Jonathan Kingdon: Lowly Origin

CHAPTER 1

Preface to a Self-portrait from the Center of the World

Why Lowly Origin? Peculiarity of bipedalism and role of geography and ecology in explaining it. Evolution by increments. Hypotheses and definitions. The beginnings of bipedalism dated to about 6 million years ago (mya), originating in East African coastal forests. "Evolution by river basin." Separate fore-/hindlimb origins. Bipedalism as the criterion for all hominins. Bipedalism and brain develop separately.

Charles Darwin, in the final words of his "Descent of Man" (1871), put it this way: "[I]t seems to me, that man with all his noble qualities—with his god-like intellect which has penetrated into the movements and constitution of the solar system—with all these exalted powers—Man still bears in his bodily frame the indelible stamp of his lowly origin" (1).

Darwin was referring to many more than one or two stages of human evolutionary history. In the preceding pages, he had invoked wormlike, fishlike, and reptilian ancestries, and it was as much to these as to four-footed primates that he contrasted a soaring intellect, exalted powers, and noble, upright qualities.

For that most eminent of Victorians—no less than for any member of another culture, past or present, historic or prehistoric—uprightness (or, more prosaically, bipedalism) was a primary and definitive difference between humans and other animals. How that stance evolved is still a great mystery, and although fragmentary fossils of very early bipeds are, at last, being uncovered, there are still many more questions than answers when it comes to giving life to these broken bones and teeth. Some new ideas about bipedalism, its precursor conditions, as well as some of its consequences are central themes in this book. Although there are many scientific papers and single chapters of books that discuss bipedalism, this is probably the first to be devoted to it as a single dominant theme—the central condition on which human evolution is predicated.

In borrowing Darwin's two concluding words as my title, I invite reflection on a moment or "stage" in human evolution that was both metaphorically and literally "lowly." I attempt to reconstruct, in the light of much new evidence and inference, the appearance, ecology, and geography of those ancestral apes that were not yet bipedal yet must already have been predominantly terrestrial. Ancestors whose nonerect gait put them on the other side of that great conceptual divide between the category "Apes" and what we call "Hominids." I also reflect, but in a much more summary fashion, on the very earliest and even more "lowly" attributes of primitive aquatic vertebrates, because I find some relevance there for hand-brain connections.

The many undeniably apelike features of human gross anatomy were sufficient for Darwin's argument, but modern genetics has greatly extended the depth and reach of his insights. From this very contemporary perspective, his words "still bears in his bodily frame the indelible stamp" reads like a prophecy. You and I now know that almost every step of our evolutionary history is written into every cell of our bodies. My genome includes sequences that date back more than 700 million years, when my ancestor consisted of no more than one cell. Locked into the genetic mosaic that adds up to a living being are huge numbers of indelible or "undeleted" genetic particles that demonstrate a patrimony that goes back not just to apes but to the start of life on Earth. In common with every other organism, each one of us is the sum of genetic additions and subtractions on an unbroken thread of life that ties us, step by step, back to that fecund moment of origin, the first and lowliest of all our "beginnings" (figure 1.1).

It can justly be argued that because evolution is the sum of so many tiny genetic increments, any focus on just one event has to be distorting and arbitrary, even for so apparently momentous an event as rising up on

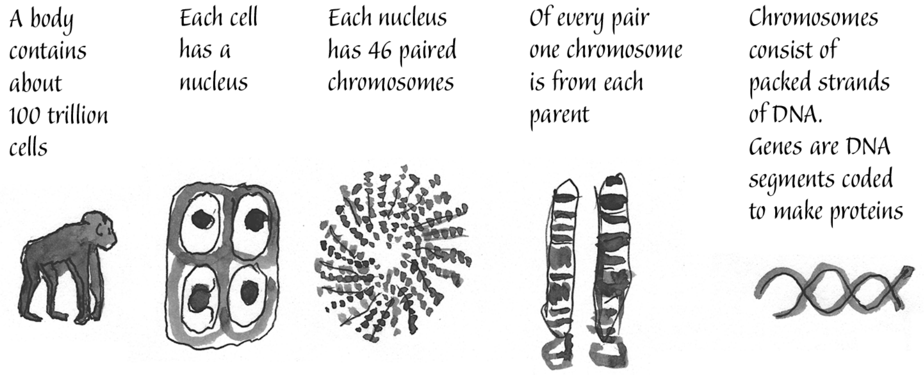

FIGURE 1.1 Building blocks of life, from DNA and proteins up to organisms.

two legs. To offset such conceptual isolation and to put bipedalism in a broader perspective, I have devised more than one framework to present my ideas. Only multiple frameworks can hint at the scale and difficulty of the enterprise. Our gait may be as plainly factual as our unquestionable existence as primates, mammals, animals; yet the puzzle of why an ape should get up on two legs is inseparable from the larger mystery of our emergence from nature as a culture-bearing species. For all the new fossils, newly mapped genome, and new awareness of the biological roots of human health, reproduction, and material culture, it is our profound and continuing ignorance of nature itself that remains the primary obstacle to self-knowledge. It is not difficult to report new discoveries from the frontiers of science; but it is less easy, as a scientist, to acknowledge that lacking the intellectual tools necessary to understand nature, we lack the means to understand ourselves. In the meantime, my multistranded narrative may hint at some of the many dimensions of human evolution while also expressing a personal confidence that the gap between nature and culture will one day be bridged by one of our greatest cultural achievements: science.

My first, largely symbolic presentation derives from an attempt, in the late 1980s to put together what I envisaged as a “Family Album,” a sort of pasted-up scrapbook of my far-flung family, the diaspora of modern humans (2). After publishing it under the title “Self-made Man,” I was challenged by a friend, who knew that I was also a painter, to attempt a “self-portrait” painted in both words and images. Not an autoimage of the artist as a young man compared with his middle-aged and elderly self, but rather a self-portrait informed by modern genetics and ecology as well as some less modern palaeontology. A portrait in which the younger self is the minimal vertebrate, an appetite-driven, wriggling backbone attracted hither, repelled thither; the youth an alert mammal-like reptile; the person in his prime a vivacious ape; and the elderly, worldly-wise wizard a contemporary, wholly modern human.

To try and retrace any part of that ancestry can be portrayed as a very personal quest, and there can be few that would deny the self-centeredness of our interest. It is in that spirit that I have adopted the metaphor of self-portrait as a medium to tell the story. But it is a self-portrait that reveals itself by increments. Each is drawn at a different stage of life, and each is set within a different landscape. Lifted out of this succession for special attention is the pivotal event on which human evolution hangs. This is not the arrival of consciousness, the ability to talk, or the evolution of a big brain. (All of these properties seem to have had very protracted histories.) Rather, it is the much more sudden event of walking on two legs, not four. What follows is not only new as an explanation, using new data, but also invokes new ways of approaching the problem of bipedal origins.

By including rudimentary vertebrates, reptiles, and monkeys in my autoportrait, I am expressing my self-awareness of *belonging* to nature, not being inexplicably different. In acknowledging the many qualities that seem more or less unique to me and my kind, I do not forget to remind myself that they must, in every case, be derived from earlier conditions that are typical for primates or other animals. Most of the characteristics that we envisage as uniquely human are actually species-specific amalgams, truly unique recombinations or composites of much more modest, preexistent increments. Some of the many unknowns in our evolutionary history will eventually become more understandable through some such incremental approach.

In such a fragmented biography, the acquisition of bipedal stance can so easily be presented as some sort of portentous coming of age: the moment in which all that followed would change irrevocably. The term hominin (or hominid) that we use to separate all bipeds from their ape cousins certainly reinforces that expectation. Yet, as many newly discovered fossils demonstrate, our monopoly of bipedalism must be seen in the context of numerous extinct bipeds. Since I first began to assemble the material for "Self-made Man," the number of new fossil hominin species has doubled, and what was envisaged as a pagoda tree of human evolution has become a bush that looks more and more like a thicket with numerous pruned branches and a succession of dead ends. While the biogeographic model presented in the following pages contributes new ideas to explain such bewildering diversity, only more fossils from more localities can tell us the true story.

The supposed bell of destiny must be muted by the awareness that not all the apes that became bipedal found themselves on a human trajectory. Getting up on two legs may have rung in a human future for our direct ancestors, but at least some bipeds, including some of the ones best known as fossils, remained “cranial apes.” That much is borne out by the fossil record. So, assuming that the distinction is a real one, what was it about our specific lineage that emancipated the earliest members of our branch from being just one more type of bipedal ape?

For clues to that puzzle, I turn to my second, less symbolic framework of ideas, locating my players in a succession of geographic and ecological contexts (without doing violence to fossil facts or the logic of known paleoecology and paleogeography). I seek answers in known anatomical changes that anticipate typically human attributes by diminishing the differences between juveniles and adults, males and females. I suggest corresponding changes in behavior that might have enhanced versatile all-group responses to various unpredictable challenges. Such social and mental versatility would have undermined the more genetically fixed responses of a species in possession of an ecological niche that existed within relatively predictable limits. Step by step, the predetermined behavior of a species with a single niche must have given way to the new competences of a species that could acquire multiple niches through an ever-expanding armory of technology, techniques, and eventually systems of communication to back them up.

For the most part, I have used the often random and accidental provenances of fossils as mere guides to the larger ecological and geographic contexts for human evolution, seeking clues in those details of African biogeography and ecology that we can still retrieve and reconstruct today. I have also sought to put the likely anatomical and behavioral responses of early hominins to a succession of environmental challenges into a sequential and spatial order that is consistent with the fossil record. A full time chart and checklist of fossil hominins has been kept for the last chapter, together with a summary of my conclusions, leaving the rest of the chapters to stress my biogeographic perspectives. Thus the first tie-up between time, place, ecology, and behavior is located on the east African coast, the second and third involve movement into the interior (each involving subtly different but highly significant divergences). The hominin trail leads on into Highvelt and other interior uplands and thence, very much later, to the Atlas Mountains (or Arabia). Each such translocation involved further refinements of bipedalism, from merely functional standing and walking to much later skills in fast running and jumping (3). In addition, there must have been a succession of mental and behavioral adjustments as the habitats and climates of particular populations changed over time. These are some of the disparate strands of analysis within which I have presented my ideas.

