

Bernard Wood

HUMAN EVOLUTION

A Very Short Introduction

OXFORD

Human Evolution: A Very Short Introduction

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Acknowledgements

For an author used to the luxury of lengthy academic papers, the occasional 500-page monograph, and to the protection afforded by technical language and multiple qualifications, boiling down human evolutionary history to the size constraints and style of a VSI is a considerable challenge. Much has changed in our understanding of human evolution in the decade or so since the first edition, and I am grateful to my undergraduate and graduate students for helping me keep up with those advances. One of the main differences between now and thirteen years ago, apart from the recovery of new fossils, is methodological developments. Advances in molecular biology have made a major impact on human evolution research. Molecular biology has not only helped resolve the relationships among the great apes, but improvements in the recovery and analysis of ancient DNA have added a powerful tool to help us understand more recent (less than a million years) human evolution. Special thanks to Brenda Bradley for helping me understand the implications of these developments. I am also grateful to Eve Boyle, Matthew Goodrum, David Patterson, Osbjorn Pearson, Peter Ungar, and Mark Weiss for their advice and expertise.

This book is for my family and my teachers, young and old, living and dead.

Finally, many thanks to Carol for her understanding.

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13 Map of the main ‘archaic’, ‘transitional’, and ‘pre-modern’ *Homo* sites
Adapted with permission from Miller and Wood, *Anthropology* p. 197 (Allyn & Bacon).

14 Time chart of ‘pre-modern’ *Homo*
© Bernard Wood.

15 Map of major Neanderthal sites
Adapted with permission from Miller and Wood, *Anthropology* p. 209 (Allyn & Bacon).

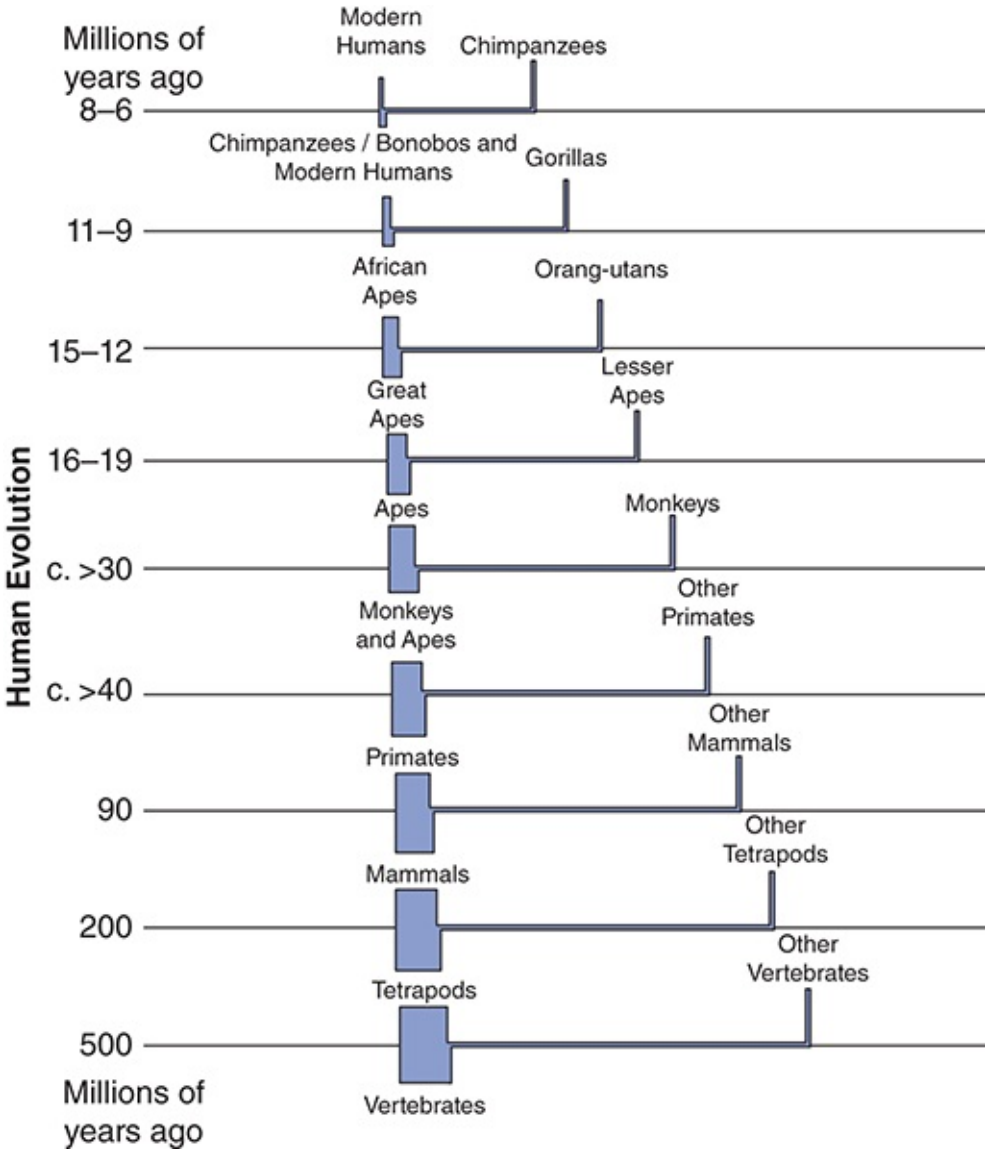
16 The ‘strong’ and ‘weak’ versions of the multiregional and recent out of Africa models for the origin of modern humans
Adapted from L. Aiello, ‘The Fossil Evidence for Modern Human Origins in Africa: A Revised View’, *American Anthropologist*, 95/1 (1993), 73–96.

The publisher and the author apologize for any errors or omissions in the above list. If contacted they will be pleased to rectify these at the earliest opportunity.

Chapter 1
Introduction

Many of the important advances made by biologists in the past 150 years, or so, can be reduced to a single metaphor. All living (aka extant) organisms, that is, animals, plants, fungi, bacteria, and all the types of organisms that lived in the past, are situated somewhere on the branches and twigs of an *arborvitae* or Tree of Life (TOL). The extinct organisms on the branches that connect us to the root of the tree are our ancestors. The ones on branches attached to our branch are our close, but non-ancestral, relatives.

The ‘long’ version of human evolution would be a journey that starts approximately three billion years ago at the base of the TOL with the simplest form of life. We would then travel up the base of the trunk into the relatively small part of the tree that contains all animals, and on into the branch that contains all animals with backbones (Figure 1). Around 500 million years ago we would enter the branch that contains vertebrates with four limbs, around 200 million years ago the branch that contains the mammals, and around 90 million years ago a slender branch that leads to one of the subgroups of mammals called the primates.



1. A diagram of the vertebrate part of the Tree of Life, which emphasizes the smaller and smaller groupings that eventually resulted in the twig (clade) that includes modern humans.

The next part of the journey takes us successively into the monkey and ape, the ape, and then into the great ape branches of the TOL. Sometime between 15 and 12 million years ago we move into the small branch that gave rise to contemporary modern humans and to the living African apes. Between 11 and 9 million years ago the branch for the gorillas split off to leave just a single branch consisting of the ancestors of chimpanzees, bonobos, and modern humans. Between 8 and 6 million years ago this very slender branch split into two twigs. One of the twigs ends on the surface of the TOL with chimpanzees and bonobos;

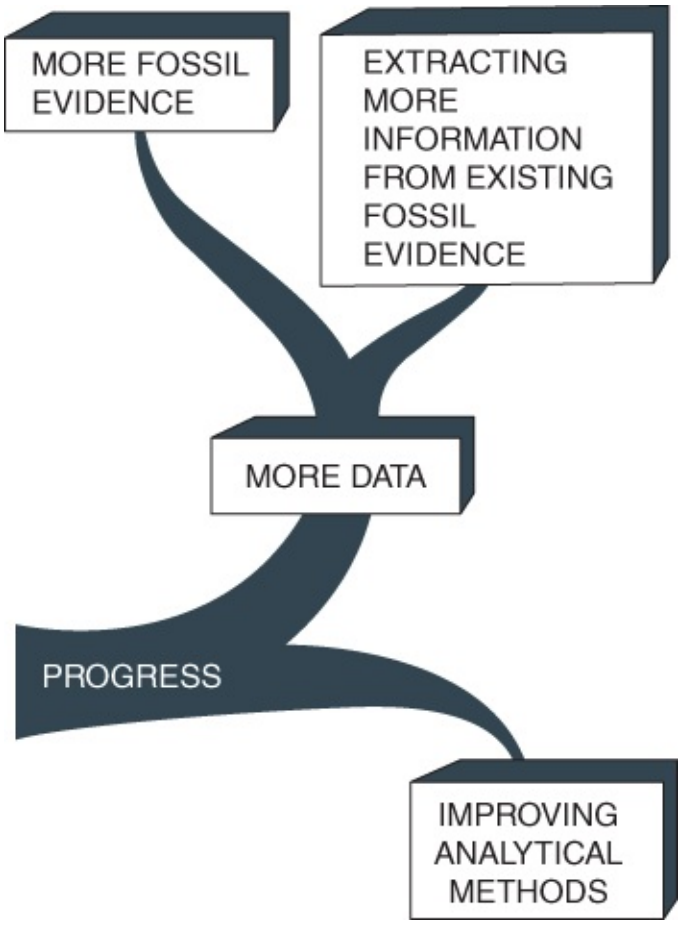
the other leads to modern humans.

This book focuses on the last stage of the human evolutionary journey, the stage between the most recent common ancestor shared by chimpanzees/bonobos and modern humans, and present-day modern humans, and palaeoanthropology—literally the 'study of ancient humans'—refers to the many scientific specialties involved in trying to reconstruct the evolutionary history of this small, exclusively human, twig of the TOL.

First, I need to explain and use some scientific jargon. Instead of 'twig' I will use the more formal biological term 'clade'. Species anywhere on the main human clade, or on its side branches, are called 'hominins'; the equivalent species on the chimpanzee/bonobo clade are called 'panins'. And instead of writing out 'millions of years' and 'millions of years ago' (and the equivalents for thousands of years) I will use the abbreviations 'my' and 'mya' and 'ky' and 'kya'.

This Very Short Introduction has three objectives. The first is to try and explain how scientists go about the task of improving our understanding of human evolutionary history. The second is to convey a sense of what we think we know about human evolutionary history, and the third is to try to give a sense of where the major gaps in our knowledge are.

We use two main strategies to improve our understanding of human evolutionary history (Figure 2). The first is to obtain more evidence (aka data). You can get more evidence by finding more fossils, or by extracting more information from the existing fossil evidence. You can find more fossils from existing sites, or you can look for new sites. You can extract more information from the existing fossil record by using techniques such as laser scanning to make more precise observations about the external morphology of fossils. You can also gather information about the internal morphology of fossils by using non-invasive medical imaging techniques such as computed tomography (CT) to obtain information about structures like the inner ear, or by using surface-penetrating microscopes to investigate the microscopic anatomy of teeth. You can also use geochemical methods to look at stable isotopes and trace elements, and molecular biology technology to detect and sequence small amounts of DNA in fossils.



2. Diagram showing how progress can be made in palaeoanthropology research. Imaging and the recovery of ancient DNA are just two of the many ways that more evidence can be extracted from the existing fossil record.

The second strategy for reducing our ignorance about human evolutionary history is to improve the ways we analyse the data we collect. These improvements range from more effective statistical methods to the use of novel methods of functional analysis. Researchers also try to improve the ways they generate and test hypotheses about the numbers of species in the hominin fossil record, and how those species are related to each other and to modern humans and chimpanzees.

I begin Chapter 2 by reviewing the history of how first philosophers and then scientists came to realize that modern humans are part of the natural world. I then explain why scientists think chimpanzees and bonobos are more closely related to modern humans than they are to gorillas, and why they think the

common ancestor of the chimpanzee/bonobo and modern human clades lived between 8 and 5 mya.

In Chapter 3 I review the lines of evidence that can be used to investigate what the 8–5 my-old hominin clade looks like. Is it 'bushy' or straight like the stem of a thin spindly plant? How much of it can be reconstructed by looking at variation in modern humans, and what needs to be investigated by searching for, finding, and then interpreting fossil and archaeological evidence? How do researchers decide where to look for new fossil sites, and how do they date any fossils they find at those sites? In Chapter 4 I explain how researchers decide how many species should be recognized within the hominin clade. I also review the methods researchers use to determine whether the hominin clade is 'bushy' and, if so, what are the details of the branching pattern.

In Chapter 5 I consider 'possible' and 'probable' early hominins. The chapter reviews four collections of fossils that represent each of the 'candidate' species that have been put forward for being at the base of the hominin clade. Then in Chapter 6 I look at 'archaic' and 'transitional' hominins. These are fossil species that almost certainly belong to the hominin clade, but which are still a long way from being like modern humans. Chapter 7 looks at species that many hominins researchers are comfortable with recognizing as members of the genus *Homo*: I call these 'pre-modern' *Homo*. I look at the earliest fossil evidence of pre-modern *Homo* from Africa, and then follow *Homo* as it moves out of Africa into the rest of the Old World.

Chapter 8 considers evidence about the origin and subsequent migrations of anatomically modern humans, or *Homo sapiens*. What features of the skeleton are only found in modern humans? When and where do we find the earliest fossil evidence of modern humans? Did the change from pre-modern *Homo* to modern humans happen several times and in several different regions of the world? Or did anatomically modern humans emerge just once, in one place, and then spread out, either by migration or by interbreeding, so that modern humans eventually replaced regional populations of pre-modern *Homo* across the world?

Finally, what will *not* be in this book? This Very Short Introduction (VSI) to 'Human Evolution' will concentrate on the physical and not the cultural aspects of human evolution. The latter, often referred to as 'Prehistoric Archaeology', is the topic of a separate VSI entitled 'Prehistory'. While I write about the role

DNA studies have played in human evolution research, interested readers should look at the ‘Molecular Biology’ VSI for more information about DNA.

Chapter 2

Finding our place

Long before researchers began to accumulate material evidence about the many ways modern humans resemble other animals, and long before Charles Darwin and Gregor Mendel laid the foundations of our understanding of the principles and mechanisms that underlie the connectedness of the living world, Greek scholars had reasoned that modern humanity was part of, and not apart from, the natural world. When did the process of using reason to try and understand human origins begin, and how did it develop? When was the scientific method first applied to the study of human evolution?

In the 5th and 6th centuries BCE Plato and Aristotle suggested that the natural world, including modern humans, forms one system, which means that modern humans must have originated in the same way as other animals. The Roman philosopher Lucretius, writing in the 1st century BCE, proposed that the earliest humans were animal-like cave dwellers, with neither tools nor language, which implies that Lucretius believed modern humans had evolved from an earlier, primitive form.

Reason is replaced by faith

After the collapse of the Roman Empire reason-based explanations for the creation of the world and of humanity were effectively replaced by faith-based ones. The Genesis narrative is well known: God created humans in the form of a man, Adam, and then a woman, Eve, and, because they were the result of God’s handiwork, Adam and Eve must have come equipped with language and with rational and cultured minds. According to this version of the origin of humanity, the first humans were able to live together in harmony, and they possessed all the

mental and moral capacities that, according to the biblical narrative, set humanity above and apart from other animals.

The biblical explanation for the different types of modern humans is that they originated when Noah's offspring migrated to different parts of the world after the last big biblical flood, or deluge. The Latin for 'flood' is *diluvium*, which is why we call anything ancient 'antediluvial' (i.e. it came 'before the flood'). Explanations involving successive floods had implications for the study of fossils. All the animals created after a flood must inevitably perish at the time of the next flood, so 'antediluvial' animals should never coexist with the animals that replaced them. With very few exceptions Western philosophers living in and immediately after the Dark Ages (5th to 12th centuries) supported a biblical explanation for the origin of humanity, yet not long after the scientific method began to be applied to the study of human origins (see below) some religious groups doubled down on biblical literalism. This resulted in the movement we call 'Creationism', and in the enterprise described, ironically, by its participants as 'Creation Science'.

During the Dark Ages some of the Greek classical texts that had survived in Europe were translated into Arabic. Some of these were later translated into Latin, which made them accessible to people like the 13th-century Italian Christian philosopher Thomas Aquinas, who integrated Greek ideas about nature and modern humans with interpretations based on the Bible.

Science re-emerges

The move away from reliance on biblical dogma was especially important for those who were interested in what we now call the natural sciences, such as biology and the earth sciences. English philosopher Francis Bacon was a major influence on the way scientific investigations developed. Theologians use the deductive method: they begin with a belief, then deduce the consequences of that belief. Bacon, who summarized his suggestions about how the world should be investigated in aphorisms that are set out in his *Novum Organum or True Suggestions for the Interpretation of Nature*, published in 1620, suggested that scientists should use the 'inductive' method. Induction begins with observations, also called evidence or 'data', then scientists devise explanations, or 'hypotheses', to explain those observations. They test the hypotheses by making more observations, which in sciences like chemistry, physics, and biology means

conducting experiments. This inductive way of doing things is the way the sciences involved in human evolution research are meant to work, but in historical sciences like palaeontology you cannot conduct experiments. So, as far as you can, you test hypotheses about processes by gathering evidence about how the world works today, and then assume it worked the same way in the past.

Anatomy starts to become scientific

Nearly three-quarters of a century before Bacon published this advice, a major change had already occurred in anatomy, one of the natural sciences that contributes to understanding human evolution. That change was brought about by Andreas Vesalius, who was born in 1514 in what is now Belgium. Vesalius' own anatomy education was typical for the time: the professor sat in his chair (hence professorships are called 'chairs') and read out loud from the only locally available textbook a safe distance from a human body that was being dissected by an assistant. After finishing his medical studies in 1537, Vesalius moved to Padua, Italy, to teach anatomy and surgery. Although Chinese, Greek, and Islamic scholars had begun to assemble reliable descriptions of human anatomy, it did not take long for Vesalius to realize that the textbooks used by his professors were based on a confusing mixture of human, monkey, and dog anatomy that had been assembled by Galen, so he resolved to write his own, accurate, human anatomy book. Vesalius' seven-volume *De Humani Corporis Fabrica Libri Septem*, or 'On the Fabric of the Human Body', was published in 1543. The *Fabrica* is one of the greatest achievements in the history of biology, and Vesalius' careful recording of his own dissections meant that researchers had access to reliable information about the structure of the human body.

Geology emerges

One of the implications of interpreting the Genesis narrative literally is that the world, and therefore humanity, had a remarkably short history. The best-known biblically based chronology was published in 1650 by James Ussher, then archbishop of Armagh in Ireland. Ussher used the number of 'begats' in the Book of Genesis to calculate the precise year of the act of Creation: according to his arithmetic it was 4004 BCE. Subsequently another theologian, John Lightfoot, part of the University of Cambridge in England, refined Ussher's estimate and declared that the act of Creation took place at precisely 9 a.m. on 23 October 4004 BCE.

The Industrial Revolution hastened the development of geology in the sense that the excavations involved in making the ‘cuttings’ for canals and railroads exposed previously hidden rock formations. Pioneer geologists such as William Smith and James Hutton paved the way for Charles Lyell in 1830 to set out a rational version of the history of the earth in *The Principles of Geology*, a book that profoundly influenced Charles Darwin. Lyell’s book promoted fluvialism and uniformitarianism as alternatives to biblically based diluvial explanations for the state of the landscape. Fluvialism suggested that erosion by rivers and streams had played a major role in shaping the contours of the earth, and the principle of uniformitarianism suggested that processes such as erosion and volcanism that we see in action today were the same ones that shaped the earth’s surface in the past. Lyell also championed the principle that, barring obvious major upheavals, rocks and strata increase in age the further down they are in a geological sequence. The same principle applies to any fossils or stone tools contained within those rocks, so unless there is evidence that fossils were deliberately buried, the lower in a sequence of rocks a fossil is, the older it is likely to be.

The implications of the new science of geology were profound. There was no need to invoke the biblical floods or divine intervention to explain the appearance of the earth. The pioneer geologists of the time also suggested that it would have taken the processes that shape the earth’s surface a lot longer than the 6,000 years implied by the Genesis narrative to produce the valleys, canyons, and mountain ranges we see today.

Fossils

Classical Greek and Roman writers had recognized the existence of fossils, but they mostly interpreted them as remnants of the ancient monsters that figure prominently in their myths and legends. By the 18th century geologists began to accept that life-like structures in rocks were the remains of extinct animals and plants, and there was no need to invoke supernatural reasons for their existence. As noted earlier in the chapter, the diluvial theory does not allow for any mixing of modern and ancient, or antediluvial, animals, so the presence in the same strata of fossil evidence of extinct animals together with fossils of creatures similar to living forms effectively refuted the diluvial explanation.

In addition to the conclusions reached by pioneer geologists about the age and

history of the earth, several other factors influenced 17th- and 18th-century scientists to consider alternatives to the Genesis account of human origins. Explorers were returning from distant lands with eye-witness accounts of modern humans living in crude shelters, using simple tools, and existing by hunting and gathering. This was so far from the state of humanity in their homeland that European travellers described the people they observed as living in a state of ‘savagery’. According to the Genesis narrative, no human beings created by God should be living in such a state.

A catalogue of life

The same explorers and traders who had returned to Europe with tales of the behaviour of ‘primitive’ people also brought back descriptions and examples of a perplexing array of plant and animal life, which in turn created a need for a way of cataloguing and organizing their discoveries. A system put forward by John Ray introduced the concept of the species, but the one that has stood the test of time was devised by a Swede called Karl von Linné, a name we know better in its Latinized form, Carolus Linnaeus.

Linnaeus’ hierarchical scheme groups similar things together in increasingly broad, or inclusive, categories. Think of the following example of a classification from the world of art. Its seven levels, or categories, are ‘Fine Arts’, ‘Paintings’, ‘Oil Paintings’, ‘20th Century Oil Paintings’, ‘Picasso’s Paintings’, and ‘Picasso’s Anti-War Paintings’. The most inclusive category, the equivalent of ‘Fine Arts’ in our example, is the Kingdom, followed by Phylum, Class, Order, Family, Genus, with the species being the smallest, least inclusive, formal category. Linnaeus’ original system has been expanded, so for example an extra category called ‘Tribe’ has been added between the Genus and Family, and the prefix Super- above, and the prefixes Sub- and Infra- below, have been added to some categories. Note that Linnaeus’ scheme does not include the equivalent of an individual painting, like Picasso’s *Guernica*. Individuals must be allocated to the smallest unit, which in our example is ‘Picasso’s Anti-War Paintings’. You cannot classify individual fossils; they have to be allocated to a species and then that species has to be classified. A unit recognized at any level in the Linnaean hierarchy is called a ‘taxon’ (pl. ‘taxa’): the species *Homo sapiens* is a taxon, and so is the order Primates. When the system is applied to a group of related organisms, the scheme is called a Linnaean taxonomy, usually abbreviated to a taxonomy. The Linnaean taxonomic system is also known as the

binomial system because two categories, the genus and species, make up the unique Latinized name (e.g. *Homo sapiens* = modern humans; *Pan paniscus* = bonobos) we give to each species. You can abbreviate the name of the genus, but not the species. So, you can write *H. sapiens* and *P. paniscus*, but not *Homo s*. or *Pan p.* This is because sometimes more than one species name in a genus begins with the same first letter (e.g. *Homo habilis* and *Homo heidelbergensis*).

Evidence of connections

Trees are common metaphors. For example, in Christianity the Great Chain of Being is sometimes represented as a tree, with modern humans at the top and other living animals placed at heights corresponding to their level of complexity. However, in contemporary life sciences the Tree of Life is not a metaphor: it is taken more literally. In a modern scientific TOL the relative size of the part of the tree given over to any particular group of living things reflects the number of taxa, and the pattern of branching within the tree reflects the way scientists think the taxa are related.

When the first science-based TOL was constructed in the 19th century, the closeness of the relationship between any two species had to be assessed using morphological evidence that could be studied with the naked eye or with a conventional light microscope. The assumption was that the larger the number of structures shared by organisms sampled from those species, the closer the species were within the reconstructed TOL. Developments in biochemistry during the first half of the 20th century meant that, in addition to traditional morphological evidence, scientists could use evidence about the physical characteristics of molecules to help assess how closely related two species were. The earliest attempts to use biochemical information for determining relationships relied on reactions between molecules on the surface of blood cells and molecules in serum, molecules we now call antigens and antibodies, respectively. Both these lines of evidence, as crude as they were, emphasized the closeness of the relationship between modern humans and chimpanzees.

Proteins are the basis of the machinery that makes other molecules like sugars and fats, and ultimately tissues such as muscles, nerves, bones, and teeth. In 1953 James Watson and Francis Crick, with the unwitting help of Rosalind Franklin, discovered that the nature of proteins, the building blocks of our bodies, is determined by a type of nucleic acid called DNA (short for

deoxyribose nucleic acid) that contains the instructions, called the genetic code, which ultimately determine what our bodies look like. So instead of scientists working out how species are related by comparing traditional morphology, or by looking at the morphology of protein molecules, they could determine relationships by comparing the DNA that dictates the structure and shape of proteins.

When these methods, first traditional anatomy, then the morphology of protein molecules, and finally the structure of DNA (the details of how DNA is compared are given below), were applied to more and more of the organisms in the TOL it became apparent that animal species that were similar in their anatomy tended to have similar molecules and similar genetic instructions. Researchers have also shown that, even though the wing of an insect and the arm of a primate look very different, the same basic instructions are used during their development. This is additional compelling evidence that all living things are connected within a single TOL. The only explanation for this connectedness that has withstood scientific scrutiny is evolution, and the mechanism for evolution that has withstood scientific scrutiny for the longest time is natural selection. We now know that factors other than natural selection also play a role, but natural selection has not been displaced as the main driver of evolution.

Evolution—an explanation for the Tree of life

Evolution means gradual change. We now know that most of these changes occur during speciation, which is when an ‘old’ species changes into a ‘new’, different, species. Although the Greeks were comfortable with the idea that the behaviour of an animal could change, they did not accept that the structure of animals, including modern humans, had been modified since they were spontaneously generated. Indeed, Plato championed the idea that living things were unchanging, or immutable, and his opinions influenced philosophers and scientists until the middle of the 19th century.

In 1809 a French scientist, Jean Baptiste Lamarck, set out the first scientific explanation for the TOL in his *Philosophie zoologique*. In the English-speaking world Lamarck’s ideas were popularized in the *Vestiges of the Natural History of Creation* (1844), a book that influenced both Charles Darwin and Alfred Russel Wallace, who independently worked out that the main mechanism underlying evolution was natural selection.

Charles Darwin's contributions to science did *not* include the concept of evolution: what Darwin contributed was a coherent theory about the way evolution could work. As we will see, Darwin's theory of natural selection accounts for both the diversity and the branching pattern, of the TOL. Darwin's thinking was influenced by Robert Malthus's *Essay on the Principle of Population* (1798) and Charles Lyell's *Principles of Geology*. Malthus stressed that resources are finite, which suggested to Darwin that imbalances between the resources available and the demand for them might be the driving force behind the selection needed to make evolution happen. Lyell's fluvial explanation for the evolution of the surface of the earth was much like the gradual morphological change that Darwin suggested was responsible for the modification of existing species to produce new ones. Darwin was also goaded into action by the work and philosophy of William Paley. Paley was a champion of the notion that animals were so well adapted for their habitat that this cannot have been due to chance. He was convinced that they must have been designed, and if so there must be a designer, and that the designer must have been God. Paley provoked Darwin to think about an alternative to the former's creationist interpretations.

