

The Fossil Record

■ CHANGING IDEAS ABOUT THE CHANGING EARTH

The past is no longer with us. To reconstruct it, we have to look at the traces that it has left in the present. Discerning those traces and figuring out their meanings is not a simple task. It has taken over 300 years for scientists to arrive at the methods that we rely on today in using the present to resurrect the distant past.

Ideas about the remote past began with pre-scientific speculation about the formation of the earth. When our ancestors looked at the landscape around them, it was not obvious to them that it contained a record of slow changes over an immense period of time. Most of the changes in the earth's surface that are noticeable to a human observer are small, swift, and local. After a storm, water running off deforested hills may cut gullies in the soil. Further downstream, that same floodwater may cause a muddy river to overflow its banks and deposit a layer of silt for miles around. At long intervals, an earthquake may shift a piece of land by a few inches, or a volcano may shower a region with ash and spill lava down its slopes.

Changes of this sort have been noticed and commented on since the dawn of history. But few of us ever see all four of these processes—erosion, sedimentation, tectonics, and vulcanism—working to alter the landscape in the course of our own lifetimes. Until about 250 years ago, nobody seems to have thought about how these forces might combine over millions of years to produce the rocks, soils, mountains, and valleys of the earth.

Throughout most of the history of Western thought, speculation about the history of the earth has been constrained by the sacred poetry of the Hebrew scriptures, in which the voice of God from the whirlwind reproves would-be geologists in words of the gravest majesty:

Where wast thou when I laid the foundations of
the earth?
declare, if thou hast understanding.
Who hath laid the measures thereof, if thou knowest?
or who hath stretched the line upon it?
Whereupon are the foundations thereof fastened?
or who laid the cornerstone thereof;

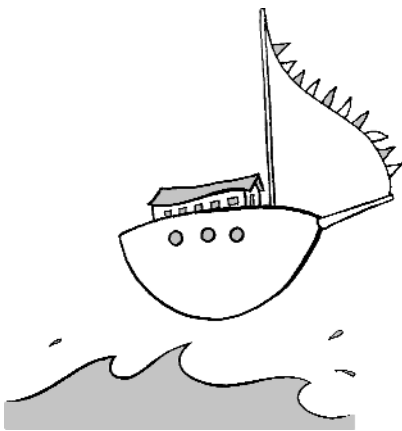
When the morning stars sang together,
and all the sons of God shouted for joy?

These lines from the Book of Job represent God as a divine mason building a world with floor plans, foundations, and a cornerstone. Few people took this poetic metaphor literally. But the creation story in Genesis, which tells how God shaped the face of the earth and planted it with grass and trees in the course of a single day, was taken very literally indeed (and still is, in some quarters). Reckoning forward from the first day of that Creation by adding together the ages of patriarchs and the reigns of kings listed in the Old Testament, biblical scholars reasoned that the universe had to be less than 6000 years old. Some Christian authorities fixed on a date of 4004 B.C. for the beginning of the world. Jewish scholars numbered the years of their calendar from a supposed Creation date equivalent to 3760 B.C.

As long as this short time scale was accepted, floods, earthquakes, and volcanoes could not be thought of as having produced the rocks and topography of the earth. The changes wrought by these processes were too small and slow to have brought the present landscape into being in a few thousand years. The minor changes that people could actually see happening in the face of the earth tended to be regarded as blemishes on the original work: signs of decay presaging the approaching end of the world, or marks left by outbursts of God's wrath.

The biggest such outburst was thought to have been the Flood of Noah, in which God had supposedly submerged the whole world under water in order to get rid of sinful humanity (see Blind Alley #1). As evidence of that universal Flood, many people pointed to the seashells and fish bones found in rocks far above the present level of the sea. Those fossil shells and bones seemed to bear out the truth of the Genesis

Blind Alley #1: The Flood Story



People all over the world recount tales of disasters long ago that ravaged the earth and threatened humanity. In the ancient Near East, the Sumerians, Babylonians, and Hebrews told stories about a great flood sent by the gods to wipe out the wicked human race. In the Babylonian version, the goddess Ishtar incites the gods to drown the world. Her plan is foiled by the god Ea, who instructs the hero Utnapishtim to build a huge vessel and load his family and all the world's animals aboard it. Safe in the ship, the people and beasts weather a great storm that destroys all other living things. After sending out a dove, a sparrow, and a raven to seek land, Utnapishtim grounds his ark on Mt. Nisir and offers a burnt sacrifice. The gods gather around, repent their acts, and promise never to do it again.

The similar flood story in the Old Testament is another member of this family of Near Eastern legends. But because it was part of sacred scripture, Jews and Christians long accepted it as historical fact. When they found fossil shells in rocks lying hundreds of feet above sea level, they took them as confirmation of a great flood that had drowned the mountains and laid down the fossil-bearing strata. When they dug up ancient human artifacts and remains, they described them as "antediluvian"—that is, dating to a time before the Flood.

The biblical Flood story has implications that can be checked out. If all the fossilized organisms died at the same time a few thousand years ago, then all the fossil-bearing rocks should contain fossils of people and other extant creatures. But they don't. If the Ark saved all the world's animals from destruction, there shouldn't be any extinct species in the fossil record. But there are. (Almost all fossil species are extinct.) If all the animals dispersed from the Ark's landing site on Mt. Ararat, then the world's faunas should grow less and less diverse the further away they are from Turkey. They don't. If enough rain had fallen to cover all the land—raising the seas an additional seven miles—then the total rainfall would have amounted to some 1.4 billion cubic miles of fresh water. How did all that water dry up in 150 days (Genesis 7:24)? Where is it now?

And so on. None of the implications of the biblical Flood story check out. It was not until this old Mesopotamian legend had been set aside that the building of scientific theories about the history of the earth's rocks, animals, and plants could begin in earnest.

story, but they also posed certain problems. For one thing, they were not really shells and bones. Most of them were composed of minerals like those found in the surrounding rocks. Some insisted that the seeming plants and animals imbedded in the rocks were not really the remains of once-living things, but just *lusi naturae*, “games of nature”—freakish, abortive organic forms produced by mysterious creative forces inherent in the stone itself. But the fossils’ detailed similarities to bones, shells, and leaves made this hard to credit.

In 1669, Nicolaus Steno, a Danish physician living in Italy, published a book that used fossils to help interpret the history of the earth. Rocks that contain fossils are always organized into **strata** or layers. We can see these layers exposed wherever a quarry or cliff face cuts a vertical section through such rocks. Different layers contain rocks of different composition: Beds of smooth slate may alternate with gritty sandstone or coarse conglomerates containing pebbles of yet another sort of stone. Steno argued that all these layers had been formed when sediments were discharged into lakes or seas by rivers, settled to the bottom, and became cemented together. Fast-moving streams carried coarse sediment that became sandstone or conglomerates; broad, slow rivers carried silt that gave rise to slate and other fine-grained rocks.

The fossils imbedded in these rocks, Steno insisted, truly were the remains of creatures that had lived in or near the seas and lakes. He showed that strange triangular fossils long known as “tongue stones” were identical to the teeth of living sharks and that other fossils found with them were clearly the remains of other sea creatures. The rocks containing such fossils, he argued, must have been laid down on the ocean floor. Other rocks, containing the remains of land plants and animals, had probably been formed from fresh-water sediments.

The layers of sedimentary rock are usually more or less horizontal, as you would expect beds of sediment to be. However, Steno recognized that some of them are tilted or folded. He concluded that the originally flat layers of sediment must have been worked on later by powerful disruptive forces capable of bending or breaking thick beds of solid stone. Steno suggested that these layers had been first lifted above the sea and then undermined by the formation of huge internal caverns. When their roofs fell in, these collapsed caverns became valleys, in which the fallen roof fragments lay as beds of tilted rock. The remaining elevations were left as mountains. Streams running down these mountains then carried silt and gravel down into the valleys, which gradually filled with new sediments.

All these ideas were generally rejected in Steno’s own day, but they influenced later geologists (Gillespie

1959, Gohau 1990). Three of Steno’s basic postulates—the sedimentary origin of rock strata, the organic nature of fossils, and the rule that overlying strata are younger than those below them—are still fundamental assumptions in reconstructing the histories of the earth, of prehistoric life, and of ancient human activity.

■ NEPTUNE VS. VULCAN

The rise of industrial economies in northern Europe in the 1700s lent new practical importance to theories about the history of the earth. As the prosperity of nations began increasingly to depend on mineral wealth, it was worth money to understand how these resources were distributed in the rocks. It was obvious that there were patterns there to be understood. The coal and metal ores that the new industrial order needed were not scattered around in random pockets. They tended to occur in particular strata, sandwiched in between layers of other sorts of rock. Miners had long ago learned to identify these mineral-bearing strata on the surface and dig down after them into the earth.

Amateur scientists began to trace and study these stratigraphic patterns. In the 1740s, a French physician named Jean Guettard, whose hobby was collecting plants, noticed that certain species of plants were found only where the underlying rocks were of certain sorts, such as limestone or chalk. Mapping the distributions of these plants, he found that their associated rocks were arranged in bands that ran across the map of Europe, sometimes for hundreds of miles. Guettard concluded that these bands represented the exposed edges of superimposed sheets or layers of rock, which had been laid down atop one another as sediments at the bottom of the sea.

If the landscape really had been carved out of stacked-up layers of sedimentary rock, then it might be possible to reconstruct the story of the earth’s creation by reading upward through those layers, starting at the bottom with the oldest rocks of all. One of the first people to try this was a German scholar named Johann Lehmann. Lehmann distinguished three major phases in the formation of the earth. He thought that the oldest rocks, which had no fossils in them, had precipitated out of a planetary suspension of liquid mud during a primitive period before the creation of life. This “Primary” period corresponded to Day 1 of the Genesis creation story, when “the earth was without form, and void.” Later rocks, containing fossil remains of plants and animals, had been laid down over the Primary rocks during the Flood of Noah. Overlying these “Secondary” strata was a third, superficial layer of recent deposits formed by erosion and volcanic action.

These ideas formed the nucleus of the first systematic theory of earth history, developed and promulgated from the 1780s on by Abraham Werner, a professor at Freiburg in Germany. Werner adopted Lehmann's account of the series of Primary and Secondary rocks. His main contribution was his explanation of volcanoes. Werner taught that the earth's deposits of coal and petroleum had been laid down during the Secondary period. When some of these flammable minerals caught fire, the heat had melted the surrounding rocks and produced volcanic eruptions, spreading sheets of lava in places on top of the Secondary strata. These strata of **igneous rocks** (rocks formed by melting) represented a brief third or Tertiary period of rock formation. Finally, erosion and floods had deposited soil, gravel, and other loose sediments on top of everything else during the most recent period, the Quaternary. Because Werner and his followers thought that almost all geological formations had been formed by the action of water, they came to be known as **Neptunists**, after the Roman god of the sea.

Their opponents argued that certain ancient rocks that the Neptunists called sedimentary were in fact volcanic in origin. For this reason, the anti-Neptunist school were sometimes referred to as **Vulcanists**. Rejecting the notion that different rock-forming processes had operated at different periods of the earth's history, the Vulcanists insisted that the forces seen at work on the landscape today—erosion, sedimentation, volcanoes, and earthquakes—had worked together throughout geological time in the same way they do now and that together they were sufficient to account for all the observable features of the earth.

This doctrine—that the laws and processes that operated in the past are the same ones we see operating in the world around us—is called **uniformitarianism**. The eventual acceptance of the uniformitarian principle was crucially important in the maturation of geology into a genuine science. It also helped to lay the groundwork for Charles Darwin's application of a similar uniformitarianism to the study of biology (Gould 1986). However, scientists today do not regard the uniformitarian principle as entirely valid over the long run. For example, the universe is now thought to have originated in an explosive cosmic event called the Big Bang, which involved processes and forces no longer at work in the world we observe. The formation of the solar planets from condensations of interstellar dust surrounding the newborn sun was another one-time-only process that has no counterpart in today's solar system, though we can get some insight into it by studying other stars younger than our own. The history of the earth and its living organisms has been profoundly affected by asteroid impacts and other catastrophic global events, which we (luckily enough) have never had a chance to witness in the brief span of human history.

But over the span of time that concerns biologists, from the origin of life some four billion years ago down to the present, the uniformitarian principle is true enough for most practical purposes. The small, local forces that we can see reshaping our landscapes today suffice to account for the formation of the rocks of the earth over the vast duration of geological time. They provide the geological background for the history of life.

■ A BRIEF GUIDE TO SEDIMENTOLOGY

Most of the fossils that paleontologists study are the remains of marine life, buried ages ago in the rain of fine mineral particles and organic detritus that falls ceaselessly through the oceans of the earth to accumulate as mud and sand on the sea bottom. When mud and sand are themselves buried and compressed by overlying sediments, they tend over millions of years to become cemented together by chemical solution and recrystallization, forming hard, dense rock. In much the same way, sugar granules in a bowl will “petrify” into a single stony lump if they get damp and then dry out again. The process takes vastly longer for sand than it does for sugar because silica is far less soluble than sucrose.

The texture of the resulting rock, as well as its suitability as a medium for the preservation of fossils, depends mainly on the size of its constituent particles. The size of those particles depends in turn on how fast the water around them was moving when they were deposited. A swiftly rushing mountain creek will wash away pebbles and gravel together with sand and silt and carry them all downstream. As it flows into flatter country and slows down, it no longer has enough kinetic energy to move the larger bits of rock. One by one, they tumble to the bottom and form deposits of coarse sediment. The smaller particles remain suspended in the water and travel further downstream. Wherever the stream speeds up, it picks up larger particles; wherever it slows down, it drops them. By the time it reaches the ocean as a broad, slow-flowing river, it may have nothing left in it but a thin suspension of clay minerals. Borne out to sea by the currents, this sediment eventually settles to the bottom as a fine-grained mud—the first stage in the formation of shale. Similar processes of sedimentation take place on a smaller scale at the bottom of lakes, or on plains flooded by overflowing rivers.

At the edges of the continents, the action of waves breaking against the rocks has the same sorts of effects that stream runoff has on dry land. High, energetic waves tear loose sizeable chunks of stone and rub them against each other in the surf until all their rough edges are worn away and they become smooth,

rounded pebbles. A lot of the rock particles produced by wave action get carried away by ocean currents, in which the particles sort themselves out by size just as they do in a river. Big pieces drop out immediately and form stony bottoms or pebble beaches near the shoreline. Sand travels further, so sandy deposits extend further away from the zone of wave action. Far out to sea, most sediments are fine-grained and may contain a high proportion of organic material. Rocks formed from such sediments are often largely made up of fossil shells and other remains of sea life. For example, the thick beds of chalk that accumulated in many areas near the end of the age of the dinosaurs are composed mainly of the calcareous shells of tiny one-celled animals called foraminifera. In general, the finer the sediment, the more likely it is that the remains and impressions of dead organisms buried in it will be preserved as fossils.

Sediments can also be formed on land by the action of air or ice. Winds blowing across dry, dusty soils can carry small particles away and deposit them as sand dunes, or as deposits of fine silt called **loess**. The particles in such windborne deposits are small, since blowing air is far less energetic than rushing water.

Rivers of flowing ice, on the other hand, can carry huge boulders for long distances. These ice rivers, called **glaciers**, form wherever the snow that falls during the winter does not melt entirely during the summer. In these chilly places, snow builds up year after year, becoming compressed into thick layers of dense ice. The weight of the accumulating ice forces some of it to begin moving away from the areas of buildup, flowing downhill with what is appropriately called “glacial” slowness. As it flows, the moving ice breaks away big and small pieces of the rock beneath it, scouring out characteristic U-shaped valleys like a carpenter’s gouge running across the earth.