Finally, as a specialist in the evolution of mammals, the perspective that I have sustained longest (and reinforced most decisively in this book) is that of the emergence of humans as the evolution of yet another mammal—a very peculiar and special one, true, but in essence just one more African mammal. I have, as long as I can remember, always seen myself in that light and seek here to share that self-image. If the reflection you see is distorted by the mirror I have constructed or by my own deficiencies of vision and knowledge, that is my responsibility. But I take heart from the certainty that I share, with you and with others before us, the impulse to try and make sense of the deeply puzzling animal that stares back at us from the mirror.

I like to think that Charles Darwin, who must have been amused by contemporary cartoons of himself as an ape or the final morph of an egg-larva-pupa transformation (figure 1.2), would have enjoyed the conceit of a hagfish (a primitive, eel-like fish) rendered as a self-portrait. After all, he concluded that the "early ancestors of man, thus seen in the dim recesses of time, must have been as simply, or even still more simply organised than the lancelet or the amphioxus." As if in anticipation of the Human Genome Project, he also invited the idea of reconstructing the past from the realities of the present: "look to man as he exists; and we shall, I think, be able partially to restore the structure of our early progenitors, during successive periods" (1).

Self-portraits require mirrors, but reflections can stare back at surprising moments and from unexpected experiences. For example, among the diversions of my backwoods childhood in Africa were hypnotic audiences over the cadavers of various wild animals while they were being butchered or skinned. Commonest were antelopes, ostriches, or wild pigs being prepared for the pot. Then there was a leopard being carefully skinned for its coat; and a zebra. Least commonplace were species such as an aardvark, a striped hyena, or a monkey, victims of some accident and dismembered or dissected out of pure curiosity.

I especially remember the brutal rending away of a baboon's pungent pelt and the revelation of its stretched-out, pink, pathetic nakedness—like a jarring rip in the invisible curtain that had kept me separate from all other animals. Through the torn skin, its flesh was difficult to dissociate from my own. As a very small child I had once spent some months playing with an equally juvenile baboon, but for all its noisy, toothy de-

FIGURE 1.2 An obituary cartoon from "Punch" of December 6, 1881. The cartoon is a plaudit, with the "evolved gentleman" taking his hat off as a mark of respect to Darwin. Darwin is posed in the dress and attitude of a classical philosopher. The circle, labeled "Time's Meter," provides the frame for a spiral of "evolving forms" with the worm theme probably referring to Darwin's late work on the earthworm.

termination to subordinate me to its ferocious, infantile will, I had somehow kept vestiges of my species-specific distance. Yet here was the racked body of a dead adult that mirrored me. As my own warm, living hands sampled the springy resilience of cool gray fingers I imagined myself suffering the helpless indignities of being played with because I, too, for an instant, was dead. This must remain one of my earliest experiences of see-

FIGURE 1.3 Acting on hunches. A 1958 sketch in which I pondered the posture of a foraging ape.

ing my self-portrait in another animal. Years later, the element of self-portraiture must have remained when I made anatomical studies and drawings, not only of a baboon but also of humans.

This book tries to extend that moment of perception; but instead of a dead baboon, the principal objects in which I seek my own ancestral reflections are fossilized apes and hominins (figure 1.3). Although evolutionary science takes over from childish intuition to guide my brush and pencil, a central preoccupation is to try and bridge the gap between my long-lost genetic self as a baboonlike quadruped and the bizarre biped I am today.

Yet another incentive to write this book has been my discomfort with the terms in which human evolution is often presented. Too often I have been unable to match stories of one mammal's evolution, that of humans, with what I know of the biology of other African mammals and their occupation of African landscapes (4). In reaction, I began to ponder those respects in which the biogeography and ecology of other living mammals might help illuminate the course of human evolution.

One of the end-products of evolutionary theorizing is a genealogical tree that places every fossil species in a temporal and relational position to other known fossil species. Because there are a limited number of fossils and a large number of theorists, the choice of trees embraces almost every permutation of postulated relationships. Just how different these trees can be is illustrated in figure 1.4, where some of the more plausible

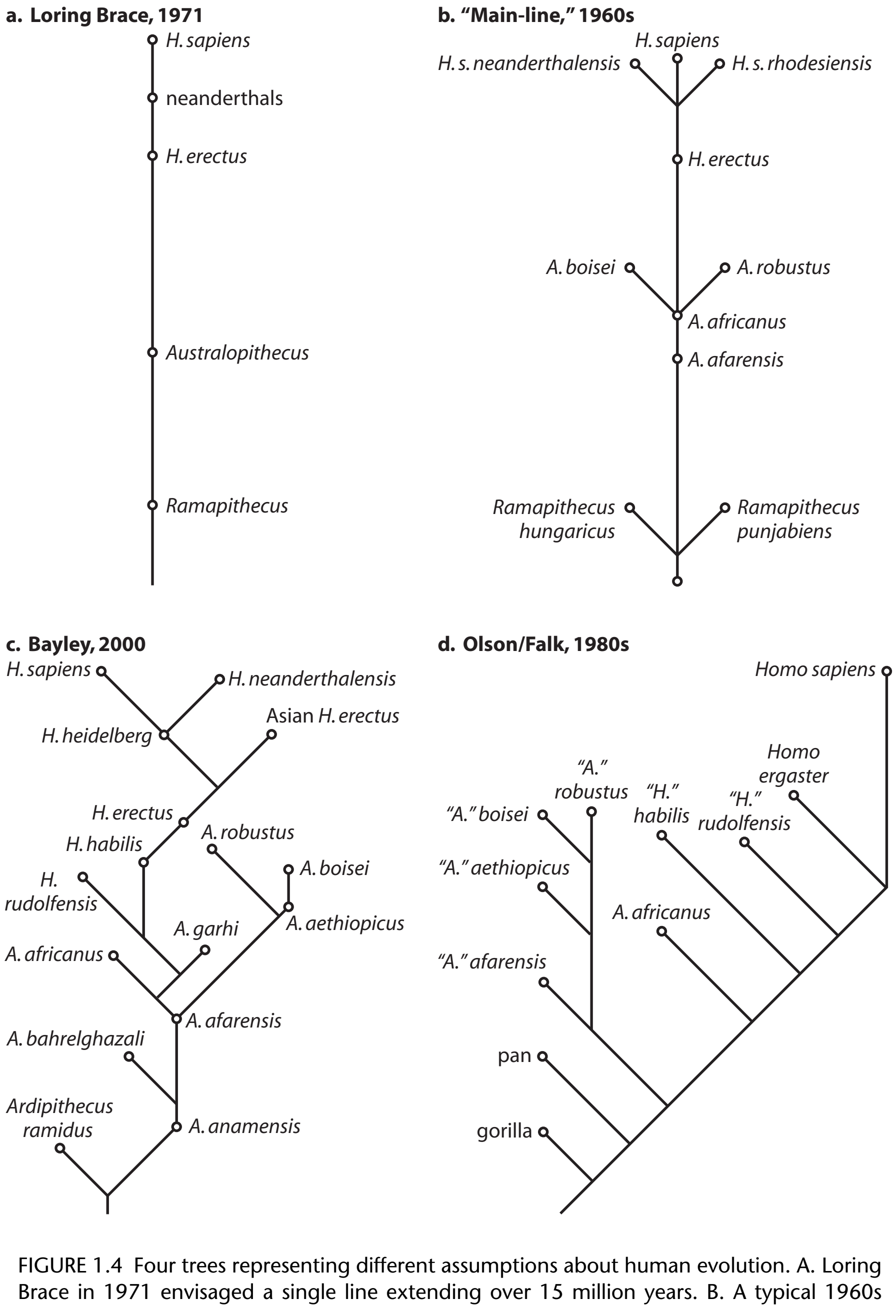

FIGURE 1.4 Four trees representing different assumptions about human evolution. A. Loring Brace in 1971 envisaged a single line extending over 15 million years. B. A typical 1960s "main-line" stem with hominids distinct for 15 million years. C. A 2000 tree with more branches but still a single tree on a 5-million-year time scale. D. The Olson/Falk tree (1981–1988), including apes on an 8- or 9-million-year time scale. (See text page 232 [figure 7.1] for my own conclusions about the human genealogical "bush.")

genealogies are displayed and their authors listed. My own conclusions about the relationship between fossil hominins correspond more closely with those of the authors Olson and Falk (5, 6) than to any others.

In a climate of conspicuous neglect of geography, these anatomically oriented authors have postulated a set of relationships that I have found broadly consistent with both the geographic and ecological patterns that have emerged from my own studies. The doubling in numbers of hominin species discovered since I began my last book on human evolution has itself been a direct stimulus to writing this book. This doubling in numbers has reinforced my discomfort with earlier explanations. Speciation, especially multiple speciation, has to take place in geographic or ecological compartments, and the evolution of discrete animals, plants, and endemic communities has been one of my long-term interests and the subject of many publications. The pages that follow seek patterns of isolation and dispersal that are at least consistent with the broad patterns that I have learned to recognize.

All animals have finite distributions that are loaded with many detailed implications for their ecological adaptations, evolutionary origins, and ability to spread or disperse. Both contemporary and ancient Africa can be understood as a pattern of ecological islands (7). Islands and isolation of any sort are intrinsic aspects of speciation, so the chapters that follow set out to contest the view that "it may be as futile to seek a specific and localized place of origin for hominids as it is for any other group" (8). Discussion of the geography of human evolution has often been so threadbare, abstract, and generalized that our many and different ancestors have no perceptible existence in time and space. There needs to be a fuller acknowledgement and awareness that our forebears were embedded in the same ecological matrices that other mammals are and have been, all with specific and finite distributions.

