mechanism advanced by Darwin was natural selection, operating on heritable variability among individuals, thus forming biological adaptations in changing environments. This mechanism of Darwinian evolution, through genetic individuality, replication, mutation (i.e., variation), and natural selection resulting in environmental adaptation, might have been operating since the origin of life. At the primitive level of molecular evolution it was shown experimentally in artificial RNA by Manfred Eigen. Later, complex adaptive systems presumably adapt to and on the edge of chaos, according to the emerging science of complexity. [*See* BIODIVERSITY.]

The origin of life, from the standpoint of genetics, was the appearance of the first replicating molecule (which could metabolize and transmit information) on earth presumably about 4 Ba. Future progressive evolution involved improving homeostasis and complexity by optimizing structural and functional diversity. Likewise, biodiversity generally increased slowly and gradually, set back occasionally by mass extinctions. Admittedly, scientists are having a hard time agreeing on the greatest mystery ever, the origin of life: on when, where, and how life first emerged on Earth from lifeless matter. Organic chemicals could have been delivered by impacts or synthesized in the atmosphere, tidal pools, or deep-sea hydrothermal vents. These earliest organic chemicals combined stepwise to form more complex organic compounds, including nucleic acids, such as the dual ribozyme and the replicating and catalytic RNA, which generated proteins.

If a self-replicating "naked gene" originated from simpler organic molecules and multiplied, it, or its progenitors, might have started molecular evolution that led to cellular life. Impacts and greenhouse effects, caused by CO_2 derived from volcanoes, prevented life from evolving until 4 Ba. Around then, precellular forms that consumed molecules from natural organic "soup" may have evolved either to early cellular animallike forms or to precellular chemosynthetic forms that did not leave fossils, giving rise to chemosynthetic cellular prokaryotes. Later, photosynthetic bacteria resembling blue-green algae (cyanobacteria) emerged, forming dense stromatolite mounds on shallow sea margins. These primitive organisms, based on carbon biochemistry and generating oxygen through photosynthesis, gave rise to all descendant complex lifeforms, including humans (Fig. 1).

IV. MOLECULAR EVOLUTION

The second major idea unifying human and life with nature is the finding that the instructions (i.e., blueprint) for forming an organism are encoded chemically (Fig. 2). A flourishing current theory states that life is derived via the RNA (ribonucleic acid) world. RNA molecules could have evolved from ribose and other organic compounds by "learning" to copy themselves. They may have started both as information and catalytic molecules, but then began to synthesize proteins that served as both catalysts and the building material of organisms. The proteins helped the RNA to replicate and synthesize proteins more effectively. They also helped the RNA make double-stranded versions of itself that evolved into DNA (deoxyribonucleic acids), possibly the most important substance in nature, substantiating life and transmitting its genetic plan over generations. DNA took over in evolution, using RNA to make proteins, which in turn helped DNA make copies of itself and transfer its genetic information to RNA and then to proteins and on to the building up of organisms and their progeny (Fig. 2).

The chemical language of life, conveying genetic information for prescribing organisms, consists then of the two closely related families of giant molecules, the nucleic acids RNA and DNA. The latter is a long, ladderlike, double-stranded, twisted molecule like a spiral staircase consisting of a sugar–phosphate polymer backbone, with four nucleotide side molecules involving only four bases, or "letters": adenine, thymine, guanine, and cytosine in DNA, and the same nucleotides, except with uracyl replacing thymine, in RNA. DNA is the repository of the genetic code and RNA is a single-stranded molecule now primarily executing DNA's plans, producing proteins on cytoplasmic ribosomes by its stored information, analogous to computer-stored data (Fig. 2). DNA's two-stranded double helix can separate and replicate by

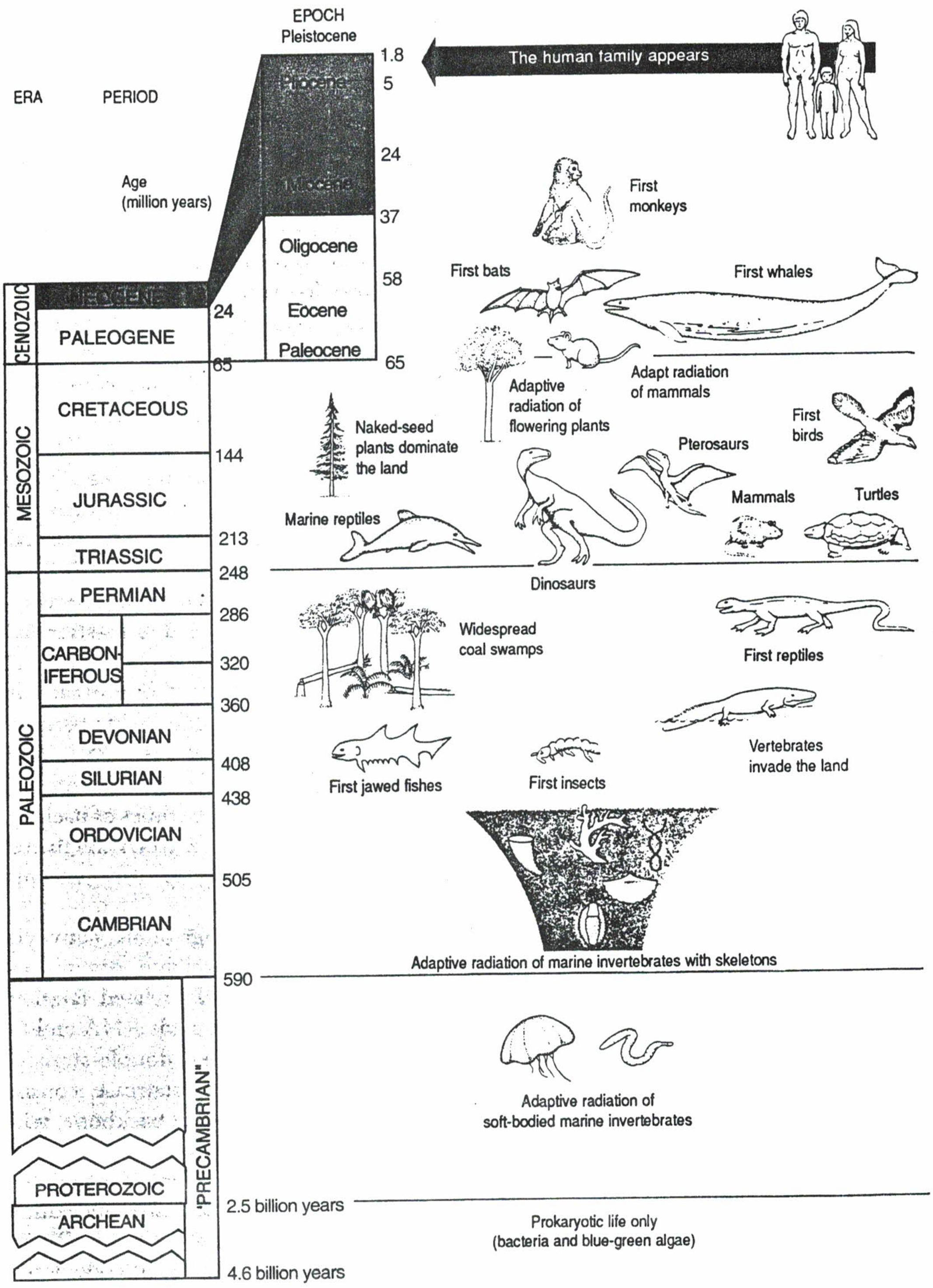

FIGURE 1 The evolution of life on Earth.

each strand complementing itself. Thus, DNA can both metabolize (produce proteins) and replicate, combining growth and reproduction.

Cloning and sequencing techniques now allow us to characterize genes directly instead of having to deduce their properties from their effect. This is a new genetics climax in the plan to obtain the complete DNA sequence of the human genome, though this goal will be achieved in the first decades of the next century. Small "model" genomes, such as the polio virus, are about 5000 letters, or nucleotides (0.005 megabases, Mb), long; the bacterium *Escherichia coli* (4.7 Mb), yeast (14 Mb), and the fruitfly *Drosophila* (165 Mb). These "model" organisms are better scaled to existing technology. The yeast genome contains genes with functions common to all eukaryotic cells and those of simple multicellular organisms. However, vertebrates, including humans, differ in their morphology and development. Therefore, the ideal small genome of minimum size and complexity with maximum homology to the human genome may be that of the pufferfish *Fugu rubripes* (400 Mb). This genome is 7.5 times smaller than the 3000 Mb of the human genome, but having a similar gene repertoire makes it the best model genome for the discovery of human genes (for update information see the "Genome" issue, *Science,* 30 September, 1994).

The 7 billion nucleotides are packed in 46 chromosomes in each of the nuclei centered in each of the trillions of cells comprising our bodies. This genetic information generates (through messenger RNA on cytoplasmic ribosomes) a second universal complementary chemical language of proteins. It consists of 20 amino acid building blocks, where 3 nucleotides in DNA code for a single amino acid molecule (Fig. 2). Proteins build the living body and provide its biochemical machinery. A length of DNA nucleotides, coding for hundreds of amino acids that comprise a single protein, is called a gene. Our 46 chromosomes in each nucleus consist of some 100,000 genes that prescribe us.

Remarkably, both the genetic (RNA and DNA) and metabolic (protein) languages, as well as the energetic currency, ATP (adenosine triphosphate), are universal to all life-forms: to microorganisms, fungi, plants, animals, and humans. Can there be a better demonstration of human unity with all life? This outstanding molecular uniformity transforms the Darwinian biological revolution into the material chemical language of life, that is, into the domain of molecular evolution. Furthermore, RNA comprises both genetic and metabolic (catalytic) ability, laying to rest the long debate over which of life's characteristics originated first: metabolism or the genetic code.

There are no substances in nature as important as the nucleic acids, RNA and DNA. These nucleic acids provided the genetic and metabolic basis of the evolutionary process generating the billions of different life-forms that have occupied the Earth since life emerged some 4 Ba. The evolutionary uniqueness of DNA and RNA resides in their dual nature, which embodies the capacity to transmit across generations both *constancy* and *diversity*. Constancy is retained through faithful DNA replication, whereas diversity is generated by the capacity to mutate, recombine, and form an infinite number of interchangeable chemical forms. Thus, a single molecule explains in one grand synthesis the constancy of inheritance and its diversity. The latter provides the material basis of evolution by natural selection.

