ROGER LEWIN

Human Evolution

AN ILLUSTRATED INTRODUCTION

Human Evolution

AN ILLUSTRATED INTRODUCTION

ROGER LEWIN

American Association for the
Advancement of Science

W. H. FREEMAN AND COMPANY
NEW YORK

Published in the United States in 1984
by W.H. Freeman and Company,
41 Madison Avenue, New York,
NY 10010. First published in Great
Britain in 1984 by Blackwell Scientific
Publications Ltd
Reprinted 1985 (twice)

Printed in Great Britain at the
University Press, Cambridge

Library of Congress
Cataloging in Publication Data

Lewin, Roger.
Human evolution.
Bibliography: P.
Includes index.

1. Human evolution. I. Title.

GN281.L49 1984 573.2 84-4188

ISBN 0-7167-1635-6
ISBN 0-7167-1636-4 (pbk.)

Preface

Palaeoanthropology—the study of human origins—has undergone a transformation in recent years. Not only has the science benefited from a remarkable series of fossil discoveries, but it has also begun to encompass radically new approaches to answering the major questions about human evolution. Moreover, there has been a dual shift in many researchers' perceptions: one represents a salutary recognition of the depth of ignorance under which the science still labours and of the real limitations to what can ultimately be known; and second, there is a greater security about genuine progress that has been made, specifically progress in asking answerable questions.

Unquestionably, it is an exciting time for palaeoanthropology, not least because the related pursuits of evolutionary biology and geology are both experiencing a degree of creative foment that from time to time occurs in the history of a science and raises it to new, high frontiers.

In evolutionary biology, there is keen debate over the circumstances under which new species arise, specifically about the process of speciation, through which biological diversity expands. This debate is forcing palaeoanthropologists to scrutinize long-held opinions on the tempo and mode of the emergence of *Homo sapiens* and its ancestral species. And in geology the traditional theme of steady, gradual change through geological time is being challenged by remarkable discoveries about the nature of mass extinctions. Geological history, and therefore the history of life on earth, is beginning to be seen as much more episodic and unpredictable than previously appreciated. This inevitably influences the larger context in which human evolution is envisaged.

Probably the most significant discovery of the century regarding human origins—or Man's Place in Nature, as Darwin's friend Thomas Henry Huxley put it—has concerned our relationship with the apes. Until biochemical studies in the 1960s showed it to be fallacious, it was widely held that the great apes (gorilla, chimpanzee and orangutan) were closely related to each other, while humans were separated by a significant evolutionary distance. As the protein biochemistry showed, and as the more recent work on the DNA behind it confirmed, humans and the African apes (chimpanzee and gorilla) are closely related to each other and as a group are relatively distant from the Asian ape (orangutan). *Homo sapiens,* in many respects, is simply a rather odd African ape.

The coming together of traditional palaeoanthropology and modern molecular biology has been one of the most significant developments in the quest for human origins, although the partnership has at times been viewed askance by both parties. The union promises to offer powerful tools for helping to establish the all-important timescales of human evolution.

Human Evolution: an Illustrated Introduction brings together the many different approaches—the established and the new—that constitute the modern science of palaeoanthropology. It introduces the reader to the full range of questions that is being asked about this rather odd African ape—ourselves. What made an ancient ape stand on two legs instead of four? What effect did the advent of stone tool technologies have on our ancestors' energy budget? What forces of natural selection favoured the remarkable expansion of the brain? Is language simply a super-efficient means of communication, or a medium of deeper thought and of shared consciousness? What did the cave art and carving of the ice age signify? Was it population pressure that ignited the agricultural revolution, or was it something more subtle? These, and many more, questions are what we need to know about ourselves and our ancestors.

This book is not meant as an exhaustive treatment of physical anthropology, geology, evolutionary biology, molecular biology or archaeology; it is an introduction to these subjects as they impinge on the story of human evolution. *Human evolution* therefore provides an effective means of gaining a wider perspective of these subjects, as well as offering the student of human origins a broad, up-to-the-minute overview of the state of this very exciting science.

Roger Lewin
Washington, D.C.

Acknowledgements

No one can write a book with so broad a scope as this without being indebted to scores of practitioners who, over the years, have been patient enough to discuss at length their specific concerns. It is surely impossible to list all by name, but I should like to mention the following, who helped either as friends or just friendly advisors: Peter Andrews, Anna K. Behrensmeyer, Barbara Bender, C.K. (Bob) Brain, Margaret Conkey, Michael Day, Niles Eldredge, Kent Flannery, Stephen Jay Gould, Andrew Hill, Ralph Holloway, Nicholas Humphrey, Glynn Isaac, David Jablonski, Donald Johanson, Clifford Jolly, Lawrence Keeley, William Kimbel, Kamoya Kimeu, Richard Klein, Misia Landau, Mary Leakey, Richard Leakey, Alexander Marshack, Robert Martin, Ernst Mayr, Theya Molleson, David Pilbeam, David Raup, Vincent Sarich, Pat Shipman, Phillip Tobias, Nicholas Toth, Erik Trinkaus, Elizabeth Vrba, Alan Walker, Tim White, Allan Wilson, Edward O. Wilson, Bernard Wood, Milford Wolpoff, and Adrienne Zihlman. My wife, Gail, has helped, as always, more than she will ever know.

R.L.