One of the most striking and surprising peculiarities of equatorial African fauna and flora is the frequency with which forest and nonforest species form pairs.* Among plants, amphibians, birds, and mammals, there are forest species whose closest relative is not another forest-adapted species but a nonforest sibling. These animals and plants apparently owe their primary success to adaptations that are not overwhelmingly governed by the weather. Free of such confining constraints, they would seem

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*I use the term nonforest because a stereotype has arisen of always contrasting forest with "savanna" or grassland when there are all manner of arid-adapted thicket formations that are emphatically *not* forest and *not* savannas. Furthermore, research on carbon isotopes in plio-pleistocene soils has suggested that open grassy "savannas" became extensive only between 1 and 2 million years ago (9).

to have responded to past oscillations of climate by evolving sibling species so that one or other form can take advantage of whatever climatic phase is currently dominant (7). It stretches the definition of "sibling species" to pair chimpanzees with humans, but it is appropriate to point out that the processes that have generated such sibling pairs may also have played a role in the evolution of both humans and chimpanzees.

Behind the evolution of such pairs are processes that are much more complex than mere two-way traffic between forest and nonforest. The habitats of today's species may differ in many important ways from those of ancestral species, but the fact that modern chimpanzees are forest-dwelling fruit eaters while omnivorous humans live in more open habitats has led to a widespread assumption about the course of human evolution. The favorite image is of forests drying out and the four-legged, forest-living ancestors of humans adapting to more open conditions by becoming erect. This, in my view, must be wrong; chimpanzee ancestors were not always tied to rain forests, and human ancestors could not have moved out into open environments until they were already bipedal. For a less simplistic scenario of bipedal origins, the abstractions of adaptation need to be broken down into increments and the dynamics of speciation related to those displayed by numerous nonhuman organisms. These comparisons suggest that in addition to taking account of climate change, African distribution patterns need to be examined in terms of the continent's surface pattern of ancient swells and basins, rivers and uplands (figure 1.5)

One challenge for species adapting to new or different habitats has been the repetitive drying out and retreat of extensive forests to a network of narrow galleries and riverine strips. During the Plio-Pleistocene, this tended to coincide with each global glaciation and gave a special importance to rivers as focal areas or refuges. With the return of humid climates, forests could expand from their riverine cores and swallow up the intervening country. In the pages that follow, both minor and major rivers and their basins play a central role in my understanding of the relationship between forest and nonforest biota.

My conviction that the human being is intrinsically one more African mammal found expression in the early 1960s, when, building on my Tanganyika childhood, I began an inventory of the mammals of eastern Africa that was, in effect, a series of essays on the evolutionary process and the diversity of its expressions. The multivolume "Atlas of Evolution in Africa" that emerged from my studies included a brief profile of *Homo sapiens* whose "peculiarities have been evolved by fundamentally the same processes that have determined the peculiarity of other mammals"

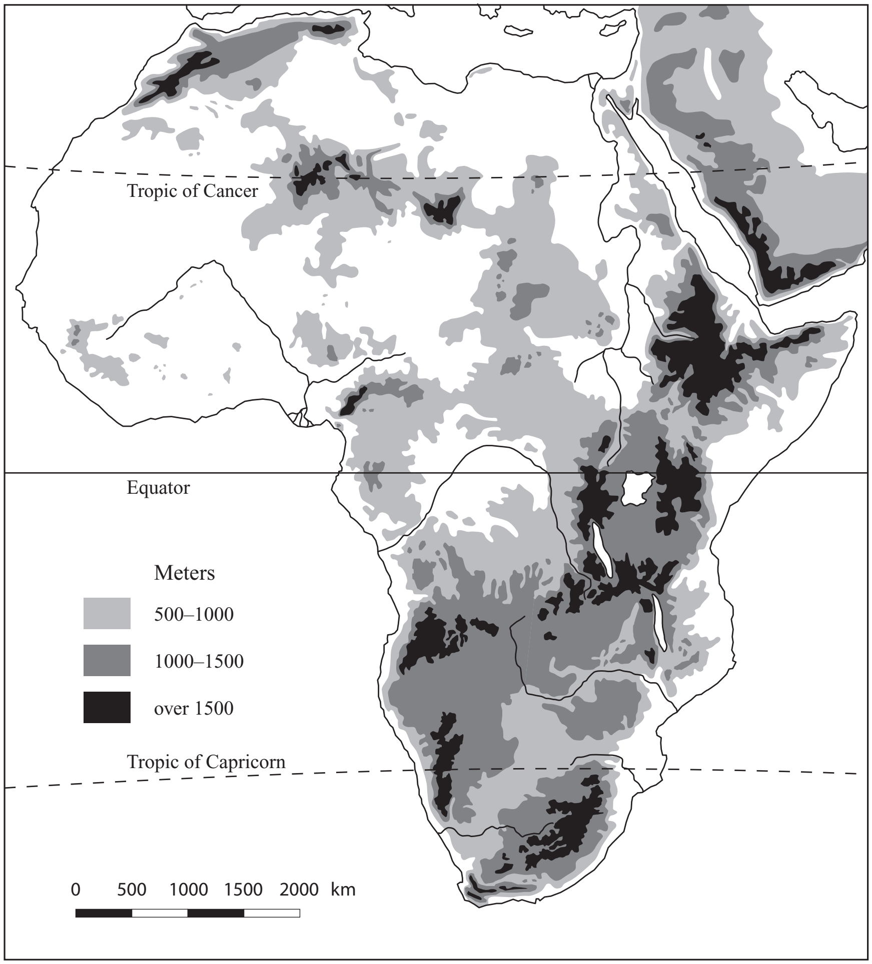

FIGURE 1.5 Africa: surface relief. Note separation into distinct northwest, northeast, east, south, southwest, Cameroon, and Saharan uplands. These areas represent discrete centers of endemism or refuges for numerous organisms adapted to cool or montane conditions. The separation of river basins and river banks has also influenced distributions and evolution. For schematic map of ancient tectonic basins, see figure 4.13.

(10). At the time, I presented this fauna as a microcosm of the mammals of an entire continent. As a sampler of Africa's diverse environments, its position as a corridor reinforced the pivotal status of this region. The fauna is, indeed, central to our understanding of evolution in Africa. In terms of my own evolution, both as a generic human and as an individual, entitling eastern Africa as "Center of the World" is a pardonable exaggeration.

Although my atlas identified some eastern endemics, I noted that the majority of mammal species belonged to a much wider area, some evolved far away perhaps, but drawn in to a region that serves as a corridor between north and south. It is the place where forest communities (stereotypically “western”) broadly overlap with those of savannas (likewise, commonly envisaged as “eastern”). This overlapping ensures that eastern Africa has the most diverse mammalian fauna in the whole continent and therefore in the world. The recurrent finding of new and ever more puzzling hominin fossils in east African soils confirms that their biogeographic history must have paralleled that of many other mammal groups. We can safely suppose that many species of prehistoric animals with distant origins were prone to finding their way to this most strategic and attractive of regions, but which species? Discriminating between local endemics and successful immigrants remains as much a challenge for studies of fossil as of living species.

From the time I was preparing my volumes up to the present, the greater part of our knowledge of fossil hominins and their environments has derived from a handful of sites on the eastern side of the continent, including the far southeast. As a result, eastern Africa has come to be portrayed as the archetypal Garden of Eden, the Center of the World for human evolution. Within limits, this updated Biblicism has some truth but, as I have already pointed out, east Africa has been an ancient theater for the excursions of habitats and fauna from very distant parts of Africa. If there is drama in human evolution, the local origins and subsequent travels of “provincials” that then made it big must be a large part of the story. One novelty of this account will be my efforts to identify the possible provenances of those provincials, however far-flung or improbable their places of origin might seem.

Consciousness of geography has been somewhat ambivalent in the literature on human origins. On the one hand, hominin sites are located and described in meticulous detail and, in the minds of many students, easily become equated with place and ecosystem of origin. On the other hand, in many theoretical models geography plays no role at all: everything hangs on the cusp of a tooth or the diameter of a fossa.

This combination is dangerous because fossils usually sample animals only once they are common and widespread. Occasionally, they may actually be in terminal decline. It is much rarer for them to be plausibly close to their place and time of origin. Mentally lifting hominins out of the communities in which they lived is equally distorting.

I see a need to relate what little we know about the evolution of prehistoric humans to more general patterns of mammal distribution. For example, it is important to know if a contemporary specimen comes from the edge or center of its range. At any given moment in time, species may give the illusion of being stable entities. In fact, they may actually be in a state of active dispersal, isolation, or even contraction and decline (11). It is therefore significant to know whether a species, living or extinct, is newly evolved and actively expanding its range; or if it represents a stable, longer established form. Some extinct species such as mollusks, pigs, and rhinos have long been viewed in this perspective, but there are now sufficient hints coming from a rapidly expanding scatter of hominin fossils to merit bolder timings and mappings of their supposed status in space and time. The maps that are offered here take full account of the fossils, but I often attempt to relate their peculiarities, localities, and dates to patterns of distribution and speciation that are inferred from living species. Some of my scene-setting may eventually prove to be misplaced or displaced, but even if some of the suggestions prove to be plain wrong, that will be of less significance than my self-reminding insistence that human evolution was never virtual but, like that of any other organism, had to have taken place in real space and real time.