V. UNITY AND DIVERSITY IN ORGANIC NATURE

The fascination of life resides in its unity and diversity. Unity is expressed by the chemical nature of life involving information transfer by the genetic code (Fig. 2), energy transfer by polyphosphates, structure and function through proteins, and cellular and tissue structures. Beyond these universals, nature consists of astounding biodiversity, involving millions of extant biological species and billions of extinct ones, most of which evolved and became extinct in the last 600 million years (My), that is, in Phanerozoic time. Clearly, extinction of species has been almost as common as origination. Only 1.5 to 1.8 million species have been documented to date, including unicellular organisms such as viruses, bacteria, algae, fungi, and protozoans, and multicellular organisms, comprising all living or-

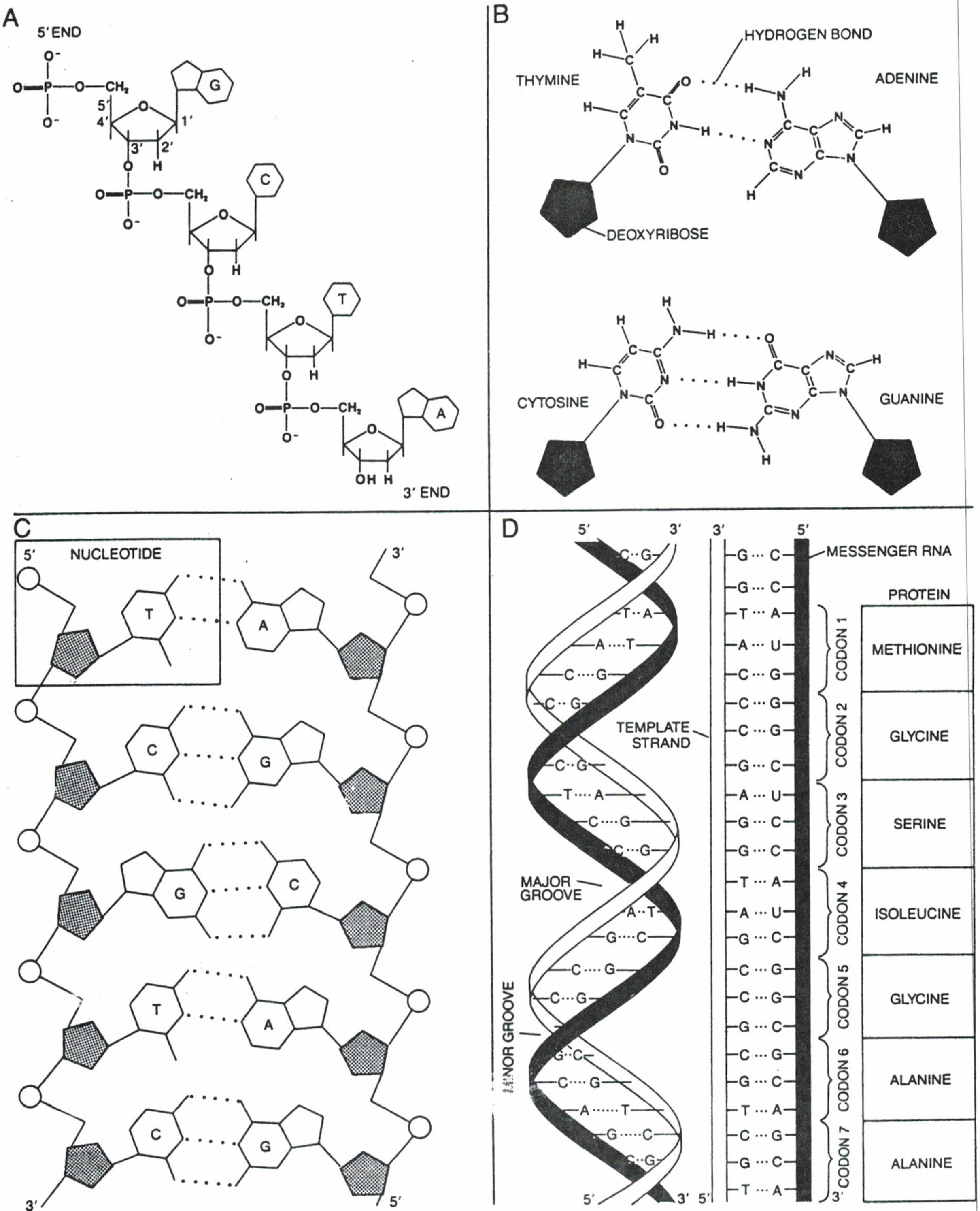

FIGURE 2 The structures of DNA, RNA, and proteins. (A) DNA backbone made of sugar and phosphate groups with attached bases; (B) nucleotide structure; (C) two-dimensional DNA structure; and (D) three-dimensional DNA structure, its transcription into a strand of messenger RNA, and the translation of mRNA into proteins. [From G. Felsenfeld (1985). *Scientific American*, October, p. 46].

ganisms. However, most extant species, involving several to dozens of millions of species (the figure is enigmatic and may differ by an order of magnitude, that is from 10 to 100 millions of species), are still unknown to science. The resolution of the enigma of how many species existed in the past and currently inhabit the Earth could highlight the evolutionary process itself and provide a sound basis for biological conservation and environmental management.

The astounding biodiversity in nature at the organismal level is based on the astronomic capacity for variation at the molecular level of RNA, DNA and proteins. Organic nature's response to environmental heterogeneity, and to the ever-changing physical and biotic stresses, was always the evolution of diversity. This is abundantly clear by observing the progressively increasing biodiversity through time from Precambrian times about 3.8 Ba, as well as in space, across the drifting continents, despite global and regional mass extinctions through the history of life on our planet (Figs. 1 and 3A–3C). The following discussion highlights the patterns and processes in the history of life, involving both diversification and extinctions.

VI. LIFE'S HISTORY: PRECAMBRIAN ORIGINS

The earth originated about 4.6 Ba, with other planets of the solar system, from a whirling cloud of dust. Radioactive dating unravels the earliest history of the Earth and the evolutionary dynamics of the emerging continents. During the first billion years of the Archean Eon of Earth history (see Fig. 1 for Earth geological eras, periods, and epochs), continents were small, but already drifting, volcanism was widespread, and radioactive elements were abundant in the lithosphere, releasing heat at a high rate. The oldest known intact rocks on Earth, the Acasta gneiss in northern Canada, are from 4 Ba, and the earliest zircon crystals, from Mount Narryer, Australia, date to 4.1 to 4.2 Ba. By the beginning of the Proterozoic Eon, 2.5 Ba, the Earth had cooled, larger continents were forming, and plate tectonic processes that operated already in Archean times continued. Banded iron formations, which formed in the presence of oxygen, accumulated in the sea about 2.5 and 1.8 Ba. Life originated apparently around 4 Ba and consisted first of prokaryotes (cells without nuclei) comprising bacteria and blue-green algae (Fig. 1).

VII. THE FOSSIL RECORD: OVERVIEW OF LIFE'S EVOLUTION

A. Prokaryotes

The fossil record represents a unique repository of information about the constant and dramatic change of organic evolution and increasing biodiversity over time, due to changes in physical (geologic, climatic) and biotic (competition, parasites, predation) diversity and stress. It reveals evolutionary diversification and extinction patterns and rates, whose dates are determined radioactively. Unequivocal evidence indicates that the first cells were prokaryotes, cells without a central nucleus containing DNA, which existed at least 3.5 Ba, in the Archean Eon, and prevailing for 1–1.5 My till the early Proterozoic Eon. This is demonstrated by stromatolite, threadlike bacterial mounds, and filamentous microfossils resembling modern cyanobacteria, or blue-green algae, from Greenland, Australia, and South Africa. The earliest prokaryotes survived presumably by anaerobic metabolism, obtaining energy by chemosynthesis and fermentation. The blue-green algae and other photosynthetic bacteria, following the anaerobes, enriched the atmosphere with oxygen as a byproduct by harnessing sunlight energy and storing it chemically through photosynthesis (Fig. 1).

Photosynthetic organisms apparently existed even earlier, 3.8 Ba, as demonstrated by the Isua banded-iron sedimentary rocks from Greenland. These are the oldest terrestrial rocks indicating the existence of liquid water, a prerequisite of life. Even the carbon content of the rocks may indicate that they involved photosynthetic organisms that utilized a certain ratio of carbon isotopes (^{13}C to ^{12}C) characterizing life. If life indeed existed 3.8 Ba as cellular forms, then its origin may date back to around 4 Ba, though fossilized cells disappeared because of strong heating during rock metamorphism. Thus, remarkably, life appeared on Earth several hundreds of millions of years after its birth as soon as the environment became suitable. However, the buildup of atmospheric oxygen may date to 2.3 to 2.2 Ba, as shown by the increasing abundance of stromatolites. This oxygen presumably set the stage for the evolution of more complex organisms, that is, the eukaryotes (Fig. 1).

B. Eukaryotes

Eukaryotes (advanced organisms, both unicellular and multicellular, with larger cells involving nuclei, chromosomes, and organelles) appeared in the early Proterozoic Eon, more than 1.4 Ba. Single-cell eukaryotes arose presumably through symbiosis by the union of two cells. The eukaryote organelles, that is, the genetic nucleus, energy-producing mitochondria, and energy-harnessing chloroplasts responsible for photosynthesis, may have all started by symbiosis as prokaryotes engulfed by other prokaryotes. The symbiosis of prokaryotes led to the evolution of novel and high-energy sources. Prokaryotes reproduce asexually by simple fissioning. The additional evolution of nuclei and chromosomes provided the structures needed for sexual reproduction and meiosis. Thus, eukaryotes "evolved" mitochondrial respiration, sex, and recombination, major emergent evolutionary innovations that increased genetic diversity and speeded up evolution, leading to multicellularity. The biochemistry invented by early life persists today not only in bacteria but also in the most complex life-forms composed of quadrillions of cells. Life's genetic library exploded in size but retains its original chemical linguistics (Figs. 1 and 2).

C. Multicellular Organisms

Eukaryotes paved the way to multicellularity after 3 billion years of unicellular "gestationary" evolution that transformed the planet atmosphere. Only about 1 Ba, multicellular complex organisms evolved, as suggested by fossil and molecular biological evidence. These gave rise to five kingdoms of living organisms: Monera, (all prokaryotes, that is bacteria and relatives), Protista (single-celled organisms with nuclei, the consumers among them are protozoans), Fungi (mushrooms, lichens, and their relatives), Plantae (Metaphyta, multicellular algae and higher plants), and Animalia (Metazoa, multicellular animals). During the first 3 billion years of life's history microorganisms prevailed in the oceans, with multicellular organisms appearing only in the last billion years (Fig. 1).

D. The Late Precambrian Radiation and Extinction

Trace fossils of tubes of wormlike, multicellular, burrowing animals in late Precambrian times occur only in rocks less than about 1 Ba. A global (Europe, North America, Australia, Africa) adaptive radiation of soft-bodied marine invertebrates, increasing in both complexity and variety (medusae, sea pens, annelid worms, and the first arthropods), occurred in the late Precambrian, originating about 800 million years ago (Ma). The best known is the Ediacara fauna of southern Australia (670 Ma), discovered in 1974 (Fig. 1). However, they seem to be a dead end and largely unrelated directly to extant living organisms. Their widespread presence is as mysterious as their disappearance (see later discussion). Other Precambrian lineages led to the great diversity of plants and animals in water, on land, in air, and just now in space.

E. The Cambrian Explosive Radiation and Paleozoic Life

The dramatic and seemingly explosive evolutionary radiation of marine invertebrates with skeletons (trilobite crustaceans, brachiopods, graptolites, bryozoans, etc.) occurred in the early Cambrian, almost 600 Ma, when most of the 26 major extant phyla appeared and others had been exterminated. These include unique, ancient, durable body plans (Bauplanes) surviving until today, such as radial symmetry (e.g., anemones, consisting of two layers of tissue), bilateral symmetry (e.g., flatworms with three primary tissue layers), and the coelomates with three body layers and a cavity in the middle layer. The latter involve segmented worms (annelids), pentamerally symmetric creatures (echinoderms, sea stars, sea cucumbers, and starfish), and bilaterally symmetric coelomates, including arthropods (insects, spiders, and crustaceans), the mollusks, the vertebrates, and others. Thus, with the initial decline of stromatolites about 1 Ba, the major eukaryote radiation and probably the first metazoans appeared between 1000 and 900 Ma. The Ediacaran faunas representing the diploblastic grades evolved extensively during the period 580–550 Ma, followed by the Cambrain faunas representing the triploblastic grades (Fig. 1).