When it reaches a warmer area where snow melts faster than it accumulates, the glacier melts too. As the rock fragments imbedded in a flowing glacier reach its melting edge, they fall to the ground, depositing a jumble of boulders and gravel known as a **glacial moraine**. If a flowing glacier reaches the sea before it melts, it may form or add to an oceanic ice sheet, which rides on top of the waves (because ice floats in water). The edges of such ice sheets eventually break off as icebergs and drift out to sea. Melting, they may drop big intrusive chunks of continental rock called **dropstones** into the fine sediments of the sea floor many miles from land. Like moraines, dropstones in fine-grained sedimentary rocks are an indicator of the presence of ancient glaciers.

Near the poles, where temperatures remain frigid year-round, sheets of glacial ice may cover the sea permanently and become three or four kilometers thick over land areas. There have been several periods in the

earth’s history when these polar ice caps spread toward the equator, covering large areas of the temperate zones with ice. These periods are called **ice ages** or **continental glaciations**. The continental ice sheets that form during an ice age swell and shrink periodically, retreating toward the poles during **interglacial** phases and advancing again during **glacial maxima**. The effects that these fluctuations had on the course of human evolution during the last great ice age, the **Pleistocene** epoch, are debated by scientists. We will return to these debates in the later chapters of this book.

At the moment, the only large land areas covered by continental ice sheets are Greenland and Antarctica. But Northern Hemisphere ice sheets extended far south into North America and Eurasia during the last glacial maximum, about 20,000 years ago. Geologists infer the former presence and extent of these ice sheets from signs of glacial erosion and from moraines deposited at the melting edges of long-vanished ancient glaciers. In reviewing the prehistory of human populations in northern Eurasia, it should be borne in mind that some evidence of early human presence at high latitudes may have been destroyed by the erosive forces of continental glaciation.

■ DATING THE ROCKS

The dispute between the Neptunists and the Vulcanists hinged largely on the question of the age of the oldest igneous rocks. This issue could not be entirely settled until there was a generally agreed way of telling which rocks were older. It was easy enough to do this as long as geologists looked at a single locality where rock strata lay on top of each other. In a given geological section, the strata higher up are always younger than those lower down in the section (if you make allowances for occasional folding and twisting). But no single section contained a sample of all time periods and rock types. It was therefore hard to say whether a layer of shale in, say, Scotland was of the same age as a similar-looking shale in Pennsylvania.

The key to this puzzle lay in the fossils imbedded in the sedimentary rocks. In the 1790s, the young English surveyor and engineer William Smith began a systematic study of the rock strata of Somerset, where he had been hired to supervise the construction of a canal. He found that the stacked-up sequence of successive rock types was different in different sections through the earth, so that a bed of red sandstone that was overlain by a layer of gray shale in one canal cut might be covered by a layer of brown sandstone in another. But the sequence of fossils was always the same from cut to cut. Therefore, the distinctive **index fossils** that were restricted to a particular part of one section could be used to match that part up with different rocks in

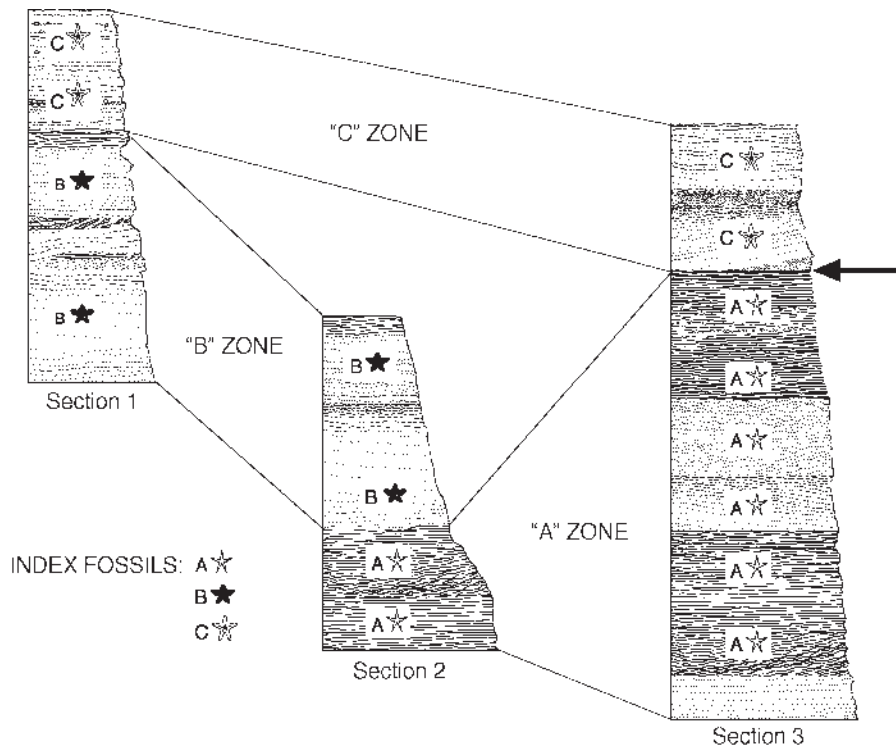


FIGURE 1.1

William Smith's principle of dating rocks by their fossils. If strata containing fossils of the species B are always younger (higher in the section) than those with A, and strata containing C are always younger than both, then these species can thus be used as **index fossils** to determine the relative ages of rocks containing them. The composite **stratigraphic sequence** diagrammed here comprises three successive units, the "A," "B," and "C" zones, though no one section contains all three. Section 3 does not contain a "B" zone, implying that it was a site of erosion rather than deposition during that period. The inferred gap or **unconformity** in this section (*arrow*) is usually also reflected in an interrupted pattern of sedimentation at that time horizon.

other areas and assign them all to the same time period (Fig. 1.1).

Armed with this insight, Smith began to classify and organize the rocks of southern Britain on the basis of the fossils they contained. With the help of a local minister who collected fossils as curiosities, he began in 1799 to publish a series of maps, charts, and books bearing such titles as *A Delineation of the Strata of England and Wales*. Other scientists soon began to build on Smith's work and to extend his system to other lands and strata. Smith lived to see himself hailed on all sides as the pioneering founder of the science of stratigraphy before he died in 1839.

The use of index fossils is the basis of **biostratigraphy**, often referred to as faunal or floral dating. Since no single locality preserves the entire record of life on earth, scientists must correlate strata from different sites in order to determine their relative ages and fit them into a single time sequence. This process begins with the tallying up of the shifting lists of organisms found in successive strata at a single site. This sequence is then

compared with similar sequences from other sites in the same area. Of course, two strata from the same time period will not always contain exactly the same suite of organisms, particularly if these strata represent different ecological zones or come from sites that are far apart from each other. Within a region, however, certain key organisms will usually be characteristic of a specific time period. By comparing the biostratigraphic sequences of the sites in a localized area, scientists can work out the time relationships between them and piece them together to form a regional biostratigraphic column. Then by comparing sites that overlap two contiguous regions (or ecological zones), a picture of relative stratigraphic relationships on a broader scale can be formed.

While Smith was walking along his canal cuts in Somersetshire and laying the foundations of stratigraphy in his mind, the Scottish gentleman farmer James Hutton was putting the final touches on his 1795 masterwork, *Theory of the Earth*. In this book, Hutton laid out detailed evidence for believing that a single set of rock-

forming processes had operated throughout the history of the earth. Hutton contended that the small-scale geological processes that could be observed acting in the present were the same processes that had fashioned the large-scale features of the earth's topography: Mountains were the result of slow uplift, and valleys and deltas were the result of gradual erosion and deposition by rivers and streams. He argued that the fossil-free "Primary" rocks, which the Neptunists saw as condensations from a worldwide suspension of some nebulous primordial ooze, showed clear signs of having been formed in the same ways as later rocks—either through the consolidation of silt and sand and pebbles washed into the world's waters by waves and streams, or through the solidification of molten stuff belched out of the earth's interior through volcanic vents. The same subterranean heat that had melted those rocks, Hutton suggested, had in some way produced buckling or heaving movements of the crust of the earth, raising former sea beds into the air to form mountains. He surmised correctly that some ancient rocks, which we now call **metamorphic**, represented sedimentary deposits that had been considerably altered by the action of heat and pressure inside the earth. Hutton insisted that all these processes had gone on throughout geological time and were still going on today. His arguments implied that the earth must be much older than was generally thought, because it would have taken an enormous amount of time for these processes to produce the current landforms. God, Hutton concluded, had created the earth as a perpetually working machine like the Newtonian solar system, perfectly designed and exquisitely balanced to keep turning over forever. In a famous phrase, he declared that the study of the earth disclosed "no vestige of a beginning, no prospect of an end."

■ THE SUCCESSION OF FAUNAS

From the union of Smith's stratigraphic principles with Hutton's uniformitarianism, the science of historical geology emerged during the early 1800s. The canonical expression of this synthesis was the English geologist Charles Lyell's massive compendium, *Principles of Geology*, published in 1830. Lyell's *Principles* had a major influence on Darwin's *Origin of Species* (1859) in at least three respects: it provided an exemplary model (of a big theoretical work supported by masses of empirical detail), it established gradual uniformitarian transformation as the normative mode of large-scale prehistoric change, and it demonstrated that the age of the earth was great enough to allow for the production of life's diversity through the slow, imperceptible processes of evolution that Darwin postulated.

The great task facing the early geologists was the reconstruction of the **geological column**—the overall

sequence of the rocks of the earth throughout its history (Fig. 1.2). No one locality preserves the column in its entirety, because there is no place on the face of the earth where sediment has been building up without interruption for four billion years. The longest single exposure is that seen in the cliff faces of the mile-deep Grand Canyon in Arizona, but even this sequence dates back only some 1.75 billion years—and about half of that time span is represented by gaps in the sequence, produced during periods in this region's history when erosion outpaced the deposition of sediments.

The complete geological column therefore has had to be pieced together by collecting fossils and rock samples from all over the world and bringing them back for publication and comparison. Two centuries of dangerous, painstaking, difficult labor and the lives of thousands of scientists have gone into this reconstruction. The job is still far from being completed, but what has been accomplished so far is one of the greatest triumphs of the scientific enterprise.

It became obvious early on in this undertaking that the creation story in Genesis was not a satisfactory account of the history of the earth. First of all, it was clear that in spite of the supposed labors of Noah and his sons, most of the species that had once lived were now extinct. In fact, this was what made Smith's stratigraphic methods work. If all the plants and animals that had ever lived were still alive today, rocks of all ages would contain the same species. Index fossils could be used to order the earth's rocks only because species had finite life spans. The mortality of species was a disturbing discovery.

Different rocks not only contained different species, they contained different *kinds* of species. Only the very youngest rocks preserved the remains of creatures much like those living today. As one traced the history of life downward through the geological column, the fossil animals and plants became more and more alien. Human remains and artifacts, for example, were restricted to the Quaternary deposits at the very top of the column. Below these, the Tertiary rocks contained various sorts of fossil mammals—but the mammals found in lower Tertiary strata were not at all like those of today. Still further back in time, there were no fossil mammals whatever, and the only large land animals were fearsome dragonlike reptiles, sometimes of gigantic size. Before that, no land animals of any sort could be found, and all the earth's organisms had apparently lived in the sea. And at the very bottom of the column, one encountered the fossil-free rocks of the Primary series, whose sediments seemed to bear witness to an unthinkable expanse of time when there had been no living things on the face of the earth.

The scientists of the early 19th century weighed two alternative interpretations of all these uncomfortable facts. One possibility was that ancient species had from

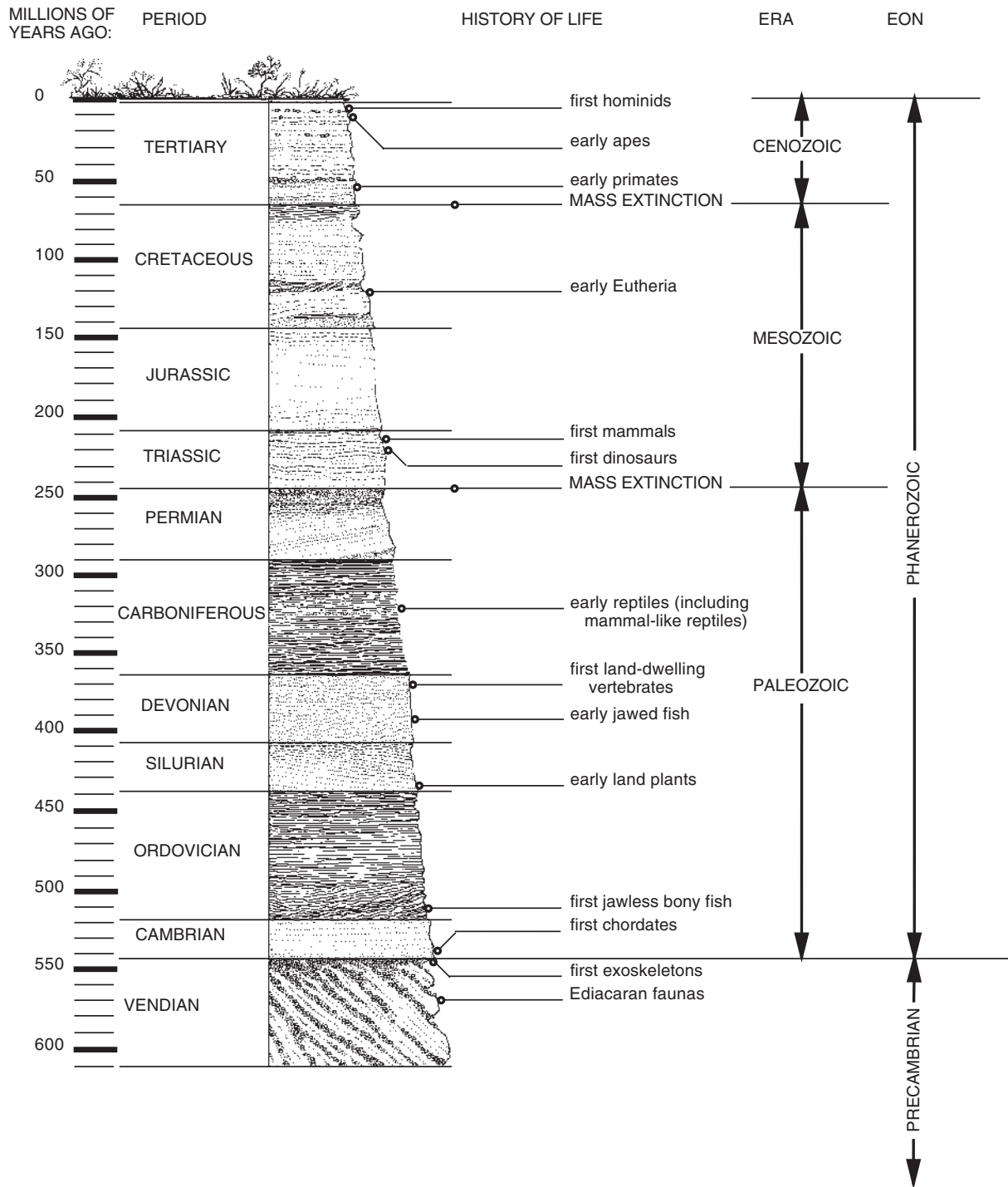


FIGURE 1.2

The geological column, showing the sequence and age of the principal stratigraphic units and some major events in the history of the human lineage.

time to time been obliterated and succeeded by specially created species belonging to new, more advanced types. The French paleontologist Georges Cuvier argued that the abrupt transitions from one stratum to another in the geological column represented brief periods of convulsive change in the earth's surface, in which most

of the planet's life forms had been wiped out (Cuvier 1831). After each of these catastrophes, new species had been created to rule the earth during a long, peaceful period of uniformitarian change. Many followers of this doctrine of **catastrophism** did not hesitate to see the hand of God at work in this cycle of extinction and

rebirth, and the final catastrophe in Cuvier's scheme was often identified with the Flood of Noah.