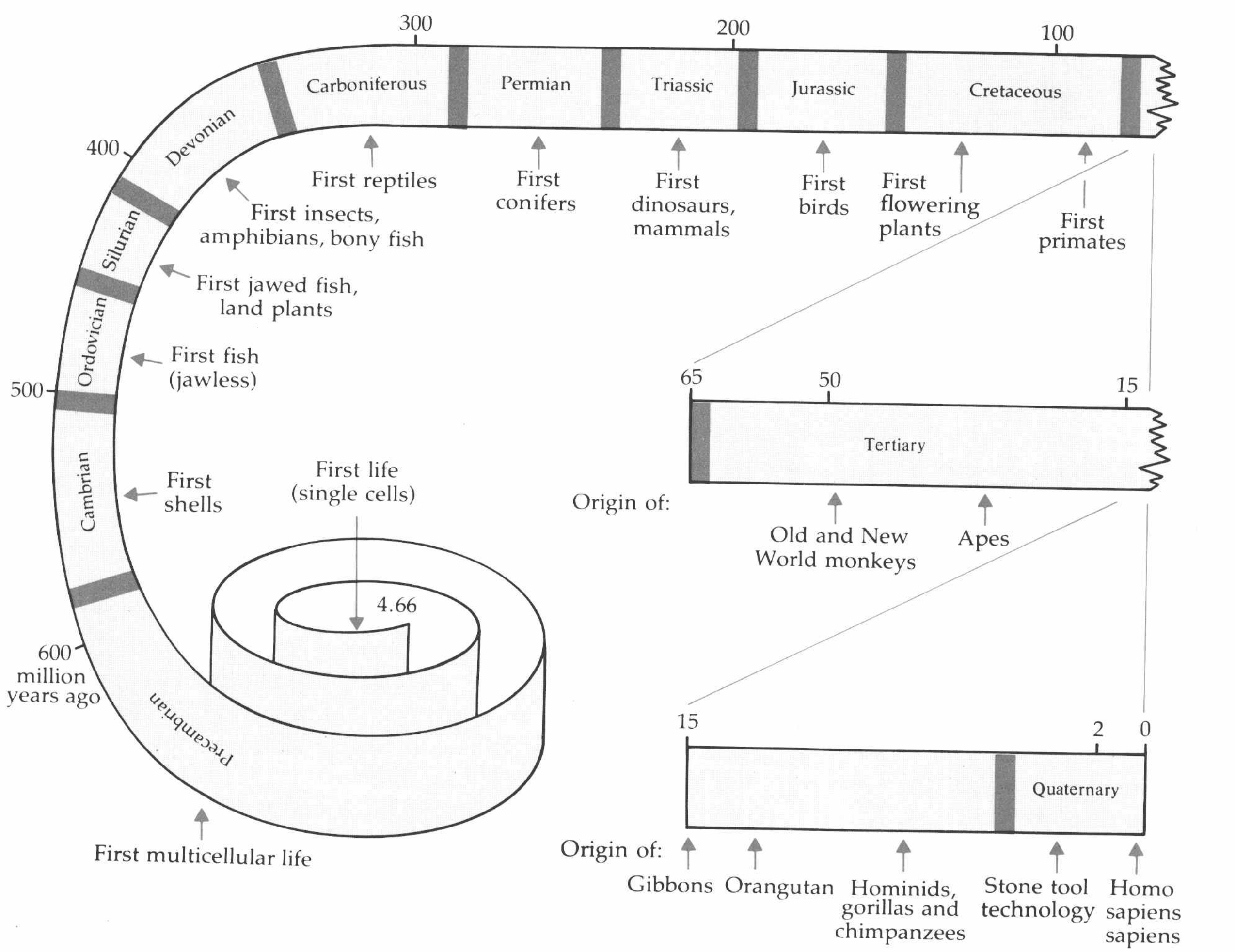
Contents

1/Human Evolution in Perspective

The species *Homo sapiens sapiens* is a relative youngster on this planet, having arisen perhaps 100 000 to 40 000 years ago; and the family to which it belongs, the *Hominidae*, has roots that reach back only five to ten million years. By comparison, life on earth has a history almost four billion years long.

One of the most remarkable things about life on Earth is the speed with which it arose following the planet's formation, 4.6 billion years ago. Direct evidence from microfossils and indirect inference from molecular data show that the first primitive organisms arose within a few hundred million years of the planet becoming cool enough to support life. Then, for the next two billion years, the most complex forms of life were algal mats growing in profusion in shallow tidal waters. A microbiological melee of blue–green algae and bacteria, these algal mats pumped oxygen into the primitive atmosphere in great quantities. This process induced changes in the biochemistry of life's simple organisms and produced monumental 'rusting' (the formation of iron oxide) through vast geological formations.

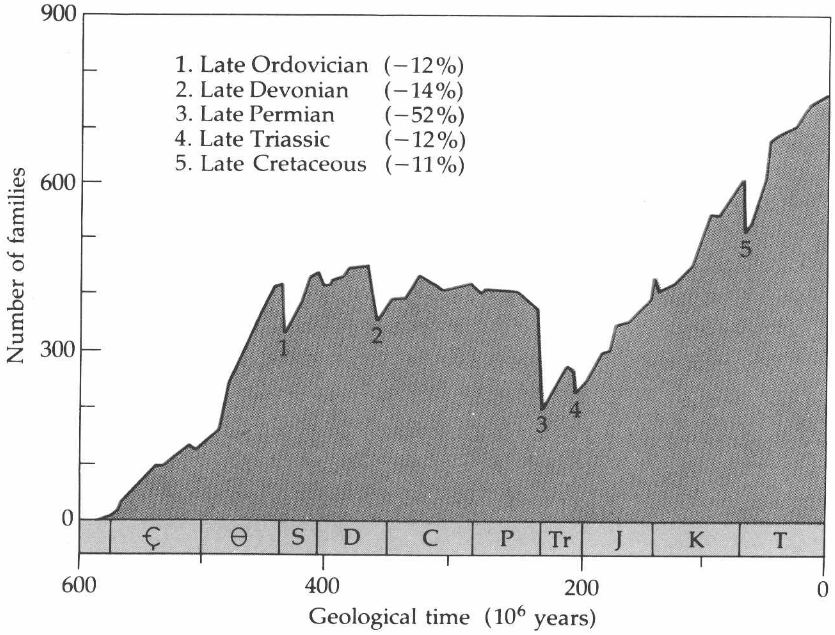
Around 1.5 billion years ago the next major evolutionary innovation occurred: eukaryotic cells arose, cells that packaged their genetic material within discrete nuclei and performed photosynthesis



Evolutionary time scale. Although life arose very early in earth history, complex life forms are relative newcomers to the planet. Primates, the order to which *Homo sapiens* belongs, arose more than 65 million years ago. The first hominids, the name given to the human family, appeared perhaps as recently as five million years ago.

and respiration within chloroplasts and mitochondria, respectively. This new form of cell was capable of a new form of reproduction: sex, which allowed a new dimension of genetic variability within populations, a crucial raw material in the evolution of diversity.

diversification. First, a huge variety of mammal-like reptiles, large and small, herbivore and carnivore, dominated the world of terrestrial vertebrates. These immensely successful creatures were eclipsed 200 million years ago by the arrival of those equally prolific reptiles, the dinosaurs.



