PALEONTOLOGY

A Brief History of Life

Ian Tattersall

TEMPLETON SCIENCE AND RELIGION SERIES

Paleontology

Templeton Science and Religion Series

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Ian Tattersall

Templeton Press

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With appreciation to the professors/friends
who taught me paleontology (but who might not
agree with everything in this book):

Elwyn Simons

David Pilbeam

Keith Thomson

John Ostrom

Fuzz Crompton

Niles Eldredge

Contents

Paleontology

Introduction

We human beings are the inheritors of a vast and almost unimaginably diverse world that has had a long and tumultuous history. We can infer many of the events of that history by looking around us at nature as we see it today, and at how the luxuriant diversity of living things is structured. But for the details of how things came to be the way they are—and for the drama, for drama there was, aplenty—we have to turn to the always fascinating but often tantalizingly incomplete fossil record.

The physical story of the planet is told principally in the rocks that form the Earth's thin skin, while the history of life on this finite globe is recounted by the fossils that some of those rocks fortunately enclose. The contemplation of the fossil record can be a humbling experience, reminding us that *Homo sapiens* is but one species among many millions that have existed, and how tiny a speck we are in the immensity of time. On the other hand, it is possible also to take comfort in the knowledge that *Homo sapiens* is not alone, that we are part of a much larger whole that will continue on its own majestic course long after our species is gone. This short book espouses the latter perspective: it is about the glorious diversity of the world, about our own place in it, and about how both it and we got to be where we are today. The book is also about how we understand this story: about how we acquire and process information about our past and that of the ecosystems from which, like it or not, we are inseparable.

The study of past life is the realm of paleontology. Paleontology is a branch of science, and science is a sector of human knowledge that differs most especially from all others in being founded on questioning and doubt. Contrary to popular belief, science does not seek to *prove* anything: "scientific proof" is one of the great myths of our age. Rather, science tries to home in on an ever-more-accurate picture of nature by proposing new ideas about it and eliminating false ones. Science is most emphatically not about ultimate causation, which is properly the province of philosophers and theologians. Instead, scientists strive to understand the proximate causes for natural phenomena: those processes that we can observe at work in the world, and about which we are able to form testable hypotheses.

The process of hypothesis testing renders science a system of provisional, rather than absolute, knowledge; it is no denigration of any scientific hypothesis to label it "only a theory." Indeed, we dignify as theories those hypotheses that have proven so resistant to attack that we can sufficiently depend on their accuracy to base further explanations upon them. So an important part of what makes science truly different from other ways of seeking knowledge is simply the limitations it imposes on the *kinds* of questions it asks about how nature works. If you can't test your hypothesis somehow, or if it cannot be based on testable propositions that *have* resisted falsification, then your question lies outside the scope of scientific inquiry.

Scientific hypotheses are usually tested by experimentation; but paleontology is a rather unusual branch of science in that it is historical. Since paleontologists are unable to rerun the tape of history, they are obliged to look at the results of experiments already made by Nature, and to reconstruct as best they can the processes that produced them. How did the riotous diversity of the living world come to be? Well, we know of only one natural process that *predicts* the kind of diversity-within-similarity that we see in the biota around us. That process is evolution. The repeated divergence of new species from common ancestral forms that lies at the core of evolution inevitably results in the pattern of sets-within-sets that we actually observe. What's more, people have for a very long time been making this observation, and drawing conclusions from it—independent of their religious, philosophical, or scientific beliefs. The physicist and science historian Jim al-Khalili has, for example, recently quoted the following from *The Book of Animals* by a ninth-century Arab intellectual, abu Uthman al-Jahith (781–869):

> Animals engage in a struggle for existence; for resources, to avoid being eaten and to breed. Environmental factors influence organisms to develop new characteristics to ensure survival, thus transforming into new species. Animals that survive to breed can pass on their successful characteristics to their offspring.

As al-Khalili points out, these words have an eerie resemblance to those Charles Darwin would use a thousand years later in summarizing his theory of evolution by natural selection.

Closer to home, a century before Darwin published his theory, Carl Linnaeus (1707–1778), the originator of the system of naming living things that scientists use today, classified human beings in the species *Homo sapiens,* within the genus *Homo,* of the order Primates. To the conventionally religious Linnaeus it was evident, purely on the basis of our anatomical structure, that we group first with the apes (which he also placed in *Homo*), all of us together forming a single larger group with the monkeys and the lemurs, in contrast to all other warm-blooded, hairy mammals. This "nested" structure is repeated throughout nature (hooded crows are a kind of crow, which is a kind of perching bird, which is a kind of bird, which is a kind of backboned animal, and so forth) and it was taken for granted in folk taxonomies long before scientists came along to make a profession out of the job. Consequently, as an explanation for why we see what we see in the living world around us, the notion of evolution is as strongly supported as any hypothesis in science. Like all science, though, evolutionary biology is a work in progress, and evolutionary biologists are constantly seeking to refine their understanding of how things got to be the way they are. Science is a process rather than a product; and as it slowly inches in toward an ever-more-accurate description of nature, it is complementary to, rather than in conflict with, the many other ways of human knowing.

Look on this book, then, as a sort of progress report rather than as a repository of fixed knowledge. Paleontology is a particularly fast-moving branch of science since it advances not simply through new analyses and new ways of extracting data from what is already known, but through new fossil finds that are constantly enlarging our base of knowledge. The fossil record is vast and constantly growing, so there is no way a short volume can do more than scratch the surface by sketching the larger picture and fleshing it out with a few carefully chosen examples. On one level my aim is to help the reader come away with an appreciation of what the record can and cannot tell us, and with a general understanding of the biological background from which modern biota and our own peculiar species emerged. More viscerally, though, I hope that the reader will gain some sense of the fun and excitement of paleontology, and of the process of discovering where we human beings fit into the natural world.

CHAPTER 1
Rocks, Time, and Fossils

Whether or not living forms exist elsewhere in the cosmos, for all practical purposes life as we know it was born here on Earth, several billion years ago. An awful lot has happened since then, and it is in the rocks composing the surface of our planet that we find the fossils that document the long history of living things. So it seems appropriate to start this book on paleontology, the science that studies those fossils, with a few words about the planet that we take so much for granted.

The geologist Preston Cloud once neatly described our Earth as an "Oasis in Space," which is, I think, about as apt a short description as it's possible to achieve. Our planet today really is an extraordinary place, with an oxygen-rich atmosphere, abundant water, a hospitable range of surface temperatures, and all the other necessities for the maintenance of life as it is familiar to us today. This amazing and comfortable environment exists, moreover, in the midst of a vast, hostile emptiness. Yet life itself came into being under very different—and very much more extreme—conditions.

The matter of origins goes back in an infinite recession, to a point that lies beyond the bounds of today's science. But scientists know the general outlines of how the Earth first began to form, some 4.5 billion years ago, out of a roiling cloud of hot dust and gases that eventually condensed to form our solar system. In early days the Earth's surface was an inferno, assailed from below by raging radioactive heat and from above by a constant bombardment of asteroids, as the remains of the debris cloud were "mopped up." Volcanoes on the hardening surface vigorously exhaled gases such as carbon dioxide, ammonia, and methane into an atmosphere initially consisting largely of hydrogen and helium. In brief, the early atmosphere was a toxic mixture of gases that would have been hostile to almost all forms of life that we know today. Equally inhospitable were the noxious oceans, which started to form as soon as the Earth's surface had cooled sufficiently to support liquid water, initially gassed out as vapor.

Still, the formation of the planet's solid outer crust proceeded rapidly as the fireball lost its initial heat. The earliest rocks known may be as much as 4.3 billion years old and are believed to be witnesses to the early operation of the processes that have governed the form of the Earth's surface ever since. Once the crust had hardened sufficiently, its surface began to be cracked by the motion of the hot, molten rock below. Imagine a pot of thick soup simmering on a stove. Warm soup rises from the bottom of the bowl at the middle, where it is hottest. On reaching the surface it flows outward to the sides of the pot, where it cools and sinks once more, ultimately to be reheated and rise again. Driven by the radioactive furnace in the planet's interior, an identical process was established under our feet well over 4 billion years ago. The upshot is that the surface of the planet was, and continues to be, divided into a varying number of more or less rigid tectonic plates that are forever in motion. New, hot magma is added on one side of each plate as it is erupted along the linear structures known as mid-ocean ridges, while old, cold rock is returned to the depths along subduction zones at the other side.

The basaltic rocks of the oceanic crust are relatively heavy. As a result the lighter rocks that compose the continents "float" above them and stand high above the ocean basins like giant icebergs. The floating continents are passively carried along on the "conveyor belts" below, like logs in a current. When one of them reaches the side of the plate on which it is sitting, it may bump into and crumple the continental mass on the adjacent plate. Forceful collisions of this kind have produced the great linear mountain chains of the world such as the Himalayas, the Rockies, and the Alps. In this way, continental topography has constantly been renewed, in the face of the erosion that constantly threatens to flatten it.

For the paleontologist, the main implication of plate tectonics is that the geography of the world is constantly changing. Today we recognize seven continents and a host of large islands scattered across the Earth's surface. But 180 million years ago, virtually all of the earth's dry land was assembled into one single supercontinent that geologists call Pangaea ("all lands"). Heat building up below it eventually split Pangaea into two giant continents: Laurasia in the north, and Gondwana in the south. Each of these then fragmented, ultimately to produce the various landmasses that we know today.

During these great movements, climates changed and biological forms shifted. Living populations were isolated or thrown into new states of competition. Species emerged and became extinct, and regions of the world developed their own distinctive assemblages of animals and plants.

Rocks and Fossils

The rocks that make up the continents of the world come in three different kinds. First there are the igneous rocks, derived from the cooling of molten magma. These include basalts and andesites and tephra ejected by volcanoes on the Earth's surface, and granites that cooled at high depths and pressures, sometimes eventually to be exposed at the surface by weathering. Over the vastness of time, weathering has operated on a grand scale: if you ever find yourself looking at an outcropping of granite, just try imagining that it probably once lay beneath several miles' thickness of rock.

Then there are sedimentary rocks, composed of particles weathered from preexisting rocks before being transported by wind and water, collected, and compacted. Finally, there are metamorphic rocks, which have been reheated enough to flow and recrystallize, as when rough limestone turns to shiny marble.

Fossils are technically any and all traces of past life, not just bones and teeth and shells. Since they are almost exclusively found in sedimentary rocks, these are the only ones we need to dwell on here, except for a passing glance at the volcanic rocks that have proven vital in dating many fossils. When rapidly accumulating sediments cover the remains of dead animals or plants, there is a chance that they will be fossilized. Typically, only the hard tissues such as teeth, bones, or shells undergo fossilization, as their original constituents are replaced by minerals. But occasionally, even soft parts may leave impressions—sometimes amazingly detailed ones—in fine-grained sediments around them.

In the ocean, where sedimentation is relatively continuous, the remains of organisms are routinely trapped in clays, muds, sands, and so forth. On land the process is a bit chancier, and fossils are most often incorporated into the sedimentary record on riverbanks and floodplains, and at the shallow edges of lakes. Such spots also have the advantage—for the paleontologist—of being favorite places for predators to attack prey that have come to drink.

When a terrestrial mammal dies, its remains are likely to be devoured and dismembered by scavengers, and its bones broken and scattered around the landscape. Factors ranging from sun, wind, and water to beetles and bacteria will usually do the rest. If a bone by chance escapes all of these vicissitudes and finds its way to a place of deposition, it will often be further battered en route. This is why most mammal fossils in museum collections are incomplete or damaged in some way, and the most commonly found vertebrate fossils are simply isolated teeth—the hardest tissues of the body.

Occasionally a carcass will be covered by sediments where it lies, and its skeleton preserved intact—naturally enough, the paleontologist's dream. But even this best-case scenario is no guarantee of preservation. As it lies in the rock pile, the fossil must be reasonably undisturbed by earth movements. To be of any use to the

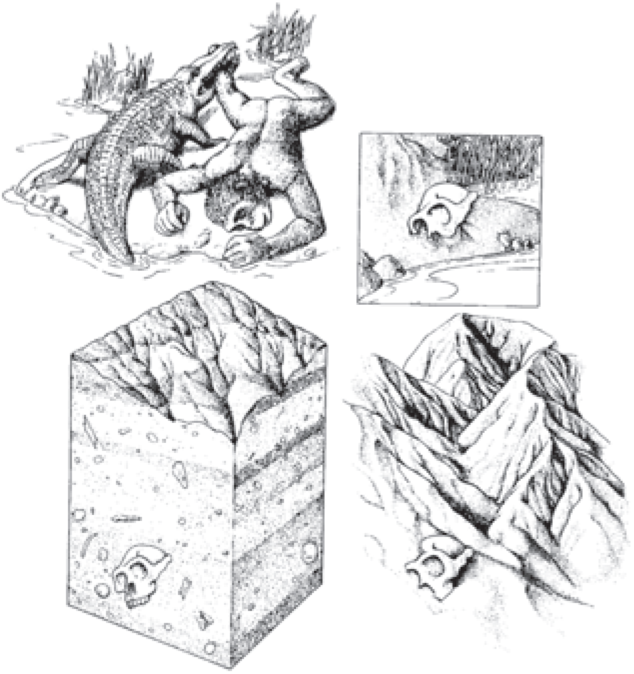


Figure 1.1. **The life history of a fossil. After death, most carcasses will be devoured by predators or scavengers (top left). What is left will either weather away or become buried in accumulating sediments (top right). Under the right conditions, mineralization will occur (bottom left). If erosion then wears away the overlying sediments, the fossil will be reexposed at the surface (bottom right), where it must be collected before it is obliterated by the elements.**

paleontologist it has to be uncovered at the surface again by further erosion—where it will be rapidly obliterated by erosion unless it is quickly found and preserved. All in all, a rather chancy proposition, which explains why fossils of many species—especially those species that are thin on the ground in the first place—are rare indeed.

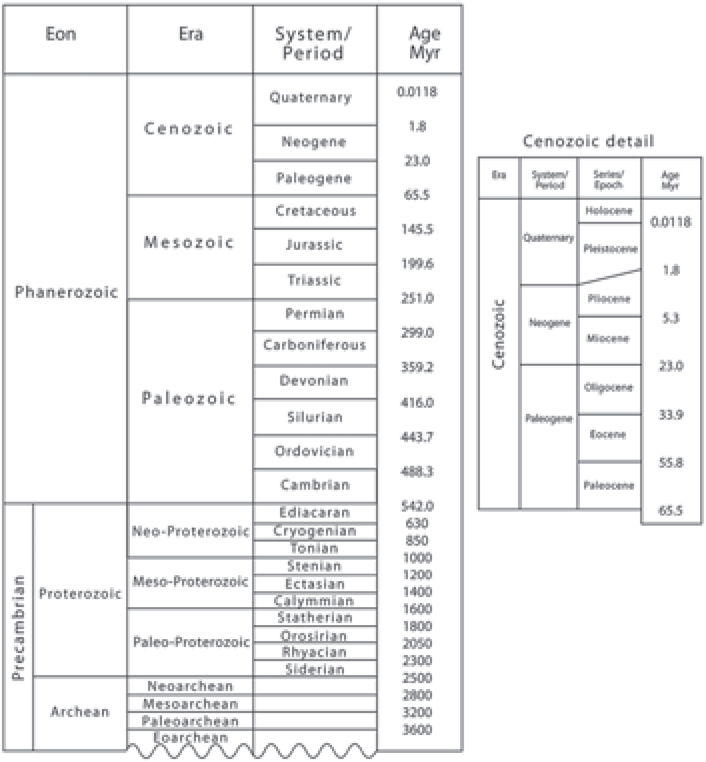
The Geological Time Scale

For the paleontologist, the most important thing about rocks is the historical record they contain. Ever since the Earth began taking on its familiar form, its continental crust has faithfully registered events happening on local and global scales. Some of this history can still be read, even though much evidence has subsequently been removed by erosion, covered by deposition, or altered by earth movements and metamorphism, sometimes on a gigantic scale.

Once it was established that the Earth was truly ancient, and had not simply been created more or less as we know it today, the first task of the early geologists was to reconstruct the historical sequence encoded in the rocks. This was not easy: for all that the working geologist could see were the rocks that happened to be exposed in any one place. And every local sedimentary basin, let alone each continent, has had its own geological history. Two basic questions thus emerged. One, at the front of every field geologist's mind, was "what was the sequence of events here?" And the other, usually asked when the geologist had returned home, or had at least struggled as far as the nearest pub, was, "How do I match it up with the sequences we see in other places?"

To approach the first question, early stratigraphers followed two rules. Sedimentary rocks accumulate in piles, one layer atop another, so the first rule was that the sediments at the bottom of any particular pile are older than the strata above. The second axiom was that these layers were originally laid down flat, no matter how earth movements might have tilted or buckled them since. Because most piles of sedimentary rock have undergone at least some deforming and tilting, together with displacement along faults that misalign the layers, stratigraphers first needed to establish the original relationships of the strata. That done, it was time to match up the sequence seen in one place with sequences seen elsewhere.

To some extent, this could be done through lithology—the characteristics of the rock layers themselves. It turned out, though, that this worked only within local sedimentary basins, because each basin has its own geological history. Basins can be large, which is why sheep in southern England graze on the same limestone soils that support the grapevines of Champagne. But every basin has its



Eon		Era	System/ Period	Age Myr
Phanerozoic		Cenozoic	Quaternary	0.0118
			Neogene	1.8
			Paleogene	23.0
		Mesozoic	Cretaceous	65.5
			Jurassic	145.5
			Triassic	199.6
		Paleozoic	Permian	251.0
			Carboniferous	299.0
			Devonian	359.2
			Silurian	416.0
			Ordovician	443.7
			Cambrian	488.3
Precambrian	Proterozoic	Neo-Proterozoic	Ediacaran	542.0
			Cryogenian	630
			Tonian	850
		Meso-Proterozoic	Stenian	1000
			Ectasian	1200
			Calymmian	1400
		Paleo-Proterozoic	Statherian	1600
			Orosirian	1800
			Rhyacian	2050
			Siderian	2300
	Archean	Neoarchean		2500
		Mesoarchean		2800
		Paleoarchean		3200
		Eoarchean		3600

Cenozoic detail

Era	System/ Period	Series/ Epoch	Age Myr
Cenozoic	Quaternary	Holocene	0.0118
		Pleistocene	1.8
	Neogene	Pliocene	5.3
		Miocene	23.0
	Paleogene	Oligocene	33.9
		Eocene	55.8
		Paleocene	65.5

Figure 1.2. Simplified International Stratigraphic Chart, showing the major divisions of Earth history with their current datings. On right, Cenozoic chart showing greater detail.

limits, so stratigraphers found another way to correlate rock formations over broader areas. They recognized certain widely dispersing organisms as "index fossils," characteristic of particular periods. The resulting correlations made possible the development of a standard timescale.

While the succession of major geological periods was basically established by the end of the nineteenth century, means of calibrating that sequence in years are quite recent. As Figure 1.2 shows, Earth history over the last 3.8 billion years is nowadays organized into three major eons that follow the initial period that is informally known as the Hadean, in acknowledgment of the fiery nature of the planet's surface in its earliest days. The first two post-Hadean eons compose the long stretch prior to the earliest fossils known to the early geologists and are grouped together in a larger unit called the Precambrian. The third eon, the Phanerozoic, covers the last 542 million years. Each eon is divided into eras. These are subdivided into periods, which are in turn composed of smaller time units known as epochs.

Chronometric Dating

Most current methods of applying real time (in years) to the geological record rely in one way or another on radioactivity. Chemical elements may exist in several alternative forms (isotopes), of which some (the radioactive ones) are unstable: their atomic nuclei spontaneously "decay" to stable states. Conversion takes place at a rate that is constant, measurable, specific to the isotope concerned, and unaffected by environmental factors. Some isotopes decay fast; others more slowly. Chemists express the rate of decay in terms of an isotope's half-life—the time it takes for half of the atoms present to decay. Geochronologists have used this property of radioactive isotopes to date rocks containing them.

There are two long-established approaches to such radiometric dating, both first developed in the mid-twentieth century. One embraces accumulation techniques, based on the buildup of stable daughter atoms. The classic accumulation technique is potassium/argon (K/Ar) dating, recently supplanted by the argon/argon (^{39}Ar/^{40}Ar) technique. Because the half-life involved is very long, these methods and others like them can be used to date very old rocks indeed—volcanic ones are preferred, because when laid down they are heated high enough to purge them of any daughter product and are often found interstratified with fossil-bearing sediments.

The opposite approach is represented by decay techniques, such as radiocarbon (^{14}C), first introduced around 1950. The unstable carbon isotope ^{14}C (radiocarbon) is produced in the upper atmosphere in a reaction governed by cosmic ray influx, and is incorporated into all living things. When an organism dies, it becomes isolated from the carbon cycle, and the ^{14}C it contains begins to decay, diminishing steadily as a proportion of the total carbon present. At 5,730 years, the half-life of radiocarbon is rather short, which means that the method can only be used on samples up to about 40,000 years old. But whereas K/Ar is used to date rocks, ^{14}C has the decided advantage of being able to date fossil specimens directly, provided enough bone protein (collagen) is preserved.

In recent years, the number of approaches to chronometric dating has multiplied, mostly for the fairly recent time frames that are of particular interest to paleoanthropologists. Most of these are "trapped-charge" methods that depend one way or another on the fact that electrons released by radioactivity may become trapped, at a measurable rate, in the lattice structure of various crystals. Good examples are thermoluminescence (TL) and electron spin resonance (ESR) dating.

What Fossils Can Tell Us

Once your dated fossil is sitting on your workbench, you need to extract as much information from it as possible. There are many different ways of going about this, involving specialists of many different kinds. The first step is to determine to what species your fossil belongs—and if necessary to create a new species to accommodate it. Then, of course, you need to situate that species in the great Tree of Life. These initial steps are absolutely fundamental to everything else that you do, and they may well prove to be the most difficult steps of all. But only when they are completed should you proceed to what most people regard as the really interesting stuff: reconstructing how your fossil lived back when it was alive, and what role it played in the ongoing soap opera of life.

Apart from its age and the location at which it was found, the most obvious information any fossil has to offer is its morphology—what it looks like. How you are built not only shows to whom you are related, but also determines how you can live. Every species is limited by its structure, both in what it can do right now and in its evolutionary potential for the future.

Of course, when you are confronted with nothing but bones or teeth, it is much easier to reconstruct what their owners might have done in life if you can find a living form whose lifestyle is reflected in features comparable to those of your fossil. The ichthyosaurs, for example, are extinct reptiles whose body form so clearly echoes those of fish that there has never been any doubt that they were swimmers—as is independently confirmed by the marine rocks in which their fossils are found.

On land, the teeth of extinct grazing mammals (and even dinosaurs) are a clear giveaway to their dietary habits, differing as they do from those of their carnivorous contemporaries just as those of carnivores and herbivores differ today. Similarly, the robust forelimbs of digging mammals, or the elongated hind limbs of leaping organisms, were as conspicuous back in the early Cenozoic as they are in the modern world.

The bottom line here is that, even when different animals or plants are not closely related by descent, if they *do* (or did) similar things, they are likely to show similar features as a result of what is called "convergence." A good solution is a good solution, whoever you are. Not every extinct animal has a modern equivalent, so not all past animal behaviors can be inferred from morphologies we see today. Nonetheless, within limits you can reverse engineer to analyze how extinct creatures moved and lived. High-tech methods are also constantly being introduced to help understand the behaviors and diets of extinct creatures. Among such methods is the analysis of certain stable (rather than radioactive) isotopes that are preserved in fossil teeth or bones. By measuring the proportions of different isotopes of carbon, for example, one can tell whether a tropical herbivore was browsing on leaves or grazing on grasses.

Predators preserve an echo of the isotopic ratios of their prey, so they can be included in the calculation, too. Carbon-isotope studies have shown, for example, that some very early human relatives were quite likely eating more meat than had been suspected. Similarly, the further up the food chain you are, the greater the ratio in your bones and teeth will be between the stable nitrogen isotopes ^{15}N and ^{14}N. On this basis, it has been suggested that our close relatives the Neanderthals were highly carnivorous: that, indeed, they may have specialized, at least regionally, in hunting extremely large-bodied prey, such as woolly mammoths and woolly rhinos.

This is merely a sampling of the ingenious approaches that paleontologists have used to flesh out the lives of their long-extinct subjects. But we should also remember that nothing lives in isolation. Every organism belongs to a much larger ecological community, itself a living thing, in which parts cannot be altered without threatening the integrity of the whole. So no matter how much you have been able to infer from an individual fossil that is sitting on the table in front of you, you will never comprehend it completely without understanding the role it played in its wider ecological community.

Helpful here is that fossils rarely occur alone. Instead, whole faunas emerge from fossiliferous rocks. Sometimes they will reflect fairly accurately the larger communities from which they were derived. At other times they are death assemblages, collections of animals that never cohabited in life but were thrown together by the forces of postmortem dismemberment, transportation, and agglomeration. Fortunately, it is usually possible to correct for these postmortem influences to provide a reasonably accurate picture of ancient faunas and habitats. As you go back further in time, and encounter organisms that are increasingly unfamiliar, things become more difficult. But geological and botanical evidence can usually be brought in to help.

To summarize, once you have identified the actors you can begin to reconstruct the plot of the play—remembering that it was not carefully thought out in advance but was rather a spontaneous drama that unfolded under many different influences. Many of these will have been external, operating entirely without regard to the excellence of the actors' adaptation to their circumstances. Indeed, adaptation turns out to be a two-edged sword. In an erratically changing world it is often unwise for a population to be too closely adapted to a single environment.

CHAPTER 2

Evolutionary Processes

THE PUBLICATION in 1859 of Charles Darwin's book *On the Origin of Species by Means of Natural Selection* caused an immediate social furor. But it did not burst in upon an intellectual milieu totally unprepared for evolutionary ideas. French scientists studying the newly recognized phenomenon of fossils around the turn of the nineteenth century had already entertained ideas of change, or at least of replacement, in ancient "antediluvian" faunas. In 1844 the Scottish encyclopedist Robert Chambers had (anonymously) published his theory that life had changed over time according to a principle of "progressive development." And in Germany, too, many proponents of *Naturphilosophie* were willing to accept some inner impetus toward development among organisms.

Protoevolutionary currents were thus already stirring widely by the middle of the nineteenth century, and Darwin had mulled privately over his evolutionary ideas for almost a quarter of a century before he went public with them. Indeed, he procrastinated for so long that he was almost preempted, entirely independently, by his younger colleague Alfred Russel Wallace, whom we now honor as the codiscoverer of evolution by natural selection. Given the huge initial public fuss over Darwin's book, it is perhaps remarkable how quickly the idea was absorbed that life had evolved—that all living organisms were related by common ancestry. This acceptance came partly because Darwin's argument for "descent with modification" was made in exquisite detail. But it was also because the mechanism he proposed for evolution—natural selection—was such a compelling one. Indeed, in retrospect many found this mechanism to be entirely self-evident, which is why Darwin's colleague and supporter Thomas Henry Huxley famously berated himself with the exclamation, "How very stupid not to have thought of that!"

Evolution by Natural Selection

Darwin's idea was elegantly simple. It was based, among other things, on his practical experiences as a pigeon fancier. As breeders of animals and plants had known from time immemorial, in every generation individuals vary among themselves in heritable features. Equally undeniably, more are born than survive to reproduce. Darwin's point was that the reproductively victorious are those whose inherited characteristics make them better adapted to the environmental circumstances in which they live, while the less fit reproduce less successfully. Just as cattle breeders can change the appearance of their cows remarkably quickly by selecting those individuals that are allowed to reproduce, Nature exerts a constant pressure on the population as a whole to become better adapted. Thus, Darwin proposed, over the generations the cumulative effect of such natural selection is to physically transform each lineage of animals—eventually into new species and beyond.

Species are, of course, the basic *kinds* of organisms that we recognize in the living world, although their exact nature continues to be hotly debated. It is generally agreed that they are the largest populations of organisms within which individuals successfully interbreed with each other, but beyond this all bets are off. This is largely because speciation, the means by which new species come into existence, is not a unitary mechanism. Instead, reproductive discontinuity may come about for wildly varying reasons, from anatomical incongruity, through failures in fertilization or development of the embryo, all the way to behavioral differences. Speciation is simply a result that we observe in retrospect. Once it has taken place, though, it is typical for any successful new species to diversify over its geographical range, as each local population accommodates to its own particular circumstances. Such diversification in turn sets the stage for future species to emerge, should some natural barrier isolate one or more sections of the population. Still, we should not think of populations as necessarily fine-tuned to their circumstances in any one place. Many random factors are at play. And being too specialized has risks: specialized forms have higher extinction rates than generalists.

As we try to understand how species may arise, it is important to separate the twin processes of species diversification and anatomical innovation, which do not necessarily proceed in lockstep. This poses a challenge for the paleontologist, who has little more than the shapes of bones (the anatomy) to deal with. How do you recognize a new species in the fossil record? This vexing problem is well illustrated in paleoanthropology, the study of the evolution of the recently evolved human family, which is very close-knit.

On the short biblical timescale generally accepted in Darwin's youth (most theologians at the time reckoned that only about six thousand years had passed since the time of the Creation), transformation via gradual generation-to-generation change was unthinkable—there just wasn't enough time. But early nineteenth-century scientists were already well aware that an immense amount of time had passed since the formation of the Earth. By 1859 the long periods required for evolution by natural selection were no longer a serious scientific issue, even if Victorian society as a whole was not yet prepared for the new perspective. So it is hardly surprising that, once the initial uproar over the idea that all living forms are related by descent had died down, the main scientific objections to Darwin's ideas came not from those who objected to the principle of evolution, but from those who opposed natural selection as its engine.

One thing that had been lacking in Darwin's original formulation had been an accurate theory of how biological inheritance worked, and the argument over evolutionary mechanisms was greatly energized with the birth of the science of genetics in 1900. Almost all of the early geneticists were committed evolutionists, but few favored Darwinian natural selection as the key agent of evolution until the late 1920s, when a remarkable convergence began to occur. This convergence later became known as the "Evolutionary Synthesis."

The Synthesis

While quite nuanced in its early manifestations, by the mid-twentieth century the Synthesis had become highly reductionist. It saw evolution as a gradual process involving little more than the long-term accretion of heritable changes within lineages of organisms, always under the guiding hand of natural selection. As environments changed, so did populations. This same process could be extrapolated over evolutionary time to include higher-level phenomena such as the origin of new species and increasing biotic diversity. Microevolution (the promotion of new morphologies or new genes and gene combinations within species) and macroevolution (the origin of new species and larger groups) thus became part of the same unitary process.

Still, while slow transformation certainly accounted for evolutionary change, to many it was hardly a complete explanation for natural variety. As a result, the origin of biodiversity had to be ascribed to external factors. The argument for the splitting of lineages necessary to produce such diversity went like this: Each species had its ecological niche. When the niche became fragmented by environmental change, separating the segments of what had previously been a continuous population, each fragment would go its own evolutionary way. Eventually, each would incorporate enough unique change to be incompatible with its siblings. Voilà—new species! And via repetition of this same process, new families and orders would eventually emerge.

The Synthesis rapidly permeated all branches of evolutionary biology, at least in the English-speaking world. And it performed a very salutary function in sweeping away a lot of accumulated intellectual baggage. But the compromises made to achieve consensus were not equal on all sides, and the ones who did least well out of the deal were the paleontologists. The systematists who studied the variety of the living world got a mechanism to explain natural diversity. The geneticists, and particularly the mathematical population geneticists, got to hold the key to that mechanism. But paleontologists were robbed of their basic unit of study. Every fossil they found had necessarily belonged to a species, which had always been the main entity of interest. Now, however, the paleontological species was an ephemeral thing. How could it be viewed as a discrete unit if every successful species transformed itself insensibly into its successor?

Delineating species through time thus became an entirely arbitrary affair, creating an acutely uncomfortable situation for students of the fossil record. On occasion it even led to the bizarre spectacle of paleontologists congratulating themselves on the deficiencies of their database, since gaps in the record provided convenient points at which to separate related species. Worse, the Synthesis relegated the paleontologists to an essentially clerical role in clearing up the details of the history of life: even in principle, there was little that fossils could contribute to theory, or to the understanding of evolutionary mechanisms.

For years, paleontologists explained discrepancies between the predictions of the Synthesis and what they were actually finding as artifacts of an incomplete fossil record. But in 1971, a concerted attack was mounted on the entire structure of the Synthesis.

Punctuated Equilibria

This attack came from Niles Eldredge, a paleontologist at the American Museum of Natural History who had been studying trilobites (ancient marine invertebrates) that were abundant in the sedimentary rocks of his native New York State and the Midwest. What Eldredge saw in his trilobites was a marked *lack* of change (stasis) over spans of millions of years. Rather than rationalize this as an artifact of an incomplete record, he preferred a literal reading of what he observed, concluding that the lack of change among those trilobites was actually saying something about their evolutionary history. There was no signal whatever of gradual honing by natural selection (which was evidently working to keep the population as a whole unchanged, by trimming off the extremes). Instead, the one change Eldredge saw was associated with a rapid event of speciation in a local trilobite population, followed by the later wholesale replacement of the ancestral form by its descendant.

Something similar had been found by Eldredge's colleague Stephen Jay Gould in his studies of Ice Age Bermudan land snails. In 1972 the two joined forces to generalize their findings in a paper

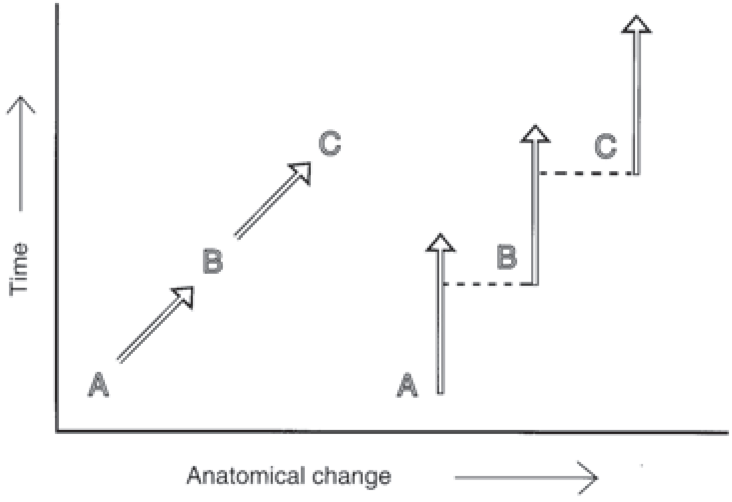


FIGURE 2.1. Two views of the evolutionary process. The arrows at left represent phyletic gradualism, whereby one species gradually transforms itself into another over time under the pressure of natural selection. On the right, the notion of punctuated equilibria views change as episodic: species are basically stable entities that give rise to new species in relatively short-term speciation events. Morphological changes may take place independently of speciation.

entitled “Punctuated Equilibria: An Alternative to Phyletic Gradualism.” Their central point was that fossil species seemed generally to come on the scene rather suddenly and to stay around in the rock record as distinctive entities for some time before abruptly disappearing. Since the local records that paleontologists investigate bear witness to the succession of faunas in particular places, this was hardly surprising. Worldwide, environments are known to have changed frequently and rapidly over time. Eldredge and Gould pointed out that when your environment changes it is much more likely that you will emigrate to more congenial surroundings, or go extinct, than that you will hang on in the same place for many generations and slowly adapt to your new circumstances.

Perhaps because of its provocative title, and certainly because of the energy with which Eldredge and Gould contrasted the theoretically based phyletic gradualism of the Synthesis with the punctuated equilibria suggested by their own observations, their publication caused an immediate stir. Paleontologists who had long labored to shoehorn their data into the framework dictated by the Synthesis were discomfited by the notion that they should usually expect to find occasional and abrupt change rather than slow, continuous transformation. Nor were they happy with the associated idea that at least some of the breaks in the fossil record should be taken as data, rather than as deficiencies. But following the predictable chorus of criticism—Eldredge and Gould were widely demonized as saltationists (advocates of evolutionary “jumps”) who denied the principle of adaptation—it transpired that, for the most part, the punctuated-equilibria model fit quite well with what paleontologists were actually finding. Indeed, many well-known evolutionary trends in the fossil record that were traditionally attributed to gradual generation-by-generation adaptation turned out to be better explained by successive species replacements.

This made it evident that, like speciation, what we used to call the “evolutionary process” is far from unitary. Instead, the factors governing evolutionary change are extremely complex. Often acting above the level of the individual, they may be entirely random with respect to adaptation. Climates and environments typically shift rapidly and erratically, far faster than natural selection could ever track. Species constantly find themselves in competition with new contenders for ecological space. There is little advantage in being the most splendidly adapted exemplar of your species if a new arrival is outcompeting your entire species into extinction. What's more, in addition to the steady background tickover of origination and extinction of individual species, faunal change may often occur in episodes of quite comprehensive replacement.

South African paleontologist Elisabeth Vrba has eloquently argued that external environmental change is the driving mechanism behind faunal "turnover pulses," which the fossil record shows have periodically occurred in her home continent. Speciation, Vrba believes, is unlikely to occur in the absence of stimulus from the physical environment, a stimulus that also spurs episodes of migration. Among other examples, she points to the major cooling event around 2.5 million years ago, during which there was a wave of first appearances in the African fossil record of open-country forms, especially grazing antelope species. This particular episode may in fact have seen the appearance of our own genus *Homo*. Vrba sees such turnovers, large and small, as routine in the history of life. She is almost certainly correct in suggesting that these have occurred across diverse groups of organisms and during relatively short bouts of environmental change.

Mass Extinctions

The most dramatic examples of abrupt turnover in the fossil record are mass extinctions, in which significant proportions of all species on Earth suddenly disappeared, to be replaced in short order by completely different biotas. The fossil record holds evidence of five main mass extinctions (and many would claim that a sixth one is occurring now, at the hands of *Homo sapiens*). The best-known mass extinction is the "K/T event" that carried away the dinosaurs some 65.5 million years ago at the end of the Cretaceous. Some 38 percent of all marine animal genera also disappeared at this time, and an even higher proportion of land animals. Flowering plants were widely supplanted by a flora dominated by ferns—as in the "fern spikes" that we often see today after forest fires.

A calamity such as this must have had an appropriately cataclysmic cause. This by itself rules out almost all of the factors to which local extinctions are usually attributed, such as pandemic disease and competition from locally evolved species and immigrants. Essentially, what is left is some kind of exotic change in the physical environment, and three culprits come to mind: (1) exceptional volcanic activity, (2) a cosmic radiation event, and (3) the impact of an asteroid or comet (a "bolide"), which could have created a nuclear winter effect. A fourth option has been to deny that there is any single cause for the K/T extinction.

The idea that a huge (ten-kilometer-wide) bolide hit the Earth was suggested in 1980 by Luis Alvarez and colleagues. Initial reaction was hostile, since many believed that the period of Earth's bombardment by asteroids was long passed. Nevertheless, the famous Meteor Crater in Arizona was evidence of a fairly large hit just fifty thousand years ago, and even without a known impact crater associated with the K/T event, the Alvarez group had compelling evidence. They showed that rocks of this time in Denmark, Italy, and New Zealand contained a thin layer rich in iridium, an element rare on Earth but a significant component of some meteorites, and suggested that this had been spread globally in a debris cloud. The iridium anomaly has now been found in many other parts of the world. In some places, the presence of "shocked" quartz grains also suggests high pressures produced by major impact.

