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Excerpt
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Chapter 1

How can we recognize common ancestors?

There are many issues that challenge us today in our investigations of the natural world. One that has always fascinated me is the structure of the universe and our position in it; and in a way following on from this, we can ask what is the nature of life and in particular how did humans evolve. The first is the stuff of astronomy, and with advancing technology we see many things today that we could not even have begun to predict in the past. The second is driven by our fascination with the world around us and in particular with ourselves, our origins and our place in the world.

It used to be thought that all we need to know about our evolutionary history will be resolved by finding more and better fossils, in the same way as it used to be thought that to understand the universe all we need is bigger and better telescopes. For both lines of inquiry, however, it is increasingly being recognized that what we really need are new ways of looking at things, at stars and cosmic rays in the case of astronomy, and at our genetic history and fossil environments in the case of human evolution. It is not enough now to find earlier and better fossils of ancestral humans; we should rather be seeking to understand their place in the web of life and their interactions with the ecosystems in which they once lived. This can be followed throughout human evolution, but of particular importance is the time when the human lineage first appeared. Can we identify our common ancestor with our closest primate relatives, or as some put it, the missing link in human evolution?

There are in fact many 'missing links' in human evolution, and Charles Darwin devoted two chapters of his book *The Origin of Species* to the problems in identifying them. Missing links are transitional forms between species, and Darwin was concerned with their apparent absence, both in living species, which he discussed at length in Chapter VI, and between related fossil species, discussed in Chapter X. He did not consider either to be fatal to his theory of natural selection, for by their nature they would have been superseded and replaced by emerging species. He would have been gratified by the current fossil record of human evolution, which is replete with 'missing links'. Each one tells us something about how we evolved as a species, when transitions occurred, and where, but none of them tell us where we first came from.

Our closest living relative among the apes is currently recognized as the chimpanzee, and it is natural to look for intermediate forms between humans and chimpanzees, both in terms of shared morphology and behaviour, and in the fossil record. Darwin is very explicit on this: "I have found it difficult, when looking at any two species, to avoid picturing to myself forms directly intermediate between them. But this is a wholly false view; we should always look for forms intermediate between each species and a common but unknown progenitor; and the progenitor will generally have differed in some respects from all its modified descendants" (Chapter X, page 413, of the sixth edition of *The Origin of Species*). In other words it would be a mistake to consider that our common ancestor with chimpanzees looked anything like either ourselves or like chimpanzees, but it is reasonable to look to see how much we share with chimpanzees, both genetically and morphologically.

Another approach to studying human evolution takes as its starting point our knowledge of modern humans, our anatomy, behaviour and genetics, and works backwards in time to look for the 'missing links' in the human fossil record. It will be seen that the further back we go, the harder it becomes to distinguish apes from humans, and the time when the human lineage arose is still unknown. We do know, however, that our closest living relatives are the apes, and I believe we need to approach this issue by looking at human origins from new directions, both by looking from the ape's point of view and by applying the new methods and technologies that are increasingly becoming available. In this way, we can extract more and more information from the available evidence. I will be looking at living and fossil apes to find genetic and morphological patterns present in the past in relation to the origin of the human lineage, extracting the likely behaviour of these now-fossilized apes, and reconstructing their place in the ecosystems in which they lived. Key points in this regard are as follows:

- Throughout three quarters of their history, fossil apes differed greatly from living apes.
- The norm for apes as shown by the fossils spanning 15 million years of evolution was of quadrupedal monkey-like adaptations.
- Fossil apes were adapted both for life in trees and on the ground.
- They were adapted for a mainly fruit diet, but some had adaptations for leaves or harder food like nuts.
- The majority of known species did not live in tropical forest but in tropical to subtropical open canopy woodland.
- Sexual dimorphism was moderate to high in many fossil apes, indicating fluid social structures.

We can infer that the last common ancestor of apes and humans shared some of these characteristics, as did early human ancestors, and major differences first came about through the acquisition of adaptations for bipedal walking early in human ancestry.