Phyla are distinguished by characters reflecting the oldest and deepest levels of evolutionary association and are hierarchically divided into classes, orders, families, genera, and species. The times of origin of the phyla and their relations remain obscure, but must have taken place in late Precambrian times more than 900 Ma, despite their spectacular explosion due to the possession of hard skeletons in the early Cambrian 600 Ma. The most spectacular assemblage of Cambrian fossils comes from the Burges shales in British Columbia. This assemblage contains many unique body plans that flourished early in the Cambrian, becoming extinct later. During Cambrian and Ordovician times, hundreds of class-level taxa originated.

Early Paleozoic biota were in the sea. The first vertebrates appeared about 500 Ma in the sea, among a rich invertebrate fauna. Colonization of land occurred about 400 Ma, involving plants, fungi, invertebrates, and vertebrates. The amphibians were the first land vertebrates that became associated with water bodies for reproduction. About 300 Ma the breeding pond was "enclosed" inside the amniotic egg, which is bounded by a hard envelope. This innovation liberated the reptiles, the descendants of amphibians, from their water dependence, thus completing the trek toward land colonization. Dinosaur reptiles prevailed in water, land, and air during the entire Mesozoic era, together with naked-seed plants (gymnosperms and cycads) (Fig. 1).

F. Life's Evolution in the Mesozoic and Cenozoic

The mammals, which originated in Triassic times, more than 200 Ma in the early Mesozoic era, radiated dramatically in Cretaceous time, becoming predominant and colonizing most habitats in the Cenozoic (Fig. 1). Placental mammals, including primates, originated 65 Ma, the monkeys 50 Ma, and the apes 30 Ma. The human family appeared 6–7 Ma, and the genus *Homo* a mere 1.6 Ma. Archaic *Homo sapiens* appeared 200,000–300,000 years ago (Ya), and modern *Homo sapiens* showed up 100,000 Ya. The agricultural revolution occurred 10,000 Ya, the Industrial Revolution about 200 Ya, and the communication revolution in the last several decades, and is still on the rise.

In 1953 humans deciphered the genetic code that prescribes all organisms. This chemical language encoded in DNA and RNA is universal to all organisms and registers genetically the history of life on Earth in the genomes of viruses, bacteria, multicellular organisms, and humans. This is a uniquely dramatic testimony to the unified evolutionary origin of all organisms from a common ancestor in early Precambrian, Archaic times. This history is condensed in humans in 46 chromosomes contained in each of the trillions of cells comprising our bodies. In recent years, we have learned to engineer the genetic code. At present, the human genetic code is being actively unraveled in the Human Genome Project, possibly the climax of all current biological research programs (see "Genome" issue in *Science,* 30 September 1994). An understanding of the chemical language of life allows us to genetically manipulate organisms, an immense, sobering power that has begun to dramatically change medicine, agriculture, and industry through genetic engineering of plants and animals by transgenic operations.

If we condense the history of life into one year to illustrate the time line of major evolutionary events, then life originated on January 1; vertebrates appeared on November 16, with land colonization on November 25; the human family appeared on December 31 at 6 a.m.; australopithecids

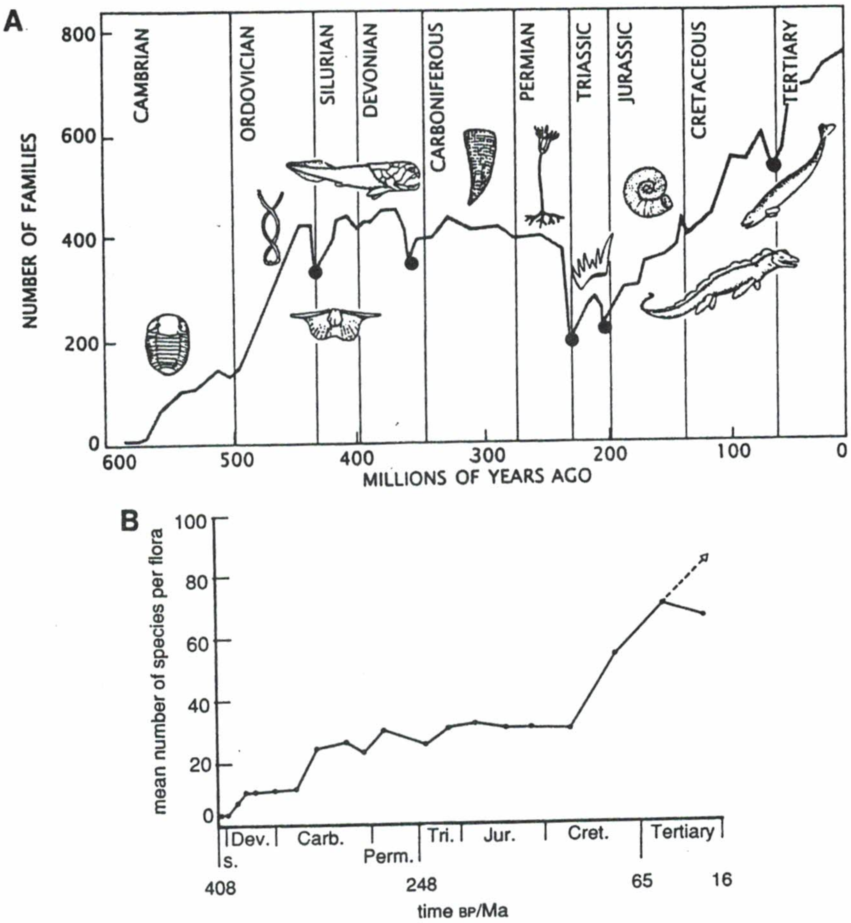

FIGURE 3 (A) Biodiversity trajectory of families of marine organisms in the Phanerozoic. (B) Biodiversity trajectory of plant species in the Phanerozoic. (C) Biodiversity trajectory of tetrapod families in the Phanerozoic. 1–6 indicate beginnings of extinctions. I, II, and III indicate 3 family assemblages that succeeded each other through geological time. [(A) from E. O. Wilson (1989). *Scientific American* **261**(3), 60–66; (B) from Maynard Smith in Chaloner and Hallam, 1989, after Knoll, 1986; (C) from M. J. Benton (1989). *Philos. Trans. Roy. Soc. London Ser. B* **325**, 369–386.]

evolved on December 31 at 1:00 p.m. and *Homo sapiens,* our own species, appeared on the same day at 11:55 p.m.; the agricultural revolution arrived at 11:58:41; and human cultural history occurred in but fragments of the last few minutes.

VIII. BIODIVERSITY: DIVERSIFICATION AND EXTINCTION PATTERNS

Large-scale evolutionary change over time clearly has various patterns, rates, tempos, and modes. The previous section dealt with qualitative evolutionary change in life's history, deduced from the fossil record, from the simplest Precambrian organisms to the extant complex organisms. Before overviewing the causes leading to variation in the trajectory of life's large-scale evolutionary change, I will first describe briefly the general quantitative evolutionary patterns of diversification and extinction.

A. Diversification: Origination and Speciation

The history of global biodiversity over evolutionary time is one of a generally increasing diversity,

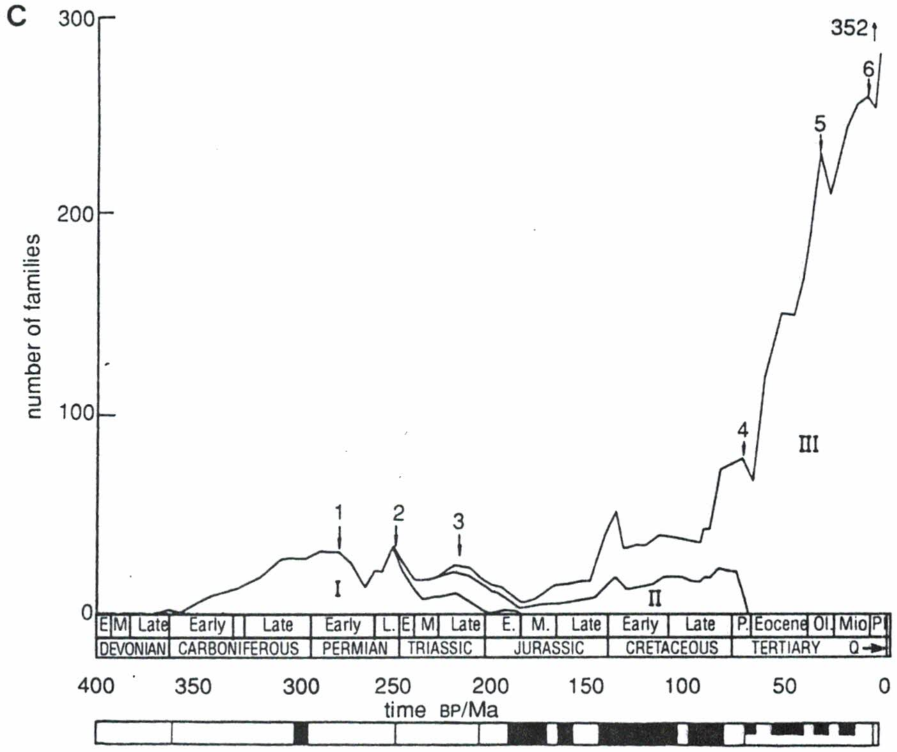

FIGURE 3 *Continued*

through speciation by either cladogenesis (i.e., fragmention of populations into reproductively isolated and ecologically compatible species in space) or anagenesis (i.e., phyletic evolution over time), in both marine (Fig. 3A) and terrestrial (Figs. 3B, 3C) organisms. The biodiversity trajectory of marine organisms indicates an initial experimental period followed by a swift rise in family number in early Paleozoic times, about 600 Ma. It remained roughly constant for the remaining 200 million years of the Paleozoic era and finally displays a slow but steady climb through the Mesozoic and Cenozoic eras to diversity's present all-time high (Fig. 3A). The rise in biodiversity was set back by five massive extinction episodes during the end-Ordovician, end-Devonian, end-Permian, end-Triassic, and end-Cretaceous periods (Figs. 3A and 4). The last of these is by far the most famous, because it ended the age of dinosaurs and opened ecological opportunities to the extensive mammalian adaptive radiation in the Cenozoic, leading, among other lineages, to the evolution of humans. A series of smaller extinctions brings the total to at least 12 extinction events, 9 of which stand out above the regular background extinction levels (Fig. 4).

The diversity of terrestrial plants (Fig. 3B) and tetrapods (Fig. 3C) increased similarly from the Devonian to the Permian. Plant diversity remained roughly constant during the Mesozoic, then began to increase in the late Cretaceous and continued to do so during the Tertiary (Fig. 3B). The rapid radiation of "modern" tetrapod groups—frogs, salamanders, lizards, snakes, turtles, crocodilians, birds, and mammals—was hardly affected by the famous end-Cretaceous extinction event. Rodent peri-Mediterranean diversification patterns in the Neogene (24–3 Ma) show three peaks of high origination rates, two in the Miocene (17.5 and 11.5– 11 Ma) and one in the early Pliocene (4.2–3.8 Ma).