There were two major problems with catastrophism. The first was that it violated the uniformitarian principle, by postulating processes of episodic destruction of a kind and magnitude unknown to human experience. The second was that it provided no explanation for the generation of new species. Some catastrophists invoked divine intervention to account for the periodic creation of new forms of life. But this sort of miraculous "explanation" was scientifically unacceptable. (A science of miracles is a contradiction in terms.) Even from a religious standpoint, it was not entirely satisfactory. Why, after all, would an all-powerful God obliterate all his living creatures from time to time and start afresh with new, improved versions, instead of producing the desired product in the first place? Surely he was not creating life over and over because he needed the practice.

The other way out of this dilemma was to adapt Hutton's model of the earth as a perpetually working machine and to suppose that today's life forms had come into being through gradual transformation of the earlier, more primitive species. This so-called **development hypothesis** was articulated in different ways by Charles Darwin's grandfather Erasmus Darwin (1794) and a few thinkers of the early 1800s, including J.-B. Lamarck (1809), E. Geoffroy Saint-Hilaire (1830), and R. Chambers (1844). But the development hypothesis was not highly thought of by most experts, because it too seemed to violate the uniformitarian principle. No one, after all, had ever witnessed one species evolving into another one. Cuvier pointed to the mummies of animals recovered from Egyptian tombs, which were estimated to be 3000 years old but displayed no differences from their modern counterparts (Ferembach 1997). This fact, he argued, shows that species have no tendency to change through time. The development theorists could only reply that 3000 years was evidently not enough time to produce detectable changes, and that it must have taken hundreds or thousands of millions of years to accumulate all the transformations seen in the fossil record. Many people found it hard to accept these enormous expanses of time.

■ RADIATION-BASED DATING TECHNIQUES

How could this question be settled? The stratigraphic methods used to reconstruct the geological column would not do the job. All they could provide were dates for one stratigraphic unit *relative to others*, based on the principle of superposition (the rule that stacked-up strata had been deposited in chronological sequence, with the ones on the bottom being older than those overlying them). These **relative dates** allowed geolo-

gists to determine that, say, rocks containing fossils of trilobites were everywhere older than rocks containing dinosaurs and that strata containing a particular species of trilobites were probably contemporaneous with strata at other localities containing the same species. But biostratigraphy was of no help in determining how many thousands or millions of years had passed since a particular layer of rock had been laid down.

Some tried to attach such **absolute dates** to the geological column by estimating how many millimeters of sediment get deposited each year on the bottoms of today's oceans and then comparing these estimates to the number of meters of rock found in various stratigraphic units. But sedimentation rates, erosion rates, and thicknesses of strata vary too much from place to place to be very useful as clocks. About all that could be said for sure was that it had taken many hundreds of millions of years to build the sedimentary rocks of the earth. To produce reliable absolute dates, geologists needed to find some physical process that proceeds at a constant rate in all times and places, producing changes in the sedimentary rocks that could be measured to determine how much time had elapsed since the rock was first laid down.

Such processes began to be identified in the 1950s, as scientists made use of the phenomena of radioactivity to develop **radiometric dating** techniques. Unstable atoms "decay" by emitting or absorbing subatomic particles and changing into something else. For example, the unstable carbon isotope **carbon-14** (^{14}C) undergoes "beta decay" by emitting an electron (beta particle) and changing into an atom of nitrogen-14 (which is stable). These decay events are unpredictable; but their average rate across a large sample of ^{14}C atoms is constant. It takes 5730 years for 50% of the atoms in a sample of ^{14}C to turn into nitrogen-14. After another 5730 years has gone by, half of the remaining C-14 will have turned into nitrogen, and the sample will be 75% nitrogen—and so on. The period of 5730 years is called the **half-life** of the ^{14}C isotope.

If we found a sealed-up canister labeled "pure carbon-14" and we wanted to know how long it had been sealed up, we could find out in two ways. First, we could take a sample and determine the ratio of nitrogen to ^{14}C in it. (The more nitrogen in the canister, the older the contents must be.) Second, we could measure the rate at which the canister's contents give off beta particles. The lower the rate of emissions, the smaller the percentage of ^{14}C remaining must be—and therefore, the older the contents are.

We do not find sealed canisters of once-pure ^{14}C in ancient archaeological sites, but we find something just as useful: tissues from dead animals and plants. Carbon-14 is produced in the earth's atmosphere at a more or less constant rate through the action of cosmic radiation on carbon dioxide molecules. Plants incorporate the

radioactive CO_2 into their tissues, and ^{14}C moves up the food chain from there. When plants and animals die, they stop assimilating ^{14}C from their environments. The ^{14}C remaining in their dead bodies gradually disappears through beta decay, while the stable isotopes of carbon remain unchanged. We can therefore determine how old a site is by determining the ratio of ^{14}C to other carbon isotopes in wood or bones from the site. We can do this either directly (through mass spectrometry) or indirectly (by measuring beta radiation).

Carbon-14 dating (also known as **radiocarbon dating**) has its complications and shortcomings. The rate of production of ^{14}C is not constant, because it varies with the amount of CO_2 in the atmosphere. Moreover, some organisms have physiologies or ways of life that cause them to assimilate less ^{14}C than other organisms do. As a result, not all organisms have the same percentage of ^{14}C in their tissues at death. Carbon-14 dates have to be corrected to take these sources of error into account. And even when all the error factors are compensated for, bone or wood that is older than about 50,000 years has too little ^{14}C left in it to be used for dating. With a time depth of only 50,000 years, ^{14}C dating is useful to archaeologists but has little utility in most paleontological contexts.

Carbon dating has other limitations. Because the death of an organism is required to start the ^{14}C “clock” running, radiocarbon can only be used to estimate an age for bone, wood, or other organic materials. It cannot be used to directly date a mineral sample or a stone tool. Even in dealing with biological materials of suitable age, there is an ever-present risk of postmortem contamination of the sample by carbon compounds of later origin. There are techniques for detecting contamination in samples, but they do not always work. These sources of error introduce uncertainty into any radiocarbon date. A ^{14}C date (or other radiometrically derived date estimate) is therefore always followed by an error estimate—for example, $25,850 \pm 280$ years. The error estimate usually represents the 95% confidence limits on the date, meaning that the estimator calculates that the chances are 95 out of 100 that the true age of the sample lies within the plus-or-minus range.

A relatively new and more precise technique called **accelerator mass spectrometry** (AMS) allows ^{14}C dates to be obtained from much smaller samples, and may in theory allow us to extend the time range for radiocarbon dating back to as much as 100,000 years ago (100 Kya). In practice, AMS has yet to extend the range of ^{14}C dating very much, because contamination is an even more serious problem when tiny amounts of ^{14}C are being used. Differing sample preparation techniques can also alter AMS age estimates by as much as 10% (Higham et al. 2006). Nevertheless, AMS has two major virtues: it can reduce the error estimates on ^{14}C dates when circumstances are favorable, and it allows

the direct dating of irreplaceable fossils without significant damage to them. Used with care, AMS radiocarbon dating has helped to provide a more accurate chronology for the later stages of our biological history.

But what about the earlier stages of that history, where even the most sophisticated radiocarbon techniques are of no use? Fortunately, there are lots of other radioactive isotopes with longer half-lives. One such isotope is potassium-40, which decays into the inert gas argon-40. It has a very long half-life—about 1.25 billion years. In certain minerals, the decay of an imbedded potassium-40 atom leaves the “daughter” argon atom trapped in the rock. If the rock is melted, the argon escapes. The ratio of potassium-40 to argon-40 in a volcanic rock can therefore be used to estimate how long ago the molten rock cooled into a solid form capable of trapping argon. Many rocks of volcanic origin can be dated using this **potassium–argon dating** technique. It is not as precise as radiocarbon dating, but it works over a far greater span of time, from around 2.8 billion years ago down to the present.

The major limitation of potassium–argon dating is that it can only be used on certain volcanic minerals. A fossil itself cannot be directly dated; and its geological context can be dated by potassium–argon only if that context is defined by strata of volcanic origin. In recent years, traditional potassium–argon dating has been largely replaced by the argon-40/argon-39 technique. This technique is more precise and can be applied to mineral samples that mix elements from more than one volcanic event. Argon–argon dating has been particularly useful in East Africa, which has been a hotbed of volcanic activity for the past ten million years. Other parent–daughter pairs of isotopes (and the parents’ half-lives) that are used in dating various sorts of rocks include rubidium-87/strontium-87 (48.8 billion years), uranium-235/lead-207 (704 million years), and uranium-238/lead-206 (4.47 billion years). Again, each of these dating techniques has its own limitations and restrictions.

When radioactive atoms give off particles, they often do damage to materials in their vicinity. The ages of some materials can be estimated by measuring the amount of accumulated radiation damage. For instance, fissioning atoms of uranium-238 embedded in the crystals of certain minerals spit out energetic particles that leave tiny **fission tracks** in the crystalline material. Melting the crystal obliterates these tracks. The time elapsed since the material was last melted can therefore be estimated by comparing the number of tracks with the amount of ^{238}U remaining in the material. Sources of error in this method include the production of irrelevant fission tracks by external radiation sources (e.g., cosmic rays) and the erasure of fission tracks by high temperatures that soften the crystalline minerals. When such errors can be ruled out or corrected for, this

technique of **fission-track dating** is useful for dating rocks ranging in age over the whole length of the geological column, from the oldest Precambrian strata up to a few thousand years ago.

When crystalline minerals absorb energy from radiation, electrons may become trapped within imperfections in the crystal lattice. Heating the material causes these electrons to escape, producing light. The amount of light produced by heating depends on the amount of radiation that has been absorbed—which in turn depends on the time that has elapsed since the material was formed or last heated. The elapsed time can be estimated by measuring either the light emission when the sample is heated (**thermoluminescent dating**) or the effect of the trapped electrons on the magnetic properties of the material (**electron spin resonance dating**, or **ESR**). These dating techniques can provide estimates for ages of two My (million years) or less. They are often used on fossil tooth enamel. Because buried rocks and fossils receive different amounts of radiation at different sites, these techniques must take account of such variable factors as the amount of uranium dissolved in the local ground water. They accordingly have relatively large margins of error, in the neighborhood of 15%. With ESR, date estimates will vary depending on whether it is assumed that the uptake of uranium occurs soon after burial (**early uptake**, EU) or is taken up at a constant rate after burial (**linear uptake**, LU). EU generally yields lower age estimates than LU. Either model might provide the more accurate date estimate, depending on the details of the particular case. However, LU date estimates usually agree more closely with dates obtained using other radiometric techniques (Schwarz and Grün 1992, Grün 2006).

For all of these radiation-based techniques, the range of error of the estimated dates can be reduced by applying them to multiple samples of the same material and taking an average. Two or more techniques can also be used to cross-check each other by applying different tests to different materials found in the same stratigraphic level. Within their margins of error (which are usually less than 10%), all these dating techniques give consistent dates across the time span of the geological column. They allow us to infer that trilobites became extinct around 250 Mya (million years ago) and that the dinosaurs died out some 185 My after that.

■ OTHER DATING TECHNIQUES

Many organic molecules exist in two forms, left-handed (L) and right-handed (D, from Latin *dexter*, “right”), each a mirror image of the other. The amino acids that link together to form proteins in living organisms are all of the L type. As time goes by, some of them will flip over into the D configuration at predictable rates. In a

living animal or plant, these right-handed amino acids are continually being removed and replaced by left-handed equivalents. But after death, they begin to accumulate in the degraded proteins of the dead organism at a rate that varies with the temperature of their surroundings. Eventually, the ratio of L to D forms will stabilize at 1:1, producing a so-called “racemic” (equal-ratio) mixture. When amino acids persist in ancient bones, teeth, or wood, the ratio of L to D forms can provide an estimate of the time since death. This technique of dating by **amino acid racemization** (AAR) can be used to estimate the age of organic material as old as 6 My. Because the rate of racemization depends on temperature, these estimates have large margins of error (around 20%). Early AAR dates were generally too old because the racemization rate was at first misestimated (Bada 1985). AAR estimates are also very susceptible to contamination by extraneous amino acids. As a result of all these problems, AAR is generally no longer used on bone. However, AAR dating on ostrich eggshell and some mollusk shell has shown more promise (Miller et al. 1993, Johnson and Miller 1997).

Similarly large sources of error attend other dating methods that depend on fluctuating environmental variables. These include **obsidian hydration dating** (based on the thickness of the hydrated surface layer that forms on buried stone tools), **fluorine dating** (based on the amount of fluorine that organic materials absorb from groundwater) and **uranium-series dating** (which depends on the rate of absorption of uranium isotopes into calcite crystals precipitating out of calcium-rich groundwater). Uranium-series dating incorporates a series of different decay phenomena, each of which has its own half-life and its own sources of error. All these methods can be used with more confidence to determine the *relative* ages of specimens from a single site. For example, one technique that helped to expose the “Piltdown Man” hoax (Chapter 6) was fluorine dating, which showed that the fraudulent fossils had been buried only recently in the gravels where they were found (Weiner et al. 1953).