What's more, a candidate for the impact crater itself has now been identified. It centers on a place called Chicxulub at the northern tip of Mexico's Yucatan Peninsula. After 65 million years, erosion has obscured the crater's outline on land, and its seaward portion has been covered by sediments. But gravity anomalies and other features show this feature to have been at least 180 kilometers in diameter—just about the size predicted by the Alvarez group. The energy released by such an impact would have been around 2 million times greater than that released by the largest nuclear device ever exploded—more than ample to create the dense, lingering dust cloud necessary for prolonged inhibition of plant photosynthesis, although high southern latitudes were probably relatively little affected.

Most paleontologists today tentatively accept an association between the K/T extinction and a bolide impact, maybe several. But this mechanism may not explain other mass extinctions. For example, massive lava floods are believed to have caused the mass extinction that occurred 200 million years ago, when over 50 percent of marine genera as well as many terrestrial forms were carried away.

As you go back in time, evidence for large traumatic events inevitably becomes harder to find. Nonetheless, some favor asteroid collision to explain the largest mass extinction of all. This one took place at the end of the Permian, about 250 million years ago, and saw the demise of as many as 95 percent of marine and 70 percent of terrestrial species. No corresponding impact structure has as yet been identified—and at that remote period it will be tough to do so—but it has been suggested that a shock on the necessary scale might also have been associated with the large-scale flood volcanism for which there is evidence at this time in Siberia. Yet further back, however, at about 380 million years ago, a major extinction seems to have taken place in a series of pulses that occurred over as long as 20 million years.

Besides the "Big Five," numerous other smaller mass extinctions are recorded in the geological column. Whatever the cause(s) in any particular instance, the most important message of the mass extinctions is that disappearances of living forms cannot always be attributed to gradual evolutionary processes. The same, of course, applies to the equally well-documented mass appearances that followed the extinctions. The net effect of these dramatic events has been biotic turnover on a gigantic scale, as the departure of older biotas liberated vast amounts of ecological space to be repopulated by the survivors, in a process known as adaptive radiation. The classic case of such radiation is the phenomenally rapid diversification of the mammals following the K/T event, as our own group took over an empty field from the dinosaurs.

Darwin lived at a time when influential geologists held the intuitively attractive "uniformitarian" view that all modifications of the Earth's surface were due to the prolonged action of mechanisms—erosion, deposition, earthquakes, volcanoes—that we can still observe today. And Darwin's pathbreaking notion, that the diversity of the living world had gradually evolved through natural selection, fit perfectly into this picture of gradual change.

Still, as demonstrated by such things as gigantic basalt floods and huge bolide impacts that I, for one, hope never to observe, the uniformitarian geological picture is at the very least not the whole story. Similarly, the grand patterns we see in the fossil record do not sum out simply to a smoothly unfolding process of adaptation, as lineages of organisms are gradually perfected by natural selection. Instead, your triumph can come about simply as the result of someone else's misfortune—and vice versa. The success or failure of species, as of individuals, is not always a matter of how well they are adapted. Sometimes it's no more than the luck of the draw.

THE MOLECULAR BASIS OF CHANGE

Evolution thus has its discontinuities, but of course it has its continuities as well. Most fundamentally, all living things are connected by unbroken lineages to our 3.5-billion-year-old common ancestor. Underlying this succession is our mechanism of heredity. In 1866, when he formulated his notion that inheritance was controlled by the discrete units we call genes, the Austrian monk Gregor Mendel knew nothing about their physical nature: he simply inferred their existence from what he observed. Nowadays we know a great deal more, and what we have learned is amazing.

Experiments on fruit flies early in the twentieth century confirmed that individual genes, passed along in the sex cells, were associated with individual traits. They also showed that those traits—and hence the genes—tended to vary together, and thus had to be linked in some way. Soon it was realized that linkage exists because the genes are distributed along microscopic paired structures, known as chromosomes, that become visible in the nucleus of each cell of the body when it is about to divide.

The story from that point onward is fairly well known. The long polymeric molecule called deoxyribonucleic acid (DNA) contains a chemical code that spells out the genes. In concert with its single-stranded cousin RNA, DNA directs the development of new cells—and new tissues, and new organisms—by specifying the structure of the proteins, the "building blocks" of the tissues, that are manufactured in the cells.

The way that DNA replicates itself as cells divide provides a mechanism for mutation, the process governing the alterations in the genes that underpin the appearance of evolutionary novelty. DNA is a fragile molecule that is sensitive to radiant energy, and mutations turn out to be spontaneous changes in the DNA code. They are surprisingly common, and these random copying errors (which do not always change the functions of the gene involved) underpin many of the hereditary changes ultimately expressed in the evolutionary histories of organisms. Mapping the changes that have taken place in the DNA of organisms over time has provided a powerful tool for tracing their evolutionary histories.

Genomics

For many years the central dogma of genomics, as the study of DNA has become known, was that information flows just one way, from the genes to the proteins. It turned out, though, that things are a lot more complicated than that. For a start, genomes (the totality of an individual's DNA) are not made up entirely of DNA that codes for proteins. Indeed, most of the human genome appears to be made up of mobile elements known by such names as SINES and LINES (Short/Long Interspersed Repetitive Elements), that don't serve a coding function. What's more, even within coding genes there are stretches of DNA, known as introns, that are edited out by the cellular apparatus instead of being translated into proteins.

Scientists have called the noncoding stuff "junk DNA," but they now find that some of it may help regulate gene expression—in which case, it may have a very important role indeed, because the relationship between the structure of a gene (its sequence of DNA bases) and the magnitude of the developmental cascade it initiates is not a simple one. Effects may be due less to the structure of the genes than to how they are regulated: the order in which they are switched on and off, and how they are expressed. To complicate things further, multiple overlapping genes may cohabit on the same stretch of DNA and produce RNAs that do not code for proteins but instead play significant roles in gene regulation.

For anyone seeking to understand how the diversity of Nature has evolved, this is very exciting. LINES and SINES have proven very useful in reconstructing relationships among organisms, and we are beginning to see how relatively small mutations at the structural genetic level can produce disproportionate developmental consequences. This has significant implications for the evolutionary process because, if a minor mutation can involve a major developmental reorganization of a body system or systems, you don't have to explain how a host of accumulating genetic substitutions, each fairly insignificant in itself, should eventually result in a coordinated innovation. One small change involving a regulatory gene can produce a major change in structure, usually problematic but occasionally helpful.

At the same time, the complexity of transcription helps us understand how the past constrains future evolution. Evolution can rarely result in optimization, not only because selective pressures are unlikely to remain uniform over extended periods, but because potential change is both random and channeled by what is there already. What's more, most selection is clearly devoted to the maintenance of ongoing integration and function—that is, assuring nonchange. Indeed, looking across the entire range of living things, it is altogether remarkable how many basic genes are still shared by the most disparate-looking organisms. It's been estimated that we share 40 percent of our genome with a banana.

Remarkably, although they have huge amounts of DNA, organisms have rather few genes. In humans, only twenty-five thousand genes control the vast array of functions necessary to produce and maintain a fully functioning adult individual. This is only possible because DNA sequences fulfill multiple functions: one gene may affect many characters, and most characters are controlled by multiple genes, which interact in complex ways. The most important evolutionary implication is that the blunt weapon of natural selection cannot impact on one character complex without simultaneously influencing many others—and not necessarily in favorable ways. The whole individual succeeds or fails in the reproductive stakes, meaning that, to make a significant difference, any potential agent of natural selection has to have a very powerful influence on survival or fecundity—in the face of many powerful competing factors.

CHAPTER 3

The Tree of Life

"How did life get to be the way it is?" is the most basic of questions, but for paleontologists it has to be asked with two important caveats. First, evolutionary events happened in the moment, unaware of the future. Second, we need to avoid judging the past by standards of our own time, even though the best way of interpreting past forms is often to compare them with living ones.

Fortunately, today's biota captures past diversity quite extensively, not least through living fossils, extant forms that have not changed much over time. Because of the branching nature of evolution, the history of life can be represented by a tree-like diagram, in which every species, living and extinct, takes its place at the tip of a peripheral twig. Those twigs are in turn assembled into ever-larger branches that reflect the descent of increasingly inclusive groups from ever-more-remote common ancestors.

Diagrams of this kind do not have to take the form of a typical slender tree, with a central trunk soaring toward its highest tip. Indeed, they should not. It turns out that one of the most economical ways of representing an evolutionary tree is in the form of a circle, as in Figure 3.1, which shows the relationships between the great subdivisions of life as they are understood today. Here the hypothetical ancestor lies in the center, and the individual branch tips are all of equal importance—emphasizing that, while evolution promotes diversity, it does not inexorably lead toward more complex states, and certainly not at uniform rates.

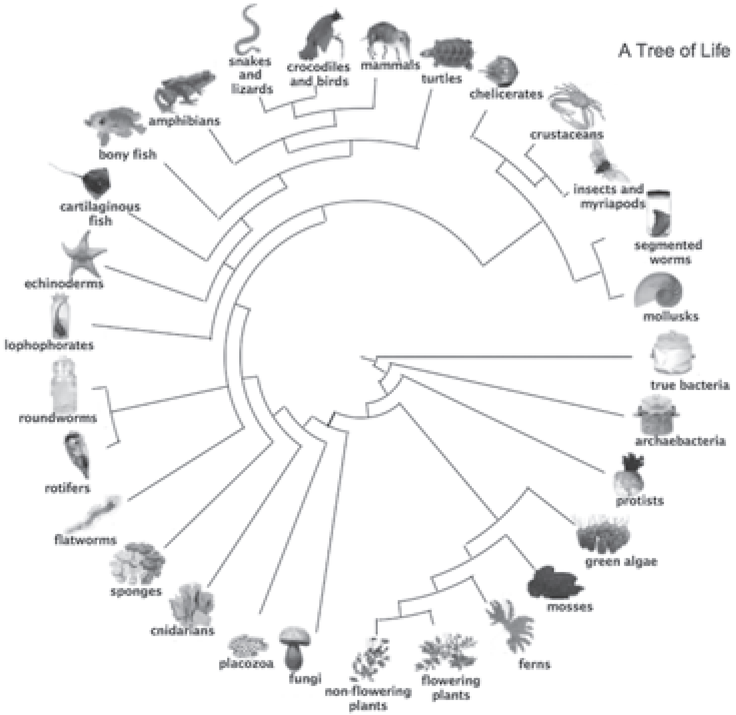


Figure 3.1. A Tree of Life, showing relationships among the major groups of living organisms. Courtesy of Rob DeSalle.

Species and Classification

Nobody knows even roughly how many living species there are in the world today: estimates range from 2 million to 20 million–plus. Still, whatever the exact number, *Homo sapiens* is only one tiny part of a huge, diversified web of Nature. Aristotle and the medieval Scholastics who followed him recognized this rather obliquely by adopting the notion of a "Great Chain of Being" (*scala naturae*), in which Earthly organisms were arranged in a continuum from the simple (slime molds) to the most complex (human beings). Once science began to assume its modern form it was discovered fairly rapidly that this gradation was not the most accurate way of characterizing Nature. But although honored in folk taxonomies from time immemorial, the organizing principle by which living things are classified by biologists today was not formalized until the mid-eighteenth century.

In his great work *Systema Naturae,* the Swedish naturalist Carl Linnaeus formalized the modern binominal system of classification in which each basic "kind" of living thing receives two names, the first indicating its genus and the combination its species. Thus human beings belong to the species *Homo sapiens* of the genus *Homo* (in which Linnaeus also bravely included the great apes, in recognition of their many anatomical resemblances to ourselves). Linnaeus then grouped his genera into Orders (in our case, Primates), Orders into Classes (Mammalia), and Classes into Kingdoms (Animalia). Since his time the number of ranks in the hierarchy of classification of living things has been greatly expanded.

We call groups at all levels of this hierarchy "taxa," and hence the science of organizing them is known as taxonomy. The Linnaean groups-within-groups approach coincides nicely with our modern understanding of the patterns produced by evolution, a process that Charles Darwin succinctly described as "descent with modification." Indeed, the splitting of lineages from common ancestral forms remains the only mechanism known to science that actually predicts the structure we see in the natural world. To the preevolutionary Linnaeus, however, the ordering of Nature was simply evident in the nested pattern of physical similarities that he saw before him.

Figuring Out Evolutionary Relationships

In building the Tree of Life and positioning species within it, the early comparative anatomists were soon joined by embryologists, paleontologists, and more recently geneticists. Regardless of technology the same comparative principles apply, but until the mid-twentieth century there were few objective ways to choose among conflicting evolutionary hypotheses. Finally, in the 1950s a revolution occurred in systematics (the science that classifies organisms based on their evolutionary relationships). Or, more precisely, two revolutions. Some systematists began devising clever ways of measuring and comparing the overall similarity of organisms. Others protested that this was misleading because it confused resemblances of two kinds: those inherited from a common ancestor and those independently evolved, which say nothing about genealogical relationship.

One common example compared a salmon, a lungfish, and a cow. The facile conclusion is that the salmon and the lungfish are each other's closest relative, because both look like fish. But in fact, in terms of descent, lungfish are more closely related to the ancestor of the land-dwelling tetrapods (including the cow) than to the ancient bony fish that was ancestral to the salmon. The similarity in body form between the salmon and the lungfish is retained from a primitive and very remote common ancestor—and is, ahem, a red herring if what you are looking for is evidence of evolutionary relationship, rather than simply of an aquatic lifestyle.

The general similarity model has now been all but abandoned, and systematists seek shared derived (changed) characters inherited from an immediate common ancestor. By grouping species based on these, they obtain branching diagrams known as "cladograms," statements about relative recency of common ancestry. These are not hypotheses of ancestry and descent: every known species is a terminal point on the cladogram, since every ancestor (represented at the nodes where the branches join) is hypothetical. In fact, in theory at least, actual ancestry is impossible to demonstrate because every ancestor was necessarily primitive in all features relative to its presumed descendants—thus lacking derived characters to connect it with any of them.

One practical difficulty is that there is plenty of convergence (a.k.a. "homoplasy") around, in the form of superficial resemblances due solely to similar adaptation. As a result, hypotheses of relationship based on small character sets tend to be fragile. The more characters you can use in your analysis, the more reliable the results are likely to be. This is where the number-crunching capacities of computers come in extremely handy.

There is now a whole range of computer-based routines for generating statements of relationship among groups of organisms, using diverse data sets ranging from morphological and even behavioral character states to DNA structure. The best of these are based on the notion of parsimony, whereby the hypothesis of relationships to be preferred is the one that requires the smallest number of character changes among the organisms involved.

The Tree of Life that we are about to look at results from the painstaking assembly of a multitude of cladograms constructed in this way. Establishing relationships among the larger groups of which it is composed has been hugely aided by the analysis of DNA sequences. This is because morphologies have often so vastly changed that there are few if any obvious similarities to compare among the largest groups, while many basic gene structures have been highly conserved over vast periods of time and are thus widely comparable across the spectrum of living things.

Structure of the Tree of Life

When Linnaeus devised his binominal classification system, the order of Nature looked pretty simple. Living things were either animals (Kingdom Animalia) or plants (Kingdom Plantae). And although early microscopists such as Antony van Leeuwenhoek had, by the late seventeenth century, already observed and described tiny single-celled bacteria, it was a long time before most biologists realized that things were a whole lot more complicated than Linnaeus and his contemporaries had thought. Attachment to the older view had much to do with the fact that the basic quality believed to distinguish animals from plants was motility—the ability to move around—which meant that van Leeuwenhoek's tiny single-celled organisms could conveniently be classified into one group or the other simply on the basis of whether they sat still on a microscope slide or not.

A century after Linnaeus, the German embryologist Ernst Haeckel hived off the microorganisms into their own kingdom Protista, creating a three-kingdom division of living things. Once rethinking had started, all bets were off, and by the mid-1970s a five-kingdom model of life's diversity had become widely accepted. Under this scheme the most fundamental division among living things was between the "prokaryotic" bacteria, which lack a membrane-bound, chromosome-containing nucleus within the cell, and the four kingdoms of "eukaryotes" that do have nuclei: the animals, plants, fungi, and protists. As always, Protista remained rather ill-defined, consisting as it did of an unwieldy assemblage of tiny forms, such as amoebas and algae, that did not obviously fit into any of the other groups.

But the complications didn't stop there. In the late 1970s Carl Woese and colleagues discovered an entirely new major category of organisms. Studying RNA sequences in prokaryotes, Woese had found that his subjects fell into two distinct groups. Although under the microscope the "bacteria" living in high-temperature environments or producing methane *look* similar to run-of-the-mill bacteria, they are entirely different genetically. Woese thus proposed three basic domains of living things: Eukaryota, Eubacteria (or just plain Bacteria), and Archaebacteria (the extremophile forms, later renamed Archaea). Exactly how these three great domains are related is still disputed, though majority opinion puts the archaeans with the eukaryotes, even though they superficially resemble bacteria. Such bizarre outcomes are not uncommon in systematics—just think back to the salmon, lungfish, and cow.

In any event, at the very base of the Tree of Life we find the bacteria. These tiny single-celled microorganisms are often reviled as the causes of many human diseases. More importantly, though, they are vital to many of the processes needed to sustain more complex life-forms. Indeed, they are the very fundament of the ecological system on which we all depend. With an estimated world population of five followed by about as many zeroes as will fit on this line of type, bacteria account for a substantial proportion of the Earth's total biomass. And while we've seen that Archaea probably group with eukaryotes, relationships so deep in the history of life are hard to demonstrate and are bedeviled by the lateral interspecies gene transfer that is common among microorganisms. Indeed, it's been claimed that, over the long haul, interdomain gene transfers can account for upward of 20 percent of the genome—in which case, the base of the Tree of Life may in fact be very tangled, looking a whole lot less like a conventional forking tree than like a woven macramé web.

Eukaryotes and Animals

The domain Eukaryota brings together the various kingdoms of organisms that have membrane-bound nuclei in their cells. Because the cellular machinery of eukaryotes has both bacterial and archaean similarities, it is suggested that the ancestral eukaryote resulted from the fusion of a bacterium with an archaeon that furnished the nucleus. How many primary subgroups should be recognized within Eukaryota is debated, but one widely adopted schema suggests eight. One leading candidate for the most primitive living eukaryote is the dreaded intestinal parasite *Giardia lamblia,* and other contenders include a long list of tiny aquatic creatures, both single-celled and multicelled. Many of these are important because, like the more evolved archaeplastids (the green plants, and red and green algae), they photosynthesize, making sugars when exposed to sunlight.

All animals have eukaryotic cells, and the vast majority, the Metazoa, are multicellular. What (literally) binds the metazoans together is an extracellular matrix of molecules providing structural support to the cells composing the tissues, and promoting adhesion among them. Most metazoans (sponges and jellyfish are exceptions) belong to a huge group known as Bilateria, the bilaterally symmetrical animals. These possess two mirror-imaged sides lying along a central axis and, just as importantly, two ends. They also have three germ layers in the embryo, permitting significantly increased complexity in adult form.

Bilateria come in all shapes and sizes, but there are three main groups. One embraces forms as diverse as squid and earthworms and the mollusks, all identified as protostomes because the initial opening in the expanding embryo becomes the mouth ("stoma") end of the two-ended creature. The second great bilateran group, also protostomes, includes the spiders, crustaceans, centipedes, and the insects, the most diverse group on the planet. Finally come the deuterostomes, which develop the anus from the initial opening of the embryo, before the mouth appears.

Being a Chordate

The deuterostomes of most interest to human beings are the chordates. Closest to the base of the chordate tree are the tunicates, a diverse group of sessile marine forms whose free-swimming larvae bear such hallmarks as a notochord, a stiffening rod that lies below a nerve cord running the length of the body. They also have gill-like pharyngeal slits and a complex nervous system. Next on the tree are the lancelets, small marine animals that retain the notochords and nerve cords into adulthood. They reproduce by external sexual fertilization and consume nutrients via a mouth and evacuate through an orifice forward of a distinct tail.

Humans belong among the Vertebrata, the backboned animals. Vertebrates today embrace all the fish, amphibians, reptiles, birds, and mammals. If we factor in all the vertebrates that ever existed, the diversity is more impressive yet. Lifeways are also astonishingly varied: vertebrates are found not only in a huge array of aquatic habitats and in the air, but on land they do everything from burrowing below ground to leaping through the forest canopy. A world without other vertebrates would be very different from the one we are used to today.

Recent molecular evidence suggests that the hagfish, a group of superficially eel-like marine scavengers, are very close to the vertebrates. But these creatures lack a vertebral column, a key feature of vertebrates, so most zoologists still prefer to isolate them in their own subphylum. Also qualifying as nearly-but-not-quite vertebrates are the lampreys. These jawless and (again) rather eel-like creatures, widespread in coastal and freshwater habitats, have a rudimentary vertebral column but still don't quite make it as vertebrates.

The Vertebrates

The true vertebrates, subphylum Vertebrata, are chordates with backbones that not only enclose and protect the nerve cord, but are composed of complex vertebrae. The vertebrates also have an elaborate circulatory system powered by a heart, a brain at the front end of the neural cord, complex paired eyes with single lenses, and a unique form of embryological development involving primordial neural crest cells that migrate out from the nerve cord to control the development of many aspects of the body.

Among the true vertebrates, humans belong to the Gnathostomata—those vertebrates that possess jaws. Several fossil groups of early jawless vertebrates are known, but all surviving vertebrates are jawed. The gnathostomes are in turn divided into two groups: the chondrichthyes (the sharks, rays, and other cartilaginous fish) and the osteichthyes (including us). The osteichthyes are divided once more into the actinopterygii (the bony ray-finned fish) and our own group, the sarcopterygii. This includes the lobe-finned fish, such as today's coelacanth, plus the land-living vertebrates known as tetrapods ("four feet").

Modern tetrapods embrace a bewildering variety of creatures, from the frogs and salamanders that develop through an aquatic larval stage, to the turtles, lizards, crocodiles, dinosaurs (including birds), and the mammals. The last five groups are amniotes, grouped together because their eggs are enclosed in a watertight amniotic sac—a feature that had evolved by the time that the land was colonized. The first amniotes were small, rather lizard-like creatures whose eggs could survive outside water, emancipating their possessors from life in the immediate vicinity of lakes, ponds, and rivers.

There is much disagreement among taxonomists about how the major groups of amniotes ought to be classified. Traditionally, four groups of more or less equal importance were recognized: the amphibians, reptiles, birds, and mammals. Nowadays, with increased attention being paid in classification to exact evolutionary relationships, one sighs for such simplicity.

To cut a long story short, among the amniotes we humans belong to a group called Synapsida, which includes all mammals plus the extinct Permian "mammal-like reptiles" and their successors. The "mammal-like reptile" designation is actually frowned upon nowadays, because reptiles are basically what's left when you've subtracted mammals and birds from Amniota—making for a very untidy group indeed. Today's birds, for example, turn out to group *inside* the dinosaur radiation, so that even though the name "dinosaur" means "terrible reptile," we can't properly view dinosaurs as reptiles at all. Better just to say that what we usually think of as reptiles belong to a group more accurately known as Sauropsida. Turtles (Anapsida) seem to be basal to this group, and all the other members are grouped together in Diapsida, which enfolds the snakes, lizards, crocodiles, birds plus dinosaurs, and a Jurassic Park–full of other extinct creatures, such as pterosaurs, ichthyosaurs, and plesiosaurs.

With the mammals we are moving into more familiar territory. Mammals are warm-blooded animals with hair and sweat glands (including some modified for milk production), three bones in the middle ear, four-chambered hearts, and a brain that includes a neocortex. Once again, we encounter a vast array of forms within this group, whose members range from the egg-laying monotremes, through the pouched marsupials, to the placental mammals whose offspring are nourished within the mother's womb to an advanced stage of development.

The best-known monotreme, the platypus, is a remarkable creature. It has the fur and milk glands of a mammal, the egg-laying and venom glands of a reptile, and the webbed feet and duck-bill of a bird. It also has a unique electrosensory system for underwater foraging. Recently, the entire genome of the platypus has been decoded, and it shows an equally bizarre mosaic of genes.

The marsupials are mainly distributed in Australia and New Guinea, with a few New World representatives, and it's amazing how far they have managed to mimic the radiation of our own more widespread group, the Eutheria or placental mammals. The placentals embrace a vast array of forms ranging from whales, through antelopes and hyenas, to bats. Our particular corner of Eutheria is the order Primates, to which we will return in detail later.

This concludes our whirlwind tour through the mind-bogglingly diverse Tree of Life. Remember, though, that we are ending with humankind for no better reason than that we humans are an anthropocentric species. We have not arrived at the top of the (circular) tree. We have simply clambered our way to the end of one of its many terminal branches.

CHAPTER 4

In the Beginning

The question, "What is life?" seems pretty straightforward; the answer is less so. Modern living things are all membrane-bound entities that metabolize (convert energy) and reproduce by means of self-replicating nucleic acids. But the first organisms were probably completely unlike even their simplest descendants today.

In the 1920s it was suggested that complex organic (carbon-based) molecules might have been formed in an oxygen-free atmosphere such as that of primordial Earth, or alternatively in the "hot dilute soup" of the newly formed oceans. But in a breathtakingly prescient letter of 1871, Charles Darwin had already imagined a "warm little pond, with all sorts of ammonia and phosphoric salts, lights, heat, electricity etc. present," in which "a protein compound was chemically formed ready to undergo still more complex changes." In the 1950s, scientists duly generated amino acids, the building blocks of proteins, by sending electric charges through a "prebiotic soup" consisting of molecules of methane, hydrogen, and ammonia in water. Once it was established that the basic components of life could indeed be spontaneously engendered from simple and abundant inorganic precursors, the question became one of the medium in which the transformation occurred.

One leading candidate is the bottom of Earth's late Hadean oceans. In this gloomy setting, warm, alkaline, mineral-rich underwater springs may have reacted with cooler seawater to precipitate out thin films of inorganic molecules consisting of silica, carbonates, clays, iron sulfides, and other minerals. Tower-like edifices of this kind, composed mostly of carbonates, are known today around submarine vents that lie away from the mid-ocean ridges. Such vents furnish much less extreme environments than the scorchingly hot and highly acidic on-ridge black smokers that support "extremophile" life today. The cooler fluids they emit are well below boiling point, but in the early days the heat gradient would probably have provided enough energy to promote the production of larger, more complex organic molecules, and eventually of self-contained cells.

To be perfectly frank, we don't know exactly how such organic chemicals began behaving like living organisms, or how they developed cellular complexity. Some scientists favor a "genes-first" notion whereby nucleic acids formed at the outset, while others prefer a "metabolism-first" scenario, in which simple metabolic pathways were initially established. However they formed, proto-organisms could have migrated into the sediments of the seabed, to initiate what has been called the "deep biosphere," the mass of microbes that live beneath the sediments of the ocean floor. With the maturing of the Earth's crust, some of these simple organisms would sooner or later have been upthrust into shallow waters, where the penetration of sunlight allowed them to build organic molecules based on carbon dioxide—and photosynthesis began.

This is, of course, just one scenario among several, though whatever the exact details, the basic ingredients for life were present very early on. Sadly, hardly any rocks survive from the Hadean to tell us what happened. The oldest known rocks, about 4.3 billion years old, simply confirm that crust formation began very early. Some 3.8-billion-year-old rocks in Greenland are claimed to contain the waste products of microbial metabolism, but they are pretty thoroughly altered by metamorphism and harbor an active population of cyanobacteria whose activities may have confused the picture. Thus, to begin the paleontological history of life, the history that is documented by physical remains of living things, we have to move beyond the Hadean and into the Precambrian, the period when the true sedimentary record begins. The first eon of this almost unimaginably enormous span of time is known as the Archaean ("the Ancient").

The Precambrian (3.8 Billion–542 Million Years Ago)

The first unarguable evidence of life comes in the form of Archaean stromatolites, layered sedimentary mats up to 3.5 billion years old whose rare modern equivalents are built mainly by photosynthesizing cyanobacteria (blue-green algae). The appearance of stromatolites coincides closely with the earliest evidence of free oxygen in the environment, witness to the fact that they photosynthesized. The advent of free oxygen changed the world, altering the atmosphere from one that was primarily composed of noxious volcanic gases to the one that is vital for almost all life-forms today.

The first evidence for free oxygen comes from banded iron formations (BIFs) that began to be deposited about 3.5 billion years ago. The source of most of today's industrial iron, the BIFs were produced as the newly available oxygen began binding to dissolved iron in the seas, producing huge bottom deposits of insoluble iron oxides. When all this chemical activity began, the oceans were a vast oxygen sink, ready to absorb all of the oxygen that the early photosynthesizers could throw at them—so oxygen-thirsty, indeed, that it took over 1.5 billion years to oxidize all the iron and sulfur they contained. Only when this was achieved, less than 2 billion years ago, did the BIFs cease to form and free atmospheric oxygen begin to rise. Even then a period of red-bed formation followed on land, as terrestrial iron was oxidized.

While all this was going on, the ancient cyanobacteria began to encounter competition from a new form of life: the "true" algae, actually primitive and microscopic photosynthesizing marine plants. The cyanobacteria were probably victims of their own success: as they pumped out oxygen, nitrates (oxides of nitrogen) began to form in the environment—and nitrates were the ideal nutrient for their new eukaryotic competitors.

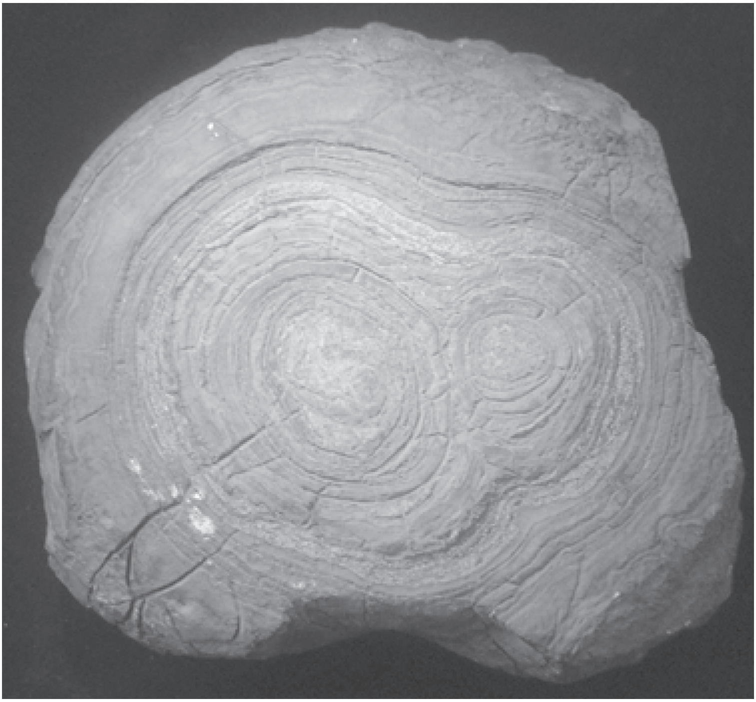


Figure 4.1. *Cryptozoon*, a cabbagelike reef-forming stromatolite that flourished in Precambrian and Cambrian times. Courtesy of Niles Eldredge.

Soon the stromatolite mats were shared with eukaryotes, and these more complex though still mainly single-celled life-forms came to dominate the shallow seas of the Earth, building huge thicknesses of limestone as they fixed seawater carbonates. To judge by the increasing variety of stromatolite architectures, this was a time of rapid diversification for the mat builders: they achieved their greatest variety around 1.5 billion years ago and held pretty steady until a gradual decline began about 700 million years ago. The initial proliferation of the new stromatolite makers has been attributed to intense competition for ecological space among the early eukaryotes, and their eventual decline to the rise of grazing eukaryotes that may have exploited them as a source of food. Certainly, today's stromatolites live only in marginal environments where potential predators are unable to thrive.

Still, while stromatolites left the most noticeable evidence of early life during the Archaean, they were not alone. Some early rocks are thought to contain possible microfossils as well as biomarkers, chemical byproducts of metabolism. Whether the metabolizers concerned were equivalent to any bacteria surviving today is debated, but they do seem to provide independent evidence of life at the very beginning of the Archaean.

Eukaryote fossils did not make their appearance until long after the beginning of the Proterozoic ("before life") Eon some 2.5 billion years ago. The first of them are rather unimpressive, basically amounting to tiny acritarchs ("of uncertain origin") that probably represent microscopic floating algae. These tiny things have been a durable feature of the fossil record ever since their appearance some 1.4 billion years ago. But not until the end of the Proterozoic, in the Ediacaran Period, do we find fossils we can truly recognize as those of animals and evidence of something that we can really call a "fauna." Meanwhile, though, the Earth itself had been through some quite traumatic times.

Snowball Earth

Geologists call the period preceding the Ediacaran the Cryogenian ("frozen"), and for as good a reason as the name of the first stage of Earth's history evokes Hades. At about a billion years ago, the Earth's continental masses came together in a single supercontinent that has been called Rodinia. With very extensive exposure of dry land, increased weathering robbed the atmosphere of carbon dioxide, which abundant tropical rainfall converted to carbonates and ultimately returned to the sea. This decline in the principal greenhouse gas set the stage for climatic cooling. Ice caps formed at the poles and advanced toward the equator. Eventually, the Earth's bright frozen mass reflected so much of the Sun's heat that the cooling became a runaway process. The result was a "snowball Earth" on several occasions between about 720 million and 630 million years ago.

The pure version of this scenario encases the Earth entirely in ice during these periods of intense cold, bringing life on the planet almost to an end. The fact that life survived has led some to prefer a "slushball Earth" idea, whereby the ice cover was never quite complete. Either way, widespread geological evidence for low-latitude glaciations supports some form of the snowball Earth hypothesis, and there is general agreement on a series of Cryogenian global cooling crises that set the stage for the future evolution of life on Earth.

What is also apparent is that, when it came, the end of the cycle was sudden. Tectonic activity didn't stop just because of the ice. Beneath its frosty veneer Rodinia was busily breaking up, and there is no doubt that volcanic vents and fissures were energetically pumping fresh carbon dioxide through the ice and into the air. With no rain to wash them out of the atmosphere, the greenhouse gases accumulated and at the end of several million years of snowball Earth, the concentration of atmospheric carbon dioxide would have risen hugely. The deglaciation would have been as self-reinforcing as the initial cooling had been: water falling on the newly exposed landscape as acid rain would have intensified weathering and the transport of nutrients to the formerly stagnant seas, causing cyanobacteria to bloom. Their photosynthesis led to a rise in atmospheric oxygen, as witnessed by the brief return of banded iron formation as volcanically derived iron was oxidized.

The exact extent to which life was banished by the Cryogenian glaciations is uncertain, but clearly it suffered a near-fatal trauma. As a result there is little fossil evidence beyond the acritarchs to document this period. Before the second major Cryogenian glacial episode at around 630 million years ago, recognizable acritarch species had lingered for as much as 100 million years; afterward, their longevity was drastically reduced, suggesting that something new was stirring ecologically. One possibility is that, in a warming world, acritarch algae had for the first time encountered predators.

The presence of predators meant that organisms were no longer limited solely by the amount of nutrition available. Ecological conditions had become more complex, and evolution had found a new stimulus. The very earliest animal fossils, putatively bilaterian embryos from China, are possibly up to 599 million years old. They suggest that, in the immediate aftermath of snowball Earth, the world was radically changing.

The Ediacaran (630 Million–542 Million Years Ago)

The record of complex life begins essentially with the impressions of soft-bodied animals belonging to a fauna known as the Ediacaran. In many ways it's amazing that these creatures should have been preserved at all. Nowadays the shallow seafloor is thoroughly reworked by the numerous organisms living down there. But in the Proterozoic, the mortal remains of the fragile Ediacaran beasts could rest in peace on the microbial mats on which they had lived. Dating between 575 million years ago and the end of the Precambrian some 33 million years later, the Ediacaran biota has excited enormous debate. Its members have been interpreted together as an entirely separate evolutionary development, and individually as the precursors of several lineages that flourished in later times. Whatever the case, the Ediacaran forms were clearly multicelled animals with distinct body plans. Some of them at least were mobile. They were also apparently diverse. They ranged from wormlike forms identified from casts of their burrows, through discoids sometimes identified as jellyfish; from apparently segmented organisms and somewhat tunicate-like, mud-filled bags of uncertain status, to quilted or frond-like creatures.

At one time these last were thought related to today's sea pens, opening the way to construing many Ediacaran forms as precursors of living groups. However, the current trend is in the opposite direction, and one authority has classified the classic Ediacaran forms together in their own phylum Vendobionta, a self-contained

Figure 4.2. ***Dickinsonia*, a probable animal that is one of the classic Ediacaran fossil forms. Courtesy of Niles Eldredge.**

group of altogether uncertain affinities. If this is the case, the core Ediacaran biota was a natural experiment that ultimately failed, leaving no descendants in the post-Precambrian world. Still, this is controversial, and molecular clock estimates suggest that ancestors of today's metazoans were already in existence 600 million years ago.

Even the term "Ediacaran biota" is ambiguous. Sometimes applied just to the bizarre vendobionts, at other times it embraces all organisms of the Ediacaran Period. In the latter sense the Ediacaran biota anticipates later times: plenty of evidence exists that bacteria of various kinds continued to flourish in the oceans, as did protists, red and green algae, sponges, shelled organisms, and worms. However, they flourished in a world that did not closely resemble the one to come. Many Ediacaran forms probably grazed on the algal mats produced by the stromatolite microbes, and as predators may even have played a role in the decline of stromatolite abundance that began at about the time they made their appearance.

Some small shelly fossils from the Ediacaran, including the tubelike *Cloudina*, bear holes apparently bored by predators, implying some increasing ecological complexity even if we don't know who the predators were. Still, few Ediacaran organisms made it into the Phanerozoic Eon, the age of "revealed life." In the first major extinction on record, they were replaced by the earliest members of the "Cambrian Explosion," who played the ecological and evolutionary games by entirely new rules.

CHAPTER 5

The Paleozoic: "Ancient Life"

THE HUGE INCREASE in animal diversity as the Paleozoic Era began appears to have been in large part a consequence of two major environmental drivers: the climatic changes that stressed the biota worldwide in the late Proterozoic and the major extension of shallow seas as Rodinia broke up. The first of these influences cleared the decks, as it were, and the second created new habitats in which the newly evolved hard-shelled bilaterans could flourish and diversify. But the Cambrian Explosion also hinged on a significant biological development: the three-layered bilateran embryo. The outer germ layer gave rise to the skin and sensory systems. The inner one generated the digestive tract and associated structures. From the middle layer the muscular and circulatory systems developed, plus a host of internal organs and, in deuterostomes, the internal support system. As body volumes grew, extra systems were needed, for the tissues could not be nourished simply by absorbing oxygen directly. Specialized circulatory and respiratory systems arose, requiring complex control that was provided by sensory organs at the head end. Here was an entirely new biology, as a result of which, by early in the Cambrian around 530 million years ago, the major groups of animals familiar in the modern biota were beginning to make their appearance.

The Cambrian (542 Million–488 Million Years Ago)

Most of what we know of the Cambrian comes from a handful of sites of exceptional preservation, known as *lagerstätten* (places of storage). In rich deposits at Chengjiang, China, and in the Burgess Shales of Canada the fine-grained rocks have conserved the impressions of soft tissues, as well as hard parts. The Chengjiang fauna is about 525 million years old and includes crustaceans and numerous kinds of trilobites, relatives of the horseshoe crabs (which also showed up as long ago as the Paleozoic). One of the trilobites, *Misshouzia*, was (like many of the other early arthropods from the site) actually soft-bodied. Related to the arthropods, even perhaps one of them, was *Anomalocaris*. This extraordinary beast was the most fearsome predator of its time: a highly mobile carnivore, up to two feet long, with a wicked forked tail. Sporting huge heads, pairs of enormous eyes, and long, barbed arms that brought their prey to a circular crushing mouth, *Anomalocaris* species were widespread in the shallow seas of the middle Cambrian.