A lifetime of walking through landscapes with the conscious awareness that my ancestors preceded me there has served to reinforce my determination to share this consciousness and assert its relevance for the way in which we reconstruct and model prehistory in Africa. Superimposed on this ancestor-inhabited world is a contemporary worldview in which new perspectives in genetics have taught us to envisage our ancestry as unbroken threads of DNA winding their way back, past innumerable catastrophes, to their earliest beginnings as single celled organisms. Along the way are billions of mutations, some of which find expression in incremental changes that can be picked up in the fossil record but which also require some knowledge to be studied and interpreted, some imagination to be visualized and portrayed.

Thus a central subject of this book is the rising up of what I call a “Ground Ape” onto two hindlegs, suggesting reasons and a location, in time and place, for that evolutionary moment. Partly because the event is incomprehensible without considering the events that preceded it, I have backtracked the trail that led up to that moment. Then, from the first, unsteady steps of a misshapen ape in an obscure province of Africa, I deduce, on the basis of other species and the inferred peculiarities of these bipeds, *where* the trails of their descendants might have led.

One difference between this account and many that have preceded it is that I try not to amalgamate adaptations. Thus, rearing up onto two of four limbs is seen as but a single adaptation within a long series of preceding and succeeding events, each of which was a discrete, perhaps modest, but essential prerequisite to becoming human. This multifaceted, piecemeal approach has shaped the "dissected" style of my analysis.

A second peculiarity of my own understanding of human evolution can be contrasted with the pictures that are painted in innumerable books, articles, and dioramas representing hominins and other extinct mammals in picturesque "National Park–like" fire-climax savannas. These depictions contradict the evidence that such landscapes became common only 1 to 2 mya (10). My own understanding of early human habitats, as expressed in this book, may derive in part from the years of my childhood and youth spent walking, hunting in, or traversing the "Itigi Thicket" of central Tanganyika. On one foray into this dry but dense and shady habitat, my companion, an entomologist, remarked that this must have been what large parts of Africa must have been like before human-set fires became widespread. His casual remark stuck in my mind, and its likely truth has been borne out by subsequent research.

Another primary difference between my approach and those of my predecessors is that I envisage standing as a relatively inefficient response to an exceptionally benign but very localized environment. This is the exact converse of previous explanations, which attempt to understand bipedalism in terms of improved efficiency under very widespread "savanna" conditions that were more difficult and trying than those in the forests or woodlands that preceded this supposed "ordeal" (12, 13).

Each chapter seeks to identify and portray some outstanding features of a particular ancestral condition. I try to locate innovations in some sort of framework of time and place and correlate changes in behavior with their anatomical and ecological contexts. The settings may be continents, ecoregions, a locality, or the provenance of a single significant fossil; the choice of which depends on sources and quality of evidence to locate particular evolutionary developments in space and time.

Fossil or molecular sources of information and supposed time frames are listed in a conspectus at the beginning of each chapter. The chapters succeed one another and develop, step by step, as an unfolding saga of hominid biogeographic history. The central focus is my analysis of the origins of bipedalism, but I have "topped and tailed" this pivotal event with my larger vision of how straightening the back, standing, walking (slowly, fast), running, and the slow elaboration of hand-eye-mind coordination must all have developed in a long, drawn-out sequence. Thus, both the beginning and final chapters of my story are a continuum of increments, always built on what went before. The evolutionary future is always constrained by its evolutionary past.

My reconstruction of the "East Coast Ground Ape," which owes an important debt to my colleague, Clifford Jolly (14), is essentially an artifact of both analysis and imagination. It represents the assertion that an intermediate form must have existed between quadrupeds and the first bipedal hominins. I contend that traditional attempts to make a single mental leap from four to two legs helps to explain our persistent inability to get to grips with the origins of bipedalism. Because we, as offspring of our first bipedal ancestors, see their innovation as definitive and momentous, I have allowed this isolated event, plucked out of a long sequence of adaptive changes, to become the book's "core event." I try to mitigate such an anthropocentric bias by demonstrating that this particular adaptation, no differently from any other, must have been in response to the dynamics of behavior, ecology, and geography that drive all evolutionary change.

Speculations on the origins of bipedalism are often fascinating exhibitions of ingenuity—expressing, above all, that this is a theater for intellectual daring (15, 16). Early anthropologists thought that moving out of the forest, making stone tools, carrying food by hand, and walking upright were "decisions" that required peculiarly human intelligence! Such naivety became totally unsustainable once it was clear that the first bipeds were cranial apes, creatures with ape heads mounted on humanlike bodies. In spite of a vastly expanded theater of discourse, explanations locating postural change in the peculiarities of a specific ecological niche still tend to be neglected. Part of the explanation for this lies in the environment of students who first begin to grapple with the subject in the intellectual hothouses of universities far from Africa, where the raw materials of study are finger-worn plaster casts of fossils, dog-eared papers on evolutionary theory, and videos on popular natural history.

Why an argument over bipedalism should have become somewhat of an intellectual arena could take up many pages, as would the merest outline of hypotheses. Russel Tuttle (17) has conveniently summarized and labeled them with his own street-smart titles as aide-memoires. The following simplified list of some 13 distinct hypotheses is built on Tuttle's titles and illustrates what a diversity of possible explanations have arisen since Darwin.

1. Freeing the hands in defense of a terrestrial way of life (Darwin 1871) (1).
2. Brachiation responsible for the postcranial features we share with apes. Broken down into three phases: gibbonlike, chimplike, and bipedal (Keith 1923) (18).

3. "The upwardly mobile" hypothesis (also Tuttle's favorite): small-bodied arboreal apes modifying their vertical climbing to run bipedally along thick branches in the canopy (Tuttle 1974, 1975, 1981) (19–21).
4. Bipedalism emerging from the need to carry babies, food, and other objects back to base (Hewes 1961; Isaac 1978; Lovejoy 1981) (16, 22, 23).
5. The avoidance of predators: extra vigilance in the savannas with frequent peering over tall grass (Dart 1926) (24).
6. Phallic display directed at females (Tanner 1981) (25).
7. Intimidation displays directed at other or same species (Westcott 1976; Jablonski and Chaplin 1993) (26, 27).
8. An aquatic phase of foraging and avoiding predators in water (Westenhofer 1942; Hardy 1960; Morgan 1972) (28–30).
9. A thermoregulatory theory whereby savanna dwellers rear up to keep cool (Wheeler 1984) (31).
10. "Two feet better than four" hypothesis; energetic efficiencies in bipedalism (Rodman and McHenry 1980) (32).
11. A "gimmick" spread by imitation then favored by selection (Dawkins *in litt.*) (33).
12. Terrestrial squat-feeding—in grassland (Jolly 1970) (14) and on the forest floor (Kingdon 1997) (34).
13. Bipedalism explained by multiple factors (Napier 1964) (35).

Hypothesis number four, what Tuttle calls the schlepp hypothesis (*schlepp* is Yiddish for carry), has been elaborated into a theory of burdens carried as male bribes or gifts to females; this approach supposedly upstaged those of other, competing primates with "an unbeatable breeding package" (16). Treading water while searching for seafood may be more tongue-in-cheek. Intimidation of competitors and predators alike has been invoked as the origin for upright displays that somehow became two-legged walking. As discussed in later chapters, such displays may, indeed, have been significant for the survival of early hominins, but I cannot envisage them as the primary cause for an erect stance. An example of recently acquired faculties being packaged and projected back to much less plausible contexts is the supposition that bipedalism can be explained by the ancestral ape getting up to escape ground radiation and keep cool. This explanation amalgamates too disparate a bunch of separate faculties as well as making many assumptions about the habitat of the earliest hominins.

Many other efforts to understand the beginnings of bipedalism have been marked by the persistent tendency to lump together whole clutches of human or protohuman characteristics. In common with most biologists, I take the view that untangling the sequence of adaptive changes through which any evolving lineage passes is absolutely vital to understanding how the members of that lineage have arrived at their own unique permutation of traits (36). If the many staged adaptations that must have preceded getting up on two legs are to be understood, it will be important to identify such stages as discrete entities and then try to order them in a sequence that is biologically workable and theoretically plausible. For example, two-legged standing, in my view, preceded true bipedal walking and need not, perhaps should not, be lumped with it. Neither stance was necessarily synchronous with the acquisition of an erect back, nor with the ability to run.

The account that follows is an effort to translate the theoretical difficulties of explaining anatomical transformation and the abstractions of speciation into identifiable Time, Place, and Mechanism.

The question of timing for the emergence of hominins, long assumed to be a very ancient event, was revolutionized by Vincent Sarich and Allan Wilson in 1967 with their elegant demonstration of a "molecular clock" that could be applied to human origins (37). Since that time, geneticists and palaeontologists have tended to favor a relatively late date for the chimp-hominin divergence (7–5 mya). An enormous gap between this date and the first proven fossil bipeds (4.4–3.5 mya) has been dramatically closed recently with the discovery of a fossil biped dated to 6 mya.

The question of place is inextricably tied to the question of how the population that was to become bipedal and their four-legged parent population became separated. The questions are connected because the genetic isolation of populations is an essential prerequisite for speciation. There have been various suggestions for the isolation of vaguely eastern or southern ape populations (38), but none has identified a habitat both ecologically distinct enough to elicit an entirely new form of locomotion nor geographically separate enough to impose the necessary isolation. My own outline addresses both shortcomings.

It is not always appreciated that the broad character of today's major plant communities is not new. Boundaries may have fluctuated wildly, but the gross pattern of humid foci strung along the equator and arid hot-spots pulsing back and forth from the north and southwest would have been well established by the mid-Miocene. A humid focus in the east was identified by the botanist Frank White as a very peculiar "region of endemism" (39). As documentation of the peculiarity of this region's fauna and flora has improved, the relative isolation of the Indian Ocean littoral forest from more westerly forests has become ever more evident (figure 1.6). It is this littoral forest that I identify as the habitat in which the vital transformation took place.