Charles Darwin made two seminal contributions to evolutionary science. The first was the recognition that no two individual animals are alike: they are not perfect copies. Darwin understood that variation was not 'noise' in the system; it was an important 'signal' that helped him understand the mechanism that generated and sustained diversity. Darwin's other contribution was natural selection. In a nutshell, natural selection suggests that, because resources are finite, and because of natural variation, some individuals will be better than others at accessing those resources. Those individuals will then gain enough of an advantage that they will produce more surviving offspring than other individuals belonging to the same species. Biologists refer to this advantage as an increase in an animal's 'fitness'. Darwin's notebooks are full of evidence about the effectiveness of the type of artificial selection used by animal and plant breeders. Darwin's genius was to think of a way that selection could occur naturally.

Selection, and thus evolution, will only work if the offspring of a mating faithfully inherits the feature, or features, that confer(s) greater genetic fitness. What Darwin did not realize (nor for that matter did any other prominent contemporary natural scientist) was that while he was putting the finishing

touches to the *Origin of Species*, the genetic basis of variation and the essential rules of inheritance were being painstakingly worked out in a monastery garden in Brno, in what is now the Czech Republic.

The flowering of genetics

The discipline of genetics was established on the basis of the observations made by Gregor (this was his Augustinian monastic name, his original forename was Johann) Mendel about the collection of artificially bred pea plants he maintained in the garden of his monastery. When Mendel presented his interpretation of the results of his breeding experiments to the Natural Science Society in Brno in 1865, he did not use the terms gene (meaning the smallest unit of heredity) or genetics. The word gene was not coined until 1909, nine years after Mendel's pioneering experiments came to the notice of evolutionary scientists. It was Mendel's good fortune that his various plant breeding experiments provided several examples of a simple one-to-one link between a gene and a trait: we now know that single gene, or 'monogenic', effects are exceedingly rare.

Mendel's simple dichotomies, yellow or green flowers, smooth or wrinkled seeds, are called 'discontinuous' variables. In primate and hominin palaeontology we mostly deal with 'continuous' variables, such as the size of a tooth, or the shape of a limb bone. These have smooth, curved, distributions, not the neat columns that result from Mendel's data. How do you get continuous curves from discontinuous columns of data? The answer is that many genes are involved in determining the size of a tooth, or the shape of a limb bone, so that what looks like a curve is in reality the combination of many sets of columns.

Our closest relatives

Not so long ago a book on human origins would have devoted a substantial number of pages to descriptions of the fossil evidence for primate evolution. This was in part because it was assumed that at each stage of primate evolution one of the fossil primate species would have been recognizable as the direct ancestor of modern humans. However, for various reasons we now know that most of these fossil taxa are unlikely to be the ancestor of modern humans. Instead, I will concentrate on what we have learned about how the great apes (aka chimpanzees, bonobos, gorillas, and orangutans) are related to each other

and to modern humans.

Among the tales of exotic animals brought home by explorers and traders were descriptions of what we now know as the great apes, that is, chimpanzees and gorillas from Africa, and orangutans from Asia. Aristotle referred to ‘apes’ as well as to ‘monkeys’ and ‘baboons’ in his *Historia Animalium* (literally the ‘History of Animals’), but his ‘apes’, just like the ones dissected by the early anatomists, were short-tailed macaque monkeys from North Africa.

With hindsight we know that the first chimpanzee was dissected in 1699 by Edward Tyson, but one of the first systematic reviews of the differences between modern humans and the chimpanzee and gorilla was by Thomas Henry Huxley. In an essay entitled ‘On the relations of Man to the Lower Animals’ that formed the central section of his 1863 book called *Evidence as to Man’s Place in Nature*, Huxley suggested that there were more anatomical similarities between modern humans and the chimpanzee and gorilla (bonobos were not recognized then) than there were between the two African apes and the rest of the primates, including the orangutan.

Darwin used this evidence in his *The Descent of Man* published in 1871 to suggest that, because the African great apes were morphologically closer to modern humans than to the only great ape known from Asia, the ancestors of modern humans were more likely to be found in Africa than elsewhere. This deduction played a critical role in pointing most researchers towards Africa as a likely place to find human ancestors. As we will see in Chapter 3, those who considered the orangutan our closest relative looked to South-East Asia as the most likely place to find modern human ancestors.

The earliest attempts to use proteins to determine primate relationships were made just after the turn of the century, but the first results of a new generation of more sophisticated analyses were reported in the early 1960s: the US biochemist Linus Pauling coined the name ‘molecular anthropology’ for this area of research. Two reports, both published in 1963, provided crucial evidence. Emile Zuckerkandl, another pioneer molecular anthropologist, used enzymes to break up the protein haemoglobin from blood red cells into its peptide components. When he used a weak electric current to separate them, the patterns made by the peptides from a modern human, a chimpanzee, and a gorilla were indistinguishable. The second report was by Morris Goodman, who used

techniques borrowed from immunology to study samples of a serum (serum is what is left after blood has clotted) protein called albumin from modern humans, apes, and monkeys. Goodman concluded that the albumins of modern humans and chimpanzees were so alike his experiments could not tell them apart.

Proteins are made up of a string of amino acids. In many instances one amino acid may be substituted for another without changing the function of the protein. In the 1960s and 1970s Vince Sarich and Allan Wilson, two Berkeley biochemists interested in primate and human evolution, exploited these minor variations in protein structure in order to determine the evolutionary history of the molecules, and therefore, presumably, the evolutionary history of the taxa being sampled. They, too, concluded that modern humans and the African apes were very closely related.

Interrogating the genome

The discovery of the chemical structure of the DNA molecule meant that affinities of organisms could be pursued at the level of the genome. This potentially eliminated the need to rely on morphology, be it traditional anatomy or the morphology of proteins, for information about relatedness. The DNA within the cell is located either within the nucleus as nuclear DNA (nDNA), or within organelles called mitochondria (mtDNA). In DNA sequencing the base sequences of each animal are determined and then compared.

Sequencing methods have been applied to the DNA of living apes and the number of studies increases each year. Information from both nuclear and mitochondrial DNA suggests that modern humans and chimpanzees/bonobos are more closely related to each other than either is to the gorilla. When these differences are calibrated using the ‘best’ palaeontological evidence for the split between the apes and the Old-World Monkeys, and if we assume that the DNA differences are neutral (aka ‘clock-like’), the prediction is that the hypothetical common ancestor of modern humans and chimpanzees/bonobos lived between 8 and 6 mya. The assumptions used by those who use molecules as ‘clocks’ can differ, and these different assumptions result in older ages for the split between the ancestor of modern humans and the ancestor of chimpanzees/bonobos.

Implications for interpreting the human fossil record

The results of recent morphological analyses of both skeletal and dental anatomy, and the anatomy of the soft tissues such as muscles and nerves, are also consistent with the compelling DNA evidence that chimpanzees and bonobos are closer to modern humans than they are to gorillas. But some attempts to use the type of traditional morphological evidence from skulls, jaws, and teeth that is conventionally used to investigate relationships among fossil hominin taxa did not find a particularly close relationship between modern humans and chimpanzees. Instead, chimpanzees clustered with gorillas. This has important implications for researchers who investigate the relationships among hominin taxa. They either need to use information about skulls, jaws, and teeth that is capable of confirming the close relationship between chimpanzees/bonobos and modern humans, or they need to find other sources of morphological evidence that can reliably recover the relationships among living higher primates supported by the DNA evidence (Table 1).

Table 1 A traditional taxonomy (A) and a modern taxonomy (B) that take account of the molecular and genetic evidence that chimpanzees and bonobos are more closely related to modern humans than they are to gorillas.

A. Superfamily Hominoidea (hominoids)
Family Hylobatidae (hylobatids)
Genus *Hylobates*
Family Pongidae (pongids)
Genus *Pongo*
Genus *Gorilla*
Genus *Pan*
Family Hominidae (hominids)
Subfamily Australopithecinae (australopithecines)
Genus *Ardipithecus*
Genus *Australopithecus*
Genus *Kenyanthropus*
Genus *Orrorin*

Genus *Paranthropus*

Genus *Sahelanthropus*

Subfamily Homininae (hominines)

Genus *Homo*

B. Superfamily Hominoidea (hominoids)

Family Hylobatidae (hylobatids)

Genus *Hylobates*

Family Hominidae (hominids)

Subfamily Ponginae (pongines)

Genus *Pongo*

Subfamily Gorillinae (gorillines)

Genus *Gorilla*

Subfamily Homininae (hominines)

Tribe Panini (panins)

Genus *Pan*

Tribe Hominini (hominins)

Subtribe Australopithecina (australopiths)

Genus *Ardipithecus*

Genus *Australopithecus*

Genus *Kenyanthropus*

Genus *Orrorin*

Genus *Paranthropus*

Genus *Sahelanthropus*

Subtribe Hominina (hominans)

Genus *Homo*

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Chapter 3

Fossil hominins: their discovery and context

As explained in Chapter 1, we use hominin for modern humans and all the extinct species on, or connected to, the twig of the Tree of Life that leads exclusively to modern humans. In this chapter I discuss what the hominin fossil record consists of, how it is discovered and recovered, and how it and its context are investigated.

The hominin fossil record

A fossil is a relic or trace of a formerly living organism. Only a tiny fraction of living organisms survives as fossils, and until people were buried deliberately the same applied to hominins. The fossils that do survive are almost certainly a biased sample of the original population: I discuss the implications of this in more detail in Chapter 4. Scientists recognize two categories of fossils. The smaller category, trace fossils, includes footprints, such as the 3.66 my trackways from Laetoli in Tanzania that I discuss in Chapter 6. The larger category, true fossils, consists of the actual remains of animals or plants, and with respect to the hominin fossil record, unless qualified, all the fossils referred to are true fossils. Animal fossils usually consist of the hard tissues that make up bones and teeth. This is because hard tissues are more resistant to being degraded than are soft tissues such as skin, muscle, or the gut. Soft tissues are only preserved in the later stages of the hominin fossil record, such as the Bog People found in Denmark and elsewhere in Europe.

Fossilization

The chances that any part of an early hominin's skeleton would be preserved in the fossil record are vanishingly small. The predecessors of modern lions, leopards, and cheetahs would most likely have had the first pick at the carcass of a dead hominin. After them would have come the terrestrial scavengers, led by hyenas, wild dogs, and smaller cats, then birds of prey, then insects, and finally bacteria. Within two to three years—a surprisingly short time—these organisms are capable of removing most of the evidence of any large mammal.

For any of its hard tissues to be preserved as fossils, the carcass of a dead hominin would need to have been covered quickly by sediment. Sediment protects the carcass from further degradation and allows chemicals in the sediments to replace the inorganic material in bones and teeth. This process takes many years, and in the meantime the sediments that surround the fossil are being converted into rock. Fossils are bone, or tooth, shaped rocks.

Diagenesis is the term scientists use to describe the changes that occur in bones and teeth during fossilization. Fossils from different sites, fossils from different parts of the same site, and even different parts of the same individual show different degrees of fossilization because of small-scale variations in the chemical environment. When they are freshly exposed, most fossils preserved in hard rocks are durable, but if a fossil is exposed to erosion by wind and rain for any length of time it can become soft and fragile, and when this happens researchers have to infiltrate the fragile bone with liquid plastic, or its equivalent, to stop the fossil from disintegrating upon excavation. Deliberate burial, which greatly increases the chance that skeletons will be preserved in good condition, is one of the main reasons why, with one or two exceptions, the hominin fossil record gets so much better about 70–60 kya.

Most hominin fossils are found in rocks formed from sediments laid down by rivers, or on lakeshores, or in the floors of caves. Generally older rocks (and thus the fossils they contain) are in the lower layers and the younger ones are nearer the surface: this principle is called the law of superposition. However, relative movement of rocks brought about by tension and compression, such as the shearing that occurs along faults in the earth's crust, can confound this general principle. Sedimentary rocks in caves are particularly prone to being jumbled up in complex ways. Water that percolates down from the surface can soften and

then dissolve old sediments, producing Swiss-cheese-like cavities that are filled by more recent sediments. So, within caves newer sediments may be below older ones.

Earth scientists use the appearance, texture, and distinctive chemistry of rocks to describe and classify them. For example, they might refer to one layer as a ‘pink tuff’, or another as a ‘silty-sand’. Just as there are rules for naming new species, there are rules and conventions for naming the strata of a newly discovered sedimentary sequence: there is the equivalent of a Linnaean taxonomy for rocks. The layer a fossil was buried in is referred to as its ‘parent horizon’. Hominin fossils found within a particular rock layer are, unless there is obvious evidence that they were deliberately buried, considered to be the same age as that layer. A fossil found embedded in a rock is described as being found *in situ*. Most hominin fossils, however, have been displaced through erosion from their parent horizon so they are called ‘surface-finds’. In order to reliably connect a surface-find to its parent horizon, it helps if the fossil has some of the parent rock (aka matrix) attached to, or embedded in, it. This is why careful scientists never completely clean the matrix from a fossil.

Finding fossil hominins

Where do palaeoanthropologists look for early hominin fossils? In the 19th century Charles Darwin argued that, because the closest known living relatives of modern humans, the chimpanzee and the gorilla, were only found in Africa then it was probable that the common ancestor of modern humans also came from Africa. So, for most of the past century, and especially the last seventy-five years, Africa has been a focus of human origins field research. But researchers cannot possibly search all of Africa, so are there places where hominin fossils are likely to be found?

Researchers look where rocks of the right age (say back to 10 mya) have been exposed by natural erosion. Erosion occurs where the earth’s crust has been buckled and cracked as large landmasses, called tectonic plates, are pushed together. This pressure produces cracks, or faults. On one side of a fault sediments are forced downwards, and on the other side they are thrust upwards: this is how the floor and walls of rift valleys are formed. These cracks in the earth’s crust are sometimes so deep that the liquid core of the earth escapes through them either as a flow of molten lava, or as a volcanic eruption. Volcanic

eruptions consist of ash (called tephra) rich in the chemicals potassium and argon. The rocks formed from these ash layers (aka tuffs) provide the raw material for dating many eastern African hominin fossil sites. Tuffs also have a distinctive chemical profile, or ‘fingerprint’, and this allows geologists to trace a single tuff not only within a large fossil site, but also across many hundreds of kilometres from one site to another. Ash that has fallen on water (aka pumice) is favoured for dating because it is less likely to be contaminated with crystals from earlier eruptions.

Fossils are exposed on the sides and floors of the valleys that form when streams and rivers erode their way through the blocks of sediment that are thrown up at faults. Locations like these are called ‘exposures’, and the places on these exposures where fossils have been found are called localities. In eastern Africa scientists look for hominin fossils in rocks of the right age that have been exposed by a combination of volcanic activity (aka tectonism) and erosion. Olduvai Gorge, in Tanzania, is probably the best-known example of a rift valley site where both tectonism and erosion have exposed rocks of the right age. Satellite imagery and recent advances in Geographical Information Systems (GIS) have been used to locate promising exposures, but very few of these turn out to have terrestrial fossils in them.

Early hominin fossils are found in a very different geological context in southern Africa. Here, they are found in caves that form when rain runs through cracks in the limestone. Small cracks expand into big cracks, big cracks become cavities, and cavities coalesce to become caves that fill with soil washed in from the surface. Leopards use the trees that grow in the entrances of the caves as a place to hide carcasses, and hyenas use cave entrances as dens. Scientists think that most of the hominin fossils found in the southern African caves were dropped by leopards: particularly complete skeletons probably represent individual hominins who entered the caves, but were unable to make their way out. Most of the fossil hominins found in southern Africa come from sites where the sediments and fossils were exposed by mining.

Although Africa is now the major focus of the search for early hominin fossils, in earlier times the search for human fossils was focused on Europe and Asia. Europe was where the first prehistorians lived and worked, so it is to be expected that they would have taken advantage of any opportunity that presented itself in their own region before looking for the fossil remains of our ancestors in more

inaccessible places. Although Charles Darwin had predicted back in 1871 that Africa would be the birthplace of humankind, in 1874 Ernst Haeckel, a prominent German naturalist, suggested that the presence of the orangutan, the only non-African great ape, in what was then called the Dutch East Indies (now Borneo and Sumatra in Indonesia) made that region a likely birthplace for humanity. Unlike Huxley, Haeckel was convinced that modern humans were more similar, and therefore more closely-related, to the orangutan than to the African apes.

Haeckel's logic caught the attention of a young trainee surgeon, Eugène Dubois, so much so that in the late 1880s he took a job in the region so he could look for human ancestors. His most famous find, the top of a brain case of a creature that had brow ridges unlike any seen on modern humans, was recovered in 1891 in the bank of the Trinil River in Java. Not all the human ancestors discovered in Asia were found in sediments sliced through by rivers. The famous Peking Man fossils came from a cave site near Beijing in China.

Teamwork

The teams that nowadays look for hominin fossils include a wide range of experts. In addition to palaeoanthropologists, geologists, dating experts, and palaeontologists who can identify and interpret the fossil remains of the animals and plants found with the hominins, teams include experts on the factors that bias the fossil record, and scientists who can interpret the chemistry of the soils in order to reconstruct ancient habitats. Researchers often have to travel to remote and sometimes dangerous places where they, along with local collaborators, search for and excavate fossils. The logistical challenges of providing water, food, and fuel in such places mean that leaders of expeditions must be good organizers as well as good scientists. They must also be prepared to spend time raising funds by writing grants, because expeditions to inaccessible central and eastern African fossil sites are expensive to mount, with the largest ones having annual budgets of tens of thousands of dollars.

The southern African cave sites are mostly much more accessible; the exceptions being the two chambers within the Rising Star system of caves. The majority of locations, including Rising Star, lie within an hour's journey time by car from Johannesburg or from Pretoria. This enables scientists to supervise research while working in universities and museums in nearby cities.

Fossils rediscovered

Some hominin fossil discoveries are made in museums. It is always worthwhile going through the collections of ‘non-human’ fossils recovered from a hominin fossil site, for even the best palaeontologists can miss things as they sort through hundreds of bone fragments. In the past when important hominin discoveries were made they were sometimes sent away to experts for their assessment, and unless great care is taken specimens can be muddled or mislabelled. For example, when a remarkably complete skeleton of a Neanderthal baby was recovered from Le Moustier cave in France it was sent to Marcellin Boule for an assessment of its age. All trace of the skeleton was lost until a researcher found the bones of a neonate among stone tools collected at the site. Fortunately, some of the bones were still in their original matrix, and this matched the rocks at Le Moustier.

Dating hominin fossils

Geologists can usually work out the temporal sequence of fossils within a small fossil site. But how do you compare the ages of fossils found at localities hundreds of kilometres apart, and how do you compare the ages of fossils from sites on different continents? To answer these questions, you need dating methods.

Most dating methods are applied to the rocks in which hominin fossils are found, or to non-hominin fossils recovered from the same horizon, so researchers must take great care to preserve the evidence that links a fossil to a particular rock layer. Some dating methods rely on knowing the time it takes for natural processes, such as atomic decay, to run their course, or they relate the fossil horizon to precisely calibrated global events such as reversals in the direction of the earth’s magnetic field. This is why some dates can be given precisely in calendar years. The best known of these methods, radiocarbon dating, is only appropriate for the later stages of human evolution. After 5,730 years (plus or minus 40 years) half of the ^{14}C there was when the organism died has been converted to ^{14}N (this is why this length of time is called its ‘half-life’). Radiocarbon dating has been used successfully for dating *Homo sapiens* fossils from Australia and Europe, but radiocarbon dates older than 40 ky are unreliable because the amounts of radiocarbon left are too small to be measured precisely. Dendrochronology, the use of tree rings, coral growth, and precisely dated lake

sediments called varves, have all been used to improve the precision of radiocarbon dating.

Most of the hominin fossils from eastern African sites (e.g. Olduvai Gorge in Tanzania, Koobi Fora in Kenya, and Hadar in Ethiopia (Figure 3)) are from horizons sandwiched between layers of volcanic ash, or tephra, which are rich in isotopes of potassium and argon. Because radioactive potassium and argon convert (or decay) into their daughter products slowly, potassium/argon (K/Ar) and argon/argon ($^{40}Ar/^{39}Ar$) dating methods can be used on older rocks that contain fossils and stone tools. Sites in southern Africa have been notoriously difficult to date, but researchers have developed a clever system that uses uranium and lead (U-Pb) to date the calcium carbonate layers that form in the caves. This has revolutionized our understanding of the age of these cave sites, and researchers suggest that most of the hominin fossils entered the caves during the drier intervals between the wetter times when the calcium carbonate accumulated.

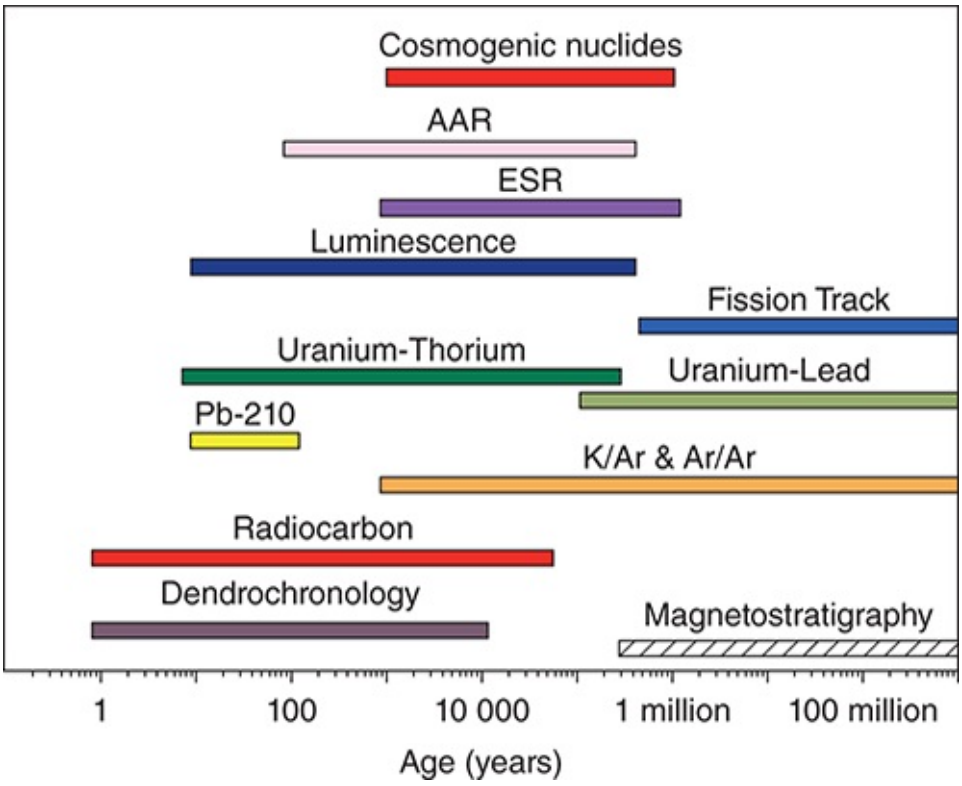


3. Sediments exposed at the Ethiopian site of Hadar. The horizontal bands represent multiple changes in depositional environments over time including rivers, lakes, and floodplains.

Palaeomagnetic dating (aka magnetostratigraphy) takes advantage of the

complex record of reversals of the direction of the earth's magnetic field. For long periods in its history the direction of the earth's magnetic field has been the exact opposite of what it is now: the contemporary direction is called 'normal' and the opposite one 'reversed'. If particles in the sediments contain any magnetic material when they settle they line up with the direction of the earth's magnetic field. This gives the rock as a whole a detectable magnetic direction, or polarity. Researchers try to find the best match between the sequence of changes in magnetic direction preserved in the hominin fossil-bearing sediments and the magnetic record preserved in cores taken from the floor of the deep ocean. Some sequences are seen more than once in the reference column, so it helps if another dating method can be used to show researchers which part of the geomagnetic polarity time scale they should focus on. A long period of palaeomagnetic stability is called a 'chron', and a relatively short-lived change in magnetic field direction within a chron is called a 'subchron'. Olduvai Gorge was the first early hominin site to be dated using magnetostratigraphy, and when subchrons were named, and not numbered as they are now, one of them was called the 'Olduvai Event'. Fluctuations in the ratio of oxygen isotopes in marine sediments (see below) are the basis of a dating system that uses Marine Isotope Stages (MIS), with odd numbers being used for warm periods and even numbers for cold periods. This system is especially useful for sites in Europe where the types of animals found are indicative of how cold and warm it was.

Other methods (e.g. electron spin resonance (ESR) and uranium series dating (USD)) can be used to date hominin fossil sites that are between the ranges of radiocarbon and K/Ar, $^{40}Ar/^{39}Ar$, and U-Pb dating (i.e. between 300 and 40 kya) (Figure 4).



4. Some of the methods used to date fossil hominins. The horizontal scale in years is log transformed, and the effective temporal range of each method is indicated by the length and location of the horizontal bars. AAR: Amino-acid racemization; ESR: Electron spin resonance; K/Ar: Potassium-argon; Ar/Ar: Argon-Argon.

Another way of determining the age of a site is to match non-hominin fossils found at the site with equivalent evidence from another site that has been reliably dated using numerical methods. If the animal fossils found at Site A are similar to those at Site B, Site A can be assumed to be approximately the same age as Site B. The use of non-hominin fossils for dating (aka biochronology) has been especially important for dating early hominins from the southern African cave sites. Nearly all of these sites contain antelope, elephant, pig, and monkey fossils, and because the same taxa have been reliably dated at key eastern African sites, researchers infer that the layers that contain equivalent fossils in the southern African caves are the same age.