Also preserved at Chengjiang are sponges, marine worms of many kinds, brachiopods (superficially mussel-like invertebrates), jellyfish, comb jellies, echinoderms, and even protists. Most excitingly, the Chengjiang fauna contains the first chordates: members of our own phylum. These include the tiny (inch-long) *Haikouichthys,* a possible relative of today's lampreys that shows some evidence for a differentiated cranium and a cartilaginous longitudinal stiffening structure, and the equally diminutive but slightly older and more primitive *Myllokunmingia*. Evidently, by quite early in the Cambrian the modern world had already begun to take form.

For variety, the Burgess Shales of western Canada are just as impressive. Their fauna was celebrated by Stephen Jay Gould in his engaging book *Wonderful Life*. These finely laminated deposits were laid down in the middle Cambrian, at the foot of an algal reef. Many Burgess animals appeared to defy classification in traditional categories, leading Gould to marvel at the sheer scale of the Cambrian Explosion and to remark that "Life is not producing this kind of diversity today." Gould viewed the Burgess fauna as "an initial phase of vigorous experimentation with all permutations of possible designs," followed later by "restriction and sorting out."

Subsequent evaluations of these creatures have been a bit more measured, partly because of a distinction that has come to be drawn between diversity (number of species) and disparity (number of basic body plans). For while the Burgess fauna displays considerable diversity, its disparity turns out to be not appreciably greater than that of arthropods today.

Figure 5.1. *Elrathia kingi*, an iconic middle Cambrian trilobite. Courtesy of Niles Eldredge.

Another way in which the early and middle Cambrian faunas resembled modern ones was that they belonged to fully formed food webs. These "networks of feeding relationships among species within habitats" reflect the fact that ecological interactions are much more complex than simple linear food chains. To discover how far back modern food webs go, researchers looked at the Chengjiang and Burgess faunas with an eye to establishing who was feeding on what and concluded that "most features of modern ecological network structure were in place by the early Cambrian." The ancient seas were already a dangerous place to be: almost every species was vulnerable to predation at some stage in its life cycle. No doubt: Modern animal life had started in earnest.

The message of other *lagerstätten* is much the same. Life flourished in the seas—although not yet on land—and trilobites continued to diversify, becoming the dominant element of the fauna and reaching their peak variety at the end of the period. But something new was brewing as well: for example, those two mobile chordate species at Chengjiang. If their lamprey and hagfish resemblances mean anything, these fossils are not merely chordates, but jawless fishes: primitive vertebrates, members of our own chordate subphylum with eyes, a brain, gill-like structures, and a notochord if not rudimentary vertebrae. Creatures like these were plausibly ancestral to the first ostracoderms (ancient armored jawless fishes) with which textbooks on vertebrate paleontology used to start.

The Ordovician (488 Million–444 Million Years Ago)

Just as the Cambrian was announced by the breakup of Rodinia, the Ordovician witnessed the reassembly of a successor supercontinent, Gondwana. Most of this great landmass lay to the south of the equator, a lot of it covered by shallow seas that supported diverse invertebrate faunas. As Gondwana drifted south, high-latitude glaciation became extensive, and while the productivity of the seas continued to increase (atmospheric oxygen was now up to about 68 percent of the modern level), the land itself remained largely barren of life, at least until the middle Ordovician. The first liverwort-like land plants appeared during the late Ordovician, possibly facilitated by fungi that had initiated soil formation, making essential nutrients available. The plants may in turn have attracted ashore the earliest terrestrial arthropods, though the only known remains of such creatures are very fragmentary.

Still, the main action remained in the seas, where animal genera quadrupled. Notable new arrivals included those ostracoderm ("shell-skinned") fishes, jawless (agnathan) forms protected by bony armor plates that formed in the skin. Although there was no bony internal skeleton, other basic fishy structures were present: brains, eyes, gills, and pressure-sensitive lateral-line sensory systems. Despite the dangers lurking in the ancient seas, many think that the armor of ostracoderms might not have originated as protection. For one thing, bone actually fulfills many functions beyond its obvious structural one—acting, for example, as both a major endocrine (hormonal) organ and as an important reservoir of calcium storage and regulation. Second, very few ostracoderm plates are known that bear signs of trauma (unlike numerous trilobite victims of *Anomalocaris* attacks).

Fishes with jaws (gnathostomes) probably evolved from an ostracoderm ancestor. The original function of jaws is unclear. One idea is that they may originally have developed as support for the gill apparatus, and only later have been co-opted for feeding. On the other hand, jaws could have emerged as the result of a single regulatory genetic event, in which case they may have been useful from the very start for grabbing prey. One of the earliest jawed fish groups to emerge contained the sharks, whose internal skeletal structure is almost entirely cartilaginous and thus rarely preserved in fossil form. Ancient sharks show up in the late Ordovician in the form of isolated scales, which tell us little other than that these creatures were already present. Most vertebrates, in contrast, actually have two bony skeletal systems, which appear to have developed independently. One system forms superficially, laid down within the skin as in the ostracoderms; the other develops deep within the body and is preformed in cartilage. In creatures such as human beings, the two systems have become combined: our skull base, for example, ossifies from cartilage, while the bone of our skull vaults is dermally derived.

The boundaries of most geological periods are marked by distinctive faunal replacements, and at the end of the Ordovician a major mass extinction occurred in which up to 60 percent of all marine genera disappeared, the axe falling particularly hard on trilobites, conodonts, brachiopods, and graptolites (a now entirely extinct group of colonial animals). Numerous theories about why this major event occurred have been put forward, the most dramatic of them implicating a giant cosmic blast of gamma rays that destroyed the protective ozone layer. More prosaically, the extinction coincided with extensive glaciation as Gondwana drifted over the South Pole. This lowered sea levels in several discrete pulses and extensively deprived shallow marine biotas of habitat.

The Silurian (444 Million–416 Million Years Ago)

Conditions were generally kinder during the Silurian, during which we begin to find terrestrial fossils larger than the plant and fungal spores of the Ordovician. Like them, though, the earliest Ordovician fossil plants are liverwort-like, nonvascular plants, lacking internal systems for distributing nutrients. At the early Silurian site of Passage Creek in Virginia, these ancient plants evidently provided very low but dense ground cover along a marshy riverside. Not much later, in Australia, we find the earliest vascular plant fossils in the form of *Baragwanathia,* a primitive spiral-leaved relative of the club mosses.

From the middle Silurian on, the emblematic land plant was *Cooksonia,* a varied genus (perhaps, indeed, a collection of genera) whose members had branching stems and, in some species at least, an internal transport system for water and nutrients. These small plants had neither leaves nor roots, though they may have grown from rhizomes (underground stems). Their aboveground stems terminated in round, spore-producing sporangia, reproductive structures that may also have played a role in gas exchange. These simple land plants laid the groundwork for the coming animal invasion of the land, heralded during the Silurian by worms, millipedes, centipedes, and scorpion-like forms.

The Devonian (416 Million–359 Million Years Ago)

The Devonian was warmer yet, with atmospheric oxygen up to about three-quarters of its modern level. Invertebrate life in the shallow seas was still dominated by brachiopods, corals, crinoids, and the rather coral-like bryozoans. Among free-swimming forms, ammonites (nautilus-like relatives of modern squids and octopuses) flourished especially. Trilobites were declining in numbers and diversity, quite plausibly as a result of predation by the multiplying numbers of jawed fish.

Primitive rooted plants gained their first terrestrial foothold, vastly accelerating the process of soil formation that had begun back in the Silurian. A splendid flora is already represented in the Scottish early Devonian Rhynie Chert *lagerstätte,* laid down by a hot spring 407 million to 396 million years ago. The Rhynie biota contains fungi, and nonvascular and diverse rooted vascular plants, and the fauna is dominated by arthropods, including millipedes, primitive spiders, and crustaceans. Many of these apparently grazed upon the plants, some of which developed spines that may have exuded defensive chemicals.

Accelerated soil formation probably helped reduce carbon dioxide in the atmosphere, heralding later cooling, as weathered carbonates were transported by streams to the ocean to be locked up in accumulating limestones. With greater soil depths vegetation flourished, and the increased terrestrial biomass enhanced the export of organic matter to the oceans, where it would have acted as a fertilizer, enriching the evolving marine ecosystems. Tall vegetation began appearing in the middle Devonian, and after about 360 million years ago we find widespread evidence of the earliest "modern tree," *Archaeopteris*, which grew over fifty feet high. It formed the first closed forest canopies and had all the major characteristics of today's woody trees, though it reproduced by releasing spores instead of seeds.

The new forests changed the world, providing a new environment that supported a terrestrial fauna including herbivores, detritus feeders, and predators that fed on both. Decomposing leaf-litter enriched streams, stimulating freshwater fish communities. Most of the nutrients eventually found their way into the late Devonian oceans, resulting in the extensive deposition of organics-rich black marine shales. And by fixing carbon dioxide, the vast tracts of *Archaeopteris* contributed to an ongoing drop in atmospheric levels of this greenhouse gas. Ironically, by doing this the forests may have sown the seeds of their own demise, for at the end of the Devonian they fairly abruptly disappeared, giving way mainly to horsetails and ferns as the climate cooled, paving the way for a minor end-Devonian extinction.

Algae continued to provide the principal food source for grazers in the ocean; but on land things were different since the expanding ground cover provided an abundant and complex food supply for animals. To cope with the effects of gravity, plants began stiffening themselves with indigestible structural carbohydrates, manufacturing as by-products noxious chemicals that could be defensively exploited against browsers. Terrestrial animals had to respond to this challenge, and one of the first groups to do so was the insects, which had evolved from a marine crustacean ancestor.

The two earliest known insects come from the Rhynie Chert. One was the very primitive springtail *Rhyniella*. The other, *Rhyniognatha*, is the earliest "true" insect. This may have been winged, and both genera appear to lie well within the larger insect radiation. If so, insects must have originated well before the Devonian began. The key to insects' subsequent success was evidently flight, which allowed them to forage at all levels of the Devonian forests.

But not just insects were busily establishing themselves on land. Other arthropods, including millipedes, took advantage of the new opportunities created by the leaf litter of the later Devonian forests. Worms probably did the same, attracting predators such as scorpions and spiders.

Back in the seas, even more momentous changes were under way. The Devonian witnessed an amazing diversification of fish. Among these were the placoderms, armored jawed fishes that flourished from the late Silurian through the Devonian. Usually considered the most basal branch of the gnathostomes, they sported heavy bony armor on the head and neck. But while they had jaws, placoderms bore bony plates in place of teeth. Sometimes these formed a fearsome self-sharpening apparatus, as in *Dunkleosteus,* a huge late Devonian form that was probably the top marine predator of its time. With the arrival of the jawed fishes, the oceans—and the rivers—had truly become a fish-eat-fish (and everything else) world.

Ancient sharks are known in the fossil record primarily from their terrifying teeth, though an exception is the fast-swimming predator *Cladoselache*. True sharks are not known until much later; but once established, they were consistently diverse and successful, as they and their relatives, the skates and rays, have been ever since.

The same can be said of the bony fish, the Osteichthyes, which originated in the early Devonian. Among them, the group known as the sarcopterygians gave rise to the terrestrial vertebrates, while the actinopterygians include almost all of the more than twenty thousand species of bony fish teeming in the world's waters today. The actinopterygians' tongue-twisting name means "ray-finned," referring to the support of the fin webbing by numerous parallel bony rays. Today nearly all actinopterygians belong to the teleost group (the odd name simply means "complete boned"): fish whose twin upper jawbones move freely relative to the skull, so that they slide forward when the mouth is opened. They are also the kind you are most likely to find on your plate when you order fish in a restaurant.

Besides the hard internal skeleton, osteichthyans all possess a swim bladder. In actinopterygians this sac contains gas and is used to control buoyancy. But in one tiny lineage—the sarcopterygians—it was eventually converted into the lungs of the first land-living vertebrates, the tetrapods ("four feet").

Tetrapod Precursors

The basic osteichthyan body plan dates back to the late Silurian and boasts a well-differentiated cranium at the front, containing the mouth and brain. Behind it, the bony vertebral column encloses the spinal cord and supports pectoral and pelvic girdles to which the paired fins attach. What makes the sarcopterygians most strikingly different from actinopterygians is their lobe-fins, each of which has a central bony element that articulates with the pectoral or pelvic girdle and is moved by a fleshy muscle complex. These complex paired fins ultimately became the fore- and hind limbs of the terrestrial tetrapods.

Sarcopterygian fish first appeared in the lower Devonian, and they rapidly diversified. One major group was the coelacanths, thought to have become extinct around 70 million years ago until a live one was fished up off South Africa in 1938. Well before this discovery, paleontologists had concluded that the lobe-fins were the group from which the tetrapods had sprung; and quite understandably, the exact function of their fleshy fins had been a major source of debate. Speculations that they had assisted the fish in "walking" over rocky seabeds seemed plausible. But some astonishing film footage taken in the 1980s from a deep-diving submersible in the Comoro Islands produced a radically different picture. It showed that coelacanths can indeed move their pectoral and pelvic fins in much the same way that you can move your upper arm in its socket. But they are not used for propulsion over the seabed. Instead, the fins maintain balance and direction in open water, the left and right pairs moving together. Much more flexible than their bulk suggests, the lobe-fins make possible very precise navigation, and the primary means of propulsion is the powerful tail fin, which operates very effectively whenever a burst of speed is needed.

A great variety of sarcopterygians existed in the Devonian, among them the Tetrapodomorpha, a group including the tetrapods proper and an untidy assortment of fish known as osteolepiforms. Among the latter the closest relatives of the tetrapods are the elpistostegids, the best known of which is the 378-million-year-old *Panderichthys*, an odd fish indeed. It has dispensed with all fins except the four lobed ones and the tail. Its body is flattened from top to bottom as in today's alligators. The pectoral (shoulder) girdle shows some tetrapod-like features, and the humerus (the equivalent of the upper arm bone) is relatively long. However, its pelvic girdle is less tetrapod-like than those of some other osteolepiform fish, suggesting that the evolution of tetrapod locomotion first involved a "front-wheel-drive" stage. Only later was there a shift to rear-wheel drive and leg power. Still, for all its resemblances to later land-living tetrapods, there's no doubt that the yard-long *Panderichthys* was indeed a fish, totally aquatic.

The land beckoned, however. For a fish to live on land, major innovations were required, including the ability to extract oxygen from the air rather than from water, and to support body weight out of the water. On the face of it, both of these are highly improbable transitions to make. Yet they not only occurred, probably on multiple occasions, but they are amazingly well documented.

We've already seen how lobe fins, articulating with front and rear bony girdles, were acquired as one solution to the problem of negotiating the watery environment. We've also seen how the aquatic elpistostegids had flattened their heads and bodies and beefed up their pectoral fins. We don't have to wait long after *Panderichthys* for evidence of what happened next, for a mere 3 million years later the fossil record presents us with a form that much more closely resembles later tetrapods. This is *Tiktaalik,* recently discovered in eastern Canadian freshwater sediments some 375 million years old.

Tiktaalik vaguely resembled modern crocodilians in overall structure. It had a flattened head with an uptilted snout and closely spaced eyes that lay atop the cranium rather than at the sides. It also had a shallow, wide body. Even more important, between the head and body there was a neck. Bony fish typically have a conical head that is firmly attached to the pectoral girdle by a series of bony plates. In contrast, *Tiktaalik* not only lacked these structures, but could move its flat head relative to the vertebral column behind it.

Inside its webbed front fins, and articulating with the pectoral girdle, are upper and lower arm bones that are equivalent to our own. There is even a rudimentary wrist, composed of a complex of smaller bones that articulate with the end of the lower arm bones in a fashion said by its describers to be "similar to the distal limb pattern of basal tetrapods. The forefins of *Tiktaalik* were capable of a range of postures, including a limblike, substrate-supported stance in which the shoulder and elbow were flexed and the distal skeleton extended." Here again is the front-wheel-drive pattern of *Panderichthys,* only more so. Evidently, *Tiktaalik* could raise itself up from the river or swamp bottom, using its front fins for support. Later this capacity would have been very useful for any air-breathing tetrapod that needed to get its body weight off its lungs, let alone for getting around.

Yet although a tetrapod, the two-feet-long *Tiktaalik* was still a fish. It clearly had a full set of gills and a spiracle (a fissure on the top of the head, also present in *Panderichthys,* that probably initially assisted in "breathing" water, but later became part of the tetrapod middle ear). What's more, *Tiktaalik*'s tail fin was shaped for propelling it through the water, its lobe fins were fully webbed, and the body bore fishlike scales. Clearly *Tiktaalik* was fully aquatic, like its osteolepiform ancestors.

Alas, the fossil record falls silent for 8 million years after *Tiktaalik.*

But the trail picks up again with two other ancient tetrapods, *Ichthyostega* and *Acanthostega*, both found in late Devonian sediments of Greenland that were laid down about 363 million years ago. *Ichthyostega* is more crocodile-like than *Tiktaalik*, and was initially viewed as essentially terrestrial, albeit with structural reminders of an aquatic past that include a generous tail. However, new discoveries suggest *Ichthyostega* was more at home in the water than on land—although its spine apparently possessed one propensity not seen in fish: a limited ability to bend up and down instead of to the sides.

The vertebrae of the spine consist of two portions, which ossify (turn from cartilage into bone) separately. The round centra (some of them barely ossified in *Ichthyostega*) abut against each other, while the neural arches above them surround the spinal cord and bear vertical flanges to which muscles attach. In *Ichthyostega* the neural arches change in orientation along the spine. This differentiation of the vertebral column into different regions happens in us and is even found in some later Paleozoic vertebrates. It might have made possible a kind of waddling gait with the body raised up off the ground, or have facilitated forward movement by flexing the spine up and down as the limbs repositioned. The rather peculiar nature of *Ichthyostega*'s ribs may also suggest limited terrestriality: broad and overlapping, they formed a substantial "cage" that might have protected the lungs from vertical pressures out of the water.

At the same time, the short appendages of *Ichthyostega* are still very finlike, even though you might want to call them limbs. The partially known front one is basically structured as in *Tiktaalik*. At the rear, the pelvic girdle appears to be firmly fixed against the spine, the limb consisting of a single upper bone (the femur) that in turn articulates with a massive tibia and fibula below. At the end of this stubby limb is a very rudimentary ankle bearing eight digits (including one that wasn't ossified: all living vertebrates are descended from an ancestor with five). But while the

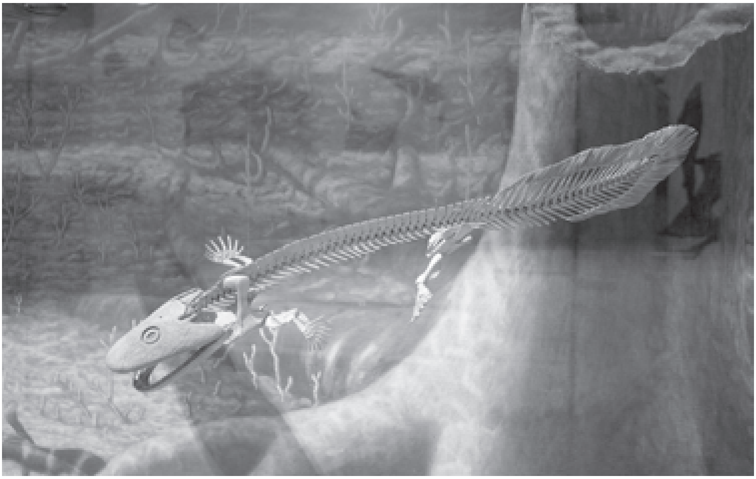


FIGURE 5.2. Reconstruction of an *Acanthostega* skeleton in a seminaturalistic setting at the American Museum of Natural History.

front appendages of *Ichthyostega* were reasonably well suited to load bearing, the hind ones were not, and probably functioned as paddles.

While clearly an early tetrapod, with a flat skull and eight digits on each appendage, *Acanthostega* had neither forelimbs nor hind limbs fitted for weight bearing. With its laterally flexible spine it is viewed as a full-time aquatic form, and it definitely retained fish-like internal gills (as *Ichthyostega* probably did also). In contrast, the specialized *Ichthyostega* may indeed have been a tetrapod experiment with weight bearing, albeit one that ultimately failed. Possibly it occasionally ventured ashore, some 363 million years ago. But at that time the actual ancestor of terrestrial tetrapods was evidently still aquatic, having acquired in the water the features that served its descendants so well when they took up residence on land. This is a classic example of exaptation, the process whereby evolutionary novelties initially become fixed in contexts entirely other than those in which they will eventually be co-opted.

I have sketched this story of the sequential acquisition of tetrapod features in a linear fashion, by singling out a few fossil taxa of many. But the Devonian certainly does not show us a linear evolutionary scenario whereby sarcopterygians single-mindedly hauled themselves ashore and stayed there. Instead, a lot of experimentation was going on in the rapidly developing riverine ecosystems. There was, though, plenty of incentive to leave the water. There were no terrestrial carnivores in the Devonian, while the waters were filled with voracious fish. Paleontologist Neil Shubin has pointed out that virtually every fish in the streams of 375 million years ago was a predator of some kind and that the commonest fish in the deposits yielding *Tiktaalik* was twice its size, with a "head as big as a basketball." In such conditions, Shubin concludes, the "strategies to succeed were pretty clear: get big, get armor, or get out of the water."

The Carboniferous (359 Million–299 Million Years Ago)

In the Carboniferous Period the process began of reassembling nearly all of the Earth's dry land into the single supercontinent of Pangaea. With this came a general uplift of dry land, many of the zones newly exposed from the sea becoming vast swamp forests. Today the club mosses are basically ground cover. But in the early Carboniferous their relatives, the lycopods, grew to enormous heights, sometimes well over one hundred feet. Below them grew a profusion of tall seed ferns and distant relatives of the modern conifers.

Besides energetically drawing carbon dioxide from the atmosphere, these forests eventually enriched it in oxygen to over 40 percent above the modern level. Besides increasing fire risk, this made it easier for the trees to manufacture their major structural component, lignin, so they could grow even larger. The accompanying drawdown of carbon dioxide soon led to global cooling, and later in the Carboniferous there was a major extinction among the lycopods, probably caused by the climatic drying associated with increasing glaciation.

The shrinking of the shallow continental-margin seas as the Carboniferous began affected the marine fauna. The trilobites dwindled to just one family. The placoderms of the Devonian disappeared, to be replaced by an efflorescence of sharks. Geological uplift increased the flow of rivers, disturbing nearshore habitats and multiplying deltaic environments in which corals and bryozoans declined, while true mollusks multiplied. The eurypterids, fearsome marine scorpion relatives, did especially well during the Carboniferous, developing numerous amphibious forms often of huge size. Bony fish thrived, too, many of them migrating to freshwater environments. Among the sarcopterygians the large predatory rhizodonts flourished, including the eponymous *Rhizodus,* at over twenty feet in length the largest freshwater fish ever documented. But wherever there are winners there are losers, and other sarcopterygians, such as the coelacanths, dwindled over this period.

One of the major effects of increasing atmospheric oxygen levels was a huge diversification among the terrestrial insects. In the middle Carboniferous, insects began to increase not only in diversity but in body size. This was almost certainly linked not only to the moist environment, but also to the fact that insects "breathe" oxygen through a system of openings in the hard external carapace. With rising atmospheric oxygen pressures the gas is more easily absorbed into the interior tissues and can travel further. The most famous giant insect of the Carboniferous is the dragonfly *Meganeura monyi,* which had an almost unbelievable wingspan of two and a half feet—five times that of the largest dragonfly today.

High oxygen levels were also presumably advantageous for the terrestrial tetrapods, which at the time were facing the problem of converting their swim bladders to an air-breathing apparatus. Sadly, the early Carboniferous tetrapod record is poor, the principal exception being a 345-million-year-old Scottish form called *Pederpes.* Mainly aquatic, *Pederpes* had some very fishy features, such as grooving along its skull for a lateral-line sensory system. But it did possess recognizable forefeet and hind feet, indicating a potential for walking on land. Unlike its Devonian precursors, but just like you and me, *Pederpes* possessed five toes on its hind feet. The forefeet probably also had five functional digits, with vestigial indications of a sixth. In essence, while the body of *Pederpes* harked back to an earlier time, its feet resembled those of later forms that are believed to have been mainly terrestrial. This apart, however, nothing much about *Pederpes* ties it to any later tetrapod group.

Land Dwellers and Amniotes

In the middle part of the Lower Carboniferous we begin to pick up evidence of the earliest forms comparable to today's amphibians—the frogs, salamanders, and giant-wormlike caecilians. Although land living and air breathing, amphibians are almost entirely dependent on streams, lakes, and ponds for reproduction. Females lay eggs that, encased in permeable membranes, dry up out of the water; and while adults breathe air, the aquatic larval stages still breathe through gills. Remarkably, the first Carboniferous amphibians, such as the 340-million-year-old *Lethiscus*, are highly specialized, indicating there was already a substantial history behind them.

The Carboniferous was clearly a time of restless innovation and experiment for the early tetrapods, especially the amniotes, the first vertebrates that were not reproductively tied to the water as their ancestors had been. The liberating factor was possession of "amniotic" eggs. These had an enveloping shell and associated membranes that prevented drying out in the air and that aided in nourishment of the developing embryo. This innovation allowed the full-time colonization of the land. Along with the first limbs, the amniote egg ranks as the outstanding evolutionary development among Paleozoic vertebrates.

Casineria, the earliest reported amniote, is thought to be around 340 million years old, approximately contemporaneous with

Lethiscus. The hands of this small and scaly creature definitely bore five digits, and its finger bones show notches indicating the insertion of strong ligaments—and thus the ability to grip. Very significant is a twisting of the lower end of the humerus, the upper arm bone. This better suits the limb to providing postural support, and strongly suggests terrestrial locomotion. Intriguingly, phylogenetic analysis implies that amniotes probably had a long unrecorded history before the time of *Casineria*.

Later in the Carboniferous, forms turn up that further strain our familiar categories. Most of us grew up with the notion that vertebrate animals can be divided into five roughly equal groups: fish, amphibians, reptiles, birds, and mammals. This approach makes enough sense if you consider only the groups living today. But as you go back in time, those apparently clean boundaries start to blur. On closer inspection, it turns out that these groupings are "grades" that consist of functionally similar creatures, rather than "clades" that contain all of the animals descended from a particular common ancestor.

Nowadays, scientists agree that when we classify animals the only really objective criterion is ancestry: what we need to be looking for is clades (of forms related by descent), rather than grades (of similarly adapted forms). As we've seen, the notion of "fish" can actually be quite misleading, because while the first tetrapods were functionally "fish," their descendants quite clearly are not. It has also turned out that, while fulfilling the dictionary definition of their name by "living both lives" (water and land), the earliest fossil amphibians were not all related by descent to those alive today. Further, we encounter the same kind of problem with the term "reptile" as well, a problem that begins to plague us as early as the late Carboniferous.

Early Tetrapod Diversity

At Joggins, Nova Scotia, some 315 million years ago, a swamp forest flourished that supported a diverse vertebrate fauna. Some unfortunate individuals became trapped in tree stumps during periodic floods and were fossilized. The most frequent victim was the yard-long and salamander-like amphibian *Dendrerpeton*.

There were others, too, including representatives of several genera that cannot be dismissed as amphibians. Yet we can't lump them as reptiles, either. We are, in short, in trouble if we try to classify these Joggins fossils using the old categories. The reptiles used to be divided up morphologically, according to the number of fenestrae (basically, holes) seen in the back half of the skull. If there were no holes (as in turtles), the forms concerned were considered "anapsids." If there was one hole per side (as in the ancient "mammal-like reptiles"—and us, for that matter), they were called "synapsids." If there were two fenestrae, the creatures concerned were "diapsids."

This made a pretty neat basis for categorization, rather as shelving books by their color does, but the resulting classification was rather unhelpful. For one thing, some forms with diapsid ancestors (e.g., lizards) have since lost one of the holes, and others (e.g., snakes) have lost both. For another, the "reptile" concept groups together organisms that the Joggins fauna tells us were already off on separate evolutionary tracks an amazingly long time ago.

The classic Joggins vertebrate is the rather lizardlike amniote *Hylonomus*. It is technically classified as an anapsid, which doesn't mean much because the no-hole amniotes are not necessarily all closely related, and there is certainly no clear link between *Hylonomus* and today's anapsid turtles. Then there is the eighteen-inch-long *Archaeothyris*, which is a primitive synapsid. Possibly together with its slightly older but lesser-known swamp mate *Protoclepsydrops*, *Archaeothyris* is now classified as a primitive member of the ophiacodontid family of the pelycosaurs. And the pelycosaurs, as we will see, are reckoned to be the stem group of the later mammals.

At Joggins there is also a slightly smaller form called *Petrolacosaurus*. This is a diapsid and belongs as such to the group containing not only the dinosaurs but almost all of today's reptiles. In a single late Carboniferous fauna, then, we find forms that foreshadow completely different groups of vertebrates, anticipating an entire future world. Running around on the floor of the Joggins swamp forest, these animals wouldn't have looked very different from each other; but each, in its own way, was a harbinger of very different things to come.

The Permian (299 Million–251 Million Years Ago)

By the end of the Permian, Pangaea stretched almost from pole to pole. Sea levels dropped, along with the area of shallow seas. Typically for a large continental landmass, Pangaean climates tended to the extremes. Much of the interior was hot and desertic, with most rainfall seasonal and concentrated along the coast. As the Permian began, vegetation similar to that of the Carboniferous still flourished; but well before the middle of the period the lycopod-dominated swamp forests were replaced everywhere except near the equator by conifers better adapted to drier or more seasonal conditions. Gingkos and cycads also showed up in the better-watered areas. Among the insects, primitive cockroaches, already abundant in the late Carboniferous, became ubiquitous; in the air buzzed dragonflies of myriad kinds, some of them still extremely large; and beetles and flies entered the record for the first time.

One of the most remarkable vertebrate finds in the early Permian is the extraordinary 290-million-year-old "frogamander" *Gerobatrachus*, from Texas. Only a few inches long, this little fossil is amazingly like a frog in many ways and appears to be the closest known relative of the group containing today's frogs and toads. Yet it has ankles resembling those of salamanders. *Gerobatrachus* thus demonstrates the close relationship between modern frogs and salamanders, suggesting that these two modern lineages split around 270 million years ago—some 60 million years after they parted ways with the caecilians.

Mammal Precursors

The emblematic terrestrial vertebrates of the Permian were the pelycosaurs. They used to be described as "mammal-like reptiles," but they clearly did not belong to the group containing today's lizards, crocodiles, and snakes. For one thing, they were synapsids, with only one skull opening. For another, reptiles are "cold-blooded" (i.e., their body temperature varies with that of the environment around them), whereas pelycosaurs are believed to have been "warm-blooded" (maintaining constant body temperatures), like modern mammals. Finally, living reptiles have teeth that are all basically conical, while those of the classic pelycosaur were of two kinds: sharp puncturing canines at the front, and shearing teeth behind. Multiple tooth types are typical of mammals. As a result of this pattern of resemblance, most paleontologists today classify pelycosaurs together with the mammals, although probably no known pelycosaur was ancestral to any later mammal.

The pelycosaurs had their roots back in the Carboniferous, as shown by the partially aquatic 315-million-year-old ophiacodont *Archaeothyris.* By early in the Permian, two distinct pelycosaur groups were diverging from an ophiacodont stem. The sphenacodonts were fully terrestrial predators, while the edaphosaurs were swamp-dwelling plant eaters. The best-known sphenacodonts are the many species of *Dimetrodon,* which flourished throughout tropical Pangaea between about 280 million and 265 million years ago.

Dimetrodon was one of the top predators of its time, with a large skull and a body that in some species grew to be well over ten feet long. It held its bulk clear of the ground, but it had a sprawling gait: as in a modern lizard, when standing still its upper limb sections projected horizontally from the body, forming a right angle with the vertical lower limb components. Its most eye-catching characteristic, though, was its spectacular "sail." This was a large and longitudinal half circle of membrane, almost certainly richly vascularized, that was supported by more or less vertical vertebral spines. Purists point out that we have no way of knowing the exact importance of this remarkable structure. But almost certainly it functioned in

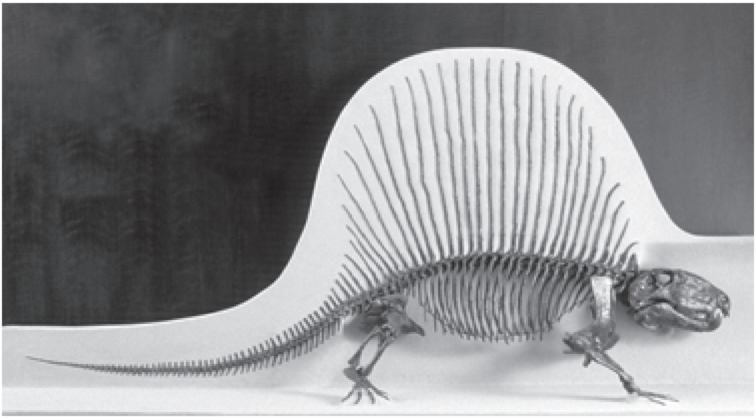


FIGURE 5.3. Mounted skeleton of the pelycosaur *Dimetrodon limbatus.* Courtesy of American Museum of Natural History.

body temperature regulation, absorbing heat from the Sun in cool air and radiating it in warmer conditions. Since the sail was there, it would be surprising if it hadn't also functioned in sexual display, like the frills and dewlaps of some lizards. But it was plainly possible to be a perfectly adequate pelycosaur without a sail, for some genera in both lineages lacked such structures.

Most pelycosaurs became extinct well before the end of the Permian, possibly as their preferred moist habitat dried out and the Earth cooled off. But before disappearing, one lineage of sphenacodonts gave rise to a group known as the therapsids, which became the dominant land vertebrates during the middle Permian.

One major group of early therapsids was the anomodonts. By the late Permian the anomodont genus *Suminia* had acquired a full set of "leaf-shaped" teeth rather similar to those seen in iguanas and some dinosaurs, strongly suggesting herbivory. Indeed, the scientists who described it believe that *Suminia* was more highly specialized for high-fiber herbivory than any other Paleozoic vertebrate and see it as evidence that the modern terrestrial ecosystem (whereby a mass of plants supports large populations of herbivores that in turn support smaller numbers of carnivores) had become fully established by around 260 million years ago, well before the end of the Paleozoic.

The theriodont ("mammal-teeth") therapsids appeared toward the end of the middle Permian some 265 million years ago and dominated the terrestrial landscape until the end of the Paleozoic. By the late Permian, therapsids in general and theriodonts in particular had acquired several innovations that would also characterize the later mammals. The head had become hinged on a double joint, allowing greater freedom of movement. The opening on the side of the skull had enlarged to accommodate larger jaw muscles, permitting a greater range of jaw movements. The teeth had become more differentiated, with larger canines at the front. And a bony secondary palate had begun to develop from the upper jawbone, permitting individuals to breathe as they ate—an important innovation for warm-blooded creatures that required more food to maintain their bodily functions.

Behind the head, the sprawling posture had been abandoned in favor of bringing the limbs beneath the body. This entailed numerous adjustments to the limb bones and the girdles with which they articulated, as well as to the fingers, which began to shorten as weight bearing was transferred from the palm to the tips of the digits.

The last theriodont group to evolve was the cynodonts ("dog-tooth"). These show several important innovations. The temporal openings in the skull are very large, permitting the muscles they accommodated to move the jaw sideways as well as up and down. This made true chewing possible, and behind the big canines were teeth that bore multiple cusps rather than simple slicing or puncturing structures. The bony secondary palate had lengthened, shifting the main airways toward the back of the throat, which is where they are in mammals. The body skeleton was lightened and simplified: the legs were brought yet farther under the body, and the ribs eventually disappeared from the back of the spine, making the whole structure more flexible and suggesting that breathing was accomplished via a fully formed diaphragm. In the rear limb, the bone at the back of the foot was prolonged for the attachment of the Achilles tendon, increasing the mechanical advantage of the leg muscles.

It is not putting it too strongly to say that by the end of the cynodonts' heyday, the basic characteristics of the mammal skull and body skeleton had become established. Indeed, it's not beyond reason to suppose that some cynodonts, at least, possessed hair, since there is some indication in the snouts of later cynodonts that they may have had whiskers.

Given that Permian sites are pretty thinly scattered, it is altogether amazing how complete a transformation series we see among the synapsids of the Permian. Indeed, from the primitive late Carboniferous *Archaeothyris*, barely differing from its reptile-like contemporaries, through forms such as *Dimetrodon* and the early theriodonts, to the cynodonts that survived the end of the Paleozoic, we see a remarkable succession of stages, each bringing us closer to the mammal condition. This succession is not, of course, a literal ancestor-descendant series. But it does give us a good idea of how a reptile-like ancestor was transformed into a mammal-like descendant.

Still, we have not yet looked at the most remarkable Permian transformation series of all, involving the conversion of the back part of the primitive amniote jaw into the hearing apparatus of mammals. Though functionally a single structure, the basic amniote lower jaw was a complex of different bones, ossifying from separate centers. The largest, composing most of the front part of the jaw and containing the teeth, was the dentary. Behind it was a jumble of smaller bones involved in muscle attachment and jaw articulation.

The early amniotes probably lacked eardrums, membranes that collect sound energy traveling through the air and transmit it to the inner ear via various structures. Not necessarily ossified, these include the stapes, initially a massive bone that served as support for the jaw. Eardrums seem to have developed separately in a number of amniote lineages, including the one that ultimately led to the dinosaurs; they were definitely present among synapsids by the time the therapsids emerged.

Throughout the Permian, the therapsid dentary expanded quite consistently, maybe because a single bone provides a more solid structure for strong biting and chewing than a mosaic does, and squeezed the other bones toward the back of the jaw. At the same time, the stapes came to fill a dual function, both in the articulation of the lower jaw with the cranium and in sound transmission. For now we'll leave the matter there, since the evolution of the mammalian ear as we know it today was a story that mainly played out during the Mesozoic Era, to which the next chapter is dedicated.

The Great Dying

The end of the Permian saw a major mass extinction—by virtually every reckoning, the largest on record (we're not sure just what happened during snowball Earth). During the end-Permian event, up to 96 percent of all marine species disappeared. Trilobites, eurypterids, and graptolites all vanished entirely, and most other marine invertebrate groups lost more than 90 percent of their species. With a loss of only 59 percent, bivalves did pretty well!

Among marine vertebrates, acanthodian and placoderm fish disappeared forever, and diversity plummeted in other groups. On land, the insects participated in the only mass extinction that is known ever to have affected them: eight orders succumbed entirely, and as many suffered hugely in diversity—a loss from which they never fully recovered, even though that might be hard to believe at a summer cookout.

Terrestrial vegetation transformed, as the luxuriant abundance of gymnosperms and seed ferns was replaced by stress-resistant low ground cover. A sudden increase in fungal spores confirms a profusion of dead trees. Although some representatives of nearly all major plant groups made it through this event, it took as much as 5 million years for terrestrial plant ecosystems to regain equilibrium.

As would be expected from such wrenching change at the bottom of the food pyramid, land vertebrates were terribly decimated. Some 70 percent of terrestrial vertebrate species went extinct, including all large herbivores.

Why did this "Great Dying" occur? Theories abound, and in truth we are probably looking at a perfect storm of circumstances. Inevitably, a major bolide impact has been touted as the cause. Although little direct evidence supports this idea, after 250 million years of erosion it cannot be entirely ruled out. A more plausible physical culprit is the gigantic flood basalt eruptions, centered in Siberia, that coincided almost exactly with the end of the Permian. While sheet lava extrusion is not normally accompanied by the volcanic pyrotechnics that produce Krakatoa-like dust clouds, it is thought that maybe a fifth of the new material produced was violently thrown in the air before settling. Such terrestrial volcanism may have been accompanied by large-scale submarine emissions of lava, possibly a factor in the rise in sea levels known to have occurred around this time.