B. Insect Diversity in the Fossil Record

Insects possess a surprisingly extensive fossil record. Their diversity exceeds that of preserved vertebrate tetrapods through 91% of their evolutionary history [see Figs. 1–5 in Labandeira and Sepkoski (1993);

see Bibliography.] The great diversity of insects was achieved not by high origination rates but rather by low extinction rates comparable to the low rates of slowly evolving marine invertebrate groups. The great radiation of modern insects began 245 Ma and apparently was not accelerated, at least at the familial level, by the expansion of angiosperms during the Cretaceous period. The basic trophic machinery of insects was in place nearly 100 My before angiosperms appeared in the fossil record, and may relate to the evolution of seed plants in general rather than to angiosperm evolution.

C. Extinction

"Mass extinction" is the term used in paleobiology to describe the relatively short interval of geological time when large and diverse segments of the world's biota underwent extinction, involving global reduction in diversity and biomass, as revealed in the fossil and geochemical record. (Figs. 3A, 3C, and 4; Table I). Both perspectives provide significant results but they must be interpreted carefully to avoid potential pitfalls. Historically, five mass extinctions have been identified in the fossil record as having been the greatest crises in the history of life during the Phanerozoic: they occurred in the end-Ordovician (~440 Ma), end-Devonian (~360 Ma), end-Permian (~250 Ma), end-Triassic (~215 Ma), and end-Cretaceous (65 Ma). In addition, four additional global events are interpreted as mass extinction phenomena, especially, those in the late Precambrian (650 Ma), end-Cambrian (500 Ma), Eocene–Oligocene (32 Ma), and end-Pleistocene (11,000 Ya) (Fig. 4 and Table I). [*See* DIVERSITY CRISES IN THE GEOLOGIC PAST.]

Background extinction describes a spectrum of smaller events, resulting from abiotic and biotic stresses leading to the regular disappearance of taxa. In general, Phanerozoic patterns of phytoplankton radiation and extinction parallel those for skeletonized marine invertebrates. In plants, extinctions tend to follow innovation. Major mass extinctions among tetrapods took place in the early Permian, late Permian, early Triassic, late Triassic, late Cretaceous, early Oligocene, late Miocene, late Pliocene, and Holocene (Fig. 3C). Many of these events appear to coincide with the major mass extinctions among marine invertebrates.

D. Patterns of Extinctions Across Life's History

Extinction may be episodic at all scales, with relatively long periods of stability alternating with short-lived extinction events (Figs. 3A–3C, 4, and 5). Most extinction episodes are biologically selective, that is, the victims and survivors are not ran-

TABLE I

Principal Extinctions and Probable Cause[a]

Extinction event	Probable cause
Late Pleistocene	Postglacial warming plus predation by humans.
Eocene to Oligocene	Stepwise extinction associated with severe cooling, glaciation, and changes of oceanographic circulation, driven by the development of the circum-Antarctic current.
End-Cretaceous	Bolide impact producing catastrophic environmental disturbance.
Late Triassic	Possibly related to increased rainfall with implied regression.
End-Permian	Gradual reduction in diversity produced by sustained period of refrigeration, associated with widespread regression and reduction in area of warm, shallow seas.
End-Frasnian (Devonian)	Global cooling associated with (causing?) widespread anoxia of epeiric seas.
Late Ordovician	Controlled by the growth and decay of the Gondwanan ice sheet following a sustained period of environmental stability associated with high sea level.
Late Cambrian	Habitat reduction, probably in response to a rise in sea level, producing a reduction in number of component communities.
Late Precambrian	Complex, including widespread regression, physical stress (restricted circulation and oxygen deficiency), and biological stress (increased predation, scavenging, and bioturbation).

[a] Based on S. K. Donovan (1989). "Mars Extinctions: Processes and Evidence," Chaps, 4–12. Belhaven Press, London.

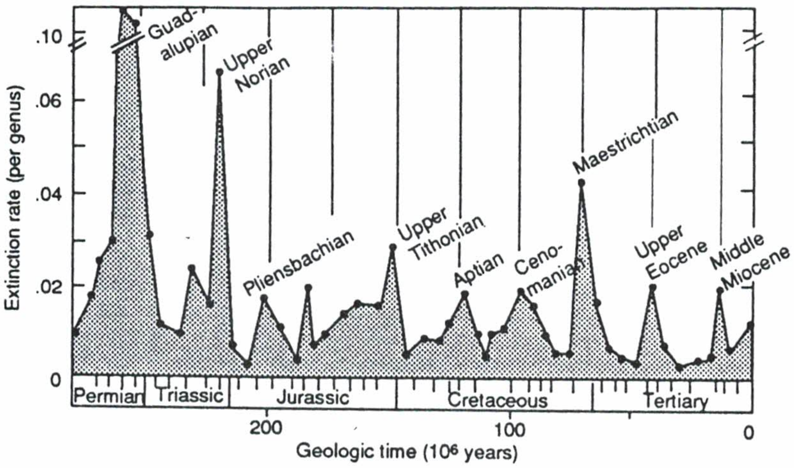

FIGURE 4 Record of percent extinction (per million years) computed from the records of 9773 genera of marine fossil animals (with the addition of the 26-My periodicity in best-fitting position). Marks along the abscissa indicate standard stages and are not sampling intervals; dots are placed at the centers of the 51 sampling intervals. [From Raup D. M., and Sepkoski, J. J. (1988). *Science* **241,** 94–96.]

dom samples of the preextinction biota. Analyzing survivorship of lineages could highlight the proximal ecological and physiological causes of extinction (Table I). The data base for extinction analysis is the distribution in space and time of about 250,000 known marine fossil species, an extremely small sample of past life. This is true because of the negligible probability of preservation and discovery of all species, as well as the problematics of the morphospecies as compared with the biological species. Thus, many sibling, morphologically indistinguishable good biological species occur in nature on the one hand, and much geographic variation within species could be wrongly interpreted as representing different species. Clearly, a better resolution derives at higher taxonomic levels (genera, families, and orders) (Figs. 3A, 3C, and 4).

Several factors may contribute to extinction resistance: broad ecogeographic and genetic spectrum, large population size, dispersal ability, and habitat selection. However, these may be more effective in background than in mass extinctions. Tropical biotas and specialist species are the first victims of extinction.

1. Precambrian Extinctions

The end-Precambrian (~650 Ma) witnessed apparently a widespread and early global extinction of the Ediacara fauna, due to combined abiotic and biotic stresses. The latter derived from sea regression and emergence of continental shelves associated with plate tectonics and climatic changes involving glaciation, anoxia (i.e., oxygen deficiency), hypersalinity, scavenging, predation, and bioturbation, all leading to the extinction of many lineages of medusoids, algae, annelid worms, and "protoarthropods."

2. Paleozoic Extinctions

a. End-Cambrian (~500 Ma)

Global mass extinctions are registered in the fossil record (Fig. 3A). Thus, at the end of the Cambrian nearly two-thirds of the 60 existing families of crustacean trilobites became extinct (Fig. 5). Major biogeographic and ecological reorganization, due to a sea level rise, led to progressive reduction in component communities or biofacies, causing a nonrandom extinction and selective survival of trilobite families. Those families, represented in upper-slope refuges, had a higher survival probability, regardless of their species richness. This increases clade survival during background extinction, supporting D. Jablonski's idea of differential causation in background as compared with mass extinctions.

b. End-Ordovician (~440 Ma)

Marine organisms, including trilobite and graptolite families, disappeared in the late Ordovician, amounting to 20% loss of diversity (Figs. 3A and

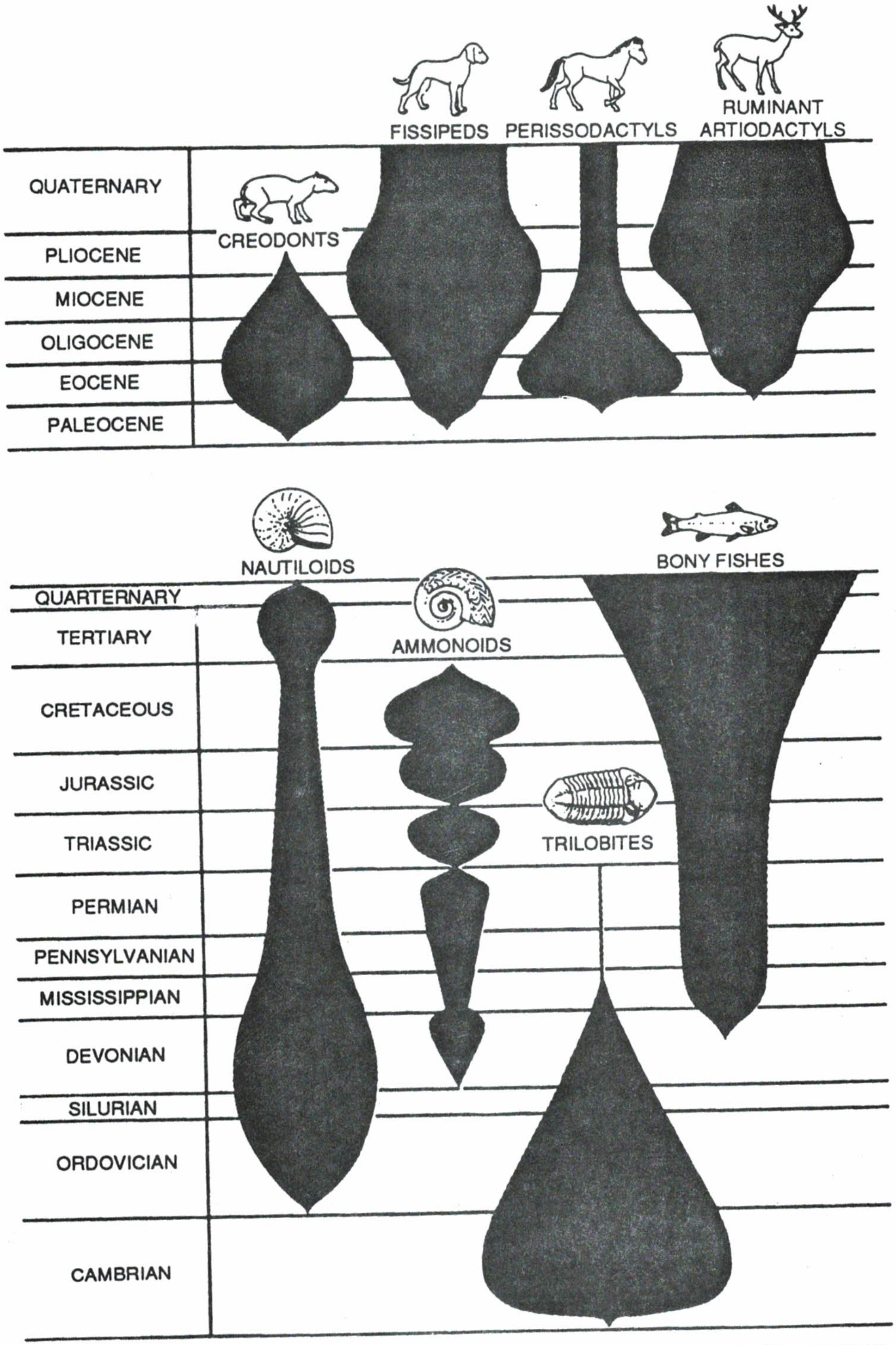

FIGURE 5 Ecological replacement of some taxa in the Phanerozoic. [From N. D. Newell (1963). *Scientific American*, February, p. 187.]

