CHAPTER 1

The Past, Present and Future of Paleoanthropology

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Paleoanthropology is the study of human evolution and that of our closest living relatives, the other primates. Humans of course are primates, and paleoanthropologists recognize the importance of understanding primate evolution as a necessary condition to understanding human evolution. This is the reason primate evolution is most commonly considered a part of paleoanthropology as opposed to the larger field of vertebrate paleontology. Paleoanthropology also includes a variety of other fields that tremendously inform the study of paleoanthropology. These include primate biology, systematics, ecology, genetics and geology. And of course, since paleoanthropologists are interested in the behavior of fossil humans, and since many of these humans left material evidence of their behavior in the fossil record, the analysis of this record, Paleolithic archeology, is also a major part of paleoanthropology. Because the material evidence of the behavior of fossil humans is so ubiquitous, while it is essentially non-existent in other animals, paleoanthropology is unique among the historical sciences.

The chapters in this book are organized around the themes that represent major areas of research in paleoanthropology. After an introductory chapter on the history of paleoanthropology, the first section of the book is on method and theory (experimental approaches, quantitative methods and life history theory). The second section on individual anatomical regions includes reviews of the evolution of the skull, brain, dentition and diet, and the limbs. The third section is devoted to environment and behavior, and includes chapters on paleoecology, geochronology, the reconstruction of social behavior using primate models, and Paleolithic archeology. In the fourth section, on genetics and race, there are chapters on the genetics of primate evolution and the genetic determinants of morphology, as well as a chapter on the race concept

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historically and today in paleoanthropology. The final three sections of the book consist of chapters describing the fossil evidence of primate evolution from their origins through the Quaternary period to the emergence of modern humans.

The history of paleoanthropology, in the sense of a general interest in understanding where we came from and how we fit within, or what our role is in the known world, is quite ancient, but the science of paleoanthropology is relatively recent (Goodrum, Chapter 2). At the end of the 18th century and especially in the first half of the 19th century, ideas of the antiquity of the earth (geologic time), transformationism (evolution), comparative anatomy and even the precursors of structural biology (unity of plan) were contributing to a new vision of natural history (or natural philosophy). For some time before that explorers brought back with them from exotic locals animals that looked strangely human-like, and our knowledge of these creatures (non-human primates) increased considerably in the 19th century. By the second half of the 19th century, Darwin had published on natural selection and human evolution, Huxley had documented the anatomical similarities between apes and humans, Mendel had discovered the basic principles of genetics, and early archeologists were beginning to amass impressive collections of artifacts of apparently great antiquity.

The first practitioners of paleoanthropology were comparative anatomists, archeologists and people willing to explore the far-reaching corners of the world in search of evidence of human evolution. The first of these were not trained in paleontology and were most commonly anatomists or physicians. Beginning in the 19th century and well into the first half of the 20th century, researchers explored the habitats of living primates, and over the years they also "harvested" vast numbers of primates. Although it has been a long time since this practice was repudiated by researchers (except in special cases such as culling), the resulting collections are among the most valuable resources of comparative data for paleoanthropologists. These same researchers began to document the behavior of primates in their natural habitats.

During the 20th century the disciplines of archeology, comparative anatomy and primatology, and fossil-collecting techniques, became more refined and sophisticated. Experimental approaches appear in the 1940s and 1950s, exploring the functional anatomy of the musculo-skeletal system and the behavior of primates in captivity. Our knowledge of genetics exploded following the discovery of heritable material (chromosomes) in cells in the beginning of the 20th century. Researchers began to embrace the idea of combining all of these approaches into the unified discipline of paleoanthropology, and by the 1970s it became increasing routine for paleoanthropological projects to combine the collection of fossils with archeology, geology, paleoecology (developed from vertebrate paleontology) in the field, and comparative anatomy and experimental biology in the lab.

The first chapter of the section on method and theory is on systematics (Strait, Chapter 3). Though limited to hominin systematics, this chapter makes it clear that there is much disagreement among researchers on the precise pattern of relationships among hominins, and even disagreement on what to call this group.[1] As Strait says, the words consensus and paleoanthropology are rarely used in the same sentence. While I am a bit less pessimistic, and see more consensus now than ten years ago, we have a very long way to go before we have the fossils and the analyses of them necessary to fully resolve the mysteries of the human fossil record. And this does not even include debate about the primate fossil record, which is at least as contentious. Although it would be satisfying to have all the answers, this would put many of us out of business. Actually, science does not work that way. There is always uncertainty in science, but in the historical sciences it is a real challenge to make convincing cases for events that occurred well before anyone who ever lived could have witnessed them. To me, that is precisely what makes paleoanthropology so exciting.

One clear pattern that emerges from an analysis of the human fossil record is that it is very complex. No one today would hold, as in the past, that humans evolved as a single lineage from a chimp-like ancestor to modern humans. It is clear that there are many branches, most of which were dead ends, experiments in being bipedal. Given the number of false starts, it is very difficult to know which among these early bipeds led to modern humans. In fact, we do not even know if any of the known fossil hominins are directly related to modern humans, and I would argue that there is a good chance that none of them are. But one of the known early hominins is probably more closely related to the genus *Homo* than are the others. Deciding which one is the best candidate is going to take some more time.