As for mechanism, I have not sought global drought crises nor even fewer trees. Rather, I see an ape population adapting to a different, more deciduous kind of forest and see its isolation as of vital relevance. Unlike many of my predecessors, I have not looked for sparser resources; rather, I can point to a different, perhaps richer, menu. I have postulated a switch to more terrestrial feeding, but instead of actively pursuing fleet prey, east coast ground apes would have found a rich supplement of small, sessile animals and plant matter from the forest floor to augment crops of fruit; the latter being predictably less diverse and growing nearer the ground than in the high forests further west.

It is not immediately obvious how grubbing about for edibles on the forest floor could culminate in bipedal walking. The argument hinges on changes in the spine, pelvis, and head-neck junction (perhaps also in the heel) being necessary precursors to standing and balancing on two legs. It was during this phase that feet changed from being claspers to becoming platforms. In common with my colleague, Clifford Jolly, I hold that it was foraging, mainly on the ground, in a squatting position that demanded these necessary modifications. Hence the title, *Lowly Origin* (34).

The fossil record makes it certain that the particular type of ape bipedalism that gave rise to humans began in Africa, which is not to say that something like it never occurred anywhere else (40). Dating of the earliest fossils has implied that bipedalism began before 4.5 mya (41), even as early as about 6 mya. While a variety of Eurasian ape fossils from about 9 or 10 mya hint at the nature of hominin ancestors, molecular clocks (based on comparing the genes of humans with chimpanzees) suggest a common ancestry up to some 6 to 7 mya (42). If this statistic is correct, the timing for bipedal beginnings contracts to some time shortly thereafter. The location of all the earliest fossils makes it likely that it was African apes from the eastern side of the continent that first became erect (38).

Eastern Africa is a big area, but it has a relatively well-understood geological, climatic, and biotic history (43), which must invite a more specific context for hominin origins. I suggest that in-depth study of the biogeography of African fauna and flora quite literally narrows the most likely location down to forests of the eastern coastal strip. That these forests have suffered sustained ecological and physical separation from forests in central Africa is attested to by the distribution patterns of nu-

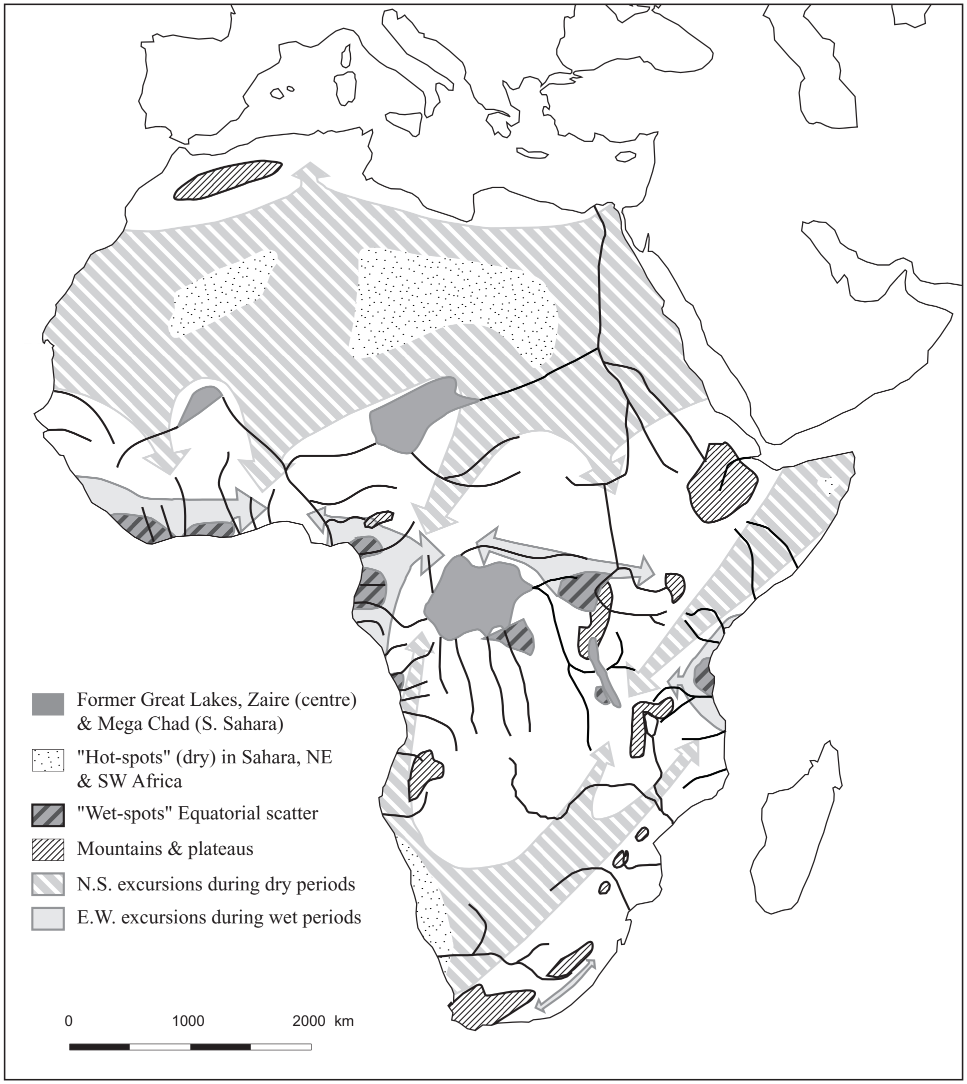

FIGURE 1.6 The dynamics of change. The pulsing of "wet-spots" (east-west, scattered along the equator), and "hot-spots" (north-south, in Sahara and northeast and southwest Africa). Former Great Lakes, Congo (center), and Mega-Chad (S. Sahara). (After Kingdon, J. 1990. *Island Africa. The Evolution of Africa's Rare Animals and Plants*. Princeton, NJ: Princeton University Press.)

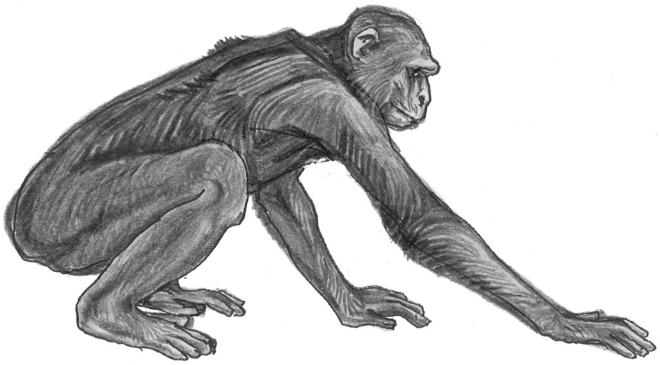

FIGURE 1.7 Reconstruction of a foraging ground ape.

merous species of animals and plants (44). The separateness of these forests is of such long standing that it represents by far the most likely mechanism to have isolated incipient hominins from ancestral chimps. More important, the forest's distinctness as a habitat may help explain *why* the eastern apes became erect.

Reconstructing the ecology of the incipient hominin apes' habitat is a less hypothetical exercise than might be thought. These isolated forests still shelter many unique and ancient organisms, and the long-term climatic constraints on vegetation in eastern Africa are relatively well known (39).

As for the immediate impetus for getting up on two legs, there are good reasons to suppose that this posture followed and was dependent on an earlier adaptive phase of "squat-feeding" (41) (as I describe in chapter 5). Squatting would have induced the reorganization of the trunk that I contend was an essential precondition for balanced standing. Instead of simply assuming that standing was a brief balancing act that spanned the quadrupedal/arboreal adaptations of the common ape-hominin ancestors, I have isolated squatting as my topic. This lowly posture (figure 1.7) signifies not only the central subject matter and title of this book; it also exemplifies one component of my piecemeal approach to reconstructing human evolution.

The ability to stand without the expenditure of much energy requires good balance. Two-legged balance, in the brief waddling of apes or the performing of poodles, is a precarious artifice because there is too much weight concentrated at the top of the column and too little stability at the bottom. In other words, these quadrupeds are top-heavy. Easy, nonenergetic standing requires a downward displacement in the distribution of weight. If structures in the upper foreparts are no longer the largest and heaviest in the body, their smallest movements will no longer destabilize balance or threaten to topple the would-be walker. To achieve such shifts in the distribution of weight in living, functioning bodies, there must be substantial changes in the relative weight of muscles, bones, and organs. I contend that this necessary slimming down of the upper part of the eastern apes' bodies came about through ecological and behavioral changes that rendered exceptionally heavy, powerful forelimbs redundant. I give the arguments, details, and rationale for this in chapter 5. It suffices here to assert, once again, that the single act of standing is inconceivable without such preliminaries. This phenomenon is commonly called "preadaptation," but I am, in the first place, trying to portray the ecological background for an "increment" that can be isolated as a manageable unit of evolution. My second objective is to highlight a conceptual approach that can enhance our ability to comprehend past events.

I contend that only an ape population that was able to exploit an intensive and reliable (rather than an extensive and irregular) food supply could permit a radical shift in the priority functions of their forelimbs. Hands and arms could, most frequently, and for long periods, be devoted to turning over leaf litter, selecting, processing, and handling foods; also, but rather less frequently, to vertical climbing and to some diagonal "propping" in the trees. As the incidence of bearing weight declined, there would come an identifiable point at which four-legged movement ceased to be as efficient as simple straightening of the legs. I contend that this point existed when the spine was balanced vertically.

The achievement of upright stance can be viewed as a moment of reorientation rather than action, a balancing act on a behavioral tightrope; the moment in which walking is still the unfulfilled potential of a standing "ground ape." Becoming fully erect can also be positioned symbolically on an ecotone between richly endowed rainforest and drier, less reliable and less homogenous "nonforests." It can also be positioned on a biogeographic boundary between the Indian Ocean coastal forests and the more diverse habitats of the eastern interior.