5). The end-Ordovician extinction involved two peaks of extinction separated by hundreds of thousands of years, characterized by the growth and decay of the Gondwanan ice sheet. This promoted widespread environmental perturbations, particularly temperature and sea level changes, which caused niche destruction and extinction. The major factors involved sea level and climatic changes were associated with chemical sea changes and anoxia. These caused the extinction of tropical, climatically stabile, stenotopic species and their replacement by cosmopolitan, generalist eurytopic species (see replacement of trilobites by nautiloids in Fig. 5). Extinction was selective among biotas (tropics versus temperate), communities (trilobites, corals, and brachiopods), niches, and species. The end-Ordovician extinction provides one of the best examples of ecological collapse. It was followed by a reestablishment of the ecological structure, setting the stage for the early Silurian radiation and the diversification of new Silurian communities.

c. End-Devonian (~360 Ma)

In the late Devonian as many as 21% of all families, 50% of all genera, and 70% of all species disappeared, involving reefal, peripheral, and shallow-water organisms, especially corals, stromatoporids, tentaculids, and brachiopods (Figs. 3A and 5). The ultimate cause of the end-Devonian extinction remains enigmatic. Tectono-glacial, paleogeographic, and bolide impact hypotheses have been proposed, each predicting a resultant temperature decline. The terrestrial ultimate causes seem more substantiated than the bolide hypothesis. The extinction lasted 3 My and was associated with lethal temperature decline as a proximate cause, creating widespread anoxia in the surface waters across the planet. This caused the global decimation of low-latitude tropical reef ecosystems and of warm-water shallow marine faunas. It was combined with higher survival of high-latitude faunas, deep-water faunas, and terrestrial faunas and floras. At the local and regional level, additional complications were added.

d. Early Carboniferous (~340 Ma)

The middle Mississippian blastoid (phylum Echinodermata) extinction event was a rapid, habitat-specific extinction. Blastoids presumably became rare worldwide or absent in shallow-water environments after the extinction. Onshore–offshore habitat shifts have been recognized as an important historial trend among marine benthos. The blastoids diversified immediately after this extinction and repopulated shallow-water habitats after a period of diminished diversity and abundance.

e. End-Permian (~250 Ma)

The end-Permian was the greatest global extinction in Earth's biota terminating the Paleozoic great experiment in marine life during an interval of intense climatic, tectonic, and geochemical change (Figs. 3A and 4). Decimation of 77–96% of marine and terrestrial species occurred in the late Permian. Marine life was devastated, experiencing a reduction of 57% of families and 96% of species, with crinozoans (98%), anthozoans (96%), brachiopods (80%), and bryozoans (79%) suffering the greatest extinction. Other severely affected groups were the cephalopods, corals, ostracods, and foraminiferans, all predominantly tropical groups or members of the reef-building community. Likewise, 75% of amphibian families and more than 80% of reptile families also disappeared. Such an enormous reduction in the biota may suggest a catastrophic event, but geochemical and faunal evidence favors a gradual process of reduction in species diversity. The most plausible causal mechanism seems to be climatic change, with a sustained period of global refrigeration, accompanied by widespread regressions and reduction of warm, shallow seas on the western and eastern margins of Pangaea. Notably, the main suborders of the decimated taxa survived the Permian to carry over into the Triassic.

3. Mesozoic Extinctions

a. End-Triassic (~215 Ma)

Multiphase late Triassic extinctions occurred in Europe involving scallops, crinoids, ammonoids, bryozoans, conodonts, and reef-building organisms (Figs. 3A and 4). Most ammonite families became extinct, except one that gave rise to the scores of families of Jurassic and Cretaceous times (Fig. 5). Likewise, primitive reptiles and amphibians were replaced by the expanding dinosaurs (Fig.

3C). End-Triassic extinctions were caused primarily by terrestrial causation facies changes, and there is no need for invoking extraterrestrial impacts. Ultimate tectonic, proximate sea level regression causing anoxia, and the loss of reefal facies, leading to reduced habitable area, best explain marine invertebrate extinction at this time. Two Jurassic mass extinctions occurred on a regional, not a global, scale, as shown by A. Hallam. They can be related to severe reductions in habitat area caused by regression of the epicontinental sea or by widespread anoxia.

b. End-Cretaceous (~65 Ma)

In the late Cretaceous (K-T), mass marine and terrestrial extinctions, extending over several million years, eliminated the ammonites, dinosaurs, and marine and flying reptiles, together with numerous families of corals, rudistid bivalves, echinoids, planktonic foraminifera, and belemnites, and also brought declines in marsupial mammals (Figs. 3A, 3C, 4, and 5). Plants, primarily tropical and subtropical lineages, also became selectively extinct (20–70% of the species, depending on latitude). Plant megafossils at the K-T boundary, most strongly in the Northern Hemisphere and less so in the Southern Hemisphere, express ecological catastrophe, some climatic selective extinction of broad-leaved evergreen species as compared with deciduous foliage, and long-term vegetational restructuring from numerous refugia (Fig. 3B). Although 50% of marine genera died out completely, and probably 60–75% of the species, many families of cephalopods and nautiloids survived with only minor evolutionary modifications (Fig. 5). This is also true for most bony fish and tetrapods. Dinosaurs, the symbols of the K-T extinction, died out at different times in different places rather than suddenly and simultaneously worldwide, sometimes surviving the iridium anomaly and sometimes coexisting with Tertiary-type mammals. Nevertheless, the demise of the dinosaurs opened the door to the explosive radiation of placental mammals, leading ultimately, among other lineages, to human evolution.

4. *Cenozoic Extinctions*

Global gradual extinctions, due to climatic change embracing both marine and terrestrial faunas and floras, occurred in the mid-Eocene–Oligocene transition in five steps over 10 My (40, 38, 36, 33.7, and 30.5 Ma), when the world changed from a "hothouse" to a "coldhouse" (Figs. 4 and 5). The major extinction event was caused by proximal cooling, glaciation, and changes in oceanographic circulation at the middle to late Eocene transition (about 40–41 Ma). Warm-humid tropical plants and animals were severely reduced. Lesser extinctions took place at the end of the Eocene (34 Ma), although extinction among taxa was selective. In the early Oligocene (about 33.5 Ma), there was significant cooling and increase of ice volume, which resulted in major changes in land floras and possibly the "Grand Coupure" immigration event in European land faunas. Major Antarctic glaciations marked the middle Oligocene (about 30 Ma), though most aboveground organisms were cold-adapted survivors, and there were relatively few extinctions.

These Eocene–Oligocene extinctions were clearly related to climatic change rather than to extraterrestrial impacts, triggered by the thermal isolation of Antarctica as Australia drifted northward and allowed the development of deep, cold, bottom water. In addition, the world Cenozoic orogenies (Andean, Laramide, and Alpine–Himalayan), which started differentially in the Paleogene across the planet, but were reinforced in the Neogene, complemented the global trend of increasing cooling, drought, and seasonality. The Cenozoic ecological theater of open country biota, starting in the Eocene–Oligocene transition, resulted then from global climatic change, extensive sea regressions, and mountain formation. The subterranean ecological zone was opened for the global convergent evolutionary experiment of adaptive radiation of small mammals underground on all continents, thus avoiding the harsh aboveground Oligocene climate. Likewise, big running mammals radiated in the extensive open biota.

5. *Miocene and Pliocene Extinctions*

Two important rodent extinctions, among other mammals, followed immediately dynamic originations (11.5–11 Ma and 4.2–3.8 Ma). The most important rodent extinction occurred in the middle to late Miocene boundary (11.5–11 Ma) (Fig. 4).

At the Miocene–Pliocene boundary and during the early Pliocene, the faunal turnover seems to increase, thus decreasing mean species duration.

6. Late Pleistocene, Holocene, and Present Extinctions

Dramatic worldwide extinctions occurred during the late Pleistocene and Holocene periods since 50,000 Ya, affecting primarily large mammals (Fig. 6). Although a global phenomenon, late Pleistocene extinctions in northern Eurasia and North America were highly variable in their severity in different regions. In North America, Asia, and Australia, but not in Africa, many of the large herbivores and carnivores became extinct rapidly, between 12,000 and 6000 Ya, with a maximum rate around 8000 Ya, when the climate had become milder and the glaciers were shrinking. South America lost approximately 46 out of 58 mammalian genera (i.e., 80%); Australia lost 15 out of 16 genera (94%); North America lost 33 out of 45 genera (73%) and at least 19 genera of birds vanished; Africa lost only 7 out of 49 genera (14%); Africa south of the Sahara lost only perhaps 2 out of 44 genera (5%); and Europe lost 7 out of 24 genera (29%). Asia also endured only a few extinctions. In general, the larger the animal, the more it was at risk of extinction. Changes in geographic ranges, reassembling into new communities affected, beside extinctions, also the relative composition of world's terrestrial biota. Marine extinctions, however, were insignificant.

IX. THE CAUSES OF BIOLOGICAL DIVERSIFICATION

Biodiversification in the Phanerozoic, in both marine and terrestrial plants and animals, displays generally increasing diversity, not only for species but also for genera and families (Figs. 1, 3A–3C and 7). The general pattern exhibits the rise and fall of families over geological time. J. J. Sepkoski described three basic patterns of marine fauna represented by Newell in spindle diagrams (Fig. 5): *Cambrian Paleozoic fauna:* highest biodiversity of trilobites and inarticulate brachiopods; *post-Cambrian Paleozoic fauna:* highest biodiversity in the Paleozoic (articulate brachiopods, rugose corals, cephalopods, crinoids, and many others); and *Mesozoic and Cenozoic fauna:* dramatic increase in biodiversity after the Paleozoic (bivalves, gastropods, echinoids, teleost fish, and modern fauna) (Figs. 1, 3A–3C, 5, and 7).

Three models of biotic diversification attempted to explain these patterns globally: (1) the *logistical model,* following the ecological theory of island biogeography, where the probabilistic rates of family origination and extinction are diversity-dependent (formulated for islands by R. H. MacArthur and E. O. Wilson, for continents by M. Rosenzweig, and for the planet by J. J. Jr Sepkoski, and (2) the *multiphase logistical model,* which focuses the Competitive interaction between successive evolutionary faunas (Fig. 5). Calculations by L. Van Valen and A. Hoffman based on Sepkoski's compendium of marine fauna in the Phanerozoic show that diversification may be diversity-dependent during low (as in the early Cambrian and Triassic periods) and high (as in most of the Paleozoic beginning in the late Ordovician) biodiversity levels.