Another clear aspect of the study of hominid systematics is the nearly universal application of the principles of cladistics analysis (Strait, Chapter 3). While there remain some detractors, the majority of researchers recognize the value of cladistic methodology in revealing patterns of evolutionary change.

The next chapter in the methods section describes experimental approaches in paleoanthropology (Ravosa, Congdon and Menegaz, Chapter 4). Since Washburn called out to biological anthropologists, in the middle of the last century, to incorporate more experimental research, lab research has developed as a major aspect of paleoanthropology. Much of this involves testing hypotheses of muscle recruitment or the nature and magnitude of strains produced by various activities, whether dietary or locomotor, which serve ultimately to test ideas of selection pressures for certain changes observed in the fossil record. Experimental research tests ideas such as "powerful brow ridges are a response to powerfully chewing: false"; "mandibular morphology responds in predictable ways to diet and the mechanical properties of food: true". Experimental approaches have allowed us to test in repeatable ways many mechanical implications that emerge from speculations ranging from the origins of bipedalism to the manufacturing of stone tools.

Chapter 5 in the method and theory section is devoted to a review of commonly applied methods of quantitative analysis in paleoanthropology (Schillaci and Gunz, Chapter 5). While multivariate methods have been applied to paleoanthropological questions for years, they are now more or less de rigueur. The authors divide their chapter into multivariate techniques used to analyze traditional (linear or angular) data and techniques for geometric morphometric data. The latter has experienced an explosion in popularity. Many researchers, myself included, have some difficulty understanding the assumptions and limitations of many of these methods, and this chapter serves to clarify some of these mysteries.

The final chapter in this section is on life history, growth and development (Kelley and Bolter, Chapter 6). The importance of these issues in interpreting the hominid fossil record has also expanded greatly in recent years, mainly, I think, due to the development of techniques to assess patterns of growth and development, especially in the dentition. Major developments in life-history research based on the fossil record have led to the recognition that the earliest hominins grew much more like great apes than humans, and that even more recent fossil humans, such as *Homo erectus* and Neandertals[2] differ from modern humans. It is clear that researchers are increasingly interested in understanding the life history of the fossil taxa they study, and that growth and development are significant if not the major processes that contribute to evolutionary change.

The next section of this book explores the evolution of various regions of the body. Shea (Chapter 7) reviews what we know about the evolution of the cranium in hominoids. He makes the important point that more needs to be done to understand the nature of the hylobatid (gibbons and siamangs) cranium and how it informs us about the evolution of the cranium in the hominids (great apes and humans). There is a tremendous range in the body mass of hominoids, with the smallest ones (gibbons) on average about 30–35 times smaller than the largest ones (male gorillas). This makes it a challenge to compare hominoid crania, as the effects of size must be accounted for. The range of variation in morphology is also spectacular, especially when fossil hominoids are included. In addition to diet and brain size, which are the most common mechanical constraints thought to mold the cranium, allometry (size and shape relationships), sexual dimorphism and other aspects of social adaptation need to be incorporated into analyses of cranial morphology.

Chapter 8 (Schoenemann) is a review of the evidence of the evolution of the hominid brain. Brains are of obvious interest in paleoanthropology given the remarkable size of the human brain. This needs explaining, but this endeavor is complicated by the fact that the brain is an extremely expensive and very poorly understood organ and that it is not preserved in the fossil record. We have the general sense that the bigger the brain, the "brainier" the species, but we also know that diversity in brain size within a species is not correlated to intelligence. It is well known that there is no correlation between intelligence and brain size in humans, the latter of which varies in normal individuals by a ratio of 1:2 (roughly 1000cc to 2000cc). The causes and consequences of brain size increase in the human lineage is a fascinating area of study. New techniques of analysis of fossils, such as high-resolution CT imaging, and a deeper understanding of the function of the brain will help us to understand more completely the reasons behind the spectacular evolution of the human brain.

Chapter 9 (Ungar and Sponheimer) focuses on research related to reconstructing the diet of our fossil ancestors, based on the anatomy of the jaws and teeth and from the dueling perspectives of the effects of the mechanical properties of food on our teeth and the chemical signals left behind by the foods we eat. All mammals, which have complex teeth and complicated dentitions, have evolved tooth forms that serve them well in processing the foods they normally eat (or they would not survive). Thus, tooth form is strongly related to broad aspects of diet, such as whether an organism routinely crushes hard or tough foods, slices through fibrous foods, or grinds more pulpy foods. Even the histology of teeth (the internal organization of cells and molecules that make up the tooth) affect the way a tooth responds to strains, and this can also be used to reconstruct diet in our ancestors. Moving away from structure, the chemical composition of teeth (and bone) reflects the aphorism that you are what you eat. There are numerous chemical indicators of diet that can be recovered from fossils. In addition, of course, what we find at sites with fossil hominins (and in some cases other fossil primates) tells us something about what they ate, whether it is the plant or animal remains found with them, food residue on their teeth or stone tools, or a general understanding of the ecology of the places in which they lived.