The incentives to get upright need have been no more than sporadic to begin with, but they would have had to be worth it. Worth could be measured in terms of extra food or compensatory food in places where and at times when it contributed toward survival (perhaps no more than seasonal gluts of milkwood or mustard bush fruit on the edges of a too-small home range).

It is only with hindsight that we can say that the ultimate worth of standing up, the hidden evolutionary prize, was the ability to find the way out of a sort of ecological and biogeographic cul-de-sac. Yet there are numerous other organisms in tropical Africa that have moved, in both directions, across the forest-nonforest boundary, and there are lessons to be learned from such species (these are explored in more detail in chapter 6). The most radical implication of "eastern ground apes" becoming transformed as they moved inland is that their occupation of a wide scatter of major river basins may have led to the evolution of more than one lineage.

There are numerous implications, not least for nomenclature, in the possibility that our own line of descent diverged at the ground ape level, not the level of "Lucy" or her kin. For many years, there has been widespread acquiescence to the inclusion of Lucies in the direct human lineage; indeed, *Praeanthropus* ("*Australopithecus afarensis*") is frequently portrayed as the prototypical first ancestor (36, 45). We must now question our assumptions about these Lucies, who were once seen as very early hominins but are now recognized as relatively late players on the hominin stage (46). Long-held models of a single lineage must suffer still further erosion as the evolutionary tree gets ever more bushy (47–49). More significantly, new data show that some of the peculiarities of our own lineage were absent from the Lucy lineage yet must have evolved by the same time. This raises numerous new questions about the ecological and behavioral roots of our own specific line. The possibility of divergence at the ground ape level will, of course, precipitate more uncertainties about the ultimate roots of humanity. Even so, I hope it will invite much more discussion and research that is couched in terms of geography, ecology and behavior; until recently these tended to be rather subordinate parts of discussion (50).

On balance, I think it very likely that Lucies, once seen as very early but now recognized as relatively late hominins, are well off the main line of human evolution; nonetheless, they remain one of the best illustrations of an early biped because their fossils are so numerous. If Lucy-like traits creep into my self-portrait as an early hominin, that is partly because any illustration at this time is, of necessity, very broad-brushed. "Evolution by River Basin" could account for this high level of convergence, a parallelism that is already implicit in the anatomy of existing hominin fossils (51, 52). Indeed, parallel anatomical adaptations in different river basin populations could have been a natural feature of this crucial moment in the emergence of humans and, perhaps, other hominins. In any event, I contend that the fossil record already provides evidence that bipedal gaits were built on an erect back, no matter whether the evolution of walking was a single or a multiple development in the descendants of eastern ground apes.

It is possible that one of the reasons why the acquisition of erectness should have remained such a controversial and enigmatic problem is that we are hostages to an iconic history in which two legs are not only the mark of our uniqueness but an automatic antithesis to four (53). Darwin's reminder that we should include limbless, hagfish-like vertebrates in our ancestry may offer us an interesting slant on the problem and open to doubt the preferred categories of the debate: quadruped versus biped; bipedalism evolving from quadrupedalism.

The fact that most terrestrial mammals, including apes, carry their weight on four legs makes the word *quadruped* seem a rational enough category, but that could once be said of "quadrumana," or "four hands"—the now obsolete and anthropocentric term for monkeys. However, "four legs" misses a distinction within the category of limbs that could substantially alter the way we study bipedalism and its origins.

Suppose we question the assumption of four-leggedness as a base line? Suppose walking on four legs is in as much need of explanation or wonder as walking on two? Justifying such a counterintuitive argument depends on how far back we are prepared to go and how fundamental we choose to get.

Organic "bodies," whether single- or multicelled, are organized to respond to numerous challenges, such as extremes of temperature, humidity, saturation, chemistry, material textures, rays, or waves such as light, noise, vibration, or water. The simplest and most universal responses to such stimuli are simple stop-go or attract-repel actions. Having the ability to sense and then react to such stimuli has an intimate bearing on the way we are built as animals, given expression in that front-end concentration of sensory equipment that we call a head. Through it we receive, process, and respond to innumerable messages via sophisticated sensory and neural pathways. We are responding at this most primitive level when we recoil from a blast of heat or cold, or even from a loud noise or a bad smell.

Some invertebrates and effectively all vertebrates are irreducibly linear. Vertebrate bodies began as segmented, finned columns that were propelled forward by a series of rhythmic muscle contractions operating on either side of the tail end of their long, thin "backbones" (54). This train of cartilaginous discs enclosed a continuous thread of nerves and overlay a digestive tube that was protected by pronglike extrusions from the vertebrae: the beginnings of ribs. As a direct reminder of such primitive antecedents I, or you, have only to see or feel spine, back muscles, gut, and

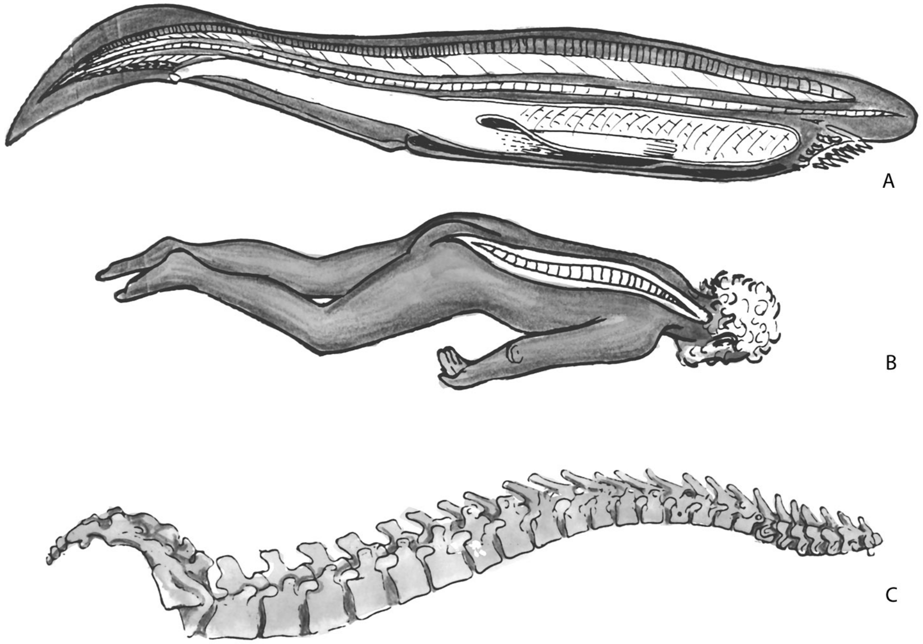

FIGURE 1.8 A. *Amphioxus*, a primitive chordate, in cross-section. B. My backbone, as felt. C. My backbone, as X-rayed.

ribs in our own bodies. As we squirm on the floor during back-strengthening exercises we can indulge the illusion of "remembering" our early vertebrate evolutionary infancy in the sensations emanating from each of these elements. We have inherited them from a pre-fish level of ancestry, together with their very necessary functions (figure 1.8).

Darwin was going back to just such elementary fundamentals when he wrote, in *Descent of Man*, that "we can see that the early progenitor of all the Vertebrata must have been an aquatic animal . . . more like the larvae of the existing marine Ascidians, than any other known form." For Darwin, the larva served to illustrate a phase, a single increment, in humanity's piecemeal emergence from its "lowly origin." Too much has been made of Darwin's supposed belief that human characteristics evolved "in concert," as a "package" (55). It is true that it needed Mendel, Crick, and Watson to show the particulate genetic mechanisms that underlie evolution and that Darwin may sometimes have smudged the boundaries between specific adaptations. However, the broad thrust of his arguments was unequivocally that evolution proceeded piecemeal, step by step, increment by increment.

It was vertebrae and associated bones toward the tail end of early vertebrates that first differentiated into hindfins and, eventually, back legs and pelvis. Like the rest of the rear end, their primary function was propulsion. For the present argument, the significance of rear-end propulsion is that from the very beginning, tail-end limbs have had quite different origins and functions from forelimbs.

The latter first evolved in close association with the head—indeed, so close that pectoral fins were actually tethered to the head of early fishes. When early terrestrial vertebrates, tetrapods, developed forelimbs from these fins, which became detached from the skull, one pair of gill arches was dragged away to become the shoulder blades or scapulae. Likewise, the anterior sources of forelimb nerve networks testify to very separate limb origins (figure 1.9). Subordinate to the brain, forelimbs still serve many vertebrates to alter and adjust their sense-driven decisions about the direction and pace of forward movements. This arrangement is particularly true of aquatic animals such as frogs and fish. There are, of course, many seal and whale species in which the forelimbs play a minor role in providing thrust during swimming, but that function belongs to the hind limbs and tail.

The differentiation of limbs goes back to the very first limbed and fingered animals. That joined-up, light-weight, multiple-rayed fins are elegant solutions to the problems of fast, maneuverable swimming in open water is proved by the survival and perfection of fins over some 500 million years of fish evolution. The delicacy of fins renders them less useful when the water is full of obstructions and tangles, as happened when plants began to flourish on land and at water's edge at the start of the Devonian, 400 mya. To progress through shallow forest swamp waters, largish animal bodies must twist and turn, squirming or levering themselves over and around stems and branches, finding a purchase with something less fragile and slippery than a cartilaginous fin. Significantly, lungfish-like fossils, their fins borne on the end of blunt oarlike stumps, first appear in the Devonian, But the major switch from fins to something more like true limbs comes with the appearance of the first, still aquatic, tetrapods after about 370 million years (56).