Reconstructing past environments

Just as the contours of the earth's surface are different from how they were

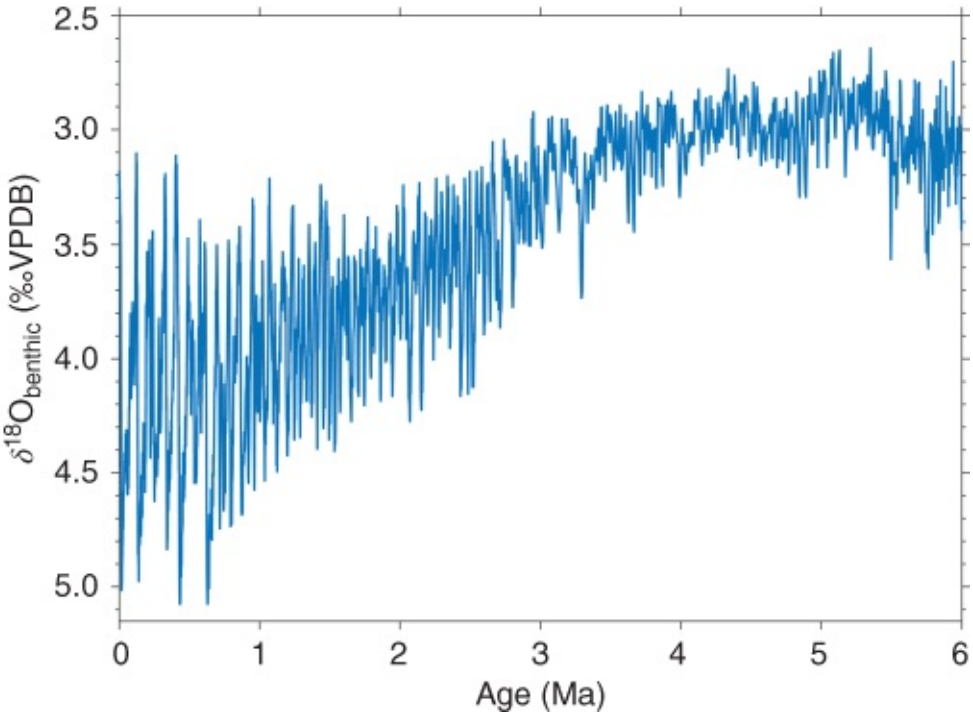
several million years ago, past environments in a region are not necessarily the same as those we see today. Researchers reconstruct past environments using geological and palaeontological evidence. Chemical analysis is used to tell whether a soil was laid down in moist or dry conditions. Palaeontologists can tell a lot about the palaeohabitat from the types of animal fossils that are found along with the fossil hominins. They use both large mammals and small micromammals (such as mice and gerbils) to reconstruct past environments. Small micromammals are especially useful because their geographical ranges are more restricted than those of larger mammals, so they are likely to provide more precise habitat reconstructions. Fossilized owl pellets are a good source of information about micromammals because owls hunt small mammals within a relatively small range.

Researchers who use larger mammals like primates to reconstruct past environments have to be careful not to assume that the habitat preferences of the ancestors were like those of their modern-day representatives. For example, although modern colobus monkeys are mainly leaf eaters who live in dense woodland, their ancestors lived in more open habitats, so the presence of colobus monkeys at a 5 my-old site does not mean the same as finding contemporary colobus monkeys. You can also learn a lot about past environments by looking at the limb bones and teeth. The limb bones reveal if the animals were adapted for open (e.g. grassland) or closed (e.g. woodland) habitats, and the height of tooth crowns and wear on the teeth are good predictors of how much grass the animals were eating.

Global climate change

Hominin evolution has taken place at a time when there have been major changes in world climate. Researchers study climate change by looking at deep-sea cores. Microscopic organisms called foraminifera (usually shortened to ‘forams’) are suspended in the water of the world’s oceans. These foraminifera take up two forms of oxygen isotope: one of them, oxygen 16, is lighter, the other, oxygen 18, is heavier. When global temperatures are higher more of the lighter oxygen evaporates, so the ratio of the light to the heavy form reduces: the opposite occurs when global temperatures are cooler. Researchers use the proportions of the two oxygen isotopes to track the temperature of the oceans, and they use ocean water temperature as a proxy for global climate (Figure 5). But the climate in a region is the result of a complex interaction between global

climate and local influences such as latitude, altitude, and the presence of mountain ranges. During the period from 8 to 5 mya the earth experienced the beginning of a long-term drying and cooling trend. Early hominin evolution took place in Africa at the time of these climatic changes, and the possible influence of climate change on the origin of the hominin lineage will be explored further in Chapter 5.



5. The oxygen isotopic composition of foraminifera from the ocean floor tracks global climate over the past 6 million years. More positive values indicate colder deep ocean temperatures and larger ice sheets.

Later in hominin evolution cyclical changes in global climate, measured using deep-sea cores, were superimposed on the long-term cooling trend. Prior to 3 mya global climate was subject to 23 ky hotter/drier and cooler/wetter cycles. Around 3 mya the periodicity of these cycles switched to 41 ky, but by 1 mya it had switched yet again to a 100 ky cycle. These 100 ky cycles are responsible for the periods of intense cold recorded in the northern hemisphere during the past million years. These long cycles had another important impact on human evolution because when so much ice is locked up in the icecaps at the north and south poles, sea levels fall and expose much of what we call the continental shelf. Reductions in sea level of this magnitude helped our ancestors to migrate

from the Old World to both Australasia and the New World.

But ocean temperatures are not always good predictors of the palaeoclimate in regions that are many hundreds of miles from the ocean. Researchers have recently been investigating what conditions were like in the lake basins where hominins have been recovered (e.g. Hadar in Ethiopia, Omo-Turkana and Olorgesailie in Kenya, and Olduvai in Tanzania). They use commercial drilling rigs to extract sediment cores, and then they subject the cores to the types of chemical and organic analyses that researchers developed for use on deep-sea cores. These lake sediment cores have provided important clues about how global climate gets modified at the regional level, and they have exposed inconsistencies among regions. Evidence of a wet and warm palaeoenvironment in one region of Africa does not mean that all African regions at that time will have been wet and warm, nor do all regions respond synchronously to changes in global climate.

Chapter 4

Fossil hominins: analysis and interpretation

Palaeoanthropologists use many methods to work out the significance of newly discovered fossil evidence, but the first order of business is to assign hominin fossils to a taxon. After that researchers work out that taxon's relationships with other fossil and living taxa, and then they infer the behaviours and habitat preferences of the taxon.

Classification and taxonomy

A subdiscipline of classification, called 'nomenclature', concerns itself with how names should be used in the Linnaean system. There is a formal code for regulating nomenclature, and scientists who think they have discovered a new species must follow this code. Rules in the code govern the types of name that can be given to a new species or genus. For example, the names of commercial products are prohibited: *Burgerking ipodensis* would not be an acceptable binomial for a new hominin species. It is also important to make sure that the name of an existing taxon is not inadvertently used for a new taxon, otherwise they will be confused.

When researchers decide to introduce a new species, they have to choose one fossil as its 'type' specimen. Researchers usually choose a relatively well-preserved fossil from among those found at the time of the initial discovery. The significance of the type specimen is *not* that it is a typical (i.e. an average) member of the species, it is significant because the taxon name is irrevocably attached to it. For example, if the type specimen of *Homo neanderthalensis* was

found to be different from all the other fossils included in *H. neanderthalensis*, they would have to be assigned to a new species, and it would need to be given a new name. The name *H. neanderthalensis* cannot be used independently of the type specimen: where it goes, the name goes, too. Seniority counts in nomenclature: if two type specimens end up in the same species, the oldest name is the one that has to be used.

When researchers write about ‘a taxon’ they are usually referring to a species, and when species are arranged in an increasingly inclusive hierarchy (i.e. larger and larger clusters of species) this is called a taxonomy, literally a ‘scheme for taxa’. Once a fossil is discovered the first thing researchers do is decide whether it belongs in an existing hominin species. Only if they are convinced it cannot be assigned to an existing species should they create a new species. The same principles apply to other levels in the Linnaean hierarchy, so researchers should only establish a new genus if they are convinced the new species cannot be accommodated in an existing hominin genus, and so on up the Linnaean hierarchy.

Most taxonomic decisions are based on a detailed assessment of the morphology of a fossil. Its morphology, or phenotype, is what the fossil looks like, both externally and internally. Morphology can be gross morphology, which is what the eye can see unaided, or microscopic morphology, which is what can be seen with a variety of types of microscope. Researchers prepare detailed qualitative descriptions of the size and shape of the fossil, but they also try to capture that information in the form of measurements as a quantitative description. In their simplest form quantitative descriptions consist of distances between defined anatomical landmarks on the fossil: these are called linear measurements. Lasers and technologies borrowed from medical imaging now allow researchers to capture details of the external morphology in three dimensions. Glenn Conroy, a palaeoanthropologist, and Charles Vannier, a medical imaging specialist, both from Washington University in St Louis, pioneered the use of computerized tomography (or CT) imaging to study the internal structure of a fossil hominin cranium from Taung in southern Africa. Subsequently Frans Zonneveld, a medical imaging specialist from Utrecht, and Fred Spoor, a palaeoanthropologist from the Natural History Museum in London, further developed these methods to provide information about the inner ear. Micro-CT now enables researchers to look at gross details of the internal structure of teeth, and synchrotron radiation micro-computed tomography (SR-µCT) enables them to look at the

microstructure of intact teeth.

Researchers must be sure the measurements made on fossils accurately reflect the size and shape of the bone or tooth before it was fossilized. Bones and teeth crack if they are exposed to daily cycles of heating and cooling, and if rock matrix gets inside the cracks it artificially enlarges the dimensions of a bone or tooth. Likewise, if a fossil bone is exposed on the surface of the ground in dry and windy conditions before or after fossilization, small particles carried by the wind can have a ‘sandblasting’ effect and remove the outer layer of bone, thus reducing its size.

The measurements and the non-metrical morphology of a newly recovered fossil are compared with those of similar specimens in existing fossil taxa. Closely related living animals (in the case of hominins this means modern humans and the African apes) are usually used as models to help decide how much variation should be tolerated within a fossil species. But Cliff Jolly, a primatologist from New York University who spent thirty years studying what happens at the boundary between distinctive groups of baboons, suggests that baboons and their close relatives may be a better analogue for hominin evolution. He points out that baboons are more widespread than chimpanzees and gorillas, and the pattern and timing of their recent evolutionary history is similar to the recent evolutionary history of hominins.

Reconstructing whole fossils from fragments

Hominin fossils that are several millions of years old are seldom found in good condition. The brain case and the face are particularly fragile and are easily trampled by hoofed animals and crushed by rocks falling from the roof of a cave. Sometimes just one fragment of the brain case is all that is left of a cranium. In a few cases more is preserved, but if the pieces are tiny reassembling them is like doing a three-dimensional jigsaw puzzle with lots of sky, no clouds, and with no picture to help you. One option is to painstakingly reassemble the pieces by hand, but this can take hundreds of hours even for a skilled anatomist who knows every detail of a skull.

Marcia Ponce de León and Christoph Zollikofer from the Anthropological Institute of Zurich pioneered ‘virtual anthropology’, which uses computer power and advances in software design to provide an alternative to reassembling

hominin fossils by hand. The fossil is scanned, a ‘virtual’ version is displayed on the computer screen, and researchers can then move and rotate each piece in any direction to see if any of the pieces fit. The software also enables a missing piece on one side of the cranium to be replaced by mirror imaging the equivalent piece from the other side. Similar software in conjunction with CT scans enables the imaging and reconstruction of structures buried deep in the bone, like the air sinuses, the bony canals of the inner ear, or the roots of the teeth.

Determining age and sex

Even if one has a complete or nearly complete skeleton, determining the sex and developmental age of hominin fossil remains can be difficult, but these difficulties are compounded when all that remain are fragments. The age at death of a fossil individual that has finished growing is difficult to determine precisely. Dental development can help determine the age of immature individuals, but once all the teeth are erupted and the roots of the teeth are formed, dental evidence, such as how worn the teeth are, is less useful.

The size and shape of the bones and teeth, the extent of muscle markings, and the size and shape of the pelvis (although pelvic fragments are rare in the hominin fossil record) are the usual ways the sex of an individual fossil is determined. The underlying assumption is that because in many non-human primates males are larger than females, then early hominin males were also likely to have been larger than early hominin females. However, when you are dealing with a sparse fossil record overall size is not always a reliable guide to sex.

Sexual dimorphism refers to all of the differences among individuals that are related to their sex, but one cannot unthinkingly extrapolate modern human or chimpanzee/bonobo sexual differences to early hominins. For example, in modern humans many pelvic sex dimorphisms occur because of compromises between the requirements of bipedalism and the need in modern human females for space in the pelvis to give birth to a large-brained infant. The same dimorphisms, however, might not apply to smaller-brained early hominins who are not bipedal in the same way that modern humans are. The pelves of small-brained early hominins almost certainly exhibit a unique pattern of sexual dimorphism.

Species and species identification

The most widely used scientific definition of a species is the biological species concept (BSC), which suggests a species is a ‘group of interbreeding natural populations, reproductively isolated from other such groups’. This is all well and good when you can observe living animals, and check who is mating with whom, but it is self-evident that this method will not work when we try to recognize species in the fossil record. However, because members of the same species mate with each other and not with members of another species, they resemble each other more than they do individuals belonging to any other species. Thus, in the absence of information about its mating habits, we can use the appearance, structure, and (if any DNA is preserved) the genetic make-up of an individual to help allocate it to a species.

But there are problems when researchers try to apply these methods to the hominin fossil record. The first problem is that we do not have complete animals in the hominin fossil record. It is customary to divide the components of animals into two categories, soft tissues (e.g. muscles, nerves, arteries) and hard tissues (e.g. bones and teeth). The vast majority of the hominin fossil record consists of the remains of the hard tissues, but because many fossils are fragmentary, the problem facing palaeoanthropologists is how to assign a fossil to a species when the only evidence you have is a broken and worn tooth, or a piece of jaw, or part of a thigh bone.

The second problem is time. Each species has a history, with a beginning (speciation), a middle, and an end (extinction or transformation into a descendant species). The average fossil mammal species lasts for just over one million years, but during that time the appearance of that species is unlikely to stay the same. Random variation and morphological responses to long-term changes in climate are likely to cause it to change, but as long as its members only mate with members of the same species then the species should continue to be distinctive. However, even if a scientist spends their whole career observing just one living species they will have collected data for just an instant of its existence. Likewise, the variation you see in museum collections of skeletons belonging to a modern species, which may, at the most, have been collected over the course of a hundred years, or so, is not an appropriate model for deciding how much variation should be tolerated in a sample made up of fossils collected at localities that span several thousands, if not tens of thousands, of years.

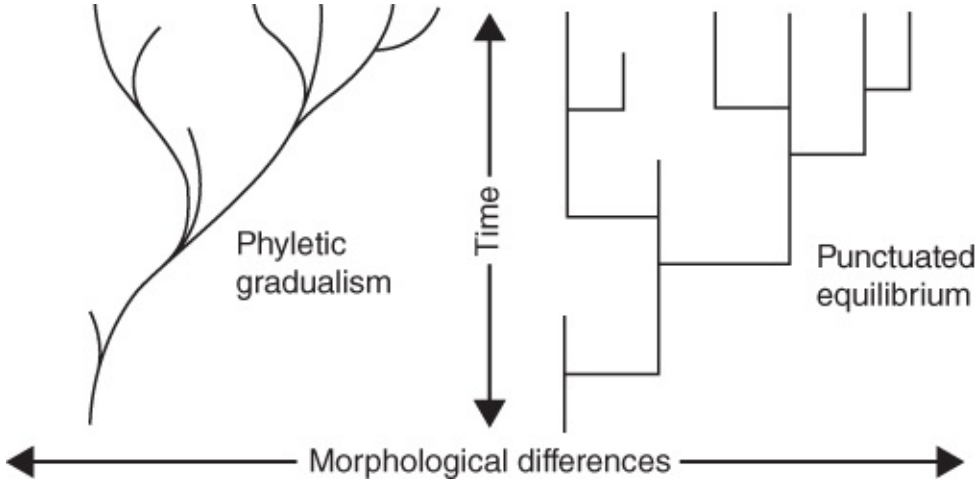
Instead of fossils, think of finding several still photographs of a long-distance running race. Palaeoanthropologists need to work out ways of telling whether they are looking at several photographs of the same running race—a long-lived species may well be sampled several times during its history—or single photographs of several different running races. In the case of human evolution this means looking at collections of modern human and other higher primate skeletons, and then using the size and shape variation within those collections as a guide to how much variation researchers should tolerate within a collection of fossils assigned to a single species. If the variation is less than that seen in the living taxa, then there are good reasons to conclude that only one species is represented in the collection of fossils. Because of the extra time involved with fossil samples palaeoanthropologists try to make an educated guess about the extra amount of variation they are prepared to tolerate in their fossil sample before they declare the variation 'too great' to be contained in a single species. But it is only an educated guess, and usually a poorly educated one at that.

Deciding how many species are represented in a collection of early hominin fossils is made more difficult because biological variation among hominins, including fossil hominins, is continuous. Therefore, where the boundaries between fossil taxa are drawn is a matter of legitimate scientific judgement and debate. Boundaries between species tend to be drawn when there is evidence of morphological discontinuity between samples of fossils. The discovery of new fossils or the introduction of new analytical methods often means that these boundaries change. Sometimes new discoveries falsify, or cause researchers to modify, their taxonomic proposals. A new species should only be established if there are really good grounds for believing the new fossil evidence does not belong to an existing species. There needs to be even stronger evidence to establish a new genus.

Speciation

Some researchers think that new species are the result of gradual change involving the whole population. This interpretation of speciation is called 'phyletic gradualism' (Figure 6), and the form of speciation associated with it is known as 'anagenesis'. Others see speciation as the result of bursts of rapid evolutionary change concentrated in a geographically restricted subset of the population. This interpretation of speciation is called the 'punctuated equilibrium' model. In the latter model in the long intervals between the periods

of rapid evolutionary change there should be no sustained trends in the direction of morphological evolution, just ‘random walk’ fluctuations in morphology. Species formation in this mode is called ‘cladogenesis’, and the term ‘stasis’ is used to describe the periods of morphological stability between episodes of speciation. Almost all researchers now accept that most of the morphological change involved in evolution occurs at the time of speciation. In some circumstances speciation may be due to quite large-scale changes in the genotype brought about by rearrangements in the chromosomes. Researchers have suggested that this may have been the mechanism underlying speciation in higher primates. Some researchers have suggested that substantial changes in the palaeoenvironment brought about by long-term shifts in climate could cause a synchronous ‘turnover pulse’ of extinction and speciation in several mammal lineages.



6. The two main models for evolution: ‘phyletic gradualism’ and ‘punctuated equilibrium’.

Particularly intensive periods of species generation and diversification are called ‘adaptive radiations’. They tend to be associated with opportunities to exploit new environments, or when extinctions in other groups mean that adaptive opportunities become available in an existing environment. For reasons that are not well understood some lineages tend to generate more species than others. All species, including modern humans, will ultimately become extinct. What is at issue is whether extinctions are determined by the intrinsic properties of a species, or by extrinsic factors such as changes in the environment (e.g. a ‘turnover pulse’), or by a combination of the two. These competing hypotheses have been tested by comparing the fossil record with independent evidence

about changes in past climates, but establishing a ‘cause and effect’ relationship between speciation and long-term changes in climate is fraught with practical and logical difficulties.

Splitting and lumping

The interpretation of hominin taxonomy (aka taxonomic hypothesis) I favour recognizes a relatively large number of species. Researchers who subscribe to taxonomies that recognize larger numbers of species are called ‘splitters’: those who prefer to recognize fewer species are called ‘lumpers’ (Table 2). Both groups of researchers are looking at the same evidence, they just interpret it differently. Most disagreements among palaeoanthropologists about how many species to recognize in the hominin fossil record are due to differences in how they interpret variation. Researchers who stress the importance of continuities within the fossil record generally opt for fewer species, whereas those who are more willing to recognize and stress discontinuities tend to recognize more species. However, when all is said and done, all taxonomies are hypotheses. If scientists explain their taxonomy, then other scientists can reinterpret the evidence in any way they choose, as long as everyone makes it clear which fossil specimens they are allocating to however many species they choose to recognize.

Table 2 Examples of ‘splitting’ and ‘lumping’ taxonomic hypotheses for the hominin fossil record

Informal group	Splitting taxonomy	Age (my)	Type specimen	Main fossil sites
Possible and probable hominins	*S. tchadensis*	7.2–6.8	TM 266–01–060–1	Toros-Menalla, Chad
	O. tugenensis	6.0	BAR 1000’00	Lukeino, Kenya
	Ar. ramidus s. s.	4.6–4.3	ARA-VP-6/1	Gona and Middle Awash, Ethiopia
	Ar. kadabba	6.3–5.2	ALA-VP-2/10	Middle Awash, Ethiopia
Archaic and transitional	*Au. anamensis*	4.2–3.9	KNM-KP 29281	Allia Bay and Kanapoi, Kenya

hominins

	Au. afarensis s. s.	3.7–3.0	LH 4	Belohdelie, Dikika, Fejej, Hadar, Maka, and White Sands, Ethiopia; Allia Bay, Tabarin, and West Turkana, Kenya
	K. platyops	3.5–3.3	KNM-WT 40000	West Turkana, Kenya
	Au. bahrelghazali	3.6–3.0	KT 12/H1	Bahr el ghazal, Chad
	Au. africanus	3.0–2.1	Taung 1	Gladysvale, Makapansgat [Mb 3 and 4], Sterkfontein [Mb 4], and Taung, South Africa
	Au. garhi	2.5	BOU-VP-12/130	Bouri, Ethiopia
	Au. sediba	2.0	MH1	Malapa, South Africa
	P. aethiopicus	2.7–2.3	Omo 18.18	Omo Shungura Formation, Ethiopia; West Turkana, Kenya
	P. boisei s. s.	2.3–1.3	OH 5	Konso and Omo Shungura Formation, Ethiopia; Chesowanja, Koobi Fora and West Turkana, Kenya; Malema, Malawi; Olduvai and Peninj (Natron), Tanzania
	P. robustus	2.0–1.0	TM 1517	Cooper's, Drimolen, Gondolin, Kromdraai [Mb 3], and Swartkrans [Mbs 1, 2, and 3], South Africa
	H. habilis s. s.	2.4–1.6	OH 7	Omo Shungura Formation, Ethiopia; Koobi Fora, Kenya; ?Sterkfontein and ?Swartkrans, South Africa; Olduvai, Tanzania
	H. rudolfensis	2.0–1.8	KNM-ER 1470	Koobi Fora, Kenya; Uraha, Malawi
Pre-modern *Homo*	*H. ergaster*	1.8–1.4	KNM-ER 992	Koobi Fora and West Turkana, Kenya; ? Dmanisi, Georgia
	H. erectus s. s.	1.8–0.2	Trinil 2	Many sites in the Old World e.g. Melka Kunturé, Ethiopia; Zhoukoudian, China; Sambungmacan, Sangiran, and Trinil, Indonesia; Olduvai, Tanzania
	H. naledi	0.25	DH1	Dinaledi and Lesedi Chambers, Rising Star Cave, South Africa
	H. floresiensis	0.095–0.060	LB1	Liang Bua, Flores, Indonesia

	H. antecessor	1.0–0.9	ATD6–5	Gran Dolina, Atapuerca, Spain
	H. heidelbergensis	0.7–0.1	Mauer 1	Many sites in Africa and Europe, e.g. Mauer, Germany; Boxgrove, England; Kabwe, Zambia
	H. neanderthalensis	0.2–0.03	Neanderthal 1	Many sites in Europe, the Near East, and Asia
Modern *Homo*	*H. sapiens s. s.*	0.2–pres	None designated	Many sites in the Old World and some in the New World

Informal group	Lumping taxonomy	Age (my)	Taxa included from the splitting taxonomy
Possible and probable hominins	*Ar. ramidus s. l.*	7.0–4.3	*Ar. ramidus s. s., Ar. kadabba, S. tchadensis, O. tugenensis*
Archaic and transitional hominins	*Au. afarensis s. l.*	4.2–3.0	*Au. afarensis s. s., Au. anamensis, Au. bahrelghazali, K. platyops*
	Au. africanus	3.0–2.1	*Au. africanus, Au. sediba*
	P. boisei s. l.	2.7–1.3	*P. boisei s. s., P. aethiopicus, Au. garhi*
	P. robustus	2.0–1.0	*P. robustus*
	H. habilis s. l.	2.4–1.6	*H. habilis s. s., H. rudolfensis*
Pre-modern *Homo*	*H. erectus s. l.*	1.9–0.06	*H. erectus s. s., H. ergaster, H. floresiensis*
Modern *Homo*	*H. sapiens s. l.*	1.0–present	*H. sapiens s. s., H. antecessor, H. heidelbergensis, H. neanderthalensis*

Note: The Denisovans are excluded because they are not a formal taxon.

Cladistic analysis

Once the taxonomy of a new discovery has been decided, researchers move on to the next stage. This involves using methods to work out how a fossil hominin taxon is related to modern humans and to other fossil hominin taxa. The

technical term ‘clade’ refers to all (no more and no less) of the organisms descended from a recent common ancestor. The smallest clade consists of just two taxa; the largest includes all living organisms. Cladistic, or phylogenetic, analysis sorts taxa according to the amount of morphology they share, but the morphology has to be of a particular kind. To be helpful for working out relationships among closely related species, the morphology used must be shared by two or more taxa, must be inherited from the most recent common ancestor of those taxa, and it must vary within the group under investigation, otherwise it cannot be used to break up that group into subgroups, or clades. For example, the features that make all higher primates mammals, such as the presence of nipples and warm blood, are no use for sorting out detailed relationships among the great apes. But to go to the other extreme, morphology only found in one species cannot be used to work out how that species is related to other taxa.

Two taxa that share specialized (aka derived) morphology are referred to as sister taxa, and that pair of sister taxa has its own sister taxon (e.g. *Gorilla* is the sister taxon of the *Pan*/*Homo* clade), and so on. The same relationships can be represented in writing by using sets of parentheses for each sister group (e.g. (((*Homo, Pan*) *Gorilla*) *Pongo*)). The branching diagram that reflects these relationships is called a cladogram.

Cladistic analysis works on the assumption that if members of two taxa share the same morphology, they must have inherited it from their most recent (aka common) ancestor. This assumption is often justified, but not always. We know that primates, including higher primates, have experienced convergent evolution, a process by which different lineages evolve similar morphology independently. The term homoplasy refers to similar morphology seen in two species that is not inherited from their most recent common ancestor. For example, it is likely that features such as thick tooth enamel, and locomotor behaviours like bipedal locomotion, evolved more than once in human evolution, thus making them candidates for homoplasies within the hominin clade.

Fossil DNA

The newest line of evidence for working out how hominin taxa are related relies on the extraction and analysis of DNA. In your family, closely related individuals such as brothers and sisters share more DNA than distant cousins do. It is the same for taxa. Two individuals within a taxon should, on average, share

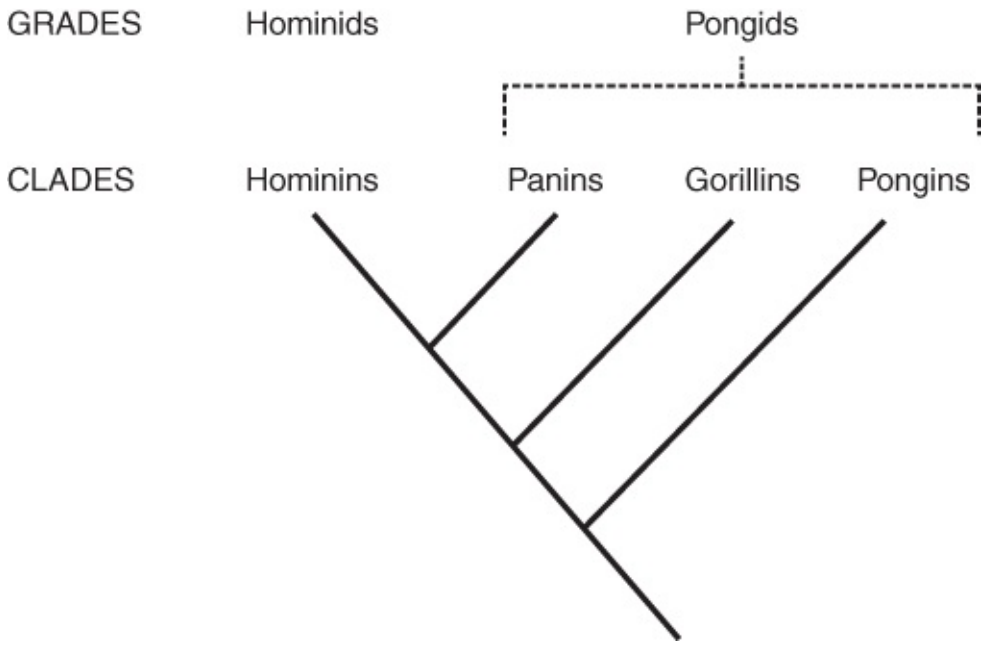
more DNA than two individuals drawn from different taxa. However, despite the importance of DNA in our lives, fossilization quickly causes nucleic acids to degrade. For example, in most circumstances, after 50,000 years only small amounts of DNA survive, and even this is broken into short fragments. A team led by Svante Pääbo, a molecular biologist from the Max Planck Institute for Evolutionary Anthropology at Leipzig, was the first to recover DNA from a fossil hominin, and I will consider fossil DNA evidence further in Chapters 7 and 8.