Still, many are dubious that volcanism alone could have produced the Pangaea-wide effects seen at the Permian's end. Might there have been an additional factor? Worldwide, rocks from the end of the Permian carry an oxygen isotope signal that may suggest an enormous release of toxic methane gas trapped in the seabed or in permafrost. The Siberian lavas were extruded over Arctic territory bounded by very shallow seas, and both of these environments would have been greatly disturbed as vast quantities of superheated rock descended on them.

Methane is a greenhouse gas. There is strong independent evidence that global temperatures increased at the end of the Permian by as much as 6°C near the equator, and by more at higher latitudes. Still, the isotope patterns seen during the early Mesozoic are not exactly what you would expect following a huge methane release, so some researchers have emphasized the potential role of an episode of oxygen depletion that affected the oceans near the end of the Permian: a condition that might well have been aggravated by global warming. Besides affecting oxygen-dependent marine organisms directly, anoxic conditions would have promoted hydrogen sulfide–producing bacteria. Large-scale release of this toxic gas would have profoundly affected life-forms, in the oceans and on land alike.

All in all, though many possible culprits exist for the late Permian extinctions, it is not possible right now to single any one out as the critical factor. In the end, as in Agatha Christie's *Murder on the Orient Express*, it may turn out that everybody did it.

CHAPTER 6

The Age of Dinosaurs

FOLLOWING THE Great Dying the world was a very different place. The new Mesozoic Era of "middle life" was rapidly dominated by the diapsid dinosaurs, while the ancestors of mammals were marginalized to specialist niches.

Geologists divide the Mesozoic Era into three successive periods: the Triassic (251 million–200 million years ago), the Jurassic (200 million–145 million years ago), and the Cretaceous (145 million–65.5 million years ago). In this time Earth's geography changed hugely: at the end of the Triassic the Pangaean supercontinent began to fragment, and by the close of the Cretaceous the world map was just beginning to take on its familiar form.

The Mesozoic was a time of major transformation in terrestrial floras worldwide. As the era opened, ferns, cycads, ginkgos, and so forth dominated. But quite early in the Triassic, coniferous seed plants began to diversify and to assume a recognizably modern aspect. As the interior Pangaean deserts of the Triassic gave way to generally more humid environments with tectonic breakup into the great continents of Laurasia in the north and Gondwana in the south, lush forest formations spread across the landscape. These were dominated by the conifers, although cycads and ginkgo relatives were also common locally, and the ubiquitous seed fern *Glossopteris* became emblematic of the Gondwanan flora. Recently, some tiny Triassic droplets of amber, 220 million years old, were found in Italy. Formed in an ancient coniferous forest, they preserve an incredibly diverse microworld of bacteria, tiny fungi, and protozoans. These organisms include very close relatives of living counterparts—implying an amazing *lack* of change in the microbiota since then.

By Cretaceous times the flora was changing again, as temperatures started rising after an initial brief cooling. Botanically, by far the most significant events of the period were the origin of the flowering plants (angiosperms) in the early Cretaceous and their subsequent diversification. By a little under 100 million years ago, many groups familiar today had appeared, and by the end of the Cretaceous the flowering plants had become dominant in most terrestrial floras.

In the seas corals flourished again, although initially sparse shallow waters limited reef development. Fish lineages rapidly diversified following the Permian extinction, providing sustenance for a burgeoning variety of marine diapsids, the most successful among these being the sauropterygians ("lizard flippers"). Sharing adaptations of the shoulder girdle that made them powerful foreflipper-propelled swimmers, the sauropterygians made their debut at the beginning of the Triassic, some 245 million years ago. Eventually some became the top marine predators of their day. The longest-lived sauropterygian group was the plesiosaurs ("near-lizards"), veterans of many a "Monster of the Lake" movie.

They were not without competition, sharing the oceans with the ichthyosaurs ("fish lizards"), formidable swimmers that appeared in the record equally early. Early Triassic ichthyosaurs looked rather lizard-like, but their descendants rapidly assumed the fish-like body proportions. Showing some remarkable convergences on marine mammals as well as fish, these marine predators probably swam at speeds of up to twenty-five miles per hour, propelled by powerful side-sweeping tails.

The flourishing of marine faunas was partly due to a rise in sea levels as the Mesozoic progressed. As Pangaea split apart during the Jurassic, high rates of seafloor spreading displaced water onto the expanding continental margins and greatly increased the area

Figure 6.1. Section through a Jurassic ammonite of the genus *Kosmoceras*. Courtesy of Niles Eldredge.

of shallow seas. In the early Cretaceous, up to one-third of the present land area is thought to have been covered by water. Almost concurrently, as the Cretaceous began, intense volcanic activity raised atmospheric carbon dioxide levels that were already high compared to today. The effect of this greenhouse gas was to warm climates worldwide, and to diminish the heat gradient between the equator and the poles. As a result, Cretaceous dinosaur fossils have been found within 15 degrees of the South Pole.

Ocean surface temperatures also rose, and ultimately equatorial waters may have become uncomfortably balmy for many lifeforms. Still, the Cretaceous saw another major diapsid group enter the marine fray: the mosasaurs. Relatives of today's snakes, these large, tail-powered predators flourished right up to the end of the Mesozoic—although they, too, eventually succumbed at the K/T boundary.

The Mesozoic was an eventful period in the evolution of all the many terrestrial lineages that lived through it. But since this is a book written by a vertebrate for other vertebrates, I am going to depart here from the strictly chronological organization I have followed so far and focus on the Mesozoic evolution of what many consider the two most significant vertebrate groups: the dinosaurs and the mammals.

First, though, I should point out that the Mesozoic was the period within which the ancestors of all of today's vertebrate groups became recognizably established. Despite poor records, each of the major lineages of the modern squamates—the lizards, snakes, and so forth—clearly had its origin within the Mesozoic. The first members of Testudines—the group containing today's turtles and tortoises—appear in the Triassic, but they are already remarkably similar to their modern relatives, so the group must have originated well before this. As for the Lissamphibia (frogs, salamanders, and so forth), recognizable members of modern lineages begin to be picked up in the early and middle Jurassic. Thus the outlines of the modern vertebrate fauna were beginning to show in the Mesozoic, although there was still a long path to travel.

The Dinosaurs

Dinosaurs are so much a part of modern folklore that it is perhaps worthwhile to start this brief account with a few words about the history of their discovery.

Naturalists, including the great French scientist Georges Cuvier, had been describing occasional fossils of giant extinct creatures since the late eighteenth century, but the notion of dinosaurs as a coherent group of extinct reptiles was not established until rather later. In 1842 the great British comparative anatomist Richard Owen coined the name Dinosauria ("terrible lizards") for a group of large fossil animals found in Jurassic and Cretaceous sediments of southern England. Reports of fossils in these rocks dated back at least to the seventeenth century, but not until 1824 did the remarkable William Buckland, dean of Oxford's Christ Church College, apply the name *Megalosaurus* ("huge lizard") to an assemblage of enormous middle Jurassic bones that he immediately recognized to be similar in shape to those of lizards. Today, *Megalosaurus* is recognized as a large carnivore belonging to the theropod group of dinosaurs. At around the same time, the physician and geologist Gideon Mantell described another giant Jurassic form, *Iguanodon* ("iguana-tooth") from deposits near the southern English coast.

The plant-eating *Iguanodon* is among the best known of all dinosaurs, with representatives described from Europe, Asia, North America, and northern Africa. Indeed, while many extinct genera are known from a handful of specimens at best, beginning in 1878 the fossil remains were discovered of at least thirty-eight well-preserved *Iguanodon* individuals, deep in a coal mine at Bernissart in Belgium. These fossils included the most complete dinosaur skeletons then known. By the end of the century an entire herd of mounted skeletons was on display in Brussels at the Royal Belgian Institute of Natural Sciences. Outdated though they now are, I still find these reconstructions the most stirring of dinosaur exhibits. What on Earth the almost exclusively adult remains of these lumbering beasts were doing jumbled up in shaly bands within the Bernissart coal deposits was loudly debated for years. Recent assessments have abandoned the idea of a single catastrophic event in favor of the notion that the carcasses were deposited one by one in river valleys incised during Cretaceous times into a Carboniferous coal-producing landscape.

A third early discovery was the early Cretaceous *Hylaeosaurus*. Also a plant eater, it was nonetheless quite distinct from *Iguanodon*, bearing armor plates along its back. Despite the varied morphologies of these three large beasts, Richard Owen grouped them in Dinosauria, a "distinct tribe or sub-order of Saurian reptiles," because all had an enlarged sacrum (the part of the spinal column that attaches to the pelvic girdle); a column-like structure of the legs, which extended directly below the body (in contrast to the sprawling gait of crocodiles); and double-headed ribs in the thorax. They were, Owen declared, the largest egg-laying and cold-blooded animals the world had ever seen.

By describing dinosaurs as "cold-blooded," Owen was comparing them to the ectothermic reptiles, whose body temperatures and levels of activity are responsive to ambient temperatures, in contrast to the endothermic mammals and birds. Endotherms maintain constant body temperatures, and (at the expense of high energy expenditure) are capable of sustained high-activity levels. Most specifically, Owen noted similarities in chest construction to crocodiles and suggested that his dinosaurs might even have had four-chambered hearts, as crocodiles do. Birds and mammals also have hearts with four chambers, in which the flows of deoxygenated blood (going to the lungs) and oxygenated blood (returning from them) are efficiently separated. Owen thus suggested that his dinosaurs might have had an "adaptation . . . approaching that of the warm-blooded Vertebrata."

Given the rather little fossil material available to him, Owen's radical deductions about the dinosaurs added up to a remarkably complete picture of these creatures. The image he evoked of the dinosaurs as heavy quadrupeds, their weight borne equally by four pillarlike legs, was not, however, congenial to everyone. In the 1820s Mantell, who owned a partial skeleton of *Iguanodon,* showed that it was not the elephant-like form envisaged by his rival. Instead, this dinosaur had possessed rather small forelimbs and much longer and stouter rear ones, on which the animal's body weight might have been exclusively borne. Such limb proportions, he pointed out, would have given *Iguanodon* a much more upright aspect than envisaged by Owen. Still, the findings of a country doctor were less influential than the opinions of the man who was to become superintendent of the Natural History Collections at the British Museum, and Owen's vision animated the first life-size reconstructions of *Iguanodon* and other dinosaurs created by the sculptor Benjamin Hawkins, at London's Crystal Palace Park, for an unprecedented dinosaur exhibition in 1853.

The discoveries in the coal mine at Bernissart corroborated Mantell's insight into *Iguanodon* locomotion a quarter-century later. These amazing finds not only confirmed the disparity between the forelimbs and hind limbs of *Iguanodon*, but they showed that the creature had possessed a large tail, thought to resemble that of a kangaroo. The Belgian paleontologist Louis Dollo eventually concluded that *Iguanodon* had been the ancient equivalent of today's giraffes, browsing high in the trees. But giraffe-like as it might have been, *Iguanodon* remained a distinctly "reptilian" giraffe.

Even before the Bernissart fossils came to light, an extraordinary find was made at the southern German Jurassic *lagerstätte* of Solnhofen: the first well-preserved example of a fossil bird. It was described by Owen in 1863 under the name of *Archaeopteryx* ("ancient wing"). Impressions of its wing and tail feathers were exquisitely preserved. They were of the rigid kind used for flight. Yet at the same time, unlike any modern bird, the Solnhofen specimen had teeth in its jaws, three clawed fingers on each hand, and a bony (rather than feathery) tail. In other words, *Archaeopteryx* combined features both of reptiles and birds. It also closely resembled a featherless fossil discovered at Solnhofen at about the same time. This was named *Compsognathus* "dainty jaw," and was immediately recognized by the English comparative anatomist Thomas Henry Huxley as a very small predatory dinosaur.

As a result of a revelation that allegedly came to him as he was carving his Christmas turkey, Huxley had concluded by the early 1870s that birds and dinosaurs were not only related, but that birds had evolved from dinosaurs. An early and energetic advocate of Charles Darwin's theory of evolution, published in 1859, Huxley found here a convenient stick with which to beat the anti-Darwinian Owen. Unfortunately, corroborating discoveries were rather slow in coming, and the evolutionary debate rapidly moved on to other ground.

Meanwhile, the dinosaur epicenter had moved to a new continent. One of the most thoughtful of all early paleontologists was Joseph Leidy, of the University of Pennsylvania, who described the first dinosaur skeleton from the United States. Found at Haddonfield, New Jersey, in 1858, and given the name *Hadrosaurus foulkii*, this was to become, ten years later, the world's first fully remounted dinosaur skeleton. Presciently, even before the discoveries at Bernissart, Leidy showed in his mount that this relative of *Iguanodon* had been a biped.

Leidy, once described as "the last man who knew everything," was famously congenial and uncombative. But his student Edward Drinker Cope could hardly be described in the same terms, and the last three decades of the nineteenth century witnessed headline-grabbing "Bone Wars" of incredible unscrupulousness between Cope and his Yale counterpart, Othniel Charles Marsh. From around 1870 onward, collecting crews sent out by both Cope and Marsh energetically spread out over the American West, stealing fossils from each other's sites, undermining each other's relationships with local Native Americans and landowners, and dynamiting fossils out of rocks in their haste to be first. Disreputable as all this was, it led to the discovery of an unparalleled trove of dinosaur diversity in the Mesozoic of the Rocky Mountain states.

Once the excitement of the Bone Wars ended with Cope's demise in 1897, dinosaur studies almost inevitably went into a more tranquil period, albeit with a steady stream of new discoveries by such luminaries as the legendary Barnum Brown and some adventurous episodes such as Roy Chapman Andrews' American Museum of Natural History expeditions to Mongolia in the 1920s. Besides unearthing a host of dinosaur bones, Andrews' team found nests filled with hard-shelled dinosaur eggs.

Together with discoveries of skin impressions, and even of natural mummies showing that some dinosaurs at least had had scaly coverings, findings like this substantiated the view of these creatures as reptilian in their general attributes. Through the 1950s, the general view of dinosaurs remained much as it was when the century began. These creatures were seen essentially as large-bodied versions of today's reptiles (basically, squamates plus crocodiles), and thus as unimpressive for anything except their size. Although evidently good enough for the times they lived in, dinosaurs had been rather sluggish and lumbering; so much so, indeed, that it was even proposed that the largest of the dinosaurs must have been at least semiaquatic, simply in order to support their enormous body weight.

What's more, dinosaurs were considered supremely unintelligent: Marsh, for example, confessed amazement at the "walnut-sized" (three-ounce) brain of the thirty-foot-long, five-ton *Stegosaurus.* How could such a tiny organ control such an enormous body? One possibility put forward was that a "secondary brain" had existed in the area of the sacral plexus in the pelvic region, to act as a relay station for signals traveling along the immense spinal cord. Today it is thought that the enlarged sacral plexus of *Stegosaurus* corresponds not to a nerve bundle, but to a space for the glycogen-storing organ also found in living birds. But the fact that a secondary brain devoted simply to moving its possessor's bulk around was once considered necessary emphasizes the dinosaurs' early image as dull-witted, slow-moving creatures.

Still, the notion of dinosaurs as modern reptiles handicapped by enormous size wasn't the only way of looking at them. John Ostrom, curator of Marsh's collections at Yale, certainly didn't think so. In 1969 he gave the name *Deinonychus* ("terrible claw") to a bipedal Cretaceous theropod dinosaur he had found in Montana, because one of the toes of each foot bore a large, curved claw that was suited to slashing. Here was the claw of a predator: a weapon later shown to have been matched by the rows of razor-sharp teeth in this dinosaur's long jaws. These deadly attributes opened the way to an entirely new perspective on this creature: as a swift and voracious hunter. Ostrom noted that with only two toes on each foot for balance, the bodily coordination of the nine-foot-long *Deinonychus* must have been exquisite as it pursued its prey, held fixed in the gaze of its forward-facing eyes.

The long-legged *Deinonychus* was evidently fast, too, and its slender arms bore elongated fingers tipped with pointed claws that any prey might fear. Even more terrifyingly, this creature probably could have turned on a dime, counterbalanced by a stiff, tapering tail whipped around by strong pelvic muscles. Finally, unlike *Stegosaurus, Deinonychus* had a brain that was a lot bigger than you'd expect for a modern reptile of its size. While this might have meant that there was just more neural matter devoted to controlling the musculature, it was also very possible that the creature was smarter as well.

Once the prevailing image of dinosaurs had been challenged by this interpretation of *Deinonychus,* the way was open to reexamine the overall stereotype: a process already begun by Bob Bakker, then a precocious undergraduate student of Ostrom's. Bakker saw dinosaurs as energetically fully equivalent to mammals and birds. To him they were active, endothermic creatures, and the internal structure of their bones showed that they had highly efficient internal energy distribution systems.

According to Bakker, locomotion held the ultimate key to the amazing success of the dinosaurs. By abandoning the primitive sprawling gait and shifting the legs directly underneath the body, the ancestral dinosaurs established ecological ascendancy by moving with unprecedented efficiency—long before the ancestral mammals. In contrast to earlier tail-dragging images, by 1968 Bakker was publishing exquisite drawings of long-necked eighty-five-foot *Barosaurus* strolling jauntily along, tails held high, and of small-horned dinosaurs in bipedal sprints. In the decades since, this dynamic new view of dinosaurs has been repeatedly substantiated. One case in point is our old acquaintance *Iguanodon*.

Reanalysis has proven the reptilian giraffe interpretation of

Iguanodon seriously flawed. To give *Iguanodon* a kangaroo-like stance, for example, Dollo had broken some of the tail bones to produce an upward curve. In life the tail had actually been held straight out, maybe curving down a little. The backbone was held horizontal, with the body balanced above the two hind limbs. The forelimbs in Dollo's reconstruction proved to have been strongly folded, giving an artificial impression of shortening. Unbending them yielded an arm long enough to have been used as additional support for the body, especially during slow movement. Ossified tendons show that tension had been distributed all along the spine and into the tail, confirming that *Iguanodon* had at least occasionally ambled along on all fours. At higher speeds, locomotion would have been bipedal.

The hand proved particularly interesting. Its three central digits and the wrist were weight bearing and specialized for locomotion, as were the powerfully built arm and shoulder girdle. The thumb and fifth digit were different, though. Dollo had shown that a curious spike (which Owen had placed on the nose of his Crystal Palace reconstruction, like the horn of a rhinoceros) represented *Iguanodon*'s thumb. It is now believed that this dagger-like appendage was defensive. The fifth digit, mobile and divergent from the others, could have been used to manipulate objects. Like its ornithopod relatives, *Iguanodon* had an unusual and efficient dental mechanism for chewing plant foods, and indeed this adaptation may have been responsible for the success of its larger group.

Who Were the Dinosaurs?

All the many dinosaur taxa now known are descended from a single ancestor that had swung its hind limbs in a fore-and-aft plane beneath the body. This locomotor habit is most eloquently revealed in a reinforcing shelf of bone at the top of the acetabulum, the recess in the pelvis into which the head of the thighbone fits.

Forms with this adaptation make up a very diverse assemblage. As early as 1887 the English geologist Harry Seeley classified the dinosaurs into two basic groups: the saurischians ("lizard-hipped") and the ornithischians ("bird-hipped"). In all land vertebrates the hip girdle is composed of three bony elements: the ilium, the ischium, and the pubis. In human beings the ilium is the large blade-like element at the side and back to which the gluteal muscles attach. The ischium is the smaller bit below it that you sit on, and the pubis is the even smaller part that lies where the two sides of the pelvis come together at the front. Such dinosaur favorites as *Tyrannosaurus* and *Velociraptor* are lizard-hipped, with a large forwardly pointing pubis, plus a grasping forefoot with divergent thumb; the equally famous *Stegosaurus* and *Triceratops* are bird-hipped, with backward-pointing pubises and reduced front teeth, or a beak. Ironically, the bird-hip conformation seems independently acquired in birds.

Each major dinosaur group is hugely diverse. Among the vegetarian ornithischians were forms as different as the huge, long-necked diplodocids such as the forty-ton *Barosaurus*; the heavily armored thyreophorans such as the ankylosaurs and the spiky-tailed *Stegosaurus*; the more lightly built cerapodans that included the duck-billed hadrosaurs, the thick-headed pachycephalosaurs, and *Iguanodon* itself; and the huge-headed, frilled ceratopsians such as the horned *Triceratops*.

The saurischians were of two major kinds. The plant-eating sauropods were mostly huge creatures with tiny heads, enormously long necks, and columnar legs supporting bulky bodies. They ambled around on all fours and included the gigantic *Barosaurus*, the barely more modestly sized *Apatosaurus* (formerly *Brontosaurus*), and the more primitive prosauropods such as *Plateosaurus*. In dramatic contrast was the second great group of saurischians, the theropods. These were for the most part lithe, agile, fast, and slender bipeds. The great majority were evidently predatory and carnivorous, though they most improbably include the ponderous, long-necked therizinosaurs, which have tiny heads with teeth like those of plant eaters. In bulk, theropods ranged from the chicken-sized *Compsognathus*, through the mid-sized *Deinonychus*, to such fearsomely huge forms as *Tyrannosaurus*, forty feet long and weighing seven tons.

Feathered Dinosaurs

Thomas Henry Huxley had early on recognized the similarities between the bird *Archaeopteryx* and the dinosaur *Compsognathus.* Later authors plumped for independent acquisition to explain this resemblance. After all, they reasoned, dinosaurs were reptiles; not birds; and they didn't fly, leaving that to the pterosaurs, an extraordinary group of large flying forms that were related to the dinosaur radiation but were not actually part of it. Instead, most paleontologists looked for bird ancestry among the thecodonts, a rather poorly characterized group of primitive diapsids.

But reexamination of the Solnhofen fossils started John Ostrom thinking again, especially after he found yet another fossil slab, from the same quarry, that bore some rather *Deinonychus*-like leg bones together with the faint impression of a feather. As a result, during the 1970s Ostrom was able to demonstrate that the ancestry of birds lay *within* the theropod dinosaur radiation. Specifically, he showed that birds were most closely related to the dromaeosaur group that contained *Deinonychus*.

Once more, the old way of classifying vertebrates—into the more or less equivalent groups of fish, amphibians, reptiles, birds, and mammals—had been upended. These traditional categories were essentially "grades," or "levels of organization," that were based on overall resemblance and harked back to the old *scala naturae*. Strictly in terms of ancestry, though, birds *are* a kind of dinosaur—which means not only that dinosaurs are not reptiles but also that they are not entirely extinct, either.

Today, birds are the only feathered forms around. And the complex structures known as feathers are fundamental to their other basic feature, their particular form of flying. Because of this, the question of bird origins is intimately tied up with the origin of bird flight. The earliest known bird is still the late Jurassic (about 150-million-year-old) *Archaeopteryx*. Indeed, the larger taxon Aves, to which all birds belong, embraces all forms descended from the common ancestor of *Archaeopteryx* and all later birds. It is reported that the strangely early *Archaeopteryx* already flew, and at the very least its feathers were of the advanced kind associated with flight. Yet it also bore clear traces of its dinosaur ancestry throughout its skeleton. These ranged from the teeth in its jaws, through its leg and pelvic structure, to its long, reinforced bony tail.

As the 1990s began, the case was just about closed that birds had originated within the theropod dinosaur radiation, specifically among the dromaeosaurs and their allies in the Maniraptora ("seizing hands"). By the mid-1990s, the developmental biologists also had a pretty good idea of how feathers could have evolved, by a series of well-understood modifications of the structure of the epidermis. Then a series of remarkable fossil discoveries in China began to shed light on the origin of flight itself.

In early 1998 a group of Chinese paleontologists announced finding exceptionally well-preserved specimens of a maniraptor they called *Sinosauropteryx*. These came from deposits in the Liaoning region that are now thought to be around 145 million years old. A close relative of the Solnhofen *Compsognathus, Sinosauropteryx* had been covered in discrete filamentous structures interpreted as "proto-feathers." The deposits also preserved soft tissues such as the eyes, and maybe some internal organs as well. One specimen had a lizard skeleton in its gut, evidence of an active predatory lifestyle that was confirmed when a third specimen turned up with the remains of a tiny mammal inside. This fit well with its massive first digit, which bore a large, knifelike claw.

Also found inside one evidently female specimen were two intact small eggs. Closer examination showed probable paired oviducts, suggesting that reproduction in these theropods was more like that of lizards than that of birds, in which eggs are relatively large and descend down a single oviduct.

FIGURE 6.2. The early feathered dinosaur *Sinornithosaurus*. Courtesy of Mark Norell.

A few months later, two more maniraptor genera were announced from Liaoning. Some 125 million years old, these pheasant-sized dinosaurs (one of which was dubbed *Protoarchaeopteryx*—for its morphology, not its age) had been swathed in a covering of downy feathers that apparently served for insulation. And they provided clear confirmation that the filamentous covering of *Sinosauropteryx* indeed represented an early kind of feather.

Both genera also possessed more rigid feathers, but neither was a flying animal. Feathers, then, were not the unique possession of birds, and the first feathers had not been used to fly! Here we have yet another excellent example (the limbs of tetrapods being a similar case) of *exaptation*: the origin of new, often radically new, features in a context other than the one in which they later become familiar. Over evolutionary history, old structures have constantly been co-opted to new uses. And how, indeed, could things be otherwise? Birds couldn't fly without feathers, but they had to have feathers before they could fly: they certainly couldn't bring feathers into existence by flapping naked wings. Still, if feathers didn't always equal flight, how had this astonishing locomotor innovation come about? The Liaoning record had an answer to that one, too.

There had been two major hypotheses about the origin of bird flight. One held that tree-dwelling proto-birds had originated as gliders, since launching from a tree is easier than taking off from the ground. Alternatively, flight might have evolved from a terrestrial running stage: an idea that gained support once it was accepted that the ancestral bird was a theropod, belonging to a group of sprinters. Then, in 2003, a Chinese team reported yet another new maniraptor from Liaoning, a small form some 125 million years old.

Called *Microraptor*, this form had advanced (flying) feathers not only on its forelimbs (wings) and tail, but on its legs as well. It seemed to have been a four-limbed glider, and its describers believed it had been arboreal. They thus concluded that "the ancestor of birds first learned to glide by taking advantage of gravity before flapping flight was acquired."

The early record of true birds is sparse and, confusingly, some of the most primitive birds have been found from quite late in time. Yet molecular analyses have consistently suggested that the diversification of modern birds well antedated the extinctions at the end of the Cretaceous. Fossil evidence to support this contention finally came in 2005, when it was reported that *Vegavis* of the later Cretaceous of Antarctica was not only a waterfowl, but quite closely related to today's ducks, implying that at least five major divergences had taken place within the class Aves before the late Cretaceous. Once again, we are confronted by the fact that evolutionary processes are far from linear. Nature is instead a great experimenter, and the old often lingers alongside the new for amazingly long periods of time.

So much for the origin of birds, which still remains obscure because *Archaeopteryx* is, awkwardly, much older than any of the

Chinese bird relatives we have been discussing (which actually appear alongside bona fide if archaic bird species). How about the origin of dinosaurs themselves?

Dinosaur Origins

Dinosaurs (including birds) are diapsids that have brought their legs under their bodies to achieve an erect posture. This excludes both their relatives the crocodilians, which retain the primitive sprawling stance, and the even more closely related flying pterosaurs. All three groups are classified, with other extinct forms, as Archosauria.

The very closest fossil relative of dinosaurs is the late Triassic archosaur *Herrerasaurus,* from 230-million-year-old deposits in Argentina. These sediments have yielded both a rich fauna and an impressive flora that includes the trunks of trees that would have been well over a hundred feet tall. *Herrerasaurus* itself was a predator, up to twelve feet long, that lacked only a few dinosaur characteristics in its hip and leg structure.

One of the earliest true dinosaurs, called *Eoraptor* ("dawn plunderer"), comes from the same Argentinian deposits as *Herrerasaurus.* Only a yard long, it is a saurischian, and possibly even a theropod. Its rather odd teeth don't reveal much about what *Eoraptor* ate, but it was a swift bipedal form with short forelimbs and clawed digits that suggest it was a predator. Other contenders for the title of "oldest dinosaur" are marginally earlier and consist of a couple of fragmentary prosauropods (plant-eating saurischians) from the middle to late Triassic of Madagascar.

The earliest ornithischians are even more poorly known, consisting principally of a form called *Pisanosaurus* from the same late Triassic formation that yielded *Herrerasaurus* and *Eoraptor*. However, by the early to middle Jurassic both ornithischians and saurischians had become well established and diverse. This diversification coincided with the breakup of the southern continent Gondwana. This split apart previously cosmopolitan Pangaean genera, freeing their descendants to follow their own evolutionary pathways.

Diversification accelerated impressively as the Mesozoic progressed: the Jurassic is littered with familiar names such as *Brachiosaurus, Stegosaurus, Diplodocus,* and *Allosaurus,* while the Cretaceous resounded to the footfalls of such luminaries as *Tyrannosaurus, Corythosaurus, Parasaurolophus, Triceratops,* and *Gallimimus*. However, remember that our knowledge of dinosaurs is shaped by geological accident: few dinosaurs, for example, are known from the middle Jurassic, but many are from the late Cretaceous.

Yet even in the late Cretaceous fewer than fifty species of dinosaurs are known worldwide, compared to many thousands of bird species alive today. Of course, dinosaurs were much larger than birds, which may have made a difference in the abundance of species. What is more, far fewer predatory dinosaurs are known than plant-eating species, which reflects the balance typical today and suggests not only that the basic structure of ecological communities has been maintained over the long haul but that our dinosaur sample is reasonably representative. Still, the known dinosaur fossil record, like those of other major animal groups, is a mere fragment of ancient diversity.

What Were Dinosaurs Like?

Between the time of *Eoraptor* and the disappearance of the dinosaurs 65 million years ago, some 165 million years intervened. During their long tenure, dinosaurs must have encountered virtually every kind of habitat available in the admittedly warm Mesozoic. In this sense they indeed ruled the world, occupying a huge range of terrestrial ecological niches from which they managed largely to exclude members of other groups.

Small carnivores, such as *Compsognathus* and *Sinosauropteryx,* were the ecological equivalents of today's foxes and jackals. Larger forms such as *Deinonychus* played the role of big cats such as lions. And the mammal fauna that dominates the modern world has never had any ecological equivalent of the terrible *Tyrannosaurus.* Dinosaurs of all sizes and relationships filled the roles of browsers and grazers, ranging in size from the small to the enormous. Except for those niches occupied by the tiniest of animals, dinosaurs dominated at every level of the food chain. In the Cretaceous skies, birds soared alongside the dinosaurs' close relatives, the pterosaurs.

Only in the oceans did the dinosaurs fail to establish themselves to any significant extent. For while the toothed bird *Hesperornis* has been compared to today's penguins, the dinosaurs left the seas largely to the plesiosaurs, ichthyosaurs, and mosasaurs.

Body size variety has its consequences, among them great ecological and structural diversity. Analysis of dinosaur limb structures has shown pretty clearly, for example, that many were fast movers. Emblematic were the agile theropods—some of which, such as the exclusively bipedal ornithomimids ("ostrich dinosaurs"), were probably capable of running at sustained high speeds. But while it is unlikely that any dinosaurs were quite as slow and lumbering as early stereotypes suggested, the large, heavy sauropods clearly could not produce anything other than short bursts of modest speed. Size (and sometimes armor) protected them from predators.

Endothermy

Today, animals that are capable of seriously sustained activity are all endotherms. Were dinosaurs also? Modern birds are. And if birds are dinosaurs, then endothermy must have evolved in at least one dinosaur lineage. Whether that was true of all dinosaur lineages is perhaps not the best question to ask. This is because a sharp dichotomy between endothermy and ectothermy, governed by the physiological mechanisms we see among vertebrates today, may not be the only possible state of affairs. Because if you are really big (with a very high volume-to-surface-area ratio), you cool off and heat up so slowly that you may have an effectively stable body temperature, independent of your physiology.

Therein lies one potential approach to the endothermy question. Numerous studies have failed so far to come up with a silver bullet, in bone histology or any other variable, that will clearly discriminate between endotherms and ectotherms. But if a trend toward endothermy was advantageous in one dinosaur lineage, it might have occurred in several. Among the saurischians, the coelurosaurs, including the maniraptor group that embraces birds, were relatively small and reached their greatest diversity toward the end of the Cretaceous. The same was true of the group of ornithischians known as the hypsilophodontids. If the body-size relationship holds, perhaps both lineages might have evolved endothermy. On the other hand, only within the maniraptors do we *know* that endothermy evolved, because all birds have it. And the maniraptors are almost the only dinosaurs that we know acquired feathers—the exception being one small-bodied early tyrannosaur from Liaoning that apparently had a filamentous covering similar to the proto-feathers of *Sinosauropteryx*.

If the initial role of primitive feathers was to provide body insulation, their presence is pretty good evidence of endothermy, because you only need to control body-heat loss if you are generating such heat internally—a costly business. Putting everything together, perhaps the best we can say is that reasonable presumptive evidence exists for endothermy in the maniraptors, and maybe even among the theropods as a whole. We only have reason to suspect endothermy among the ornithischian hypsilophodontids.

Diet

However a vertebrate functions, it's ultimately going to need a source of energy, which will come from what it eats. Dinosaur diets are occasionally directly indicated by fossilized stomach contents (such as the lizard inside that *Microraptor*, or the conifer needles, seeds, twigs, and fruits found in the stomach of one mummified ornithischian). More usually, however, diet has been indirectly inferred. Studies of teeth, which are the primary organs of food acquisition and ingestion, or of the mechanics of jaw movement, allow you to speculate about meat eating vs. plant eating, but not much more. Analysis of wear-scratches on teeth can additionally suggest how gritty the diet was, suggesting that among the sauropods, for instance, forms such as *Diplodocus* browsed higher above the ground than did *Camarasaurus* and its like.

Quite detailed "last meal" information is provided by coprolites (fossilized feces). The problem lies in knowing who produced them. Fortunately, one dromaeosaur skeleton was fossilized with coprolites inside it, packed with lizard bone fragments. In another case, some coprolites pretty confidently attributed to a titanosaur (a large sauropod) showed that dinner had consisted entirely of five species of grass.

One extraordinary demonstration that some theropods, at least, were highly active predators came from the extraordinary finding of the skeletons of a *Protoceratops* (ornithischian) and a *Velociraptor* (theropod) locked in mortal combat. Discovered in 80-million-year-old sandstones in Mongolia, and displayed at the American Museum of Natural History in 2000, this astonishing tableau was frozen in time when a sand dune suddenly collapsed and covered the attacking *Velociraptor* and its victim.

Another unusual line of evidence on dinosaur feeding came from tooth-marked bones showing that the theropod *Majungatholus* fed not only on sauropod dinosaurs but practiced cannibalism on its own species as well.

Evidence continues to accumulate on dinosaur diets—bone chemistry is especially promising—but studies are already converging on the rather general notion that ornithischians and sauropods were largely if not entirely herbivorous, while the theropods were mostly carnivorous (though some of their bird relatives had taken to seed eating by the early Cretaceous).

Social Behavior

Dinosaur trackways identified at numerous sites around the world have confirmed that dinosaurs held their legs beneath their bodies, some moving fast bipedally while others ambled more slowly on all fours. They also confirm that some dinosaurs, at least, traveled in large groups. In the 1940s, numerous sauropod footprints were uncovered at the Davenport Ranch in Texas. These had been made by at least twenty-three individuals who were moving over muddy ground at an estimated four to five miles an hour. Overlapping tracks indicated that the largest individuals led the way, with smaller ones trailing. But while these sauropods were traveling in file, equally large herds elsewhere seem to have moved along on a broad front. Either way, the dinosaurs were social: something not unexpected among herbivores.

Trackways of carnivorous theropods are less common. Again, you might expect this, since predators are invariably thinner on the ground than their prey. Did such dinosaurs hunt alone or in packs? At another Texas location, along the Paluxy River, numerous sauropod and theropod tracks were mixed. An initial interpretation was that a herbivore herd had been pursued there, some 107 million years ago, by at least three predators. Now scientists are more cautious, pointing out that there is no way of knowing how long after the sauropod tracks the theropod footprints had been made.

Once the discoveries of Roy Chapman Andrews in the Gobi Desert had confirmed that dinosaurs were egg-laying creatures, and that they laid multiple eggs in nests, the question became whether or not they cared for their young. There are two phases of parental care: the building of nests and incubation of the eggs, and the subsequent guarding and feeding of the young. In the mid-1970s a large concentration of dinosaur nests was found near Choteau, Montana. These contained both eggs and hatchlings, all associated with the fossil bones of a hadrosaur called *Maiasaurus.* Even spacing of the nests suggested that numerous individuals had come to this colony to lay and incubate eggs. It was also suggested that the parents had fed the hatchlings, since some of these, too small to leave the nest, showed wear on their teeth. However, since dental wear is not definitive evidence of chewing, second-stage parental care must remain at this point no more than plausible.

Even more remarkable, one Gobi theropod had been named *Oviraptor* (egg stealer) after its remains were found in a nest containing eggs believed to have been laid by *Protoceratops.* Seventy years later, a similar egg was found that contained an embryo of *Oviraptor* itself. Far from being stolen, the eggs were being incubated.

A powerful reason for believing that the parents actually reared the chicks once the eggs were hatched is that not only birds, but crocodiles—the other living archosaurs—do so today. At this point we cannot know how extended or elaborate that parental care might have been. However, it's a reasonable bet that dinosaurs typically cared for their young, at least during the very earliest phases of their development outside the egg. Growth studies suggest that very small theropods took about three years to attain full adult body size, while a medium-sized species might have taken about four to twelve years and a *Tyrannosaurus* around eighteen. A really large sauropod might not have reached its maximum body mass until around twenty-five. Life expectancies are even tougher to guess, but small theropods may have lived three to four years, medium-sized ones to seven to fifteen years, and big ones to twenty-four to thirty years. Giant sauropods such as *Brachiosaurus* might have made it to fifty years or more. But remember that food web: no matter how big you have the potential to become, you're always at risk of being gobbled up while you're still small.

Why No More Dinosaurs?

After dominating land faunas for most of the Mesozoic, the non-avian dinosaurs abruptly disappeared (along with much of the rest of the biota) at the end of the Cretaceous, some 65.5 million years ago. What could explain this apparently sudden event, remembering that to geologists "sudden" is not necessarily the same as "instantaneous"? We've already discussed the K/T crisis in Chapter 2, so there's little need to say much more here, except perhaps to note that all reports of dinosaur fossils in sediments postdating the K/T boundary have been satisfactorily explained by reworking, whereby fossils are eroded from older sediments by wind and water, then redeposited in younger ones.

The claim has also been made—on rather sparse data—that dinosaur diversity was significantly dwindling toward the end of the Cretaceous, perhaps because of a general cooling around that time due to lessening volcanism and falling atmospheric carbon dioxide. Such cooling might in turn have affected nonavian dinosaur physiology in ways we are not in a position to fully appreciate. On the other hand, we know that the extreme volcanism producing the Deccan Traps occurred right at the end of the Cretaceous, almost certainly warming the atmosphere by several degrees.

The best dinosaur record from the last 10 million years or so of the Cretaceous comes from western North America. It shows a fairly high diversity of dinosaurs at the beginning of this period, and an increase in the body size of the biggest saurischians and ornithischians toward the end. This information suggests that the terrestrial environment in the final years of the dinosaurs was productive, and that food was abundant both for herbivores and for the carnivores that predated on them. The end of the Mesozoic world certainly wasn't strongly predictable on existing climatic or environmental trends.