History of investigations into human evolution

The question of human origins has intrigued people from before the time of Charles Darwin. Karl Linnaeus first formulated the question of man's origin when he assigned humans to the order Primates (then called Anthropomorpha) and described them just like any other plant or animal. This was not accepted by some early scientists, who placed humans in their own separate class, and even T.H. Huxley placed humans in their own group, the Anthropini, despite the fact that he recognized their similarities with the African apes. Charles Darwin in *The Descent of Man* took the view that "from a genealogical point of view it appears … that man ought to form merely a family, or possibly even only a subfamily" in the order Primates. He says further that "If the anthropomorphous apes be admitted to form a natural sub-group, then as man agrees with them, not only in all those characters which he possesses in common … but in other peculiar characters, such as the absence of a tail and of callosities and in general appearance, we may infer that some ancient member of the anthropomorphous sub-group gave birth to man." Darwin finally goes on to warn that we should not expect any ancestor that "was identical with, or closely resembled, any existing ape or monkey". It was generally recognized by these nineteenth century scientists, therefore, that humans are primates, are grouped with apes and their common ancestor resembled neither ape nor human.

With regard to *where* humans evolved, Darwin is more direct. "It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzees; and as these two species are now man's nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere." He further recognized that early humans were frugivorous (fruit-eating) and lived in a hot climate. T.H. Huxley agreed with Darwin's conclusions both with respect to Africa being the original home of mankind and to chimpanzees and gorillas being most closely related to humans (Figure 1.1). The German zoologist Ernst Haeckel, in his *History of Creation*, devised 22 stages in the evolution of life, and in the absence of fossil evidence, he placed apes in stage 20 and humans in stage 22. The acquisition of upright walking, the presence of a large brain and the power of speech marked their separation at stage 21. These early scientists were working with near absence of fossil evidence, but it was stemming from

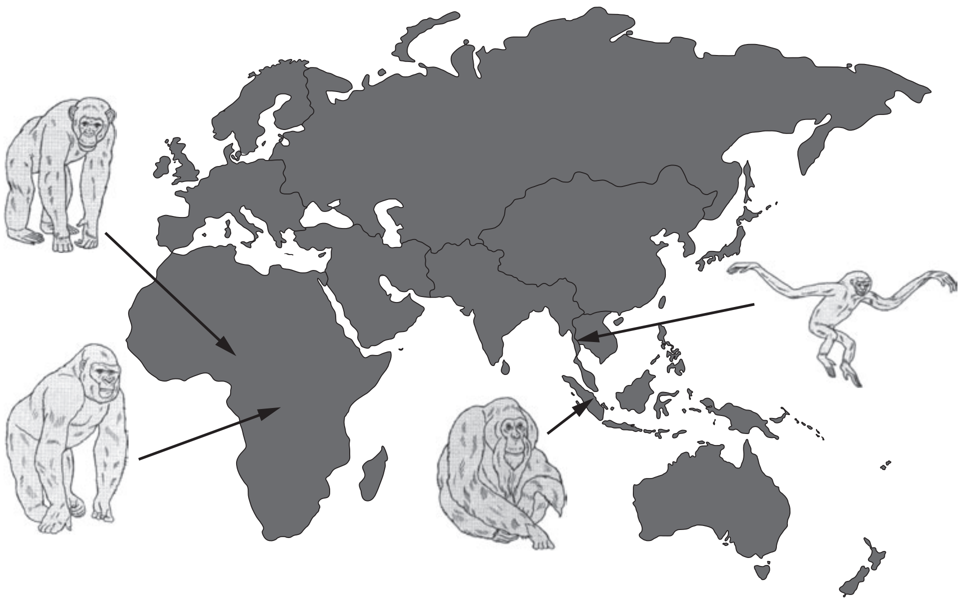

Figure 1.1 Distribution of the extant apes, chimpanzees and gorillas in Africa, and gibbons and orang utans in Southeast Asia.

their insights that early twentieth century scientists like Raymond Dart, Ralph von Koenigswald, Eugene Dubois and Louis Leakey devoted much time and expense looking for the 'missing link' or the common ancestor between humans and apes.