Researchers undertaking fossil DNA analysis must take particular care to prevent and detect contamination. When people handle fossils, they inevitably leave hair and skin cells on the fossil and these are a potent source of contamination. Scientists must make sure they are detecting DNA amplified from the fossil hominin and not DNA from other sources. In a study of cave bear fossils researchers detected more than twenty different modern human DNA sequences on a single cave bear fossil. Tens, if not hundreds, of people will have handled most hominin fossils, especially those found many years ago. Working out which of many DNA sequences recovered from a modern human fossil really belongs to that individual is a challenge. And the challenge of stitching small DNA fragments together to reconstruct a whole genome requires technical ingenuity and a great deal of computing power.

Grades

Homoplasy complicates attempts to sort early hominins into clades. An alternative is to sort hominin species into grades, a category that emphasizes what an animal does rather than what its phylogenetic relationships are. Sport Utility Vehicles are the equivalent of a grade, whereas all the cars produced by the Ford Motor Company, including its range of SUVs, are the equivalent of a clade. Grades may also be clades, but they are not necessarily so. For example, leaf-eating, or folivorous, monkeys are a grade, but they are not a clade because folivorous monkeys from the Old and New World are, respectively, just one component of much larger Old and New World monkey clades, and pongids are a grade but not a clade because the grouping excludes hominins (Figure 7). A clade comprises all the descendants of a common ancestor, not just some of them. Palaeoanthropologists are more likely to agree about grades than clades, but determining the branching pattern of the TOL is something that must be pursued, even if the results are controversial. I will refer to some of these

controversies in later chapters.



7. Comparison of the concepts of clades and grades as applied to living higher primates.

Function and behaviour

In addition to classifying fossils and arranging them in a cladogram and then a phylogeny, palaeoanthropologists also use the fossil record to work out how an extinct species functioned and behaved. Researchers try to learn as much about an extinct animal as they would expect to know about a living one. What did it eat? How did it move around? Did it live in social groups, or was it solitary? Palaeoanthropologists attempt to answer these questions by looking at as many lines of evidence as they can to infer function and behaviour, then they combine this information with evidence about the palaeohabitat to generate hypotheses about how that species was using its environment. The problem is that they collect this information over a much longer time-scale than is the case when researchers study living taxa. Accounting for these time-scale differences is an ongoing challenge.

Functional morphology means looking at a bone or tooth and considering what functions it performs best and most frequently. For example, you would only need curved finger bones if you spent a lot of time holding onto branches, so

curved finger bones are a sign that climbing was a part of that animal's locomotor repertoire. The shapes of finger joints and the length of the fingers and thumb also provide clues about how well early hominins could have gripped objects. Holding the shaft of a hammer needs a power grip, whereas the ability to hold and use a small, sharp stone tool uses a precision grip and a different combination of arm, forearm, and hand muscles. Similarly, the thighbones of animals that bear all their weight on their hind limbs are differently shaped from those whose weight is distributed across all four limbs.

Diet is a crucial aspect of an organism's biology. Those who study living animals can observe and record exactly where and when an individual forages, what food items are available, and which of those items an individual chooses to eat, but how do you reconstruct the diet of an extinct organism for which none of this can be observed? Traditionally this would have been done by looking at the part of the body that comes into contact with the food we ingest—the teeth. It is a palaeontological truism that the shapes of tooth crowns carry a strong dietary signal. Blade-like postcanine teeth are for slicing meat or grass, and teeth with flatter crowns are for breaking open fruit items. But there are several problems with using tooth morphology to reconstruct diet. First, there is good evidence that the shape of tooth crowns is conservative in the sense that there is a substantial lag between a change in dietary strategy and changes in tooth morphology. Second, there are many animals whose diet is not restricted to a single food item, so their dietary signal is more ambiguous. Third, we know from living animals that when their preferred foods are scarce local populations adapt by eating food items their teeth are not obviously suited to process. Lastly, tooth shape seems to be a better guide to the physical properties of food items (e.g. does the food item fracture or tear?) than it is to the type of food ingested. Given these problems researchers have explored other ways to reconstruct the diet of fossil hominins.

Scratching the surface

First, they looked at the rate and manner in which teeth wear. Wear, which is a loss of any tooth volume, large or small, occurs when teeth come into contact with items that are harder than the enamel covering the surface of a tooth. Minerals in plants and extraneous grit are two of the major drivers of tooth wear. Gross tooth wear leading to flattening of the cups and exposure of the underlying enamel is obvious to the naked eye, but gross wear is the end result of many

episodes of microwear. Researchers have also exploited how the chemistry of the hard tissues, specifically the proportion of isotopes of carbon and oxygen in enamel, can be used to reconstruct diet.

One would have thought that with all of these methods in play, by now we would have a pretty good idea about the diets of extinct hominins. But that is not the case. One of the main reasons hominin diets are still a matter of controversy is that the methods described above operate at very different temporal scales. At one end is tooth shape, the super-tanker of dietary signals, which is slow to react to changes in the availability of food items. At the other end is microwear, which reflects the physical properties of the foods eaten by that individual in the few weeks before its death. So, for microwear to be a useful indicator we must assume that what was being eaten immediately prior to the end of the animal's life reflects its diet in the longer term. Tooth chemistry lies between these two temporal extremes in the sense that, depending on how the enamel is sampled, the stable isotopes in enamel taken from a particular tooth will sample more, or less, of the few hundred days it takes to form the enamel cap of a hominin tooth crown. Another reason that diet is so difficult to reconstruct from the size and shape of teeth is that it is not clear what drives selection on tooth morphology. Is it to cope with the foods that members of a species prefer to eat, or is it to allow them to process foods they fall back on during periods of food scarcity?

Comparable complications apply to attempts to reconstruct social behaviour, locomotion, and dexterity. Reconstructing the behaviour of extinct animals is difficult, and it is especially challenging to do this for closely related fossil hominins.

Gaps and biases in the hominin fossil record

Over many decades palaeoanthropologists have accumulated hominin fossils from thousands of individuals going back to between 8 and 6 ma. While this number looks impressive, the majority are concentrated in the later part of the hominin fossil record. Besides this temporal bias, the hominin fossil record has other biases and weaknesses. The science of working out these biases, and trying to correct for them, is called taphonomy. Whereas some of the hardest parts of the skeleton such as the teeth and the mandible are well represented in the hominin fossil record, the postcranial skeleton, that is the vertebral column, the ribs and the limbs, and particularly the vertebral column and the hands and feet

are poorly represented. The relative durability of different parts of the skeleton (e.g. mandibles are generally heavier and are made of denser bone than vertebrae) is partly responsible for the differential preservation of body parts. Lighter bones like vertebrae are likely to be swept along in the floods that follow torrential rain, and then carried out into a lake, where they will be mixed in with the fossilized bones of fish and crocodiles. In contrast, heavier bones like jaws, and teeth, which are especially dense, will fall to the bottom of the floodwaters, get trapped in the stones on the bed of the stream or river, and will be preserved with the bones and teeth of other terrestrial animals.

Another factor influencing differential preservation is which parts of the carcass predators find most tempting. Leopards like to chew on the hands and feet of monkeys, and if extinct large carnivores had similar preferences, then these parts of hominins would be in short supply as fossils. Thus, we know less about the hands and feet of fossil hominins than we do about their teeth. Body size also has a significant influence on whether a taxon is likely to have a fossil record. Large bodied mammals are more likely to be fossilized than small ones, and larger individuals within a taxon have a greater likelihood of being fossilized than smaller individuals. There is every reason to think that these same biases affect the hominin fossil record.

Some environments are more likely to lead to fossilization and subsequent discovery than others. Thus, we cannot assume that more fossil evidence from a particular period or place means that more individuals were present at that time, or in that place. It may just be that the circumstances at one period of time, or at one location, were more favourable for fossilization than they were at other times, or in other places. Likewise, the absence of hominin fossil evidence at a particular time or place does not have the same implication as its presence. As the saying goes, ‘absence of evidence is not evidence of absence’. Similar logic suggests that taxa are likely to have arisen before they first appear in the fossil record, and they are likely to have survived beyond the time of their most recent appearance in the fossil record. Thus, the first appearance datum (or FAD) and the last appearance datum (or LAD) of taxa in the hominin fossil record are likely to be conservative statements about the times of origin and extinction of a hominin species.

The same reservations apply to the geographical distribution of fossil sites. Hominins almost certainly lived in more locations than there are fossil sites.

Early hominin sites in Africa cover less than 3 per cent of the surface area of that continent, and we should not fall into the trap of thinking that all of the significant events in hominin evolution occurred in the locations where fossils are exposed by natural erosion or by mining activity. The drunk looks for their keys under the lamp-post because that is the only place with enough light to see, not because it was where they dropped them! Our equivalent of the lamp-post is places where sediments are exposed. The best examples are the East African Rift Valley where cracks in the earth's crust have exposed fossil-bearing sediments, or the caves in southern Africa where miners in search of lime have removed or exposed fossil-bearing sediments.

Environments in the past were often different from the ones we see now: parts of the world we now think of as being unattractive habitats were not necessarily that way in the past, and vice versa. Lastly, not all environments are conducive to preserving bones and teeth. Some soils are so acidic that bones and teeth rarely survive. For a long time, it was assumed that fossils would never be found in forested palaeoenvironments because of the high levels of humic acid. This turned out to be a fallacy, but there are sites where archaeologists would have expected to see stone tools and bones together, and where they only find stone tools: the bones and teeth were dissolved before they could be fossilized.

Chapter 5

Early hominins: possible and probable

Eight million years ago much of Africa was covered with thick forests interspersed with rivers and lakes, and most primates were tree-dwellers. During the period from 8 to 5 mya the earth experienced the beginning of a long-term drying and cooling trend. The drying occurred because an increasing share of the earth's moisture was locked up in ice sheets that began to extend further and further away from the north and south poles. Temperatures fell, even in Africa.

Hominin evolution likely began in Africa at the time of these climatic changes. Due to the increasing dryness, forests were replaced with open woodland, and areas of grassland began to appear. We tend to think that the grassland-adapted animals we associate with the modern-day African savannahs, such as antelopes and zebra, have always been there, but they, and the savannah they inhabit, are relatively recent phenomena. The common ancestor of modern humans and living chimpanzees/bonobos probably lived in the forests. Some of its descendants, though, began to adapt to life on the ground in more open conditions.

The fossil evidence for what may be the earliest hominins is found in sites which the other fossil and chemical evidence suggests was a mosaic of habitats—woodland, grassland, lakes, and gallery forests along rivers: no convincing early hominin fossils have been found in an exclusively forested environment. This suggests that if these fossils do belong to early hominins, then the earliest hominins were adapted to both tree living and ground living. Trees would have provided fruit, nesting sites, and protection from predators. Patches of grassland would have provided new food sources such as tubers, while lakes and rivers would have offered fish and molluscs. Although some early hominin fossils are

found in caves it is unlikely that early hominins lived in the caves. Without reliable sources of heat, light, food, and water caves do not make attractive habitats for primates.

How to tell an early hominin from an early panin

There are many differences between the skeletons of living chimpanzees and bonobos and modern humans, particularly in the brain case, face, and base of the cranium, teeth, hand, pelvis, knee, and the foot. There are also other important contrasts between the skeletons of modern humans and chimpanzees/bonobos, such as the rates at which they develop and mature, and the relative lengths of the limbs, but you need better-preserved skeletons than are usually seen in the early phases of the hominin fossil record to be able to detect these types of differences.

However, all the differences listed in Table 3 are differences between the living members of the panin and hominin clades or lineages. Scientists searching in 8 to 6 my-old sediments for the earliest hominins must consider a different question: what were the differences between the first hominins and the first panins? These are likely to have been much more subtle than the differences we see between contemporary hominins and panins. Although the *Pan*/*Homo* common ancestor was neither like a living chimpanzee/bonobo nor like a modern human, most researchers agree that it was probably more like the former than the latter. The logic goes like this. Genetic and morphological evidence suggests that gorillas are the living animals most closely related to chimpanzees/bonobos and modern humans. Gorillas share more morphology with chimpanzees/bonobos than they do with modern humans (gorilla bones are more likely to be confused with the bones and teeth of chimpanzees/bonobos than with the bones and teeth of a modern human). Therefore, the common ancestor of chimpanzees and bonobos and modern humans was probably more like a living panin than a modern human. Its skeleton would most likely show evidence of being adapted for life in the trees. For example, its fingers would have been curved to enable it to grasp branches, and its limbs would have been adapted to walk both on all fours, and on the hind limbs alone. Its face would have been snout-like, not flat like that of modern humans, and its elongated jaws would have had relatively modest-sized chewing teeth, prominent canines, and large incisor teeth.

Table 3 Major differences between the skeletons of a modern human and a living chimpanzee

	Modern Human	Chimpanzee
Forehead	Steep	Low
Face	Flat	Projecting
Cranial vault	Widest higher up	Widest at the base
Brain size	Large	Small
Canine teeth	Small	Large
Base of skull	Angled	Straighter
Thorax	Barrel-shaped	Conical
Lumbar vertebrae	5	3–4
Limb bones	Straight	Curved
Limb proportions	Lower limb long	Lower limb short
Wrist	Less mobile	More mobile
Hand	Cup-shaped and long thumb	Flat, long fingers, and short thumb
Foot	Arched and big toe straight	Flat and big toe angled
Pelvis	Neonatal head is a tight fit	Neonatal head has ++ room
Development—bones and teeth	Slow	Fast

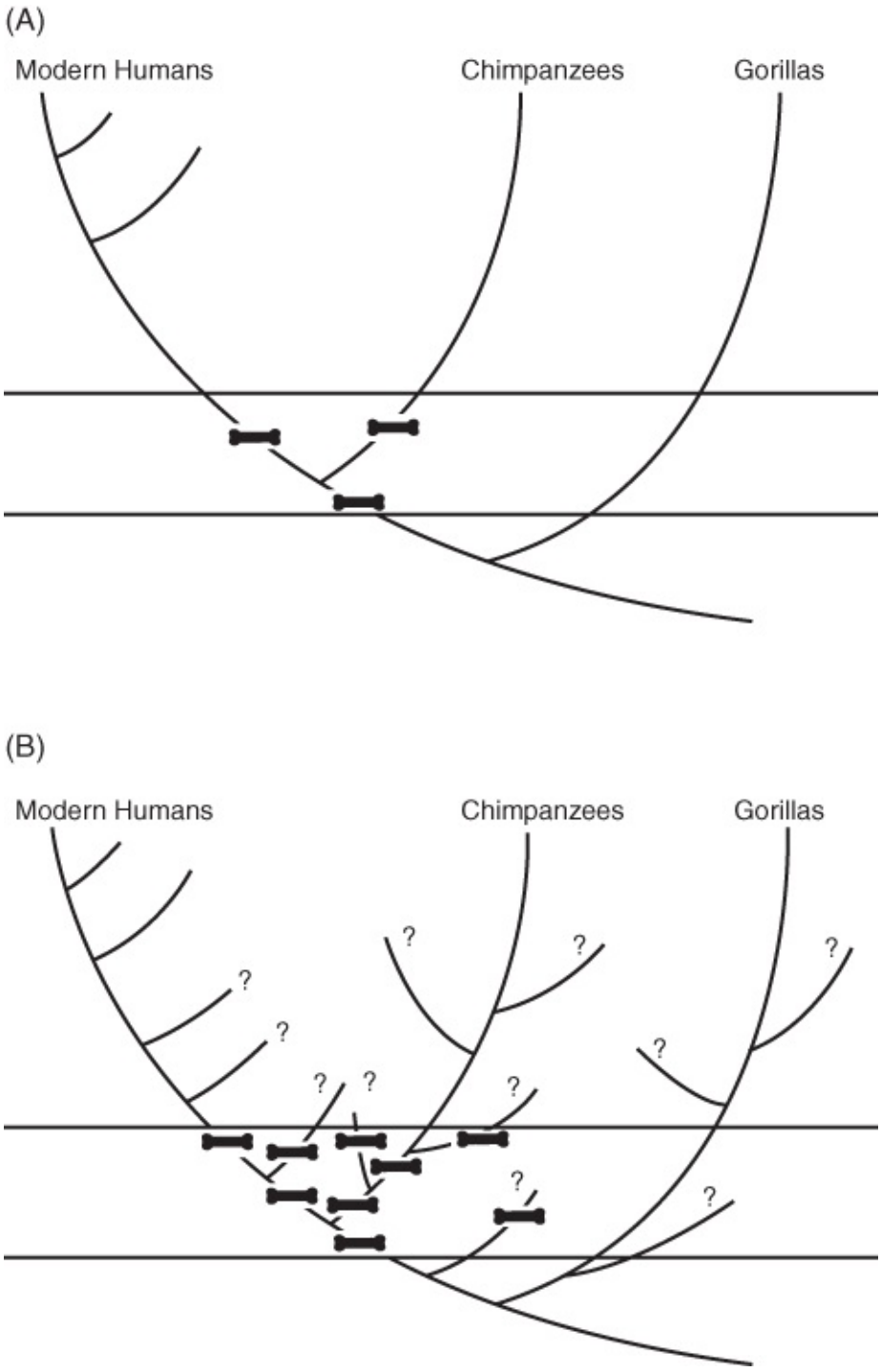
The first hominins

Researchers surmise that probably relatively little changed between the hominin and panin common ancestor and the earliest panins. But in what ways would the earliest hominins have differed from that common ancestor? Researchers predict that, unlike the earliest panins, the earliest hominins would most likely have had smaller canine teeth, larger chewing teeth, and stronger lower jaws. There would also have been changes in the skull and skeleton linked with more time spent upright and with a greater dependence on the hind limbs for bipedal walking. These changes probably included a forward shift of the foramen magnum, the

place where the brain connects with the spinal cord, so that the head is better balanced on a body with a more vertical trunk, as well as wider hips, straighter knees, and a more stable foot.

Simplicity versus complexity

Splitters and lumpers have very different models in mind for the early stages of hominin evolution (Figure 8). A lumper would entertain only three possibilities for an 8–6 my-old higher primate that was more closely related to modern humans and chimpanzees/bonobos than to gorillas. It would either belong to the common ancestor of hominins and panins, or be a primitive panin ancestral to living chimpanzees/bonobos, or a primitive hominin ancestral to modern humans. A splitter, especially one like me who considers it likely that the first hominins and panins were just two of a number of closely related lineages, would consider other options for the same 8–6 my-old higher primate. These options include belonging to an extinct clade that is the sister taxon of the *Pan/Homo* clade, or to one, or more, extinct panin and hominin subclades.



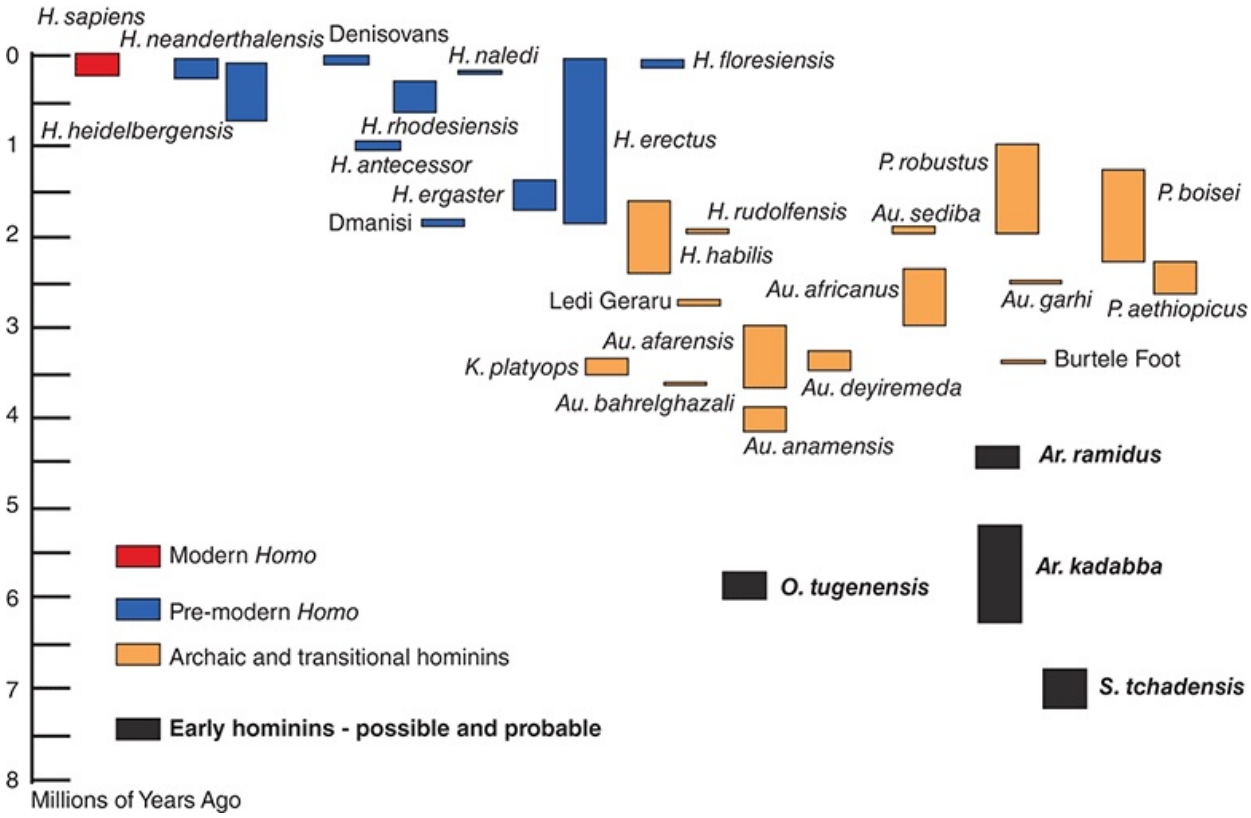
8. ‘Lumping/simple’ (A) and ‘splitting/complex’ (B) interpretations of the higher primate twig of the Tree of Life.

Splitters would also expect to find evidence of homoplasies in this 8–6 my period. Homoplasy complicates the task of sorting real hominins from taxa that

may have independently evolved, and would thus share, one or more of the features researchers traditionally assume are only seen in hominins. Some researchers, and I am one of them, think we need much better evidence than we at present have to be confident we can sort the earliest hominins from non-hominins with any degree of reliability.

Contenders for the title of the earliest hominin

Researchers have put forward four species, spread across three genera, as contenders for the earliest hominin (Figure 9). One of the main problems in determining whether or not the fossils are actually primitive hominins is the small amount of fossil evidence we have for them. The fossil evidence for all four could fit comfortably in a supermarket trolley, and there would still be plenty of room to spare. Furthermore, the supermarket trolley does not necessarily contain the same evidence for each of the four contenders. Currently there is a distorted cranium, parts of several lower jaws and teeth of one, mostly teeth and some hand and foot bones of a second, some teeth and parts of the thigh bones of a third, and an associated skeleton, cranial fragments, lower jaws, many teeth, but few useful limb bones, of the fourth.



9. Time chart of ‘possible’ and ‘probable’ early hominin species.

The oldest of the four contenders is *Sahelanthropus tchadensis*, known from fossils discovered by Michel Brunet and his team from 2001 onwards. It has been dated using biochronology and a relatively new isotope method to between 7.2 and 6.8 mya.

Sahelanthropus tchadensis is an important taxon for several reasons. First, it was found at a site called Toros-Menalla in Chad, in west central Africa. This region, which today is on the southern fringes of the Sahara Desert, was very different around 7 mya. The geological and palaeontological evidence suggests that *S. tchadensis* lived in a complex habitat of lakes, grassy woodland, and rivers bordered by forests. We know this because geologists looking at the rocks can identify traces of sediments that could only have been laid down on a lakeshore, and because vertebrates found at the site include freshwater fish and representatives of forest dwelling, woodland, and grazing animals. Second, the evidence for *S. tchadensis* includes a remarkably complete, but distorted, cranium that has been ‘straightened out’ using virtual anthropology techniques,

which allows it to be compared more meaningfully with other later hominins and with chimpanzees.

The brain of *S. tchadensis* is chimp-sized, but the upper part of its face has brow ridges reminiscent of those seen in hominins much less than half its geological age. The mandible is thicker than the jaws of living chimpanzees, and the canines are worn down only at the tip and not also on the sides as they are in chimpanzees. Are the brow ridges, the robust lower jaw bone, and the canines that wear down only at the tip sufficient evidence to be sure that *S. tchadensis* is a primitive hominin, and not the common ancestor of chimpanzees/bonobos and modern humans, or a member of the panin lineage, or a member of another, extinct, clade? It is unfortunate that limb bones found with other *S. tchadensis* fossils have been kept under wraps for years: when properly analysed they should help clarify the relationships of *S. tchadensis.*

If *S. tchadensis* is an early hominin, then the location of the site in west central Africa means early hominins occupied much more of the African continent than just eastern and southern Africa.

The second oldest potential primitive hominin species is *Orrorin tugenensis*, the name given to fossils found in sediments in the Tugen Hills of northern Kenya. Its age has been determined using potassium/argon dating to around 6 my. One specimen, a lower molar tooth crown, was discovered in 1974; the remaining twelve specimens have been discovered since 2000.