Paleontologists are thus increasingly receptive to the notion of a catastrophic event, or even of a series of catastrophes. The best candidate for such an event is the bolide impact that produced the Chicxulub crater—which might have been one of several if Earth was passing through a meteor shower at around that time. The Chicxulub impact might not have been a unique cause of the dinosaurs' demise—many other possibilities have been mentioned, and some could have worked in synergy—but it is almost certainly implicated in the process.

Whatever happened was something short-term, that preferentially affected the terrestrial fauna. Dinosaurs had monopolized the terrestrial ecological niches that could be occupied by primary feeders larger than a small dog, while the largest survivors of the K/T event on land were crocodiles and crocodile-like forms that can survive extended periods without feeding. Over the longer term they can get by on detritus, and it has been suggested that detrital remains sustained the crocodiles during the period when the environment was in the greatest shock and primary production was at its lowest.

The mammals also took a large hit at the K/T boundary. But the major lineages made it through, almost certainly surviving for reasons having to do with their small body sizes and probable nocturnal habits. Being insignificant sometimes has its advantages.

Mammals and Their Relatives

By the end of the Permian, the complex lower jaws of the synapsids (a.k.a. the "mammal-like reptiles") had become dominated by the dentary bone that progressively squeezed the other jawbones toward the back, where the mandible articulated with the cranium. Several lineages of synapsids perished in the great end-Permian extinction, but the cynodonts, the group in which this trend was most pronounced, survived into the Mesozoic. Diverse cynodont fossils are known: enough to gain a pretty clear picture of how the mammals emerged from a cynodont ancestry. Possibly the most intriguing aspect of that transition is how mammals acquired their unique and sensitive hearing apparatus.

Origin of the Mammalian Ear

The best-known early Triassic cynodont, some 246 million years old, is the cat-sized *Thrinaxodon*, a lightly built carnivore with shortish limbs structurally intermediate between the sprawled configuration of the Permian therapsids and the later below-the-body mammal arrangement. Still, *Thrinaxodon* showed suggestions of the flexible double articulation of the skull with the vertebral column that is seen in mammals. It had a solid secondary palate, and the teeth in its jaws were quite mammal-like, with well-differentiated canines and cheek teeth bearing multiple cusps. However, as in reptiles and earlier synapsids, these teeth were replaced throughout life, lacking the precise occlusion between upper and lower teeth characteristic of the mammal dentition.

Behind the dentary, several small bones still lay where the jaw contacted the articular bone of the cranium. These small elements were only loosely connected to the dentary and possibly to each other. One, the angular, helped support a membrane, the tympanum, that also attached to the cranial base. Sounds picked up by the tympanum were transmitted to the neighboring quadrate bone, part of the jaw joint, and then in turn to the stapes that connected across the middle ear.

Among mammals, the dentary articulates directly with the squamosal bone above, rather than with the articular via the small bones behind it. Three tiny bones transmit sound vibrations from the tympanum (eardrum) across the middle ear, to be converted into nervous impulses toward the brain. In the transition from the primitive therapsid articular region to the mammalian version, via something like what is seen in *Thrinaxodon,* several modifications had to occur. These key changes are amazingly documented in known fossils.

In an early Jurassic (200-million-year-old) cynodont called *Diarthrognathus* ("double jaw joint"), we can see the modification of the jaw joint in progress. *Diarthrognathus* lived up to its name in having two jaw joints per side, one between the quadrate and the articular as in earlier cynodonts, and one, new-style, between the dentary and the squamosal. The same is true of its approximate contemporary *Morganucodon,* a tiny genus that was traditionally classified as a mammal because, like us, it had only one replacement set of teeth and a finite growth period, while retaining multiple tiny bones at the back of the jaw.

Among the latest cynodonts and earliest mammals, the quadrate/articular joint diminished and eventually disappeared, the two bones involved becoming incorporated into the middle ear mechanism as the incus and malleus, respectively. Because the dividing point between evolved cynodonts and primitive mammals is so arbitrary, and because the Jurassic record is proving to be amazingly diverse, many paleontologists now prefer to classify forms such as *Morganucodon,* along with true mammals and various extinct groups, into a broader category called Mammaliaformes.

The earliest known mammaliaform to possess an entirely mammalian-style jaw joint and single-bone mandible is the tiny (two-gram) *Hadrocodium* from the early Jurassic of China, some 195 million years ago. It also shows advanced features of the secondary palate; a precisely occluding dentition that is well differentiated into the familiar incisor, canine, premolar, and molar categories; multicusped cheek teeth; and a raised and forwardly shifted jaw joint.

The auditory modifications revolutionized hearing. Primitive amniotes literally hear through their lower jaws. Sound travels from the jaw, through the joint, to the middle ear via the stapes. The jaw can pick up vibrations only when it is in contact with the ground. But with a freed-up eardrum communicating directly with the brain via the tiny delicate bones of the middle ear, a mammal can detect minute sound vibrations traveling through the air, and has effectively acquired an entirely new sense.

If it seems almost impossible to imagine bones migrating from the back of the jaw to a space within the cranium above, a fossil has recently been found that catches them in the act: the 125-million-year-old *Yanocodon,* a hamster-sized creature from China. Despite a somewhat archaic spine and sprawling limb posture, *Yanocodon* classifies closer to placentals than to monotremes. In the spectacularly preserved type specimen, the three bones of the middle ear (very similar to those of today's platypuses) are visibly attached to the mandible via an ossified cartilage. Because something similar exists in mammal embryos today, *Yanocodon* suggests that the transition in ear structures resulted from a relatively simple shift in developmental timing. That this change occurred more than once is suggested by a similar conformation of the ear bones in the early Cretaceous Australian monotreme *Teinolophos.*

Mammal Endothermy

Several lines of reasoning suggest that by the early Mesozoic, mammal precursors had acquired some degree of endothermy. This is most convincingly demonstrated by fossils that possess respiratory turbinates at the front of the nasal cavity. These are thin, scrolled bones that play a role in heat exchange, and their presence is taken to indicate a constant high body temperature. Some late Paleozoic therapsids may have had turbinates, and they were definitely present in some advanced cynodonts and forms such as *Morganucodon*. High metabolic rates may thus have preceded the emergence of mammals in the strictest sense, spurred by the adoption in various later therapsid lineages of an active "foraging-predator" lifestyle that contrasted with an earlier "sit-and-wait" type of predation.

While mammalian endothermy is associated with specialized thermoregulatory structures like hair and sweat glands today, it is hard to know if this was always the case. In the absence of very early fossilized hair impressions, we have to rely on inference. It has been argued that hair (perhaps originally acquired as sensory whiskers) probably did not become an essential form of insulation until tiny body sizes and nocturnality became the norm for mammaliaforms in the early Jurassic—plausibly in consequence of the dinosaurs' ecological marginalization of all except the smallest competition.

Several fairly early mammaliaform fossils actually bear fossilized hair impressions. Earliest is the middle Jurassic (164-million-year-old) *Castorocauda* ("beaver tail"), from China. More mammal-like than *Morganucodon* but less so than *Hadrocodium*, *Castorocauda* has a flattened tail and adaptations that suggest swimming and burrowing. It is thus regarded as semiaquatic, and as evidence that, at least by the middle Jurassic, not all early mammaliaforms were insectivorous.

This unexpected diversity in lifeways is confirmed by the late Jurassic *Fruitafossor* from Colorado, boasting very odd tubular teeth and the skeleton of a specialized digger. Evidently, much more biodiversity was present among Jurassic mammaliaforms than has traditionally been thought, and we are probably seeing as yet only the tip of the iceberg.

Combining ecological considerations with such things as turbinate development and the adoption of highly aerobic energetics, we can speculate a little more about what Jurassic mammaliaforms were like. Almost certainly, the structures preserved were associated with mammal-like lungs and respiration. If so, the Jurassic forms would have had mammalian-type diaphragms and cardiovascular systems, necessitating the enlargement of those organs (heart, kidney, liver, and so forth) that contribute to raised rates of basal metabolism. Brain casts of Jurassic mammals show that, despite small sizes, typically mammalian features had been acquired, especially in the forebrain and cerebellum. Hearing and smell seem to have become the dominant senses during the Jurassic, probably spurred by lifestyles centered on nocturnal predation on insects, and it's a reasonable bet that the egg-laying Jurassic mammals nursed and tended their young.

Cretaceous Mammal Diversity

While the origin of Mammalia as strictly defined goes back into the Jurassic, the modern lineages originated much more recently. Still, although paleontologists have traditionally identified the Cenozoic, the "Age of Mammals," as the period within which today's major groups of placental (eutherian) mammals diversified following the demise of the dinosaurs, DNA comparisons have consistently suggested an earlier, late Cretaceous origin for many of them, following the origin of Eutheria earlier in the period. A recent meta-analysis of large quantities of DNA data from around twenty-five hundred different mammalian species recently suggested that there was a burst of diversification among placentals some 93 million years ago (when dinosaurs still dominated terrestrial ecosystems), and thereafter no comparable radiation until well within the Age of Mammals.

According to this analysis, the end-Cretaceous mass extinction that carried away the dinosaurs had no immediate effect on rates of mammal speciation. However, it is possible that this result is skewed because the DNA comparisons were limited to extant eutherians, whereas plenty of eutherian lineages are now extinct. If we knew more about those, the picture might change appreciably. Moreover, a reappraisal of the DNA data has very recently led Japanese researchers to move the origin of the modern placental radiation up to about 84 million years ago, bringing molecular and paleontological estimates more closely into line.

Nonetheless, despite discoveries of early fossil mammals in Mongolia and elsewhere, there is still no definitive Mesozoic evidence for any placental relatives, even in the latest Cretaceous. What's more, recent paleontological analyses have concluded that placentals probably originated in Laurasia, close to the K/T boundary. Still, none of this rules out a complex evolutionary history for mammals during the Cretaceous.

Today's mammals are of three basic varieties: the egg-laying monotremes, the pouched marsupials, and our own group, the placentals, which give birth to live offspring at an advanced stage of development. Although reproductively primitive, the living monotremes are quite specialized in many ways (adults don't have teeth, for instance). Now restricted to Australasia, they were once distributed more widely in Gondwana, as shown by an early Cenozoic fossil from South America. A variety of Australian monotreme fossils appears as early as the lower Cretaceous. As we've seen the oldest of them, *Teinolophos,* suggests parallel development of modern ear morphology in monotremes and therians (marsupials plus placentals). In China, the early Cretaceous (125-million-year-old) therian *Akidolestes* is reported to show extensive postcranial similarities to monotremes.

The essential unity of the mammals is reflected in their possession of closely comparable genomes and developmental processes. Significantly, simple genetic changes can independently divert the latter to produce similar morphological results. Thus, during the middle Mesozoic, precisely occluding tribosphenic molars evolved independently in the major mammal lineages. In the south, a Gondwanan lineage is thought to have given rise to the monotremes, while the northern continent of Laurasia was the birthplace of both marsupials and placentals.

The earliest marsupial yet reported is *Sinodelphys*, from the same early Cretaceous Yixian beds of China that yielded *Akidolestes.* Exquisitely preserved, this fossil has impressions of fur and even of some soft tissues. About six inches in total length, and weighing under an ounce, *Sinodelphys* shows clearly marsupial affinities in its wrist, ankle, and front teeth—even though it is 50 million years older than the earliest known member of any surviving marsupial lineage. The back teeth are very insectivore-like, and various characteristics of the shoulder, limbs, and feet indicate that it was a climber, adding further to the ecological range of mid-Mesozoic mammals.

Besides *Akidolestes, Sinodelphys* shared its environment with a wide range of other extinct mammaliaforms. These included *Repenomamus,* a much larger creature the size of an opossum, whose dietary habits were evidently very different from those of its smaller mammaliaform brethren. Indeed, the stomach contents of one fearsomely toothed *Repenomamus* indicate that its last meal had included a baby *Psittacosaurus*—an ornithischian dinosaur that matured to the size of a deer.

The astonishing Yixian fauna also includes a multituberculate, *Sinobataar.* First appearing in the middle Jurassic, the multituberculates flourished for some 100 million years before becoming extinct in the middle Cenozoic. Rather rodentlike, they are the only known true mammal group to have become totally extinct. Finally, the very same deposits yielded the earliest eutherian mammal yet found, the mouse-sized *Eomaia* ("dawn mother"). This gives us a minimum date of 125 million years ago for the divergence between today's two large therian lineages, and reinforces the notion that the split occurred in the northern continent of Laurasia. *Eomaia,* fossilized with its lush hairy coat still visible, is the most primitive placental mammal yet known. Fascinatingly, its pelvis indicates that this early member of our own lineage still reproduced much like a marsupial, with the young born at an incredibly early stage of development.

It is always hard to figure out exactly how very small extinct mammals moved, since they didn't need to have adaptations to support great body weight and lived in a world full of irregular surfaces whether they lived in the trees or on the ground. Still, both the hands and feet of *Eomaia* bore the narrow claws typical of climbing forms, and other features of the skeleton also suggest that this tiny eutherian was a scrambling climber capable of tree living. Given that the other Yixian mammaliaforms were probably more committed to the ground, the eventual success of the eutherians may have been founded on an initially arboreal way of life.

Somewhat older than the Yixian fauna is one from Daohugou, in Chinese Inner Mongolia, that has produced an ancient mammal like no other. It has the necessary jaw joint and differentiated teeth, but it is so different from all other mammals that an entire new order had to be invented to contain it. *Volaticotherium* is a squirrel-sized creature with a hair-covered patagium—a gliding membrane stretched between the elongated fore and hind limbs—the impressions of which are exquisitely preserved in the finely laminated shaly rock slab that encloses the remains. *Volaticotherium* was clearly a glider, and no primitive one either: it was capable of planing much in the style of the modern colugos, which are skillful climbers in the trees and can cover well over a hundred yards in a single glide.

By 2006, when this extraordinary find was described, paleontologists already realized that Mesozoic mammaliaforms had been much more diverse than once thought. Nobody, however, had imagined this. Gliding is actually not an unusual means of locomotion in mammals—it seems to have evolved up to seven times, in three disparate lineages—but finding evidence of it this far back in the fossil

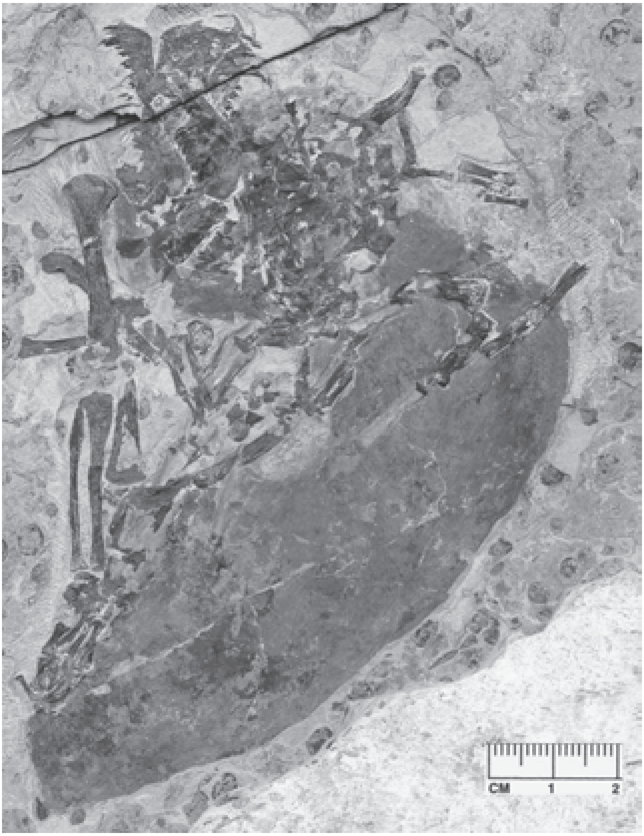


Figure 6.3. The Cretaceous gliding mammal *Volaticotherium*. Courtesy of Meng Jin.

record is truly remarkable. Indeed, the next earliest evidence of any kind of mammalian flight at all is provided by a bat fossil only about 50 million years old. All in all, such extraordinary and unexpected finds as *Volaticotherium* serve as a heavy hint of more surprises to come, as Mesozoic mammaliaforms become better known.

CHAPTER 7

The Age of Mammals

With the demise of the dinosaurs the mammals proliferated on land, and soon in the seas, too, where fish diversified along with mollusks and corals. As the Cenozoic ("new life") Era began some 65.5 million years ago, the Earth was relatively warm, though the subsequent tendency was toward cooling and increasing temperature contrast between equator and poles. The most notable break in this trend was the "Paleocene-Eocene Thermal Maximum" around 55 million years ago, when world temperatures sharply peaked.

Oceans are major distributors of heat around the globe, and climates worldwide were greatly influenced by continental repositioning as the remnants of Pangaea continued reconfiguring toward today's familiar geography. When Australia separated from Antarctica around 34 million years ago there was significant general cooling, as the frigid new Arctic Circumpolar Current brought cold water to the surface and isolated Antarctica from the warmer waters to its north. A major ice sheet developed on the formerly forested Antarctica, and sinking cold water began a northward flow that affected ocean temperatures right into the northern Atlantic and Pacific: an event correlated with a major faunal replacement at higher latitudes that amounted to a minor mass extinction. Radical changes also occurred some 3 million years ago when the formation of the Isthmus of Panama rerouted the world's major oceanic currents to create the "great conveyor" that dominates oceanic circulation today. Cooling temperatures and high precipitation thereafter combined to produce an ice cap over the northern polar regions, 30 million years after its southern counterpart began to form.

The linking of North with South America united these landmasses for the first time in a couple of hundred million years. Evolution had been proceeding almost entirely independently on each for this entire time, so each continent had an entirely distinctive fauna and flora. With the creation of the Isthmus of Panama, animals could again move freely between the two remnants of Pangaea, resulting in what has been called the Great American Interchange. The flow was unbalanced. Only a handful of South American forms moved north, while at least twenty-nine North American placental genera moved south. They wreaked havoc on the South American natives, with the resident marsupial carnivores taking the heaviest hit. Today at least half the mammal genera living in South America are descended from North American immigrants. Ironically, many of them, including camel relatives and tapirs, belong to groups now extinct in the north.

The Cenozoic Timescale

Geologists still disagree vociferously over how best to subdivide the Cenozoic. To cut a very long story short, seven epochs are generally recognized over this time (see Figure 1.2 on page 13), though how they should be grouped is disputed. Our current epoch, the Holocene, began some 11,000 years ago but is only arbitrarily separated from the preceding Pleistocene, the epoch of the Ice Age.

We've seen that ice ages have been an intermittent feature of Earth's history for at least the last 2.7 billion years. But when we talk about "the Ice Age," we habitually refer to the most recent set of glacial episodes in the Northern Hemisphere, starting in the late Pliocene about 2.6 million years ago. Since that point the Earth has been in the grip of a cycle of polar ice sheet expansions (glaciations) and contractions (interglacials), under the control of a number of influences that include variations in the planet's orbit around the Sun, and the tilt and orientation of its axis of rotation relative to that orbit.

All these changes affect the solar radiation received on the Earth's surface at different times of the year. Past global temperatures are recorded in cores drilled into the Antarctic and Greenland ice sheets and the sediments of the ocean floors. These show that early on in the current glacial regime temperatures fluctuated largely according to relatively short (twenty-three-thousand- and forty-one-thousand-year) cycles governed by variations in the orientation and tilt of the Earth's axis. In contrast, over the past nine hundred thousand years or so the major influence has been the longer cycle, of about one hundred thousand years, that is controlled by the planet's orbit.

A host of other influences also operates, including the abundance of greenhouse gases in the atmosphere, heat distribution by oceanic currents, and the sheer volume of the ice sheets themselves. The net result is that, over the past million years or so, the Earth has swung from periods of maximum cold (when the ice caps are at their largest), through more temperate interglacial periods (such as the one we are now in), and back again, at roughly one-hundred-thousand-year intervals. Within these larger cycles there have been numerous oscillations.

Developing a sequence of glacial advances and retreats was fiendishly difficult for early geologists, for all they had to go on was surface evidence of ice action, and each ice sheet advance severely disturbs the evidence left by the previous one. Nowadays geologists prefer to use data from ice and seabed cores, which provide continuous records of the climatic conditions when they were made.

In colder times, due to a variety of influences, seawater contains less of the light oxygen isotope ^{16}O compared to its heavier counterpart ^{18}O than it does in warmer ones. This difference is preserved in the carbonate shells of planktonic foraminifera that are preserved in accumulating muds on the seafloor. Isotopic measurements in cores through these sediments thus record fluctuations in seawater surface temperatures over time. The same is true for cores made through what remains of the polar icecaps. The longest of these comes from East Antarctica and has produced a record of variation in climate and ice volume over the past 740,000 years. This record covers eight major glacial cycles and is in comforting agreement with a large number of deep-sea cores, some of which stretch far back to cover most parts of the Cenozoic. As a result, the Pleistocene timescale now consists of a sequence of numbered Stages (some divided into substages), the numbers increasing as one goes back in time.

One final note about Ice Ages: they have a huge effect on geography. When it gets cold, rain falling on the polar regions freezes instead of returning to the seas via rivers and seepage. Thus as ice caps expand, sea levels fall. Land is exposed, often creating dry bridges between areas formerly isolated by water. Even with the continents disposed pretty much as they are now, during parts of the Ice Ages the map of the world was therefore very different from the one familiar today. Currently, the three largest islands in the world are Greenland, New Guinea, and Borneo. A mere twenty thousand years ago, at the height of the last glaciation, the world's largest island was Madagascar. The others were joined by land bridges to the adjacent continents.

Such geographic changes have had enormous effects on the biota. Among mammals, for example, speciation is improbable if populations are continuous. Fragmentation of populations is promoted by the higher sea levels typical of interglacials, while competition between closely related species, a major factor in determining larger evolutionary patterns, is stimulated by lowering sea levels that permit mingling once speciation has occurred in isolation. Similarly, in warmer times terrestrial vegetation zones move uphill and away from the equator, taking their faunas with them. When it cools down, the reverse occurs. In other words, Ice Age cycles (as long as they don't run out of control, as in snowball Earth) inescapably promote diversity and innovation in the living world—and the competition that inevitably follows. Under such conditions you would expect to find the most evolutionary action, and it was in just this kind of milieu that our own ancestors emerged.

Faunal Change over the Cenozoic

During the Cenozoic both the physical and the living worlds took on their familiar modern appearances. This period is also especially interesting as the time when the mammals diversified and gave rise to our own particular group, the primates. Today there are almost thirty Orders of mammals, and of course mammals themselves constitute only the tiniest corner of nature: there are some thirty-six phyla of animals alone. Since it is impractical to cover such a huge waterfront, let's glance briefly at the overall chronology of events over the Cenozoic before looking at the evolution of two representative mammal groups—to the extent, of course, that any Order can be described as representative of such an astonishingly varied Class of animals. If you prefer looking at specific organisms, as we have mostly done so far, you may want to skip forward here to the accounts of whale and primate evolution at the end of this chapter. But if you are content to sit back and watch the passing parade of animal life changing before your eyes as the epochs unroll, you may—like me—find endless fascination in contemplating the ebb and flow of the cast of characters over the many acts of the Cenozoic evolutionary play.

The Paleocene (65.5 Million–55.8 Million Years Ago)

With the dinosaurs gone from the land, the pterosaurs from the air, and the plesiosaurs and ammonites from the seas, the Paleocene was a time of enormous experimentation, particularly as mammals energetically exploited their new ecological opportunities.

There is no really good fossil evidence of any of today's eutherian groups before the K/T event, although isolated teeth suggest that primitive hoofed mammals and possibly even primates were already in existence when that calamity befell. DNA comparisons suggest that many placental orders had earlier origins, but the clear message of the fossil record is that in the late Mesozoic there was at best a handful of placentals around, in contrast to a quite high diversity of marsupials. In the Paleocene all that rapidly changed. Even in the earliest Paleocene, placental fossils are rare in North America where the record is best, while marsupials are numerous and diverse in the same deposits. Yet by the end of the Paleocene, a relatively short epoch of some 10 million years, virtually all of the vastly diverse modern eutherian orders were in existence. This was truly an adaptive explosion.

In the North American record, the most numerous and diverse of the early placentals were primitive relatives of today's ungulates (hoofed mammals). To judge by their low-crowned teeth, none were yet grazers. Most probably foraged on the floors of the tropical and subtropical forests that covered most of North America and Eurasia. In wetter regions conifers dominated the forests, and swamps teemed with crocodilians. Where drainage was better, flowering plants were busily diversifying, providing a wide array of fruits that were increasingly exploited by coevolving placentals.

Alongside the ungulates on the forest floors were larger forms such as the pantodonts. These stubby browsers eventually became the largest mammals of their time, the size of modern cows. There were also possible diggers, in the form of clawed taeniodonts and tillodonts, both similarly destined for extinction. The underbrush was the domain of a variety of insectivores, all of them small and most of them rather shrew-like.

The forest canopies supported faunas that partly reflected the past and partly looked to the future. The wave of the future was represented by the earliest "archaic" primates such as *Plesiadapis*, somewhat squirrel-like arboreal forms with long tails and faces.

Their digits were clawed, but at least one member of the larger group is known that had a divergent hallux (big toe) like later primates, which they also foreshadowed in the form of flattish molar teeth that suggest they ate fruit.

A variety of carnivores preyed on these vegetarians. Most common were the creodonts, short-limbed creatures looking a bit like big weasels. Unlike weasels, though, they lacked the efficiently shearing carnassial teeth typical of the order Carnivora—very primitive members of which were also around, in the form of a rather rare group known as the miacids. None of these mammalian predators was any bigger than a jaguar, and most were much smaller. Thus the top predators of the time remained the crocodiles and, remarkably, a bird: the six-feet-tall and flightless *Diatryma*, a robust and chunky meat-eater with a fearsome great beak.

The European and North American mammal records are reasonably similar, but in eastern Asia the picture is rather different. Oddly, while pantodonts were rare in Europe, they were very diverse in China. The primates and multituberculates that were ubiquitous in North America and Europe were sparse at best. In their place were numerous anagalids, ancient precursors to rabbits and rodents, and, by the end of the Paleocene, maybe the earliest rodents themselves.

At around the end of the Paleocene, coinciding with the Paleocene-Eocene Thermal Maximum, there was a dramatic extinction among benthic (bottom-living) foraminifera in the oceans. These organisms had sailed through the K/T event. Yet at the end of the Paleocene around half of their species became extinct, just as many planktonic forms were busily diversifying. The culprit seems to be methane that had been trapped in the bottom sediments along the continental margins and was released by warming ocean temperatures or by some change in seawater chemistry. This event poisoned the benthic fauna and ultimately filled the atmosphere with a potent greenhouse gas. Once much of the excess methane had been absorbed by the oceans themselves the spike subsided, but not before conditions were set for very warm times in the Eocene Epoch that followed.

The Eocene (55.8 Million–33.9 Million Years Ago)

As the Eocene began, the whole Earth was subtropical to tropical, well-watered and clothed in dense forest formations. Close to the poles, broad-leafed evergreens flourished that could never have tolerated frost, and palms and cycads were abundant despite long periods of seasonal darkness.

The oceans, too, were warm, with mollusks and echinoderms and reef-building corals becoming amazingly diverse along with an associated bony fish fauna. During this time various lineages of mammals took to the seas, including the ancestors of whales and sea cows. One group of benthic foraminiferans, the nummulites, proliferated on the floor of the shallow Tethys Sea, north of Africa. Though single-celled, these grew to huge sizes, each one secreting a chambered shell the size of a nickel that served as a tiny greenhouse containing algae whose waste products nourished their hosts. Nummulites are a major component of the limestones of the Giza Plateau near Cairo and provide much of the volume of the stone from which the Great Pyramids were built.

Right around the beginning of the Eocene, plausibly due to the establishment of a land bridge across the proto–Bering Straits, there was massive east-west faunal interchange. Numerous groups arrived in North America, largely from Asia and including rodents and ancient perissodactyls (the odd-toed ungulates, the group that later came to contain today's horses, tapirs, and rhinos). There were also dichobunids, small deerlike animals with long, slender legs, that were the ancestors of today's artiodactyls (the even-toed ungulates: sheep, deer, cattle, hippos, and so on). Between them, these early perissodactyls and artiodactyls seem to have supplanted the primitive hoofed groups of the Paleocene.

The canopies of the North American Eocene forests supported an abundance of two major primate groups, the omomyiforms and the adapiforms. These are jointly celebrated as the earliest "primates of modern aspect," the adapiforms in particular functionally resembling the lemurs that live in Madagascar today. Such primates were also common in Europe, where tillodonts also appeared for the first time, and rodents and pantodonts arrived from Asia. Artiodactyls and perissodactyls made their European debut as well, to the detriment of the resident primitive ungulates. Similarly, the primitive European creodonts succumbed to the arrival of the true carnivores over the course of the Eocene. In Asia the rodents multiplied in the early Eocene to the exclusion of their anagalid predecessors, and perissodactyls (though not yet the artiodactyls) are found for the first time.

After the early Eocene, temperatures began to cool. Possible reasons range from a slowdown in rates of seafloor spreading, through increased weathering due to uplift of mountain ranges, to changes in oceanic circulation patterns. Probably each factor had its role to play, but the upshot was that tropically adapted marine floras and faunas were stressed worldwide, leading to significant middle-Eocene extinctions that included the nummulites.

On land the mammals responded to changing vegetation through the middle Eocene with a sharp reduction in diversity. In North America, where the record is once again best, gains included the bizarre rhino-sized uintatheres, knobbly skulled beasts descended from much smaller-bodied early Eocene immigrants from Asia, and the large perissodactyls known as titanotheres. Losses predominated, though, including a drastic decline in multituberculates as the rodents multiplied, and the disappearance of the *Plesiadapis*-like archaic primates that ceded to the rodents and more modern primate forms. Taeniodonts, tillodonts, pantodonts, and the archaic ungulate genera all virtually disappeared—as, apparently, did the land connections that had led to the cosmopolitan world of the early Eocene. All in all, some 80 percent of all the North

American land vertebrate genera that had been present 47 million years ago were gone 10 million years later. Those that were left were almost all harbingers of things to come.

After a final warmer blip toward the end of the Eocene, polar glaciation began with the isolation of Antarctica some 34 million years ago. During the brief warm interlude the first members of the rhinoceros family appeared in North America. The three-toed horse *Mesohippus* became common, and the artiodactyls began to diversify, among them the first peccaries and humpless camels, found alongside their distant relatives the oreodonts. Among the predatory forms were members of the weasel and dog families, and the sabertooth-like nimravids. Rodents included abundant rabbits and beavers, pocket gophers and squirrels, while the carnivorous creodonts made their last appearance at this time.

Asia and Europe experienced similar patterns, each showing more endemism toward the end of the Eocene due to the loss of intercontinental connections. The upshot was that in each area the fauna looked very different—and much more modern—at the end of the Eocene than it had at the beginning. Africa and South America are poorly known in this period, but it seems that change was much less radical in the latter, setting the fauna up to evolve more or less in its own way right up to the Great Interchange at the end of the Tertiary.

European paleontologists had long recognized a major faunal replacement at the end of the Eocene. Some have looked for a cataclysmic event to explain this; but climate change is more probably implicated, especially since the loss of species was preferentially of arboreal forms, notably the primates, and of leaf feeders (as inferred from their teeth) compared to mixed feeders that were capable of processing a wider array of tougher foodstuffs. Significantly, the replacements of the endemic species that were lost in Europe were largely Asian immigrants.

Recent detailed analysis of this event (which was always difficult to date precisely, because it was detected mostly in faunas preserved in isolated fissure deposits, rather than in regular geological sequences) suggests that the supposed end-Eocene replacement actually occurred early in the following Oligocene Epoch, a time of climatic cooling. In Europe dwindling temperatures were reflected in the transformation of subtropical forests into more temperate formations and in Antarctica in the formation of an ice cap. As the ice cap built up, sea levels around the world dropped, plausibly exposing land bridges between Asia and Europe. The Asian fauna invaded the European archipelago, and the rest was history.

THE OLIGOCENE (33.9 MILLION–23.1 MILLION YEARS AGO)

Climatic deterioration in the early Oligocene, some 33 to 34 million years ago, is documented in numerous oceanic cores. In the southern ocean some cores have confirmed that this cooling was associated with Antarctic glaciation, since they contain heavy sand and gravel particles that could only have been transported out to sea by icebergs that dropped them upon melting. Consequent changes in the marine fauna included the substantial replacement of archaic whales by members of modern groups that benefited from upwellings of cold, nutrient-laden water that nourished huge planktonic blooms. All in all, the world's oceans were beginning to look very much like today's, as the continents neared their modern positions and the marine faunas sorted themselves into distinct tropical, subtropical, temperate, and cold zones.

Onshore, cooler conditions were associated with drying. Angiosperms continued diversifying even as forest cover diminished, and more open grassy environments proliferated. Oligocene faunas worldwide reflect this shift, the major exception being Africa, where Oligocene sediments are known from only one—possibly atypical—area: the desert to the west of Egypt's Fayum region, a well-watered depression adjacent to the Nile south of Cairo.

During the late Eocene and early Oligocene this desert, now 150 miles inland, was perched close to the northern edge of the African continent. Sluggish rivers meandered through lush tropical forests that supported a rich fauna of primates and also a splendid diversity of afrotheres, members of an endemic group that include elephants and their relatives, sea cows, hyraxes, the bizarre embrithopods and ptolemaiids, and elephant shrews. Apart from a couple of very primitive medium-sized mastodons, which most likely already showed some development of a trunk, the most striking of all of these Fayum afrotheres was the rhino-sized *Arsinoitherium*, a distant browsing relative of elephants and hyraxes whose enormous head bore two large and two tiny horns made of solid bone. Apart from the primates and afrotheres, the Fayum deposits have yielded a host of other mammals that include bats, insectivores of many kinds, artiodactyls, one unique family of rodents, creodonts, and whales. They have also yielded quantities of reptiles: altogether, a fauna of great diversity and strongly endemic tendencies.

Oligocene faunas elsewhere reflect drier, more open surroundings. European mammals show generally Asian affinities, while in Asia itself many older groups disappeared or diminished to be replaced by rhinoceroses, new kinds of rodents, and a wide variety of artiodactyls that included early ruminants. Preying on these was a whole array of carnivores, including the nimravid sabertooths, true cats, and the civets, which had expanded greatly from their Eocene roots. And although the Asian Oligocene in general witnessed a reduction in the diversity of large mammals, it also produced the biggest land mammal ever recorded, the rhinoceros relative *Paraceratherium* that stood up to eighteen feet tall and may have weighed as much as twenty tons.

The best Oligocene mammal record of all comes from North America which seems, like Europe, to have maintained at least intermittent Asian connections. From warm, well-watered forest in the late Eocene, the environment progressed to cooler, drier woodland in the early Oligocene. One sign of this change is that the formerly ubiquitous North American primates all but disappeared across the Eocene-Oligocene boundary. Another is the replacement of the formerly abundant water-loving species such as crocodiles and turtles by such land-bound reptiles as tortoises.

Still, the remaining mammals proved quite adaptable, and there was no across-the-board Oligocene replacement in North America, possibly because most of the archaic fauna had already succumbed to earlier events, while the survivors were better prepared for the stresses to come. Resistant forms included the ubiquitous oreodonts, their relatives the early camels, various three-toed horses, and rhinos of various sizes and proclivities. All seem to have been browsers; there is no indication yet of specialized grazers. The latter typically have very high-crowned teeth, something not yet in evidence among the herbivores of the northern continents. In contrast, the small mammal fauna looked quite modern, including many varieties of rodents such as squirrels, beavers, and hamsters.

Conditions may have been drier yet in South America, where evolution was proceeding more or less in isolation. The resident Oligocene herbivores tended to have higher-crowned teeth than those elsewhere in the world, suggesting that they had for some time been dealing with the tough, resistant vegetation typical of more arid climates. On the other hand, primates had arrived in South America by the late Oligocene, and primates are not renowned for their ability to flourish outside forest settings. Still, they are not famous either for crossing substantial tracts of water, something they must have done to get across from Africa, their almost certain source. In the Oligocene, the South Atlantic was substantially narrower than at present, and it's possible that the primates got across it by hopping along a now-sunken chain of islands on natural rafts. And maybe they survived once they reached South America because parts of that continent were wetter, and thus more forested, than those that have so far been decently sampled for fossils. The little we currently know opens questions that will only be answered by better fossil records from both sides of the South Atlantic.

The cold snap at the beginning of the Oligocene seems to have had a general winterizing effect on northern biotas, which were consequently more resistant to further rounds of cooling. Nonetheless, in North America faunal diversity dwindled in the cool, dry conditions of the later Oligocene, although some genera such as the oreodont *Leptauchenia* roamed the brushy plains in huge numbers. Some pretty unusual forms were produced at this time, too, such as the energetically burrowing mylagaulid horned rodents.

In Europe, diversity also dropped off. Archaic artiodactyls suffered particularly as the continents progressed toward modern geography and Europe's fauna became better integrated with the Asian one. Toward the very end of the Oligocene there was some warming. This was followed by renewed cold, however, and the Antarctic ice cap expanded. Worldwide, climates were becoming more unstable.

The Miocene (23 Million–5.3 Million Years Ago)

During the 18 million years of the Miocene the map of the world took on its familiar form. The Atlantic widened to something close to its modern dimensions, India was busily slamming into the underbelly of Asia and uplifting the Himalayas, and Arabia was detaching itself from the northeastern corner of Africa along the Red Sea rift and moving toward Asia. Australia was approaching its modern position, and most of Europe became permanently attached to Asia. By the end of the Miocene, the only major tectonic repositioning still left to occur was the uplift of the Panamanian isthmus.

This was a period of major mountain building as the continents came together. Most dramatically seen on an east-west axis across southern Eurasia, from the Pyrenees through the Alps and Carpathians to the Himalayas, this tectonic activity was also happening north-south on the western side of the Americas. In Africa itself, the main tectonic event was a great doming up of the longquiescent continental surface along the line of the huge north-south Rift Valley. This had the effect of drying out the eastern side of the continent, formerly watered by humid winds from the west, as it fell into the rain shadow of the raised Rift.

Along with all of this tectonic activity came a warming trend after the ice shock at the end of the Oligocene. A general warming through the early Miocene climaxed in a "mid-Miocene climatic optimum" between about 18 and 15 million years ago. Warmer oceans saw major reef building, and mollusks diversified once again. With proliferation at the bottom of the food chain, predators flourished once more, and the Miocene oceans are perhaps most famous for *Carcharocles,* a gigantic relative of the great white shark. Almost entirely known from its enormous teeth, this huge beast is estimated to have grown to fifty feet or more in length and is thought to have preyed mostly on whales. By the end of the Miocene, all of the major varieties of whales we know today were on the scene, along with early seals, sea lions, and walruses belonging to an entirely independent group of secondarily aquatic mammals, most closely related to bears.

On land a parallel trend prevailed, with temperate and even subtropical humid floras establishing themselves even at quite high latitudes. Major faunal interchanges occurred, as connections were established between previously isolated landmasses. In the early Miocene there were several pulses of mammal emigration from Asia into North America: first mainly of ungulates, but later of a wide variety of herbivores and predators. Movement the other way was less busy, but still significant. One notable early emigrant was the three-toed horse *Anchitherium,* which had reached Europe as well as Asia by the end of the early Miocene, although many other North American émigrés failed to disperse that far south.