One of these, *Acanthostega*, illustrates both the piecemeal nature of evolution and also exemplifies the potential for fundamental differentiation between limbs at the front and back of an animal. The forelimbs of this newtlike tetrapod were similar to those of lobefinned lungfish, but the powerful hind legs were furnished with eight digits, not fin rays (figure 1.10). Other species had five, six, and seven digits, but the number eventually stabilized into the five-fingered standard possessed by most

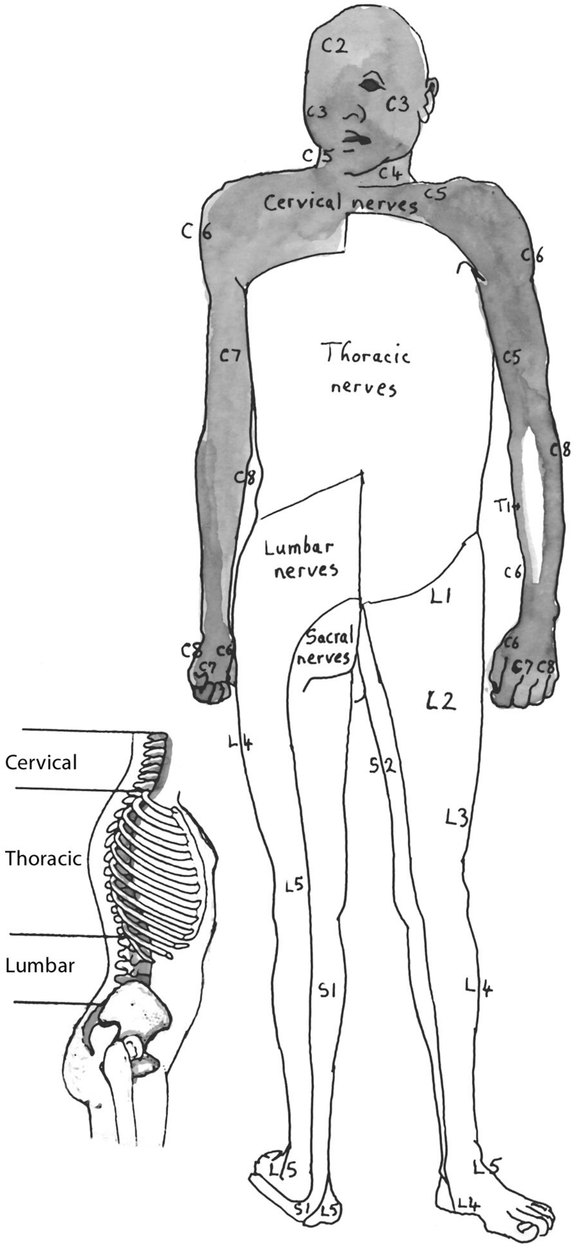

FIGURE 1.9 Cervical nerves serve the surfaces of both head and forearms.

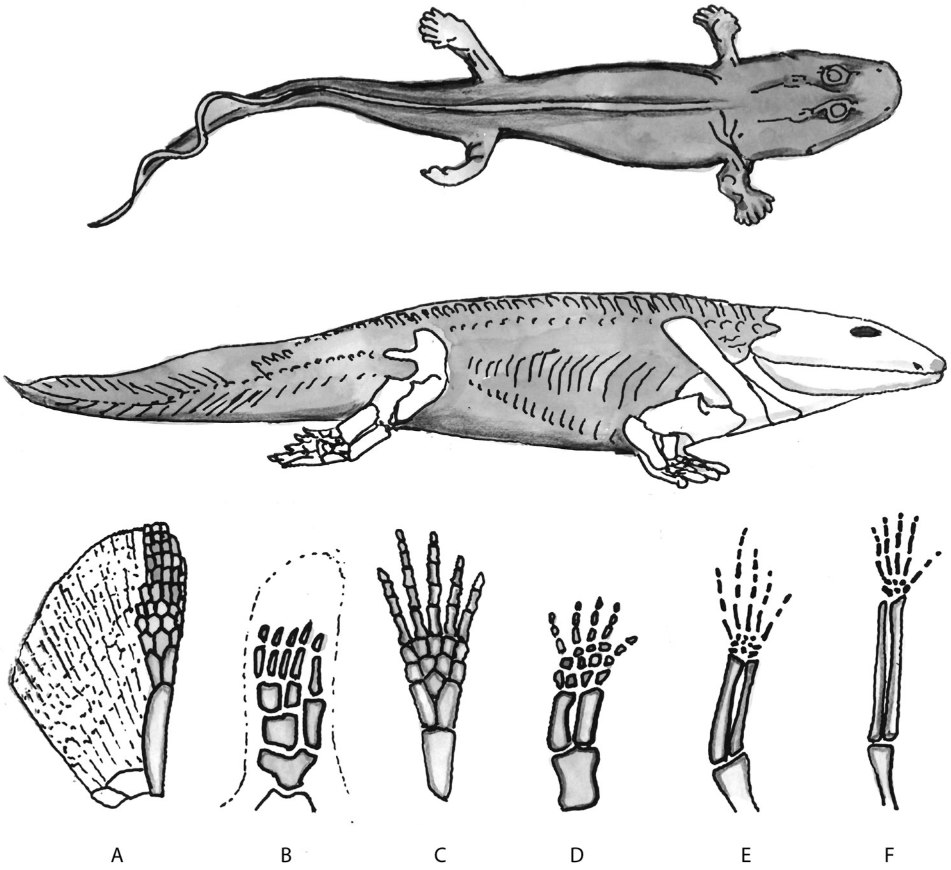

FIGURE 1.10 Top: The Devonian tetrapod *Ichthyostega*. (Note the close association of forelimb bones with the head.) Bottom: Evolution of the forelimb. A. Breast fin of a shark (shaded section illustrates the components that persist in higher vertebrates). B. Lobe-finned fish. C. Generalized amphibian. D. Five-fingered early amphibian. E. Lizard. F. Human. (In part after Ahlberg, P. E., and A. R. Milner. 1994. The origin and early diversification of tetrapods. *Nature* 368: 507–514; Ankel-Simons, F. 2000. *Primate Anatomy: An Introduction*. San Diego, CA: Academic Press; and McLeod, M. 2000. One small step for fish, one giant leap for us. *New Scientist* 19 August 2000.)

modern amphibians, reptiles, and mammals (57). Another tetrapod, *Ichthyostega*, which was broadly contemporaneous with *Acanthostega* and was also a large (>1 meter long) predator, had powerful front limbs that supposedly helped keep its air-breathing throat apparatus clear of the ground during forays out of the water. By 338 mya, tetrapods were fully terrestrial and highly diverse in form (58).

Because the fore-ends of primitive vertebrates were the first to en-

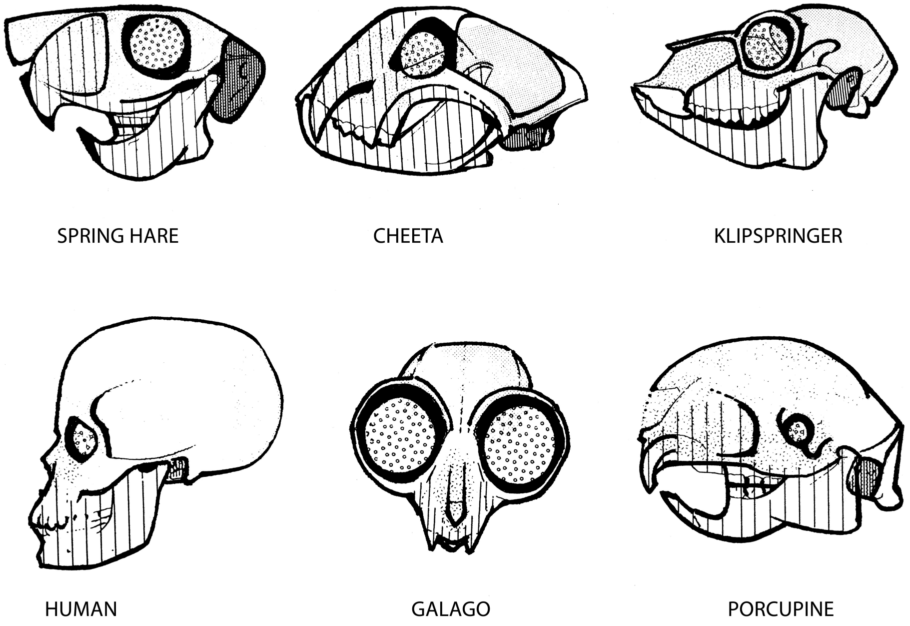

FIGURE 1.11 Skulls of six mammals to illustrate the enclosure of functional activities, such as seeing, chewing, smelling, thinking, etc., in discrete capsules. A. Spring hare. B. Cheetah. C. Klipspringer. D. Human. E. Galago. F. Porcupine. (From Kingdon, J. 1971–1982. *East African Mammals. An Atlas of Evolution in Africa* [3 vols., 7 parts]. London: Academic Press.)

counter both food and obstacles, basic sense organs and a mouth developed there. The need to respond to light, chemical, electric, or vibrational signals led to the differentiation of cells until they developed into eyes, nose, and ears, each encapsulated in compartments that shared the upper part of what became the skull. The lower section of this structure became a hinged mandible, and eventually both jaws developed teeth. My skull still consists of a series of connected capsules (figure 1.11), and it is in the relative size and permutations of connecting bridges, struts, and welds that the species-specific differences among animal skulls become obvious.

The fact that my fore-end, including my forelimbs, encountered and "processed" the environment while propulsive force resided at my rear-end remained an inherited "given" long after my aquatic ancestral "self" had spawned land-dwelling mammals (indeed, even to the point where some had become tree-dwelling primates).