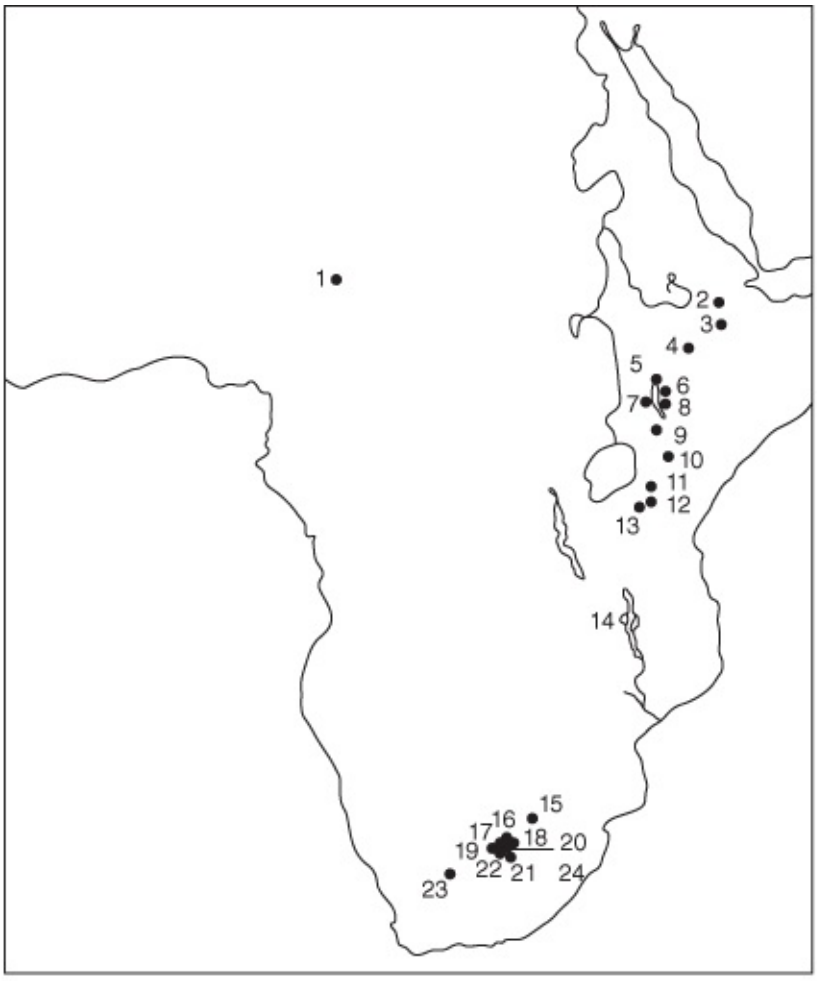
The evidence for *Orrorin tugenensis* is still frustratingly fragmentary. Its discoverers, Brigitte Senut and Martin Pickford, two palaeoanthropologists based at the Collège de France in Paris, base their conclusion that *O. tugenensis* is a hominin on dental and postcranial evidence. Senut and Pickford claim that the enamel covering the molar and premolar teeth of *O. tugenensis* is much thicker than the enamel of panins. They also claim that the bone surrounding the neck of the thigh bone, just below the hip joint, is preferentially thickened on the top and bottom, as is the case in undoubted bipedal hominins. This contrasts with apes, which have equally thick bone all around the neck.

Critics of the view that these fossils belong to an early hominin make three points. First, they say that the morphology of the *O. tugenensis* femur is not as clear as its discoverers make out. Secondly, they claim that it is only an

assumption that thick enamel is confined to the hominin clade. Thirdly, they suggest that aside from the thickness of the enamel the preserved tooth crowns of *O. tugenensis* are otherwise ‘ape-like’.

Until we have more evidence about *O. tugenensis*, it is best to treat it as a creature closely related to the common ancestor of panins and hominins: to my mind there is not enough evidence to be sure it is a hominin.

The other two collections of fossils that might be from a primitive early hominin are both included in the same genus, *Ardipithecus*. The temporally older fossil collection, which comes from the Middle Awash region of Ethiopia and dates to 5.7–5.2 mya, is assigned to *Ardipithecus kadabba* (Figure 10). The fossils of *Ar. kadabba* include a mandible, teeth, and some postcranial bones. Many aspects of the fossil evidence, such as the tall, pointed, upper canines, resemble chimpanzees. Little of the morphology of the fossils in this collection resembles that of the archaic hominins discussed in Chapter 6. The case for regarding *Ar. kadabba* as a hominin is not a strong one. Researchers decided to establish a second species of *Ardipithecus* for this material because its discoverers thought its canines were more ape-like than those of the previously discovered, but temporally later, *Ardipithecus ramidus*.



1 Koro Toro and Toros-Menalla
Au. bahrelghazali, S. tchadensis
2 Hadar *Au. afarensis*
3 Middle Awash/Gona *Au. afarensis*
Ar. kadabba, Ar. ramidus,
Au. garhi
4 Konso *P. boisei*
5 Omo *Au. afarensis, P. aethiopicus,*
P. boisei
6 Koobi Fora *P. boisei ?Au. afarensis*
7 West Turkana
P. aethiopicus, P. boisei, K. platyops
8 Allia Bay *Au. anamensis*
9 Kanapoi *Au. anamensis*
10 Lukeino *O. tugenensis*
11 Peninj *P. boisei*
12 Olduvai Gorge *P. boisei*
13 Laetoli *Au. afarensis*
14 Malema *P. boisei*
15 Makapansgat *Au. africanus*
16 Gondolin *P. robustus*
17 Kromdraai *P. robustus*
18 Drimolen *P. robustus*
19 Sterkfontein *Au. africanus*
20 Swartkrans *P. robustus*
21 Gladysvale *Au. africanus*
22 Cooper's *P. robustus*
23 Taung *Au. africanus*
24 Malapa *Au. sediba*

10. Map of Africa showing the main 'early' and 'archaic' hominin fossil sites.

The fossil evidence of *Ar. ramidus* comes from the Middle Awash and Gona regions of Ethiopia: the earliest evidence is from around 4.5 mya and it may have persisted to less than 4 mya. The initial evidence from Aramis in the Middle Awash consisted of teeth, parts of several jaws, some hand and foot bones, and part of the underside of a cranium. Subsequently more fossils were found at Gona, and later still the discovery of an impressive associated skeleton from Aramis, plus many other teeth, was announced.

The discoverers of the Aramis evidence for *Ar. ramidus* suggest that the location of the foramen magnum, the opening for the spinal cord on the underside of the cranium, indicates that *Ar. ramidus* was more upright than is the case in the living apes. The joint for the big toe is ape-like, so its discoverers suggest that it combined climbing with walking bipedally on large branches. The thin enamel of *Ar. ramidus* suggests that its diet was closer to that of chimpanzees/bonobos than to the diets of undoubted early hominins, an interpretation supported by measurements of the stable-isotopes in its enamel. It has been claimed that the remains of the animals and the plants found with *Ar. ramidus* point conclusively to a woodland habitat, but others have drawn very different conclusions, suggesting that evidence from stable isotopes recovered from soils is consistent with a more open habitat.

The strongest evidence for linking *Ar. ramidus* with hominins is the position of the foramen magnum, which is further forward than in chimpanzees, but closer to its location in bonobos. Of the four potential hominins two of them, *S. tchadensis* and *Ar. ramidus*, have the best, but different, cases for being included in the hominin clade.

Whereas ‘splitters’ recognize the four collections of fossils as separate taxa, ‘lumpers’ take the view that all four taxa are either different species within a single genus, *Ardipithecus*, or perhaps they sample just one species, *Ar. ramidus sensu lato* (i.e. interpreted loosely).

Chimpanzees and bonobos have almost no fossil record

If modern humans and chimpanzees/bonobos are each other’s closest living relative, then both are parts of evolving lineages that have been separate for the same length of time. As we will see in Chapters 6–8, modern humans have a substantial fossil record, much better than that for many other mammals. But the

fossil record for chimpanzees and bonobos is virtually non-existent. In stark contrast to the evidence covered in this book, the *only* panin fossil evidence in the last 8 my is a handful of 500 ky-old isolated teeth from a site called Baringo, in Kenya.

In the past the lack of fossil evidence of panins has been 'explained' because it was assumed that the ancestors of modern chimpanzees and bonobos also lived in the forest, and because there is little chance of erosion in the forest, then there are no exposures, and thus fewer places where fossils could be uncovered by erosion. Others suggested that high levels of humic acid in the soils of forests dissolve bones before they can be fossilized. Neither of these explanations is wholly convincing. Fossils are difficult to find in forests, but they are there. They just do not happen to include any fossil evidence belonging to panins. Of course, some of the fossils assigned to *Ardipithecus, Orrorin*, and to *Sahelanthropus* could be panins, but no one has been anxious to forgo the chance of being the discoverer of the earliest hominin in favour of being the discoverer of the earliest panin, or of a hitherto unrecognized extinct lineage more closely related to modern humans than chimpanzees and bonobos! This is strange, because from the point of view of the wider biological interest it would be much more interesting to find fossil evidence of an early panin ancestor, or evidence of a hitherto unrecognized extinct lineage, rather than fossil evidence of yet another early hominin. If we could find out what an early panin looked like, it would mean that researchers would have a better chance of identifying 'real' hominins. There are other reasons why it would be helpful if researchers found an early panin. At the moment researchers assume that the common ancestor of hominins and panins, and early panins, were panin-like. But it would be much better to *know* what early panins were like rather than having to make informed guesses about them, and this information would also help the researchers who are trying to identify homoplasies in the *Pan/Homo* clade.

Chapter 6

Archaic and transitional hominins

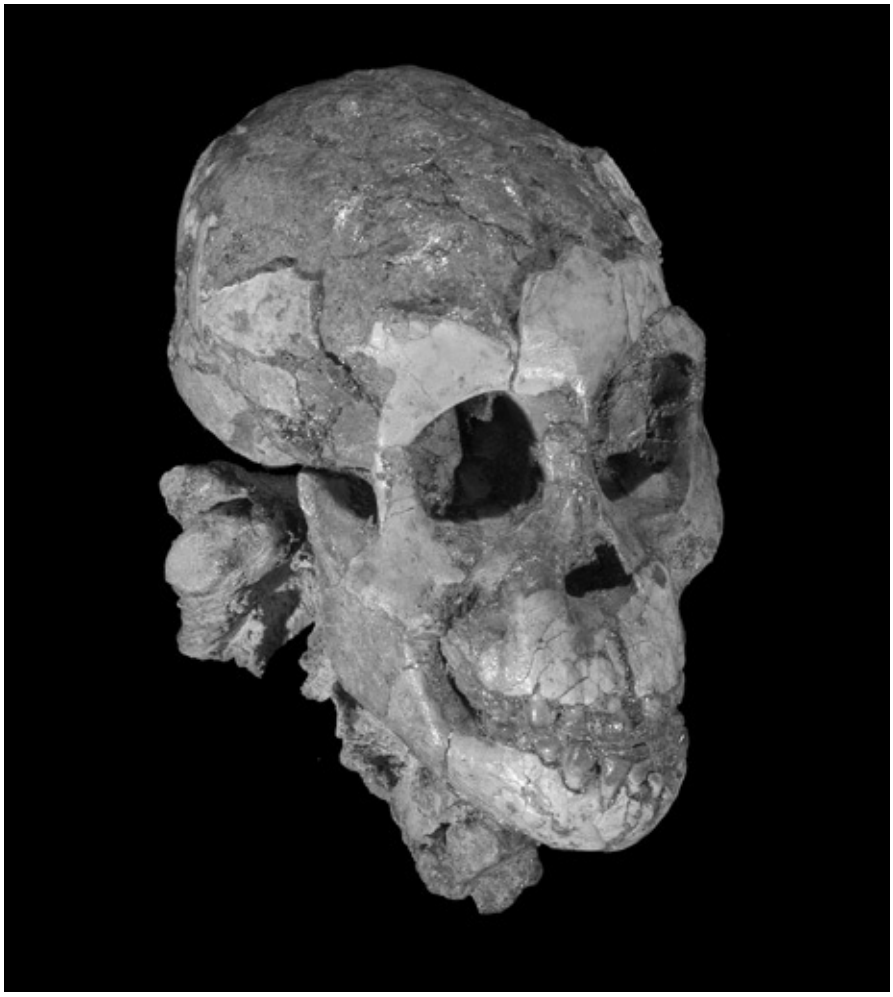
In this chapter I deal with creatures that are almost certainly hominins. They share more of their morphology with modern humans than they do with chimpanzees and bonobos, yet they do not show the changes in jaw and tooth size and in body size and shape that characterize hominin species we are more comfortable including within our own genus *Homo*. So, I call them ‘archaic’ hominins. At the end of the chapter I also consider a group of hominins that seem to be part archaic hominin, and part *Homo*: I call these ‘transitional’ hominins.

Archaic hominins from eastern Africa

Half a million years later in geological time than *Ar. ramidus* we begin to see signs of an undoubted hominin, *Australopithecus afarensis*, with a much more comprehensive fossil record than any of the potential primitive hominins discussed in Chapter 5.

This species was established in 1978 to accommodate fossils recovered from Laetoli in Tanzania and from the site of Hadar in the Afar region of Ethiopia—see below for why the genus is called *Australopithecus*. The evidence for *Au. afarensis* consists of several supermarket trolleys-worth of fossils, including two well-preserved skulls, several well-preserved crania, more than thirty lower jaws, lots of teeth, and sufficient limb bones to be able to generate reliable estimates of its size and body weight. Almost all of the evidence comes from sites in Ethiopia, with Hadar contributing the lion’s share.

The Hadar part of the collection includes the famous ‘Lucy’, which made the headlines because it was the first time researchers had recovered such a well-preserved early hominin. When it can be shown that a collection of fossils very likely comes from the same individual (aka an associated skeleton) researchers can match jaws and teeth with limb bones, and arm bones with leg bones, which means they can make more accurate estimates of stature, body weight, and the relative length of the limbs. Zeray Alemseged and his team also recovered a remarkably well-preserved associated skeleton of an infant from the site of Dikika (Figure 11), and at 3.3 my it is a little older than Lucy.



11. The associated skeleton of the child from Dikika.

The picture of *Au. afarensis* that emerges is of a hominin weighing from 35kg (75 lb) to 55kg (125 lb). Its brain volume was between 400 and 500 cc, larger

than the average brain size of a chimpanzee and substantially larger than the 300 to 325 cc estimates for the brain size of *S. tchadensis* and *Ar. ramidus*. However, when brain size is related to the size of the body (blue whales have larger brains than modern humans, but they weigh more than we do) the brain of *Au. afarensis* is only a little larger than that of an equivalent-sized chimpanzee. Its incisor teeth (the four teeth in each jaw you see when people smile) are much smaller than those of chimpanzees, but the chewing teeth (the two premolars and three molars on each side that are at the back of the jaw—you need to make someone laugh out loud to see them) of *Au. afarensis* are larger than those of chimps. This suggests that its diet included more hard-to-chew items than does the diet of chimpanzees. The shape and size of the pelvis and lower limb remains suggest that although *Au. afarensis* was capable of walking bipedally it was maybe not adapted to travel long distances bipedally. Its upper limb bones suggest that it was a more capable climber than modern humans.

The oldest preserved trails of hominin footprints, and the oldest hominin trace fossils, are the 3.66 my-old footprint trails discovered at Laetoli, Tanzania, and excavated by Mary Leakey. The hominin footprints are just one of many trails made by large and small animals, ranging in size from horses to hares. The foot- and hoof-prints are well preserved because the animals happened to walk across a flat area where a layer of volcanic ash had recently been moistened by a rainstorm. The type of fine volcanic ash at Laetoli has a chemical content that makes it behave like cement, so when the sun dried out the layer it became rock hard: the process is much like the one used outside a Hollywood restaurant to preserve the hand- and footprints of film stars. These trace fossils provide graphic evidence that a contemporary early hominin, presumably *Au. afarensis*, was capable of walking bipedally. The size of the footprints and the length of the stride are consistent with estimates of stature made using the limb bones of *Au. afarensis*, suggesting that the standing height of individuals was between 3 and 4 feet.

Fossils from a site in Kenya called Kanapoi that date from 4.2–3.9 mya belong to a different hominin, *Australopithecus anamensis*, that could well be ancestral to *Au. afarensis*. The canines of *Au. anamensis* are more chimpanzee-like than those of *Au. afarensis*, yet the chewing teeth are very different from those of chimpanzees. Hominin fossils collected at Bahr el ghazal in Chad in 1995, not far from the site where *S. tchadensis* was found subsequently, have been assigned to *Australopithecus bahrelghazali*, but some researchers claim,

probably correctly, that these remains do not belong to a separate hominin species, but to a geographical variant of *Au. afarensis*.

Two other discoveries fall within the time range of *Au. afarensis.* In 2009 part of a foot was recovered from 3.4 my-old sediments at Burtele in the Woranso-Mille study area in Ethiopia. Its ape-like, opposable, big toe resembles the foot of *Ar. ramidus*, and distinguishes it from what we know about the foot of *Au. afarensis.*

The other discovery is a collection of fossils from near to Burtele that has been assigned to a new species, *Australopithecus deyiremeda*. Its discoverers claim that the tooth enamel and the part of the mandible containing the roots of the teeth are both thicker than they are in *Au. afarensis.* If these suggested differences are confirmed by future discoveries, it could be that the diet of the new species was different from that of *Au. afarensis.*

The 2.5 my-old *Australopithecus garhi*, found at Bouri, in the Middle Awash, is 'odd' in several ways. Limb bones found with it suggest it was a biped, yet its chewing teeth are a good deal larger than those of the other three eastern African australopiths described above, and they are nearly as large as the teeth of *Paranthropus boisei* (see below). Although no stone tools have been found with the *Au. garhi* fossils, animal bones found close by show tell-tale signs that flesh had been removed using a sharp-edged tool. The evidence of 2.5 my-old cut-marked bone from Bouri is claimed to be the earliest undisputed evidence that hominins were deliberately removing flesh, but if the grooves on bones from Dikika are cut-marks, as has been claimed, then these would push evidence for the deliberate defleshing of animal carcasses back to 3.3 mya.

Archaic hominins from southern Africa

All the australopith taxa introduced thus far have been found at sites in eastern or central Africa. Those regions are not necessarily the only parts of Africa occupied by the australopiths, nor are the localities within those regions necessarily where the hominins spent most of their time: they were simply places on the landscape where, for one reason or another, one or more hominin bones had accumulated. Maybe they were transported there by the run-off from a rainstorm, or the site may have been close to the food cache or the lair of a predator. Most of the sites have been dated by applying isotope-dating methods to volcanic ash either in the same horizon as the hominin fossil evidence is likely

to have come from, or in layers above and below the fossil-rich layer.

In 1924, nearly fifty years before the discovery of the remains belonging to *Au. afarensis*, the skull of a hominin child was unearthed in southern Africa, but the context was *very* different. It was discovered when a small cave was exposed during mining operations at the Buxton Limeworks at Taung. Most of the fossils from the cave were extinct baboons, which were being shipped to Professor Raymond Dart at the University of the Witwatersrand in Johannesburg because of his interest in the evolution of the brain. Mixed in with the true fossils recovered from Taung were natural endocasts, a rare form of trace fossil. Although natural endocasts look like brains, they consist of solidified sand and silt that has entered the brain cavity, where it faithfully preserves the impressions the brain leaves on the inside of the brain case. Dart realized that one of the skulls and endocasts was different; the brain was larger and the face was smaller than that of the baboons. It was more like an ape than a monkey, but its teeth were not ape-like. So Dart called the new taxon *Australopithecus africanus*, which means literally the 'southern ape of Africa'.

When Dart wrote about his discovery in *Nature* in 1925, he received a frosty reception. Most researchers were either ignorant of, or had forgotten, Darwin's prediction about Africa being the origin of humankind. However, Dart managed to recruit a distinguished ally, the palaeontologist Robert Broom, who had made a name for himself by collecting fossils of mammal-like reptiles. Broom was so convinced that Dart had found an important link between our ape ancestors and modern humans that he started to look for other caves that might contain the bones of *Au. africanus*, or of creatures like it.

Broom searched for more than a decade before a second hominin-bearing cave site, Sterkfontein, was discovered. It contained remains that scientists now interpret as belonging to the same species as the Taung child. Hominins were discovered at two more caves, Kromdraai and Swartkrans, but their chewing teeth and jaws were bigger than those of *Au. africanus*, so they were allocated to a different genus and species, *Paranthropus* (which means 'beside Man') *robustus*. Its slightly larger chewing teeth just about put it into the 'megadont archaic hominin' category. Hominin fossils found at other southern African cave sites (e.g. Drimolen and Makapansgat) belong, respectively, to *P. robustus* and *Au. africanus*. Two 2 my-old associated skeletons recovered from Malapa have been assigned to a separate species, *Australopithecus sediba.* Their discoverers

claim that because the two skeletons show a distinctive mix of features seen in *Au. africanus* and early *Homo* (see below), *Au. sediba* is distinct from the former. Much of the anatomy they preserve is not well known in either *Au. africanus* or early *Homo*, and my instinct is to be parsimonious and assume the fossils from Malapa sample a sub-population of *Au. africanus.*

Interpreting the southern African hominins

One problem with interpreting the hominins recovered from the southern African caves is that for a long time they could not be dated as reliably as those from sites in eastern Africa. With one exception, at the southern African cave sites early hominin fossils are mixed in with other animal bones in hardened rock and bone-laden cave fillings, or breccias, and until recently these sites were dated by comparing the remains of the mammals found in the caves with fossils found at sites in eastern Africa. On this evidence the ages of the *Au. africanus*-bearing breccias were estimated to be between 2.4 and 3 my. It turns out that the best way to date these sites is to date the flowstones that coincide with periods when the climate is relatively wet. Robyn Pickering discovered that they could be dated using a method that uses uranium and lead (U-Pb). Not unexpectedly she found the same-aged flowstones in different caves, which means that we have a much better idea of both the absolute and the relative ages of the fossils that are capped by flowstones. The U-Pb method suggests that most of the hominin fossils from Sterkfontein are between 2.0 and 2.6 my-old, whereas the hominins from Swartkrans are *c*.2 my-old. Pickering and her colleagues suggest that the hominin bones entered the caves when the climate was drier.

Our current understanding of *Au. africanus* is that its skeleton was much like that of *Au. afarensis*, but its chewing teeth were larger and its skull was not as ape-like. Its average brain volume is a little larger than that of *Au. afarensis*. The postcranial skeleton suggests that *Au. africanus* could walk bipedally, but would still be able to climb in trees. The other animal fossils and the plant remains found with *Au. africanus* suggest that its habitat was grassy woodland. As for *P. robustus*, its chewing teeth are larger, its face is broader, and its brain is slightly bigger than that of *Au. africanus*. Some researchers think that the locomotion of *P. robustus* may have differed from that of *Au. africanus*, but there is not enough evidence to be sure of this.

Neither *Au. africanus* nor *P. robustus* lived in the caves. Their bones were either

dropped into cave openings by leopards, or they belong to individuals who had either fallen into the caves or who had explored them and found them easier to enter than to leave.

Really megadont archaic hominins in eastern Africa

In 1959 Mary Leakey discovered a 1.9 my-old fragmented cranium at Olduvai Gorge in Tanzania. The OH 5 cranium has much larger chewing teeth and jaws than *P. robustus*, but its incisors and canines are small, both absolutely and in relation to the size of its premolars and molars. Whatever this creature was eating, it evidently did not need large incisor teeth to bite into it.

The OH 5 cranium was made the type specimen of *Zinjanthropus boisei*, but most researchers have dropped the genus *Zinjanthropus* and place this eastern African taxon into either *Australopithecus* or *Paranthropus*: I will refer to it as *Paranthropus boisei* because most researchers support the hypothesis that *P. robustus* and *P. boisei* inherited their shared morphology from a recent common ancestor. Further evidence of *P. boisei* came with the discovery of a mandible with a large, robust body, large chewing teeth, and small incisors and canines at the Peninj River, on the shores of Lake Natron, in Tanzania. Since then many more fossils belonging to *P. boisei* have been found at Olduvai, and at sites in Ethiopia, Kenya, and Malawi.

The features that set *P. boisei* apart are found in the cranium, mandible, and the dentition. It is the only hominin to combine a massive, wide, flat face with exceptionally large chewing teeth and small incisors and canines. Despite these large jaws and chewing teeth, its brain (around 450 cc) is similar in size to the brains of australopiths like *Au. africanus*. The earliest evidence of *Paranthropus* in eastern Africa is a variant that has a more projecting face, larger incisors, and a more ape-like cranial base. Some researchers assign these pre-2.3 mya fossils to a separate species, *P. aethiopicus*. Despite the richness of the cranial evidence for *P. boisei*, very few postcranial remains have been found in association with cranial remains we can be sure belong to *P. boisei*. What little we do know suggests that its postcranial skeleton was much like that of other archaic hominins.

Most palaeoanthropologists interpret the large-crowned, thick-enamelled chewing teeth, the large mandibles with wide bodies, and the crests on the crania

of large individuals as evidence that the diet of *P. boisei* was highly specialized. One interpretation suggests that its peculiar anatomy enabled it to eat fruits or seeds with hard outer coverings, another that it may have been adapted to eat grass or sedges. Others disagree and say that *P. boisei* may have been a dietary generalist, the higher primate equivalent of a bush pig. Its large chewing teeth and mandibles would have enabled it to cope with a wide range of dietary items including plant foods, insects, and grass. Its stable isotope signature sides with grass or sedge consumption.

There is no morphological reason why *P. boisei* or *P. robustus* could not have made primitive stone tools. Pointed bones found with *P. robustus* show wear that matches that produced by contemporary hunters and gatherers when they use pointed sticks to break into termite hills for the energy-rich and palatable termites.

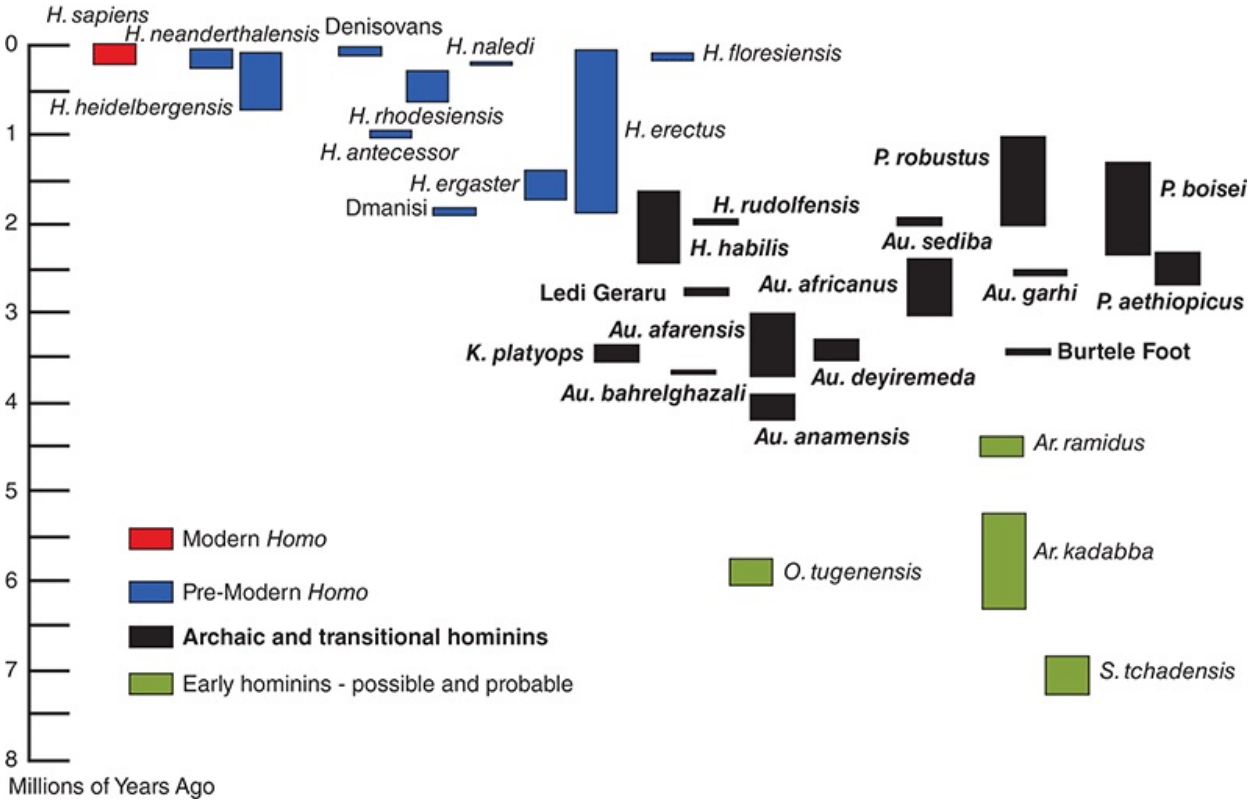
The largest specimens of *P. boisei*, almost certainly males, were almost twice the weight of the smallest, presumably female, individuals (around 150 pounds compared to 75 pounds). In living primates such a wide range of body size is associated with a social system in which there is competition among males for access to females. In comparable living primates males establish this hierarchy through threats mediated by displaying their large canine teeth. The absence of large canines in *P. boisei* suggests that if there was a dominance hierarchy then male *P. boisei* individuals must have used some other means for establishing it. Perhaps the sheer size of their faces, combined with orangutan-like skin folds, could have been the means they used to establish their place in the hierarchy?

