

The History of Our Tribe: Hominini

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BARBARA HELM WELKER



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About the Book

Where did we come from? What were our ancestors like? Why do we differ from other animals? How do scientists trace and construct our evolutionary history? *The History of Our Tribe: Hominini* provides answers to these questions and more. The book explores the field of paleoanthropology past and present. Beginning over 65 million years ago, Welker traces the evolution of our species, the environments and selective forces that shaped our ancestors, their physical and cultural adaptations, and the people and places involved with their discovery and study. It is designed as a textbook for a course on Human Evolution but can also serve as an introductory text for relevant sections of courses in Biological or General Anthropology or general interest. It is both a comprehensive technical reference for relevant terms, theories, methods, and species and an overview of the people, places, and discoveries that have imbued paleoanthropology with such fascination, romance, and mystery.

Reviewer's Notes

KRISTIL L. LEWTON

Barbara Welker's *History of Our Tribe: Hominini* fills an important gap in current mid-level undergraduate human evolution texts. It is the only book of its kind to offer both an introduction to and a concise synopsis of human evolution broadly, including paleoanthropological methods (dating, classification, etc), morphology and behavior of extant and extinct primates, and encyclopedic entries on all known species of human ancestors. The book uses images from open access internet sources, as well as original drawings. In addition, links to useful websites where more information can be sought are included throughout the text.

The general layout and organization of the text are intuitive and the sequence of topics follows a logical progression that would nicely suit a typical undergraduate human evolution course. Background topics are introduced and explained as needed in a concise format that does not distract from the main themes and emphases of the text.

One very useful feature of this text is the complete, encyclopedic entries for each fossil hominin species. The entries for each species follow the same layout, starting first with the geologic dates associated with the taxon and important fossil sites and discoverers, followed by phylogeny, discovery and geographic range, physical characteristics, and environment and way of life. Each species entry includes a summarized list of the primitive and derived traits for that taxon, which will prove to be enormously helpful for students.

Dr. Kristi L. Lewton is an evolutionary anatomist and biological anthropologist. Dr. Lewton received her Ph.D. in anthropology from Arizona State University, conducted postdoctoral research at Harvard University, and is currently an Assistant Professor at Boston University. Dr. Lewton's research focuses on the evolution of primate locomotor systems, the functional anatomy of the pelvis, and reconstruction of locomotor behavior in fossil species.

Acknowledgements

The proposal for this book was chosen by the Open SUNY Textbook program in March 2014. The book represents nine months of writing and research. Three students helped me immensely during the project. Tyler Blank spent an entire semester researching new discoveries and editing and indexing the manuscript. Keenan Taylor spent a semester researching relevant ecology and anatomy in order to produce his beautiful illustrations that greatly enrich the book. Finally, Blain Shinkle had the daunting task of bringing order to the references that I cited. Many thanks to the external reviewer, Dr. Kristi Lewton, a biological anthropologist and evolutionary anatomist at Boston University. She expertly edited the manuscript and greatly improved it. Many times I was so caught up in thinking and writing that I neglected grammar and forgot the reader; Kristi consistently and gracefully put me back on track.

Acknowledgements: eCampusOntario

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Introduction

Where did we come from? What were our ancestors like? Why do we differ from other animals? How do scientists trace and construct our evolutionary history? I have attempted to answer those questions and more.

The title of this book is a bit tongue-in-cheek. Primate taxonomy has changed immensely in recent years, and while the changes make the subject more difficult to master, the classification of great apes is much improved. Like it or not, we are great apes. We used to have our own family, Hominidae, as distinct from the other great apes, making us the *hominids*. All great apes are now hominids. At the level of the subfamily, the Asian great ape (the orangutan) splits off, leaving us and our fellow African great apes in the subfamily Homininae. We are *hominines*. The gorillas then come out at the tribal level (Gorillini), leaving humans and possibly chimps, depending on who is doing the lumping or splitting, as members of the tribe Hominini. We are *hominins*. When we refer to hominins, we mean humans and our extinct bipedal relatives. Of course, the title likely first conjures a cultural aspect of human social organization, that is, the tribe, because most people are not familiar with new and improved human taxonomy.

That brings up my sense of humor. I am a naturally silly person, and I hope my nonsense will not be off-putting to the reader.