A bigger movement occurred about 18 million years ago, when Arabia bumped into Eurasia, forming the first bridge south into Africa which, as we've seen, had up to that time been populated mainly by endemic groups. Some African forms promptly made their mark in Eurasia, most notably the proboscideans, which had spread as far as North America by about 16 million years ago. Primates, too, made it out of Africa, although they remained restricted to the subtropical and tropical regions of southern Eurasia. Most of the traffic, though, went the other way, with a veritable flood of Eurasian forms into Africa. The ancestors of modern rhinoceroses, pigs, antelopes, giraffes, and many others entered Africa for the first time, along with their predators, the true cats and civets. This intrusion saw the rapid extinction of afrotheres such as the ptolemaiids and arsinoitheres.

With the Miocene we begin to get reasonably good fossil records in South America and Australia, two continents poorly documented earlier in the Cenozoic. Australian Miocene mammal, bird, and reptile faunas are currently known only from humid, forested environments, whereas known South American faunas encompass more open environments as well. South America was home to a wide variety of endemic groups, plus the primates that had arrived in the Oligocene and the caviomorph (porcupine-related) rodents whose ancestors had apparently immigrated in the late Eocene. This highly endemic fauna became extremely diverse during its Miocene isolation. The same was true in Australia, where the totally endemic mammal fauna consisted of an enormous radiation of marsupials that in certain respects mimicked what placentals were doing in other parts of the world.

At about 14 million to 13 million years ago, things began to change. A much colder isotopic signal occurs in seabed cores from the southern ocean. These also yield a lot of ice-rafted debris that indicates significant expansion of the Antarctic ice sheet. Things changed less in the tropical oceans, suggesting that today's steep climatic gradient between the tropics and poles was establishing itself. The significant drop in average world temperatures indicated was possibly due to high deposition of organic carbonates that depleted the atmosphere of the greenhouse gas carbon dioxide.

The effects of cooling were far reaching, on marine and terrestrial biotas alike. Open habitats began to displace forests in Africa, Eurasia, and North America. Woodlands and scrublands at first, these areas were converted to true grasslands late in the Miocene, around 7 million years ago. Forest dwellers dwindle in the record, and browsers were largely supplanted by grazers. Among other arboreal forms, the higher primates that had flourished in the forests and woodlands of southern Europe following their earlier exit from Africa, were gone by about 9 million years ago. In Africa itself, shrinking forest cover at the very end of the Miocene may have forced our own hominid precursors to the ground, at least part-time.

The final shock of the Miocene occurred right at its end when a remarkable geological event took place, apparently in association with the formation of the West Antarctic ice sheet. In the middle Miocene, Africa had nudged up against Eurasia, almost closing off the Mediterranean Basin, a depression of oceanic depth with relatively few rivers flowing into it. Evaporation from the almost landlocked Mediterranean Sea was extreme, necessitating a constant inflow of water from the Atlantic via the Straits of Gibraltar. But when Africa moved up against Europe at Gibraltar, shortly after 6 million years ago, this water supply was cut off. Within a very few years the Mediterranean dried up virtually entirely, creating a ten-thousand-feet-deep and two-thousand-mile-long Death Valley that must have furnished some of the most inhospitable environments since the Hadean.

Around the fringes of the Mediterranean Desert some forest lingered, inhabited by tapirs, antelopes, pigs, proboscideans, and other forms with histories on both sides of the basin. Despite tough conditions in the region, these fringe forests appear to have allowed a diverse assemblage of mammals to travel between Europe and Africa in this period, known to geologists as the Messinian Stage.

The effects of the Messinian event were not simply local. Evaporation of all that seawater caused the formation of huge salt deposits on the floor of the Mediterranean basin, a process that repeated itself on several occasions as the Atlantic broke through and refilled the basin over a giant waterfall, only to be blocked off again by the continuing northward movement of Africa. As this evaporite formation locked up an enormous amount of salt on the seafloor, the world's oceans became less saline and froze at a higher temperature. In turn, this accelerated formation of the Antarctic ice shelves which more readily froze, quickening global cooling and lowering sea levels and probably exposing a Bering Straits land bridge over which North American camels and dogs entered Eurasia. Elsewhere, the replacement of forests by savannas and steppes continued, resulting in another wave of extinctions, especially in North America. Whether cause or effect, the Messinian event reverberated around the world. Its end marked the end of the Miocene, as the Straits of Gibraltar reopened definitively.

The Pliocene and Pleistocene (5.3 Million–0.001 Million Years Ago)

In terms of both geological events and human evolution it makes sense to consider the Pliocene and Pleistocene Epochs together; even the boundary between them is disputed.

A brief post-Messinian warming was followed, at about 2.6 million years ago, by a global descent into the cycle of the Ice Ages. In Africa a good deal of forest persisted through the early Pliocene, with scrublands and tree savannas where the Sahara is now, extensive gallery forests around lakes and rivers farther south, dense forests in the western equatorial regions, and vast expanses of woodland and warm-temperate forest in the south. In this mosaic of habitats lived a varied fauna with many herbivore genera that are familiar today, alongside an array of now-extinct proboscideans such as gomphotheres and deinotheres, a fearsome array of carnivores such as the sabertooths *Dinofelis* and *Machairodus*, and early members of our own hominid family.

The formation of the Isthmus of Panama, starting about 3 million years ago, changed the world. There are some indications of earlier glacier formation in the Arctic, but the diversion of the great oceanic conveyor abruptly changed the pattern of heat distribution across the globe. Permanent ice-cap formation started in the Arctic, and sea levels began to fall worldwide, marking the start of the Ice Ages cycle of glacial and interglacial episodes.

During cold glacial periods the Arctic ice cap expanded southward, to cover a vast swath of northern America and Eurasia. In the west it reached New York City, and in the east it approached London. At higher elevations subsidiary ice caps formed, most famously on the Alps and the Pyrenees. Periglacial environments varied enormously depending on local topography and proximity to the ocean, but in general the ice masses yielded more or less directly to tundra, where low grasses, sedges, and lichens grew on the thin layer of soil above the permafrost. Farther south, and in more sheltered spots, the vegetation grew higher, with pine forests at first, then mixed pine and deciduous formations. To furnish all that glacial ice sea levels dropped—by over three hundred feet at the last glacial maximum some twenty thousand years ago—and vast tracts of land were exposed at the continental edges.

Mass faunal migrations occurred as temperatures and environments shuttled backward and forward between glacial and interglacial states. Most stable was North America, where most of the archaic forms such as three-toed horses, giant camels, and primitive proboscideans, had already disappeared early in the epoch. Still, mammoths emigrated from Eurasia across the dry Bering Strait to dominate a fauna quite similar to the modern one that included a variety of horses. Among the artiodactyls were peccaries, deer, and antelope; in the south were giant ground sloths and armadillos, reminders of South American contact. Predators included bears and saber-toothed cats, along with the larger cats familiar today—and even an American cheetah. Numerous dogs included the famous dire wolf that replaced the American hyena. The American bison, emblematic of the Great Plains, was a late emigrant from Eurasia, only appearing around three hundred thousand years ago.

A major extinction of the larger-bodied North American forms at the end of the Pleistocene, some ten thousand years ago, has been controversially attributed to "overkill" by the first human hunters to arrive in the New World—and it is certainly true that fully modern humans have had a major impact on local ecologies virtually everywhere they have gone.

The Bering land bridge assured that the Eurasian Ice Age fauna was generally similar to the American one. Deer of many kinds abounded, among them the "Irish elk" *Megaloceros*—actually a giant fallow deer with antlers sometimes measuring over twelve feet across—and the ubiquitous reindeer, staple of early hominid hunters. Woolly mammoth and woolly rhinoceroses were the largest animals on the landscape, and a fearsome array of predators included sabertooths, lions, hyenas, bears, and a host of smaller forms such as foxes and minks.

Early in the Pleistocene, the European fauna was generally typical of cold tundra and steppic conditions. But with the onset of the one-hundred-thousand-year glacial-interglacial cycle about a million years ago, an alternation set in. In relatively mild Atlantic Europe, the warmer interglacials saw the replacement of steppes, on which reindeer and woolly mammoth roamed, by pine forests and mixed forests of beech, oak, and hornbeams in which deer flitted and wild boar rooted. Ironically, these were more difficult conditions for early human hunters than those typical of colder times. Hominids themselves had arrived in Europe by about 1.4 million years ago, and endemic evolution there culminated in *Homo neanderthalensis*, eventually a victim of the extinction of European large-bodied mammals that took place after *Homo sapiens* arrived there about forty thousand years ago.

Almost all of today's African mammal species were already in place during the Pleistocene, following a peak of diversification during the early Pliocene. African climatic vagaries were more closely related to humidity than to temperature, but even during the driest periods, small refugia of tropical forest lingered in parts of western Africa, supporting the fauna still found in this province today. Farther east, wooded grasslands began opening up into true savannas, while extensive woodland formations occurred to the south. In addition to the mammals you see on safari today, the savannas and woodlands of Africa supported a wider variety of grazers, browsers, predators, and hominids than currently.

Initially proliferating about 5 million years ago, fossil antelopes have been important in reconstructing the effects of climate change in Plio-Pleistocene Africa. Analysis of antelope fossils from South African sites suggested that a major faunal "turnover pulse" occurred around 2.5 million years ago (i.e., at about the time of onset of the northern glacial cycle), in which browsing forms typical of moist woodlands were replaced by grazing types typical of dry savanna environments. Some think that a significant correlation exists between the corresponding environmental events and the appearance, at around the same time, of the first stone tools and the earliest fossils classified in our own genus *Homo*. However, while East African fossils do reveal a significant replacement of mammal species between about 3.0 million and 1.8 million years ago, there is no specific signal around the 2.5-million-year mark. The jury is still out.

The Holocene (Ten Thousand Years Ago to the Present)

The last eleven thousand years of interglacial conditions are normally awarded their own epoch (the Holocene, or recent), even though there is no indication that (other things being equal) the world has emerged from the Pleistocene climatic cycle. Faunas today are pretty much as they were when the ice caps had shrunk to their preindustrial dimensions, with the highly important exception of an ongoing extinction event (sometimes known as the Sixth Extinction) that is due to the effect of one species, *Homo sapiens*, on environments worldwide.

As the last glacial cycle was ending, only one kind of hominid was left standing: *Homo sapiens*. Before this point, all human beings were hunters and gatherers, living by the highly sophisticated exploitation of Nature's bounty. Constantly on the move, their ecological role was not hugely different from that of any other generalist species. But once a settled, agricultural lifestyle had been adopted—a change that took place independently in several centers worldwide in the period between about eleven and seven thousand years ago—the rules changed entirely. A species that had formerly lived in tiny numbers, and had been integrated into the environments it occupied, found itself for the first time in opposition to Nature. All else follows from there. The story of the Holocene is virtually exclusively the story of the impact of one species, *Homo sapiens,* on our planet—an impact with whose enormously ramifying consequences we have yet to come to terms.

Before we pursue that enigmatic species, let's pause for a more in-depth look at two of the most interesting mammal groups of our world: the whales and the primates.

CHAPTER 8

Of Whales and Primates

THE MAMMALIAN menu is a rich one, especially in the Cenozoic. It includes armadillos, otters, kangaroos, shrews, civets, water rats, bats, elephants, rabbits, colugos, and rhinos, and each has its own fascinating story. Since it's impossible to cover this vast waterfront here, let's look more closely at the evolution of one "extreme" mammal order, the whales, and our own group, the primates.

WHALES

The ancestral mammal was a land dweller. Yet many mammal groups, including most notably the otters, the seals, and the dugongs, have returned to a mainly or entirely watery existence. But none of these secondarily aquatic forms has made this transition with quite the degree of commitment shown by the members of the order Cetacea: the baleen whales, plus the toothed whales and the dolphins and porpoises. Even the dugongs, which spend their entire lives grazing in warm, shallow waters near the shoreline, retain forelimbs that are still recognizably arms, albeit greatly modified; modern cetaceans, on the other hand, are at home in the deep ocean, with entirely flipper-like forelimbs and a whole host of other adaptations to a specialized aquatic existence.

Whale body shape is fusiform (spindle-shaped) and hydrodynamic; the tail is modified into a fluked and powerfully propulsive structure (which moves up and down, mirroring the axis of bending of the terrestrial mammal vertebral column and contrasting with that of fish, which bends sideways); the hind limbs are so reduced as not to be apparent externally (something seen also in the dugongs); and there are extensive modifications to the respiratory, auditory, visual, and other body systems. The shift from a terrestrial to a fully aquatic lifestyle, with all of the physical and physiological accommodations involved, is as radical an ecological transition as any organism can make; fortunately, we have a truly remarkable fossil record showing how whales achieved it.

When dealing with a group as highly specialized as the whales, it is often difficult to find anatomical characteristics that will help identify that group's closest relatives. Because of this, for many years the relationships of whales to other mammals were rather unclear. The favorite candidate for a cetacean stem group was the mesonychids, superficially wolf-like primitive hoofed predators that flourished on the northern continents during the Paleocene and the Eocene. These included such extraordinary forms as the Mongolian Eocene *Andrewsarchus*, possibly the largest mammalian terrestrial predator that ever lived. They were thought to be artiodactyl relatives, but they also had rather distinctive triangular teeth that vaguely resembled those of toothed cetaceans, which they also resembled in some points of ear structure.

Mesonychyids were thus considered close to whale ancestry until some biologists began thinking that, on other structural grounds, the closest relatives of the cetaceans might be the artiodactyls themselves. The initial idea here was that the whales were the closest relatives of the artiodactyls as a group. Even this seemed a bit odd to some, implying as it did that cows were more closely related to whales than to the more structurally similar horses. But worse was to come.

Early molecular systematic findings supported a general relationship between the whales and artiodactyls, while casting doubt on the comfy cohesiveness of the artiodactyls as a group. The real stunner came later, though, when on a whole variety of genetic markers the cetaceans turned out to fall well *within* the Artiodactyla. Not only that, but they consistently grouped alongside the semiaquatic hippopotamuses.

This finding contradicted conventional wisdom, but the molecules seemed to insist that whales and hippos formed their own clade, which rapidly became known as the "Whippos." And although paleontologists weren't too happy with this because the earliest fossil evidence of the hippo family dates from the middle Miocene while cetaceans were already around some 40 million years earlier, they soon also had fossil evidence to confirm the whale/artiodactyl link.

The key piece of morphology that unites all artiodactyls is the shape of the ankle joint. In living artiodactyls this has a double-pulley shape that is found nowhere else, not even in mesonychids. Quite understandably, whales had been traditionally excluded from comparisons of this feature because they have no feet, and hence no ankle joints. But in 2001 two independent groups of paleontologists discovered Eocene whale fossils that still possessed rear limbs and feet—and that showed the characteristic artiodactyl ankle structure. This was evidently a feature that had been primitively present in the ancestor of whales and artiodactyls, which obviously could not have been a mesonychid.

As a result, while the mesonychids are still considered to be somehow related to the whale-artiodactyl group (Cetartiodactyla), paleontologists now believe that whales are derived from a very early artiodactyl. Where this leaves the hippos is problematic, but one fossil study suggested (uncontroversially) that the origin of hippos lies deep within a group of artiodactyls known as the anthracotheres, and (more controversially) that the hippo+anthracothere group is more closely related to early whales than to pigs or to ruminants.

Since fossil anthracotheres go back only to the middle Eocene (by which time whales were recognizably whales), there is an obvious problem of timing. So while the unity of the overall Cetartiodactyla group seems to be pretty well established at this point, phylogenetic structure within it will have to await close scrutiny of the early record to see if any of the primitive artiodactyls actually possesses previously unrecognized hippo characteristics.

Going from a terrestrial to an aquatic lifestyle requires radical reorganization of the body plan, and the whale fossil record is now good enough to show convincingly how this reorganization was achieved. The early members of the whale lineage are loosely drawn together into a group known as the archaeocetes, the earliest of which belong to the genus *Pakicetus* and close relatives. Some 52 million years old (early Eocene), *Pakicetus* was a creature of about the same general size and shape as a wolf. Although its fossils are found in river sediments along an ancient shoreline, recent finds indicate that *Pakicetus* was terrestrial, with the skeleton of a runner—including that ankle joint. Whalelike features are confined to its long and flattish skull, equipped with a dentition reminiscent of both mesonychids and later whales. Along with the shape of the ear region, its teeth are the primary reason for regarding *Pakicetus* as a cetacean, for there is little about it that foreshadows an aquatic lifestyle. So while the lineage culminating in today's whales was already in existence by the early Eocene, the way of life certainly wasn't.

Next in line were the ambulocetids and their relatives, the remingtonocetids, whose fossils come from roughly 49-million- to 43-million-year-old middle Eocene deposits representing nearshore marine and swampy environments. Best known of the ambulocetids is *Ambulocetus natans*, which translates as "walking and swimming whale." Finally we are looking at something that anticipated whales in its lifeways as well as in anatomical details. About the size of a sea lion, *Ambulocetus* was a bulky creature with stocky limbs, large feet, and a long, strong tail. With its low-slung body and elongated jaws containing triangular pointed teeth, *Ambulocetus* has been described as a "mammalian crocodile," although its spine structure suggests that, while well able to walk on land, it also swam by undulating its spine up and down, propelled by its large hind feet. Its long and tapering tail evidently lacked the flukes that make today's cetaceans such powerful swimmers. But it is a marvelous intermediate between the terrestrial *Pakicetus,* which at most waded in the rivers along which it lived, and the more evolved whales to come.

At about 47 million years old, the early protocetid whale *Rodhocetus* has yet shorter arms and legs, a smaller pelvis, a more muscular tail, and an emphasis on the webbed feet—which still show that telltale ankle joint—as paddling devices. The cetaceans of the middle Eocene were still evidently hedging their bets, retaining the ability to move around on the land even as they were becoming adroit swimmers. But this equivocation didn't last long, and slightly younger forms such as *Georgiacetus,* another protocetid, have hind limbs that did not attach solidly to the spine via the pelvis, and so could not have been used to support the body on land. They could, on the other hand, have been used as effective propulsors in the water, moved by undulation of the spine.

The late Eocene cetacean fauna (around 41 million to 35 million years ago) was dominated by the basilosaurids and dorudontids. The basilosaurids, in particular, were enormous (up to sixty feet long), with long, sinuous bodies. They were full-time aquatic creatures, and although they were long known to have possessed flipper-like forelimbs, it came as a surprise when fossils were discovered proving that *Basilosaurus* had also possessed tiny but complete hind limbs. Unlike the vestigial hind limbs of modern whales, these had projected beyond the body wall. Useless for locomotion, they simply serve as reminders of *Basilosaurus*' terrestrial ancestry. A fluke was probably present on the tail of *Basilosaurus,* but these creatures probably swam rather as sea snakes do, undulating their bodies. Stomach contents preserved inside one skeleton of the long-jawed and fearsomely toothed *Basilosaurus* show that the individual had recently eaten fish, including sharks. If any further proof were needed that here was a full-time oceanic predator, *Basilosaurus* shows a migration rearward of the single nostril: the

Figure 8.1. Shadow drawing by Bonnie Miljour of the Eocene whale *Basilosaurus*. Courtesy of P. D. Gingerich.

first stage toward the characteristic blowhole of modern whales. So did the smaller dorudontids, which also still possessed tiny hind limbs but were more dolphin-like in their proportions, and probably swam using their tail flukes.

Today's cetaceans fall into two main groups: the Odontoceti (toothed whales, plus dolphins and porpoises) and the Mysticeti (baleen whales). Both are probably derived from a basilosaurid ancestor, going separate ways shortly before the Eocene-Oligocene boundary. Subsequently, both groups independently showed backward and upward migration of the nostril(s), ultimately to form the modern blowhole. In both cases this involved telescoping the cranium: elongating the basal part of the skull and foreshortening its upper part, something that seems to have taken place independently in several lineages. But while following parallel telescoping trends, odontocetes and mysticetes diverged in their use of sound. Odontocetes specialized in emitting high-pitched sounds for echolocation related to predation and navigation, while the mysticetes co-opted low-frequency sounds for interindividual communication, sometimes over vast distances. The first morphological evidence for echolocation comes from an early odontocete, *Squalodon*. Its family Squalodontidae flourished between around 33 million and 14 million years ago, but apparently went extinct as it lost out in competition with the toothed whale groups that ultimately gave rise to today's multifarious odontocetes.

Unlike the predatory odontocetes, all modern mysticetes are filter feeders, employing plates of the coarse hairlike substance known as baleen to strain shoaling microprey (the tiny shrimplike krill are a favorite) out of the water. But the acquisition of baleen may not have been the basal adaptation of the group. The earliest mysticetes, such as the late Eocene *Llanocetus*, retained largish adult teeth (albeit possibly with some incipient baleen present), and were probably predatory on larger vertebrates. Soon the teeth were reduced, as in the late Oligocene *Aetiocetus*, which apparently also possessed baleen; and in the slightly later *Eomysticetus* they were gone entirely, replaced by a full set of baleen plates. The basic formula that led to the later success of the mysticetes had been fully established. From the Miocene onward, mysticete history consisted essentially of the ongoing differentiation of the baleen whale groups that now roam the seas.

The Primates

As primates ourselves we find primate evolution intrinsically fascinating, and the primate fossil record has received more intensive scrutiny than any other. But despite all this attention, a satisfactory definition of our own mammalian order still eludes. Today's primates consist of the lemurs of Madagascar and the bushbabies and lorises of Africa and Asia (together generally known as the "lower primates"); the tiny and enigmatic nocturnal tarsier of island Southeast Asia; and the New World and Old World monkeys, the greater and lesser apes, and human beings (together, the "higher primates").

How you divide up the order Primates depends on how you see the position of the tarsier: there are arguments to be made for classifying it with both the lower primates and the higher ones. In either case, the lower and the higher primates form compact monophyletic groups. And nobody doubts that the living order Primates as a whole is monophyletic, descended from a single unique common ancestor. Still, there has been a lot of evolutionary water under the bridge since that common ancestor existed, which makes it hard to identify a common diagnostic group of features that all primates share.

As a result, primatologists have tended to point instead to a series of "evolutionary trends" that appear to characterize the order as a whole, the higher primates showing them in more developed form than the lower primates do. They include increasing dominance of the sense of vision over that of smell; improved grasping and manipulative capacities (initiated by divergent first digits and the replacement of claws with nails); and enlargement of the higher centers of the brain.

Among the mammals the primates are loosely grouped, with the tree shrews, the colugos, and perhaps the bats, into a larger unit known as Archonta. Exact relationships among these forms are debated, as is whether the fossils traditionally identified as the earliest primates should actually be considered as primates or simply as another group of archontans. These ancient putative primates, the plesiadapiforms, are nearly all Paleocene (there is one rather dubious tooth from the very latest Cretaceous, and a few stragglers into the Eocene), and none of them can be linked with any certainty with the euprimates, or primates of modern aspect, that replaced them as the Paleocene ended.

As exemplified by the eponymous *Plesiadapis*, the plesiadapiforms are "dental primates," with rather blunt-cusped chewing teeth and some resemblances to later primates in their locomotor apparatus. They were arboreal, and possibly specialized like many later primates in feeding on terminal branches. But most retained claws on all digits, had small brains in relation to their body size, and possessed large and very specialized front teeth. Their evident success in the Paleocene forests was presumably due to exploitation of the abundant fruit produced by the rapidly diversifying angiosperm plants, nocturnal habits also helping reduce the competition they faced.

The plesiadapiforms rapidly disappeared as the first primates of modern aspect proliferated in both North America and Eurasia during the Eocene. The new primates came mainly in two forms: the omomyiforms and the adapiforms. A cynic might say that the

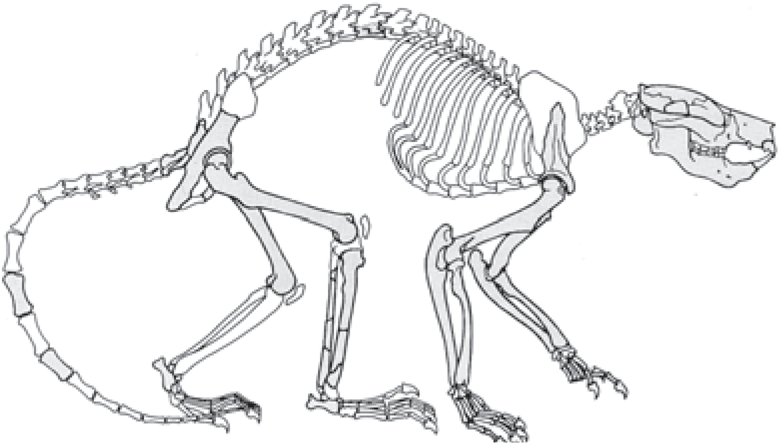


Figure 8.2. The skeleton of the Paleocene primate *Plesiadapis tricuspidens*, from France.

omomyiforms were the small ones (many were mouse-sized) and the adapiforms the larger ones (up to about the size of a house cat); but many reckon the omomyiforms have some affinity with the tarsiers, while the adapiforms are more lemur-like (though it is hard to demonstrate direct connections between any known adapiform and any of today's very diverse lemurs of Madagascar).

Members of both groups evince the basic primate trends: grasping hands and feet with divergent first digits; flat nails backing sensitive pads instead of claws; reduced snouts, suggesting a deemphasis of the sense of smell (which nonetheless remains important); and forward-facing (stereoptical) eye sockets fully ringed by bone, implying greater optic stability and enhanced vision. A newly discovered omomyiform skull from China has small orbits, suggesting the diurnal activity habit that was also probably typical of many adapiforms. Brains also seem to have been a bit bigger relative to body size than those of plesiadapiforms.

Modern lemurs and lorises have very specialized and slender front lower teeth that point forward to produce a grooming comb.

In the Egyptian Fayum, 40-million-year-old fossils have been found of two primates that also possessed tooth combs. One of these is said to resemble a bushbaby and the other a loris, suggesting that the roots of these modern lower primate groups go back at least to the late Eocene. Similarly, some teeth from the early Oligocene of Pakistan (around 30 million years old) are said to resemble those of dwarf lemurs from Madagascar. This suggests an ancient origin for this group, too—as is also implied by the molecular record.

By the close of the Eocene, lower primates had virtually disappeared from North America and Europe, probably due to climate change that led to the replacement of dense forest by more open temperate habitats. In tropical Africa and Asia, in contrast, the lower primates hung on, albeit marginalized to nocturnal niches by competition from the emerging higher primates. Only in Madagascar, a vast island reached by higher primates (human beings) only two thousand years ago, did lower primates continue to flourish and diversify in diurnal as well as nocturnal niches.

The higher primates—monkeys, apes, and humans, collectively known as Anthropoidea—place vastly greater emphasis on vision relative to smell. Compared to the modern and ancient lower primates, the anthropoids have enhanced manipulative abilities, larger brains, and more complex social lives; almost all are exclusively diurnal. Their exact ancestry remains unknown, but they form a cohesively monophyletic group that had its roots in an Old World primate stock, most plausibly African, at some time in the late Eocene.

Some 26 million years old, the late Oligocene *Branisella* is the earliest South American monkey. Known only from jaws and teeth, it quite strongly resembles the late Eocene Fayum early anthropoid *Proteopithecus* and is clearly an immigrant into a continent that had effectively been isolated since the breakup of Gondwana. The best guess is that its ancestor had managed to cross the then-much-narrower Atlantic from West Africa by rafting on matted vegetation, either directly or via a series of now-sunken stepping-stone islands along the mid-Atlantic ridge. *Branisella* seems to have lived in a relatively open environment, but South American primates subsequently diversified into the extraordinary variety of forest dwellers familiar today. Although mammals are generally very poor long-distance overwater dispersers, South America's caviomorph rodents and possibly its emballonurid bats must have made a similar voyage. In all of these cases, molecular estimates place the date of this event somewhere in the range of 31 million to 25 million years ago.

Apart from some 45-million-year-old isolated teeth from Algeria and some controversial fossils from eastern Asia of about the same age, the earliest Old World higher primates come from Fayum deposits in Egypt dating from the late Eocene into the early Oligocene (about 37 million to 30 million years ago). Today's Fayum desert was then a well-watered, low-lying region supporting lush tropical forests that harbored three principal higher primate groups. The oligopithecids and parapithecids were quite small-bodied and vaguely monkeylike forms that later became extinct. In contrast, the cat-sized propliopithecids may lie fairly close to the ancestry of the later Old World higher primates as a whole (some even think specifically to the hominoid group). They had rather apelike teeth, smallish brains, and limb structures that recall those of certain highly agile South American monkeys.

The oldest Old World monkey fossils are also known from Africa, in deposits up to about 20 million years old. The best-known genus is *Victoriapithecus,* which seems to have predated the split between today's two large Old World monkey groups, the leaf-eating colobines and the more generalist cercopithecines. The oldest known definitely colobine fossil is no more than about 9 million years old. Perhaps oddly, it is only after about 7 million years ago that monkey fossils really become abundant in Africa, plausibly because monkeys accommodated better to climatic drying than the formerly diverse hominoids (Hominoidea is the superfamily embracing humans and apes).

Following the contact of Afro-Arabia with Eurasia some 18 million years ago, the African primate fauna was able to spread into Eurasia. Between about 11 million and 8 million years ago, the single cercopithecine genus *Mesopithecus* colonized a huge swath of Europe and Asia, as far east as Afghanistan. It was possibly the progenitor of the even more successful species *Dolichopithecus,* whose range extended from Europe as far afield as Siberia and Japan between about 4.5 million and 2.5 million years ago—until the late Pliocene glacial shock.

The hominoids themselves emerged in Africa in the earliest Miocene, about 23 million years ago or perhaps a little earlier. The best-known early hominoid is *Proconsul,* various species of which are known in East Africa between about 23 million and 14 million years ago. The size of a small chimpanzee, the species *Proconsul heseloni* is known from a virtually entire skeleton, plus bones of numerous other individuals. It had a very apelike dentition and (like modern apes) lacked a tail. But in other respects it was remarkably generalized, with the skeleton of a runner rather than of a versatile climber—despite having occupied a densely forested habitat.

Modern apes have very mobile shoulders and specializations of the hands that allow them to curl up their long fingers while walking. None of this is seen in *Proconsul,* whose postcranial adaptations might better be described as monkeylike. But *Proconsul* is only one genus among many. By now literally dozens of extinct hominoid genera of Miocene and later ages have been described. Up through the middle Miocene all are African; but following Africa's contact with Eurasia, hominoid fossils are found widely in Europe and in southern regions of Asia as well.

They ranged enormously in size, from the comparatively tiny ten-pound East African *Micropithecus,* to the huge Chinese *Gigantopithecus*. This monster, known only from teeth and jaws, is estimated to have weighed six hundred pounds or more. And in contrast to today's few species of apes, which represent a mere shadow of earlier hominoid diversity, Miocene hominoids were adapted to a great variety of ecological niches, ranging from deep tropical forests to semitemperate woodlands. Particularly interesting is the 12-million- to 9-million-year-old *Sivapithecus,* from northern India and Pakistan. This form has an extraordinarily orangutan-like skull and dentition, in combination with a generalized skeleton that entirely lacks the suspensory specializations of the orangutan.

In Europe, too, the Miocene hominoid fauna is diverse. Remarkably, we find there the most active recent contenders for an evolutionary position close to our own family Hominidae (which undoubtedly had its roots in Africa, not in Europe), or at least to the larger group that contains both us and the great apes. One of these contenders is the Greek *Ouranopithecus*. Dated to about 9 million years ago, this hominoid lived in a fairly open, shrubby habitat—nothing like anywhere you'd find a modern ape. The interpretation of *Ouranopithecus* as a close hominid relative is, however, controversial, and no postcranial elements are known.

More complete is a newly described hominoid from Spain named *Pierolapithecus.* A 12-million- to 13-million-year-old partial skeleton is said to show features consistent with some postural uprightness. Its describers suggest that *Pierolapithecus* was close to the form that ultimately gave rise to the African and Asian great apes on the one hand, and to us on the other. *Pierolapithecus* was a moderately large (about seventy-pound) fruit and leaf eater with a shortish face (from back to front) and a broad, shallow rib cage. Its adaptations to upright posture were evidently acquired in an arboreal context, since it lived in tropical forest and retained many features indicating an arboreal lifestyle.

There has been a lot of debate about the implications for hominoid evolution of *Pierolapithecus*' unusual morphology. Some would place this genus closer to African apes than humans, rather than equidistant from both, while others question any special affinities at all to the human/ape group. Still, whatever consensus eventually emerges, this intriguing creature emphasizes that Miocene ape evolution was by no means simple, and that a lot of evolutionary experimentation was going on among hominoids of the period. Certainly, although there are virtually no fossils known that fall in any modern ape lineage—unless they have been mistakenly identified as hominids—it looks increasingly as if the locomotor specializations of today's apes are relatively recent in origin—as indeed are ours.

The late Miocene was a time of unsettled climates and environments, and it offered precisely those conditions in which one would most expect to find evolutionary innovation. It was from the resulting ferment that the hominid lineage eventually emerged, even as the energetically diversifying monkeys were squeezing the hominoid fauna in what remained of its traditional forest habitat, and overall hominoid diversity was dropping like a stone.

CHAPTER 9

Walkers and Toolmakers

Look closely at a chimpanzee—preferably in its environment, not yours. Its psychological resemblance to you is almost frightening. When you look into its eyes, you *know* something complex is going on behind them. Almost all of you is there. But not everything. It's frustrating not to know exactly what the missing ingredient is, but as you stare it seems so small, as if the chimpanzee were but a single short cognitive hop away from you.

Chimpanzees have incredibly complex social lives. They love, they hate, they form alliances, they go to war. They hunt bushbabies with spears, and colobus monkeys in organized gangs. They use leaf sponges to soak up water, and they crack open nuts using stone anvils and hammers. They deliberately murder each other. All this and much more makes them eerily like us in so many cognitive ways—although physically, it's maybe another matter. Chimpanzees are quadrupeds, with hands and wrists that are specialized for weight bearing, albeit in a clever way that allows them to retain slender digits with good manipulative abilities. And of course they are quite capable of walking around upright, although common chimpanzees don't do this quite so much as their close cousins the bonobos—which, significantly, also copulate facing each other, as part of an impressive repertoire of such behaviors. Clever and adaptable as they are, though, chimpanzees and bonobos are essentially forest dwellers, with all the necessary physical equipment for life in the trees. Modern humans, on the other hand, with their tall, slender, bipedal bodies, are built for life out in the open, away from the shelter of the forest.

Over the past 7 million years or so, an eye-blink in evolutionary time, the apes and we have taken very different evolutionary paths. And your eyes tell you instantly that it has taken a fair bit of change for each of us to get to our present physical state from that of our latest Miocene common ancestor. Still, there is that nagging matter of cognition. So near—but also so far. And the archaeological record, the archive of hominid behavioral evolution, tells us that there have in fact been many intermediate steps on the cognitive level, as well as on the physical one, since our common ancestor with the apes. In this chapter we follow these developments, with the aim of trying to understand what it is, ultimately, that makes us *Homo sapiens* unique—and when we got that way.

In the Beginning

Along with their close fossil relatives, human beings belong to the zoological family Hominidae (some prefer the subfamily Homininae; it's of no practical consequence). Defining the group isn't easy. Clearly, the further back we go in evolutionary time, the less like us our ancestors will have been; and the search for the earliest hominid is complicated by the fact that nobody is sure exactly what it *ought* to look like. What's more, right at the beginning there will have been little to distinguish early hominids from early apes; and since fame and fortune are more likely to await the discoverer of an early hominid than the finder of an early ape, it's perhaps hardly surprising that current claimants for the title of "earliest hominid" are a rather motley assortment.

What all of these pretenders have in common is principally the claim that they were upright bipeds. Walking upright on the ground has become the de facto qualification for inclusion in Hominidae. But it might be wise to remember that more than one hominoid lineage may well have adopted upright locomotion as a solution to moving around in the more open environments that were expanding in late Miocene Africa as the climate dried and became more seasonal.

With these caveats in mind, we can still look at the putative early hominids from the perspective of one original bipedal stock. If we do this, the first thing that impresses is their variety—a variety that suggests that the history of Hominidae has been from the beginning very similar to that of all other successful mammalian families. That is to say, multiple new hominid species have emerged to triumph or perish in the ecological arena, in a process of continual evolutionary experimentation with the obviously multiple ways there are to be a hominid.

This variety contrasts very distinctly with the traditional paleoanthropological expectation that human evolution has been a single-minded, unilinear slog from primitiveness to perfection. The notion of one unique, gradually perfecting human lineage fits well with the undeniable fact that there is only one hominid species in the world today: a single entity that we are tempted to project back into the past, to produce a chain of ancestors becoming steadily less like us as they recede into the mists of time. But analysis of the hominid fossil record, which has vastly expanded over the past few decades, shows very clearly that this was not the pattern at all. At virtually all points in human evolutionary history, several hominid species have coexisted (and at least intermittently competed). That *Homo sapiens* is the lone hominid in the world today is a highly atypical situation.

The earliest claimant for hominid status is *Sahelanthropus tchadensis*, from central-west Africa. Faunally dated to the late Miocene, between 7 million and 6 million years ago, it is known mainly from a distorted and broken-toothed cranium and thus offers only indirect evidence of bipedality. In a quadruped, whose skull juts forward from a horizontal spine, the large hole (foramen magnum) through which the spinal cord exits the skull points back. In a bipedal modern human it is shifted under the skull, pointing down to aid in balancing the skull atop a vertical vertebral column. A forward shift and downward orientation in the foramen magnum of *Sahelanthropus* suggests bipedality.

Beyond this, *Sahelanthropus* is quite puzzling. On the one hand, its tiny cranial vault contained a brain no bigger than that of a small chimpanzee. On the other its face, instead of being long from back to front as seen in apes and as might have been expected in a primitive hominid, is actually rather short—to a degree, indeed, that is not otherwise matched among hominids before about 2 million years ago. All known dentitions of *Sahelanthropus* are badly damaged, but one canine tooth is clearly smaller than in apes (and thus more hominid-like) although its rather pointy shape is not typical of later hominids. All in all, most paleoanthropologists continue to accept *Sahelanthropus* as a very early hominid, though a vocal minority views it as an ancient ape.

If *Sahelanthropus* is a hominid, it lays to rest the otherwise rather attractive "East Side Story" scenario, whereby rising landscape along the line of the East African Rift Valley isolated the area to its east from humid winds out of the west. Rainfall in eastern Africa consequently declined, the story goes, accelerating the fragmentation of the forests there and forcing the earliest hominids to the ground, even as their ape relatives continued to luxuriate in the humid forests of the west.

The leading rivals of *Sahelanthropus* come from 6-million-year-old rocks in the Baringo Basin of northern Kenya. Dubbed *Orrorin tugenensis,* they consist of some jaw fragments and three partial femora (thigh bones) claimed to show adaptations to bipedality. The problem is that the parts of the femora that would show this for certain are missing, making functional interpretation tricky—although bipedality does seem plausible. On the plus side, the cheek teeth (molars and premolars) in the pieces of jaw are squarish, with the thick enamel typical of early hominids. They are apparently well on the way to the condition of "postcanine megadonty" (large chewing teeth) that characterizes later and better-established members of the early hominid radiation.

Not so the cheek teeth of another early hominid wannabe named *Ardipithecus ramidus*. This one, from 4.4-million-year-old deposits at Aramis, in northern Ethiopia, has rather apelike narrow molars with thin enamel, although the canines are smaller than in any modern ape, if rather pointed. The key to the hominid status of *Ardipithecus ramidus* is a small piece of skull base containing the foramen magnum, which is said to be oriented downward. Not far away, from deposits dating from between 5.8 million and 5.2 million years ago, come some jaws containing teeth rather similar to those from Aramis, plus an isolated toe bone. These were jointly given the name *Ardipithecus kedabba.* The toe bone, rather curved, was controversially claimed to be similar to those of later early hominids, and to be prima facie evidence of bipedality.