In 2001 Meave Leakey and colleagues recovered hominin fossils from West Turkana, Kenya, dated to between 3.5 and 3.3 my. The most complete specimen, a cranium, is deformed by many matrix-filled cracks, but despite the cracking there are facial features that do not match the face of *Au. afarensis*, the hominin best known in this time period. Meave Leakey's team was convinced their find was sufficiently distinct from *Au. afarensis* to justify assigning the fossils to a new genus and species called *Kenyanthropus platyops*.

Transitional hominins

In 1959 at Olduvai Gorge, near where they had recovered the *P. boisei* cranium, Louis and Mary Leakey made the first of a series of remarkable discoveries of

what they came to realize was a much more human-like early hominin than the archaic hominins I have considered up until now. Even today scientists are debating whether these remains belong to a primitive species of our own genus *Homo*, or whether they belong to a larger-brained archaic hominin (Figure 12).



12. Time chart of ‘archaic’ and ‘transitional’ hominin species.

Finds made in 1960 included some teeth, part of the top of a cranium, some hand bones, and most of a left foot, and the next year the Leakeys found the incomplete skull of an adolescent, more cranial fragments, a lower jaw, and teeth. The cranial remains showed no sign of the bony crests characteristic of larger-bodied *P. boisei* individuals, and the premolar and molar teeth were substantially smaller than those of *P. boisei*. Although the brain was still small, Louis Leakey and Phillip Tobias, a distinguished South African anatomist from the University of the Witwatersrand who was initially commissioned by the Leakeys to describe their 1959 *Zinjanthropus* cranium, were convinced that impressions on the inside of the cranial cavity provided evidence of a distinct Broca’s area, the part of the brain that at the time was believed to be the sole control centre for the muscles involved in speech.

Leakey and Tobias recruited hand expert John Napier, and the trio argued that the new material justified establishing a novel species, *Homo habilis*—literally 'handy man'—within the genus *Homo*. Prior to their proposal the consensus was that all *Homo* species should have a brain size of at least 750 cc, but the brains of the new Olduvai discoveries were only about 600–700 cc. Leakey and his colleagues argued that the Olduvai evidence for *H. habilis* satisfied the functional criteria for *Homo*, namely an upright posture, a fully bipedal locomotion, and dexterity. The latter inference was based on their interpretation of the hand bones, along with their conviction that *H. habilis* and not *P. boisei* had made the stone tools that had been found in the same levels at Olduvai.

Similar looking fossils have since been recovered from other sites in eastern and southern Africa, with the single largest addition to the collection coming from the site of Koobi Fora in northern Kenya. The brain size of the enlarged sample of *H. habilis* ranges from just less than 500 cc to about 800 cc. Some of the faces are small and projecting and others are large and flatter. The lower jaws also vary in size and shape. The few limb bones that we can be reasonably confident belong to *H. habilis* show that its skeleton was like that of the archaic hominins in that it had long arms relative to the length of its legs.

Taking all the new evidence into account, there is little other than brain size and some differences in the shape of the teeth to distinguish *H. habilis* from the archaic hominins. When we relate the size of its jaw and teeth to estimates of its body size, *H. habilis* is more similar to the australopiths than to later *Homo*. The conclusion that *H. habilis* was capable of spoken language was based on presumed links between Broca's area in the brain and language production that are no longer valid: we now know that language function is more widely distributed across the brain. The postcranial skeleton of *H. habilis* differs very little from that of *Australopithecus* and *Paranthropus*. The hand bones found at Olduvai suggest *H. habilis* was capable of the manual dexterity involved in the manufacture and use of simple stone tools, but this is also true of *Au. afarensis* and *P. robustus*.

In addition to doubts about whether *H. habilis* should be in *Homo*, researchers generally agree that the crania, jaws, and teeth of *H. habilis* are more variable than one would expect for a single species. Many, but not all, researchers now divide it up into two species: *H. habilis* proper (technically called *H. habilis* s*ensu stricto*, i.e. in the 'strict sense') and *Homo rudolfensis*. Compared to *H.*

habilis proper the latter has a bigger, wider, flatter face, and larger chewing teeth, which suggests that its diet may have differed from that of *H. habilis*. We know nothing for certain about the limbs of *H. rudolfensis*.

Chapter 7

Pre-modern *Homo*

All the fossil hominin taxa I have considered thus far are relatively small (*c*.25–55 kg) compared to most modern humans. Brain size and limb proportions are only known for a few individuals belonging to archaic and transitional hominin taxa. In all cases where there is enough information to make even a rough estimate of brain size, the brains are all below the absolute and relative size of later *Homo* taxa. All the taxa have relatively shorter legs than modern humans. This would have made them less efficient bipeds than we are, but it does mean that they would still have been able to climb into trees for shelter or for food. The large chewing teeth and thick mandibular bodies of the archaic and transitional hominins, and the very large chewing teeth of the hyper-megadont archaic hominins, suggest that their diet routinely or occasionally included tougher or more abrasive food than the diets of modern humans. All the archaic hominins and the transitional hominins seem to belong to a different grade from modern humans. So when and where in human evolutionary history do we see the earliest evidence of creatures that are more like modern humans?

Homo ergaster

Fossils recovered from sediments at Koobi Fora and West Turkana in northern Kenya, which are a little less than 2 my-old, provide evidence of ‘early African *Homo erectus*’, or *Homo ergaster*. Robert Broom had previously suggested that a lower jaw from Swartkrans might be evidence of such a creature, but it was not until the better evidence from eastern Africa that researchers were willing to accept the existence of a hominin close to 2 mya with a body whose size and shape is more like that of modern humans than any of the archaic or transitional hominin taxa. In addition, in relation to the size of its body, the teeth and jaws of

H. ergaster are smaller than those of the archaic and transitional hominins, which suggests that the diet of *H. ergaster* probably differed from that of the archaic and transitional hominins. This is consistent with a change in the stable isotope signal between teeth likely to belong to *H. habilis* and *H. ergaster*. Others have suggested that *H. ergaster* may have been the first hominin to routinely cook food. Cooking makes tough foods easier and raw foods less risky to eat, but the earliest sound archaeological evidence of the ability to control fire presently comes from the *c*.1.0 my Wonderwerk Cave in South Africa and the *c*.800 ky site of Gesher Benot Ya'agov in Israel.

The longer lower limbs of *H. ergaster* would have allowed it to travel long distances efficiently. Clearly some adult modern humans are adept at climbing trees to recover nuts and honey, but for most modern humans their long legs get in the way, and their arms have lost the ape-like ability to use branches efficiently for locomotion. In all these aspects *H. ergaster* is more specialized than earlier hominins. However, in one important respect, brain size, it shows little advance over the two transitional hominin taxa. Why large brains do not appear until much later in human evolution is still a puzzle to palaeoanthropologists. Perhaps it is related to the avoidance of the extra risk in the later stages of pregnancy. The likely shape and size of the pelvis of *H. ergaster*, combined with what can be inferred about the brain size of a *H. ergaster* neonate, suggests that the head was still small enough to be oriented transversely all the way through the birth canal without the need for it to be rotated after negotiating the pelvic inlet, which is what happens in modern humans.

Out of Africa: who and when?

The earliest evidence of hominins beyond Africa is 2.1 my-old stone tools found at Lantian in China, but 'absence of evidence is not evidence of absence' so we must be sure to continue to look for evidence of hominins outside Africa before this time.

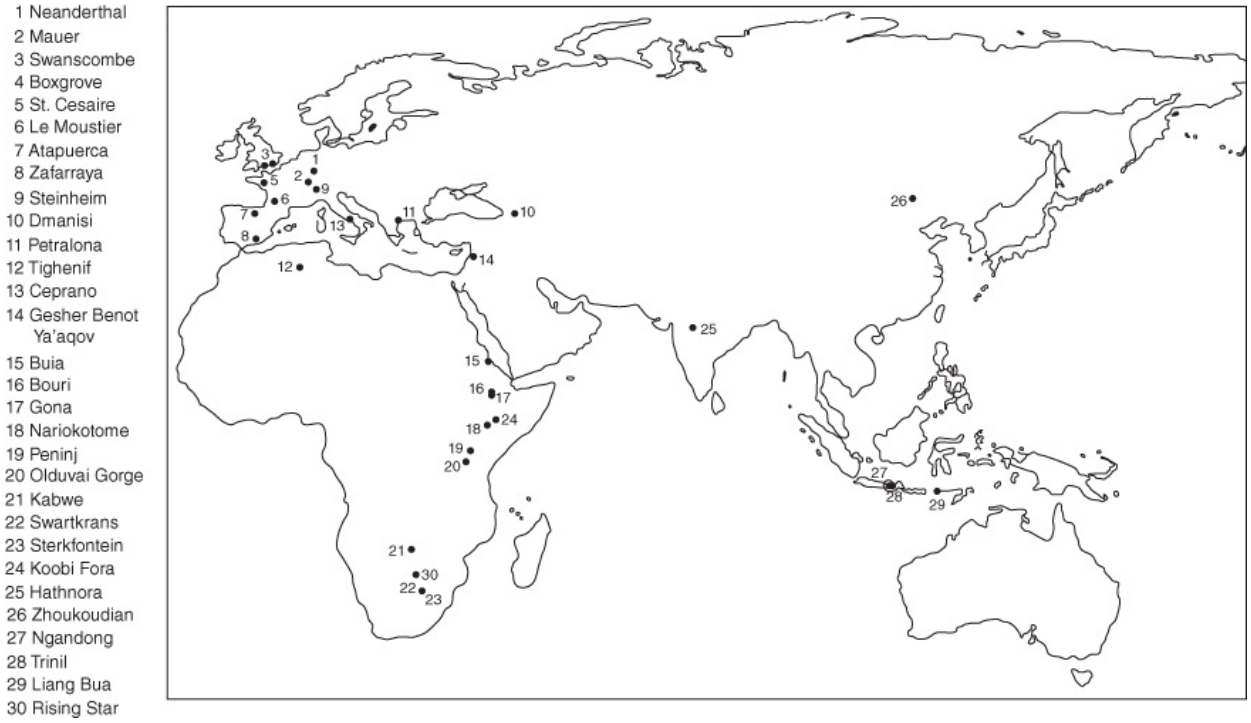
Around 1.8 mya there is good fossil evidence of a relatively primitive *H. ergaster*-like hominin at Dmanisi in Georgia. There are no absolute dates for the sediments from the site, but the age of the lava beneath the sediments, their magnetic direction, and the fossil animals found with the hominins, all support an estimated age of 1.8 my. The Dmanisi hominins are an intriguing mix of

relatively primitive morphology (e.g. a small brain and primitive cranial base) combined with a relatively more modern human-like postcranial skeleton. It is also noteworthy that the stone tools recovered from the same horizon as the Dmanisi hominins resemble those found in the oldest, Bed I, sediments at Olduvai Gorge, Tanzania. After Dmanisi, the next well-dated evidence of hominin occupation outside of Africa is the 1.5 my-old site of 'Ubeidiya in Israel, but so far the only hominin fossils found at the site are some teeth.

By at least one million years ago there is evidence of a new type of hominin, *Homo erectus*, from sites in Africa, China, and Indonesia. If you met a *H. erectus* in the street you would be unlikely to confuse it with a modern human, but it would look more like a modern human than any archaic or transitional hominin. Some researchers, but not all, are persuaded that *H. erectus* reached Indonesia as early as 1.7 mya, and perhaps as early as 1.9 mya. If so, *H. erectus* would most likely have been established on the Asian mainland sometime before that. At present the 2.1 my-old stone tools found at Lantian are the earliest reliable evidence of hominins on the Asian mainland.

The best-known fossil evidence of *H. erectus* comes from sites along the Solo River in Indonesia, and from the Peking Man site (now called Zhoukoudian) in China. As we saw in Chapter 3, Eugène Dubois found the first *H. erectus* fossils on the island of Java. Encouraged by finding a small piece of lower jaw at a site called Kedung Brubus in northern Java in 1890, Dubois turned his attention to the part of Java where the Solo River has exposed sediments that we now know may date back to around 2 my. He organized an elaborate excavation of the sediments that had been exposed in the banks of the river during the dry season near the village of Trinil, and in 1891 the excavators uncovered some teeth, a femur, and a skullcap (technically this is called a calotte). Remember that in 1894 the only two hominin taxa known were *Homo sapiens* and *Homo neanderthalensis*. Initially Dubois thought the calotte belonged to an extinct giant gibbon, but he evidently changed his mind because in 1894 he gave it a different genus name, *Pithecanthropus*, which is now included in the genus *Homo*. The Trinil specimen lacks the large brain and tall rounded brain case of modern humans—its brain volume was about 60 per cent of the average for modern humans—but the femur found close by looked like a modern human femur, which is why Dubois called his new species *Pithecanthropus erectus*. However, not all researchers are convinced the femur is as old as the calotte. It may belong to a much more recent skeleton that was 'reburied' in the river

gravels. The search for hominins at Trinil has continued, but the last hominin to be recovered from the site was in 1900 (Figure 13).



13. Map of the main 'archaic', 'transitional', and 'pre-modern' *Homo* sites.

The next phase of the search for hominin remains in Java focused upstream of Trinil where the Solo River cuts through the sediments of the Sangiran Dome. It was here that in 1936 a German palaeontologist, Ralph von Koenigswald, recovered a cranium that resembled the Trinil skullcap, but with an even smaller brain. Several more specimens were recovered before the Japanese occupation of Java curtailed research, during which Ralph von Koenigswald protected the hominin fossils by burying them in his garden. When the search for early hominins in and around the Sangiran Dome was renewed after the war, researchers recovered mandibles, several crania, and some postcranial evidence.

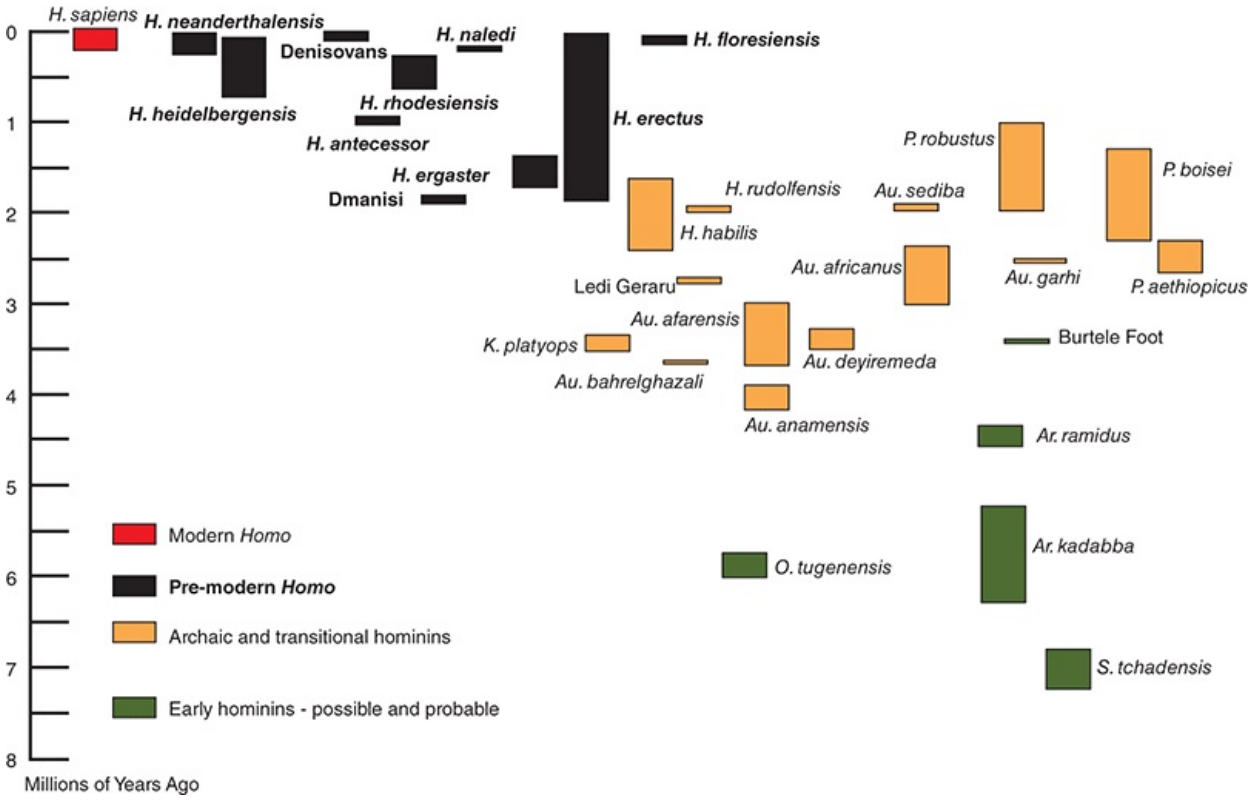
The search for early hominins in China began in the early 1920s when a Swedish palaeontologist, Gunnar Andersson, and a junior colleague from Austria, Otto Zdansky, started their excavations at the Zhoukoudian (formerly Choukoutien) Cave, near Beijing. There were plenty of quartz artefacts, but apparently no evidence of fossil hominins. However, in 1926, when Zdansky was looking

through the excavated material from Locality 1 that had been shipped to Uppsala, he realized that an upper molar and a lower premolar labelled as ‘ape’ teeth were actually hominin. They were given to Davidson Black to describe and evaluate, and along with a well-preserved lower molar tooth found in 1927, he assigned them to a new genus and species, *Sinanthropus pekinensis*. That year Black and two colleagues, Weng Wanhao and Anders Bohlin, resumed excavations at Zhoukoudian. The first cranium was found in 1929 and excavations continued until they were interrupted by the Second World War. Nearly all of the fossils recovered from Locality 1 were lost during the war. They were given to a unit of US marines for safe-keeping, and it is not clear whether the fossils were lost before the marines reached a port, or whether they were lost at sea, but they never reached the USA. Their whereabouts remains a mystery, but fortunately excellent casts had been made by Franz Weidenreich, who had previously published meticulous qualitative and quantitative descriptions of the fossils. Some of the morphology of the Zhoukoudian fossils was distinctive, but in many other ways the *Sinanthropus* fossils resembled those belonging to *Pithecanthropus erectus* from Java, so much so that in 1940 Franz Weidenreich suggested both sets of fossils should be included within a single species in *Homo* called *Homo erectus*. Since the Second World War fossils similar to those belonging to *Pithecanthropus* and *Sinanthropus* have been found at other sites in Java (e.g. Ngawi and Sambungmacan) and China (e.g. Lantian), and at sites in southern Africa (e.g. Swartkrans) and eastern Africa (e.g. Melka Kunturé, Middle Awash, Olduvai Gorge, and Buia).

Despite the recovery of a relatively large number of *H. erectus* crania, relatively little was known about the limbs of *H. erectus* until crucial postcranial evidence was recovered from eastern Africa. These discoveries included a pelvis and femur from Olduvai Gorge (OH 28), two fragmentary partial skeletons from Koobi Fora (KNM-ER 803 and 1800), and an unusually well-preserved associated skeleton of a juvenile male from West Turkana—the ‘Turkana Boy’ (KNM-WT 15000). It is this evidence that suggests the limb proportions of *H. erectus* were modern-human-like.

In Africa there is evidence that later *H. erectus* may have evolved into pre-modern *Homo* in the form of *H. heidelbergensis*, but in Indonesia the later *H. erectus* material seems to get more specialized. This makes it less likely that the Indonesian hominins evolved into archaic *Homo* and more likely that Asian *H. erectus* was a ‘dead end’. China and Indonesia (the latter especially because of

the relatively recent evidence from Ngandong) seem to have been among the last outposts of *H. erectus* (Figure 14).



14. Time chart of 'pre-modern' *Homo.*

Characteristics of *Homo erectus*

The low crania of *H. erectus* are all widest at the base. There is a substantial and more or less continuous bony ridge, or torus, above the orbits, and a pronounced blunt ridge (or keel) of bone, the sagittal torus, runs in the midline from the front to the back of the brain case. At the back of the cranium the sharply angulated occipital region has a well-defined sulcus above it. The two layers of dense bone in the cranial vault (aka the inner and outer tables) are thick. The volume of the cranial cavity of *H. erectus* varies from *c*.730 cm^3 for OH 12 (and 550 cm^3 if D4500 from Dmanisi is included) to *c*.1250 cm^3 for the *c*.300 ky-old Ngandong 6 (Solo V) calotte. Most of the smaller-brained individuals are earlier in time, and all of the larger-brained individuals are later in time.

The limbs of *H. erectus* are modern-human-like in their proportions (i.e. the absolute and relative lengths of the components of the limbs), but the robust long bone shafts are more flattened from front to back (femur) and from side to side (tibia) than they are in modern humans. The pelvis has a large socket (aka acetabulum) for the head of the femur and the bone between the socket and the crest of the ilium (you can feel this on yourself either side level with your hips) is thickened. Both of these features are consistent with a habitually upright posture and long-range bipedalism. There is little or no fossil evidence relevant to assessing the dexterity of *H. erectus*, but if *H. erectus* manufactured hand axes then dexterity would be implicit.

Homo heidelbergensis

By 700 kya at sites like Bodo in Ethiopia and Kabwe in Zambia there is evidence of hominins that lack the characteristically shelf-like brow ridges we see in *H. erectus*. These crania have separate thicker and rounded brow ridges over each eye socket, and their brain cases are larger (*c*.1200 cm^3) than those of *H. ergaster* (*c*.800 cm^3) and *H. erectus* (*c*.750–1000 cm^3). There is also a further reduction in the size of the jaws and chewing teeth. What little we know of the postcranial skeleton of *H. heidelbergensis* suggests that the limb bones are substantially thicker and stronger, and the joint surfaces larger, than those of modern humans. The name *H. heidelbergensis* seems a strange one for a fossil hominin we see first in the African fossil record, but we use it because a jaw found in 1907 near Heidelberg in Germany is likely to belong to the same taxon. Fossils from a cave in Spain called Gran Dolina, which was exposed when a railway line was being driven through the Sierra de Atapuerca, dating to *c*.1 mya have been assigned to a species of pre-modern *Homo* called *Homo antecessor.* A *c*.1.2–1.1 my-old mandible from a nearby cave, the Sima del Elefante, has been provisionally assigned to the same taxon. The discoverers of the fossils at both locations suggest *H. antecessor* may be ancestral to *H. heidelbergensis*, but there is little consensus about how these species are related.

Homo naledi—a hitherto unknown pre-modern *Homo* taxon, with a hitherto unknown combination of morphology

Approximately 1,550 hominin bones and teeth—it is not clear whether they have ever been truly fossilized—from at least fifteen individuals have been recovered

from the Dinaledi Chamber of the Rising Star cave system, which is within a kilometre of the site of Swartkrans, in southern Africa. The fossils, which display remarkably little inter-individual variation, sample a hominin with an unusual mix of characteristics. Its cranium resembles *H. ergaster*, but with a smaller brain case (*c*.550 cm^3), the dentition combines modern human-like tooth crowns with primitive mandibular premolar tooth roots, the hand morphology is mostly modern human-like yet the toe bones are curved, and the pelvis and hip-joint are relatively primitive.

Initially, the interpretation of this material was made more complicated by the total absence of any information about the age of the fossils, and the lack of any credible hypothesis for how these remains come to be in a difficult-to-access pitch-dark cave a long and tortuous crawl from what is claimed to have been the only possible entrance. Nor is there a credible hypothesis to explain why there are no other mammal fossils in the Dinaledi Chamber. The implications of this new evidence are critically dependent on the age of the remains, because the mix of modern human-like and more primitive (i.e. mosaic) morphology would suggest one thing if the remains are 2 my, but quite another if they are only 200 ky old. Subsequent research addressing the stratigraphic context and dating of the *H. naledi* fossils—that maybe should have been done *before* the initial publication of the fossil evidence—suggests they date from around 250 kya.

Researchers have recovered 131 hominin fossils, from at least three, and most likely four, individuals, from a different chamber in the Rising Star cave system. Unlike the situation in the Dinaledi Chamber, non-hominin mammalian fossils were recovered from the Lesedi Chamber, but it is not clear they are the same age as the hominins, which are undated.

Homo naledi most likely samples a relict population descended from early *Homo*: it has little to say about the early history of our genus.

Homo floresiensis—a ‘dwarfed’ pre-modern *Homo* taxon?

The announcement in 2004 of a new hominin taxon, *Homo floresiensis*, based on a collection of hominin fossils recovered from excavations at a cave called Liang Bua on the Indonesian island of Flores, shook the palaeoanthropological community. With a brain size of *c*.400 cm^3, an estimated stature of just over 3

feet, and with limb proportions and a pelvis like Lucy's, its discoverers were faced with a considerable interpretative challenge. Were the newly discovered remains primitive enough to be accepted as the first evidence for a transitional or archaic hominin outside of Africa even though the youngest evidence was no more than 60 ky old? Or was the small size the effect of island dwarfing operating on a normal-sized pre-modern *Homo* taxon that resembled either *H. ergaster* or *H. erectus*?