I wrote this book to fill a perceived gap between basic texts in physical anthropology and advanced books that cover paleoanthropology and fossil hominins in great detail. I designed it with my 200-level Human Evolution course in mind. I wanted more than is available in an introductory text without overwhelming students with the jargon, complex anatomy, numerous fossil sites, etc. of an advanced text. I also tried to avoid the general tedium of textbooks, but I am not sure if I succeeded. The book can also serve as a supplemental text (since it's free!) for any course that covers aspects of human evolution, such as Introduction to Anthropology, Introduction to Physical Anthropology, Human Ecology, Old World Prehistory, etc.

After presenting an overview of the discipline of paleoanthropology, I introduce nonhuman primates so as to show students where we fit and what we can learn from their ecology and behavior. I trace the evolutionary history of the primates, with a special emphasis on the ancestry of the hominins. An overview of human and hominin anatomy is presented so that students can understand how bodies changed over time as hominins came down from the trees, moved out of the forests, and began their globe-trotting adventures. The remainder of the book is dedicated to all of the extinct hominin species as well as the earliest members of our own species, *Homo sapiens*.

The hominins are organized chronologically, and this book includes the following information where available: (1) brief introduction; (2) phylogeny or evolutionary history; (3) discovery and geographic range wherein paleoanthropologists, sites, and famous discoveries are covered; (4) physical characteristics; and (5) environment and way of life, including relevant aspects of behavior and culture. I have tried to keep the hominin sections uniform and encyclopedic in nature so that students can quickly find what they need. Student aids and additional references are included.

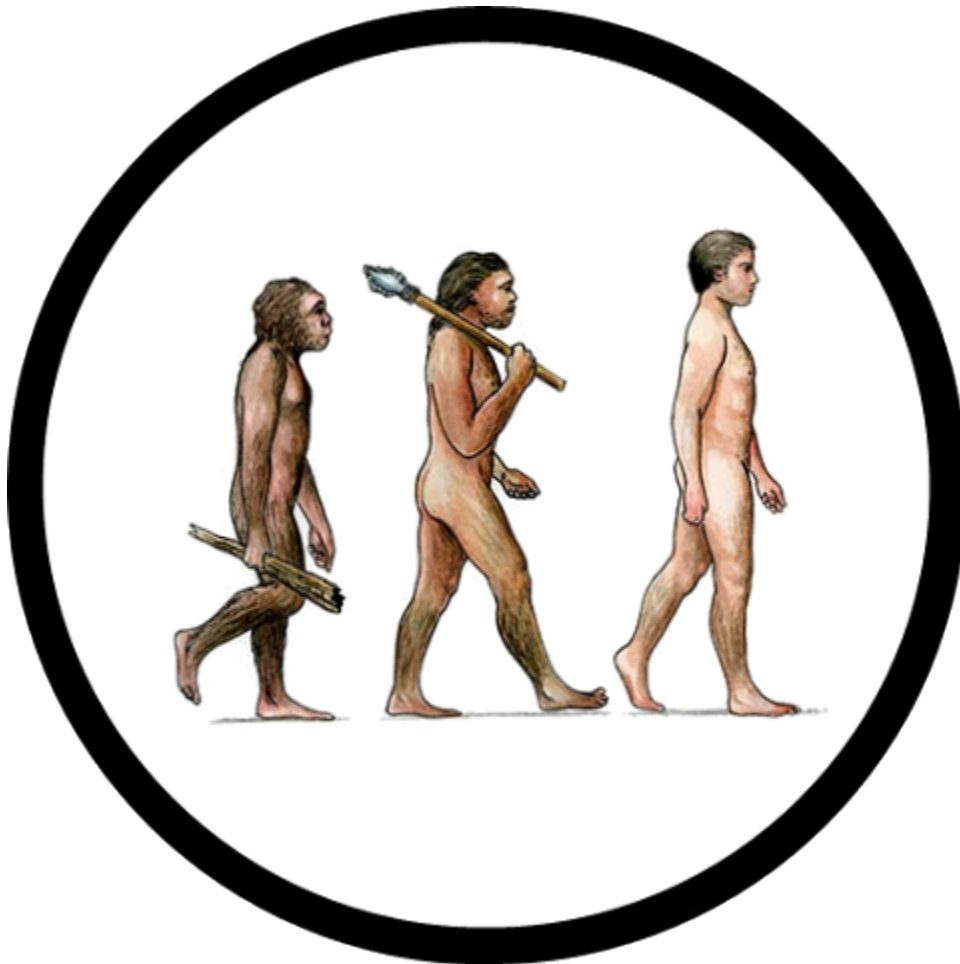
And now, a little about why the crazy monkey lady (as students are wont to refer to me) wrote a book on human evolution. I am an anthropologist, physical anthropologist, anatomist, primatologist, and behavioral ecologist. I have thus been trained in both animal and human behavior, from a cultural and biological perspective. I have taught comparative primate and human anatomy. I have been teaching General Anthropology, Physical Anthropology, Human Evolution, Human Ecology, Human Osteology (skeletal anatomy), and primate courses for 18 years. I have approached the topic of human evolution from the perspective of my training and experience. Thus I have covered what I learned about the various species, in terms of fossils, paleoanthropologists, sites, anatomy, and cultural remains; I have also focused where possible on their ecology and environment, the