■ DATING BASED ON THE CYCLES OF THE EARTH

When sediments are deposited in still water, iron-containing minerals in the sediments tend to line up with the earth’s magnetic field. The resulting rocks retain a magnetic signature showing which way the compass needle pointed when they were laid down. When this **remanent magnetism** is measured across a sufficiently long stratigraphic sequence, it becomes apparent that the earth’s magnetic field changes polarity at irregular intervals, so that what was previously the north magnetic pole becomes the south pole and vice versa. This produces a succession of “normal” and “reversed”

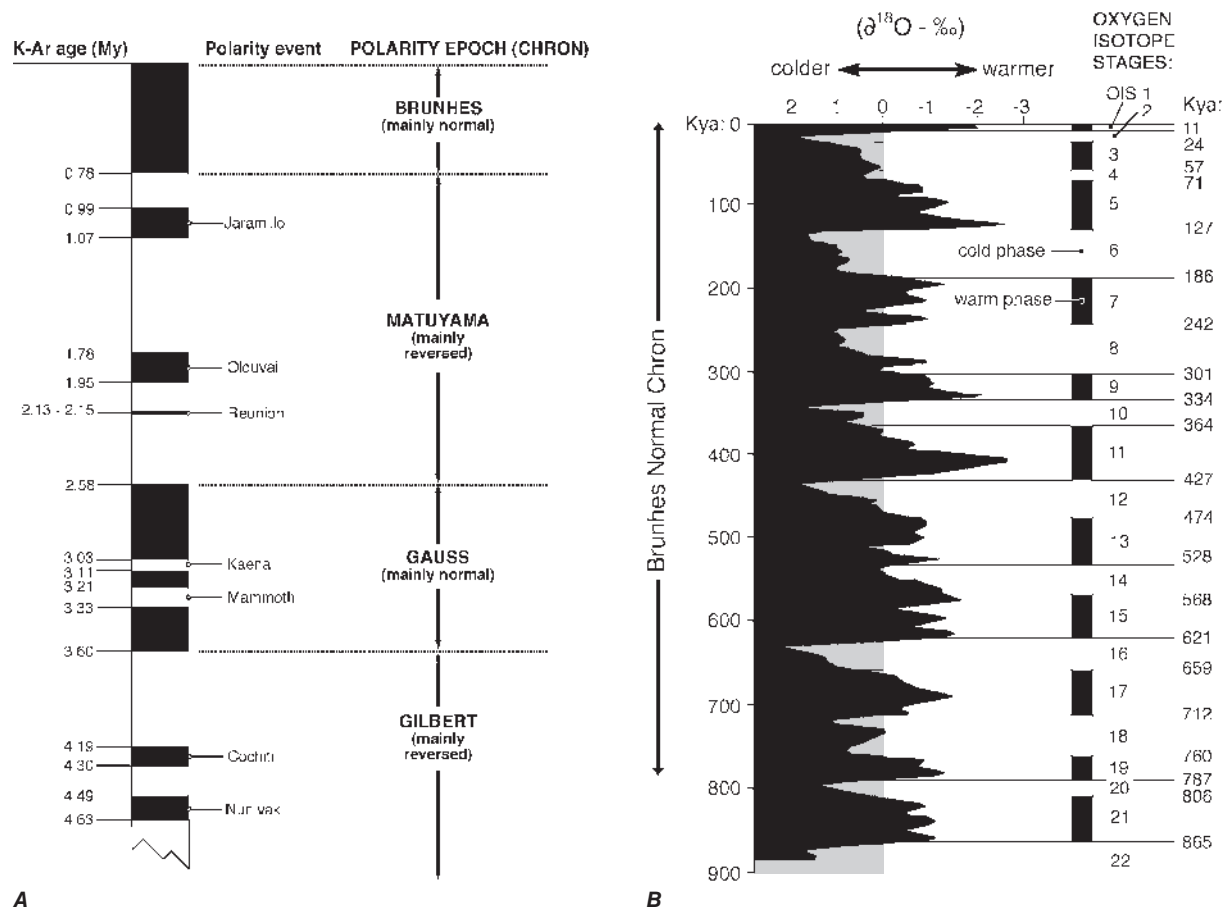


FIGURE 1.3

Geochronological sequences. **A:** Sequence of normal and reversed geomagnetic periods for the late Cenozoic. **B:** Alternation of warm and cold periods across Oxygen Isotope Stages 1 through 21, inferred from oxygen-isotope ratios in fossil foraminifera. The boundaries between stages are drawn on the basis of Milanković cycles. (After Butler 1992, Klein 1999, and Gradstein et al. 2005.)

periods of varying length (Fig. 1.3A), which is the same everywhere in the world. The magnetic “signature” of a rock stratum can therefore help to determine its age.

Inferring a date from a paleomagnetic sequence is no easy matter. Simply identifying a **reversal** (from normal to reversed polarity or vice versa) is not enough, because it must be determined which reversal it is. To do this, a date must be found for some part of the sequence using other techniques. Without such chronological anchors, a local reversal might correspond to any number of different reversals in the global paleomagnetic sequence. For example, the preferred dates for the Gran Dolina site at Atapuerca in Spain are now some 300,000 years older than those originally presented, because it was determined that the local paleomagnetic sequence had to be shifted back one reversal event on the global chart (Chapter 5).

Earth’s history has witnessed countless climatic changes, many of which led to major shifts in the types

of organisms inhabiting the oceans and land masses of the planet. Many of the climatic changes that have occurred during the last 65 million years, and probably during earlier periods as well, can be explained by the astronomical theory of M. Milanković (or Milankovitch). Milanković noted that the motion of the earth through space fluctuates in a predictable way with respect to such variables as the shape and position of the earth’s orbit, the angle of the axis of the earth’s rotation, and the wobble of the earth on that axis as it spins. These **Milanković cycles** (Imbrie and Imbrie 1979, Berger et al. 1984, Berger 1992) all have different periods, and so they continually move in and out of phase with each other. When the cycles line up in a certain way, the earth’s atmosphere receives less sunlight, and the planet grows cooler. During the coldest phases of these cycles, mean annual temperatures at high northern latitudes were as much as 16°C colder than they are today. Even near the equator, mean temperatures dropped some

3–5 °C, and intermediate regions experienced intermediate amounts of cooling (Stanley 1989).

The most recent of these cooling events resulted in a fluctuating advance and retreat of continental ice sheets during the **Pleistocene epoch** (Flint 1971, Van Couvering 2000a,b; Stanley 1989). The Pleistocene (from the Greek meaning “most recent”) lasted from around 2 Mya until the latest retreat of the continental ice some 12 Kya. The Pleistocene was characterized by a series of climatic oscillations between cold **glacial** periods and warmer **interglacial** phases. In the colder periods, annual snowfall exceeded annual snowmelt in high latitudes and at high altitudes, resulting in the growth of glaciers. Tremendous amounts of water became tied up in these masses of ice, and sea levels fell correspondingly. At the last glacial maximum, sea level was 100–140 m lower than it is today (Flint 1971). Within the glacial periods, there were brief episodes of warmer temperatures characterized by small-scale ice retreats. These periods are called **interstadials**, and the intervening periods of maximal cold are known as **stadials**. By convention, the term “interglacial” is restricted to the warmest periods of the Pleistocene, when glaciers were completely absent from temperate lowland regions. We are living in one such interglacial period. Geologists exclude this latest interglacial from the Pleistocene and dignify it with its own special name as the **Holocene** or Recent epoch, mainly because it contains us.

In 1909, A. Penck and E. Brückner defined four Pleistocene glacial maxima on the basis of their observations in the Bavarian Alps. These glacial periods were named (from oldest to youngest) the Günz, Mindel, Riss and Würm. This four-phase scheme was subsequently extended to all of Europe. Similar systems were adopted for other northern continents, and the four glacial periods were thought to correspond to “pluvials” (periods of increased rainfall) in Africa. But over the years, it became increasingly clear that this scheme was far too simplistic and that the whole Pleistocene world did not march in time to the same four-beat pattern (Van Couvering 2000b).

The complexity of Pleistocene climate fluctuations is most clearly seen in sediments sampled by drilling into the deep ocean bottoms, where sedimentation is unremitting and the Pleistocene stratigraphic sequence contains few gaps (Shackleton 1967, 1975, 1987, 1995; Bassinot et al. 1994). The distribution of oxygen isotopes in microfossils from these sediments provides an indirect record of planetary temperatures. Ocean water contains two stable isotopes of oxygen, ^{16}O and ^{18}O . Both isotopes combine with hydrogen to form water (H_2O). When seawater is evaporated from the oceans and deposited in glacial ice, those water molecules formed with ^{16}O are evaporated more easily than those with the heavier ^{18}O isotope—and so the proportion of ^{18}O to ^{16}O in the remaining ocean water is increased.

When oxygen gets incorporated into the skeletons of foraminifera and other marine organisms, the $^{18}\text{O}/^{16}\text{O}$ ratio in these remains reflects the ratio present in the seawater at the time these animals lived. We can therefore measure the amount of water locked up in ice—and therefore estimate the overall temperature of the earth—by determining the $^{18}\text{O}/^{16}\text{O}$ ratio in the fossil shells trapped in sea-bottom sediments.

The **oxygen-isotope stages** (OIS) for the past 900 Ky are presented in Fig. 1.3B. By convention, the odd-numbered stages represent warm periods, with OIS 1 being the current or Holocene interglacial. Designating the present as an interglacial period may be a bit unnerving, but the expert consensus is that the Pleistocene is not over and that we can expect the glaciers to return. In fact, data from the deep-sea studies indicate that the intensity of each successive glacial advance has tended to increase over the most recent glacial periods (Stanley 1989). This could mean that the next one will be a humdinger—unless the well-documented human influences on today’s climate disrupt the Milanković cycles.

The OIS chart reveals 11 glacial periods during the last 900 Ky, but there are also numerous stadials and interstadials in each of the 22 OIS recognized here. It may be significant that none of the warm phases over this period are quite as warm as OIS 1—except for the last major interglacial, OIS 5e. None of the other warm periods reach this level (Fig. 1.3B), and they are of rather short duration (perhaps 10–15 Ky). Maybe the glaciers will be returning sooner than we think! The dates given for the temperature fluctuations shown in Fig. 1.3 of course cannot be inferred from the $\delta^{18}\text{O}$ data themselves and must be determined by other methods, including both radiometric and relative dating techniques.

■ THE PROBLEM OF OROGENY

Until the middle of the 20th century, there was a big mysterious piece missing from geological theory. It seemed clear that sedimentary rocks had been formed by the accumulation of mud, sand, and gravel under lakes and seas. But it was not clear how these rocks had been lifted above the waters to become exposed on dry land. The lifting processes, whatever they were, had to be at least as powerful as the processes of erosion, or else the continents would long ago have been worn away by ice, wind, and rain and scattered as sediment beneath the waves.

In the aftermath of an earthquake, it was sometimes found that a block of the earth’s crust had been thrust upward a few inches along one side of a crack or **fault** in the rock. Such faults often extended for hundreds of miles. Perhaps sudden sliding or slipping movements along these faults were the cause of earthquakes. Study

of the sedimentary rocks on opposite sides of fault lines showed that movement along some faults had continued in the same direction for a long time, so that once-continuous rock formations had become displaced from each other by many vertical feet or horizontal miles. If this process of earth movement went on long enough, it might result in the buckling of the moving crust and the formation of mountains.

It was evident that faults, earthquakes, and **orogeny** or mountain-building all had to be connected somehow. The newest mountains (the ones that are highest, least eroded, and most jagged) invariably are found in areas rich in faults and shaken frequently by earthquakes—for example, along the western edges of North and South America. But what colossal forces could be responsible for shoving vast chunks of the continents around and heaving beds of solid rock up out of the ocean floor to stick up miles above the sea surface?

Some 19th-century geologists conjectured that the earth is still cooling from its original molten state, and that as it cools it shrinks. In theory, the shrinking of the earth might cause the crust of the dwindling planet to wrinkle and buckle like the skin of a drying apple, producing mountains and valleys. But this account did not explain why the mountainous “wrinkles” were found in some regions and not in others. And as more was learned about geophysics, it became clear that the earth is not cooling at all—that it in fact continually gives off more energy than it receives, radiating surplus heat produced in its interior by the decay of radioactive atoms.

■ CONTINENTAL DRIFT

In 1915, a German scientist named Alfred Wegener proposed that all the continents of the earth had at one time been fused together into a single immense land mass. He called this imaginary supercontinent Pangaea, which is Greek for “all earth.” Wegener marshaled data from geography, stratigraphy, and paleontology to support his ideas. He showed, for instance, that the Atlantic edges of Africa and South America fit together like pieces of a huge jigsaw puzzle and that when the two were put together, the older stratigraphic rock formations of one continent matched up neatly with those of the other.

Wegener also noted that his theory would help to account for the otherwise puzzling distribution of certain plants and animals. There are some groups of organisms that are found on all the southern continents but do not occur in more northern lands, either alive or as fossils. If the continents had always held their present positions on the globe, these taxa would have had to get into Africa, Australia, and South America by traveling through Eurasia and North America without leaving any traces of their passage. But if those southern continents had been attached directly to each other in the

past, their shared fauna and flora would no longer pose a mystery.

Wegener’s hypothesis of **continental drift** was listened to with interest and mentioned politely in geology textbooks. But it was not taken too seriously for many years, because Wegener was unable to come up with a plausible mechanism that could have moved the continents around in the way his theory required. The rocks of the earth’s crust are of two basic sorts: magnesium-rich igneous rocks such as basalt, which form the bedrock of the ocean basins, and lighter and softer rocks rich in aluminum, which make up the substance of the continents. Wegener’s theory seemed to demand that the soft rocks of the moving continents had somehow plowed their way through the harder and denser rocks of the ocean basins, like a ship made of butter sailing through a sea of clay. This was clearly impossible.

The mystery was gradually cleared up in the 1950s and 1960s, as research ships began exploring the topography and stratigraphy of the deep ocean floor. It was found that the basaltic rocks of the ocean basins are divided by fault lines into **crustal plates**. These plates are in motion relative to each other. In some places, adjoining plates are moving apart, leaving gaps or **rifts** in the crust, through which molten rock from the earth’s mantle wells up to form new basalts and chains of volcanic mountains. In other places, where plates are colliding, the edge of one plate is riding up over another, heaving the buckling edge of the top plate skyward to form jagged new mountain ranges and forcing the bottom plate down into the mantle to be remelted.

The movements of the continents are now thought to be driven by convection currents produced in the hot, fluid rock of the mantle by the planet’s internal heat. As the basaltic rocks move around and around in these great, slow cycles of subduction and re-eruption, they carry the lighter, overlying continents along, tearing them apart and thrusting them together like islands of froth circulating on the surface of a gently simmering pot of soup. The resulting theory of **plate tectonics** has solved the riddle of orogeny, filled the old gap in our understanding of sedimentary processes, and vindicated the insights of Alfred Wegener.

The continual disappearance or **subduction** of crustal material into the planetary interior contributes to the steady loss of ancient rocks. The earth has had a solid crust for over four billion years, but the oldest rocks known are less than 3.8 billion years old. All the older rocks have long since been drawn down into the mantle, or have been eroded away and redeposited as new sediments on the ocean floor. Because rocks do not last forever, older rocks get harder to find as we move down the geological column—and so the fossil record becomes more and more fragmentary the farther back

in time we look. We accordingly know far more about the origins of humankind than we do about those of (say) vertebrates; and we know almost nothing at all about the origin of life itself.

■ LIFE: THE FIRST THREE BILLION YEARS

Although the origin of life is still a mystery, we have a fairly detailed idea today of what it would take to upgrade nonliving carbon-based molecules into self-reproducing systems. Because carbon is one of the most common chemical elements, the rocks and air of the early earth must have contained a lot of simple carbon compounds—carbon monoxide and dioxide (CO, CO₂), hydrogen cyanide (HCN), hydrocarbons, and so on—just as many of the sun's other planets do. Once the ocean had condensed out of the earth's steamy primitive atmosphere, some of these carbon compounds would have dissolved in its waters. Others would have floated in oily wisps on the sea surface. When concentrated in certain favorable sites—by natural distillation in evaporating lagoons, for instance, or by binding to the surface of clay minerals—these compounds could have reacted with each other and combined to produce somewhat more complicated organic molecules, including amino acids, sugars, purines, and pyrimidines. Polymerized amino acids are **proteins**, and polymerized sugars with purines and pyrimidines attached are **nucleic acids**—and proteins and nucleic acids are the key constituents of life.

The major stumbling block in understanding the origin of life is a chicken-and-egg problem. In today's world, the nucleic acid DNA carries the hereditary information in all self-reproducing organisms. DNA needs specific protein catalysts to replicate itself. But those protein catalysts are themselves synthesized by reading out instructions coded in the DNA. It is not clear how instructions for making the proteins needed to make DNA could have gotten encoded in a DNA molecule. The first self-replicating molecules may have been compounds capable of catalyzing their own synthesis—for example, ribonucleic acid (RNA), which carries the hereditary information in some viruses (Orgel 1998). Perhaps proteins and nucleic acids teamed up only belatedly, after a long period of independent evolution. At the moment, we have no way of telling. We may never know until we find and study other earthlike planets. It is hard to understand phenomena, such as the origin of life or of the universe, for which we have a sample size of one.