Chapter 10 reviews the evolution of the postcranial skeleton from apes to humans. The goal here is to, firstly, set the stage for the evolution of bipedalism by discussing the evolution of the trunk and limbs in fossil apes, and then to survey major transformations in the postcranium of hominins. It is almost universally agreed that humans evolved from a suspensory ancestor. There are a large number of features of the skeleton of apes and humans that are unique, and plausibly related to suspensory behaviors (hanging below the branches of trees). These features develop gradually from more monkey-like anatomy in the earliest apes (pronograde quadrupedalism, or walking on the tops of branches), to an essentially modern ape morphology in the apes that lived just before the chimpanzee–human divergence. While the wonderfully complex fossil record of apes shows that many similar looking anatomies evolved in parallel a number of times, there is no doubt that there is a consistent trend toward a shift from monkey-like to ape-like in the plausible ancestors of the living apes and humans. By 6–7 Ma (mega-annum, or millions of years ago), fossils representing taxa with some, as yet unknown, form of human bipedalism are known from Africa, and by 6–4 Ma these evolve into *Ardipithecus*, with a curious mixture of bipedal and climbing characters (Simpson, Chapter 22). The transition to modern human postcranial form, however, is reasonably well documented in the fossil record from *Australopithecus* to *Homo erectus* (Hammond and Ward, Chapter 23; Antón, Chapter 26). After *Homo erectus*, the changes in the postcranium leading to modern humans are more or less fine-tuning, though there are important differences, especially between fossil *Homo* and modern humans, who are essentially domesticated (wimpy and less robust) versions of our ancestors, as far as our skeletons go.

Chapter 11 introduces the next section of the book, on environment and behavior. Though behavior is discussed in other chapters, here we are looking mainly at data from fields outside of morphology. The first chapter, by Reed, covers the rich and highly informative field of paleoecology. As Reed describes it, modern paleoecology takes a multiproxy approach that applies as many sources of information as possible to reconstruct the paleoecology of fossil localities. These include comparisons of species composition with modern communities and distributions of adaptations present in a site, regardless of species composition (running, digging, climbing, diet, etc.), known as ecomorphology. They also include evidence from the sediments in which fossils are found, the landscapes in which sites are found, and the chemicals (isotopes) found in both the sediments and the fossils themselves. Paleoecologists also employ information from larger-scale processes such as orogeny (mountain-building), glaciation and continental drift. A paleoecological analysis of a fossil locality would not be complete without an understanding of its taphonomy, that is, a reconstruction of the circumstances by which the fossils found in a spot came to be deposited there. Sometimes it is because the organisms died in that spot, but many times it is because their remains were transported, most commonly by water, from more distant spots. It is the taphonomist's job to determine to what extent the assemblages of organisms at a site are autochthonous (local and representing a moment in time) or allochthonous (mixed, both in time and space).

Chapter 12 (Plavcan) tackles the challenging topic of reconstructing social behavior from the fossil record. Social behavior has been implicated in everything from basic survival to brain-size increase and the emergence of culture and language. There have always been speculations about the evolution of these features of humans and this chapter describes the limitations of the evidence and the extent to which a rigorous approach can reveal very interesting patterns. As with paleoecology, the reconstruction of behavior uses the approach of analogy to living species, with the idea that if patterns of, for example, sexual dimorphism in body mass or canine size, are the same in a sample of fossils of a particular taxon and a living taxon, a reasonable hypothesis is that the living and extinct species share aspects of their social behavior related to sexual dimorphism (sex ratios, relations within and between the sexes, care of infants, etc.). Other morphological features implicated in the reconstruction of behavior (other than diet and positional behavior) include brain size and orbital dimensions (nocturnal primates have larger eye sockets on average). There are many caveats to reconstructing behavior from the fossil record when there lacks a direct mechanical explanation linking behavior and anatomy (like powerfully built jaws and powerful chewing), but this does not make it less worthwhile or important. Consider how much we have learned about dinosaurs from the discovery of their nests and grouping patterns and the surprising insights this has provided about their strategies for rearing their young. The advances in reconstructing social behavior in primates and humans is at least an order of magnitude more advanced, but also more complicated.

Chapter 13 (Deino) covers the world of geochronology as applied to paleoanthropology. Geochronology is simply the telling of time using data preserved in the geological record, including rocks and fossils (which actually are also rocks). The age of fossils is one of the most sought after pieces of information about them, even if it is sometimes misinterpreted. There is no doubt that we need to place fossils in a chronological sequence to understand the evolution of a lineage, but the fact that a fossil taxon from a particular site may be older than another from another site does not necessarily mean that the fossil taxa actually evolved in that order. In other words, we cannot assume that the ages of fossils represent the actual origins and extinctions of species. We call the order of appearance of fossil species in the fossil record first and last occurrences, meaning the oldest and youngest *known* ages, to distinguish from their real biological origin and extinction, which are basically unknowable. However, in most cases it seems to work out that morphologically more primitive taxa are older in the fossil record than are more modern-looking fossils. Deino describes all of the current methods used to assess the age of fossil localities. Outside of paleoanthropology, it is probably less well recognized that fossil dates are most often based on the rocks in which they are found rather than the fossils themselves, so it is most often the sites and not the fossils that are dated. New techniques, however, are being developed to date fossils directly. Recent advances in the field of geochronology have vastly improved the precision and accuracy of dating methods, and have expanded the reliable ranges of many techniques, so that today nearly the entire time-period of primate and human evolution is covered by reliable dating techniques, when the geological circumstances are favorable.