Episodic nature of life's history. Since the origin of multicellular organisms in the late Precambrian, life's history has documented a steady rise in diversity, as recorded here by the increase through time in the number of families of marine vertebrates and invertebrates. Interrupting this rise, however, have been a series of mass extinction events (numbered 1–5), which have reduced diversity by the figures shown in parentheses. Each extinction was followed by rapid radiations of new organisms. Courtesy of David Raup.

Before about 800 million years ago life, which was still confined to oceans, was exclusively represented by single-celled organisms. The origin of multicellular organisms at this point marked another major evolutionary step. And during the next 400 million years most of the 30 or so existing major body forms or phyla had appeared, plus many more that have since vanished. This Cambrian Explosion, as it has been characterized, probably reflects an unencumbered invasion of empty ecological niches.

Dry land remained untouched by life until about 400 million years ago, when plants, fungi, invertebrates and finally vertebrates became terrestrial. The first terrestrial vertebrates, amphibians, had to remain near water because their mechanism of reproduction, which involved eggs vulnerable to desiccation, demanded it. Around 300 million years ago, the origin of the amniote egg, secured in a tough shell, freed the amphibians' descendants, the reptiles, of their dependence on water. The conquest of dry land was complete.

The Age of Reptiles, which spanned a great swath of history from 300 million to 65 million years ago, witnessed two distinct waves of evolutionary

The end of the dinosaurs' reign, 65 million years ago, was sudden in geological terms, and is known as the Cretaceous extinction. However, their sudden demise was not especially cataclysmic from a biological perspective: their numbers declined over a five or ten million year period. Climatic changes were probably the principie cause of the dinosaurs' extinction, although there is persuasive evidence of asteroidal impact around 65 million years ago that might have delivered the *coup de grace*.

Before the Cretaceous extinction very few vertebrate species were smaller than a cat. After the extinction there was virtually no vertebrate larger than a cat. The living world had changed dramatically, and the Age of Reptiles had given way to the Age of Mammals.

Mammals have their origins some 200 million years ago, being descendants of the mammal-like reptiles, but it was not until the dinosaurs had vanished that they became abundant and began to occupy the large animal niches. Although they never matched the gargantuan size of some of the dinosaurs, some terrestrial mammals, from their diminutive origins, reached impressive proportions. The mammalian evolutionary odyssey, from tiny beginnings eventually to give rise to some very large species, is a common pattern repeated throughout the history of life.

Primates, the mammalian order to which humans belong, were probably already in existence when the Cretaceous extinction occurred: they were small, arboreal, nocturnal insectivores. Arboreality is a strong theme of primates, as are their grasping hands, excellent vision and high sociality. These small primates, the prosimians, gave rise to New and Old World monkeys some 50 million years ago. The apes arose 20 million years later in the Old World tropics, and became as diverse and abundant as monkeys are today.

Deteriorations in global climate from 20 million years ago onwards had a great impact on these large primates, creatures of the tropics. Many of these apes became extinct. Between ten and five million years ago one of them changed, giving rise to the direct ancestors modern African apes and humans.

Kingdom Animalia
Phylum Chordata
Class Mammalia
Order Primates
Family Hominidae
Genus Homo
Species Sapiens

Taxonomic classification of modern humans. Typically, modern humans are assigned to a further subdivision, the subspecies *Homo sapiens sapiens*, in order to separate us from a discrete, earlier and now extinct group, *Homo sapiens neanderthalensis*.

The history of life is dramatically episodic, with great waves of extinction followed by bursts of adaptive radiation. Indeed, there is some evidence that major extinctions occur regularly – about every 26 million years – perhaps as a result of periodic impacts of comets or asteroids. Although the passage of time sees the origin of more and more complex forms, this is merely the outcome of the essentially random process of evolution operating on the material available at each stage. It is not in any sense a progressive programme of improvement.

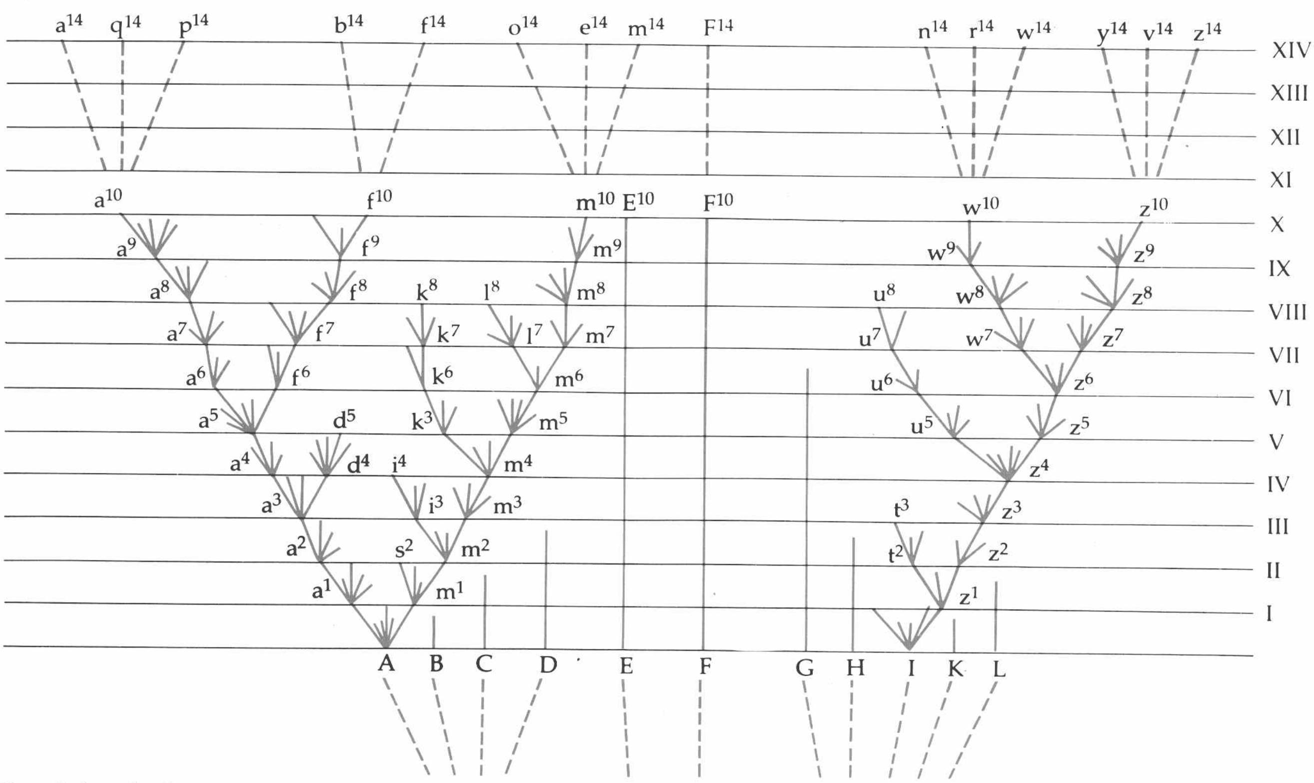
If a glance at the history of life teaches anything, it teaches that every species will eventually become extinct. Today, the earth is populated by perhaps two million species, most of which are insects, a great proportion are plants, 8000 are amphibians and reptiles, 8600 are birds, and only 4000 are mammals. This two million represents just one per cent of all the species that have ever lived. The average 'life-span' of an invertebrate species is between five and ten million years, and for vertebrate species it is about one-half this or even less. Hominid species, according to the fossil record, survive for only one or two million years. *Homo sapiens sapiens*, the latest species on the hominid lineage, has existed so far for only 0.1 million years. The planet Earth can expect to continue for another ten billion years before the sun's hydrogen fuel becomes too depleted to support life on Earth.