Global rates of speciation seem to be independent of diversity. Van Valen, Maiorana, and Hoffman suggested that while the probabilistic rates of family origination and extinction in the Phanerozoic decrease, the family diversity increases with geological time (Figs. 3A–3C). There is no significant intercorrelation between either family extinction or origination rate and diversity. The rates seem to be diversity-independent. Finally, (3) the "*lithospheric complexity*" *model* is another nonequilibrium model for global biodiversity developed by Joel Cracraft, suggesting that speciation and species extinction are determined by environment (climate gradients and barriers, and topographic barriers to migration, etc.). The biosphere in this model can never reach equilibrium and is in a constant flux due to the incessant geological–climatic change, despite mass extinctions that temporarily reverse the trend. Clearly, this model is diversity-independent in contrast to other models, including the famous "Red Queen" hypothesis of L. Van Valen. The Red Queen hypothesis visualizes a never-ending evolution of taxa due to biotic stresses and interactions only, even in the absence of any change in the physical environment. Clearly,

FIGURE 6 Extinction of large mammals in the Upper Pleistocene and Holocene. [From N. D. Newell (1963). *Scientific American*, February, p. 190.]

the dichotomic either/or approach was always wrong in evolutionary studies. To argue that either abiotic or biotic change only predominates is unrealistic. As usual in biology, interactions of complex factors drive evolution. Our present major ignorance is in quantifying the relative importance of the various evolutionary interacting abiotic and biotic forces in the evolutionary process, which involves both diversification and extinction.

X. THE CAUSES OF EXTINCTIONS

A. Overview: Patterns and Theories

Speculation on the causes of extinctions in the geological past dates back to the early days of geology in the early nineteenth century when Georges Cuvier's catastrophism model (1822) was replaced by Charles Lyell's gradualism and W. Whewell's uniformitarianism models. However, little thought has been given to the possibility that mass extinctions might show some regular cyclic pattern. Furthermore, suggestions of driving mechanisms for major extinction events varied from terrestrial, such as gradual or abrupt changes in climate and/or sea level, to sudden extraterrestrial large-body impacts.

The study of mass extinctions only recently became one of the major areas of evolutionary biology. The main factors for this are the spectacular and provocative hypothesis that (1) the latest Cretaceous mass extinction (K-T) was caused by an impact of a huge bolide; (2) mass extinctions are periodic, with a periodicity of approximately 26 million years since the end of the Permian, and are caused by comet showers triggered by an unseen solar companion; and (3) the biotic effects of mass extinctions are qualitatively different from all other phenomena in the history of life on Earth.

Extinction is an evolutionary and ecological problem. All plant and animal species that have been driven to extinction were primarily affected by environmental changes leading to background extinction. Species become extinct because they are unable to cope with rapidly changing environments, being constrained by their own slow evolution, or because their ecological niches disappear and their adaptive repertoire is no longer relevant to the new environments. Or, because of biotic factors (parasites, diseases, and competitors). Both causes, either singly or in combination, can lead to species extinction individually and/or massively. Extinctions are biologically not random, either taxonomically or ecologically. For this reason, extinction must play an important role in the evolution of life in a Darwinian selective sense.

Prediction of the extinction of populations and species requires ecological, demographic, genetic, and evolutionary information. Loss of genetic diversity due to genetic drift or other factors in small populations can diminish future adaptability to a changing environment. Resistance to background ("normal") extinction may be ineffectual during mass extinction. In general, but with many exceptions, groups surviving great extinctions were generalists and conservatives, supporting the idea of "survival of the unspecialized," which was already recognized by Darwin. According to Jablonski, mass extinctions tend to remove not only more clades, but different clades from those lost during times of background extinction. Traits conferring resistance during mass extinctions (e.g., broad ecogeographical range at the clade level) are, according to Jablonski, poorly correlated with traits that enhance survival and diversification during background times. Removal or reduction of dominant groups during mass extinctions provides opportunities for diversification of taxa that had been minor constituents of the preextinction biota. Thus, evolution can proceed in directions not predictable from the background extinction preceding the mass extinction.

Extinction is most pronounced in animals. Each of the three successive land floras, the lower vascular plants (mosses and ferns), gymnosperms, and angiosperms, evolved rapidly followed by a long period of stability (Fig. 7). Extinction may be caused by either or both abiotic (physical) and biotic causes, and/or their interaction, which may predominate. Extinction can operate on individuals, species, higher taxa, and even entire ecosystems.

Background extinction, that is, the ongoing process of the normal rate of replacement of one species

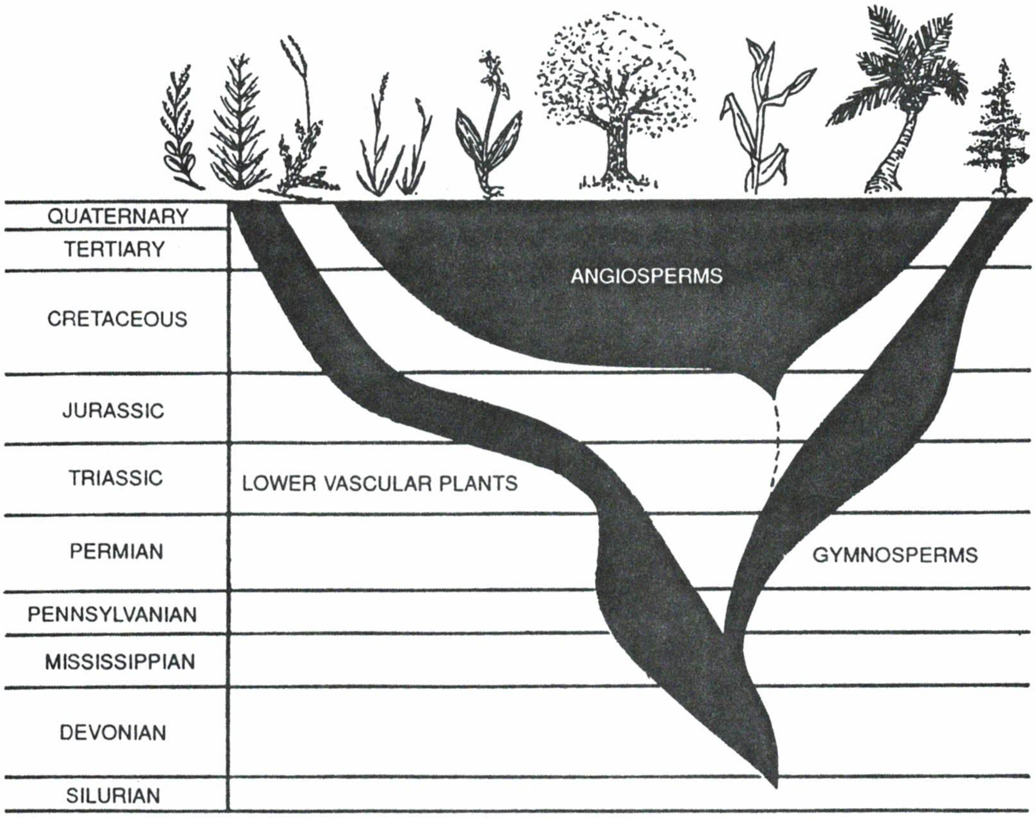

FIGURE 7 Biodiversity trajectory of land plants in the Phanerozoic. [From N. D. Newell (1963). *Scientific American*, February, p. 183.]

by another, known as Van Valen's law, may be caused by physical and biotic factors or their combination. However, their relative importance may vary in space and time and is largely unknown. Recent introduction of predators, competitors, pathogens, and parasites into new areas, primarily islands, either small (e.g., in the Pacific Ocean or West Indies) or large (e.g., Australia), emphasizes the relative importance of biotic factors under relatively slowly evolving environments. However, abiotic factors, such as climatic changes, fluctuations of sea level, and transgression–regression phenomena, occurred throughout evolutionary history and more recently due to the dramatic changes of the global environment resulting from anthropogenic influences.

Transgression-dependent anoxic events have been associated with several extinctions in end-Ordovician, end-Devonian, end-Triassic, end-Jurassic, Cenomanian (mid-Cretaceous), and end-Cretaceous times. The idea of an association of extinction with anoxia–eustatic cycles is generally supported, as claimed by Hallam. Although we have clues as to the combinatorial factors causing specific extinctions (Table I), such as in the late Permian, the relative importance and interaction of the cause(s) in specific extinctions are largely unknown, and no simple current theory of community ecology provides a satisfactory explanatory model. Such a theory is expected to emerge from the integration of current hypotheses and new empirical insights.

Mass extinctions are regarded by some as caused by one single factor, usually the same factor for all extinctions. This could be an extraterrestrial impact, an extraordinary volcanic eruption, or a major paleogeographical, oceanographic, or climatic change, but it is always just one single driving force that is conceived as being the ultimate cause of all extinctions during the time interval interpreted as a mass extinction. D. M. Raup and J. J. Sepkoski suggested in 1984, primarily on the stratigraphic ranges of marine families, that the fossil record of the past 250 My is regularly spaced in geological time and shows a 26-My periodicity caused by climatic changes, meteoritic impact, and other signals in environmental history that may corroborate periodicity. The case for or against extraterrestrial causes of extinctions depend on further clarification of the timing of extinction in the stratigraphic record. However, recent data appear to be more against than in support of "the cause" as a single factor, and also question the periodicity idea.

B. Evaluation of Current Extinction Theories

In-depth statistical analysis challenges the 26-My periodicity. J. A. Kitchell and D. Penna showed in 1984 that the best-fitting time-series model is a stochastic autoregressive model that displays a pseudoperiodic behavior with a cycle length of 31 My for the past 250 My. Periodicity in a time series is insufficient evidence that a periodic external force is causally responsible. Cyclical-like genetic cycles and supercycles caused by cyclical selection (V. Kirzhner, A. Korol, Y. Ronin, and E. Nevo) demonstrated that causality should be evaluated with independent evidence. The periodicity lengthens and weakens when the analysis is extended to the entire Phanerozoic. The history of the probability of extinction for the entire Phanerozoic, based on time-series analysis, has decreased uniformly over Phanerozoic time, whereas the inertia or stability of the biotic system after the late Permian has increased. Moreover, in 1987 S. M. Stigler and M. J. Wagner challenged the 26-My periodicity conclusions on statistical grounds. Important questions concerning mass extinctions include, among others, proximate and ultimate timing (terrestrial, solar, cometary) causes, periodicity, and organismal response. Whether a mass extinction is periodic, pseudoperiodic, or random, and whether the signal is simple or complex, earthbound or extraterrestrial, are now under intensive critical and stringent testing in several laboratories, including broad sampling of evidence for the cause(s).

The supposed 26-My periodicity of extinction since the mid-Permian has also been challenged by the work of C. Patterson and A. B. Smith with fish and echinoderms, which together make up about 20% of the available marine Phanerozoic data analyzed by Sepkoski. Only 25% of these fish and echinoderm extinctions are real, reflecting disappearance of a monophyletic group. The remaining 75% is noise, chiefly involving "extinctions" of nonmonophyletic groups, mistaken dating, and families containing one species only. They concluded that periodicity in their sample is a feature of the noise component, not of the signal. Similarly, family appearances and extinctions in the ammonoids, summarized by M. R. House in 1989, are significantly correlated with temperature and sea level fluctuations, associated with anoxic or low-O_2 events, supporting the species–area theory. The tetrapod record is largely equivocal regarding the theory of periodicity of mass extinctions. Overall, the tetrapod data are suggestive, but by no means conclusive, evidence against periodicity.

Ammonoides lived for about 320 My, from the early Devonian to late Cretaceous. They experienced major extinctions at the end of the Devonian, Permian, Triassic, and Cretaceous, and smaller extinctions primarily in the Paleozoic. Extinctions were preceded by decline in diversity and followed by low diversity and individual abundance. Character novelties were gradually elaborated and diversified as in other taxa. Innovation appears steadier than the rather more spasmodic and irregular extinctions. Earthbound, nonperiodic environmental and paleogeographical changes best explain the evolution and extinction of ammonoids.