Perhaps the point was too indirect, or even too obvious, for Darwin to pursue, for while he emphasized that organisms retain general structures from their aboriginal progenitors and he explicitly described hands as acting "in obedience" to human will (at the same time noting "free, independent action in the arms and upper body" of *Homo sapiens*), *The Descent of Man* makes no mention of functional separation between forelimbs and hindlimbs predating the radiation of higher vertebrates. Yet it is in the context of deep Darwinian time frames that the evolution of standardized forelimbs and hindlimbs in terrestrial animals becomes no less a gravity-fighting contrivance than walking on two legs. It is somewhat of an exaggeration to portray our many quadrupedal ancestors as occupants of a mere interlude in our evolutionary history. It is no stretch to suggest that restricting propulsion to the back legs alone is as much a "return" as it is an innovation. When the primitive connection between head and forelimbs is remembered, the latter's emancipation from serving as supportive props becomes somewhat less revolutionary. The development of a way of life that rebalanced the tyranny of foursquare gravity becomes as remarkable for what it "restored" as for the novelties it unquestionably introduced. As for human two-leggedness being "revolutionary" (and supposedly uniquely beautiful) (59), human gaits scarcely compare for balance, grace, and speed with those of ostriches or emus!

This diversion into the nether regions of vertebrate history therefore serves to remind us that "quadrupedalism" is mainly a contrivance that land-living animals have evolved to overcome the many problems of gravity and the need for faster movement. Among the reasons for this reminder that forelimbs have historical neural connections with the head, one has been to demystify bipedalism; second, challenge the assumption that not using the forelimbs for propulsion was an event of absolutely unprecedented originality; and, third, to prepare the ground for discussing later head-hand linkages. A further purpose is that if you have been persuaded that the functional anatomy of a hagfish is even remotely relevant to an ape standing up, the next leap ahead, to the earliest primates (in chapter 2) will be that much easier to embrace.

Reconstructing some of the series of events that must have gone on before and after becoming erect may also help to underline the incremental nature of the evolutionary process itself (figure 1.12). Each such increment needs to be studied as a complex of interrelated changes, set in time, place, and environment. And I have already indicated that a historically plausible sequence of "increments" has provided the substance and the structure for each of the succession of chapters that follows. So why lift one increment out of its proper temporal sequence?

The reasons are twofold. One is to establish the central topic of the book. The other is to reinforce my descriptive technique of breaking "bipedalism" down into component parts. Thus, I interpret an erect back,

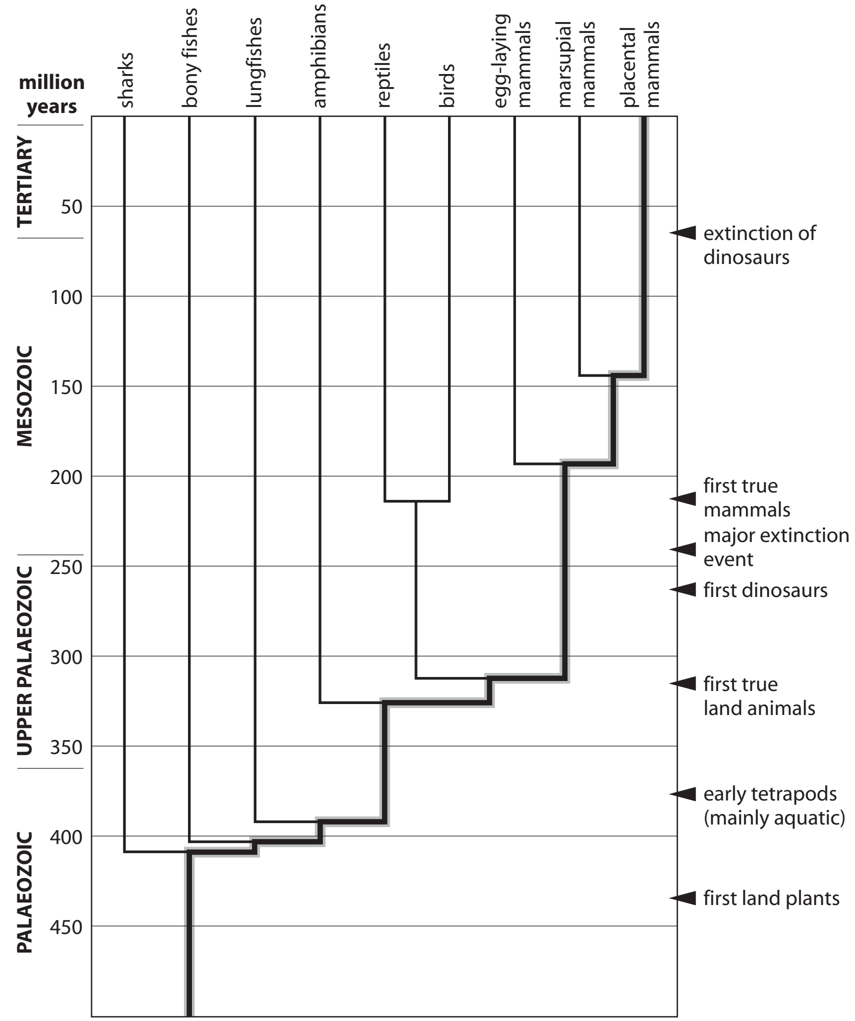

FIGURE 1.12 The radiation of vertebrates through time, with the human line of ancestry traced in bold.

balancing on two legs, walking, and running as four distinct entities. I acknowledge that they may have important structural connections, but each can be productively studied as a separate adaptive response.

To balance on two legs is an essentially static activity. Alone, it has not gotten you anywhere. However, if you were previously four-legged, it is an anatomical and physical feat; it is also a necessity for economic locomotion. Conceptually, it is a “moment”; chronologically, standing comes before walking and after quadrupedalism. Yet the realities of adaptive change in intelligent, active, versatile animals make it unlikely that any such "moment" could ever find such a neat, static niche. As more than one wag has remarked, what came between four legs and two? Three? The witticism is less outlandish than it may seem, as is explored in chapter 4.

In the context and format pursued in this book, standing is, above all, an evolutionary moment. Many living mammals have literal moments of standing up on their hind legs. These are easy to document, but the evolutionary moment in which an ape becomes habitually erect is a temporal unit that is more difficult to visualize, describe, or study. There are other important theoretical reasons for trying to reconstruct the series of events that must have gone on before and after becoming erect.

The difficulty of reconciling four-legged walking, especially knuckle-walking, as the immediate precursor of bipedalism has led to a polarization of views as to whether it was a short, sudden, instant adaptation or a protracted, sporadic response to particular stimuli—an activity that merely increased in its incidence. It is a polarization that has some theoretical importance because a sudden "flip" from one mode of locomotion to another supports the idea of "punctuated equilibrium" (60) and combined "packages" of adaptive change, whereas protracted, step-by-step change in specific domains is, by definition, more gradualist (61). In asserting that there was no sudden leap, no magic response to some cosmic change, I am supporting and augmenting Jolly's 1970 proposition that a (literally) lowly but important intervening stage of evolution should be registered. Furthermore, in laying out a road map of human evolution with a succession of wayside stops, I am suggesting that greater attention be paid in future to identifying and reconstructing the ecology of identifiable ecological "islands." This topic should be an essential dimension of evolutionary studies because the genetic isolation of populations is a key component of speciation.

In the pages that follow, I draw on several new lines of evidence to suggest places, mechanisms, ecological contexts, and times for what I regard as the plural beginnings of hominin evolution.

Becoming erect can be seen as a symbolic moment for the irreversible separation of the human lineage from all other animals; it has also become the rather arbitrary taxonomic criterion for separating all human-like hominins from all apes (62). I think this is a false duality. Standing was but a momentary pause in a long series of adaptive changes, but it was predicated on the accumulated benefits of earlier evolutionary phases: the primacy of vision, diurnal habits, taillessness, and the spatial mobility of an ape with brachiating ancestors. These piecemeal preconditions for bipedalism were followed by no less piecemeal and extraordinary consequences for our own evolution as humans. An incremental perspective on evolution suggests that the set of adaptations that culminated in erectness had no inevitable connection with adaptations for big brains. That much is corroborated by the fossil record. We know that brains enlarged in our own lineage, but the first really successful bipeds seem to have had no need for brains larger than those of apes. In chapter 5, I propose that our intellectual beginnings may have started in an initially insignificant sidebranch of the ground apes.

Furthermore, the development of what we like to call cleverness must have been equally subject to incremental change and equally tied in to selection for a particular type of mental versatility. A step-by-step improvement in cleverness must have involved change in quite separate sensory, motor, physiological, and behavioral, mental, and neural skills. Each of these modifications must have had its own ecological and behavioral contexts. So while this book does not set out to examine the evolution of intelligence, I share with others the conviction that many parallels must have existed between physical and mental development (63). Staged changes in ecology and behavior must have corresponded with piecemeal changes in the way in which evolving humans constructed mental models of the world or worlds in which they found themselves. These would have included literal “models” (including the physical constructs we call tools) whereby they could eke out a living through their own and their social group’s actions.

The conviction that all our adaptive traits, including intelligence, derive directly from animal ancestors is still a very minority view. It is a conviction that has profound implications for our worldview and for how the only truly bipedal animal will have to conduct itself if it is to survive. Matt Cartmill summed up both the simplicity and the magnitude of the personal choice we all have to make: “to seek to show that all things human are prefigured or paralleled in the lives and adaptations of our fellow animals—is at bottom to doubt the reality of the moral boundary that separates people from the beasts. Whether we fear or welcome the dissolution of that boundary is the real issue” (64). It is an issue that has as much bearing on long-term human survival as it has for new human moralities.

The intellect that Darwin celebrated “penetrating the movements and constitution of the solar system” still bears the stamp of numerous increments of change. Each increment is embedded in a distant past, but identifying their sources and their transformations will be the task for future self-portraitists seeking to chart the architecture of that mysterious amalgam that is a living human being.

My own self-portrait is more explicitly physical. So, having explored some of my rudimentary vertebrate dimensions and identified the evolution of bipedalism as a pivotal topic for the book, I now backtrack from the latter and, with apologies to neglected amphibian and reptile ancestors, leapfrog to sketch out my (and your) life as an early mammal and primate.

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