2/Darwin and Natural Selection

In his most famous book, 'On the Origin of Species', published in 1859, Charles Darwin studiously avoided the issue of human evolution, but for one sentence in its conclusion: 'Light will be thrown on the origin of man and his history'. Darwin was principally concerned with presenting a persuasive case by which to establish the fact of evolution and with suggesting a mechanism, that of natural selection, by which organic change might occur through time. None of Darwin's many intellectual predecessors who broached the subject of evolution had managed to achieve this.

During his 40 000 mile, five year-long voyage around the world aboard HMS Beagle, the young Darwin observed the patterns of geology and of life, both extant and extinct, on many continents. What he saw impressed him greatly and was to become the core of the 'Origin'. However, as a keen pigeon fancier and lover of horses, Darwin was sensitive to the power for selective change of careful domestic breeding. And it was with an essay on 'variation under domestication' that he began his 'one long argument,' as he described the 'Origin'.

Extrapolating from the efficacy of domestication, Darwin argued as follows: 'Why, if man can by patience select variations most useful to himself, should nature fail in selecting variations useful, under changing conditions of life, to her living products. . . . I can see no limit to this power, in slowly and beautifully adapting each form to the most complex relations of life.' Unlike the conscious selection of the domestic breeder, however, natural

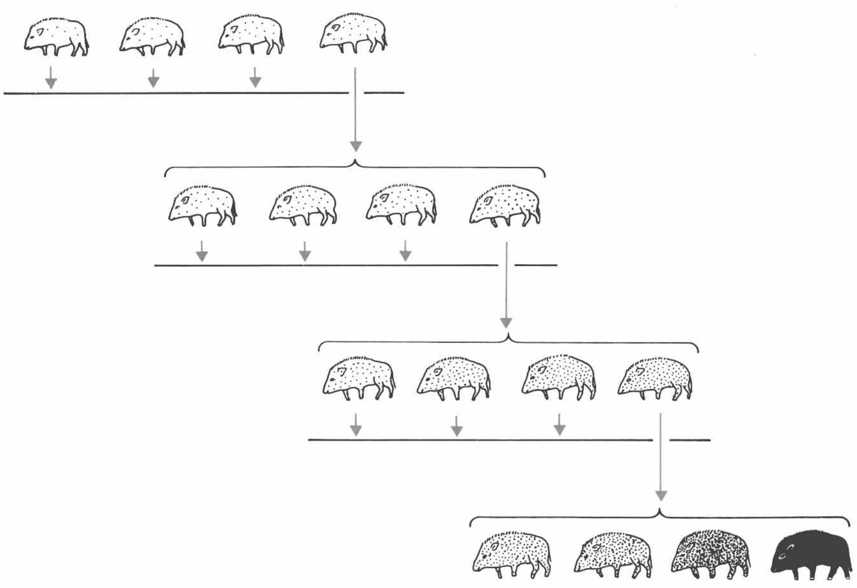


Darwin's only diagram in 'Origin of Species'. The capital letters A–L represent species in a genus, some of which changed through time (A and I), while the remainder produced unchanging descendants. The space between horizontal lines was meant to represent 1000 generations, so that after 10 000 generations species A had given rise to three new species (a^{10}, f^{10}, and m^{10}), and after 14 000 generations to eight new species (a^{14}, q^{14}, p^{14}, b^{14}, f^{14}, o^{14}, e^{14} and m^{14}). Similarly, with species I. As species descendants of A and I proliferated they eclipsed the related species, most of which (except F) became extinct after 14 000 generations.

selection is not necessarily progressive and certainly not directed or purposeful. But neither is it totally random. In natural selection, genetic variation within a population, which is random, passes through the selective filter of environmental pressures, which is not random.

Darwin described the essence of natural selection as follows: 'More individuals are born than can possibly survive. A grain in the balance will determine which individual shall live and which shall die—which variety or species shall increase in number, and which shall decrease, or finally become extinct.' The nearly-perfect match between organisms and their way of life, viewed by natural theologians as the product of a Great Designer, is explained by natural selection as a passive adaptation through the differential survival of the fittest individuals.

If, for example, a dark coat colour confers a survival advantage in a population, perhaps through more effective camouflage, then those individuals with the darkest coats will have an improved chance of survival and, therefore, an improved chance of passing their genes to subsequent generations. Through time dark coats will predominate. And through long enough periods, given sufficient change through adaptation, new species will emerge, new forms of life will arise.