Chapter 14 is a review of Paleolithic archeology, the record of the technology, and its impacts, during the course of human evolution until the origins of agriculture. Schick and Toth cover the record from before the appearance of the first direct evidence of tools in the fossil record (comparisons with chimp tool use) to the appearance of modern humans. Archeologists often say that they study garbage, and certainly in the Paleolithic this is the case. The vast majority of the Paleolithic record consists of broken or intact tools left behind, and the remains of the animals used for food and processed using these tools. While there is some curation of tools (keeping and "sharpening" them for repeated uses), much of the Paleolithic record, especially its earliest manifestations, is more like what you would find at a favorite picnic site rather than a kitchen (disposable utensils, a temporary set-up and a bunch of left-over bones). As humans become more modern, we see evidence of spatially organized, longer-term habitations, curated tools, and evidence of increasingly sophisticated techniques of tool manufacture, food acquisition, and overall resource exploitation. One of the most interesting fairly new discoveries in Paleolithic archeology is the recognition that "modern" tools appear at different times (diachrony) in different places in the archeological record, and that most often the oldest most advanced tools for a particular archeological time period are found in Africa. Another important point in this chapter is that, despite the undeniable signal of increased complexity in the archeological record over time, it is not a purely linear record. There are many variants of every archeological "tradition" and, as I mentioned, diachrony in the appearance of "innovative" tools and techniques.

Chapter 15 (Disotell) summarizes the state of the art in genetic approaches to understanding ape and human evolution. The major applications of genetics in paleoanthropology are the estimation of relations and divergence dates among living species using biomolecules (first proteins, then mitochondrial DNA and eventually nuclear DNA) and the very recent actual gene-sequencing of fossil specimens. From the beginning of the modern era of molecular anthropology in the early 1960s, researchers have for the most part concluded that humans and African apes share a more recent ancestor that either one shares with Asian apes. This conclusion was in stark contrast to the view of the vast majority of morphologists during this early period, who grouped all great apes together to the exclusion of humans.[3] The revisiting of the African ape and human clade in the modern era (originally proposed by Huxley), based on modern, lab-based analyses, is I think one of the most significant developments in the history of paleoanthropology. It calls into question the idea that there is a vast gap between apes and humans, and reveals the fact that humans are in fact embedded within the great apes, the hominids, which includes the great apes and humans. Regarding divergence dates, the most widely discussed, the chimp-human divergence, is currently placed at roughly 6 Ma, although somewhat older dates are not excluded. The most recent developments in molecular anthropology are the identification of gene sequences in fossils, allowing a direct comparison with living humans. At this point this research is, if not in its infancy, in its childhood, and I expect many more spectacular developments in this field. Recent results indicate that, while Neandertals are distinct from modern humans, they share up to 4 percent of their known genome with modern humans, specifically European and Asian modern humans (see Wolpoff and Caspari, Chapter 17; Harvati, Chapter 28; Collard and Dembo, Chapter 29).

Chapter 16 (Sherwood and Duren) segues from genetics to the genetics of morphology, which, of all the topics in this book, is the area of research that is likely to develop the most in the next decade. A goal of many researchers interested in phylogeny is to understand the genetic basis of morphology, so as to make a direct connection between morphological comparisons among species and the evolutionary changes that drive them at the level of the gene. Since the 1930s it has been recognized that there are constraints to morphological change, that morphology needs to remain integrated, and that the genetic background of morphology must constrain morphology. But specifics have been lacking until recently. Several examples of genes and their relationship to morphology are given in this chapter, but the main message is the complexity of the relationship between genes and morphology, and the long research road ahead in mapping out this relationship. We are beginning to unravel these connections in teeth, limb proportions and the cranium, but there is a great deal of potential in this field.

Chapter 17, by Wolpoff and Caspari, covers the history of paleoanthropology as it relates to the concept of race. I put this in the genetic and race section to emphasize the degree to which this issue reflects the history of biological anthropology, genetics, and the specific preconceptions that persist today about human variation. The definition and cultural meaning of race, and how these have evolved, are among the topics discussed in this chapter. The history of ideas about the origin of human races, specifically, monogenism and polygenism (ideas that humans evolved from a single or from separate populations), while very different from ideas about modern human origins today, is nevertheless mirrored to some extent in the current debate.

Wolpoff and Caspari take the opportunity to update their ideas about the multiregional model of human evolution (see references in Chapter 17). It needs to be noted, however, that this is a minority view among paleoanthropologists, most of whom support the African replacement model (see Hublin, Chapter 27 and Collard and Dembo, Chapter 29). This of course does not mean that Wolpoff and Caspari are incorrect, and they do raise some interesting points.[4] While all the authors in this book who discuss the genus *Homo* recognize separate, more or less clearly defined species (e.g., *Homo habilis, Homo erectus, Homo heidelbergensis*, etc.), Wolpoff and Caspari do not, writing instead about a "single species lineage". The debate about where to draw the lines between species is a very difficult one in any field of paleontology, but especially in paleoanthropology. However, the view that most or all *Homo* fossils are part of a single evolving species lineage does not necessarily follow from this difficulty. As you will see in this book, most researchers have decided where to draw the species lines, although to be sure there is much debate about the details, and a number of important fossils persist in being very difficult to assign. I encourage readers to carefully consider the provocative arguments of Wolpoff and

Caspari as well as all other theories before drawing their final conclusions about the course of the evolution of our genus. Here is a good chance to consult the primary literature, cited by the authors in this book, to enable you to draw your own conclusions.