Hallam suggested in 1987 that the famous end-Cretaceous (K-T) mass extinctions were not a geologically instantaneous event and were selective in character, with a high proportion of both terrestrial and marine groups surviving with little or no change. Likewise, he has forcefully argued in 1989 the case for sea level change as a dominant causal factor in mass extinction and radiation of Phanerozoic marine invertebrates, on both small and large scales. In many cases, the major extinction factor was apparently not regression, but the spreading of anoxic bottom water associated with the subsequent transgression. The sea level–extinction relation was also formulated ecologically.

An ecological mass extinction model involving mantle–core interactions, at the end of the Paleozoic and Mesozoic, appears plausible. This may involve magnetic field reversal patterns, together with changes in sea level, volcanicity, and climate, causing mass extinctions. Our minds should always be open to alternative scenarios, but we must also entertain a healthy degree of skepticism and beware of simplistic, single-factor models. To what extent the hypothesized large bolide impact was responsible for the K-T extinction, or was merely a contributing or coincidental factor to an already deteriorating environment, is currently being tested and debated by paleontologists. Clearly, the linking of biostratigraphy and chemostratigraphy has great potential for unraveling the evolutionary history of life on Earth.

These features are incompatible with the original L. W. Alvarez hypothesis in 1980 of the K-T extinction being caused by a single asteroid impact that produced a world-embracing dust cloud with devastating environmental consequences. By analysis of physical and chemical evidence from the stratigraphic record, Hallam and colleagues have shown that a modified extraterrestrial model in which stepwise extinctions resulted from encounter with a comet shower is less plausible than one intrinsic to the Earth. The latter involved significant disturbance in the mantle, causing plate tectonics and increased volcanism. Sea level fall and rise, and concomitant increased volcanicity, would also have caused seasonal extremes of temperature on the continents to increase, thus augmenting environmental stress on the dinosaurs. Increased volcanism may cause devastating atmospheric consequences, including acid rain, reduction in the alkalinity and pH of the surface ocean, global atmospheric cooling, and ozone layer depletion, all leading to selective ecological disaster among terrestrial plants and animals.

C. Climatic Causes of Extinction: Patterns and Theory

Climatic diversity is a major determinant of biotic diversity. Climate change might have contributed to both background and mass extinctions. A direct influence for climate on Phanerozoic extinctions has been argued by S. M. Stanley. Slowly changing boundary conditions can cause stepwise or geologically abrupt responses in climate models and result in slow to rapid transition between climate and states. These could cause extinction and/or origination events, that is, negative or positive climatic selection, locally, regionally, or globally. Theoretical and empirical results support the concept of geologically abrupt climate change, that is, those lasting thousands to hundreds of thousands or millions of years. Climate–life transitions often coincide in Earth history. If biotic turnover is indeed significantly affected by climate change, ecosystems may be more sensitive to forcing during early stages of evolution from an ice-free to a glaciated state, as recurred several times in evolutionary history (e.g., Precambrian, Ordovician, Devonian, Eocene–Oligocene, and Pliocene–Pleistocene). Thus, climate instability represents an important mechanism for causing stepwise to rapid environmental change and biotic turnover, in addition to other factors, terrestrial or extraterrestrial.

Long-term climatic change occurred from a "hothouse" to a "coldhouse," or from ice-free Earth in the mid-Cretaceous (100 Ma) to a bipolar glacial state (antarctic and arctic), with periodic glacial expansion into northern midlatitudes in the Cenozoic. These lead to global climatic heterogeneity and seasonality, documented by the oxygen isotope record. Likewise, there has also been significant increase in cooling and aridity during the last 30–40 My, climaxing in the Pleistocene glaciations. This started with the Eocene–Oligocene extinction, the most significant biotic turnover in Cenozoic biota, and continues in our current biota and ecosystems and their catastrophic change and destruction by human activities. Three of the Cenozoic biotic extinctions coincide with climatic change of glaciation and cooling: 31–40 Ma

(Eocene–Oligocene), 10–14 Ma (middle Miocene), and 2.4–3.0 Ma (Pliocene–Pleistocene). Smaller extinctions are also correlated with the O_2 record. Other extinctions are associated with ocean anoxic conditions, and changes in organic carbon, which affected atmospheric CO_2 levels.

Climate model experiments suggest that the long-term trend over the last 100 My may be largely determined by climate changes induced by plate tectonics and mountain formation (orogenies, i.e., earthbound). Similarly, plate tectonics-induced changes in the seasonal cycle may have triggered the Ordovician and Carboniferous glaciations. The climate change in the late Precambrian coincided with the breakup of a supercontinent, analogous to the breakup of Pangaea in the Mesozoic. Over the past half-billion years, the face of the Earth has changed markedly. The pieces of Gondwana assembled during the period 540–300 Ma at the South Pole and united to become the supercontinent Pangaea. The latter moved northward across the equator and eventually broke up to form the familiar continents we find today. These developments may have been linked with an increase in atmospheric CO_2, due to enhanced seafloor spreading rate. This may demonstrate a close global link between geological and climatic changes affecting biotic evolution.

Remarkably, two additional climate–extinction events are well correlated in the Phanerozoic: the late Ordovician (440 Ma) and late Devonian (360 Ma), coinciding with glaciations following long intervals of ice-free conditions. In general, increasing glaciations are associated with sea level fall. The biggest of all extinctions in the late Permian (250 Ma) has often been related to changes in sea level, but glaciation and salinity changes associated with extensive evaporite formation may have been substantial, implicating thermohaline instabilities as a contributing mechanism. The late Triassic extinction occurred during a peak in Phanerozoic evaporite formation. Finally, a significant evolutionary event, the expansion of soft-bodied metazoans in the late Precambrian (after 670 Ma), followed the most widespread phase of late Precambrian glaciation.

Even the celebrated K-T extinction may have involved terrestrial causes such as a general fall in sea level, which might have affected seasonality, and the decrease in ocean productivity, independent from a hypothesized impact. Preliminary evidence indicates that ecosystems may be more sensitive to the climatic stress of cooling (e.g., mid-Paleozoic and mid-Cenozoic) during the initial stages of environmental change. Later, more extensive glaciations had a lesser effect on biota, possibly because of resistance and increasing adaptation of organisms to stress through natural selection. Though multiple causes may contribute to extinction events, terrestrial, geological-climatic, and consequently biotic stresses may override extraterrestrial factors in relative importance.

Two complementary causes seem to be responsible for the Upper Pleistocene–Holocene extinction: climate and humans ("prehistoric overkill"). Climate change, correlating with late Pleistocene and Holocene extinctions, occurred on global, regional, and local scales, as is evident by palynological data. Vegetational shifts occurred across the globe from tundra and boreal conifer forests, from about 18,000 years before present (B.P.) to present closed-canopy deciduous forest starting about 10,000 years B.P., following postglacial warming. During this time the fauna changed drastically, primarily by large terrestrial mammal extinctions. Although a global phenomenon, late Pleistocene extinctions were most severe in North America, South America, and Australia, and moderate in northern Eurasia. In Africa, where nearly all of the late pleistocene "megafauna" survived to the present century losses were slight, but become alarming at present, when apes, elephants, and big game are under very severe wild hunting by humans ("human overkill") (Fig. 6). Climate change today in the composition and chemistry of the atmosphere involves devastating changes of greenhouse gases (carbon dioxide, methane, nitrous oxide, and chlorofluorocarbon-11[D], decreased stratospheric ozone concentrations, and increased ultraviolet input. The consequent increases in ultraviolet radiation, alarming global warming, and pollution are likely to affect drastically biodiversity, ecosystems, agriculture, and human health. Climate model simulations confirm a climatic causation (involving increased seasonality) for the biotic turnover of flora and vertebrate fauna, as described in the foregoing.

Climatic extinctions in the Pleistocene–Holocene times involved mammoths, mastodonts, horses, camels, sloths, and peccaries, among others (Fig. 6). The disappearance of large herbivores led to the extinction of large carnivores and scavengers dependent on them. This model of climatic extinction was designated "coevolutionary disequilibrium" by R. W. Graham and E. L. Jr. Lundelius (1984). The change from Pleistocene to Holocene environments, with major reorganization of vegetational communities, was certainly very unfavorable for large mammals. Each species is considered to have responded independently to the climatic and vegetational changes at the end of the Pleistocene, thus destroying that delicate balance and resulting in extinctions, climaxing at our times.

Across the planet the addition of a new predator, *Homo sapiens,* complemented and aggravated climatic change in causing the terminal Pleistocene extinction. Large herbivores (e.g., ground sloths) became extinct, even though their supposed habitat remained. Artefacts were found associated with 5 of 37 genera of large vertebrates that disappeared (mammoths, mastodonts, horses, camels, and giant tortoises; (Fig. 6), and worldwide extinction of megafauna is roughly correlated with the first appearance of humans in North America. On islands, almost all recent extinctions of species derive from human activity. Victims include New Zealand's moas, Madagascar's giant lemur, and many bird species on Hawaii and other tropical Pacific, Atlantic (West Indies), and Indian oceanic islands. Rarity of species is the precursor of extinction. Small environmental effects can sometimes cause large ecological changes that lead to extinctions.

The modern crisis of extinction is approaching the catastrophic proportions of late Cretaceous times. Current estimates of extinction rates underestimate the actual values by a large factor, particularly in the tropics. The human demand for space, hunting, fishing, lumbering, grazing, farming, road building, deforestation, industrialization, use of insecticides, pesticides, and herbicides, effect of introduced species (biological invasions) and habitat destruction all lead to accelerating destruction of ecosystems, biodiversity, endemic species, and genetic diversity. Pollution, fires, insect outbreaks, disease vectors, alien grasses, and species migration increase the causes of mass destruction, potentially climaxing in the elimination of the delicately balanced and fragile tropical rain forest. [*See* GLOBAL ANTHROPOGENIC INFLUENCES.]

Humans are primarily responsible for the extinction of birds and mammals during the last 2000 years, most significantly on oceanic islands, but also in continental North and South America, Africa, and Australia. The African savannah's big game and tropical forest fauna and flora are under increasing pressure. Both biodiversity and genetic diversity are currently being reduced at an alarming rate, causing the extinction of populations, species, ecosystems, and biotas. At present, the rate of extinction is accelerating and it will likely continue to increase because of the human population explosion. This growth directly led to global changes caused by excessive predation, introductions of competitors and pathogens, habitat destruction (primarily the deforestation of the tropical rain forest), and extensive land conversion for agriculture and industrialization. The distinctly human driving forces of change, or anthropogenic stresses, primarily the catastrophic population explosion from the present 5 billion people to possibly 10 billion in the next century, severely threaten the future of both the biosphere and humans. A contrasting cornucopian economic view assumes that greater numbers of people will help us to solve environmental problems by modern techology and economy. Ecological predictions, however, clearly indicate that future human survival depends on stopping our population explosion and conserving the biosphere.