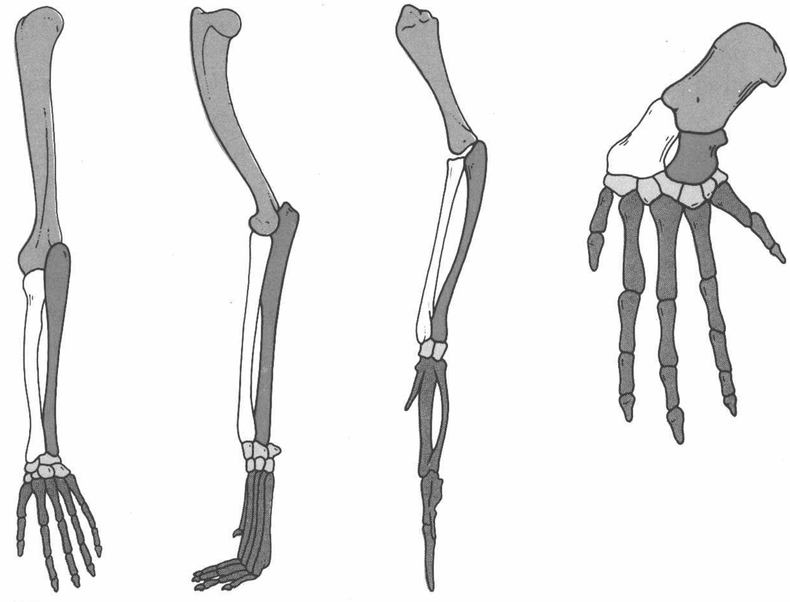


Natural selection. Selective advantages of large body size and dark coat colour confer differential survival and ultimate reproductive success on those individuals with those characters. As a result, the population mean for these characters will shift, generation by generation, towards larger size and darker coats.

The essence of natural selection as Darwin saw it was the steady accumulation of tiny incremental modifications—descent with modification as he called it. It is a slow and gradual process. 'Natura non facit saltum', nature does not make jumps, he wrote in the 'Origin'. This, as will be seen later, has been a point of contention among evolutionary biologists for many years.

Darwin admitted that his theory had problems, but he adduced massive support for the fact of evolution. Drawing on his experience on the voyage of the Beagle, he noted that fossil successions throughout the world showed, in each case, a distinct continuity, a degree of relatedness over time not readily explicable by special creation. He noted, too, that living organisms within a class are plainly related to each other within discrete geographical areas. He noted that one should not be surprised that on continents that experience similar climatic conditions which are widely separated on the globe, the forms of life inhabiting them might be quite different: '. . . the course of modification in the two areas will inevitably be different.' Why should the patterns of life on oceanic islands be more similar to those on a neighbouring continent than to the patterns of life on ecologically similar islands elsewhere on the globe? he asked. 'It must be admitted that these facts receive no explanation on the theory of creation.'

Homologous structures—for example, the common pattern of bones in the human hand, the horse's leg, the bat's wing and the fin of a porpoise—also speak of descent with modification, Darwin argued. Descent with modification also explains why 'the embryos of mammals, birds, reptiles and fishes should be so closely alike.'



The principle of homology. The biological derivation relationship (shown by colours) of the various bones in the forelimbs of four vertebrates is known as homology and was one of Darwin's arguments in favour of evolution. By contrast, the wing of a bird and the wing of a butterfly, although they do the same job, are not derived from the same structures: they are examples of analogy.

With surprising rapidity, Darwin's argument for the fact of evolution was embraced by the intellectual community. (The idea of natural selection was, however, the subject of debate many years afterwards.) With the intellectual climate so transformed, Darwin subsequently felt able to publicize his views on the more sensitive subject of human evolution. In 1871 he published 'The descent of man, and selection in relation to sex', which was an uncompromising discussion about man's place in the natural world.

'The main conclusion arrived at in this work, namely that man is descended from some lowly organized form, will, I regret to think, be highly distasteful to many', he wrote. 'We must, however, acknowledge, as it seems to me, that man with all his noble qualities, with sympathy which feels for the most debased, with benevolence which extends not only to other men but to the humblest living creature, with his godlike 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.'

Like his great friend and champion, Thomas Henry Huxley, Darwin was greatly impressed by the anatomical similarities between humans and the African great apes, the chimpanzee and gorilla. From this, he speculated on the location of man's origins. 'In each great region of the world the living mammals are closely related to the extinct species of the same region. It is, therefore, probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man's nearest allies, it is somewhat more than probable that our early progenitors lived on the African continent than elsewhere.' A century after this was written, the facts appear to support the great man's speculation.

1796. *Zoonomia* in which Erasmus Darwin discussed ideas on 'transmutation' that presaged much of Charles Darwin's theory.

1802. *Natural Theology* by William Paley who argued that the Natural World is the product of divine design, an argument that remained strongly held for half a century.

1809. *Philosophie Zoologique* by Jean Baptiste de Lamarck who proposed an internal force that drives organisms up an evolutionary ladder. Lamarckism remained strongly supported until the end of the century in some academic quarters.

1830–1833. *Principles of Geology* by Charles Lyell: the foundation of modern geology and the essential context to Darwin's evolutionary ideas.

1858. Joint paper by Darwin and Alfred Russel Wallace to the Linnean Society, the first public presentation of the theory of natural selection.

1859. *On the Origin of Species* by Charles Darwin.

1863. *Evidence as to Man's Place in Nature* by Thomas Henry Huxley, Darwin's friend of advocate, who outlined uncompromisingly what Darwin had only implied in the *Origin* about human history.

1866. *Versuche über Pflanzen-hybriden,* the description by Johann (Gregor) Mendel of his breeding experiments that revealed the principles of Genetics that were to become so important in providing a scientific basis for variation. Mendel's publication remained unnoticed for more than 30 years.

1871. *The Descent of Man* by Charles Darwin in which he stated bold and detailed evolutionary ideas applied to human origins.

1900. Mendel's work was rediscovered and described in publications by Hugo de Vries, Carl Correns and Erich Tschermak.

1901. *Die Mutationstheorie* by Hugo de Vries, a popular evolutionary theory that emphasized mutations over selection.

1937. "Genetics and the origin of species." Theodosius Dobzhansky presents the genetic input that would be so important in the emerging Modern Synthesis.

1940. *The Material Basis of Evolution* by Richard Goldschmidt, a major statement of the Mutation Theory.

1942. *Evolution: The Modern Synthesis* in which Julian Huxley outlined the marriage of Genetics and Ecology in establishing natural selection as the core of evolutionary change.

1942. "Systematics and the origin of species" by Ernst Mayr, who laid the foundations of many modern ideas on speciation.

1944. "Tempo and mode in evolution" by George Gaylord Simpson, one of the modern greats. Again, seeds of many current ideas are to be found here.

Major publications in the history of evolutionary biology.