Chapter 18 is the first chapter in the second part of the book, on the fossil evidence of primate and human evolution. The earliest fossils thought to be primates appear in the Paleocene, the first epoch of the Paleogene, the subject of this fifth section, though there is debate about which taxa are actually primates and which are closely related to primates, but have not quite crossed the threshold. Silcox describes the adaptive complexes that define the primates and how attributes of each of these appear at different times during the early evolution of the primates. She makes the important point that primate origin is a process rather than an event, and that the accumulation of attributes typical of primates today took some time. It is not surprising, therefore, that the earliest primates bear little resemblance to living primates, having only recently diverged from the common ancestor of primates. What is remarkable is the diversity of the earliest primates, which probably reflects their success within evolving forest ecosystems in a world devoid of many creatures that died out with the dinosaurs.[5]

Chapter 19 picks up the evolutionary history of the primates with the evolution of the anthropoids (Old and New World monkeys, apes, and humans). Beard, in this chapter, enumerates the characters needed to identify a fossil as an anthropoid, and surprisingly perhaps, points out that they mainly relate to subtle features of the dentition. Once again, the development of features typical of living anthropoids took some time, which makes the identification of the earliest member of this clade challenging. Beard and previous authors use the terms "stem" and "crown," which I think deserve a bit of attention in this introduction.

Fossil stem taxa do not have direct descendants, having evolved before the last common ancestor of living taxa in their group. They are more closely related to living taxa in their group than to anything else. Crown taxa include living forms as well as fossil taxa that evolved after the divergence of the last common ancestor of living taxa. In terms of anthropoids, a stem anthropoid is a fossil taxon that evolved before the last common ancestor of all living anthropoids, for example, a very primitive taxon like *Eosimias*, but that diverged from stepsirhines before the living anthropoids diverged from each other. A fossil crown anthropoid would be *Aegyptopithecus* (see Harrison, Chapter 20), which evolved after the New World monkeys (platyrrhines) diverged from the catarrhines but before the living catarrhines (Old World monkey vs hominoids) diverged from one another. Crown taxa are among the branches of living taxa (like the crown of a tree) whereas stem taxa are earlier branches (lower down and not in the crown). While ancestral anthropoids are highly arboreal, as has long been considered the case, many of them were tiny, among the smallest primates ever, which differs from the classic view that anthropoid origin was accompanied by an increase in body size. The other important message in the chapter is that anthropoids appear to have originated in Asia and dispersed at some point into Africa. Interestingly, although early primates disperse throughout Eurasia and North America, anthropoids never make it to North America until the end of the Pleistocene, when humans make the trip from Siberia.

Chapter 20 takes the review of primate evolution forward in time to the era of catarrhine origins (Old World monkeys, apes, and humans). Harrison focusses on fossil stem catarrhines, those that lived before the two living branches of catarrhines diverged (cercopithecoids and hominoids). The oldest fossil evidence of catarrhines is over 30 Ma, and catarrhines were confined to Africa until about 17 Ma. There is no consensus on which fossil taxa are most directly related to living taxa, which, as noted earlier, is not surprising, because these fossil forms appear before the obvious diagnostic characters of catarrhines and hominoids appear. There is an intriguing gap of 10 to 15 Ma between the stem catarrhines from Egypt and Arabia on the one hand (propliopithecoids) and the stem catarrhines from Eurasia on the other (pliopithecoids). Between the appearances of each of these clades we see the appearance of the crown catarrhines, the Miocene hominoids. Pliopithecoids such as *Pliopithecus* were once thought to be ancestral to living hylobatids, mostly on the basis of size and their slender builds, but we know today that pliopithecoids are stem catarrhines, having diverged from other catarrhines before the two living clades (Old World monkeys and apes). As with the previous stages of primate evolution described in this book, there are many taxa that appear at and shortly after the origin of the clade, but only a few survive to become crown taxa, even fewer are thought to be direct relatives of living taxa.

Chapter 21 explores the fossil evidence of the Hominoidea, and introduces the section of the fossil record on Neogene and Quaternary hominoids. The same theme introduces this chapter as the last. It is difficult to define a taxon and at the same time include its earliest members, because the obvious attributes of a taxon today (for hominoids, large brains, suspensory positional behavior) are not obvious, or are simply absent, in the earliest members of the group. In this chapter I try to describe the fossil evidence for the transition from a monkey-like *Proconsul*, which is pronograde (arms and legs of equal length with the palms and soles facing down), to *Rudapithecus* and other Late Miocene apes, which are suspensory, swinging below branches rather than walking atop them. Among the controversies discussed in this chapter is the apparent appearance of suspension probably several times during the course of ape evolution. In the end, I conclude that suspensory evidence in *Morotopithecus* and *Oreopithecus* is probably of parallel origin. I suggest that there is evidence in the Early Miocene for adaptations that allowed apes to disperse into Eurasia, for a subsequent evolution of more modern apes in Eurasia, and for a new dispersal back into Africa of more modern taxa. Many researchers have questioned this scenario, and I encourage readers of this book to seek out these alternative views, cited in the references for that chapter.