Once a molecular complex appeared that was capable of making copies of itself, natural selection would have begun to work on those copies, preserving any variations that out-reproduced the others. Naked molecules of nucleic acids that turned up in local puddles of

organic chemicals may have been the first self-copying systems. However, they could not spread beyond those puddles until they became enclosed in some sort of envelope that let them take a bit of the puddle along. Resembling a stripped-down version of a modern bacterium, the first living cell would have been a minute droplet of a watery solution of proteins and other chemicals, wrapped in a fatty cell membrane to separate it from the surrounding water. It contained a single strand of DNA, which carried the necessary information to produce several different sorts of proteins. Those proteins catalyzed the cell's metabolic processes (including DNA replication), participated in the cell membrane, and operated to produce more proteins from the genetic instructions coded in the DNA.

The smallest and simplest self-reproducing systems on earth today are almost this simple. These tiny organisms, called **mycoplasmas**, are biochemical cripples that need to get their food and energy by absorbing fairly complex molecules directly from the surrounding fluid—for example, in human lungs, where they cause a form of pneumonia. The earliest cells may have made a meager living in this way by floating around in the thin organic soup of the early ocean, waiting to bump into nourishing molecules of ammonia and sugar.

More advanced microorganisms, including bacteria, are more self-sufficient. A key step in the evolution of self-sufficiency was the development of enzymes that enabled microbes to make their own sugar. Some of them did this, as some bacteria still do, by using light energy from the sun to drive metabolic reactions that combined the smelly gas hydrogen sulfide (H₂S) with CO₂ to yield the sugar **glucose** (C₆H₁₂O₆) plus elemental sulfur (S) and water: $12\text{H}_2\text{S} + 6\text{CO}_2 \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 12\text{S} + 6\text{H}_2\text{O}$. The main disadvantage of this strategy is that H₂S is not very common. A later modification used different light frequencies to power more complex reactions in which the ubiquitous compound water, H₂O, replaces H₂S in the system, so that oxygen instead of sulfur is given off as an end product: $6\text{CO}_2 + 6\text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$. This new process of **photosynthesis** was a great evolutionary success. Bacteria equipped with it, known as **cyanobacteria**, rapidly became the most abundant life forms in the ancient oceans, and they remain one of the most abundant forms of life today.

Life could not have come into being until around 4 billion years ago, when the earth's surface had cooled enough to let liquid water condense on it. Filaments of carbonaceous matter found in 3.5-billion-year-old Australian chert are interpreted by some as fossils of bacteria (Schopf 1999), but the authenticity of these and other supposed traces of exceedingly ancient life is disputed (Brasier et al. 2002, 2005; Altermann and Kazmierczak 2003, Lepland et al. 2005, De Gregorio and Sharp 2006).

More solid evidence of life appears around 2.8 billion years ago, in the form of indisputable fossils—stacked-up bacterial mats called **stromatolites**—and complex organic compounds in ancient shales. Photosynthesis had probably begun by this time (Olson 2006), but the earth's atmosphere was not yet oxidative. Fine-grained sedimentary rocks older than 2.2 billion years contain granules of pyrites and other easily oxidized minerals. If the air back then had been rich in corrosive oxygen gas, those minerals would have oxidized and decomposed into other compounds while they were being broken up into fine granules of sediment (Knoll 2003). The definitive onset of an oxidative atmosphere is signaled by the deposition around 2 billion years ago of the world's major deposits of iron ore, laid down when reduced (ferric) iron ions that had been dissolved in the primitive ocean combined with oxygen, turned into insoluble ferrous oxide, and precipitated out as vast beds of rust-colored, iron-rich sediments on the floor of the sea (Klein and Buekes 1992).

The release of vast amounts of oxygen gas into the air and water of the earth by cyanobacteria must have had much the same catastrophic effects on microbial life that the chlorination of a swimming pool has. By the time a new equilibrium was finally reached around 2 billion years ago (Strauss et al. 1992), most of the earth's original life forms had been killed off. Those that survived did so only by retreating into deep, dark crevices and crannies where the deadly oxygen could not penetrate. Their modern descendants, the **anaerobic bacteria**, still populate such refuges today, buried deeply in soils and sediments or hiding inside the guts of people and other animals. They occasionally break out and take revenge on oxygen-breathing organisms by infesting their tissues, causing such infections as peritonitis and gangrene.

Atmospheric oxygen was a disastrous setback for the earth's anaerobic organisms, but it presented the cyanobacteria and their descendants with fabulous metabolic opportunities. Earlier life forms had metabolized glucose by breaking each six-carbon glucose molecule apart into two molecules of a three-carbon compound called **pyruvate**. In the new oxygen-rich world, that pyruvate could be further combined with the readily available oxygen to yield carbon dioxide and water. This novel **aerobic** form of respiration brought an almost tenfold increase in the energy generated by metabolizing a sugar molecule. The pyruvate wastes that had been the ashes of the fire of life now became a plentiful new fuel.

One group of microbes managed to cope with the flood of oxygen by enclosing its vulnerable DNA in an inner, protective membrane, forming a cell **nucleus** separated from the surrounding **cytoplasm**. A branch of this group set out on a new evolutionary path by

forming a partnership with some cyanobacteria. They did this by growing larger and bringing the cyanobacteria “indoors,” enclosing them within pinched-off inpocketings of the host cell's surface. The imported cyanobacteria brought with them not only their own separate DNA, but also all their valuable enzymatic machinery for aerobic respiration.

These cells appear to have incorporated at least two different strains of “domesticated” bacteria, specialized for doing different jobs. The cyanobacteria that did the job of making air and water into glucose kept their photosynthetic green pigment, chlorophyll, and turned into **chloroplasts** (Chu et al. 2004). Those that handled the task of aerobic respiration, oxidizing the glucose back into CO₂ and water to yield energy, became **mitochondria**. The resulting **eukaryote** (Greek, “true nucleus”) cell was a relatively large membranous sac containing the cell nucleus, ribosomal protein factories, and other components suspended in a watery broth of dancing organic molecules, transporting raw materials, waste products, and energy back and forth between the cell contents, the cell surface, and the imbedded chloroplasts and mitochondria (Fig. 1.4).

All later plants and animals are descended from those first eukaryotes. Plants have retained both chloroplasts and mitochondria. We animals and our relatives, the fungi, lost our chloroplasts early on (or are descended from primitive eukaryotes that had not yet acquired them), and so we are not able to make our own food. But almost all the cells in our bodies contain mitochondria descended from the immigrant bacteria of long ago. Even today, after more than a billion years of symbiotic evolution, our mitochondria are still separated from the cell's cytoplasm by a double barrier (their own membranous envelope surrounded by a pinched-off vesicle of cell membrane), reproduce separately from the rest of the cell, and have their own DNA. As we will see later, mitochondrial DNA has played an important part in the study of recent human evolution.

The earliest fossils generally accepted as eukaryotes are simple collapsed spherical sacs from northern China, dated to around 1.8 billion years ago (Zhang 1997). Their fossils are recognizable as eukaryotes because they are several times larger than even the largest bacteria, although they are still one-celled and visible only through a microscope. Fossils that can be seen by the naked eye—coiled-up, millimeter-wide ribbons called *Grypania*—date back even further, to about 2.1 billion years (Han and Runnegar 1992). These ribbons may be fossils of early multicellular algae. But some living cyanobacteria clump together in similar-looking colonies, so it is not clear whether *Grypania* is an early fossil eukaryote or a colonial bacterium.

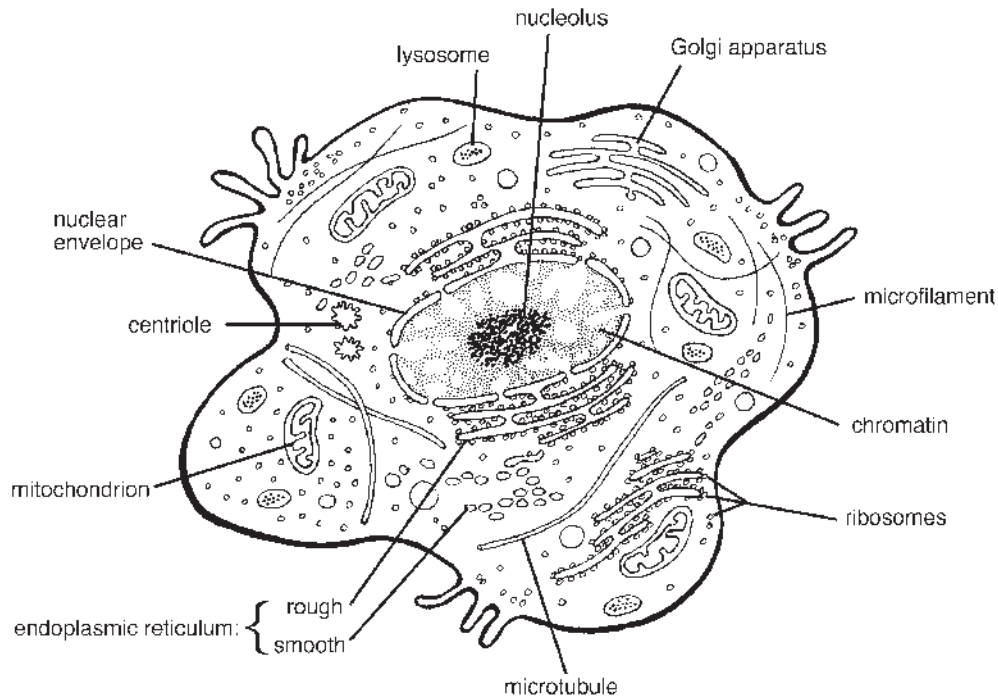


FIGURE I.4

Diagram of a eukaryotic (animal) cell, showing some of the principal internal structures. Nuclear DNA and proteins form linear complexes called chromosomes, which appear throughout the nucleus as a diffuse material called **chromatin** when the cell is not actively dividing. The **nucleolus** is a center for the assembly of protein-making units called **ribosomes**. These nuclear structures are surrounded by a double-walled **nuclear envelope** confluent with a complexly folded **endoplasmic reticulum**. Part of that reticulum is called “rough” because it is studded with ribosomes synthesizing proteins. The **Golgi apparatus** is another system of folded sacs, within which various chemicals are stored and processed. **Microtubules** and **microfilaments** are structural elements involved in maintaining and changing the shape of the cell. Large organic molecules are hydrolyzed into smaller ones inside digestive sacs called **lysosomes**. **Centrioles** function in cell division. **Mitochondria** are centers for the respiratory processes that provide energy for the other chemical reactions of the cell. (After Campbell 1993.)

■ MULTICELLULAR LIFE

Just as eukaryotic cells originated as colonies of bacteria, so multicellular organisms originated as colonies of eukaryotic cells. Most multicellular organisms, including human beings, develop as **clones**—that is, all their component cells are genetically identical, derived from a single progenitor cell by repeated cell division. In multicellular organisms, that progenitor cell is usually formed by the fusion of two smaller cells called **gametes** (eggs or sperm). Each gamete is derived from one parent. It contains one copy of the total genetic complement, or **genome**, of the species to which the organism belongs. The progenitor cell formed from the fusion of two gametes therefore has two copies of the genome. So do the cells that are cloned from it as the embryo develops. Biologists refer to these two-copy cells as **diploid** and the one-copy gametes as **haploid**. When the new diploid organism eventually produces its own

haploid gametes, the separate genomes derived from its two parents get mixed or **recombined** in the process, so that each gamete carries genes from both parents. When these gametes combine with those from another individual, the resulting new progenitor cell (the fertilized ovum, or **zygote**) will develop into another organism that inherits genes from four grandparents but is genetically different from all of them.

This intricate two-parent reproductive arrangement is called **sex**. It represented a major advance in the mechanics of evolution, because it made it easier for favorable mutations that cropped up in two different individuals to get together in their descendants. Bacteria manage to do something similar in other ways, partly by picking up bits of DNA from dead bacteria and sticking them into their own genomes, but this system will not do for multicellular plants and animals. Although all the cells of a many-celled organism are cloned from a single starter cell, they wind up forming different organs

in the adult, with divergent structures and functions. Such organisms therefore need to have a hierarchically arranged genome, in which some of the genes function to switch other genes on or off during development, so that the cells in different organs can develop in different ways in spite of their genetic sameness. Many-celled organisms therefore need to have more delicately adjusted and integrated genomes, and cannot evolve by simply scrounging up genetic information from things they eat. The invention of sex in one-celled eukaryotes provided a more useful and sophisticated method of genetic recombination, which aided and accelerated the evolution of multicellular life.

The earliest multicellular animals must have been tiny and soft-bodied. They have left no traces in the fossil record. Sponges have been recovered from 580-million-year-old rocks in China (Liu et al. 1998). Tiny, globular, many-celled fossils found in slightly younger Chinese rocks appear to represent the early embryonic stages of some multicellular animal (Xiao et al. 1998). Undisputed multicellular animals, in the form of small, nondescript conical shells, occur all over the world in deposits dated to the very end of the **Vendian period** (Fig. 1.2), about 550 Mya. Immediately after that, at the beginning of the **Cambrian period**, these so-called “small shelly faunas” are replaced by a great variety of fossil marine animals that appear seemingly out of nowhere. Because this sudden “Cambrian explosion” of fossils is a worldwide marker of this time horizon in the sedimentary rocks, the boundary between the Vendian and Cambrian periods has been adopted as a line separating the two primary divisions of the geological column: the **Precambrian eon** and the following **Phanerozoic** (Greek, “visible animals”) **eon**, roughly corresponding to the “Primary” and “Secondary” rocks of the early geologists.

For a long time, it had been thought that the Precambrian was devoid of multicellular fossils. Their abrupt appearance and great diversity at the beginning of the Cambrian period was perceived as a troubling mystery. Then in 1946, fossils of multicellular organisms were recovered from Vendian deposits around 570 My old at the Ediacara copper mine in South Australia. Since then, geologists have found similar **Ediacaran** faunas in Precambrian rocks from other parts of the world as well.

Unfortunately, these Precambrian discoveries have not cleared up the mystery of the Cambrian explosion. Most of the larger Ediacaran organisms are not likely ancestors of any Cambrian life forms. They appear to have been flattened mats of pasted-together tubes, growing outward from a central core or axis. In cross-section, these things probably looked like an inflatable swim-mat or air-mattress. Nothing much like this body plan is found in any organisms known from later periods. One theory about these creatures holds that the hollow tubes acted like greenhouses, in which photosynthetic

or chemosynthetic bacteria grew in a protected environment and provided their tube-making host with nutrients (McMenamin and McMenamin 1989, Runnegar 1992, Seilacher 1994).

Why was that protected environment necessary? Vendian **trace fossils** hint at an answer. These fossils can be described as worm tracks in mud—traces left by multicellular animals moving in or along the surface layer of the ocean floor. The unknown creatures that left these Precambrian tracks were probably grazing on the thin mat of cyanobacteria and other one-celled organisms that covered the bottoms of the Precambrian seas. The hollow tubes of the Ediacaran “air-mattress” creatures may have protected their internal microorganisms from being eaten by these wormlike or sluglike grazers.

M. and D. McMenamin (1989) have called this late Precambrian phase in the history of life the “Garden of Ediacara,” with reference to the Garden of Eden in the Bible. And here at the dawn of multicellular life, there does appear to have been something rather like a Peaceable Kingdom. Ediacaran life consisted mainly of microscopic plants and bacteria living directly or indirectly by photosynthesis. A few larger organisms lived off the bacteria, either by filtering them out of sea water (as those Vendian sponges did), or by slurping them up from the sea floor (the worm tracks), or by culturing them internally and metabolizing their byproducts (the “air-mattress” creatures). But there are no signs that multicellular animals had started eating each other. No jaws, teeth, or defensive structures—no shells or carapaces or spines or spikes—are seen in the Ediacaran fossils. We can assume that the contest between predator and prey had not yet begun, or at any rate had not yet progressed beyond a very low level of intensity. This was a world without weapons or armor, and therefore it was a world without speed and a world without brains.