Eugene Dubois had been inspired by Haeckel's work, which provided him with what we would call today a 'search image'. Neanderthals did not qualify for his search image, as he thought that they were only a low sort of human, a primitive race. For Dubois, "Only the fossil remains of the transitional form between ape and man could prove evolution irrefutably. There could be no denying evolution, with such a fossil in hand. To find the right fossil, the one with anatomy that was half-man, half-ape . . . what a grand thing it would be, to be the man who found the missing link!"

In 1887, Eugene Dubois set out to Indonesia (at the time the Dutch East Indies) with the express purpose of finding the missing link between humans and apes, and against all the odds he was successful. First he found a molar tooth which he thought looked like a chimpanzee tooth. Soon after he found a skull cap which must have housed a brain very much larger than that of any living ape, and a leg bone which indicated that his fossil had been an upright two-legged walker. These are two elements of Haeckel's stages, and Dubois could hardly be blamed for not finding the third, as evidence of speech does not fossilize, at least not at this early stage. After some juggling with names, Dubois eventually named his fossil *Pithecanthropus erectus*, which translates as erect ape man. He claimed it was neither ape nor human but was the transitional form that must have existed between man and the anthropoids.[1] Despite its large brain, nearly twice the size of even the largest gorilla, he never accepted it as a human ancestor, although most others did so over time.

The earliest fossil human found was not in fact greeted with acclaim but was largely ignored. This was the Neandertal skull found in 1848 in Gibraltar. Many claims were made for it, but when it was first found it was not even identified as a human ancestor. It was thought by many to be a pathological modern human, with its great brow ridges and robust skull, and in fact there was little interest in it. A few years later, a similar skull was found in the Neander valley in Germany (Neander Tal). It was named by Professor William King as *Homo neanderthalensis* at the 33rd meeting of the British Association for the Advancement of Science in 1863. King described the fossil in more detail the following year, and T.H. Huxley provided an account of the Neandertal skull in *Man's Place in Nature*. He identified some of its characters as ape-like, although he recognized its human qualities: "In no sense can the Neanderthal bones be regarded as the remains of a human being intermediate between men and apes."

At the same time as these early Neandertal fossils were being found, the first fossil apes came to light from much older Miocene deposits in Europe (Figure 1.2). Some of these have been claimed to be ancestral to living apes and even humans, but all too often the search for the chimpanzee–human common ancestor has been sidelined by using the chimpanzee as a model. Such a procedure was in fact first suggested by Huxley, but using one of the descendant species like this as a model for the common ancestor would be putting the cart before the horse, for it not only does not answer the question of what the common ancestor was like, but it also actually prevents us from even asking the question. In fact, few mammalian lineages have remained unchanged since the time of the late Miocene, and it is simplistic to assume that the hominin lineage has undergone significant evolutionary change since the common ancestor but the chimpanzee lineage has not. Robert Broom was equivocal on this matter: "there is much difference of opinion as to whether the ancestor was a higher anthropoid such as the gorilla or chimpanzee, (or) an earlier anthropoid like the fossil Miocene ape *Dryopithecus*", although he had previously rejected all dryopithecines as possible ancestors on the grounds that they had

[1] Anthropids are the Old World monkeys and apes, the superfamilies Cercopithecoidea and Hominoidea.

Figure 1.2 The first fossil apes of *Dryopithecus* and *Pliopithecus* found in southern France during the nineteenth century, consisting only of jaws and teeth. These fossils were known to Darwin and Huxley, but they did not comment on them.

large canines and shearing third premolars, and he considered this condition could not be reversed to arrive at the australopithecine and human condition.