Chapter 22 concerns the fossil evidence of the earliest hominins (taxa more closely related to *Homo* than to any other living genus.) Once again, the thorny issue of defining a taxon is addressed. Simpson asks, "How can we identify the earliest hominins?" While one might think hominins should be defined by features that distinguish us from our closest living relative (the chimpanzee), such as large brains, language, and other complex forms of behavior, in fact, these attributes appear much later in human evolution. The features that do seem to appear in conjunction with hominin origins are bipedalism and canine reduction. Simpson reviews the evidence for the earliest hominins, including *Sahelanthropus, Orrorin*, and *Ardipithecus.* A combination of evidence of bipedalism and canine reduction does in fact characterize all of these taxa. There is a question about the placement of *Ardipithecus kadabba* and *Ardipithecus ramidus* in the same genus, given the noticeably more primitive morphology of the former. Only more fossils of *Ar. kadabba* will resolve this debate. *Ardipithecus ramidus* is a great example of the fact that one can never really anticipate what we will find in the fossil record. *Ar. ramidus* has a very unanticipated combination of arboreal (an opposable big toe) and terrestrial (a bipedal pelvis) adaptations that many paleoanthropologists have stated could not exist together. Simpson notes as well that there is disagreement, even in this volume, about the interpretation of the significance of *Ardipithecus ramidus* for understanding human evolution. This involves both the adaptations of the last common ancestor of chimpanzees and hominins and the phylogenetic relations of these early hominins, and once again I encourage readers to pursue these debates in the literature.

Chapter 23 reviews the evidence of the earliest hominins with clear evidence of shared derived characters with the genus *Homo*. *Australopithecus* and *Kenyanthropus* (or the australopiths) are nearly universally regarded as hominins, unlike the taxa described in Chapter 22, about which debate continues (though I am convinced that they are also hominins). *Australopithecus* and *Kenyanthropus* have moved further in the direction of modern hominins in terms of canine size and, where known, bipedalism, and also show signs of their own autapomorphies (specializations). While we think of humans as having small jaws and teeth compared with living great apes, fossil humans actually had larger jaws and teeth, on average, than living apes. In other words, humans went through a phase of masticatory hypertrophy and megadontia, that is, our ancestors had very large jaws and teeth. Hammond and Ward review the four species of *Australopithecus* and the somewhat controversial *Kenyanthropus*, which some would include in *Australopithecus*. Readers should refer to Chapter 3 (Strait) for a discussion of the taxonomy of this group of early humans. The goal of this chapter is not the taxonomy but the paleobiology of this taxon. Readers should note as well that the "robust australopithecines," that is, *Paranthropus*, are considered separate in this book, which is also somewhat controversial. In addition to human-like and specialized characteristics, *Australopithecus* also appears to have been strongly dimorphic in body mass, most like the living great apes *Gorilla* and *Pongo*. We also know that australopiths are slightly encephalized (they have larger brains relative to body mass) compared with living and fossil great apes, but that they grew (as indicated by the timing and pattern of their dental development) more like apes than humans. While australopiths are not modern by any measure, and in many ways are intermediate between modern humans and modern apes, they are clearly more closely related to modern humans than they are to the earliest hominins.

Chapter 24 covers the other "australopith," the robusts, or *Paranthropus*. Wood and Schroer provide a summary of the lively history of debate about *Paranthropus*, which for many years was synonymized with *Australopithecus* (and still is, according to some). *Paranthropus* is a separate phenomenon with its own fascinating part in the story of human evolution, whether or not it is a separate genus. It is for this reason that I wanted it to have its own chapter. *Paranthropus* has variously been interpreted as an *Australopithecus* on steroids, an interesting dead-end, and even a tool-using close relative of *Homo*. The evolution of *Paranthropus* can be traced from the more primitive *P. aethiopicus*, with its small brain, prognathic face and large front teeth, to

P. bosei and *P. robustus*, with their larger brains, orthognathic (flat) faces, and very small front teeth. There is debate about the relations among these taxa, which again I urge readers to explore. The relatively large brains, flat faces and short cranial bases of *Paranthropus* have led some to suggest that this genus might actually be more closely related to *Homo* than *Australopithecus*. Most researchers in fact believe that *Paranthropus* went down a doomed path of increasing dietary specialization, reflected in its enormously enlarged jaws and teeth, and that it either could not compete with contemporaneous tool-using early *Homo* or was too specialized to be able to respond to changing ecological conditions.

Chapter 25 opens the final section of the book and introduces us to the genus *Homo*, covering the earliest members of our genus. While some consider these species (*Homo habilis* and *Homo rudolfensis*) to be australopiths, most researchers recognize synapomorphies (shared derived characters) with later *Homo* not found in *Australopithecus*. Early *Homo* in general has larger brains and smaller or at least less prognathic faces than most australopiths. Their anterior (incisors and canines) and postcanine (premolars and molars) teeth are also more "balanced," with size proportions resembling modern humans, though in absolute size all teeth are larger than in modern humans. Australopiths tend to have very large anterior teeth and most *Paranthropus* have very small anterior teeth and huge postcanines. There are many mysteries about early *Homo*, not the least of which is its postcranium. There are very few diagnostic specimens of early *Homo*, which are limited to cranio-dental material, found in association with postcrania. There is some indication that *Homo habilis* was similar to *Australopithecus* in limb proportions (relatively long and powerful upper limbs and short lower limbs), while other fossils that may be attributed to early *Homo* (possibly *Homo rudolfensis*) look more modern. Until we find a relatively complete skeleton of each taxon we will not know what the body of each species of early *Homo* looked like. It is interesting that early *Homo* is in many ways intermediate between australopiths and later *Homo*, because early and later *Homo* (*Homo habilis, H. rudolfensis* vs *H. erectus*) actually overlap in time.