■ THE CAMBRIAN REVOLUTION

Quite suddenly at the end of the Precambrian, in the space of a few million years of transition, hundreds of genera of armored fossil animals appear, covered with shells, carapaces, spines, spikes and plates of keratin, chitin, and calcium carbonate. Among the most common and familiar of these Cambrian newcomers are the trilobites, which vaguely resemble armored seagoing centipedes. These creatures, once wildly successful but now extinct, represent a major group (phylum) of animals called **arthropods**—segmented animals with external skeletons of chitin and many jointed legs. Other arthropods are still wildly successful today. They include centipedes, spiders, scorpions, and all the innumerable hosts of insects on the land and crustaceans in the sea.

Most of the other major groups of living invertebrates are represented in the Cambrian, including molluscs, brachiopods (lamp shells), echinoderms (starfish and their relatives), and several phyla of worms, as well as a lot of strange-looking creatures of uncertain relationships.

Unlike their Ediacaran predecessors, these Cambrian animals lived by eating other multicellular organisms, killing them and consuming their tissues just as humans and most other animals do today. The advent of the new ecology of predators and prey is signaled by the widespread appearance of some common anatomical features in many Cambrian animals.

The most fundamental of these is **bilateral symmetry**. In contrast to most Precambrian organisms, the primitive members of most of the Cambrian phyla have a head end, a tail end, and left and right sides. This tells us that these creatures were specialized for moving in one particular direction. The head, which is the end of an animal that first encounters new stimuli as it moves forward, is usually distinguished from the other parts of the body by having eyes, feelers, or other special sense receptors. Such heads presumably housed some sort of central nerve ganglion to receive incoming stimuli from those receptors and coordinate the animal's responses to them.

Heads, tails, and sense organs do not necessarily imply a predatory lifestyle. They all must have been present in some form in the wormlike microbe-grazers that left those tracks in the Precambrian mud. But bilateral symmetry and its correlates make it easier to evolve predatory adaptations. The advent of predation in the Cambrian is attested to by the appearance in many Cambrian animals of three key anatomical innovations: jaw-like organs around the head end of the gut for seizing prey, strong propulsive swimming paddles adapted for swift evasion or pursuit, and **defensive armor** against predators. Precambrian fossils are rare not only because Precambrian rocks are rare, but also because few Precambrian organisms had any hard parts. The widespread simultaneous emergence of defensive structures in

many Cambrian phyla—mollusc and brachiopod shells, the calcareous plates of echinoderms, trilobite exoskeletons, and so on—bears witness to the onset of new selection pressures caused by the “invention” of predation. With the advent of this new ecology, the Garden of Ediacara was closed, and the harmless air-mattress creatures of the Precambrian swiftly vanished from history. The arms race between the eaters and the eaten has been a major engine of evolutionary change throughout the subsequent history of animal evolution.

Cambrian members of our own phylum, the Chordata or **chordates**, had no bones or other hard parts; but fossils of them have been found recently at two Lower Cambrian sites in China where soft-bodied animals have been preserved in great detail (Chen et al. 1999, Shu et al. 1999). Some of the Chinese fossils appear to represent primitive chordates something like the living lancelet, *Branchiostoma*, a wormlike animal about 5 centimeters long that survives today in shallow seas off the coasts of Asia. *Branchiostoma* and its Cambrian relatives exhibit four main characteristics that we find in all chordates (Fig. 1.5). The first is a rubbery stiffening rod called the **notochord**, a kind of primitive backbone that runs down the back of the animal. The second chordate trait is another cord, made of nerve cells—the **spinal cord**, lying between the notochord and the skin. The third chordate trait is **segmented muscles** attached to either side of the notochord. These muscle segments, or **myotomes**, are the “flakes” that separate from each other when you eat a cooked fish with a fork. In a living fish or lancelet, they wiggle the animal's propulsive tail and send it scooting through the water. Nerve impulses passing through the spinal cord coordinate the contractions of these blocks of muscle with each other and with stimuli that the animal detects in its environment. The fourth chordate trait seen in *Branchiostoma* is a series of holes called **gill slits** in the side walls of the throat. *Branchiostoma* feeds by pumping sea water out through these slits and swallowing any solid leftovers. All vertebrates, including ourselves, exhibit these four chordate characters in one form or another. In humans, the noto-

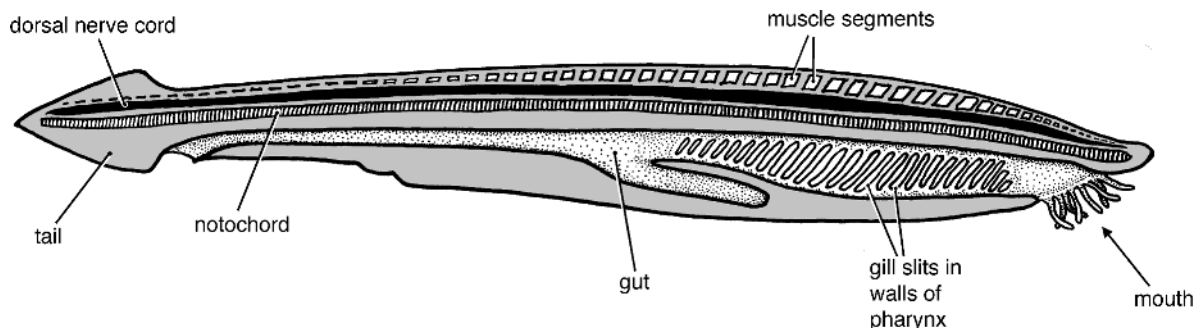


FIGURE 1.5

Major characteristics of the phylum Chordata, diagrammed as they appear in a primitive living chordate (*Branchiostoma*).

chord and gill slits are transient embryonic structures, but the segmented muscles and spinal cord persist throughout life.

The lancelet is a chordate, but it is not a vertebrate in the strict sense. Unlike true vertebrates, it has no jaws, no brain, no eyes or other complex sense organs at the front end—just gill slits and a ring of tentacles around the mouth. Vertebrates are distinguished from more primitive chordates like *Branchiostoma* by two major innovations: the head and the skeleton.

The first of these innovations to evolve was a true **head** with eyes and brain, which was more or less simply added onto the front end of the animal in front

of the notochord. Some of the Cambrian chordates from China evidently had heads, though they appear to have lacked eyes (Chen et al. 1999, Shu et al. 1999). More advanced cranial structures are seen in other early chordates called **conodonts**, which were equipped with a pair of big eyes and rows of prey-shredding calcareous spikes inside the mouth (Fig. 1.6A). True vertebrates added a second big innovation—an internal **skeleton** of bone or cartilage, with a brainbox surrounding the brain and a string of vertebral elements forming a primitive backbone around the notochord. The first vertebrate skeletons appear in the **Ordovician** period, which followed the Cambrian (Fig. 1.2). Known only from

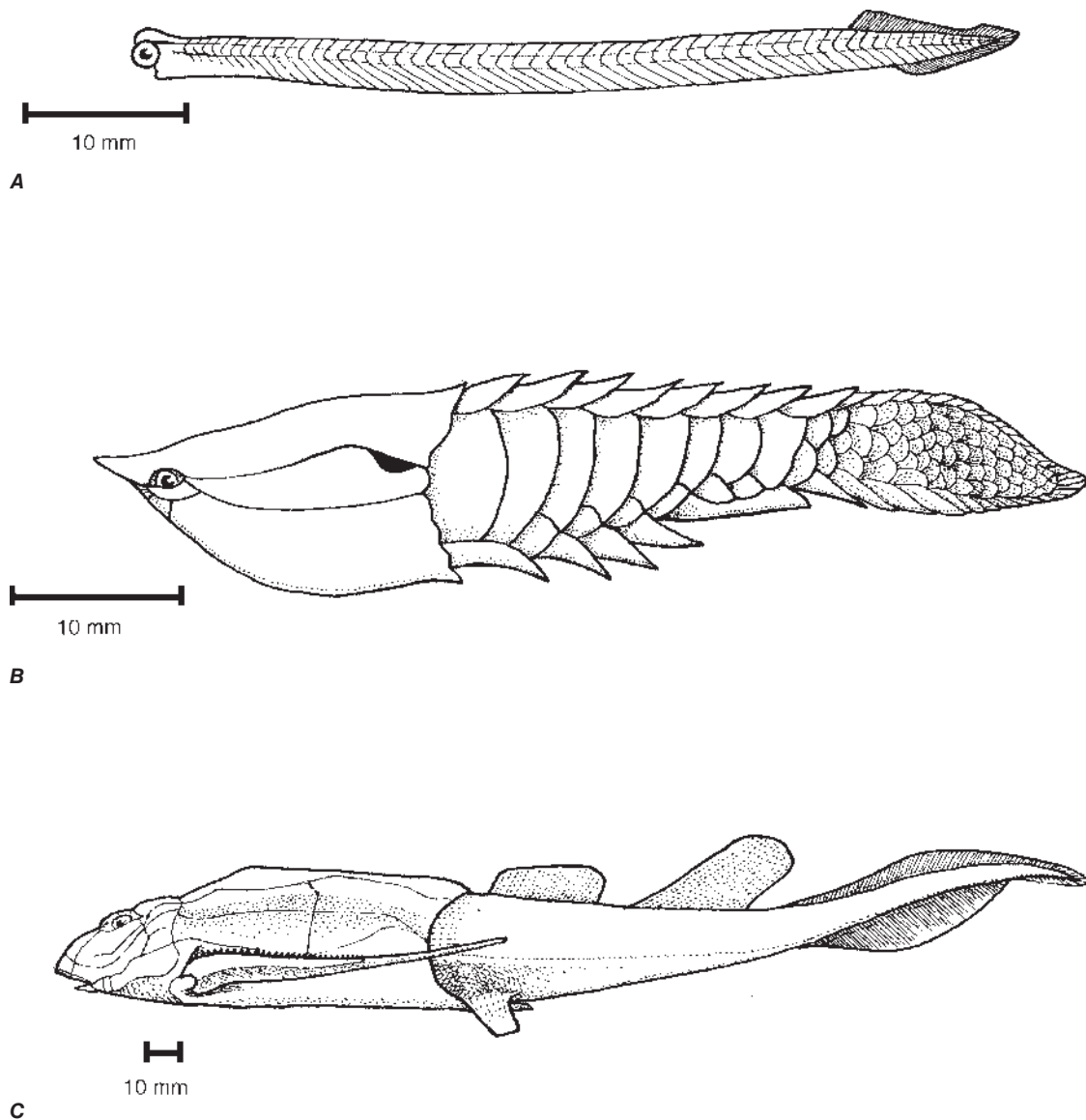


FIGURE 1.6

Paleozoic fishes. **A:** Lower Carboniferous conodont (*Clydagnathus*). **B:** Armored jawless fish (*Anglaspis*). **C:** Early jawed fish with pectoral and pelvic fins (*Botbriolepis*). (A, after Sweet and Donoghue 2001; B–C, after Moy-Thomas and Miles 1971.)

fragmentary remains, these Ordovician vertebrates appear to have been primitive fishes something like living lampreys, which are found today in rivers and lakes and seas all around the world. Lampreys have no jaws, but they have eyes of the standard vertebrate sort, along with a skull and vertebrae formed from cartilage, and they also have a small but clearly vertebrate brain elaborated out of the front end of the spinal cord.

Most of the jawless fish known as fossils from the Ordovician onward had more rigid and elaborate skeletons, made of bone instead of cartilage. In addition to having a braincase and vertebrae, these early fish had an extensive layer of osseous plates lying beneath the skin, forming a sort of dermal armor that helped ward off attacks from predators. The bony shield over the vulnerable head was especially solid (Fig. 1.6B). We still preserve many of these **dermal bones** in our own skulls.

■ JAWS, FINS, AND FEET

Vertebrate jaws evolved from (or developed as an anterior extension of) the rows of bones that form in between the gill slits. The first vertebrates with jaws

appear in the fossil record in the early **Devonian** period, about 400 Mya. These early jawed fish sported another innovation that was crucial for the emergence of human-kind: four **paired fins**, comprising a front pair of **pectoral fins** just behind the head and a hind pair of **pelvic fins** back near the anus (Fig. 1.6C). In most of these Devonian fish, the vulnerable eyes and brain were still protected by a head shield of bony armor. But the rest of the body wore a sort of flexible chain-mail coat of small scales made of a bonelike tissue called **dentine**, coated with hard, shiny **enamel**. The scales inside the mouth were pointed, with sharp tips to help hold and tear prey. We still have a set of these enamel-coated scales in our own mouths: our teeth.

The scales on the bodies of most modern fish have been pared down into delicate little translucent chips. Human beings, however, are descended from a group that retained the big, primitive, enamel-covered scales for a long time. These fish are called **sarcopterygians**, from the Greek for “fleshy fins,” because their fins were thick and muscular (Fig. 1.7A). It was lucky for us that their fins were robust, because this made it easier for those fins to function as arms and legs when some of these fish began coming out of the water. The larger bones inside the fins of some fossil sarcopterygians can

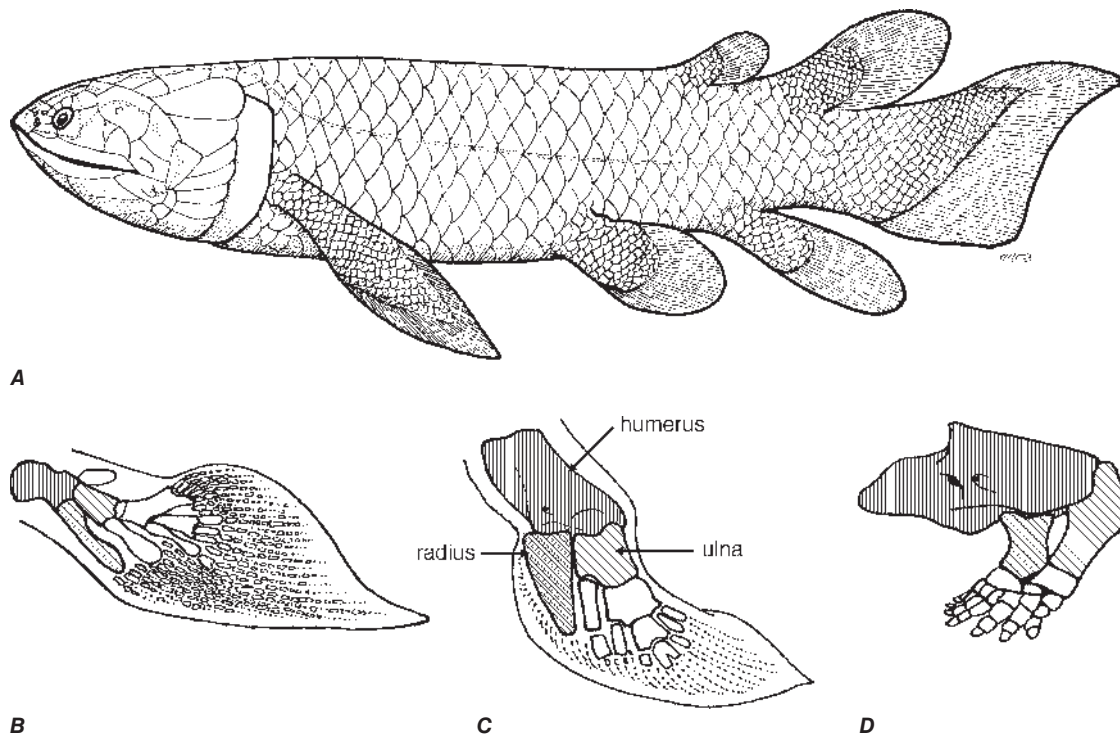


FIGURE 1.7

Fins and limbs. **A:** Devonian sarcopterygian *Holopterygius*. **B–D:** Pectoral fins of *Eusthenopteron* (**B**), a sarcopterygian fish close to the origins of the tetrapod stock; the transitional fish-like Devonian tetrapod *Tiktaalik* (**C**); and the early tetrapod *Acanthostega* (**D**), showing homologies and successive stages in the evolution of the humerus, radius, and ulna. (**A**, after Moy-Thomas and Miles 1971; **B–D**, after Shubin et al. 2006.)