Other workers took a more balanced view of human origins. W.K. Gregory observed that: "Many anthropologists have specialized almost exclusively in their own field and have not acquired a practical knowledge of the evolution of the mammals, so far as it is known in many orders and families of mammals throughout the Tertiary and Quaternary Periods. Such specialists are impressed by the great and obvious differences between mankind and the existing anthropoids. They often magnify the phylogenetic importance of these differences, sometimes to the extent of supposing that the derivation of man is still veiled in complete mystery, ... (and that) chimpanzee and gorilla have retained, with only minor changes, the ancestral habitus in brain, dentition, skull and limbs, while the forerunners of the Hominidae, through a profound change in function, lost the primitive anthropoid habitus, gave up arboreal frugivorous adaptations and early became terrestrial, bipedal and predatory, using crude flints to cut up and smash the varied food." I believe that it is a deeply buried assumption in the views of many scientists that humans are indeed 'different' from the rest of the animal kingdom, and this is in fact a throwback to nineteenth century thinking, which classified humans in their own family.

Björn Kurten, a remarkably perceptive biologist, proposed in his book that "Man did not descend from the apes. It would be more correct to say that apes and monkeys descended from early ancestors of man. The distinction is real: in the traits under consideration, man is primitive, apes and monkeys are specialized." Louis Leakey was another perceptive biologist, and he brings out two issues that give many people cause for concern when regarding our relationship with the apes when he said:

> People will stand in front of a chimpanzee in a zoo, or a stuffed gorilla in a museum, and say: 'I just could not believe that I am descended from that!' Scientists do not believe it either, nor do they ask anyone else to believe it; but they do claim that the great apes and man had a common ancestor long ago. But man on the one hand and apes on the other represent different branches and different specializations that have arisen from that common stock . . . . It has been all too common to write or speak of the great apes as PRIMITIVE members of the ape-human stock, and from this to argue that physical characters that occur in the apes are also PRIMITIVE characters, and as such, characters which one might expect to find in pre-human fossils that were in the direct line leading to man himself.

Mike Rose made a particularly telling point when he said: "When I look at the postcranial bones from the Miocene apes, I get a fairly consistent pattern from many species, but it is nothing like what we see in modern apes. Maybe we should consider the ones that survived as the bizarre ones." I believe we should indeed take the Miocene apes as 'normal' and their present survivors as highly derived, which means most emphatically that we should not use any of the living apes as a model for the ancestral pattern for humans.

Fossil apes and human evolution

Now we should consider how much fossil apes can tell us about human evolution and what kind of information we can expect to get from a study of fossil apes. For a start they provide an approximate age *when* a particular lineage arose, including the human lineage; they also tell us *where* it existed in the past; and therefore they tell us where and when the ancestors for two lineages may have lived, and in particular where and when the last common ancestor of apes and humans lived. In addition, they tell us *which adaptations* were present in different lineages of fossil ape, which can then be compared with the adaptations seen in early humans, the order in which adaptations appeared and which were important to the life of the animals. This is important in itself, but if the adaptations are related to the *environment* with which they were associated, they should allow us to interpret the place fossil apes and humans occupied in that environment. These issues are based on the assumption that morphological adaptations relate to habitat and can be interpreted for fossil apes by comparison with living primates.

In contrast to all these things that the study of fossil apes tells us about ape and human evolution, it needs to be stated that most species of fossil ape tell us little about the evolutionary relationships of living taxa. The evidence for this comes from genetics and morphology of living species; although I will provide some background on this, the main part of this book is about the fossils, and therefore the main emphasis of this book will not be on evolutionary relationships but on the adaptations and the environment of the ape ancestors of humans. This is based on my belief that any realistic assessment of the last common ancestor of apes and humans must be interpreted in terms of where, when and how it lived, and this means its location and environment. I will be describing the ranges of adaptations present in fossil apes in relation to their environment, and in interpreting the types of habitat occupied by the Miocene apes I will be drawing upon my years of work in Kenyan forestry. I should explain a little about my work in Kenya as a background to the ecological interpretations I will present later in this book.

My first job in Africa was in the Kenyan Department of Forestry, at a remote forest station high up on the slopes of the Aberdare Mountains: Kiandangoro Forest Station is set in the midst of montane forest at an altitude of 2400 metres. There are dense bamboo thickets through which elephants had carved pathways, and following these paths was virtually the only way of penetrating them; by contrast the montane forest was easier to get through except that it seemed to be mostly growing on near vertical slopes. I had many close encounters with the local wildlife, including a close inspection from a leopard one night while asleep in a rather flimsy tent. I also had the good fortune to walk through a large herd of buffalo in dense vegetation without seeing a single one. The forest guards who had gone on ahead and who were safely perched up in trees could see the whole event unfolding, which they told me about in graphic detail afterwards.