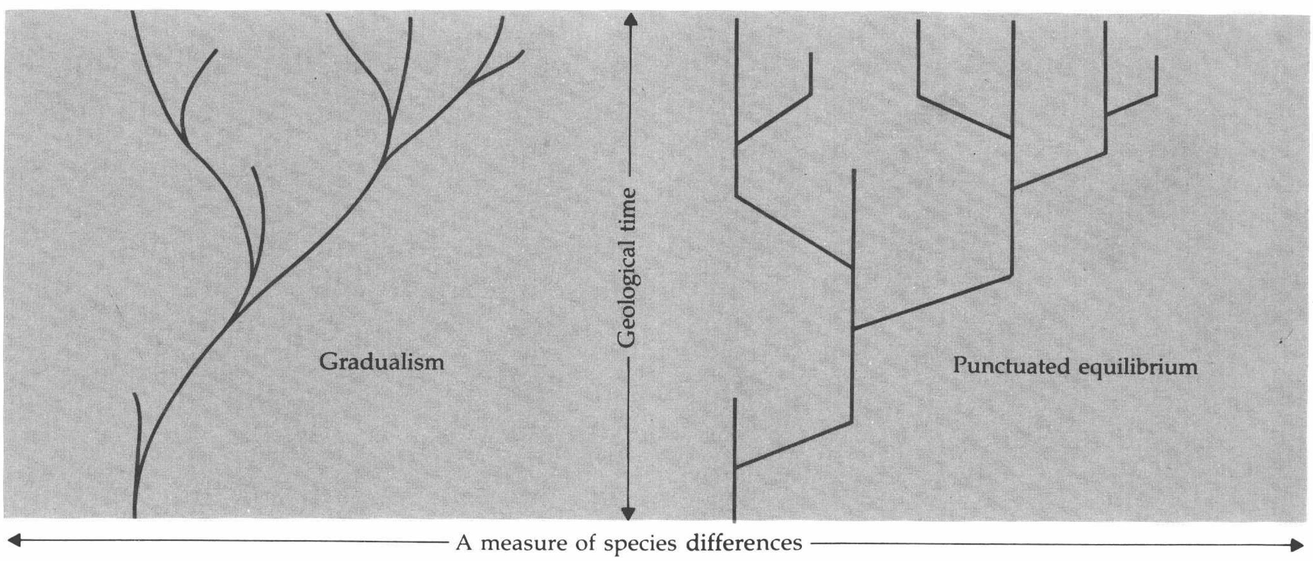
3 / Modern Evolutionary Ideas

The history of evolutionary ideas reveals how very complex the ultimate questions of biology are: 'How do species arise?' and, 'How is it that species are apparently so clearly suited to the demands of their daily lifes?' Ideas have come and gone, some to return later in refashioned form. Periods of consensus have settled a calm confidence over the field, subsequently to be replaced by a foment of new and reincarnated ideas in an atmosphere of excitement and sometimes heated debate. The 1980s is unquestionably a period of intense and healthy turmoil in evolutionary biology, with a melding of new ideas and new data generating a tremendous sense of creative tension amid urgent debate.

Although some nineteenth century scientists were immediately persuaded by Darwin's arguments that natural selection was the main agent of evolutionary change, substantial numbers clung to other ideas, including the Lamarkian notion of an internal driving force reflecting an organism's 'needs' directing that change. Then, when Mendelian genetics was rediscovered at the turn of the century, a new school emerged; these were the mutationists led principally by Hugo de Vries. Shifts in an organism's genetic constituents provided the major propulsion for evolutionary modifications, they argued, an idea later charicatured by the phrase 'hopeful monster'. The mutationists viewed evolution as proceeding by sudden bursts of change propelled by internal events, namely mutations. Effects of the external environment, via selection, were relegated, at best, to a minor role.

The early decades of this century saw evolutionary biology in some intellectual disarray. By the 1930s and 1940s, however, a consensus began to emerge, later to be known as the modern synthesis, a term coined by Julian Huxley, grandson of Thomas Henry Huxley. The modern synthesis, which was the product of a marriage of the rapidly maturing field of genetics with the more established ideas of selectionism, all in the context of population biology, brought a rare unanimity to this traditionally tumultuous branch of science. The principal architects of the modern synthesis were, with Huxley, Theodosius Dobzhansky, Ernst Mayr, Sewell Wright, Ledyard Stebbins, George Gaylord Simpson and Bernard Rensch.

At its most extreme, the modern synthesis viewed



Two modes of evolution: gradualism and punctuated equilibrium. Gradualism views evolution as proceeding by the steady accumulation of small changes over long periods of time. Punctuated equilibrium, by contrast, sees morphological change as being concentrated in 'brief' bursts of change, usually associated with the origin of a new species. Evolutionary history is the outcome of a combination of these two modes of change; however, there is considerable debate as to which mode is the more important.