be matched up, bone for bone, with the major bones in our own arms and legs (Fig. 1.7B–D). Surviving sarcopterygian fish include the ocean-dwelling coelacanth *Latimeria* and three species of lungfish that inhabit seasonal bodies of fresh water in the southern continents. Land vertebrates, or **tetrapods** (Greek, “four feet”), evolved from sarcopterygians in the late Devonian. Unlike the rather stiff, flipper-like fins of the earlier sarcopterygians, the modified fins—which we now must call arms and legs—of these Devonian tetrapods stuck out sideways and bent downward to reach the ground. They were both stouter and more limber than the ancestral fins. Their joints, bones, and muscles were big and strong enough to carry the animal’s weight when it was out on land, but flexible enough to allow the limbs to swing freely back and forth in the cyclical movements of walking. The little plates of bone that had lain at the bases of the ancestral fins were expanded into **scapulae** (shoulderblades) and **hipbones** (Fig. 1.8), providing bigger areas of attachment for the enlarged limb muscles. The fan of radiating bony fin supports found in the fins of sarcopterygian fish (Fig. 1.7B) became strengthened and simplified into a single stout proximal element (the **humerus** in the arm, the **femur** in the thigh) and a pair of distal elements (the **radius** and **ulna** in the forearm, the **tibia** and **fibula** in the lower leg), terminating in a cluster of wrist or ankle bones (**carpals** or **tarsals**) and a spray of **digits** (fingers or toes). Each digit contained a basal bone called a **metacarpal** or **metatarsal** and a terminal string of small bones called **phalanges**. Most of these early tetrapod elements persist in human limbs.

The viscera of these land-going fish were supported and protected by enlarged ribs curving down from the

backbone toward the belly. At the tail end of the trunk, the hipbones grew up to touch the ribs and down to touch each other in the midline of the belly, thus forming a complete bony ring—the **pelvis**—that provided a firm foundation for the hind limb. In most living tetrapods, including humans, the ribs that touch the hipbone fuse together with their vertebrae in the adult to form a single composite bone called the **sacrum** (Fig. 1.8).

Getting around on land is one of the two biggest problems faced by a fish out of water. The other major problem it confronts is water loss. The early land vertebrates evolved eyelids and tear glands to keep their eyes from drying out, but (like the frogs and salamanders, which are their least-changed modern descendants) they retained the moist, glandular skin of their fishy forebears. Therefore, they had to stay in humid surroundings to avoid desiccation. They also had to return at mating time to the water, as frogs do. Out of the water, their ejaculated sperm would not have been able to swim to the eggs and fertilize them, and the jelly-covered eggs would have been unable to develop into water-breathing, tadpolelike larvae.

These early tetrapods were not the first organisms to colonize the land. If they had been, there would have been nothing for them to eat when they got there. Plants had preceded the vertebrates onto land by some 30My, and various invertebrate groups—including the ancestors of insects—followed the plants onto the land not long afterward. The abundance of edible arthropods on land may have been one of the things that led some sarcopterygian fish to start coming out of the water.

The appearance and spread of land plants altered the earth’s atmosphere. Changes in the chemistry of the

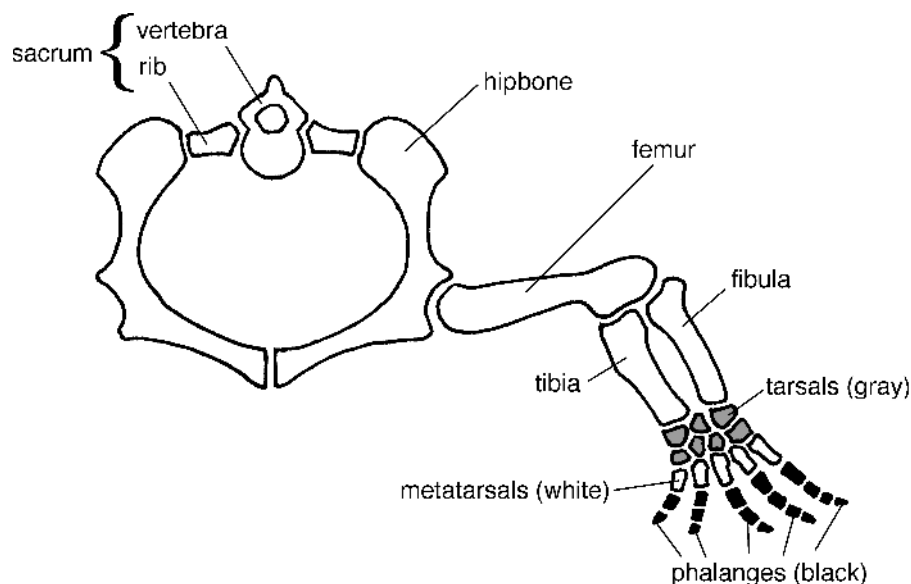


FIGURE 1.8

Diagrammatic anterior view of pelvis and one hind limb of an early terrestrial vertebrate.

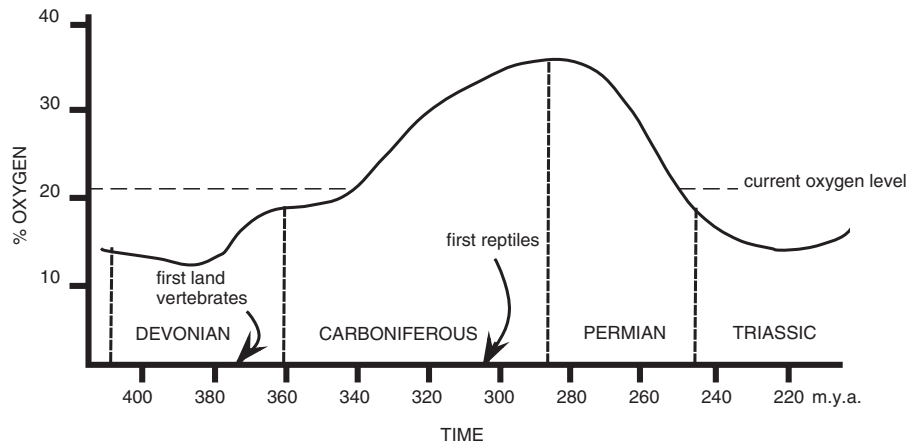


FIGURE 1.9

Atmospheric oxygen levels in the late Paleozoic and early Mesozoic. (After Graham et al. 1997.)

sedimentary rocks suggest that levels of oxygen in the air began to rise some 380–400 Mya (Fig. 1.9), at about the same time that plants were colonizing the continents. During the **Carboniferous** period that succeeded the Devonian, great forested swamps spread across the continental lowlands, and land plants underwent an evolutionary radiation. Much of our coal today is mined from deposits laid down in these swamps—which is why this period is called the Carboniferous, from the Latin word for “coal-bearing.” The air’s oxygen content continued rising until it reached a peak some 280 Mya in the early part of the next period, the **Permian**. It plunged back down again during the Permian to its earlier level, and then it rose more slowly up to an intermediate level like that of the present.

Some biologists think that these fluctuations in atmospheric oxygen were driving major events in animal evolution. They contend that the increasingly oxygen-rich air of the Late Devonian made it easier for vertebrates to move out of the water onto the land at this time (Graham et al. 1995). The high oxygen levels in the Carboniferous—and the high metabolic rates that must have gone with them—also may have made it easier for insects to evolve the machineries of flight. The Carboniferous witnessed the evolution of giant insects, looking like dragonflies with a wingspread a meter across, which probably would not have been able to live in the less oxygenated air of other periods in the earth’s history.

■ THE REPTILIAN REVOLUTIONS

During the Permian and the period that followed it, the **Triassic**, the continents slowly drifted together near the equator, forming a single supercontinent that geologists call **Pangaea** in belated tribute to Alfred Wegener. The huge size and low latitude of Pangaea promoted the

spread of deserts. And as the world’s land masses grew drier and merged together, plant life suffered. The diversity of fossil land plants fell at the end of the Permian—one of only two times that this has ever happened in geological history (Niklas and Tiffney 1994). Oxygen in the earth’s atmosphere dropped along with plant diversity throughout the Permian, hitting a low point in concert with the final consolidation of Pangaea during the Triassic (Fig. 1.9).

The coalescence and drying-out of the Permian continents contributed to the success of the next major innovation in the human lineage—the development of an egg that could be laid on land. The new eggs were covered with a tough, leathery shell, stiff enough to support the egg against gravity and impervious enough to keep out bacteria. Because their shells were not entirely watertight, they needed to be laid in damp soil to keep from drying out, as the eggs of many reptiles still do today. This slight permeability of the eggshell had its useful side, however, because it allowed the egg to absorb water from its moist surroundings and grow larger between laying and hatching—again, as the eggs of many modern reptiles do (Carroll 1988, Stewart 1997). The shell also had to be porous enough to let oxygen in and carbon dioxide out, so that the embryo could breathe. All this presents a tricky set of conflicting demands for an eggshell to have to juggle. Some scientists think that the high oxygen levels of the late Carboniferous atmosphere were what made the evolution of this new egg possible (Graham et al. 1997).

The new eggs had a complicated structure (Fig. 1.10). The developing embryo sported a **yolk sac** of the usual vertebrate sort—a bag connected to the gut, containing liquid food to sustain embryonic metabolism and growth. But in the new egg, a second baglike intestinal outgrowth was added on behind this to receive the embryo’s urinary wastes. (These now had to be stored

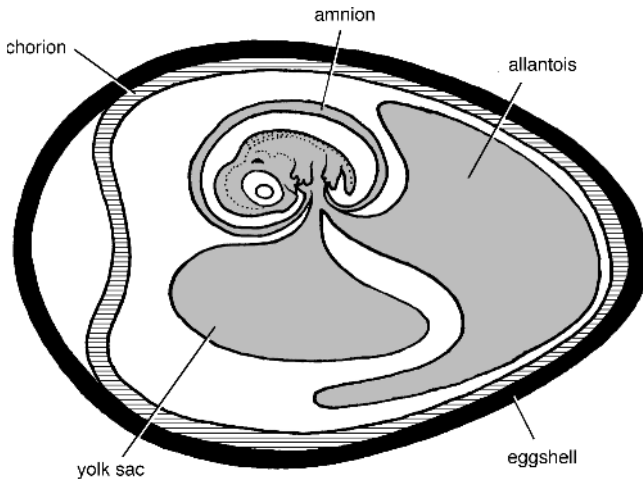


FIGURE 1.10

The amniote egg (diagrammatic).

inside the egg, because there was no longer any surrounding body of water to dump them into.) This new sac, the **allantois**, also served the embryo as a sort of lung, spreading out under the shell to provide a large surface richly supplied with blood vessels for absorbing oxygen from the air and discharging CO_2 . Between the allantois and the shell, the entire embryo was wrapped in an outer protective membrane called the **chorion**. Finally, an innermost membrane called the **amnion** enclosed the embryo proper within its own private water bath of amniotic fluid, separating it from all the other apparatus and goings-on inside the eggshell.

Most reptiles and all birds today continue to lay eggs of this sort. So do three species of mammals (two echidnas and one platypus). Other mammals (and a few reptiles) have given up laying shelled eggs, allowing the zygote's early development to take place inside the secure refuge of the mother's egg ducts. But the embryos of these animals still retain the chorion, amnion, allantois, and yolk sac. All mammals, reptiles, and birds are therefore classed together as **amniotes**, after the amnion—whether or not they still lay amniote eggs.

The animals that were laying these eggs were the first **reptiles**, known as fossils from the late Carboniferous. In addition to their famous eggs, the ancestral reptiles displayed two other key adaptations to a fully terrestrial life. The first was **internal fertilization**. In primitive tetrapods, the males had fertilized the eggs as they emerged from the female's reproductive tract, just as male frogs and toads do today. But eggshells make this impossible. If the egg is going to be laid with a shell around it, the male has to introduce sperm directly into the body of the female before the shell forms, so that his gametes can reach the ova to fertilize them. Other animals that lay eggs protected by an impervious

coating—sharks, insects, spiders, and so on—have adopted internal fertilization for similar reasons.

The other key innovation developed in the ancestral reptiles was a **cornified epidermis** covered with a thick layer of dry, dead skin cells. This horny layer curtailed evaporation from the body surface, thus solving the last big problem faced by a fish out of water. The leathery skin and new reproductive adaptations of the early reptiles allowed their descendants to move completely away from ponds and swamps and take up a new style of life in the dryer uplands.

We can trace the separate lineages of birds and mammals all the way back to the Carboniferous period. The first reptiles (Fig. 1.11A) had a solid skull roof, like those of sarcopterygian fish and the primitive land vertebrates. But other Carboniferous reptiles evolved openings in the sides of the dermal armor of the skull. There were two main groups of these reptiles—a group with two holes on each side, and another group with only one hole (Fig. 1.11B, C). The descendants of the early two-holed or **diapsid** reptiles include the dinosaurs and birds, as well as all living reptiles with the possible exception of turtles (Kumazawa and Nishida 1999). The one-holed group, the **synapsids**, included the ancestors of the mammals. The hole in the side of the synapsids' dermal skull roof can still be traced in the human head, where it is represented by the **temporal fossa**—the area full of muscles on the side of the skull, between the dermal bones at the crown of the head and those of the cheekbone (Fig. 1.11).

The first synapsids were still thoroughly reptilian—lumbering, scaly, cold-blooded carnivores with a sprawling alligatorlike posture. They included in their numbers, however, some of the first plant-eating terrestrial vertebrates. Although these synapsid experiments in herbivory turned out to be evolutionary dead ends, they signaled the dawning of a new sort of ecosystem.

On land and sea alike, the earth's major food chains begin with green plants. But in the sea, most green plants are microscopic. Out at sea, beyond the coastal shallows, the ocean bottom lies in permanent darkness, and so photosynthetic plants must float near the surface of the waves. Under these circumstances, one-celled plants have a competitive advantage. Larger, many-celled plants are less efficient at absorbing sunlight (Niklas 1994), and they tend to get shredded by wave action at the sea's surface. Accordingly, most of the plants in the sea are single-celled—and so most of the herbivores are tiny as well. Most of the oceanic animals that we can see without a magnifying glass are animals near the top of the food chain: carnivores that eat other carnivores.