In Chapter 26 Susan Antón describes the evolution of the first member of the genus *Homo* with modern human proportions. From the neck down, *Homo erectus* looks much like modern humans, though important differences remain in the details. It is certainly a dramatic departure from early *Homo*, despite the fact, as I noted earlier, that the two overlap in time. The transition to a more modern postcranial skeleton seems to have occurred fairly rapidly. Of course, the skull of *Homo erectus* is more modern as well. The cranial capacity is larger than in early *Homo*, but generally smaller than in modern humans, though there is some overlap in size between the two. *Homo erectus* also has smaller, flatter faces and smaller teeth than early *Homo*. *Homo erectus* is the first hominin taxon known to have dispersed out of Africa, by about 1·8 Ma, though some believe that a more primitive taxon also dispersed from Africa, leading to the evolution of *Homo floresiensis* (Jungers, Chapter 29).

The wide distribution in space and time of *Homo erectus* distinguishes it from earlier hominins, and may be the reason that there is debate about the number of species that might be represented within the umbrella name of *Homo erectus*. This is unresolved at present, but the fact that this debate exists reminds us of the success of this hominin, which lived for about 2 Ma and was present in southern, eastern and northern Africa and in Eurasia from southeast Asia to Georgia. While the first stone tools are found in association with early *Homo*, with *Homo erectus* we see the first finely crafted, symmetric tools with many different forms, a real toolbox, as well as the first evidence of the controlled use of fire.

Chapter 27 targets the next phase of human evolution, which, for lack of a better term we can call the "pre-Neandertal" phase of human evolution. The fossils discussed by Hublin in this chapter are, broadly speaking, intermediate between *Homo erectus* and *Homo sapiens*, in terms of brain size, facial and dental dimensions, and behavioral complexity. Specimens are sometimes said to represent the ancestors of Neandertals, some the ancestors of modern humans, and some the ancestors of both. This reflects their intermediate morphology. Many specimens from Europe in the range of 300 to 600 ka combine attributes of *Homo erectus* and Neandertals, leading some to suggest that European Middle Pleistocene hominins are the ancestors of Neandertals, while modern humans emerged contemporaneously in Africa. After 200 ka, fossil hominins in Europe have clearer Neandertal affinities. The accumulation, or accretion, as described by Hublin, of Neandertal features in these European hominins makes it difficult to draw the line between species. The pre-200-ka group is traditionally assigned to *Homo heidelbergensis* (after the Mauer mandible, found near the German city of Heidelberg), while more recent fossils are assigned to Neandertals (either *Homo neanderthalensis* or *Homo sapiens neanderthalensis* [see Harvati, Chapter 28]). Complicating the issue is the presence of one group of specimens very similar to *Homo heidelbergensis*, also from about 300–600 ka, in Africa (*Homo rhodesiensis* or *Homo heidelbergensis* sensu lato) and a second group of post-300-ka specimens that have features of modern humans. It is possible that modern humans evolved from the African Middle Pleistocene hominin *Homo rhodesiensis* while Neandertals evolved from European *Homo heidelbergensis*. However, this early split between Neandertals and modern humans is inconsistent with the molecular data, which suggest a more recent divergence (Disotell, Chapter 15).

Chapters 28 and 29 take over where Chapter 27 leaves off, reviewing the evidence for the origins of the Neandertals and modern humans, respectively. In Chapter 28, Harvati surveys the fossil evidence of the Neandertals. As suggested by Hublin, Harvati describes the features of the Neandertals as accumulating gradually in Europe, with definitive Neandertals appearing around 200 ka, and "classic" or full-blown Neandertals in the Late Pleistocene, after about 70 ka. The Neandertals are a European and western Asian phenomenon, which may make their importance in paleoanthropology somewhat exaggerated. Most researchers in paleoanthropology are also of European origin, or were trained by researchers with ties to Europe, such that the central role that Neandertals occupy could be interpreted as a bit of Eurocentrism. On the other hand, they are the best-known of our closest fossil relatives, and they are fascinating. And, lest we forget, recent genetic analysis indicates that living Eurasians and Neandertals share up to about 4 percent of their DNA (Disotell, Chapter 15). Harvati discusses the adaptation of Neandertals and the possible reasons for their extinction, both of which are active areas of research and debate today. The degree to which Neandertals resemble modern humans in their strategies for exploiting resources, their mode of communication and their belief systems, are all areas of intensive research today.

Chapter 29, the other side of the coin, so to speak, concerns modern human origins. As noted, most evidence, both genetic and fossil, suggests that modern humans first evolve in Africa, and spread into Eurasia around 100 ka. Collard and Dembo focus on the various models that have driven research into the origins of modern humans, and the evidence in support of each. Models range from the multiregional hypothesis, which predicts that modern humans originate from disparate populations around the world, to the African replacement hypothesis, which predicts that humans originated from a localized population in Africa. Collard and Dembo disentangle the subtleties of these and other hypotheses that combine aspects of both, and survey the fossil evidence to see which hypothesis is most consistent with it. They conclude that the bulk of the evidence, both from genes and morphology, is consistent with the African replacement model, or a variant thereof (the [African] hybridization and replacement model), which allows for some gene transfer between African founding "modern" populations and non-African, non-modern populations. Of course, if, for example, modern humans that had dispersed thousands of years earlier interbred with Neandertals in Europe 60,000 years ago, and this accounts for the 4 percent of the Neandertal genome that we find in living Eurasians, does this not mean that we are both the same species? This is the defining criterion of the biological species concept, that populations that can successfully interbreed and produce offspring over several generations are in fact members of the same species. These are questions that paleoanthropologists will be pondering for years to come.