And that's it for evidence of hominids before about 4.2 million years ago. Even if all these forms *were* bipeds they make a pretty oddly assorted group. But if all of them were hominids, descended from a unique common ancestor that wasn't ancestral to any ape, they show that in those early days our ancient precursors were vigorously testing the possibilities opened up by terrestrial bipedal locomotion. Not that any or all of them was or were fully terrestrial. Almost certainly none was, despite having adaptations to upright posture. The faunas associated with all of them indicate fairly closed forest conditions, and it's clear that full emancipation from the trees came only much later in human evolution. Nonetheless, the issue of how hominids came to be bipedal is crucially important, since the consequences of this way of getting around were absolutely fundamental to all later developments.

Despite the fragmentary nature of the record, there are some things about the origins of bipedalism that can reasonably be assumed. The first is that the forest-dwelling hominid ancestor was already predisposed to postural uprightness (maybe like *Pierolapithecus*). Since modern humans lack in their wrist anatomy any sign of the specializations that enable today's apes to bear their body weight on their forelimbs while retaining nimble fingers, it is also pretty certain that the ancestor retained a relatively generalized body form. Almost certainly, the hominid ancestor did not adopt an apelike solution to terrestrial life because it had a yet greater propensity to arboreal uprightness. There has been a lot of argument about the key advantage that caused the first terrestrial hominids to walk bipedally. But the plain fact is this: the unusual form of locomotion would never have been adopted if the ancestral hominid had not found this a natural and comfortable way to get around. Everything else simply followed.

The Australopiths

The earliest well-documented hominids belong to the genus *Australopithecus,* first described from South Africa in 1924. Because the taxonomy of these early hominids is not well worked out, many paleoanthropologists like to apply the informal name "australopiths" to the entire radiation of early hominids of which *Australopithecus* forms part. The most ancient of these hominids, *A. anamensis,* comes from northern Kenya and consists mainly of jaws and teeth from two sites in the Turkana Basin dated to between 4.2 million and 3.9 million years ago. But there are also both ends of a tibia (shin bone) that provide strong evidence for upright locomotion. If a little primitive-looking, the jaws and teeth are also comfortingly reminiscent of better-known australopiths from a little later in time.

The chewing teeth of *A. anamensis* are said to indicate a dietary shift to tougher foods compared to the softer, fruit-dominated diet of chimpanzees. A smaller size difference between the canine teeth of males and females than is seen in apes might also have correlated with some change in social structure. The habitat within which this hominid ranged seems to have varied from dryish bushland to riverine forest with woodland beyond.

Based on preserved materials, the describers of *A. anamensis* felt it plausible that their new form was ancestral to *Australopithecus afarensis,* a much better-documented hominid from sites in Ethiopia and Tanzania dated in the 3.8-million to 3.0-million-year range. Its most spectacular representative is "Lucy," the partial skeleton of a

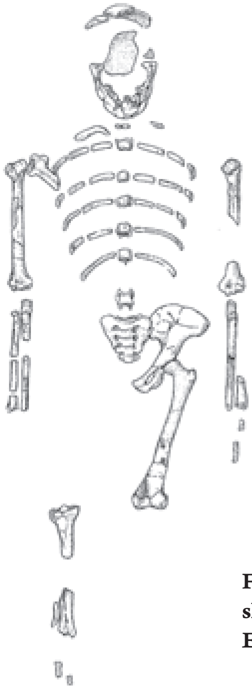


Figure 9.1. Drawing by Diana Salles of the "Lucy" skeleton of *Australopithecus afarensis*, from Hadar, Ethiopia.

female who lived some 3.2 million years ago at a place now called Hadar, in Ethiopia. In life Lucy was not much over three feet tall, and weighed only about sixty-five pounds. In a classic example of sexual size dimorphism, males of her species were a good bit larger, reaching maybe one hundred pounds or so.

Associated skeletons are vanishingly rare in the hominid fossil record before the (very late) invention of burial, so Lucy gives unique insight into human precursors of this antiquity. Better yet, she is supplemented by a trove of other fossils, adult and juvenile, that help us paint a pretty complete portrait of *A. afarensis*. Most significantly, individuals of this species were without doubt bipedal when they were on the ground. Lucy's legs are relatively short but nonetheless those of a biped; and in contrast to the long, narrow pelvis of apes, hers is even broader than ours. Despite having rather long feet with somewhat curved toes, from the hips down Lucy was clearly a committed biped, albeit not in quite the way we are today. Her upper body, however, speaks of her arboreal ancestry in its relatively long arms and torso that tapers upward to the narrow shoulders. Her hands, too, were those of a climber: long, with somewhat curved and powerfully grasping fingers.

A body structure like this was bound to provoke extensive debate about how its possessor actually lived and moved. After a quarter-century of argument it is now generally agreed that *A. afarensis* was bipedal when on the ground but spent a lot of time in the trees. Members of the species almost certainly depended on trees for shelter and for much of their sustenance. Such a lifestyle agrees with what is known of the environments that *A. afarensis* inhabited, which typically included a mosaic of riverine or lakeshore forest, with woodland and bushland beyond.

The most spectacular demonstration of early hominid bipedality comes from Laetoli, in northern Tanzania, whence *A. afarensis* fossils have also been reported. Here, some 3.6 million years ago, hominids walked across a plain covered in sloppy wet volcanic ash. The footprints they left behind later hardened and were preserved, to be reexposed by erosion and paleoanthropologists in the 1970s. While the details are debated, these arrow-straight trackways were unquestionably left by small hominids who were walking bipedally. They appear to have been crossing a rather open plain (a dangerous place for tiny defenseless creatures to be, teeming as it was with large predators) that lay between two more densely forested areas where they would presumably have been much more at home.

So again: why bipedality? To repeat, a large part of the answer must be that the arboreal precursor was already highly disposed to holding its trunk erect, and thus found it most natural to move around bipedally when forced to the ground by the shrinking of its ancestral habitat. Maybe that's actually the whole explanation. Nonetheless, the question has traditionally been posed in terms of the "key advantage" conferred by bipedality.

In this role, many have pointed to the freeing of the hands from locomotion so that they could be used to carry objects, to manipulate them, or even to make tools with them. The ability to do these things is certainly a major consequence of the new locomotor style, although bipedality was adopted long before stone tools started to be made. Others have suggested that by moving around upright you can spot predators from farther away, or that you can engage in more effective threat or even sexual displays, or that you can more effectively wade through streams. One particularly compelling observation was that by standing upright in the open tropics, you reduce the amount of your body directly exposed to the sun's vertical rays and at the same time maximize the body area that is exposed to cooling breezes. This point is important if you are out in the open savanna (and it might well correlate with the loss of body hair that is so notable a characteristic of human beings today), because in hot environments it is critical not to overheat the brain. In the absence of any specialized brain-cooling mechanisms, hominids can only achieve this by cooling the entire body.

There are cogent objections to all such putative key advantages. Maybe the problem is that, once you have adopted bipedality, *all* of the advantages—and *dis*advantages—of this way of getting around are yours. The significant thing is standing up in the first place. Almost certainly, this had principally to do with the postural adaptation of the hominid ancestor, although once on the ground in a bushy environment hominid bipedality may have been encouraged by the advantages it offered when feeding in the lower branches of trees. Nonetheless, the early hominids were still hedging their bets. They were facultative rather than obligate bipeds: they were not stuck with terrestrial bipedality as their only option, as we are. Though tempting, it's wrong to view the australopiths' have-it-both-ways locomotion as somehow transitional between arboreality and obligate bipedality, even though it may have been a prerequisite for the latter. In any event, this basic body form was clearly a successful one, since it remained remarkably stable for millions of years, even as various australopith species came and went.

Finally, before leaving this subject I should stress that we really have no idea what kind of pelvic adaptations the very first hominid bipeds possessed. By the time we get to Lucy we have a form whose pelvis and legs were radically altered from the ancestral condition. But unless this anatomical change had for some odd reason happened long ago in the trees, it must have taken place after movement on the open ground had become an important part of the hominid repertoire. There is still a lot to learn.

For all the accommodations of *A. afarensis* to a semiterrestrial lifestyle, above the neck these hominids had not moved far from the ape condition. Today's *Homo sapiens* has a tiny face tucked beneath the front of a huge globular braincase. This contrasts strongly with modern apes, which have large faces that jut out in front of rather small braincases—very much as the faces of the early hominids did. The brains of *A. afarensis* were not significantly larger than those of comparably sized chimpanzees today, and like apes these ancient hominids also had long, stout tooth rows that were set in well-buttressed jaws.

For this reason many paleoanthropologists refer to the early hominids as "bipedal apes," and there is certainly no good reason to infer that they were a lot smarter than today's apes—which is not to demean them in any way. Hardly a week goes by in which an ape is not discovered to do something that we thought only we did. But clearly the apes don't process information about the world around them exactly as we do, and thinking of the early hominids as junior-league versions of ourselves is plain wrong. Like all of our extinct relatives, they were creatures that need to be understood in their own unique terms.

Between about 4 million and 2 million years ago, australopith species proliferated in Africa, though none seems ever to have contrived to leave that continent. In South Africa, whence australopith species were first described, two distinct lineages traditionally have been recognized: the gracile forms, from sites in the 3.0-million- to 2.5-million-year range, and the slightly later robust ones, principally distinguished by the massiveness of their dentitions and their supporting architecture. Additionally, a slightly earlier skeleton, some 3.3 million years old, has been reported from the South African site of Sterkfontein. It is still partly enclosed in the matrix in which it was discovered, but is said to show differences not only from the later South African australopiths but from its approximate coeval Lucy: for example, its legs are not particularly short compared to its arms, and the hand is very humanlike in having a relatively long thumb and short fingers. A preliminary assessment still places this hominid as a "climber in the trees . . . and bipedal on the ground." But its distinctive characteristics, if substantiated once the skeleton has been freed from the surrounding rock, will emphasize how at this stage australopiths were still experimenting with variations on the primitive hominid theme.

A robust lineage of australopiths has also been recognized in eastern Africa, starting at about 2.5 million years ago and persisting, alongside hominids of more modern aspect, until as recently as 1.4 million years ago or even less. Their huge, flat molars and premolars had been thought adapted for eating tough, gritty, fibrous foods (roots, tubers, and the like). The graciles, in contrast, were believed to have preferred an ancestral diet mostly of fruit. However, a recent microscopic study failed to reveal the differences in dental wear that you'd expect from such radically different diets, and stable carbon isotope analyses indicate that some of the South African robusts, at least, were quite omnivorous and may have included animal protein in their diet. This inference fits quite nicely with the recent and as yet untested suggestion that the massive, flat teeth of the robusts might have been well suited for cracking the shells of arthropods and small crabs—an abundant resource in the lakes and watercourses of Plio-Pleistocene Africa.

Observations like this also accord well with the fact that, as more isotope studies are done, the stronger the suggestion becomes that australopiths of all kinds were incorporating into their diets a component that had originated in sedges and certain grasses. Because it is vanishingly unlikely that any australopith actually ate sedges, the conclusion must be that they were feeding on animals that grazed on such plants (because your tissues are full of evidence about what you have eaten). Among other things, this implies that we can't use chimpanzee hunting as a model for the australopiths' pursuit of animal protein—because, although chimpanzees quite efficiently (if only occasionally) hunt small mammals such as blue duiker and colobus monkeys, these forest-living prey do not feed on plants that carry this signal. More likely, the telltale component came from small-bodied grass-eaters that do incorporate this sign. Candidates for this role include forms such as hyraxes, or juveniles of larger-bodied grazing species. These would have to have been pursued in more open environments, necessarily using different techniques. But then again, the signal might have come from termites (this time, a chimpanzee favorite) or from those arthropods.

Knowing exactly where the isotopic signal originated is especially important because the adoption of a high-quality diet was an essential prerequisite to the expansion of the hominid brain that was to come. The brain is an energy-hungry organ: in modern humans it consumes around a fifth of all the energy used to power the body. Enlarging the brain demands a compact and reliable source of calories such as animal fats and proteins. In retrospect, early hominids must have had such a source. The idea of carnivory among early hominids is not a new one. In the late 1940s, long before anyone worried about energetics, Raymond Dart—the man who had recognized the first australopith specimen for what it was—began dramatically promulgating a "killer ape" origin for the hominids. Noting that australopith fossils were usually found in association with lots of broken animal bones that he took to be the remains of australopith meals, he concluded that the human family had been born in violence, inaugurating the "blood-spattered, slaughter-gutted archives of human history."

Later it was realized that the animal bones had been broken and accumulated by natural forces, including predators, scavengers, and the elements. It came to be believed that at most the australopiths had been scavengers, living chiefly on plant foods and availing themselves now and again of what was left of carcasses killed by carnivores. It was noted that the australopith fossils had been broken in much the same way as all the others, and that one piece of australopith skull even bore twin holes that were fitted exactly by the two canines of a leopard mandible. These had evidently been made as the leopard dragged the remains of the poor australopith away to stash them up a tree for safekeeping.

As a result of observations like these, Man the Hunter eventually became Man the Hunted. A good argument can be made that the biologically defenseless early hominids—they were small, slow, and had even lost their dagger-like canine teeth—most likely exhibited many of the characteristics of prey species, even as they fed on smaller animals such as those hyraxes that putatively provided the isotopic signal. Looking at the australopiths as prey species has a significant effect on our perspective on them, as we will shortly see. In any event, since it's tough to scavenge hyrax carcasses for a living, it is beginning to look as if, away from the deep forest, the omnivorous australopiths may have been beginning to actively hunt small grazing prey. And why not? While chimpanzees shun dead carcasses (and it is hard to know what might have made such things attractive to early hominids), at least in some places they do eagerly hunt—even if for them the sharing of the meat plays a greater role in cementing social relationships than it does in supplementing their diet.

The First Toolmakers

One of the problems in figuring out how the australopiths actually lived is that, at least for most of their existence, they left no archaeological traces—no direct record of their behavior. Indeed, a record of this kind is almost uniquely the legacy of later hominids, although stone anvils on which chimpanzees broke nuts four thousand years ago have recently turned up in West Africa.

The study of archaeology only begins with the use of the first stone tools—truly durable testaments to actual human activities that announce the arrival of the Paleolithic, the Old Stone Age. So far, nobody knows exactly who made the very earliest stone implements. These ancient tools—small, sharp-edged flakes knocked from a small cobble using a hammer stone—come from sites in Kenya and Ethiopia that are dated to about 2.5 million years ago, but sadly suggest nothing beyond their use in butchery. Only in one instance, at Bouri in Ethiopia, is there anything close to an association between very early stone tools and any kind of hominid. Significantly, though, this hominid was an australopith.

At Bouri, in sediments about 2.5 million years old (in which stone tools themselves were oddly rare), were found both the fossils of a hominid that was dubbed *Australopithecus garhi* (though it doesn't differ much from *A. afarensis*) and animal bones that bore cut-marks: traces left by the stone tools that had been used to dismember the carcasses of medium- to large-sized ungulates. Whether or not the prey had initially been killed by the tool wielders is impossible to say, although no carnivore tooth marks were reported on the cut-marked bones. There is no guarantee that the toolmaker/butcher was indeed *A. garhi*, but pending further finds, this australopith must be the leading candidate.

If this scenario is accurate, here is an excellent example of a theme that has marked the story of human evolution ever since: new behaviors do *not* tend to be invented by new kinds of hominids. Technologies have come and gone totally out of phase with new kinds of hominids, which makes sense: new technologies must be invented by an individual, who has to belong to a preexisting species. And, on current evidence, the first stone tool makers were more than likely small-brained hominids with large faces and archaic body proportions.

When you find stone tools, you have direct evidence of a very specific kind of behavior, and less direct evidence of a particular level of cognitive performance. We'll follow up on this in a moment. But before leaving the australopiths let's turn again, briefly, to the implications for their lives of the notion that they were prey (as well as predator) species, whose lifestyle had necessarily to take the danger of predation into account. Even today, only in our cocooned Western world and its derivatives can individual humans comfortably ignore the danger of predation. Especially during the Plio-Pleistocene, when the African plains teemed with large predatory animals, the risk of attack was omnipresent.

In their recent book *Man the Hunted*, Donna Hart and Bob Sussman point to a slew of strategies that would almost certainly have informed the lives of hominid species spending at least part of the time in relatively open environments where danger lurked behind every bush. Remember that from the point of view of the species, successful strategies are those that favor the survival of the group as a whole, rather than of its individual members. Hart and Sussman identify seven such strategies:

1. Live in large groups. Hart and Sussman suggest groups from twenty-five to seventy-five, a lot larger than most traditional estimates. There *is* safety in numbers.
2. Versatility. Use the trees *and* the ground for greatest security. We know from the way they were built that the australopiths were incomparably well equipped for that. We also know that this two-way strategy was very successful, for otherwise, the basic australopith structure would never have endured as it did.
3. Be flexible in your organization. Forage for scarce resources in small groups, but come together for protection where possible.
4. Have multiple males in your social groups. Reproductively, males are the more dispensable sex, and especially where the

males are significantly larger than the females, they can provide vital protection for females and infants.

5. A corollary of the last strategy: Take advantage of the fact that upright posture gives an appearance of greater body size, especially among larger males that might have been able to mob predators quite effectively.
6. Select sleeping sites for maximum protection from nocturnal predators, something that the climbing abilities of australopiths ideally suited them to do.
7. Be smart. Intelligence confers the ability to monitor the environment, to communicate with other members of the group, and to outwit potential predators.

These rules of thumb do not, of course, exactly specify how australopiths lived. Trying to guess their lifestyle has always been vexed by the fact that signals from different sources are mixed. For example, the only living (lesser) apes with little sexual dimorphism in canine size (like the australopiths) live in pair-groups, while those with the largest body-size dimorphism (apparently comparable to at least some of the australopiths) are the gorillas, among which one male dominates a small group of females—although subordinate males, and of course juveniles, may also be around. And significantly, as Hart and Sussman point out, the apes are forest-dwellers, and the early hominids were not.

All in all, most likely the australopiths were edge species, living largely in the wooded zone between deep forest and more open country. If their social organization was indeed more strongly influenced by their predator-infested habitat than by their arboreal ancestry, it seems very plausible that they lived in largish groups with multiple males and females, all ranged in a social hierarchy of some sort. Inside such groups, social relationships would have been intense and complex, and vocalizations, gesture, and body language would all have been important in communication. Further, since primate edge species tend to be refuging, returning to favored protected spots to sleep each night, it seems reasonable to conclude that australopiths roamed widely during the day to forage, while seeking nocturnal security at a limited number of relatively fixed points.

In the absence of an archaeological or other record all this must, of course, remain speculation. This makes it particularly frustrating that—even at the latest stages of australopith evolution, after stone tools had begun to be manufactured—we cannot expect to find positive confirmation of refuging habits. The reason is that the earliest stone tools seem to have been made as and where required, rather than at favored localities as later in hominid evolution. Nonetheless, it may be significant that at one time there was much discussion among archaeologists of potential "home bases" around which the early toolmakers ranged, or at least of "central-place foraging."

One can speculate a lot more about the lifestyles of the earliest hominids. For the time being, however, all is inference, and we cannot read more into the evidence than it will bear. Alas, such direct evidence as we have is slender indeed. What is certain, though, is that we cannot see these early toolmakers simply as primitive versions of ourselves, or as creatures that were somehow intermediate between us and the apes, either behaviorally or cognitively. Whoever they were, they were doing their own thing.

EARLY *HOMO*

Although it has lavished much introspection on itself, the genus *Homo* remains poorly defined. Starting with the single species *Homo sapiens*, our genus has grown by accretion over the past century and a half as the fossil record has expanded. Along the way a sort of ratchet action has assured that, with each new addition, the morphological variety perceived as permissible within it has increased. One result is that, in the period between about 2.5 million years ago (approximately coincident with the first appearance of stone tools) and something under 2 million years ago, there is by now a motley assortment of mostly fragmentary fossils contending for the title of "earliest *Homo*," none of them with much morphological claim to that role.

The earliest widely recognized species allocated to *Homo* is *Homo habilis* ("handy man"), a name applied in the early 1960s to a handful of fossils from 1.8-million-year-old rocks of Tanzania's Olduvai Gorge. Their discoverer Louis Leakey promoted his fossils as primitive *Homo* principally because he associated them with the crude stone tools found in the same sediments. Leakey was a leading advocate of "Man the Toolmaker," the notion that the critical defining feature of the human genus was not any particular morphology, but a behavior: the making of tools. True, he also believed that a couple of fragments of cranial vault indicated a brain fractionally larger than that of australopiths. Equally true, the chewing teeth of the new form were a lot smaller (and thus humanlike, at least in this respect) than those of a robust australopith found nearby. But it was an enormous leap to make these slender indications the basis for a new species of the genus that also included *Homo sapiens*; and it was almost certainly a leap too far.

Nonetheless, no australopith was suspected at that time of making stone tools, and in cognitive as well as technological terms, this invention was unquestionably huge. Stone tool manufacture must have had an enormous effect on hominid lifeways and potentials. Of course, many vertebrates are now known to use implements: New Caledonian crows form and use stick tools, as chimpanzees do, along with those hammers and anvils for cracking nuts. But it is nonetheless true that the making of stone tools (and, even more, their spontaneous invention) places you in a new cognitive league—even if not our own. Apes coached intensively in stone toolmaking (even individuals who performed heroically in other cognitive tests) have performed rather unimpressively. They get the idea of cutting with a flake detached from a stone. But none has ever grasped the practicalities of regularly hitting one piece of rock with another at precisely the angle and force required to detach a sharp flake.

Kanzi, the most famous bonobo subject of such experiments, eventually took to throwing rocks on the floor to shatter them. You can't blame him for that. Smashing rocks the right way to get a sharp cutting flake is not only difficult for neophytes, but painful on the hands to boot. Still, it seems that, whatever exactly the cognitive spark may be that underwrites the ability to make stone tools, it is lacking in today's apes. Yet if the evidence from Bouri is to be taken at face value, this spark was present in later populations of the small-brained bipedal apes, a conclusion made more secure by the fact that there is no really good fossil evidence that a new *kind* of hominid entity was on the scene until more than half a million years after stone tools began to be made. From the very beginning, hominid biological and technological innovations were out of phase.

The implications of stone toolmaking don't stop with the manufacture of the tools themselves. Appropriate stone is not found everywhere. The tools associated with cut-marked bones at ancient butchery sites are typically made of foreign materials not available at the locality itself. Since entire cobbles have been pieced together from fragments found at such sites, they must have been brought in as raw material by the hominids, to be made into tools when needed. Often, their nearest possible source was several miles away: clear evidence of foresight on the part of the individuals who made the tools.

Alas, it is unclear what else this meant for the toolmakers, or for how they subjectively experienced the world. Part of the fault is ours: we are simply incapable of inserting ourselves into the minds of beings that don't think as we do. We can try to imagine what it would be like to have their particular attributes or limitations, but that is not the same as being in their place. The bipedal apes weren't chimpanzees. But they weren't us, either. In the end, however much effort we expend trying to understand their cognitive states, we wind up simply with our own mental constructs.

The first indications of a truly new kind of hominid that we can unreservedly welcome into our genus appear a little under 2 million years ago, at a time when the robust australopiths, at least, were still flourishing. The relevant fossils come from rocks around Lake Turkana, in northern Kenya, that have yielded an enormous trove of hominids dating mostly from between about 1.9 million and 1.5 million years ago. Among them are several crania that early on were attributed to *Homo erectus,* although in recognition of the fact that this famous extinct hominid species seems to have been limited to eastern Asia, many paleoanthropologists now prefer to assign them to the local species *Homo ergaster*.

This new species is best represented by the spectacular 1.6-million-year-old skeleton technically identified by its museum catalog number (KNM-WT 15000) but more informally known as

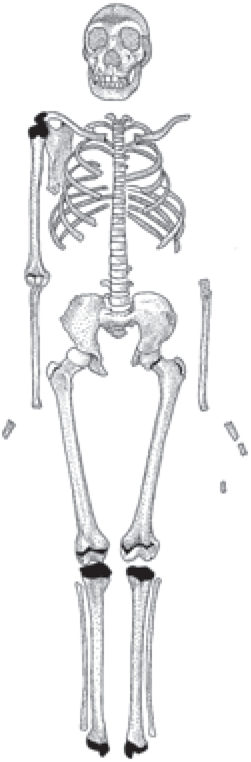


FIGURE 9.2. Drawing by Don McGranaghan of the "Turkana Boy" skeleton, KNM-WT 15000, from West Turkana, Kenya.

the "Turkana Boy." Here we have a total break with the past. Nothing in the fossil record anticipates the morphology of this new form, and it is very clearly not a simple extrapolation of what had gone before. In light of this, it is very likely that we see in the Turkana Boy the results of a single change in a regulatory gene complex that was small in terms of DNA structure, but that had ramifications throughout the body.

The Boy was adolescent when he died, probably after about eight years of life, though he had developed to the stage of a modern twelve-year-old and his skeleton already shows many adult features. Starting at the top, his skull houses a brain a bit more than half of the modern size, compared to the one-third typical of the bipedal apes. This is, perhaps, a fairly modest increase. But the skull in which the brain was housed was radically different in proportion from any australopith's and anticipates in many ways what is seen more fully expressed among later hominids.

The biggest surprise, though, comes below the neck. As far as we can tell, all australopiths were relatively short-statured, rarely if ever attaining a height of much more than four feet. In contrast, while the adolescent Turkana Boy was only about five-feet-three-inches tall when he died, had he lived to adulthood he would have topped six feet, taller than most people today. He was proportioned much as modern people are, particularly those who live in hot, dry climates similar to the one he experienced. So while there are many minor differences between the Boy's skeleton and those of hominids who came later, we can see in him the arrival of an essentially modern body form.

Here at last was an obligate biped: a tall, striding creature completely emancipated from the ancestral forest and woodland. At a time when open savanna was expanding, a hominid had emerged that was fully equipped to exploit this habitat. The Turkana Boy doesn't just show an incremental improvement over his known predecessors; he represents a revolutionary new way of doing hominid business. If we can judge from indirect cranial evidence, new hominids of this kind may—possibly—go back as far as about 1.9 million to 1.8 million years ago. We have nothing to suggest, however, that anything other than a radical short-term reorganization of the entire skeleton was involved in the origin of this unanticipated phenomenon.

Yet this radically new hominid continued to make stone tools effectively identical to those already produced for a million years by its more archaic precursors. Stone tools associated with the first *Homo ergaster*, and right through the time of the Turkana Boy, are uniformly of the Mode 1 style that dated back to Bouri and Gona times: small, sharp flakes knocked by a hammer stone from a small cobble (a "core") from which more than one flake may have been removed. Although the cores themselves may have been used as pounding or chopping tools, especially in breaking bones for marrow extraction, the sharp, slicing flakes were almost certainly the primary implements. Though simple, the flakes were very effective: experimental archaeologists have efficiently butchered entire elephants using replicas of them. Maybe this technology was a victim of its own success, for hominids seem to have been content with it, more or less as it was, for a very long time.

It's frustrating to know so little about how the physical break with the past reflected new behaviors. For the first time, however, we can be more or less certain that hominids had lost their ancestral hairy coat. In the woodlands, shelter would always have been available to allow periods of cooling off. Out on the tropical savanna this was no longer the case, and keeping the body (and brain) cool would have been a major consideration. Uniquely, human beings cool down through the evaporation of sweat produced by specialized glands, something that is impeded by a dense covering of hair. And once this covering had been shed, dark pigmentation of the skin would have been needed to protect it from the damaging effects of harsh tropical ultraviolet radiation.

In becoming obligate bipeds, hominids sacrificed speed for endurance, another influence on their living strategies. Out on the savanna hominids would have been subject to more consistent predation pressures than ever before, and since they were less capable than their predecessors of profiting from arboreal or rocky refugia, they must in some way have accommodated behaviorally to their new and possibly more dangerous circumstances. Much has been made of the unique ability of modern humans to throw objects accurately. Possibly it was at this stage that this skill began to be honed, in a defensive context or even a hunting one. Hand-eye coordination has certainly been a significant aspect of the hominid behavioral repertoire ever since. Food resources, too, were different, and differently distributed. Exactly how the hominids adjusted to the new realities of savanna life—maybe by digging for tubers, or by scavenging, or profiting from their newly acquired endurance by hunting larger animals more intensively, or all of these—it is impossible to say. The first putative uses of fire—employed by later hominids not only for cooking but for protection—come from a couple of sites in East and South Africa that date from about 1.8 million years ago, when *Homo ergaster* was already around. However, these are isolated intimations, and a gap of a million years follows before evidence appears of fire domesticated in hearths.

As for cognitive advance, only with the next innovation in stone toolmaking do we have any good basis for inference. At about 1.5 million years ago or perhaps a bit before, and again in eastern Africa, we begin to pick up evidence of a new kind of stone tool. This is the Mode 2 or "Acheulean" hand axe, a large, teardrop-shaped implement that was carefully worked on both sides to a predetermined symmetrical shape, using multiple blows. The earliest stone toolmakers were simply after an attribute: the sharp cutting edge. Exactly what the tool looked like didn't matter. In stark contrast, the Acheuleans fashioned stone cores to a mental template that must have been in their minds before stoneworking started.

This concept was revolutionary and must be accepted as evidence of another cognitive advance. But again, it's hard to say what exactly that means. The ability to envision a specific form within a lump of rock represents a level of abstraction that clearly lies beyond the simple (or maybe not-so-simple) ability to realize that if you smash a rock the right way you will obtain something with which you can cut. But knowing what it means in terms of a broader perception of the world is difficult.

What's more, despite sometimes being produced locally in vast quantities, the hand axe was not an innovation that spread like wildfire as hominids moved within and beyond Africa. Even in the East African heartland, simple flake tools continued to be made alongside hand axes—and their cousins, the obliquely edged cleavers—for another million years. More puzzlingly, Mode 2 reached Europe a full million years after it appeared in Africa, and it is only rarely found in eastern Asia. Once more, we see a disconnect between innovation in the biological and cultural realms, and it is hard to know just what to make of the meager archaeological evidence we have.

Because the brain of *Homo ergaster* was significantly larger than that of australopiths, we do know that the trajectory of hominid brain enlargement had already begun. But how that larger brain was organized remains a closed book, and precisely what enlargement meant in terms of increased cognitive complexity is impossible to specify. What's more, the cognitive leap implied by the invention of the Acheulean took place well after a larger brain had been acquired. If, as one might suppose, the cognitive potential that was realized in the Acheulean had originated with the larger brain, this new potential lay fallow for a very long time before being exploited by its possessors.

That might seem odd, but in fact it is not surprising at all. Remember that exaptation, whereby an innovation originates well before being exploited in a new context, is a common feature of evolution—as we saw, for example, in the origin of tetrapod limbs and of avian feathers. Those innovations eventually turned out to be indispensable for terrestrial and aerial movement, respectively; but both were in place well before the adoption of the forms of locomotion with which we associate them today. Our human mind is a reductionist thing, and we like to perceive direct connections between causes and effects that we can currently observe; but in the matter of both technological innovation and the evolution of human cognition, such connections invariably turn out to be elusive.

Out of Africa (for the First Time)

With *Homo ergaster*, for the first time, a hominid was truly at home out in the open. It is probably no coincidence that right after the revolutionary new body form appeared, we find the first evidence of hominids who had journeyed beyond Africa. This movement was clearly not the result of intentional exploration. For the vast bulk of hominid history, spreading into new areas simply involved population expansions, frequently punctuated by contractions, extinctions, or diversions. Such expansion was evidently facilitated by the new physical mobility in an environment that was becoming increasingly widespread.

The best evidence for early exit from Africa comes from the 1.8-million-year-old site of Dmanisi in the Caucasus, on the eastern fringes of Europe. Dmanisi was the last place anyone would have expected to find ancient hominid fossils. Indeed, the first of them surprised medieval archaeologists excavating the remains of an ancient town. Quickly the paleoanthropologists moved in, and now the site has yielded five crania, three mandibles, and a number of postcranial bones. These extraordinary finds help clarify the mystery of how, after millions of years, hominids had contrived to leave Africa, presumably via a route that took them across the Sinai Peninsula.

Part of the explanation for this new mobility must involve the emancipation of hominids from the fringes of the shrinking African forests. As the forests retreated, any hominids dependent on woodland for survival would have found themselves ever more limited geographically, while their savanna-adapted relatives found the opposite. Paleoanthropologists have vigorously debated the critical ingredient that promoted hominid expansion at this point. Was it the enlarging brain and presumed greater intelligence? Was it improved technology, allowing the exploitation of a greater range of environments? Or was it the new locomotor adaptation itself?

The Dmanisi hominids allow us to eliminate at least two of these possibilities, for the Dmanisi hominids had quite small brains and made Mode 1 stone tools. That leaves modern body form itself, and the striding locomotion that we see so evidently exemplified in the Turkana Boy is emblematic of what makes modern humans physically so unusual today. Human beings are literally walking machines. They may not be fast, but they possess stamina and endurance that allow them to keep moving long after fleeter quadrupeds have collapsed of exhaustion. That is the basis of the ambush hunting typically practiced by hunting and gathering peoples, who simply wound and then outlast their quarry.

This does not mean that the Dmanisi hominids were ambush hunters. But two partial skeletons, although of considerably shorter stature than the Turkana Boy, are said to show the essential morphology of the modern human skeleton—thereby suggesting that the key to these hominids' mobility may have been striding locomotion. Despite their small brain sizes and rather archaic skull structure, then, the Dmanisi hominids were not simply bipedal apes.

What, then, to make of them? So far they have had quite a wild taxonomic ride. Back in the early 1990s, when only a single mandible was known from Dmanisi, it was given the name of the southeast Asian species *Homo erectus*. Some linear thinkers still view this species as a stage in human evolution that occupies an intermediate position between the australopiths on the one hand and the later hominids on the other. Viewed this way, *Homo erectus* is essentially a receptacle to embrace all of the hominids that existed in its time period, which lasted in Indonesia until about forty thousand years ago. That would make this a very long-lived and very variable species indeed.

But with fresh cranial discoveries the new Georgian hominids began to be compared to *Homo ergaster*, their putative African ancestor. Soon, however, they gained an independent identity when the new name *Homo georgicus* was applied to a very large and robust mandible that emerged from the site. Subsequently the entire assemblage has been moved back to *Homo erectus*, but that's clearly not the end. With the discovery of a large and very striking cranium that apparently matches the large mandible, it's possible that the whole lot may once more become *Homo georgicus*. Because all of the crania were found pretty close together, nobody wants to notice that they make a very motley assemblage. But if and when the matter is reappraised, the question of how many hominid species are found at Dmanisi may be reopened.

Still, this hasn't occurred yet, and it may never. Meanwhile, whatever exactly they are, the Dmanisi fossils are impressive evidence that hominids had begun their takeover of the Old World by 1.8 million years ago. Their initial spread into Asia didn't take long. Genuine *Homo erectus* has been controversially dated in Indonesia to Dmanisi times, and there are well-established dates going back to 1.66 million years, about the age of some very primitive stone tools reported from a site in Pakistan. Early dates have also been reported from China, though these are less certain.

In Europe, the first hominid fossil is a jaw fragment from the Sima del Elefante at Atapuerca, in Spain, that may exceed 1.2 million years old. A site in Italy has yielded stone tools that are even older. Another locality at Atapuerca, some eight hundred thousand years old, has yielded hominid fragments assigned to the new species *Homo antecessor*—which is alleged to have practiced cannibalism. What do these dates mean?

Well, since the further-flung eastern Asian record goes back well before the European one (if we forget Dmanisi), it seems likely that the first hominid emigrants from Africa turned rapidly eastward on leaving their native continent, staying in the subtropical zone all the way to the Pacific. Europe was isolated by more rugged terrain and harsher climates, and it evidently posed greater difficulties to colonizing hominids, who did not pull off the trick there until rather later. But again, since the Atapuerca fossils are associated with Mode 1 tools, it was obviously not improved technology that allowed the penetration of Europe for the first time.

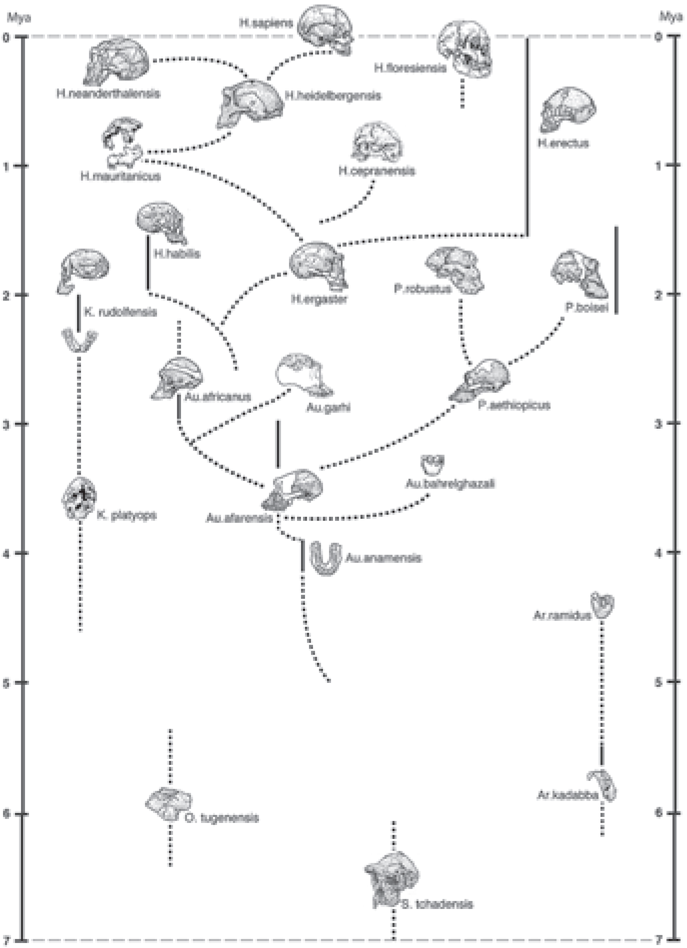


Figure 9.3. Highly provisional hominid family tree, showing consistent diversity within the family over time (except now).

Whatever exactly happened, the pattern is clear. Once hominids had occupied the new territories of Eurasia, new species were locally spawned, exactly as you'd expect. One of the most bizarre examples is *Homo floresiensis*, recently discovered on the Indonesian island of Flores. Surviving until a mere twelve thousand years ago, this form bucks all hominid trends in being extremely diminutive in stature (the one skeleton known was hardly any taller than Lucy) and in having an exceedingly small brain, not to mention huge feet. Some paleoanthropologists have had difficulty swallowing this highly anomalous find as a proper hominid species and have sought to show that the skeleton (along with a few other bits and pieces) is simply a pathological example of *Homo sapiens*, or even of *Homo erectus*. Odds are, though, that it is a real evolutionary phenomenon. And if it is, it provides yet another example of the hominid tendency to diversify locally, although it also exhibits some very primitive features that may ultimately help us understand what the earliest emigrants from Africa were truly like.

CHAPTER 10

A Cognitive Revolution

The African hominid record dwindles a bit between about 1.5 million and 1.0 million years ago, as hominids were spreading to other areas of the Old World. It contains few specimens with larger braincases than the Turkana Boy's. Some, indeed, had smaller ones, and it is not at all evident how most of these fossils are best classified. Morphologies are quite diverse, and the picture only starts to clarify a lot later in time.