My next posting in Kenya was to assist with the running of the Nyeri Division, which controlled the montane forests of Mount Kenya and the Aberdares. Although collectively described as forest, in fact the vegetation ranged from magnificent camphor forests on the southeast mountain slopes, where the moisture-laden winds blowing in from the sea dumped most of their water load, to the dry cedar forests of the northwest, the winds having deposited most of their moisture content before reaching there. On the northern slopes there are no trees at all, the dry forest having been replaced by ericaceous vegetation. Above the upper limits of the tree line, at about 3000 m, was a wonderful landscape of heathers, giant groundsel and *Senecio*.

My third posting was to western Kenya, both to seek out new areas to set aside for planting new forests around the shores of Lake Victoria and to manage Kakamega Forest. Kakamega Forest is an 'island forest', the furthest eastern outlier of the Central African and Ugandan lowland forests (technically part of the Guinea-Congolian lowland rainforest). It officially extends over 240 km^2 and has a great variety of habitats: species-rich areas in broad river valleys (Yala River), intermediate semi-deciduous forest with less complex canopy structure covering much of the area away from the valleys and more open areas of bushland on rocky outcrops. Local farmers have excised much of the land, both officially and unofficially, for settlement, so that well under half of this area is now under forest. The mammal fauna has been well documented by Jonathan Kingdon in his magnificent series on East African Mammals, and the monkeys have been extensively studied, including the formation of mixed-species groups of monkeys. What is particularly interesting about this region is that the forest vegetation is interrupted by grass glades, areas with stable borders of *Acacia* and tall herbaceous vegetation. These may have been the result of clearing of the forest, although where the forest is being cleared at present for agriculture, the trees grow back if given the chance. The surrounding forest has many pioneer tree species that rush to fill any clearing, for example *Maesopsis eminii*, which is a common species at Kakamega, and which is known to readily expand into surrounding grasslands. The glades have shallow dry soils, unlike the grass dambos of the Central African forests, which are part swamp. Since rainfall over the Kakamega Basin is in excess of 2000 mm, spread evenly throughout the year, with even the driest month receiving about 100 millimetres, it is evident that the grass glades are not climatically controlled but are present as a result of some other factors. As far as I know, this has not yet been studied, but other possible solutions are that there is a hard pan close to the surface of the soil, which impedes drainage of the soil and prevents the growth of deep-rooting trees, or there may be chemical contaminants in the soil preventing growth of trees (Figure 1.3).

Kakamega Forest is in the north of Nyanza Province, and in the south there were almost no forest areas receiving any protection. My job was to locate suitable areas and to persuade the local population of the benefits of building up forests. This was not an easy task, and while a measure of agreement was reached for several areas, in the long term the needs of the local people for land to grow crops on has prevailed. In the course of my work in the region I met many interesting people, and one of the lessons I learned was the tragedy of living with contradictions. Subsistence farming was the norm in that part of Kenya, and the farmers were able to feed their families by expanding into the woodlands surrounding their farms. They did this by cutting down the trees, and they could tell me of several instances where the clearing had destroyed their water supplies. They were well aware of cause and effect, the existence of

Figure 1.3 Kakamega Forest, Kenya. (a) The interior of the semi-evergreen forest, which is classified as intermediate tropical forest, i.e. intermediate between lowland and montane forest. (b) The forest edge, with rainforest stepping down to a line of Acacias and down again to a line of high herbaceous (*Acanthus*) vegetation, and finally down to grassland. (c) The transitional border is more or less permanent, and fires started in the grassland do not penetrate into the forest. Grass glades are very extensive within the forest boundaries, and they appear to be edaphic in origin rather than climatic, but the nature of the soil factors is not known at present. A black and white version of this figure will appear in some formats. See plate section for colour version.