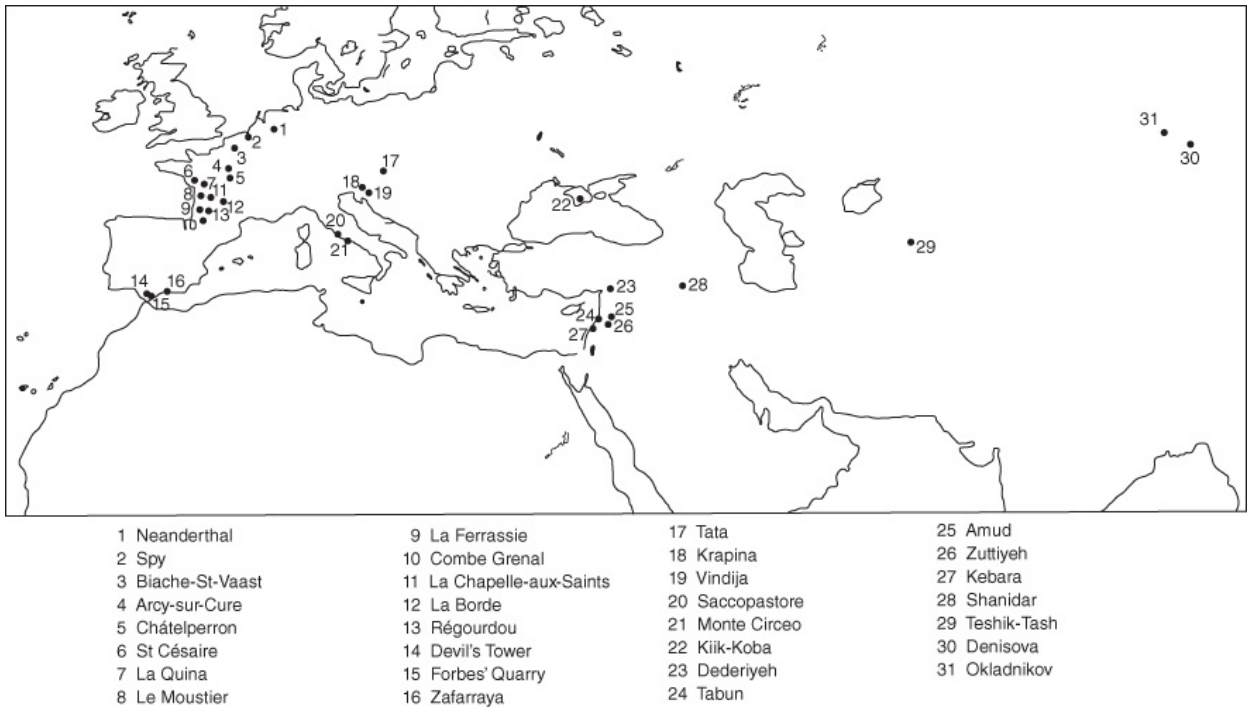
Some researchers opted for even more exotic explanations. These included the suggestion that the Liang Bua hominin fossils sampled a few pathological individuals in an otherwise normal population of pre-modern *Homo*, or they sampled a population in which a diminutive stature and microcephaly were the norm. However, the proportions and morphology of the brain case of *H. floresiensis* are not consistent with microcephaly, and it more closely resembles the brain case of *H. erectus* than it does that of normal, or microcephalic, modern humans. A second tranche of hominin fossils recovered from Liang Bua, which confirmed the small size and primitive nature of the mandible, the dentition, and the postcranial skeleton of *H. floresiensis*, makes the 'pathological/microcephaly' hypothesis very difficult, if not impossible, to sustain. The discovery of a *H. floresiensis*-like mandible at another site on Flores most likely extends the temporal range of *H. floresiensis* back to *c*.700 kya.

But if the Liang Bua hominins are the product of island dwarfing, the jury is still out concerning the nature of the 'pre-dwarfed' hominin. Was it a transitional or archaic hominin, or was it one of the pre-modern *Homo* taxa recognized in Africa? The presence of stone tools suggests that humans reached what are now the islands of the Philippines by *c*.700 kya. What sort of hominins were they, and how were they related to *H. floresiensis*?

Homo neanderthalensis

The best-known species in the 'pre-modern *Homo*' category is *Homo neanderthalensis*, better known as the Neanderthals (some researchers prefer the modern German 'Neandertal', but as the name comes from the Linnaean binomial 'Neanderthal' is technically correct). Neanderthals, which are morphologically distinctive, cranially, dentally, and postcranially, seem to have been confined to Europe and the Asian mainland. Neanderthals are 'best known' in two senses. They have the most comprehensive fossil record of any extinct

hominin, and they are also the extinct hominin that most readers of this VSI are likely to have heard of (Figure 15).



15. Map of major Neanderthal sites.

The earliest evidence of hominins that show signs of Neanderthal-type morphology comes from a site called the Sima de los Huesos, one of several caves in the Sierra de Atapuerca, near Burgos in Spain, where a Spanish team have unearthed a treasure trove of hominin fossils dating to *c*.450 kya. But the name, *H. neanderthalensis*, recognizes the location of the type specimen, an adult partial skeleton called Neanderthal 1 that was recovered in 1856 from the Kleine Feldhofer Grotte in the Neander Valley, in Germany. With hindsight it was not the first evidence of Neanderthals to come to light, for a child's skull found at Engis in Belgium in 1829, and an adult cranium recovered from Forbes' Quarry in Gibraltar in 1848, also display the distinctive (see below) Neanderthal morphology. No faunal or archaeological evidence from the Feldhofer cave was reported in 1856, and there seemed to be no prospect that such evidence could ever be obtained. However, in a remarkable example of archival research contributing to palaeoanthropology, in the mid-1990s Ralf Schmitz and Jürgen Thissen managed to glean enough information about the whereabouts of the cave to go back to the much changed Neander valley and locate the remnants of the

cave sediments discarded by the miners in 1856. The excavations they undertook in 1997 recovered fauna, artefacts, and hominin fragments, one of which fitted exactly onto the outside of the lower end of the femur of the original Neanderthal 1 skeleton. In 2000 they recovered more fauna, archaeological, and hominin skeletal fragments, including two cranial fragments that belong to the original Neanderthal 1 calotte. Their attempts to date the rediscovered sediments suggest the Neanderthal type specimen was *c*.40 ky old.

The next major Neanderthal discovery was made in Moravia (Sipka, 1880), then came discoveries in Belgium (Spy, 1886), Croatia (Krapina, 1899–1906), Germany (Ehringsdorf, 1908–25) and France (Le Moustier, 1908). The first Neanderthal outside of Western Europe was found at Kiik-Koba in the Crimea in the early 1920s, after which came discoveries on Mount Carmel in the Levant (Tabun, 1929) and in central Asia (Teshik-Tash, 1938). In the meantime, two sites in Italy (Saccopastore, 1929 and Guattari/Circeo, 1939) had yielded Neanderthal remains. Further evidence was added after the Second World War, first from Iraq (Shanidar, 1953) and then from sites in Israel (Amud, 1961; Kebara, 1964) and Syria (Dederiyeh, 1993). New fossil evidence for Neanderthals continues to be discovered in Europe and Western Asia, for example at St Césaire in France in 1979, Zafarraya in Spain in 1983, and at Lakonis in Greece in 1999.

Full-blown (aka classic) Neanderthals, that is fossils that show all of their distinctive morphology, including a large nasal opening, a streamlined face that projects forwards in the midline, a rounded top and back of the cranium, a cranial cavity that is on average larger than that of modern humans, and distinctive limb bones with thick shafts and large joint surfaces, are mostly known from sites that are between 100 and 30 ky-old. No Neanderthal fossils have been found in Scandinavia—it was probably too cold even for Neanderthals—but they have been found in eastern Asia as far as Siberia, and there are credible reports of discoveries in China.

There are two opposing views about the relationship between Neanderthals and modern humans. One suggests that Neanderthals are morphologically too specialized to have made a significant contribution to the modern human gene pool, and that the differences between them and modern humans merit recognition as a separate species. The opposing view considers the morphological differences between Neanderthals and modern humans to be

relatively trivial and supports their inclusion in *H. sapiens*. The first interpretation is the more correct one.

DNA from Neanderthals

Fortunately, other lines of evidence are now available for assessing the taxonomy of the Neanderthals, for researchers have been able to extract both mitochondrial (mtDNA) and nuclear (nDNA) from Neanderthal, and other, fossils. In 1997 Svante Pääbo and colleagues showed that short fragments of mtDNA recovered from a large chunk of the shaft of the right upper arm bone of the Neanderthal 1 type specimen were almost certainly remnants of the ancient DNA (aDNA) of that individual. The average number of sequence differences between modern humans and the Neanderthal 1 sequence was three times greater than the average sequence difference between any two randomly selected modern humans. Furthermore, the Neanderthal 1 sequence was no closer to the sequences of modern Europeans than it was to the sequences of modern humans from other regions of the world, plus the sequence differences were interpreted as suggesting that Neanderthals diverged from the modern human lineage more than half a million years ago!

Since this quantitatively modest beginning, ancient DNA research has made huge strides. In 2006 James Noonan and colleagues used new methods of high-throughput sequencing and analysis to generate the first Neanderthal genomic library, which showed that the genomes of Neanderthals and modern humans are 99.5 per cent alike. Four years later Richard (Ed) Green and colleagues reported a draft sequence of the Neanderthal nuclear genome, and when they compared their draft with the draft nuclear genome of the chimpanzee and with the nuclear genomes of five modern humans, a small portion (*c.*1–4 per cent) was more similar to non-African modern human samples than to the only African modern human that had been sampled, which suggests a modest but significant amount of admixture between Neanderthals and modern humans.

In 2016 Matthias Meyer and colleagues recovered mtDNA from one of the *c.*450 ky-old hominins from the Sima de los Huesos, and when, two years later, they extracted nuclear DNA from the same individual, plus at least one other, it confirmed what had been suspected from the morphological evidence—the Sima de los Huesos hominins are closely related to Neanderthals.

The Sima de los Huesos research is an example of the strand of hominin aDNA studies that is trying to push back the recovery of aDNA into ever-deeper time. A relatively new sub-field of aDNA research uses the DNA recovered from recent modern human fossils to reconstruct how modern humans populated the major regions of the world. We will discuss this in Chapter 8.

A surprise from Siberia

In 2008, researchers excavating the *c*.48–30 ky level in Denisova Cave in the Altai Mountains in Russia recovered a tiny bone that came from the end of the little finger of a human hand. The morphology was not sufficiently distinctive to assign it to a particular hominin taxon, but the circumstances of its fossilization and post-depositional history were such that its DNA was particularly well preserved. The expectation was that it belonged to one of the Neanderthals whose Mousterian tools were known from Denisova, but instead of its mtDNA being within the Neanderthal range Krause and his colleagues concluded it was distinct from *both* modern humans and Neanderthals. Krause et al. suggested the hominin pinky bone belonged to a taxon that most likely shared a common ancestor with modern humans and Neanderthals between 800 ky and one million years ago.

More recently nuclear DNA has been extracted from tooth crowns whose crown morphology is distinct from both modern humans and Neanderthals, and when Alan Rogers and colleagues compared that DNA with the genomes of modern humans and Neanderthals, they concluded that the Neanderthal and Denisovan lineages separated only a few hundred generations after their ancestors split from the modern human lineage sometime between 770 and 550 kya. They also suggested that after the Neanderthal lineage separated from the Denisovans *c*.400 kya the Neanderthal population expanded and then fragmented into largely isolated local groups, and apparently more than one of these contributed genes to modern humans. But even after 300 ky of separation it seems that Neanderthals and Denisovans may have occasionally interbred, because when Viviane Slon and colleagues looked in detail at the genome of one hominin individual from Denisova Cave, the 90 ky-old Denisova 11, they stuck their necks out and suggested that it had a Neanderthal mother and a mainly Denisovan father. The Denisovans are the first example of a genome in search of a distinctive phenotype, but some researchers suggest that fossils from Chinese sites—such as Dali, Jinniushan, Maba, and Xinjiang—may be the phenotypic expression of the

Denisovan genome.

Several research groups have found evidence that Denisovans contributed genes to modern humans. This admixture is most evident in the genomes of aboriginal modern humans from Papua New Guinea and Australia, and the nature of the admixture suggests that exchange may have occurred *c*.50 kya. Among the genes we apparently inherited from the Denisovans are ones that help modern humans live at high altitudes, and others that help us fight infections. According to the genome reconstructed from its aDNA at least one Denisovan individual had dark skin, brown hair, and brown eyes.

Interpreting Neanderthals

Long before evidence from aDNA became available, many were convinced that Neanderthals evolved into modern humans. This interpretation was supported by the original dates given to a sequence of hominin fossils in the Near East, which suggested that the Neanderthals found in the caves at Tabun and Amud were older than the more modern-human-looking fossils from sites such as Qafzeh. However, the results of more accurate dating methods have stood that traditional interpretation on its head, because there is now good evidence that the more modern-looking Qafzeh fossils pre-date the Neanderthal remains.

Neanderthals have been particularly prone to erroneous interpretations involving pathology. For example, the skeleton from La Chapelle aux Saints is badly affected by osteoarthritis, but because it was used for one of the most reproduced reconstructions of Neanderthals, all Neanderthals were assumed to have a bent back and round shoulders. It was also seriously proposed that Neanderthals were modern humans affected by congenital hypothyroidism, also called cretinism. This conclusion was made on the basis of the rough correspondence between the distribution of Neanderthal sites and the contemporary ‘goitre belt’ that extends across Europe to the Near East. But this is an example of ignoring the difference between correlation and ‘cause and effect’. Cretinism results in distinctive marks on the skeleton that are not seen in Neanderthal fossil bones.

It seems that Neanderthals were one of the first, if not the first, hominins to regularly bury their dead, and, if this is the case, it helps explain why the quality and quantity of the hominin fossil record is so much better for Neanderthals than it is for earlier hominins. Some graves show evidence of ceremony, and

researchers have also claimed that Neanderthals had an interest in art, with convincing evidence that Neanderthals were decorating cave walls in Spain long before the first evidence of modern humans in that part of the world.

Aside from providing information about relationships, another outcome of the Neanderthal and Denisovan genome sequencing projects is the ability to make predictions about soft tissue and neuro-behavioural characteristics that are not preserved in the fossil record. For example, some Neanderthals most likely had red hair, and among the genes shared between modern humans and Neanderthals are ones that have been linked with mood disorders.

Chapter 8

Modern *Homo*

Conventional wisdom

For much of the last century many believed that the transformation from pre-modern *Homo* populations to modern humans took place more or less independently in Africa, Europe, and Asia. So, for example, in Europe the Neanderthals would have evolved into European modern humans, and in Asia late surviving *H. erectus* would have evolved into Asian modern humans. In its extreme form this ‘multiregional hypothesis’ embraced the now thankfully discredited notion that geographical variants of modern humans (the term ‘race’ has little, or no, biological meaning with respect to modern humans) had distinctly different evolutionary histories.

A weaker form of the multiregional hypothesis was espoused by researchers such as Franz Weidenreich, who played a critical role in the analysis of the remains of *H. erectus* from Zhoukoudian. This combined the hypothesis that regional variants of pre-modern *Homo* had each evolved into modern humans, with the proposal that subsequent to their independent evolution the differences between these regional variants were reduced by gene flow—either by migration or by inbreeding—between the regions. Nonetheless, contemporary supporters of this weak multiregional hypothesis (WMRH) argue that, despite any such gene flow, each region has kept enough of its own character to make regional populations of modern humans distinctive and recognizable. They support the WMRH because they see morphological evidence of continuity between pre-modern *Homo* and modern human populations in each of the major regions of the world. Under this scenario it would be difficult to draw a line between, say, Neanderthals and early modern humans in Europe, and between *H. erectus* and

early modern humans in Asia. Supporters of the WMRH argue that these gradations, together with the melding effect of gene flow between regions, justify including *H. erectus* and all the regional hominin variants that came after it in a single species. If there were to be a single species for *H. erectus* and all subsequent hominins then that species would have to be *Homo sapiens* because Linnaeus' species name for modern humans has historical priority over all the other names (e.g. *H. neanderthalensis* and *H. heidelbergensis*) subsequently given to pre-modern *Homo* species.

The suggestion that Neanderthals contributed a small portion of their characteristic nDNA to modern humans has breathed molecular life into the corpse of the WMRH, but there is scant evidence of any regionally distinct morphology that exclusively connects pre-modern *Homo* and modern humans in the major regions of the Old World.

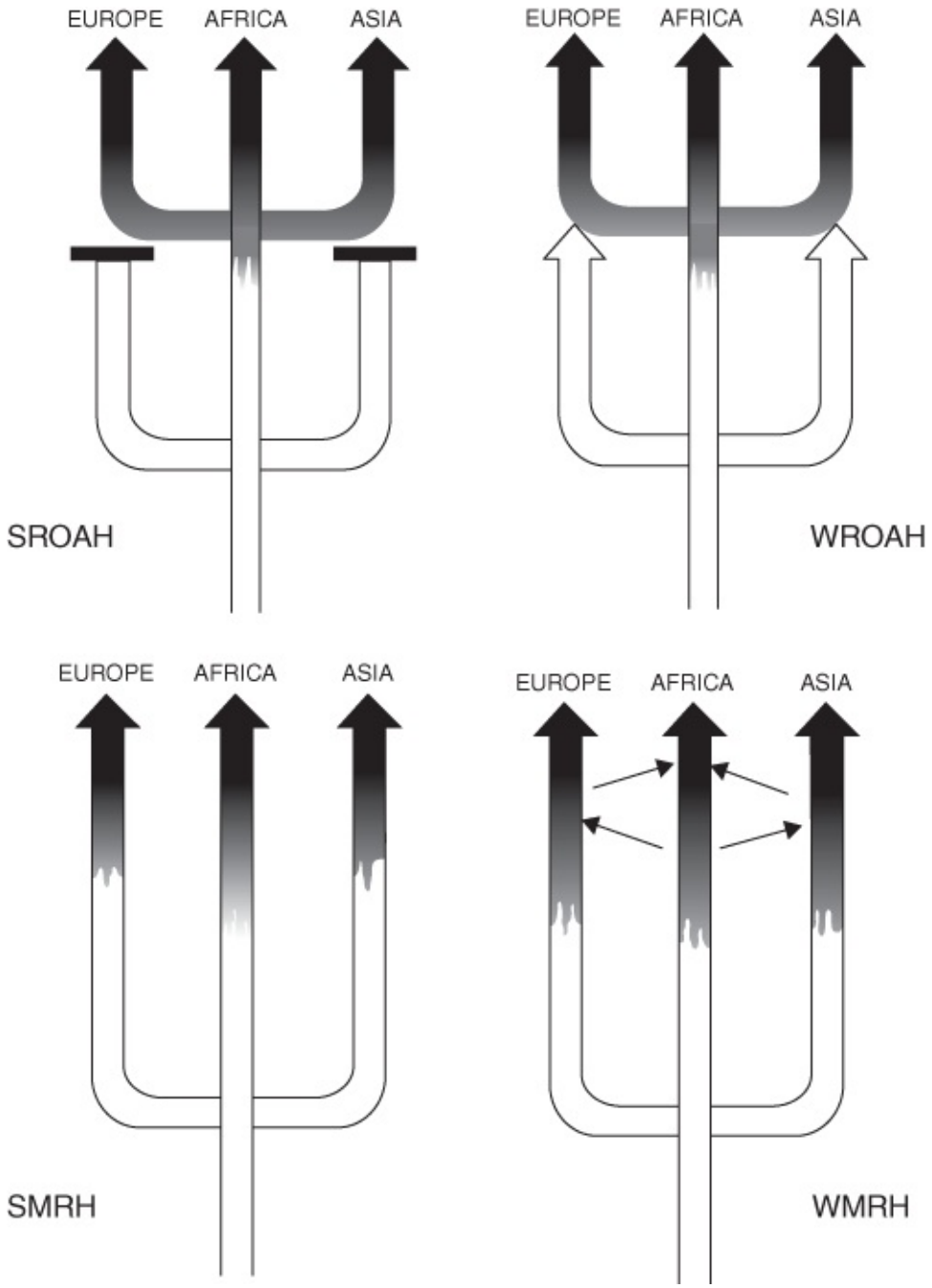
Eurocentrism in palaeoanthropology

The first fossil modern human was found in 1822, when the so-called 'Red Lady' ('red' because the bones were stained with red ochre, but the skeleton almost certainly belonged to a male, not a female) was recovered from a cave at Paviland on the Gower Peninsula, just west of Swansea, Wales. However, the discovery that is nearly always cited as the first fossil evidence of modern *Homo* (i.e. *Homo sapiens*) in Europe was made in 1868 at the Cro-Magnon rock shelter at Les Eyzies in the Dordogne, France. The apparent historical priority of Cro-Magnon, combined with the archaeological evidence of sophisticated small stone awls, and needles and fish hooks made from bone recovered from European sites, plus cave art, suggested to many researchers that continental Europe was not only the cradle of modern civilization, but also the birthplace of our own genus, *Homo*, and our own species, *H. sapiens*. But as researchers look further afield for evidence such as cave art, they are finding it in non-traditional locations, such as images in a cave in Borneo that may be as old as *c*.40 ky.

A challenge to Eurocentrism

The notion that Europe was the place where modern humans evolved was challenged by two developments. The first was the recognition, beginning in the latter part of the 19th century, and intensifying in the second quarter of the 20th

century, that there was fossil evidence of human ancestors more primitive than Neanderthals in Asia. Subsequently, of course, came the realization that the early phases of hominin evolution most likely occurred in Africa (Figure 16).



16. The ‘strong’ and ‘weak’ versions of the multiregional and recent out of Africa models for the origin of modern humans.

The second began in the 1930s when Dorothy Garrod, a distinguished Cambridge archaeologist, discovered fossils resembling modern humans in caves on Mount Carmel, in what was then Palestine. The Mount Carmel discoveries, together with the recovery of modern-human-like fossils and evidently ancient stone tools in Kenya by Louis and Mary Leakey, and in Egypt by Gertrude Caton-Thompson (also affiliated with the archaeology department at the University of Cambridge), began to convince the more outward-looking European archaeologists that important events in both the early and the later stages of human evolution may have taken place outside of Europe. In 1946 Dorothy Garrod introduced a course called 'World Prehistory' into the undergraduate archaeology course at Cambridge and her successor, Grahame Clark, continued in the same vein by encouraging his graduate students to excavate in Africa. The point of this diversion into the history of prehistory is to emphasize that by the 1950s and 1960s some students of human evolution were already comfortable with the idea that important events in the evolutionary history of modern humans may have taken place outside Europe.

Discoveries, new dates, and molecular evidence

In the 1980s three lines of evidence combined to prompt some researchers to contemplate the radical proposition that Africa, far from being an evolutionary sideshow and a cultural backwater, may have been the birthplace of modern humans and of modern human behaviour.

The first of the three new lines of evidence was the redating of the collections of hominin fossils in the Near East. This made it clear that instead of the Neanderthal fossils from Kebara and Amud pre-dating the more modern-human-looking fossils from Skuhl and Qafzeh, it was the other way round. This meant that researchers could not use dating evidence to make the case that Neanderthals evolved into modern humans.

The second line of evidence was the discovery of modern-human-looking fossils in southern Africa and in Ethiopia. Initial dating efforts suggested the Omo I cranium from Ethiopia was *c.*130 ky-old, but a more recent attempt to date the Omo I cranium using isotope dating indicated it was close to 200 ky. A collection of fossils from Herto, also in Ethiopia, added to the evidence suggested that modern-human-like crania were present in Africa between 200 and 150 kya. More recently new fossil finds and archaeological discoveries from

Jebel Irhoud in Morocco dated to just over 300 kya have revived debate about the location and timing of the appearance of modern humans in Africa. The authors do not claim that the Jebel Irhoud hominins are anatomically modern human, but they do suggest they document the ‘early stages of the *H. sapiens* clade’.

The third line of evidence came not from palaeoanthropology, but from the application of molecular biological methods to the study of modern human variation. The pioneering study applying these methods was published in 1987 by Rebecca Cann, Mark Stoneking, and Allan Wilson, molecular biologists at the University of California at Berkeley. The researchers focused on mtDNA because mutations occur in mtDNA at a faster rate than they do in nDNA, because mtDNA does not get reshuffled between chromosomes when germ cells divide, and because it does not have the innate repair mechanisms found in nDNA, so once mutations occur in mtDNA they tend to persist. When Cann et al. compared mtDNA from nearly 300 modern humans from across the world, they found 133 different versions of modern human mtDNA, and when they arranged them in the shortest tree that connected all the variants while minimizing the number of mutations, the shape of the tree and the distribution of variation within it was striking. It had a deep African branch with a second branch that contained the mtDNA variants found in many Africans and all of the people from outside sub-Saharan Africa. There was also more variation within the sub-Saharan African branch of the tree than in the rest of the world put together, and most of the mtDNA variants seemed to have had an African origin.

Mitochondrial Eve

Cann and her colleagues claimed these results implied that modern humans had been in Africa longer than anywhere else in the world, and that the population of modern humans in Africa was probably larger than in the rest of the world combined. The more individuals there are, the more likely it is that mutations will occur. They also made three other claims in their paper. First, the amount of difference in mtDNA between two population samples is a function of how long those populations have been undergoing independent evolution. Second, the differences between sub-Saharan modern humans and the other modern human populations suggested that modern humans originated in Africa around 200 kya. Third, they claimed that after modern humans left Africa they did not interbreed with any of the archaic populations they would have encountered as they moved

into the other main regions of the Old World. In effect, Cann and colleagues were suggesting that all modern humans were inherited from an ancestral population that had its origins in Africa, and because you inherit your mtDNA intact from your mother the inferred evolutionary history of mtDNA is effectively a history of maternal inheritance. The press dubbed it the 'Mitochondrial Eve' hypothesis, but Cann and colleagues never claimed that all modern human mitochondrial DNA can be traced back to a single *c*.200 ky-old African female. Some refer to it as the 'strong recent out of Africa' hypothesis (or SROAH), but as we will see most researchers who support a 'recent out of Africa' model for modern human origins support a less extreme version (i.e. they concede that Neanderthals and aboriginal hominins in other regions may have made minor contributions to the modern human genome—see above).

Let battle commence

So, the battles lines were drawn. In the 'red corner' the weak multiregional hypothesis (WMRH), and in the 'blue corner' the weak recent out of Africa hypothesis (WROAH). Remember that researchers who were unwilling to support the strong version of the multiregional hypothesis were more inclined to support a weaker interpretation that included gene flow between regions. Similarly, when other researchers tried to repeat Cann and colleagues' analysis using more up-to-date molecular methods, and more rigorous statistical techniques, they came up with different results, but they still pointed to Africa as the origin of a substantial amount of modern human mtDNA variation.

The male and the nuclear perspectives

While researchers were working on ways to refine the evidence for modern human origins that could be extracted from regional variations in modern human mtDNA, other research groups had set about tackling other parts of the genome. One of the parts of the nuclear genome they paid particular attention to is the DNA from the part of the male, or Y, chromosome, which has no equivalent on the female, or X, chromosome. Because it has no female counterpart, the DNA on that part of the Y chromosome does not get reshuffled during germ cell division: the technical term for it and the mtDNA is that they are both 'non-recombining' regions of the genome. So, this part of the Y chromosome DNA is like mtDNA except that it is transmitted from one generation to the next by males to their sons.