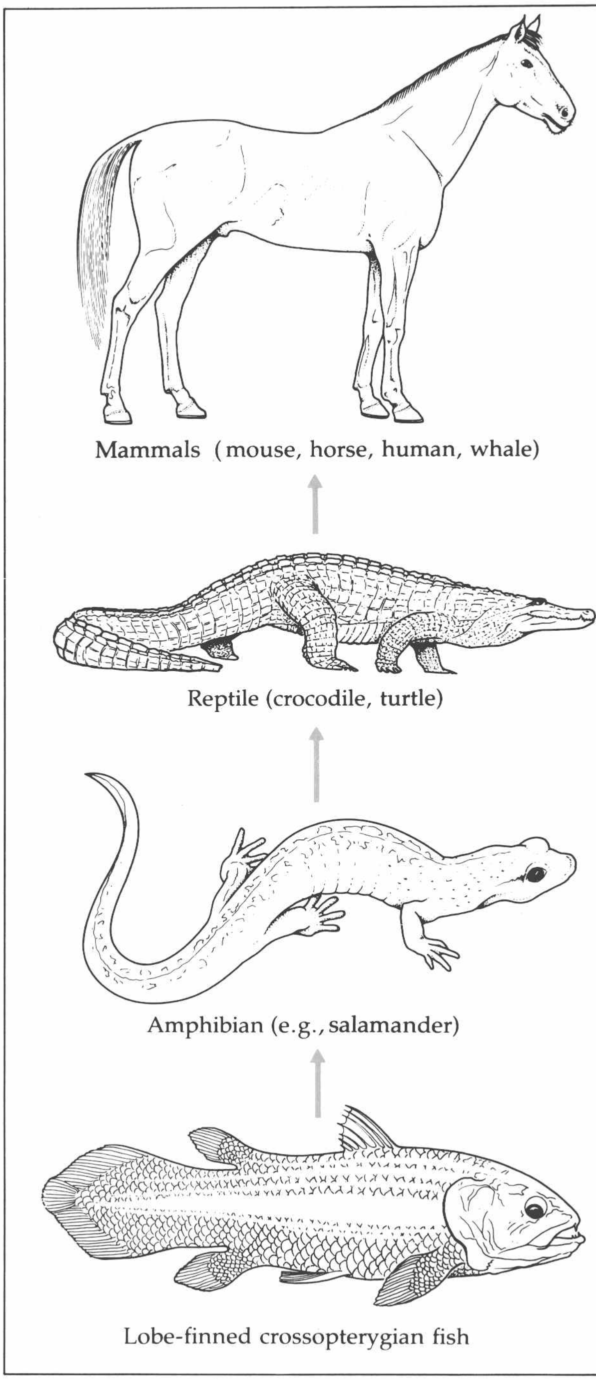
organisms as capable of infinite genetic (and, therefore, morphological) variation, with selection moulding a species from an infinite and continuous set of possibilities. Evolutionary change was characterized as a shift in gene frequencies, with traits being treated as discrete units. The overall effect of the modern synthesis was to rehabilitate the idea of evolutionary change as the product of the gradual accumulation of small incremental changes, the ultimate agent of change being natural selection. The implication was that the outcome of the all-powerful natural selection is near-perfect adaptation of species to their environments.

In 1972, two American palaeontologists, Stephen Jay Gould and Niles Eldredge, urged a reconsideration of saltational change—so-called punctuated equilibrium. The fossil record, for the most part, does not reveal a continuum of transitional forms between species. Each species in the record is relatively unchanging through time: it enters as the clear descendant of an earlier species; and when it disappears it is often replaced by a clear descendant of its own. Although such a chain of species may display undisputed relationship between one species and the next, typically there is a morphological gap in the fossil record between ancestor and descendant.

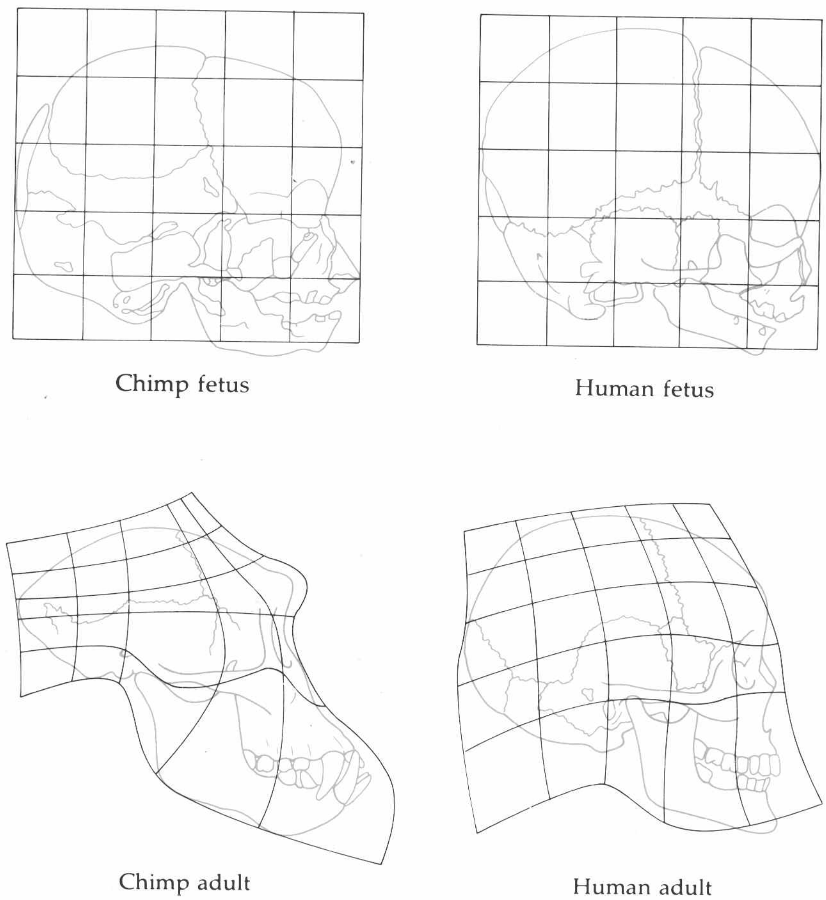
Darwin argued that the gaps resulted from an incomplete fossil record. Gould and Eldredge believe, incomplete though the record may be, it truly reflects the mode of evolutionary change: periods of morphological stasis are punctuated by bursts of change, or speciation events. These bursts might occur over 50000 years, periods relatively long by biological standards but brief in a geological context.

Punctuated equilibrium is compatible with the mode of speciation championed since the 1950s by Mayr, that of allopatric speciation. New species typically arise, he says, in small isolated populations where 'genetic revolutions' are possible and new variants will not be diluted in a large pool of average genotypes.

Gould and others also object to the apparent implication of the modern synthesis that the range of variation available to selection is totally unconstrained and anything is possible. (The same observation had been made earlier by Conrad Waddington, but it was eventually submerged by the selectionism of the modern synthesis.) The counter argument holds that events of history and the rules of embryological development represent two important sources of constraint, and of opportunity, on evolutionary change. For example, the first terrestrial vertebrates had four legs, not because this was selected as the most efficient mode of locomotion but



The principle of historical constraint. Evolution, in many ways, is a conservative process. The preservation of a four-limbed body over vast tracts of time and through very different environmental circumstances illustrates the power of historical constraint. For example, the horse has four legs not just because it is a very efficient way of moving about on dry land but because its fish ancestors also had four appendages.



Neotony in human evolution. Although the shape of the cranium in human and chimpanzee fetuses is very similar, a slowing down in development through human evolution has produced adult crania of very different forms, principally in the shape of the face and the size of the brain case. The changes in grid shapes indicate the orientation of growth.

because the first land animals descended from fish with four fins.