On the land, things are reversed. Small plants are at a disadvantage in capturing sunlight on land, because they have to grow in the shadows of their larger neighbors. Therefore, wherever circumstances permit, the

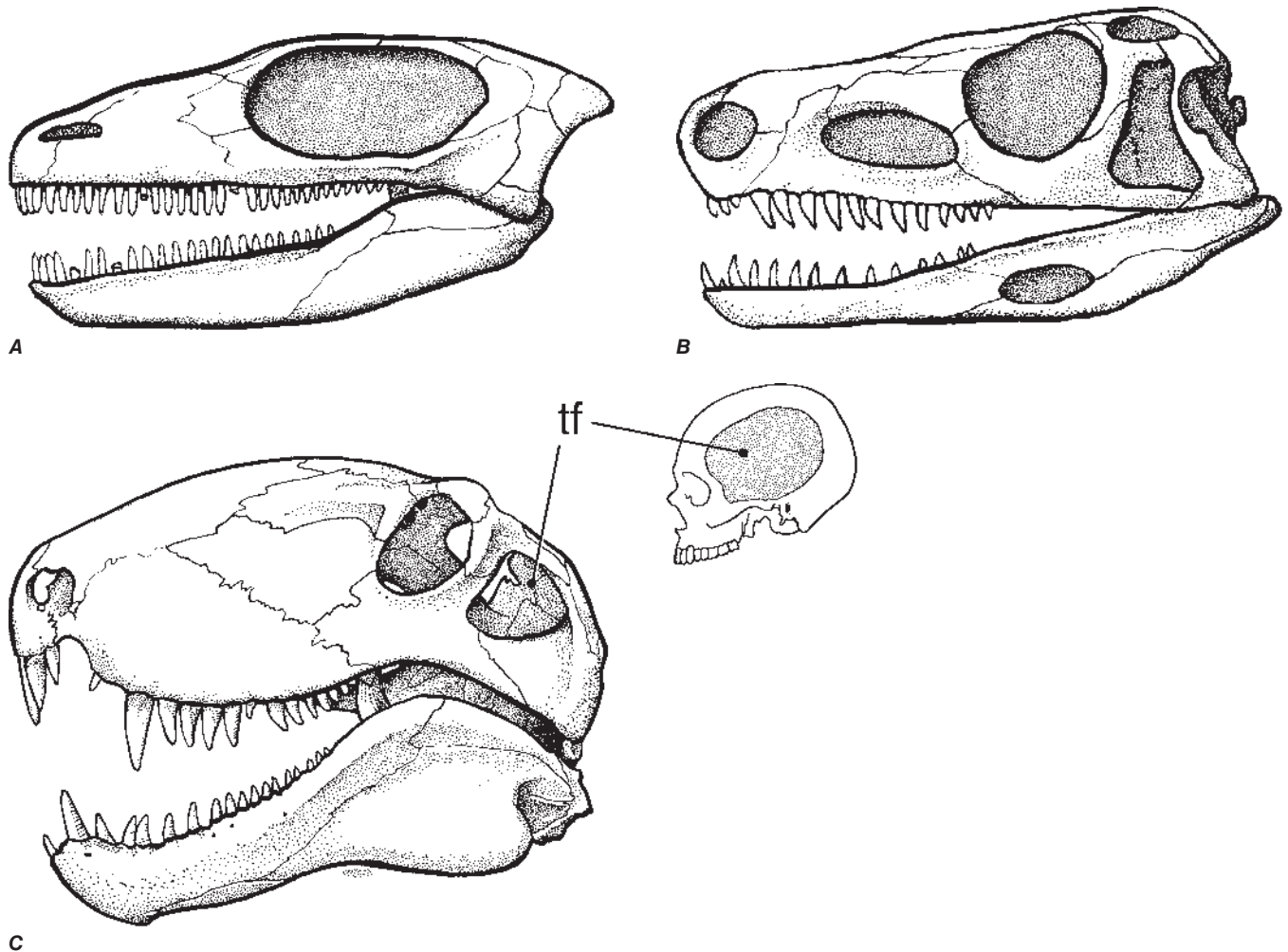


FIGURE 1.11

Skulls of three types of early reptiles: **(A)** the Lower Permian anapsid *Nyctiphruretus*, **(B)** the Lower Triassic diapsid *Euparkeria*, and **(C)** the Lower Permian synapsid *Dimetrodon*. The temporal fossa (tf) in the human skull (inset) is the homolog of the single temporal opening of *Dimetrodon*. Not to same scale. **(A–C)**, after Romer 1956.)

surface of the continents is covered with trees and other tall plants, whose spreading crowns are adapted to intercept sunshine and deny it to their competitors. To compete in this battle of shadows, land plants have to invest a lot of their glucose production in making **cellulose** and other stiff, long-chain sugar polymers, which they use to support their towering tissues against the pull of gravity and the buffeting of rain and wind. These polymers contain a lot of energy, as the heat given off by burning wood or paper attests; but it is hard to release by any means short of combustion. Some bacteria can crack these **structural carbohydrates** apart, but animals cannot. Therefore, all animals that eat land plants either specialize in easily digested tissues like fruits or seeds, or else rely on anaerobic microbes in their guts to do the job of breaking down structural carbohydrates into sugars.

Early land plants bore neither fruits nor seeds, and early land vertebrates had no way of digesting cellulose. The terrestrial food chains of the Carboniferous therefore lacked big herbivores. Terrestrial ecosystems of the modern sort, in which big herbivores outnumber big carnivores, began to appear when some groups of Early Permian synapsids evolved the two key adaptations that leaf-eating vertebrates need: **(a) shredding teeth** to reduce plant leaves and stems to a slurry that gut bacteria can work on efficiently and **(b) capacious intestines** to provide space for this silage to sit and ferment. The intestines of the Permian herbivores are not known from the fossils, but we know from their ribs that they had big, bulging abdomens (Fig. 1.12). Most leaf-eating vertebrates, from duckbilled dinosaurs to horses and gorillas, have evolved these two specializations in some form or other (Hotton et al. 1997).

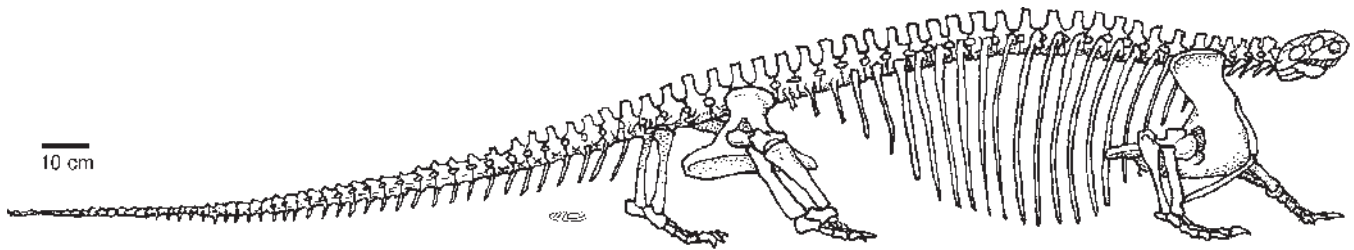


FIGURE 1.12

The skeleton of the plant-eating Early Permian synapsid *Cotylorhynchus*. (After Stovall et al. 1966.)

■ THE TWO GREAT EXTINCTIONS

The synapsid reptiles were the dominant large land animals of the Permian, but their rule was short-lived. The end of the Permian saw perhaps the greatest mass extinction in the history of life on this planet. The causes of this ecological catastrophe remain unclear. The coming-together of Pangaea may have had something to do with it. One theory holds that massive volcanic eruptions that occurred in Siberia at that time released vast amounts of greenhouse gasses into the atmosphere, causing a spike in world temperatures and driving already-stressed animal populations to extinction (Hallam 2004). For whatever reason, most animal species disappeared at this time. It has been estimated that more than 80% of all multicellular animals may have become extinct at the end of the Permian—including most of the synapsid reptiles (Raup 1991).

The surviving synapsids made a modest comeback during the Triassic period that followed the catastrophe. But their ecological space was mostly taken over during this period by the diapsid (two-holed) reptiles, including the ancestors of the dinosaurs. The first dinosaurs made their appearance around 200 Mya, in the late Triassic. The old-fashioned view of dinosaurs was that they were slow, cold-blooded, stupid, lumbering behemoths who died out because they could not adapt to changing times. The current fashion is to think of typical dinosaurs as active, nervous, birdlike creatures with warm blood and feathers. A lot of ink has been spilled in debates over warm blood in dinosaurs, but the point is a moot one, especially for the biggest and most herbivorous dinosaurs. Any very large land animal will have a more or less constant body temperature, because its great bulk takes a long time to warm up or cool off; and any large herbivore will have an elevated body temperature because of all the heat given off by its gently rotting internal compost. And if birds are surviving small dinosaurs, as the consensus has it nowadays, then at least some of the smaller dinosaurs must also have been warm-blooded and birdlike.

By the end of the Triassic, the dinosaurs and other diapsids had replaced the synapsids as the dominant

land vertebrates. But one lineage of one-holed reptiles hit on a way to survive in the shadow of the dinosaurs. They became tiny, nocturnal, and warm-blooded, scurrying around in the darkness under the roots and leaves of the forest floor, protected against the chill of the night by a coat of insulating hairs. They were fierce predators—on beetles and worms and such—and they were also fiercely protective mothers, guarding and incubating their eggs and also feeding their hatchlings on fatty secretions from modified sweat glands on their bellies.

These were the early **mammals**, from which we are descended. The suite of innovations that made their way of life possible included a lot of the key inventions in the human lineage. We will look at these mammalian innovations in more detail in Chapter 3. For now, they can all be summed up in two phrases: **small size** and a constantly **high metabolic rate**. Most of the distinctive mammalian features of the teeth, jaws, skin, lungs, and reproductive system are corollaries of these two items.

The mammals stayed small and inconspicuous for the next 135 million years. They did not stop evolving during that period. Their teeth became more complicated and efficient at grinding and slicing food. Some of them evolved keener senses of smell or hearing. Others began eating plants. One group took to bearing live young. But despite these innovations, mammals retained their nocturnal habits and their small size, from a few grams up to no more than five or six kilograms (Hu et al. 2005). During the **Jurassic** and **Cretaceous** periods that followed the Triassic (Fig. 1.2), mammals did not grow big or presume to compete with the dinosaurs. It took an astronomical collision to bring them out into the sunshine and raise them into prominence as the dominant land animals.

The collision involved a medium-sized asteroid, a rocky piece of space debris some 10–15 kilometers in diameter. It struck the earth 65 Mya, near what is now the northern coastline of Yucatan, in Mexico. We can still trace the faint outlines of that impact, which left a crater 200 kilometers across. Sedimentary rocks all around the world from this time horizon carry material

thrown up by the impact—dust with enriched levels of the metal iridium, tiny spheres of molten glass, amino acids not found in terrestrial sources, and so on. The incandescent re-entry of these millions of tons of splattered material may have produced a brief but titanic pulse of infrared heat waves, powerful enough to set all the world's forests on fire and cook all the terrestrial animals that were too big to hide under a rock (Robertson et al. 2004). In the strata overlying the thin layer of asteroid debris, no one has ever found an undisputed fossil of a dinosaur.

It is now generally agreed that the Mexican asteroid impact caused the extinction of the dinosaurs at the end of the Cretaceous. Many other groups of animals also vanished at this time, resulting in a second great mass extinction rivalling that at the end of the Permian. The abrupt faunal changes occurring at these two horizons are used to divide the Phanerozoic eon into three so-called **eras**: the **Paleozoic** (“ancient animals”) era preceding the Permian extinction, the **Mesozoic** (“middle animals”) era following it, and the **Cenozoic** (Greek, “recent animals”) era following the asteroid impact (Fig. 1.2).

■ THE MAMMALS TAKE OVER

The Cenozoic, which is the shortest of the three eras, is sometimes called the Age of Mammals for the same reason that the Mesozoic is called the Age of Reptiles. In both eras, the large land animals belonged respectively to those two groups. The 65-million-year-long Cenozoic is divided into only two subunits: the **Tertiary** period and the later and much shorter **Quaternary** period, which lasted only some two million years. (The words “Tertiary” and “Quaternary,” which mean “Third” and “Fourth,” are the sole surviving reminder in modern geology of the four-period model of the early Neptunists.)

The increasing brevity of the stages recognized at the top of the geological column reflects the fact that younger rocks are more plentiful than older ones. It also reflects the early geologists' underestimates of the amount of time that elapsed before *Homo sapiens* came on the scene. Those underestimates were rooted in an older, more anthropocentric view of the world than ours. For people who believed deep down that all things were made for man's benefit, it was hard to grasp the fact that the earth was devoid of human beings throughout more than 99.9% of the history of life. We have adopted an anthropocentric focus of our own in writing this book, and most of the rest of it will be concerned with the human lineage during the Cenozoic in general and the Quaternary in particular. But it is worth pausing at this point to note how rapid our success and how vanishingly brief our tenure on this planet thus far has been.

The asteroid impact at the end of the Cretaceous exterminated all the large land animals, but it had less profound effects on plant life. Outside of North America, where the asteroid struck down, latest Cretaceous floras look pretty much like early Cenozoic floras (Hallam 2004). Cenozoic mammals have therefore tended simply to take over the ecological roles for large animals that were left vacant when the dinosaurs went away. The duckbilled, sauropod, and ceratopsian dinosaurs of the Cretaceous have been replaced as large herbivores by such creatures as elephants and hooved mammals. Raptorial dinosaurs have been supplanted as large terrestrial predators by big cats, wolves, and their kin. Dolphins and seals have slipped into the niches for large marine carnivores once occupied by plesiosaurs and ichthyosaurs. And so on. In addition to taking over all this ecological space from the vanished great reptiles, mammals have also held on to the general niches that they occupied in the Mesozoic, including the roles of small herbivores (multituberculates in the Cretaceous, rodents and rabbits nowadays) and of small nocturnal insect-eaters such as shrews.

Mammals have not, however, made many incursions into the niches for small *diurnal* animals. Most of those niches are still occupied by the surviving diapsids. If you go for a midday walk in the wilds on almost any continent, you will see a number of small diapsids—lizards, snakes, and above all birds—and you may encounter some large mammals; but the only small mammals you are likely to see belong to a few groups (including squirrels, mongooses, and monkeys) that have hit on ways of competing with the birds in the daytime (Charles-Dominique 1975). At small body sizes, the diapsids still rule the day and the mammals rule the night, now as in the Cretaceous.

Cenozoic mammals have of course made some ecological innovations of their own. Grasses and grasslands did not evolve until the Tertiary (Jacobs et al. 1999), and so today's herds of grazing mammals with special teeth for grinding the gritty, siliceous leaves of grass had no equivalents in the Cretaceous. Mesozoic reptiles also never came up with anything like the filter-feeding adaptations of the baleen whales, which short-circuit the sea's food chains by allowing the very largest predators to feed directly on some of the smallest ones. Perhaps the most original mammalian innovation was the nocturnal flight of bats, made possible by the evolution of their leathery wings and the extraordinary sonar-like echolocation that permits them to zoom through the air safely in total darkness. This breakthrough, which probably took place around the beginning of the Cenozoic, has been a great success. So have the specializations of the teeth and jaws that have allowed the rodents to become extremely effective small herbivores, with no real counterpart among non-mammalian vertebrates. Most mammals today are either rodents or bats.

One general feature of Cenozoic mammalian evolution is of special relevance to the human lineage—namely, a trend toward evolving bigger brains. In many groups of mammals, we find that the modern forms have brains that are conspicuously larger than those of their similar-sized relatives in the early Tertiary (Jerison 1973, Martin 1973). This trend shows up in many mammal lineages with widely differing

lifestyles, including rodents, carnivores, primates, whales, and hoofed mammals. Brains, as we will see later, are metabolically expensive organs. Perhaps the trends toward brain enlargement that we see in many groups of Cenozoic mammals were made possible by underlying improvements in metabolic efficiency, which we have no way of detecting in the fossil record.