The final chapter in this book covers one of the newest and strangest discoveries in paleoanthropology, *Homo floresiensis* (Jungers, Chapter 30). *Homo floresiensis* is a small hominin known only from the island of Flores, in the eastern end of the Indonesian archipelago. The specimens were recovered from a cave deposit and include several individuals, but the most complete, a skeleton (LB1), has received the most attention. No one could have predicted the discovery of these diminutive hominins, especially on a remote island that has never been connected to another land mass. The discovery was so unusual and unexpected that it has spurred many detractors, all of whom have tried to explain the morphology of *Homo floresiensis* as a consequence of pathology. None of these attempts have been convincing, and the majority of researchers today are convinced that *Homo floresiensis* is a real species and not an aberrant modern human. The combination of characteristics found in *Homo floresiensis* is simply bizarre. It has a very small, chimp-sized brain, yet it is associated with fairly complex tools and evidence of hunting. It has long been thought that hunting and complex tool kits require relatively large brains. It is not clear what is going on in *Homo floresiensis*, but there is some evidence of reorganization similar to that seen in human brains. In the morphology of the skeleton, *Homo floresiensis* is more like *Homo habilis*, or even *Australopithecus*, than like later *Homo*. All of this makes *Homo floresiensis* fascinating and there are many opinions, some better informed than others, about its origins and adaptations. *Homo floresiensis* may well represent a long separate lineage of hominin that made its way to the far reaches of the Indonesian archipelago independent of the dispersal of early *Homo erectus* into Asia. Once again, I encourage readers to learn more about *Homo floresiensis* by reading the primary literature, including a special issue of the *Journal of Human Evolution* from 2009 (Volume 57, issue 5).

The goal of this book is to provide readers with an introduction to paleoanthropology, but not just the evidence from the fossil record. My intention was to put together chapters from leading experts working in paleoanthropology today that would serve as a sort of "what paleoanthropologists do" primer. Not a "paleoanthropology for dummies," but a volume that reveals to a broad audience exactly what paleoanthropologist do, how a diversity of disciplines inform paleoanthropology and the degree to which paleoanthropology is a rich, multidisciplinary endeavor. I hope this book goes a long way to answering the question "how do they know that?" about primate and human evolution. Readers will not find a plethora of references at the end of each chapter, but a list of key sources of information. However, an internet search of any of these or the terms in the index of this book will quickly bring a great deal of additional information to the reader. There are other resources, especially journals, which provide detailed information on the data of paleoanthropology. This book was conceived as a source of information for people with an interest in human evolution. My hope is that students at all university levels, other anthropologists and other biologists will find this a useful and quick source of information on the state of the art. Having read and edited all the chapters, and having learned a great deal from them, I also hope that my colleagues, who, like me, focus on one area of the field, will find chapters on other areas useful to them, as a refresher. Science writers should find this a helpful source of information for background and fact checking, and, finally, I really hope that other members of community of readers of science at all levels will enjoy this book.

NOTES

1 "Hominin" throughout this book refers to the group that includes humans and all of our ancestors more closely related to us than to chimpanzees, our closest living relatives. Not all paleoanthropologists accept this nomenclature, preferring instead to call this group the hominids. However, a large majority of researchers include all the great apes and humans in the hominids, African apes and humans in the hominines, and humans and our ancestors in hominins.

2 Some authors prefer the spelling Neandertal, which is the modern German spelling, while others prefer Neanderthal, the historic spelling, and the one most common in the literature until recently. I was not able to get this standardized in these chapters, so both spellings appear in this book. Regardless of the spelling of the common name, the spelling of the nomen (taxon name) *Homo neanderthalensis* or *Homo sapiens neanderthalensis* will not change, by rule of the International Commission of Zoological Nomenclature.

3 It is important, however, to remember that Huxley (1871) concluded that African apes and humans are more closely related to each other than either is to *Pongo*, based on morphological criteria.

4 Wolpoff and Caspari exaggerate the estimate of the contribution of Neandertal genes to the modern human genome (5 percent). The actual estimate is 1–4 percent, with an average of 2·5 percent. The other estimates they provide about admixture with Neandertals are based on models and not direct comparisons (Disotell, personal communication).

5 I apologize to friends, colleagues and others who are interested in the evolution of the strepsirhines (lemurs and their kin), platyrrhines (New World Monkeys) and cercopithecoids (Old World monkeys.) The study of the evolution of these clades is also part of paleoanthropology (articles are published on them in the *Journal of Human Evolution*), but I did choose a somewhat anthropocentric approach, and thus branches divergent from the clade leading to the Hominoidea are not included in this book. Excellent sources of information on the evolutionary history of these clades can be found in Walter Hartwig's edited volume *The Primate Fossil Record*, Cambridge University Press, 2002.