Although the rules of embryological development remain to be elucidated, it is clear that the embryo grows as an integrated whole. The fact that embryos of widely different organisms pass through very similar stages, as Darwin noted, seems to indicate that channels of development are indeed tightly constrained. The combined constraints of history and development must, therefore, limit the range of variation upon which selection can subsequently act.

The constraints of embryological development also present evolutionary opportunities. Small alterations in the timing of events in early development, for example, might produce a substantial change in the mature organism—not quite the 'hopeful monster' variety, but a more dramatic change than envisioned by a simple shift in gene frequencies. Indeed, there is a good deal of evidence that much of evolutionary change derives from shifts in the timing of developmental events, a pertinent example of which is with humans. In many ways mature humans are reminiscent of juvenile apes: our small faces and globular cranium are examples of this. A crucial step in human evolution, the enlargement of the brain, can be seen as the result of a slowing down of embryological development in an ape-like ancestor. Instead of ceasing at birth, brain growth continues well into childhood, eventually producing a much larger and more complicated piece of mental machinery.

With natural selection remaining at the core of modern theory, constrained as it is by history and embryology, evolutionary change can be viewed as a combination of relatively rapid shifts and of gradual modifications. Major evolutionary innovations are likely to be the product of punctuational rather than gradual change. And there is decreased emphasis on viewing species as conglomerations of near-perfect adaptations. As French novelist Francois Jacob said: 'Evolution is a tinkerer, not a precision engineer.'

4 / Primate Heritage

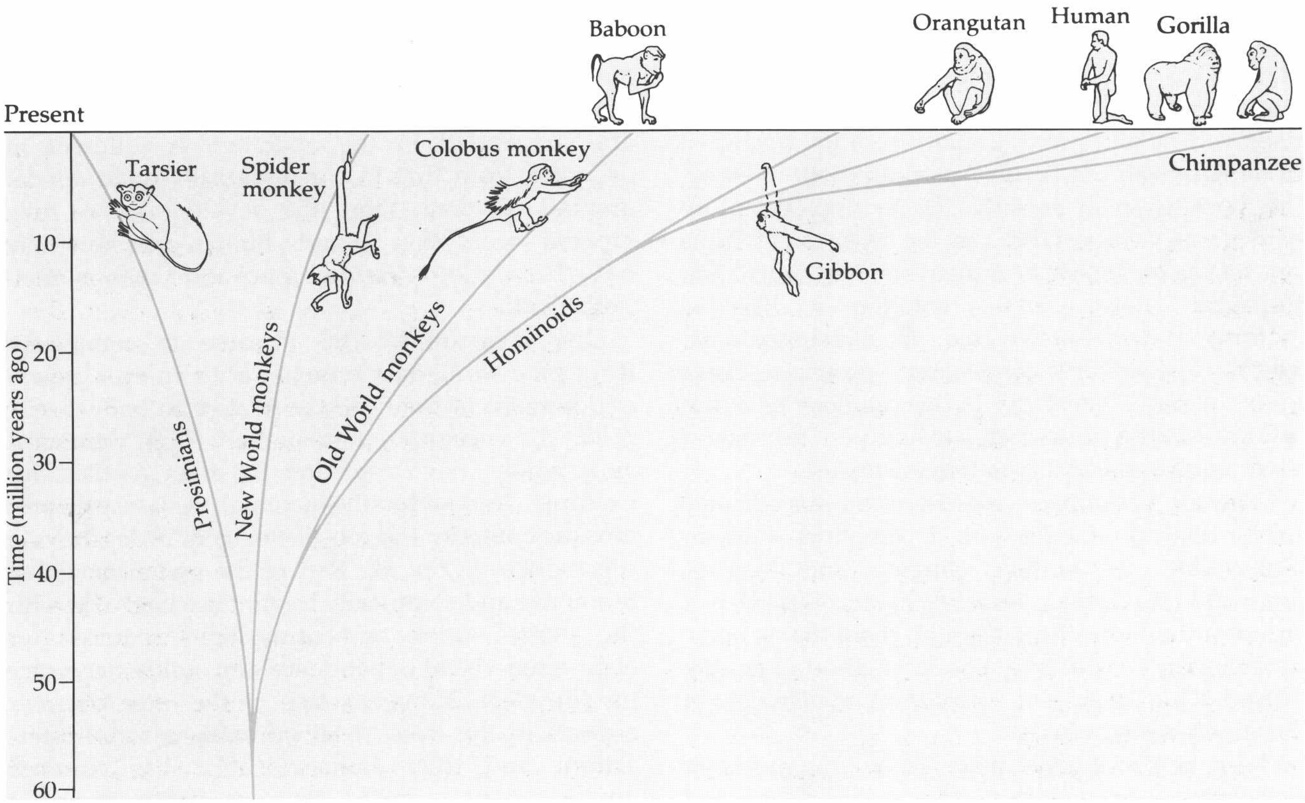
Primates are quintessentially creatures of the tropics. *Homo sapiens,* having inhabited virtually every corner of the globe, is therefore something of an unusual member of this interesting vertebrate order. By contrast, many of the characteristics that might be taken to separate man from the rest of his fellow primates—such as extreme intelligence, upright walking, and intense sociality—are, in fact, merely extensions of typical primate features, not discontinuities from them.

The Cretaceous extinction that spelled the end of the reign of the dinosaurs also terminated many mammalian lines, particularly among the marsupials. Primates, in the infancy of their evolution at the time, were among the mammalian orders to survive the extinction. It is salutary to contemplate the course of history had the primate line been extinguished 65 million years ago! However, survive it did, and it experienced the kind of adaptive radiation typical of many mammalian groups through the Cenozoic period.

The earliest primates were small, nocturnal, arboreal animals, not unlike the modern tree shrew. Life in the trees is the natural habitat for the vast majority of primates and even those that have adopted a terrestrial life style, such as baboons and ring-tailed lemurs, are never far from the safety of branches aloft. It is not surprising, therefore, that adaptations to arboreality form the essence of what it is to be a primate.

The first primates were insect-eaters, a feature, incidentally, of many vertebrate orders in their evolutionary beginnings. For primates, the combination of predating on insects while suspended precariously on thin branches and twigs, led to a suite of important adaptations.

The predatory weapon was the hand, which developed a high level of manipulative facility. The hand eventually acquired an opposable thumb, which aided in grasping prey, and sensitive finger pads backed by nails rather than claws, which extended primates' exploratory dimensions in their



Primate family tree.