adaptive significance of their morphology and behavior, and their behavioral ecology and socioecology, such as social organization, mating systems, male and female strategies, cognition and abilities, etc. My goal was to create a more holistic and enjoyable textbook by bringing the species to life. I have learned from the paleoanthropologists and strived to understand past species from my own perspective, founded in comparative primate anatomy, ecology, and behavior. My hope is that students will gain both an evolutionary perspective and a more synthetic understanding of hominins and themselves.

I hope readers will enjoy and benefit from the book. I have tried to keep it interesting, accessible, and uniformly organized. In proposing to write an open textbook, I wanted to provide students with a useful reference at no cost. While I think of some textbooks as expensive sleeping aids, at least mine is free!

PART I: AN INTRODUCTION TO PALEOANTHROPOLOGY

I. Paleoanthropology



Human evolution. “Human Evolution Icon” by Magnetic Hyena is licensed under CC BY-SA 3.0.

WHAT IS PALEOANTHROPOLOGY?

Paleoanthropology, a subdiscipline of anthropology, is the study of extinct primates. While the majority of researchers doing this kind of work are anthropologists, paleontologists (within the discipline of geology) may also study fossil primates. The primary method used by paleoanthropologists is the analysis of fossil remains. However, they increasingly rely on other scientific disciplines to gain a better understanding of the environmental forces that played a role in our evolution, as well as the formation of the fossil record. For example, **geologists** identify processes of sedimentation and fossilization, and date fossils and their associated sediments using a variety of techniques (see DATING TECHNIQUES below). A variety of disciplines are involved in helping to reconstruct ancient environments and biological communities. **Paleontologists** identify ancient floral and faunal fossils. **Palynologists** analyze particles in ocean and lake cores, as well as pollen in terrestrial sediments (see Figure 1.2), to determine the predominant flora in a given area at a particular time. **Taphonomists** help determine how fossil assemblages were formed.

In the 1920s, **Raymond Dart** proposed that early hominins (bipedal primates, like ourselves) found in South African caves had inhabited those caves. In addition, he interpreted puncture wounds found in some of the skulls as evidence that those hominins made and used weapons for hunting and male-male aggression. The taphonomist **C. K. Brain** argued in more recent times that either hominins fell through cracks into subterranean caves after having been cached in trees by leopards, or their bones were dragged in by rodents, such as porcupines, for gnawing. We now realize that while those early members of our tribe likely used simple tools, they were not big-game hunters or warmongers (see Chapter 15 for more information).



Pollen grains under scanning electron microscope. "Misc pollen colorized" by Dartmouth Electron Microscope Facility, Dartmouth College is in the public domain.