The results from studies of the Y chromosome were like those from the mtDNA studies. Twenty-one out of twenty-seven Y chromosome variants originated in Africa, and there was more variation in the Y chromosome of Africans than in all the people from other parts of the world. The mtDNA results were no ‘flash in the pan’. Much the same results have come from studies of nuclear genes, and like those in mtDNA and in the Y chromosome, nuclear gene studies are providing evidence of admixture between archaic and modern human genotypes.

The predominant message from DNA studies, be it from mtDNA, the Y chromosome, or the rest of the nuclear genome, is that most of the modern human genome originated in Africa. Another is that for the past 2 my Africa seems to have been the source of ‘pulses’ of hominin evolutionary novelty. The first pulse was the emigration of a *H. ergaster*-like hominin, the next a *H. heidelbergensis*-like hominin, and then perhaps several waves of migration of modern-human-like hominins, perhaps not looking very different, but with different cultural capacities and skills. One researcher, Alan Templeton, who pointed out the evidence for a series of migrations, gave his paper the apt title ‘Out of Africa Again and Again’, but it is now generally agreed that modern humans are derived from a relatively recent, *c*.75–45 kya, migration out of eastern Africa.

Migration or gene flow?

Novel genetic variants can reach beyond Africa in two ways. People can take them with them when they migrate, or they can transmit them by interbreeding. The latter mechanism involves Africans interbreeding with people in an adjacent region of the Old World, these people then in turn interbreeding with other people further away from Africa, and so on. The genes are transmitted rather like the baton in a relay race. This is the type of gene transmission implied in the ‘diffusion wave hypothesis’, which, as its title implies, suggests that novel genes spread in waves.

Modern humans beyond Africa

There are two discussions about the arrival of modern humans beyond Africa, be it in Europe, or anywhere else. One concerns the arrival of modern-human-looking people themselves, in other words the earliest fossil evidence of modern

humans. The other discussion concerns the arrival of modern human behaviour, in other words the earliest archaeological evidence of people doing things that archaeologists are satisfied only modern humans would have been able to do. Not surprisingly, the discussions about what constitutes modern human behaviour are even more spirited than those surrounding what constitutes modern human morphology. Once palaeoanthropologists managed to escape from the trap of equating modern human morphology with the morphology of modern Europeans, it became easier for them to recognize modern humans in different parts of the world. Archaeologists have also recognized that there is more to modern human behaviour than what our ancestors were doing in Europe *c*.40 kya. For example, the alleged lack of cave art in Africa was sufficient to dismiss Africa as a potential source of modern human behaviour. There are two good reasons to reject this argument. First, there *is* cave art in Africa; archaeologists had not been looking hard enough. Second, to have cave art you need caves, and in many parts of Africa there are no caves.

Ancient DNA chimes in

Before aDNA research was being recruited to help investigate the relatively recent evolutionary history of modern humans, the conventional wisdom was that the modern humans living in each of the major regions of the world are the direct descendants of founder populations derived from the most recent wave of modern human migrants from Africa. This scenario suggests that regions closer to Africa would have experienced longer periods of local continuity than regions further from Africa. Another expectation was that there would be more evidence of admixture between modern humans and Neanderthals closer to the likeliest locations for that admixture—the Near East for example—than in locations further afield.

The results of applying a series of tests based on within-population sequence variation to aDNA recovered from relatively recent fossils assigned to *H. sapiens* suggests that the reality is more complex than the conventional wisdom I have outlined. Regional continuity seems to be the exception, not the rule, and there are many instances where sequences from sub-recent modern human fossils from a region are more than subtly different from the sequences of the modern humans living in that region today.

‘Ghost’ populations

When David Reich and Nick Patterson applied these tests to European aDNA data, they concluded that the peopling of Europe involved hypothetical ancient ‘ghost’ populations. For the most part we only have the equivalent of circumstantial evidence for these ‘ghost’ populations, but in 2013 Eske Willerslev and colleagues published the genome of a 24-old ky boy from a site called Mal’ta in south-central Siberia, and its sequence matched the one predicted by Reich and his colleagues for the hypothetical ‘ghost’ population they called ‘Ancient North Eurasian’. Reich and his colleagues have predicted the existence of comparable influential populations in other regions of the world, such as the Basal Eurasians, two groups in North America, and the East African Foragers, but the fossil equivalents of these and other hypothesized ‘ghost’ populations have, thus far at least, proved to be elusive.

Modern humans in Europe

The earliest fossil evidence of modern humans in Europe comes from a *c*.40 ky-old site called Pestera cu Oase in modern-day Romania, and the earliest evidence of modern human behaviour in Europe comes from sites in modern-day Bulgaria dated to between 43 and 40 kya. Modern humans in Europe overlapped with the Neanderthals for up to 10 ky, with the most recent evidence for Neanderthals coming from sites such as St Césaire in France, Zafarraya in Spain, and Vindija in Croatia that are all dated to *c*.30 kya (Table 4).

Table 4 The main morphological and behavioural differences between modern humans and Neanderthals

	Modern humans	Neanderthals
MORPHOLOGY		
Brain size	Large	Very large
Brow ridges	Weak	Thick and arched
Nose and mid-face	Flat	Projecting
Cranial vault	Straight sides	Bulging sides
Occipital region	Round	Bulging
Incisor teeth	Small	Large

Thorax	Narrow	Broad
Pelvis	Small and narrow	Large and wide
Limb bones	Straight	Curved
Limb joints	Small	Large
Hand–thumb	Short	Long
Development—bones and teeth	Slow	Faster
BEHAVIOUR		
Stone tools	Small and specialized	Larger and cruder
Composite tools	Yes	No
Shaped bone tools	Yes	No
Personal decoration	Yes, and well developed	No

Modern humans in Asia

Although there is earlier evidence of modern-human-like fossils in the Near East at Qesem and Misliya Caves, the earliest evidence of modern humans in Asia is a *c*.100 ky-old collection of teeth from a limestone cave at Daoxian in southern China. The forty-seven teeth are modern-human-like in the sense that they have small and simple crowns with short and slender roots. This is consistent with a report of a modern-human-like finger bone recovered from Al Wusta in Saudi Arabia that is at least 85 ky-old. There is much older, 385–172 ky, evidence from a site called Attirampakkam in Tamil Nadu, India, of the types of stone tools (e.g. blades and points) that in other parts of the world have been associated with modern humans.

Modern humans reach Sahul and Oceania

Researchers have suggested that modern humans may have occupied one, or more, parts of Sahul, the landmass that includes Papua New Guinea, Australia, and Tasmania, by 65 kya. When water is locked up in polar ice caps and glaciers, the parts of the continental shelf that are exposed provide connections between landmasses that today are separated by water. If hominins were in Sahul by 65

kya then they must have been in Sunda, the landmass that includes mainland South-East Asia and the present-day islands that make up Indonesia, sometime before that.

But even if there was temporal overlap between modern humans and late *H. erectus*, the discovery that *H. floresiensis*, a ‘dwarfed’ form of early *H. erectus*, persisted until 60 kya on the island of Flores is a reminder that temporal overlap does not necessarily mean that their geographical ranges overlapped: different kinds of hominins could have lived on separate islands and not necessarily have come into contact with one another. The hominins that crossed the open water between Sunda and Sahul must have been able to construct rafts, or some other form of craft, as well as containers for food and water to sustain them during the voyage. In any event, by 35–30 kya modern humans in the Pacific region were skilled enough seafarers to reach many remote islands in Oceania including Timor, the Moluccas, New Britain, and New Ireland.

Modern humans in Sahul

The existing hominin fossil record suggests that modern humans were the only hominins to enter the region we call Sahul, so there is no question of overlap with earlier groups. The time of the initial arrival of modern humans in Australia is unknown, but archaeological evidence suggests they may have arrived by 65 kya, and there is excellent, well-dated, fossil evidence that confirms they were there between 40 and 35 kya. Modern human fossils in Australia show substantial morphological variation. The people living around Lake Mungo, in what is now New South Wales, had steep foreheads, taller brain cases, and flat faces, while the populations at Kow Swamp and Coobool Creek in Northern Victoria had more sloping foreheads, lower brain cases, and projecting faces. Some researchers interpret these morphological differences as evidence of more than one wave of immigrants, but most see no more variation than one would expect to see through time if a new species dispersed across a large new territory such as Australasia.

Modern humans in the New World

There were three routes from the Old World to the New, a direct crossing of the Bering Straits, island hopping from one Aleutian island to another, or across the

Atlantic. Today all three require a sea voyage, but for several periods during the past 40–30 ky the fall in sea level and the thick ice caused by the intensely cold conditions would have closed the Bering Straits and linked some of the Aleutian Islands, although the intense cold would have been a powerful deterrent to a journey from Siberia to Alaska. It is possible that modern humans following migrating herds of mammoths ventured unwittingly into the New World during cold episodes, but there is no evidence of a modern human occupation site in Alaska until 12 kya.

The conventional wisdom is that the immigrants made their way south along a relatively ice-free corridor in Alaska and western Canada, and then went on to populate all of North, Central, and South America relatively rapidly. However, there is remarkably little evidence of human occupation along what is presumed to be the route south. And some New World archaeologists use this negative evidence in support of other scenarios, including one suggesting that the first occupants of the New World may have travelled there directly from Europe.

For a long time archaeologists accepted distinctive stone tools called Clovis points as the earliest evidence of modern humans in the New World, but more recently researchers have unearthed evidence of a stone industry more primitive than the Clovis at several sites including Duktai in Alaska, Meadowcroft in Pennsylvania, Cactus Hill in Virginia, and Topper in South Carolina in North America. In South America the best-known sites are Taima-Taima in Venezuela, Pedra Furada in Brazil, and Monte Verde in Chile. Meadowcroft’s radiocarbon dates indicate it was inhabited by at least 14 kya, and perhaps as early as 20 kya. Monte Verde, which provides excellently preserved evidence of modern human behaviour in South America around 12.5 kya, was occupied year-round and there is evidence of a dwelling that was large enough to have housed 20 to 30 people.

No matter when, where, and how modern humans arrived in the New World, it did not take them long to spread rapidly into a diverse range of environments. It is likely there were several migrations of modern humans into the New World, each of which made their own contribution to the genetic and cultural diversity of New World populations.

Chapter 9

The future of human evolution

In this chapter I interpret ‘future’ in two senses. First, what are the next few decades likely to bring in terms of new evidence about human evolution? Second, are modern humans still evolving, and if so, what changes are we likely to see?

More fossils from existing sites

Researchers will continue to look for additional fossil evidence. Some will continue their work at existing fossil sites, others will look for new locations. Those who work at existing sites attract less attention, but adding information to the existing site samples of recognized hominin species is a significant scientific contribution. The hyper-megadont archaic early hominin *Paranthropus boisei* is particularly distinctive, to the extent that its crania, mandibles, and teeth are unlikely to be confused with those of other early hominins. By now researchers working at different sites have assembled quite large (20+) samples of some tooth types, so we looked at how increases in the sample size affected estimates of tooth size. What we found was that once you had collected 8–10 teeth, size estimates, as expressed by the mean value, became remarkably stable. What larger samples did was to change the range—the larger the sample, the more we learned about the nature of variation in *P. boisei* tooth crown and root morphology. So, collecting more examples of the same hominin is an important contribution to our understanding of human evolution. But even adding one, or two, new fossils can provide critical information about an existing taxon. This is particularly true for early hominin taxa in which the crania of males and females differ in both size and shape. Even a few cranial fossils make it less likely that you will make the mistake of thinking that smaller crania belonging to presumed

females, or larger crania belonging to presumed females, sample different species.

An excellent example of the importance of long-term field research at the same site is the results of many decades of collecting fossils at Hadar in Ethiopia. These efforts have expanded the sample of *Australopithecus afarensis* to the extent that it can now be used as the equivalent of a comparative reference sample to help researchers make decisions about the significance of variation in other smaller, and less comprehensive, site samples of early hominins.

New sites also help

Each new hominin fossil site provides evidence about the morphology and behaviour of early hominins. Even if the new site samples an already recognized hominin taxon, it will provide additional evidence about that taxon's morphology, its range, its age, and the types of habitat it preferred. It is important to realize that the fossils found at a site are just a tiny sample of a much larger population that lived in the past. Some researchers fall into the trap of assuming that site samples capture all of the variation displayed by the parent population, but common sense suggests this would be extremely unlikely. Each new site sample helps to build up a more realistic 'profile' of a taxon. Also, the nature of the fossil record is such that we only have access to evidence that geological processes allow us to see. Geological contingency is no respecter of an animal's actual geographical and temporal range, so site samples can only ever provide minimum estimates of the temporal and geographical ranges of a taxon. Each extinct hominin taxon almost certainly appeared *before* the oldest fossil evidence for it, and it almost certainly persisted *after* the most recent fossil evidence. The same logic applies to its range. New sites nearly always help narrow the gap between the *actual* and the *observed* temporal and geographical ranges.

What are the chances of finding new taxa?

Researchers have been looking for fossil evidence for human evolution for well over a century, so surely all of the taxa involved in our evolutionary history, especially the taxa involved in the early stages of our evolution in Africa, must have been discovered by now? There are several reasons why this is unlikely to

be the case. First, Africa is a large continent, and even if one errs on the generous side, the locations of the existing fossil sites cover no more than 2–3 per cent of its land surface. Second, it was not long ago that researchers realized that fossil hominins may go back to 8–7 mya, so it is only relatively recently that researchers have been looking in regions where sediments of that age are accessible. For both of these reasons, it would be foolish to assume that we know all the actors in the early phases of the human evolutionary drama, and as we saw in Chapter 8 ancient DNA extracted from relatively recent modern humans suggests that the taxonomic diversity that is evident in the hominin fossil record from 4 mya persisted until relatively recently.

Squeezing more evidence from the existing fossil record

Just as the future will bring new fossil evidence, it will also see changes in the way researchers extract evidence from the new and the existing fossil evidence. Our understanding of human evolutionary history has been revolutionized by researchers applying technical and analytical advances that have taken place in sciences other than palaeoanthropology. There will be improvements in the power of existing methods, and if the past is anything to go by, newly developed methods will be exploited to analyse the fossil record.

Two areas, molecular biology and imaging, will play even larger roles than they do now. Advances are almost certainly going to be made in the ability of molecular biologists to extract ancient DNA from fossils, and in the mathematical models that are used to interpret the DNA sequences that are extracted. In the past few decades, imaging modalities developed for use in clinical medicine have been successfully employed to recover information about the inner morphology of bones and teeth. As we accumulate these data from the bones of fossil hominins, information about the size and shape of the bony canals of the inner ear will help researchers better understand their posture and locomotion, and information about the density and orientation of the bony struts inside the medullary cavity of bones will help researchers better understand what activities individual hominins were performing. More detailed information about the microscopic anatomy of teeth will help researchers better understand the types of food the hominins were able to process, as well as providing important information about growth and development.

The lessons of history

No matter what about the past is being studied, there is always pressure to develop a comprehensive narrative for why something happened. What were the causes of the French Revolution? Or the First World War? Or the war in Vietnam? For all three of these examples scholars try to re-analyse the evidence within the public domain, or unearth fresh evidence. How will we know when we have enough evidence to justify generating a comprehensive narrative for human evolutionary history? The evidence we have for human prehistory is orders of magnitude less than it is for recent events in human history, and that is unlikely to change. A comprehensive explanation based on an incomplete data set is almost certainly wrong. Our task is to generate a narrative that can accommodate new evidence.

Contemporary human evolution

Cultural evolution has now largely, but not entirely, superseded the type of morphological evolution we can track by looking at bones and teeth. Technology has not only effectively blunted the influence of natural selection on the human phenotype, but it has also enabled many modern humans to enjoy improved life expectancy at each stage of their lives, with most of us enjoying long and productive lives. But this has not always been the case. Until relatively recently all modern human communities, in all regions of the world, combined high fertility with high mortality, with most of that mortality being the result of contracting communicable diseases early in life. This ubiquitous pattern began to change in the 18th century to one of lower fertility and lower mortality, with most mortality now occurring later in life as a consequence of non-communicable diseases. Although this change began in Europe, and intensified there at the time of the Industrial Revolution, it has since spread to many other parts of the world. But there is a price to be paid for living longer, which is exposure to the non-communicable diseases associated with ageing, such as heart and chronic respiratory disease, diabetes, and dementia.

No free lunches

Researchers are beginning to suspect there is an evolutionary link between these pre- and post-modern survival strategies. It makes intuitive sense that *before* the transition to modernity there would have been positive selection for genes that

increase fertility, and that seems to have been the case. But geneticists are familiar with a phenomenon called pleiotropy, which is when the same gene can have more than one effect. Some genes have different effects at different phases in the life cycle, and the effects of genes can be influenced by changes in the nutritional status of an individual.

The phenomenon of pleiotropy seems to have been at work in the case of some of the genes that improve the chances of an individual having more offspring. Stephen Stearns and colleagues suggest that when high fertility was an imperative, the genes that would have been selected for were those that were advantageous in the context of fertility. It turns out that some of the genes that improve fertility have a deleterious effect later in life. This is because they predispose those individuals to heart disease, especially so when those individuals are well nourished. When you did not live a long time these ‘downstream’ deleterious effects did not matter, but as soon as life expectancy increases, the ‘dark side’ of these genes is exposed.

So, the future of our species is less likely to be influenced by whether our bodies are up to the task. The weak link is more likely to be that our genomes were shaped in circumstances very different from those we face today. The agenda of a relatively new area of medical research, evolutionary medicine, tries to understand how our well-being is threatened by our evolutionary history.

Timeline of important events and discoveries relevant to human origins and evolution

6th c. BCE	Greek philosophers treat modern humans as part of the natural world
13th c. CE	Thomas Aquinas reconciles Greek ideas with the biblical narrative
1543	Vesalius prepares the first detailed and accurate description of the anatomy of modern humans
1758	Carolus Linnaeus assembles the first comprehensive taxonomy of living organisms and establishes *Homo sapiens* as the binomial for modern humans
1800	Georges Cuvier establishes the principles of scientific palaeontology
1809	Jean Baptiste Lamarck sets out the first scientific explanation for the Tree of Life
1822–3	The first fossil modern human discovery at Paviland on the Gower Peninsula, just west of Swansea, Wales
1829	Discovery in Engis, Belgium, of what later was recognized as a Neanderthal child's cranium
1830	Charles Lyell presents a scientific version of the origin of the Earth
1848	Discovery at Forbes' Quarry in Gibraltar of what was later recognized as an adult Neanderthal cranium
1856	Discovery of the Feldhofer Neanderthal skeleton
1858	Alfred Russel Wallace and Charles Darwin independently conclude that evolution is best explained by natural selection
1865	Gregor Mendel publishes the results of his experiments of the inheritance of discrete traits
1864	Feldhofer skeleton made the type specimen of *Homo neanderthalensis*
1868	Fossil evidence of modern humans discovered at the Cro-Magnon rock shelter at Les Eyzies in the Dordogne, France

1890/1	Eugène Dubois discovers the first early hominin from Asia at Kedung Brubus, Java; Dubois discovers a hominin skull cap at Trinil, Java
1894	Dubois makes the Trinil skull cap the type specimen of *Pithecanthropus erectus*
1907–8	Hominin mandible from Mauer, Germany, made the type specimen of *Homo heidelbergensis*
1924	The first African early hominin is discovered at Taung
1925	Raymond Dart makes the Taung child the type specimen of *Australopithecus africanus*
1926	Hominin teeth confirmed to be among the fossils recovered from what was then called Choukoutien (now Zhoukoudian)
1927	Davidson Black makes one of the Choukoutien teeth the type specimen of *Sinanthropus pekinensis*
1938	Robert Broom makes TM 1517 the type specimen of *Paranthropus robustus*
1940	Franz Weidenreich transfers *Pithecanthropus erectus* and *Sinanthropus pekinensis* to *Homo erectus*
1959	OH 5 recovered by Mary Leakey and Louis Leakey makes it the type specimen of *Zinjanthropus boisei*
1964	Louis Leakey and colleagues make OH 7 the type specimen of *Homo habilis*
1968	Camille Arambourg and Yves Coppens make Omo 18.18 the type specimen of *Paraustralopithecus aethiopicus*
1975	Colin Groves and Vratislav Mazák make KNM-ER 992 the type specimen of *Homo ergaster*
1978	Don Johanson and colleagues make LH 4 the type specimen of *Australopithecus afarensis*
1986	Valery Alexeev makes KNM-ER 1470 the type specimen of *Pithecanthropus rudolfensis*
1989	Colin Groves transfers *Pithecanthropus rudolfensis* to *Homo* as *Homo rudolfensis*
1994	Tim White and colleagues make ARA-VP-6/1 the type specimen of *Australopithecus ramidus*
1995	Tim White and colleagues transfer *Au. ramidus* to *Ardipithecus ramidus* Meave Leakey and colleagues make KNM-KP 29281 the type specimen of *Australopithecus anamensis*
1996	Michel Brunet and colleagues make KT 12/H1 the type specimen of *Australopithecus bahrelghazali*
1997	Jose-Maria Bermudez de Castro and colleagues make ATD 6–5 the type specimen of *Homo antecessor*
	Svante Pääbo and colleagues show that short fragments of DNA they recovered from the humerus of the Neanderthal 1 type specimen are almost certainly remnants of its mtDNA
1999	Berhane Asfaw and colleagues make BOU-VP-12/130 the type specimen of *Australopithecus garhi*
2001	Brigitte Senut and colleagues make BAR 1000'00 the type specimen of *Orrorin tugenensis* Michel Brunet and colleagues make TM 266–01–060–1 the type specimen of

	Sahelanthropus tchadensis
2004	Yohannes Haile-Selassie and colleagues make ALA-VP-2/10 the type specimen of *Ardipithecus kadabba*
2005	Peter Brown and colleagues make LB 1 the type specimen of *Homo floresiensis* Sally McBrearty and Nina Jablonski report the first panin fossils from Baringo, Kenya
2010	Lee Berger and colleagues make MH1 the type specimen of *Australopithecus sediba*
	Richard Green and colleagues report a draft sequence of a Neanderthal nuclear genome and suggest it shows evidence of a modest amount of admixture between Neanderthals and modern humans
	Johannes Krause and colleagues show that mtDNA recovered from a hominin finger from Denisova is distinct from both modern humans and Neanderthals
2012	Nick Patterson and David Reich present a method for predicting ‘ghost’ populations that contributed to the genome of contemporary modern humans
2013	Eske Willerslev and colleagues suggest the genome of a 24 ky-old boy from Mal’ta in south-central Siberia matches the sequence predicted for the hypothetical Ancient North Eurasian ‘ghost’ population
2015	Lee Berger and colleagues make DH1 the type specimen of *Homo naledi*
2016	Matthias Meyer and colleagues extract nuclear DNA from several of the 450 ky-old Sima de los Huesos hominins
2018	Viviane Slon and colleagues claim that a 90 ky-old individual from Denisova was a hybrid resulting from a mating between a Neanderthal mother and a Denisovan father

Further reading

Chapter 2: Finding our place

P. J. Bowler, *Life's Splendid Drama* (Chicago University Press, 1996): a historical account of the efforts of scientists to reconstruct the history of life on earth.

R. M. Henig, *The Monk in the Garden* (Houghton Mifflin, 2000): describes Gregor Mendel's plant-breeding experiments, and deals with how Mendel's work was rediscovered.

E. Mayr, *What Evolution Is* (Basic Books, 2001): a good introduction to the principles of, and evidence for, evolution.

J. A. Moore, *Science as a Way of Knowing* (Harvard University Press, 1993): beginning with the Greeks it traces the history of the major developments in biological research.

C. Zimmer, *She Has her Mother's Laugh* (Dutton, 2018): an excellent introduction to heredity.

Chapter 3: Fossil hominins: their discovery and context

J. Kalb, *Adventures in the Bone Trade: The Race to Discover Human Ancestors in Ethiopia's Afar Depression* (Springer-Verlag, 2001): focuses on the competition among scientific teams searching for early hominin fossils.

V. Morell, *Ancestral Passions* (Simon & Schuster, 1996): describes the Leakey family and many of their important discoveries.

P. Shipman, *The Man Who Found the Missing Link: Eugene Dubois and his Lifelong Quest to Prove Darwin Right* (Simon & Schuster, 2001): describes the efforts made by Eugène Dubois to find fossil hominins in Java.

C. C. Swisher III, G. H. Curtis, and Roger Lewin, *Java Man: How Two Geologists' Dramatic Discoveries Changed our Understanding of the Evolutionary Path to Modern Humans* (Scribner, 2000): chronicles efforts to generate absolute dates for the Javan hominins.

Chapters 4–6: Fossil hominins: analysis and interpretation; Early hominins: possible and probable; Archaic and transitional hominins

L. Humphrey and C. Stringer. *Our Human Story* (NHM, 2018): accessible review of the fossil evidence for human evolution.

I. Tattersall, *The Fossil Trail: How we Know What we Think we Know about Human Evolution*, 2nd edn (Oxford University Press, 2008): a very readable account of the history of the discovery and interpretation of the hominin fossil record.

B. Wood (ed.), *Wiley-Blackwell Encyclopedia of Human Evolution* (Wiley-Blackwell, 2013): detailed entries for nearly all the fossils and hominin species included in these chapters and Chapters 7–8.

B. Wood and A. Henry, *Wiley-Blackwell Student Dictionary of Human Evolution* (Wiley-Blackwell, 2015): a more accessible version of the above.

Chapter 7: Pre-modern *Homo*

Chris Stringer, *Lone Survivors* (St Martins Griffin, 2013): a reliable guide to the later stages of human evolution.

Chapter 8: Modern *Homo*

D. Reich, *Who We Are and How We Got Here* (Pantheon Books, 2018): one of the pioneers of the analysis of ancient DNA explains the complex evolutionary history of regional populations of modern humans.

J. H. Relethford and D. A. Bolnick, *Reflections of our Past: How Human History is Revealed in our Genes*, 2nd edn (Routledge, 2018): a clear and even-handed account of the implications of the inter-regional and inter-individual DNA differences among modern humans.

A. Rutherford, *A Brief History of Everyone Who Ever Lived: The Human Story Retold Through our Genes* (Weidenfeld and Nicolson, 2016): accessible account of how we come by our genomes.

Useful websites

<http://humanorigins.si.edu/>This is the website of the Human Origins Program at the Smithsonian Institution. It is careful, up-to-date, and authoritative.

<http://www.msu.edu/~heslipst/contents/ANP440/index.htm>This is a time-space chart of hominin fossils.

<http://www.becominghuman.org>This website is maintained by Arizona State University's Institute of Human Origins. The information is reliable and the images are carefully selected. You can see and learn about the hominin fossil record here.

http://www.talkorigins.orgThis website summarizes the major hominin fossil finds.

http://www.sciam.comThis site has links to biographies of scientists.

http://www.ucm.es/paleo/ata/portada.htmThis site has details of the important excavations at Atapuerca in Spain.

<http://www.neanderthal.de>An excellent site that features the discoveries from the Neanderthal Valley, near Düsseldorf, Germany.

<http://www.chineseprehistory.org>Provides images and background to fossil hominin discoveries from China.

<http://www.leakeyfoundation.org>The Leakey Foundation website has excellent links to other sites where readers can find information about the hominin fossil record.

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