D. Challenges to Mass Extinction: Simplistic Theories

A. Hoffman and others have recently challenged the periodicity and single-cause models, suggesting that many phenomena designated traditionally as mass extinctions are in fact clusters of extinction episodes roughly associated in geological time, within periods of a few million years (see Table I). He and others suggested that different causes led to the latest Ordovician, late Devonian, mid-Cretaceous, latest Cretaceous, and late Eocene–Oligocene extinctions. Thus, different environmental causes, and coincidental combinations thereof, might lead to extinctions and so they can hardly be considered as individual events. Even the largest of all global extinctions, the Permo-Triassic, attributed by Hoffman to a single factor and characterized as a noncatastrophic extinction (i.e., due to atmospheric and ocean depletion and enrichment of O_2, respectively, causing marine nutrition deficiency), may not be an exception; it involved climatic, tectonic and geochemical change. As rightly emphasized by D. H. Erwin, few complex events stem from a single cause. More common is a complex web of causality, a web that can be difficult to untangle, and the end-Permian extinction is no exception. The most plausible explanation according to Erwin would appear to be a three-phase model combining elements of several mechanisms. The extinction began with the loss of habitat area as the regression dried out many marine basins, converting the two-dimensional coastlines of the mid-Permian to more linear coasts. The increased exposure of Pangaea as the regression progressed exacerbated climatic instability. This instability, coupled with the effects of continuing volcanic eruptions and an increase in atmospheric carbon dioxide (with some global warming), led to increasing environmental degradation and ecological collapse. Furthermore, Hoffman believes that much of the evidence for the 26-My period mass extinction derives from arbitrary, ambiguous, and imprecise decisions concerning geochronometry, that is, he questions the absolute dating of stratigraphical boundaries, the culling of the data base, and the definition of mass extinction as opposed to background extinction. In his view, rapid but apparently staggered appearance of major new taxa, such as at the Cambrian–Ordovician boundary, elevated taxonomic pseudoextinctions. Thus, the apparent periodicity of mass extinctions may result from stochastic processes, and periodicity theory may overdramatize the patterns that are truly obtainable from the fossil record.

Carbon isotope ratios in marine carbonate rocks have been shown to shift at some of the time boundaries associated with extinction events, for example, the K-T and Ordovician–Silurian. The Permian–Triassic boundary, the greatest extinction event of the Phanerozoic (Fig. 3A), is also marked by a large carbon ratio depletion. New carbon isotope results from sections in the southern Alps show that this depletion did not actually represent a single event, but was a complex change that spanned perhaps a million years during the late Permian and early Triassic. These results suggest that the Permian–Triassic extinction may have been in part gradual and in part "stepwise," but was not in any case a single catastrophic event. Both the carbon isotope shifts and the chemical events (including an iridium anomaly) may have causes related to a major regression of the sea.

According to Jablonski, a substantial and rapid fall of sea level seems to provide the best correlation with marine invertebrate mass extinction episodes throughout the Phanerozoic, presumably due to reduction in the neritic habitat area. Climatic deterioration has been claimed as the proximal cause in a number of cases, for example, in the global Eocene–Oligocene and regional Pliocene–Pleistocene extinctions. Clearly, associations between climatic deterioration and extinctions do not always reveal cause–effect relationships. However, if many such associations occur across phylogeny, the causality may become more robust and plausible. One of the major unresolved problems and future challenges in extinction theory is the biological selectivity of victims and survivors.

XI. THE EVOLUTIONARY PROCESS

The evolutionary process is based on several major driving forces and their interactions, including mutation (in the broad sense), recombination, migration, natural selection, and stochastic processes. Unfortunately, we know very little even today about their relative importance in the evolution of natural populations and the role of evolutionary constraints. Clearly, however, genetic diversity in nature is the basis of the evolutionary process through its twin processes of speciation and adaptation (i.e., in successful originations), but it also may substantially affect the probability of extinction. The evidence derived from extant natural populations of plants and animals, at the local, regional, and global scales, is best explained by ecological heterogeneity and change in space and time. These involve physical (climatic, geological, hydrological) and biotic (pathogenic, predatory, and competitive factors) changes and stresses. It is plausible to assume that the interaction of abiotic and biotic ecological heterogeneity and stress are also the major determinants of background and mass extinctions, according to the extent and severity of the stress.

Natural selection, in its various forms and in combination with stochastic factors, appears to be a major differentiating and orienting force of evolutionary change at the molecular (genotypic) and organismal (phenotypic) levels, locally, regionally, and globally. This holds primarily at the individual level, but also at higher, group selection levels (species and higher taxa) in the taxonomic hierarchy all the way up to whole biota. Likewise, it presumably assumes a major role in originations and extinctions across individuals, species, ecosystems, and biota. Critical testing and analyses, in nature and the laboratory, are still greatly needed to substantiate this conclusion. Theory should attempt to cope with the accumulating evidence at the single and multilocus genetic structure of protein and DNA levels and their interface with developmental biology and organismal evolution, as well as in origination and extinction. The explosive accumulation of genetic maps (locus maps of complex genomes) will substantially highlight evolutionary patterns and processes. Clearly, evolutionary success, in overcoming environmental stresses and even global changes, depends at least partly on the genotypic and phenotypic (morphological, physiological, and behavioral) resources available during ecological crises at all scales, local, regional, and global.

Microevolution appears to extend smoothly into macroevolution. Alternative views have been voiced by leading paleobiologists, including Gould, Eldredge, Stanley, and Vrba, who argue for a hierarchical model in which macroevolution is decoupled from microevolution. The aforementioned basic evolutionary forces appear to operate at all levels. However, selection at higher taxonomic and ecosystematic levels may be important in evolution. The instability of arctic and subarctic species has been advocated by C. S. Elton. In contrast to intuition, as emphasized by R. May, stability becomes less likely in complex ecosystems like the tropical rain forest. Complex ecosystems are composed of numerous food chains involving primary producers (diversifying according to light, temperature, water, and nutrients) and secondary consumers (herbivores, predators, and parasites). Hence, these complex ecosystems are vulnerable to slight, domino effect changes, because they may be at the transition phase between order and chaos. This was emphasized by S. A. Kauffman in his 1993 discussion on the origins of order and the roles of self organization and selection in evolution.

XII. CONCLUSIONS

The universe unfolds a large-scale evolution of order emerging from chaos and primordial uniformity. The expanding and inflating universe, following the Big Bang 15 Ba, evolved in a hierarchical cosmic order of galaxies, quasars, stars, planets, and life. The emergence of life and later consciousness from inanimate matter are wonders equal in significance to the cosmic birth. Organisms evolved from star stuff and the atoms comprising their bodies were born in primordial nuclear fires at the birth of time or were derived from dying suns. The solar system was born about 4.6 Ba. Life's origin is still a scientific mystery, although its evolution from inanimate matter is highly plausible and decipherable. Overwhelming geochemical, biochemical, biological, and fossil evidence reveals that life originated about 3.8 or possibly 4 Ba. Based on replication, metabolism, and transmission of information over generations, life evolved relentlessly over time at varying tempos.

Overall, the evolution of life displays an increase in biodiversity and complexity of organisms, ecosystems, and biota. Although originations proceeded to increase biodiversity, background regional and global mass extinctions recurred through the Earth's history, always followed by innovation and diversification. Originations and extinctions, that is, the stuff of evolution, are associated primarily with terrestrial abiotic (geological, climatic, environmental) and biotic (parasites, diseases, predators, competitors) factors. Extraterrestrial impacts (asteroids, comets, bolides) might have affected the evolution of life, but their relative importance may be secondary, and at any rate are currently hotly debated. The disentangling and assessing of the relative importance of terrestrial and extraterrestrial factors may prove hard to resolve, but the paramount importance of climate–life interactions is indisputable. Likewise, though several massive extinctions clearly recurred in the Phanerozoic, the predominant background and mass extinction of species, ecosystems, and biotas, analogous to individual mortality, has operated through evolution, opening ever-new ecological niches for life's evolutionary experimentation, innovation, and emergence.

The dogged evolution of life from simple lifeless objects to complex living organisms is based on a combination of stochastic and deterministic factors. However, from molecular to organismal evolution, and from the original few life-forms that evolved from inanimate matter to our current all-time high biodiversity and complexity, evolution has been primarily dominated by natural selection despite its strong interaction with stochastic processes.

Cosmic evolution, on physical, biological, and cultural (human) levels, appears to display a trajectory from simplicity to complexity. This trajectory toward increasing complexity depends on self-organizing, materialistic, physical, chemical, and biological laws. Cosmic evolution seems to have been continuous ever since the Big Bang, about 15 Ba to the present. The universe may either proceed to expand relentlessly or crush and recycle, depending on cosmic conditions. As long as the sun provides planet Earth with free energy, and unless extraterrestrial, astronomical, terrestrial, or human forces destroy the biosphere, life's evolution will keep ticking without any obvious target except that of better survivorship against all odds and expansion by adaptive radiations into all open ecological niches.

Evolution is based on a unified chemical language and genetic code, generating an infinite biodiversity of individuals, populations, and species. Thus, unity and diversity are the cornerstones of ever-increasing biological evolution. Only humans can instill meaning in this ongoing game of survival. Only humans can understand the past and present and attempt to responsibly plan and control the foreseeable future.

The origin of the mind from living matter, together with the origin of life from lifeless matter and matter's origin from radiation after the Big Bang explosion, are the three highlights of universal history. The mind reveals evolutionary insights, wonders, and mysteries and manifests the evolution of biodiversity within a unified cosmic evolution, proceeding from chaos to increasing order and diversity. Mind's cosmic awareness closes the circle of thinking matter consciously and scientifically examining and reflecting on its own origins and past, present, and future evolution. Though cosmic evolution may seem comprehensible but meaningless, the relentless search for origins and evolutionary patterns and processes, as well as for beauty and harmony, is the mind's meaningful creation. A human, as suggested by David Bohm, is "a microcosm of the universe." Understanding and seeking truth, wondering and enjoying the beauty and mysteries of the macrocosmos and microcosmos, may be the only meaningful creations generated by our mind.

As so aptly said by Albert Einstein, "The most beautiful experience we can have is the mysterious. It is the fundamental emotion which stands at the cradle of true art and true science." Moreover, as cogently written by physicist Steven Weinberg, "The effort to understand the universe is one of the very few things that lifts human life a little above the level of farce, and gives it some of the grace of tragedy." Unquestionably, a unique and deep grace, wonder, and mystery inhere to a fragment of the universe that aspires to comprehend the whole. In a sense, the universe came to know itself. Cosmic evolution indeed displays the most dramatic holistic saga ever: the lawful, stepwise, and gradual evolution of energy and simple matter into the immense complexity of life, and the slowly yet ever-increasing level of biodiversity since 4 Ba, with new forms replacing old ones (background extinction), occasionally set back by mass extinctions. The climax of that Primeval Fireball is the evolution of thinking-matter, brain-mind, capable of reflecting on the origin and evolution of life and our place in the universe.

Glossary

Hubble's law The reddening of light from a star that is moving away from us due to the Doppler effect, which states that velocity is proportional to distance, i.e., the change in the observed frequency of a wave due to relative motion of source and observer. This leads to Hubble's law, which states that velocity is proportional to distance.

Infinite density The density of the universe at the Big Bang when density and the curvature of space-time would have been infinite. The Big Bang is the singularity at the beginning of the universe, that is the point in space-time at which the space time curvature becomes infinite.

Irregularity The early state of the universe, which shows no definite order or shape.

Nucleosynthesis, or nucleogenesis The theoretical process(es) by which atomic nuclei could be created from possible fundamental dense plasma.

Symbiosis An association of dissimilar organisms to their mutual advantage.

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