The First Cosmopolitan Hominid Species

In 1976, paleontologists found a distinctive thick-boned skull at Bodo in Ethiopia. Some 600,000 years old, it had a big, broad, and flattish face. Its brain capacity was estimated at about 1,250 cubic centimeters: not too far below the modern average. No postcranial bones were discovered along with it, but you'd guess that its skeleton had been very massively built. Most significantly, Bodo is the earliest known member of a hominid species found widely in the Old World. Similar African fossils come from Zambia and South Africa; European representatives of the same species were found in Germany, France, Greece, and maybe the United Kingdom; and a couple are known from China as well. The first of these specimens to be named was a mandible from Germany that was dubbed *Homo heidelbergensis* for the nearest city, and all such specimens now bear this name, regardless of where they were found. Many are poorly dated, but two European dates of around 500,000 and

400,000 years ago are probably quite reliable, and some specimens may be as little as about 200,000 years old.

It seems probable, then, that the highly distinctive *Homo heidelbergensis* originated in Africa at some time before about 600,000 years ago, and that within a hundred thousand years or so it had begun to spread to almost all parts of the Old World. This was the first truly cosmopolitan hominid species, though it seems clear that it did not completely replace all of the endemic hominids whose territories it invaded.

The earliest *Homo heidelbergensis* evidently made rather crude stone tools, but during the tenure of this species several very intriguing cultural developments occurred. The site of Terra Amata, in southern France, close to 400,000 years old, contains traces of the world's earliest artificial shelters. One such structure was made of saplings stuck into the ground in a large oval and brought together at the top. The perimeter was reinforced with a ring of stones and, just within the entrance, a shallow scooped-out area containing blackened stones and bones indicated a hearth.

Although it doubtless represents a vitally important aspect of the lives of the Terra Amata hominids, this hearth is not the earliest one known. The most ancient well-documented claim of domestic fire use actually comes from Gesher Benot Ya'aqov in Israel, a 790,000-year-old site that lacks hominid fossils but where thick lenses of ash indicate that hominids had regularly used fire. Oddly, since this innovation must have made an enormous difference to hominid life, it is only from Terra Amata times onward that the remains of hearths become a regular feature of archaeological sites.

Evidence for early fabrication of shelters comes in only slowly, but the 350,000-year-old site of Bilzingsleben offers traces of structures, too. Also potentially (but not necessarily) the work of *Homo heidelbergensis* are some long and elegant wooden throwing spears, some 400,000 years old, found in a bog at Schoeningen in Germany. Because wood preserves only exceptionally, we have no earlier record of its use in tool manufacture. But these unique spears are a revelation, for they were carefully shaped to concentrate the weight at the finely pointed front end. Stone flakes at Schoeningen were simple but may have been hafted into wooden handles to form complex tools.

Symbolic Intelligence

However imperfectly perceived, findings such as these suggest that during *Homo heidelbergensis* times something significant was stirring in the cognitive realm. Whatever the exact payoff of a larger and more energy-hungry brain than any hominid had ever possessed, it must have related somehow to an increasingly complex way of processing information about the world. The control of fire, the construction of shelters, the fabrication of complex tools: these are all major advances toward the highly distinctive lifeways that hominids have shared ever since. Nonetheless, not all complex ways of interacting with the world are the same, and a critical modern cognitive feature was evidently still lacking.

Today's *Homo sapiens* is unique, as far as we can tell, in living in a world that is literally of its own creation. Other species, even quite intelligent ones such as chimpanzees, bonobos, and orangutans, live entirely in the real world. They react directly, with varying degrees of subtlety, to the stimuli coming in from around them. Not so *Homo sapiens.* Other than reflex reactions such as withdrawing our hands instantly from a hotplate, our responses are typically indirect, based on our own individual constructions of our circumstances.

We exhibit this unusual behavior because in our brains we deconstruct our environments into a mass of intangible symbols, which we combine and recombine to produce new mental realities. We may not be able to do anything about the predicaments in which we find ourselves. But we are able to envision alternatives, based on our mental ability to produce those all-important symbolic constructs. If you experience the world around you essentially as a continuum you can't do this, although you can certainly react to circumstances in complex ways.

You could, of course, argue that a rudimentary ability to predict future needs can be discerned in the planning of those ancient stone tool makers who picked up and carried rocks in the expectation of making implements later. However, those future needs are previously observed, while the symbolic ability is able to conjure up new situations entirely. In the case of the earliest stone tool makers, anticipation was plausibly produced by an intuitive, nondeclarative form of intelligence, and the same is almost certainly true of the thinking that guided most later and more sophisticated Stone Age toolmaking as well. Only if an object is overtly symbolic can we be sure that its maker was thinking symbolically, and nothing in the record left behind by *Homo heidelbergensis* can be unambiguously interpreted as a symbolic object.

It is important not to confuse symbolic thought with mental complexity. All symbolic creatures are intellectually complex, but not all intellectually complex beings are or were symbolic. Sequences of behavior directed at the production of useful objects, with an anticipated end in view, may show a high degree of intuitive intelligence, but they don't necessarily demonstrate symbolism. Only overtly symbolic acts and objects can do that, and these will rarely be purely utilitarian. Of course, one can claim that a lack of symbolic objects at an archaeological site cannot be taken as proof that the site itself was not formed by symbolic creatures. But the absence of any good evidence of symbolism over the entire record of a species is at the very least highly suggestive.

For all its encephalization, *Homo heidelbergensis* falls into the general hominid pattern of innovation in the sense that its arrival is not announced by a new stoneworking technique. Instead, this occurred in the middle of its tenure. Although conceptually distinct, Mode 1 and Mode 2 stoneworking industries are grouped together in the early Paleolithic category. Only at some point over about 300,000 years ago do we find a new Mode 3 technology inaugurating what is known as the middle Paleolithic in Europe and the Middle Stone Age in Africa.

"Prepared-core" Mode 3 stone tools are radically different in concept from what preceded them. A stone core was carefully fashioned, with multiple blows to both sides, until one well-placed final blow, probably from a soft hammer of bone or antler rather than from a brittle stone, would detach what was essentially a finished tool with a single cutting edge around all or most of its periphery. Once again, as with the shift from Mode 1 to Mode 2, we see evidence here of a more subtle level of cognition than any documented earlier. And again, alas, we have no idea just how this innovation reflected larger changes in the way in which the hominids involved perceived and subjectively experienced their world. Were the lives of late *Homo heidelbergensis* significantly different from those of their early precursors 300,000 years earlier (as ours, for instance, are from those of the first *Homo sapiens*)? We simply don't know, but my guess is that they weren't. We think of technological and cultural change as being constants in our own lives today, but among our forerunners, change was evidently both sporadic and rare.

The Neanderthals and Their Relatives

Archaeologically, *Homo heidelbergensis* is relatively poorly known. In contrast, *Homo neanderthalensis,* a species known across a wide swath of Europe and western Asia between about 200,000 and 30,000 years ago, is the best documented of all extinct hominids. Neanderthals are particularly fascinating for a whole host of reasons. For one thing, they represent an endemic European lineage of hominids estimated by molecular systematists to have split with the (African) one leading to *Homo sapiens* at over a half-million years ago. This long period of separate evolution is confirmed paleontologically by the presence at Atapuerca, over 530,000 years ago (and thus coeval with the European branch of *Homo heidelbergensis*), of a population of hominids clearly antecedent to *Homo neanderthalensis*, but not at all the same thing.

What's more, while the Neanderthals had brains fully as large as ours, the Atapuerca hominids had possessed smaller cranial vaults, indicating that brains independently enlarged over time in the Neanderthal and *Homo sapiens* lineages. Interestingly, during the same period a similar trend was going on in *Homo erectus*, isolated in its eastern Asian redoubt. Given the well-known energetic constraints on brain enlargement, the occurrence of this phenomenon in three separate lineages of *Homo* indicates a very powerful predisposition toward it in our genus. Understanding precisely what advantage that predisposition played to is going to be crucial if we are ever to comprehend fully the emergence of our own cognitively unique species.

The Neanderthals, who by about 200,000 years ago had evidently outcompeted *Homo heidelbergensis* into local extinction in their European redoubt, left a remarkable record of achievement. For one thing, they were hugely skilled practitioners of the complex prepared-core technique. Still, while they produced stone tools beautifully, they did so rather monotonously in the sense that, like their forebears, they produced remarkably similar tools wherever and whenever they went.

While early analyses recognized a very large range of Neanderthal stone tool types, more recent reappraisals have shown that many represent stages in the same "reduction sequences," reusing scarce materials. To make a really good Mode 3 tool, you need a predictably fracturing material such as flint, which isn't available everywhere. Implements made of such valuable materials were thus continually resharpened by Neanderthals, who knew good stuff when they saw it. Each time they were re-edged, the tools became smaller and changed their form, giving a spurious impression of variety in basic types. In contrast, tools made from abundant inferior materials were much cruder and were not reworked.

But while the Neanderthals were great craftspeople, the spark of restless inventiveness that animates modern technologies just doesn't seem to have been there.

Not that the Neanderthals introduced no innovations. They seem, for example, to have invented burial of the dead at some time about 70,000 years ago. Frustratingly, it's hard to know exactly what this new practice implied. To us burial is part of a larger ritual system, with echoes of the afterlife and spiritual belief, and it is intimately tied up with our symbolic capacities. But among the Neanderthals it may well have reflected something more immediate or more confined. It might, for example, have been a material expression of the same kind of emotion that elephants appear to experience for deceased relatives rather than, as in our case, being equally the product of an intellectual construct overlayering such emotions.

To have spiritual feelings you need to be able to envision dimensions that transcend your immediate experience of the world, and it is not at all evident that the act of burial in itself implies that ability. Certainly, we have no clear evidence that Neanderthals ever buried their dead with grave goods. The practice of burying with the deceased objects that would be useful in an afterlife, or critical in making the journey there, has been a widespread feature among modern human societies from very early times. It is indicative of the unique human ability to envision worlds alternative or complementary to the one we experience every day. It is good evidence of symbolic mental processes.

On the other hand, while the absence of complex burial from the Neanderthal record is certainly not *proof* that these hominids were incapable of spiritual beliefs, this seems to be the implication. Our modern symbolic ability is superimposed on structures and behaviors that have very deep origins in our history. We do many things that are now mediated by our symbolic capacities, but that our forebears must have done in their absence—as the comparative study of primate behavior very strongly suggests. Burial may be an excellent example, having taken on new overtones and new meanings with the advent of symbolic thought.

The most famous Neanderthal interment is probably the "flower burial" at Shanidar Cave in northern Iraq. The shallow grave of an individual buried there some 60,000 years ago was unusually rich in the pollen of spring flowers, leading to the notion that flowers had been deliberately placed in the grave before it was filled. However, the presence of the pollen has also been attributed to the activity of rodents, still present today, that hoard quantities of blossoms in their burrows.

Perhaps, then, a more suggestive observation at Shanidar is the skeleton of an aged male who had been afflicted by a withered arm, perhaps from birth. That this individual contrived to lead a long life in the harsh Neanderthal environment has been taken to imply that mechanisms of social support had aided in his survival. What this might mean for the specifics of Neanderthal life and worldview is less clear, especially given that similar claims have been made for a vastly older and smaller-brained individual from Dmanisi, who had survived to a very old age with virtually no teeth.

None of this is intended to belittle the Neanderthals, who endured for a very long time in a range of Ice Age environments that were for the most part difficult indeed. Even during milder interludes, plant resources were scarcer than in warmer climes, and *Homo neanderthalensis* was clearly an accomplished and adaptable hunter, responding flexibly to the resources available locally. Indeed, at least in one place isotope studies suggest that these hominids specialized in the hunting of very large and difficult animals, namely woolly rhinoceroses and mammoths.

Altogether, one has to admire the way in which the Neanderthals coped with tough conditions, and pretty clearly what made this possible was cultural rather than physical accommodation. It has been calculated that the amount of subcutaneous fat needed to insulate the delicate internal organs of a Neanderthal from harsh external conditions would almost have equaled its basic body weight: obviously not a practical proposition in an active hunter! They must have possessed clothing and other cultural accoutrements that their cousins in the tropical regions of the Old World could well have managed without; and their ability to accommodate culturally to prevailing conditions allowed the Neanderthals to flourish, if at low population densities, across a wide swath of the Old World.

Clearly, then, Neanderthals were hominids of considerable cognitive sophistication who interacted with the world around them in an unprecedentedly intricate way. But there is no good evidence that they processed their knowledge of that world in the very unusual way that we do. And while Neanderthals certainly had highly complex means of communication, it is highly doubtful that they had language, using a finite number of vocal elements to make infinite numbers of different statements. There has been a long debate over whether they possessed the physical equipment necessary to produce the sounds we use in speech, and it turns out that the answer is probably no. Archaeologically, there is little to bolster the notion that Neanderthals were articulate in the way we are—though to put this in context, there is little to suggest that the earliest *Homo sapiens* used language either.

Finally, for all their cultural and presumed cognitive complexity, the Neanderthals were not at all like *Homo sapiens* physically. Their bodily structure reflected their long history of independent evolution, as dramatically illustrated by a recent reconstruction of an entire Neanderthal skeleton, cobbled together from partial skeletons preserved at diverse sites. The Neanderthal skeleton is robust, with a primitively wide, flaring pelvis and a broad, upwardly tapering rib cage. This contrasts strongly with the relatively narrow pelvis and thorax of *Homo sapiens,* which is also more compact in its limb joints. Together, these features suggest differences not only in structure but in gait between the two kinds of hominid.

Above the neck, the differences are even more striking. Although Neanderthals had brains at least as large as ours, these were

FIGURE 10.1. Reconstructed Neanderthal skeleton (left) contrasted with one of a *Homo sapiens* of comparable height. Photo by Ken Mowbray.

housed in a skull of very different shape, with a low cranial vault retreating sharply behind a large, jutting face with oddly swept-back cheekbones. Considering all of the features distinguishing the skeletons of *Homo neanderthalensis* and *Homo sapiens,* it is hard to imagine that, on meeting, the two forms would readily have recognized each other as reproductive partners.

Indeed, molecular anthropologists have concluded that gene exchange once the two populations came into contact was biologically negligible, if there was any at all. This conclusion is independently reinforced not only by the fossil record, which discloses no plausible physical intermediates, but by the direct extraction of mitochondrial DNA from a dozen Neanderthal fossils. While varying among themselves as would be expected, the Neanderthal mtDNA samples are all highly distinct from their counterparts in modern *Homo sapiens*. So although some paleoanthropologists still persist in looking upon the Neanderthals as a bizarre variant of *Homo sapiens* (for no better apparent reason than that both species had big brains), there is no reasonable doubt that they were an entirely independent evolutionary entity—and thus the best mirror we have in which to measure our own uniqueness.

The Origin of *Homo Sapiens*

While the lineage culminating in *Homo neanderthalensis* was flourishing in Europe, developments in hominid evolution were proceeding apace in Africa. Unfortunately, though, we see them through the lens of a very imperfect fossil record. In the several hundred thousand years following Bodo times, we find a number of reasonably large-brained hominid fossils that are too distinctive to be reasonably shoehorned into *Homo sapiens* as we know it today. The relationship of these specimens to our own species remains equivocal, but we may pretty confidently suppose that our ancestry lay somewhere within the rather miscellaneous assortment of hominids that occupied Africa over the past half-million years or so, some of which were contemporary with the earliest putative African *Homo sapiens.*

The most ancient candidate we have for *Homo sapiens* status is a rather fragmentary skull from Kibish, in southern Ethiopia, that may be some 195,000 years old. Conveniently, this date coincides quite closely with what molecular anthropologists have lately been estimating for the origin of our species based on DNA diversity in modern populations.

Sadly, the specimen itself leaves much to be desired, although it is clearly much closer to modern humans than anything else of comparable antiquity. Its archaeological associations are slender, but a few unimpressive lithics from the same deposits have been ascribed to the Middle Stone Age. Younger at 160,000 years, but considerably better preserved, is a cranium from the Ethiopian site of Herto. Lacking a lower jaw so we can't see if it had possessed a modern chin, and somewhat damaged in the very diagnostic region above the eyes, the Herto specimen appears nonetheless quite plausibly *Homo sapiens*.

No living sites were found at Herto, but both Acheulean and Middle Stone Age stone implements are found in the same sediments, implying that our species was born in a very archaic technological context indeed. This impression is strongly reinforced by the earliest unequivocally modern human remains. Some 93,000 years old, these come from Jebel Qafzeh, in the Levant, which *was* a living place. The copious archaeological associations there are with the Middle Paleolithic Mousterian—the same culture as the Neanderthals, who seem both to have preceded and succeeded moderns in this area. Indeed, in the Levant, Neanderthals and moderns seem to have come and gone, and possibly to have coexisted, over a period of many tens of thousands of years. During this time they wielded virtually identical tool kits. There is no reason to suspect any significant behavioral differences between the two species.

Back in Africa, some stirrings of technological innovation are evident over the past few hundred thousand years, although not in direct association with *Homo sapiens.* Mode 4 tools—long, thin "blades," traditionally identified with the Cro-Magnons, the earliest *Homo sapiens* who invaded Europe at only about 40,000 years ago—begin to show up sporadically in Africa several hundred thousand years ago, in otherwise Middle Stone Age contexts. Such "advanced" behaviors as pigment grinding and, later on, shellfishing and long-distance exchange of valued materials, also appear in Africa relatively early. Still, to repeat, it is not clear that any aspect of Old Stone Age economic activity necessarily reflects an awakening of symbolic mental processes, and not until after about 100,000 years ago, though still in Africa, do we begin to detect what we can seriously consider as evidence of a symbolically mediated view of the world.

At the site of Klasies River Mouth on Africa's southern coast, Middle Stone Age living sites about 100,000 years old have been said to show a symbolic organization of living space. More tangible evidence of symbolism comes from Blombos Cave, another coastal site not too far away. There, in Middle Stone Age levels about 75,000 years old, were found a couple of ochre plaques engraved with regular geometric markings. One of these is particularly striking and has been accepted by many as the world's earliest overtly symbolic artifact. This conclusion is strengthened by the finding in adjacent deposits of small gastropod shells that were apparently pierced for stringing: an early necklace. In all recorded societies body ornamentation is, and was, loaded with social meaning and overtones of status, so these shells are generally seen as tokens of symbolic processes in the minds of the hominids who pierced them. Similar "beads" of even greater antiquity, comparable to Klasies, have recently been reported from sites in northern Africa and Israel.

While these findings reinforce the notion that the human spirit was astir in Africa as long ago as 100,000 years, we have to wait a long time to see evidence of this spirit in full flower. A poor record means that we know little of what was going on in Africa following about 70,000 years ago, though these were times of climatic vicissitudes and drought that made much of southern Africa uninhabitable for tens of thousands of years. Whether any direct connection will ever be shown between the early indications of symbolism at Blombos and later ones elsewhere is hard to predict. What is certain, however, is that when the uniquely human spirit next found recorded expression, it was expressed with a vengeance.

A Creative Explosion

At some time under forty thousand years ago, the first fully modern Upper Paleolithic peoples began to trickle into Europe, presumably from an ultimately African point of origin. And unlike their anatomically modern predecessors in the Levant, these Cro-Magnons soon began to leave abundant evidence of virtually the entire panoply of human symbolic behaviors. The record they left behind is nothing short of extraordinary. Not only did these people make sophisticated tools out of a wide range of materials whose particular properties they clearly intimately understood, but, starting at least thirty-five thousand years ago, their artistic creations—the ultimate expression of symbolism—stand among the most deft and powerful images ever made. Not only did the Cro-Magnons render exquisite and immaculately observed animal images on cave walls, but they accompanied them with geometric signs of all kinds—some of which clearly represented local idioms. In fact, they often made these images in the most improbable and difficult of locations, for reasons that can only have sprung from the unfathomable intricacies of the human spirit.

Painting, engraving, sculpture: all were established at this early stage, not only in special contexts but also in domestic ones, as utilitarian objects were liberally decorated—knife handles, spear-throwers, and, later on, harpoons. These people made notations on plaques of bone and antler, some of which have been interpreted as lunar calendars. At well over thirty thousand years ago, vulture-bone flutes of sophisticated sound ability testify that they were playing music. Technologies diversified locally, reflecting the restless inventiveness that has characterized modern humans ever since. Both social grouping patterns and hunting techniques became more complex, as reflected in the structure and contents of their living sites, which clearly and routinely display a division of space into zones where different activities were carried out. The list goes on: by twenty-six thousand years ago we have evidence of the arrival of tailoring, in the form of sharp, tiny-eyed bone needles; and occasionally clay statuettes were fired at high temperatures in simple but remarkably effective kilns.

The Cro-Magnons expressed the unique human capacity in its fullest and purest form. Their lives were drenched in symbol—and though they may not have been the first such people, the Cro-Magnons are the first to have left us a record that leaves no doubt they were *us*, in possession of *all* of the basic capacities that underpin our modern lifestyles today.

It is probably no coincidence that these were the people who, in ten thousand years at most, contrived to dislodge the Neanderthals from the entire huge area that they had occupied, and to nudge them into extinction. Whether this exclusion was achieved by direct conflict, indirect economic competition, or both, we don't know for sure. What is clear, though, is that something similar may have been happening to *Homo erectus* (and to *Homo floresiensis*) in eastern Asia at about the same time, and that more archaic hominid types also failed to persist in Africa.

We should not make too much out of extinction, which is after all the inevitable fate of all species, however successful. Nonetheless, over the long span of hominid history, several hominid species had routinely contrived to coexist in the world—even on the same landscape—at any one moment. In contrast, with the arrival of symbolic *Homo sapiens*, something extraordinary had evidently emerged on the scene: an entirely new entity, intolerant of competition from its kin, whose destructive capacity is far from exhausted today.

The Origin of Human Cognition

Something profound had happened. As smart and resourceful as the Neanderthals may have been, symbolic *Homo sapiens* is not a simple extrapolation of what had gone before; it is a qualitatively different entity, not an incremental improvement. The ability of an organism to imagine alternate worlds rather than simply react to the real one (which itself is a matter of perception: are you, for instance, principally olfactory or visual?) evidently changes the rules of the ecological and evolutionary games entirely.

In order to understand the emergence of this new quality of ours, we have to remember that the very first people who looked exactly as we do evidently did not behave like us. Indeed, the first *Homo sapiens* possessed technologies that were identical not only to those of their predecessors, but to those of the other hominids—Neanderthals, Middle Stone Agers—with whom they coexisted. And, significantly, they did not displace those others. It was only at some point well within the tenure on Earth of anatomically modern *Homo sapiens* that the new cognitive capacity expressed itself, at some time after about one hundred thousand years ago. Odd though this may intuitively seem, it should not surprise us. We have seen multiple examples throughout this book, and especially in this chapter, of a fundamental disconnect between structural and behavioral innovations.

Any new behavior has to be permitted by the structure that is already there, and new behaviors cannot propel appropriate new structures into existence. What seems to happen is that there is often a lag, potentially of very long duration, between the acquisition of a new structure (which may be maintained simply because it doesn't get in the way, or because it is genetically linked with something that *is* immediately useful) and its recruitment to a new role. With symbolic *Homo sapiens* we are clearly looking not at *ad*aptation but at *ex*aptation, the familiar process (think tetrapod limbs or avian feathers) whereby new structures are only co-opted well after their origins to the roles in which they are now familiar. This phenomenon of exaptation is a hugely important component in the evolutionary process—and an entirely routine one.

Almost certainly, as part of the radical developmental reorganization that produced the highly derived modern human skeleton, some neural innovation was acquired that exapted the human brain for symbolic thought. Presumably relatively small in structural genetic terms, this innovation capitalized upon hundreds of millions of years of accretionary vertebrate, mammal, primate, and hominoid brain evolution.

Whatever it was, it seems to have acted much like the keystone of an arch. By superimposing itself upon the neural legacy of the immediate *Homo sapiens* ancestor, it created a structure with an entirely new potential. For, while the symbol-ready brain was clearly a *product* of a long history, the potential it created was not *predicted* by that history. Much more than simply an improvement on what was already there, it allowed a radical change in the way information was processed in the higher centers of the brain. Clearly, this new brain was backwardly compatible: its first possessors were able to continue doing business just as before, exactly as the first *Homo ergaster* had done in the remote past. As a result, before the full potential of its new biology could be expressed, *Homo sapiens* had to discover what it was newly able to do, and this could only have been achieved through the action of a cultural stimulus. The biology, after all, was already there.

What might the stimulus have been? For a variety of reasons the obvious candidate is the invention of language. For one thing, language is the ultimate symbolic activity. Indeed, it is impossible to separate it from symbolic thought as we experience it today. Like thought, language involves abstracting our perceptions of the world into a vocabulary of discrete mental symbols, and recombining them to create new constructs and meanings. It is, indeed, hard for us today to conceive of language and symbolic thought as entirely separate entities.

What makes language an even more attractive candidate as a releaser for symbolic thought is that it is also the ultimate communal property: something that would readily spread within a population that was exapted for it, even in the unlikely event that the symbolic ability was initially co-opted as an internal conduit to thought. Its communal quality makes language significantly more plausible as a population-level releaser than such essentially internalized candidates as the ability to envision multiple levels of intentionality (technically known as “theory of mind”): I know that you know that he knows . . . and so forth.

We also know that structured languages are quite readily invented spontaneously by prepared human minds, as in the case of a sign language (governed by rules similar to those of vocal languages) recently made up by deaf Nicaraguan schoolchildren. Indeed, I am greatly attracted by the notion that language was invented not by adults but by children—who are famously more receptive to new ways of doing things than adults are, and who like to distinguish themselves from their elders. Finally, although articulate language makes heavy demands on the vocal tract, it is evident from cranial base morphology that the structures that make it possible were already in place. They had been there at least since the origin of *Homo sapiens* as a recognizable anatomical entity some two hundred thousand years ago—having clearly arisen initially in an entirely nonlinguistic context.

Together with the emergent (rather than selected) nature of the human capacity, the accretionary history of the human brain helps us understand why we are in many ways such odd and inconsistent creatures. We possess the rationality that is conferred by our symbolic capacity, but we are not entirely rational beings. Many of our conscious decisions are at least partly processed through some very ancient brain centers indeed. As a result, we make bad decisions for bad reasons. We are notoriously poor at assessing real risk. We are very inefficient judges of value. At least corporately, we seem to be almost incapable of placing our own long-term best interests ahead of short-term gain.

All of this and a whole lot more tells us that our vaunted brains are not optimized for anything—which is probably a very good thing, since any form of optimization would involve tradeoffs, most of which would be awful to contemplate. Instead, we have a rather rickety general-purpose brain that happens to possess some remarkable capacities. The human brain is not something that any human engineer would put together. This jury-rigged aspect not only makes the brain the unique instrument it is, but it is what makes our paradoxical species simultaneously so admirable and so despicable. After all, it is hard to argue that, as a whole, *Homo sapiens* displays any consistent human condition. For every saint you can find a sinner, for every philanthropist a thief, for every open mind a closed one—sometimes, all in the same person.

Where did the release of the odd modern human capacity take place? Pretty certainly, this almost unimaginable transition from a nonsymbolic, nonlinguistic state to a symbolic, linguistic one happened first of all in a small, relatively isolated population of *Homo sapiens* that lived in Africa, plausibly eastern Africa. From studies of genetic diversity in living human populations, molecular biologists reckon that at some time around sixty thousand to eighty thousand years ago, the worldwide population of *Homo sapiens* underwent a dramatic contraction. This event correlates well with the African climatic vicissitudes I've already mentioned, and it may have involved the reduction of the entire *Homo sapiens* population to no more than a few hundred individuals, or to a few thousand at most. Small populations provide optimal conditions for the fixation of genetic or behavioral novelties. It is entirely credible that it was among the stresses of such a contraction event that the modern human capacity began to be exploited. Subsequently, with the relaxation of environmental conditions, newly symbolic humans were able to range once more beyond Africa, just as successive waves of hominids had previously done.

The fossil record is fairly unhelpful on just how *Homo sapiens* spread out of Africa, although it's evident that more or less the entire Old World had been populated by about forty thousand years ago. However, by comparing the distribution of genetic markers in populations around the world, molecular biologists have been able to come up with a fairly finely calibrated account, mostly but not entirely based on mitochondrial DNA (passed along in the maternal line) and Y-chromosome DNA (paternal). Given the greater general mobility of males than females, the patterns of genetic diversity derived from the two sources differ a little, but the larger picture is clear.

About sixty thousand years ago, the human population started to expand and diversify again in (probably eastern) Africa. Some lineages stayed in that continent, heading both west and south. Others struck out north, either continuing into Europe, where colonization and the elimination of the resident Neanderthals began about forty thousand years ago, or eastward into Asia. The initial wave of Asian colonization stayed to the south, crossing Asia Minor and then hugging the Indian coastline on the way to Southeast Asia. Once there, one major group expanded north into China, where fossils confirm they were present by about forty thousand years ago. Ultimately, descendants of these people spread back westward into central Asia. Another group went into the deep Southeast, occupying the Indonesian archipelago by around forty thousand years ago—which coincides approximately with the latest dates we have for *Homo erectus* in that region.

Modern humans may have arrived in Australia even earlier, although today's aboriginal Australians are probably descended from later immigrants. Genetic and cultural sources both indicate that the Pacific islands were colonized from the west rather than from the Americas, beginning only within the past few thousand years. The far end of the route north through China was Siberia, and from there the New World was ultimately colonized, either via a Bering Strait land bridge or by following the coastline in boats. The modern indigenous populations of the Americas appear to have been established as a result of multiple immigration events. The exact number is debated. Some geneticists favor three, others two, all within the last twenty thousand to fifteen thousand years or so, and one perhaps as recently as seven thousand years ago. Most archaeological evidence suggests that North America did not become significantly inhabited until about fourteen thousand years ago, although one date of a thousand years earlier from a site in Chile suggests that an initial wave of immigrants had coasted all the way south by that time.

Within each major region of the world there have been multiple dispersals of human populations since the initial arrivals, and probably a lot of local extinctions as well. Populations have restlessly washed back and forth as long as humans have had their wanderlust. As a result, when molecular anthropologists calculate trees of human population relationships based on genetic markers (particularly using nuclear DNA), they very often find them to have a webby appearance, indicating a very complex history of interchange. Molecular anthropologists also discovered that, on average, even very widely separated human groups show a whole lot more internal genetic variation than occurs among them. For all the variety that we are prone to perceive, *Homo sapiens* really is a very close-knit species, and a very young one.

The Origin of Spirituality

In any catalog of human universals, spirituality and religious feeling always figure high on the list. No property of our unique and complex mind is more profoundly implanted in the human psyche, or more widespread among human societies, than the feeling that we human beings are part of a larger whole—that there is something greater out there than we are directly able to perceive. The ability of the human mind to harbor such notions is, of course, directly related to the symbolic capacity: the ability to conceive of alternate worlds that nobody has actually seen or that are not directly accessible to human perception.

In this sense, our collective spiritual sensibility is clearly a coproduct of the switch to symbolic cognition that marked the origin of *Homo sapiens* as we know ourselves today. If the unique human spirit was ever breathed into our species, it was at the point when this unique form of symbolic cognitive functioning was acquired.

But the apparently universal *need* for this sensibility (among societies, at least; it evades some individuals) suggests that there is more: an apparently ingrained interaction of our higher centers with more ancient, broadly emotional regions of the brain, to produce a longing that begs spiritual fulfillment. Perhaps this yearning has at least partly to do, as Freud suggested, with the insult to the human ego that death represents, and that religious belief can transcend. Equally, though, it might involve a highly functional mechanism for sustaining the self-aware individual in an indifferent and arbitrary world—from which, for most of its history, members of *Homo sapiens* have not been nearly as insulated as we typically are in the Western world today.

But the individual is not the entire story here. For via its close cousin religion, spirituality also fulfills an apparently essential social function. Religion might, indeed, be described as the connective tissue of virtually every society ever recorded. Many primate societies might be characterized more or less adequately as the sum total of all the interactions among their members, but no human society could be described in this way. The ethereal cannot be ignored. A common belief in humanity's place and role in the world, frequently expressed via accounts of its origins, is perhaps the most fundamental expression of the social dimension of the human psyche.

Such shared beliefs within populations have turned out to be the strongest social glue that exists. In the most intensely social animal of them all, it was inevitable that religious beliefs should have been regularly co-opted to political ends, thus in turn feeding back into social and economic organization. To give just one example, without the intermingled and inextricable forces of religion and community, Lower and Upper Egypt would never have been united, turning the Nile Valley into the economic powerhouse of the ancient world through public works of unprecedented scale.

Significantly, no society has ever managed to entirely eliminate religious or spiritual beliefs among its members—although, illustrating the inescapable human paradox, it is improbable that any society has ever been able to impose them universally, either.

Primate behaviorists have made much out of the fact that the basic underpinnings of human religious awareness, as of morality and fairness, are to be found in the advanced sociality of primates in general and of higher primates in particular. Dogs, too, have recently been shown to have a sense of "justice." And certainly, whatever it is that human beings are today, in cognition and belief as well as in all aspects of their physical being, it is founded upon a long history that ultimately goes back not merely to the origin of the primate order but well beyond. None of what we are would be possible in the absence of any detail of that history.

But the background from which we sprang was about being primate, rather than about being human; and spirituality as we experience it certainly cannot be defined as anything other than something that, as far as we know, only modern humans have. It was presumably even lacking—except in potential—among the very first beings that were physically structured exactly as we are.

Conversely, although the nature of spirituality is inevitably defined by our own modern sense of being human, we can be pretty sure that as far back as there was symbolic consciousness, there was spiritual awareness. Throughout recorded history, significant new discoveries of all kinds have immediately unleashed energetic exploration of the possibilities inherent in them, and there can be no doubt that, as soon as it became possible to imagine worlds lying beyond the one of everyday experience, such worlds *were* imagined.

Indeed, we have historical evidence at a very early stage that this was the case. If you are ever fortunate enough to visit those phenomenally expressive Ice Age cave art sites of southern France and northern Spain, the earliest of which date to between thirty thousand and forty thousand years ago, you will immediately understand this in the most visceral way possible. Ancient though it may be, Cro-Magnon art has a power that must be experienced to be comprehended; and though it was *of* this world, like religious art today it was clearly not solely *about* this world. Sadly, while it clearly reflected its makers' understanding of their environments, and their explanations of their own place in them, the exact referents of this art are lost to us, presumably forever. But whatever elements it may have contained of the mundane, it was clearly also art of magnificent transcendence.

Of course, the Cro-Magnons were hunters and gatherers, not sedentary and postindustrial as we are. And we know that, as conceived by the remarkable human mind, the content and expression of alternative worlds varies vastly with the circumstances of the individuals and societies concerned. In his book *Dominion,* my colleague Niles Eldredge points out that hunter-gatherers and sedentary agrarians tend to see their places in the world very differently. Historically documented hunter-gatherers seem to have viewed themselves as part of the ecosystems around them. They lived from their bounty and by their rhythms. Because like all human beings they were incapable of imagining cognitive frameworks alternative to their own, they tended to imbue Nature with a human spirit, and thus by extension to embrace themselves within it. They felt themselves to be *part* of their surroundings, which in turn they imbued with spiritual significance.

Agrarians, on the other hand, find themselves in opposition to Nature. Rain doesn't fall at the farmer's convenience, and life for agriculturists is a constant battle to shift the odds in their favor. The battle has constantly intensified as populations, no longer under purely natural constraints, have continued to grow.

The exigencies of the settled condition have led to an entirely new view of humanity's place in Nature, a view that Eldredge points out is nowhere better captured than in the founding documents of the Judeo-Christian tradition. These were, of course, recorded by the near descendants of the very first sedentary peoples who responded to climate changes at the end of the Pleistocene by planting crops and domesticating animals. In Genesis

1:26–28, perhaps the closest thing we have to the direct testimony of the first farmers, God says:

> Let us make man in our image, after our likeness: and let them have dominion over . . . every . . . thing that creepeth upon the earth. So God created man in his *own* image . . . male and female created he them. And God blessed them, and God said unto them, Be fruitful, and multiply, and replenish the earth, and subdue it; and have dominion over the fish of the sea, and over the fowl of the air, and over every living thing that moveth upon the earth.

Eldredge's book is about the ultimate impact of this mind-set on world environment; and although other elements of this extract might be emphasized, the word he sees as most significant in it is "dominion." This view of creation helps justify the struggle of the authors of Genesis to modify Nature, and to impose their will upon it, as agrarians have to do. The results of the humanly heedless exercise of the authority thereby granted are the subject of a vast literature; and beyond noting how gratifying it is that, after many years of neglect, increasing attention is now being paid by Christians to the injunction to "replenish the earth," it is beyond our scope to pursue the issue here. Still, Genesis reveals our basic human need to justify particular ways of doing things. Symbolic human beings not only want to know *what*, they also need to explain *why*. Traditionally, religion has provided the necessary explanations.

In this way spirituality, by way of its more politically and structurally focused cousin religion, has served (and continues to serve) the vital function of explaining and giving coherence to the world around us. It reflects the profound human need to *know*. But human need to know in particular ways. It is clear that our jury-rigged minds are highly reductionist, craving straightforward stories about the world, however murky and complex the facts may actually be. We long for simple cause-and-effect chains. Such accounts of the world are mainly what both science and religion provide at different levels of understanding. Indeed, it has often been remarked that, in traditional societies, religion served a function similar to that served by science in our own.

After all, religions typically provide explanations for why the world is the way it is, and for what we are doing in it, even if they do so by shifting those explanations to a plane that is intrinsically and intentionally beyond immediate human understanding. Still, while the perception of commonality of role is of course valid as far as it goes, it certainly doesn't capture the entire picture: science and religion do not furnish alternative explanations, take one and leave the other.

This is because, while science and religion reflect very different ways of knowing, those ways are entirely complementary. Science is a wonderfully compact way of knowing about the observable world, because it seeks to establish the rules by which Nature is ordered. And if you know the principles on which the world works, you no longer need to know all of the individual observations from which those principles were inferred. By now accumulating such knowledge would, of course, be a task beyond hopeless—as it was even in the time of nineteenth-century paleontologist Joe Leidy, one of the many "last men who knew everything." Back in the days of the very first farmers, it may have been possible at least to be familiar with all of the basics by which society and the economy functioned. But once science as a way of looking at the world gathered steam, society itself soon became dependent on scientifically gathered knowledge, and on the technological advances that knowledge made possible. Today, science has made itself indispensable. Society as we know it could not function without it.

Still, that doesn't mean that religion is redundant. Far from it. Scientific knowledge is provisional and inherently limited to what we can observe and measure in the material environment. Science cannot deal with eternal verities and ultimate causation, because these issues cannot be cast in testable scientific terms. Yet the human thirst to know the ultimate foundations of life and the universe is at least as great as that to understand proximate causes. Evidently the human symbolic capacity gives us not only the ability but also the imperative to reach out to possibilities that lie beyond the scope of science.

Despite the widespread perception that there is a conflict between scientific and religious belief (your story against mine), many scientists have preferred to underscore the intrinsic differences between the two forms of knowledge, and to operate on a "good fences make good neighbors" basis. This fits well with Jesus' injunction to "render unto Caesar the things that are Caesar's, and unto God the things that are God's."

But an alternative (or perhaps more appropriately, additional) perspective on the matter might emphasize that the search for knowledge in *all* of its dimensions is underpinned by the same identical human curiosity about the universe, and about our own place in it. Shifting the emphasis in this way, one can envision a single trajectory of developing knowledge, something like a two-stage rocket. Starting firmly in the material world, you can ride the scientific first stage to the point at which its fuel is exhausted, the point that lies at the limits of testable knowledge. From there—if you wish, or feel the need, as most people seem to—you can ignite the spiritual second stage, and be transported to the limits of the human ability to understand.

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Index