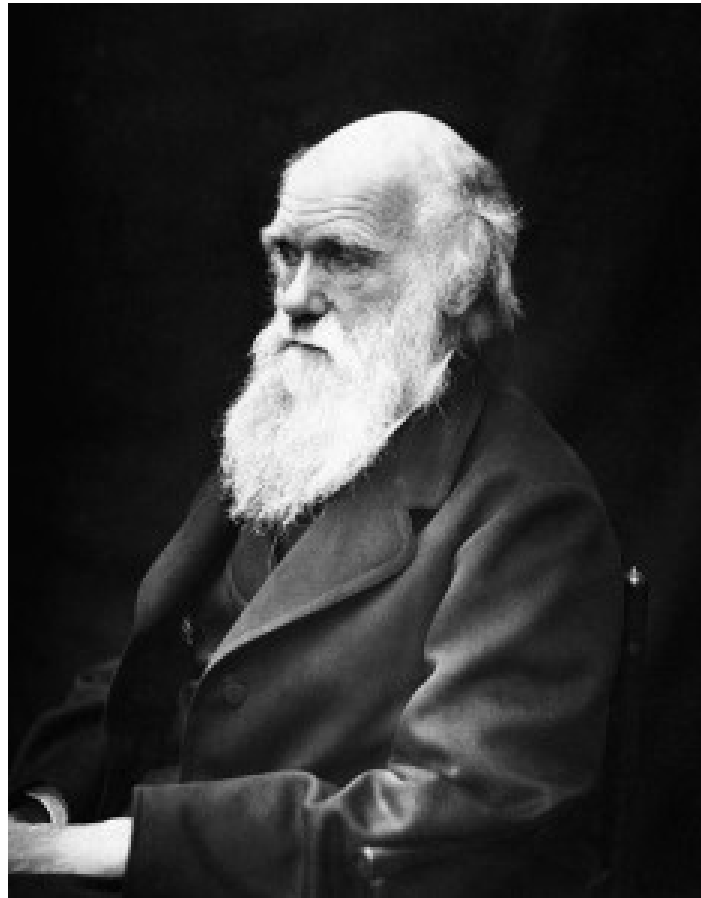
HISTORY OF THE DISCIPLINE

While paleoanthropology, as a formally recognized science, is fairly recent, questions and beliefs related to our origins extend back to the earliest members of our species and possibly even earlier. All modern humans living in traditional (e.g., hunter-gatherer bands, tribes, or chiefdoms) or state-level societies have a set of beliefs associated with their origins. However, any ideas that fall outside the realm of science are part of a culture's religion and are termed creation myths.

The most influential fields to have contributed to the science of paleoanthropology are geology, biology, and archaeology. Geologists (even those who were not recognized as such, e.g., Charles Darwin) are primarily responsible for the realizations that (1) the earth is ancient, and it formed via natural processes; (2) the earth was originally covered with water, and life began in that "primordial sea"; (3) life on earth originated with simple forms, with some descendent species becoming more complex over time, as can be seen in the fossil record; (4) species change or go extinct in response to environmental change; (5) new species are the result of a portion of a population adapting to new or changed environmental conditions; (6) the same forces, such as volcanic eruptions, that operate today are those that shaped the earth and caused changes in the fossil record via extinctions and speciation events; and (7) layers and deposits are continually developing or eroding so that organisms are buried and fossils come to light, respectively. The idea that the same forces that operate today are those that shaped the earth and caused changes in the fossil record is termed **uniformitarianism**. Charles

Lyell coined the term and is heralded as the father of modern geology. He greatly influenced Darwin and thus contributed to Darwin's synthetic view of the evolution of life on earth. Geologists use various methods to date fossils or fossil-containing sediments and have developed a **chronology** (i.e., a timeline) for the earth as a whole, as well as depositional layers in areas where fossils have been discovered.

Biologists and geneticists have refined the theory of **evolution by means of natural selection** by determining how traits are inherited. Scientists from a variety of disciplines have classified the known species of the world based on evolutionary relationships (also see Chapter 2).



Charles Darwin. "Charles Darwin 01" by J. Cameron is in the public domain.

Archaeology has played and continues to play a strong role in paleoanthropology via the study of the **archaeological record**, that is, the record of past human activity via cultural remains and **anthropogenic** (human-induced) changes to the environment. Thomas Jefferson has been referred to as the first archaeologist, in that his methods were more scientific than his fellow **antiquarians**. Antiquarians tended to be after the "goods," without regard for careful interpretation of the archaeological record. Most would be considered looters by today's standards. They took items of great cultural and historical significance for personal or museum collections. Some items have been returned to their countries of origin, but the damage is done when the archaeological record is disturbed or destroyed. Once an item has been removed from the area where it was found, scientists can no longer learn from its context, for example, from associated artifacts or the location of the artifact in geographic space and time.

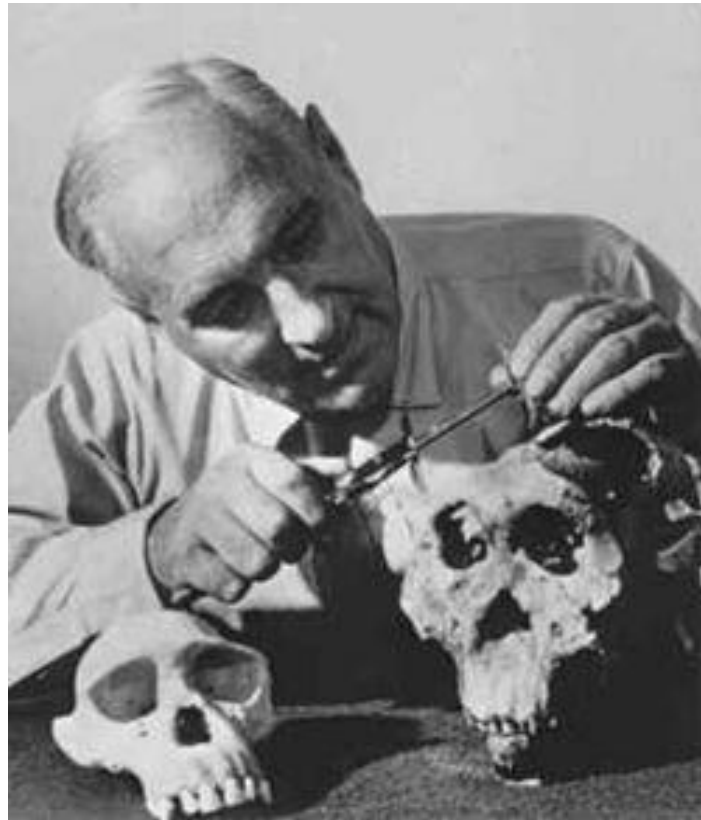
Archaeologists and geologists played a key role in recognizing that “stones and bones” were evidence of earlier hominin activities. In addition, the fact that some of the bones were from extinct animals supported the idea that humans had been around for a long time. Archaeological methods of excavation and analyses, such as the **provenience** (i.e., the three-dimensional location within a site) and association of **artifacts** (i.e., portable human-made or altered objects), help archaeologists and paleoanthropologists reconstruct past behavior. Just as taphonomy plays a role in determining how fossil assemblages came to be, it is also useful for archaeological assemblages.



Eugène Dubois. “Eugene Dubois” is in the public domain.

According to *Merriam-Webster Online*, the first known use of the term “paleoanthropology” occurred in 1916. However, the earliest paleoanthropologists were not labeled as such and came from a variety of occupations, such as anatomists and physicians. The first hominin fossils discovered were the neandertals in the 1800s. However, paleoanthropologists disagreed about whether neandertals were ancestors of humans or were modern humans. **Eugène Dubois** was the first person to intentionally search for a fossil hominin. He went to Asia with the sole purpose of finding evidence that humans evolved there, as was the reigning belief in Western Europe. In 1891, he discovered a skull cap (known as a **calotte**) and femur on the **Solo River** in **Trinil**, Java. More discoveries in China and Java during the first half of the 20th century supported the Asian origin theory until Raymond Dart and his contemporary, **Robert Broom**, began discovering much more ancient material in South African quarries

and caves. Further discoveries by **Louis** and **Mary Leakey** in East Africa cemented Africa as the birthplace of humanity, and the race to find human origins and ancestors was on.



Louis Leakey. "Louis Leakey" is in the public domain.

RECONSTRUCTING PALEOENVIRONMENTSA variety of tools can be used to determine the type of environment past species occupied. As mentioned, paleontologists can use floral and faunal analyses and what they know about ancient species or their extant relatives to determine environment type, for example, the presence of aquatic-, grassland-, and/or forest-dwelling species. Palynologists examine particulates in aquatic and terrestrial strata (i.e., layers or sediments) to do the same, primarily focusing on floral analyses. A variety of isotopic tools can be used to categorize floral and/or faunal communities at a given site, such as hydrogen, oxygen, and carbon isotope fractionation and nitrogen isotope ratios. For example, calcium-rich remains such as eggshells, bones, and teeth can be analyzed isotopically to determine what types of vegetation those animals consumed and hence, the type of environment in which they lived. The strontium-to-calcium ratio in bones and teeth can be used to determine the amount of animal versus plant matter in the diet. Based upon that technique, scientists now believe that paranthropines, a group of hominins in East and South Africa dating from the early- to mid-Pleistocene (see Chapter 16), ate some animal matter. However, whether they were consuming insects or larger prey is not known.

For more information on the aforementioned methods, consult Henke W, Tattersall I. 2006. *Handbook of paleoanthropology*. New York (NY): Springer.

DATING TECHNIQUES

Dating techniques fall into two categories, relative and absolute. **Relative dating techniques** (1) ordinarily rank **strata** relative to one another through time (see Figure 1.6) or (2) use what is known about deposits in one area, such as volcanic ash or lava, to relatively date deposits in another area. Jefferson is credited with the **Law of Superposition**, which posits that as you go deeper into the earth, layers get older, as long as strata have not been disturbed due to human, animal, or geological activity. Thus artifacts or fossils found in one layer are either older or younger than those in a deeper or shallower layer, respectively. **Absolute dating techniques** use similarities in (1) floral and faunal assemblages or (2) sedimentary and/or chemical composition of deposits in order to match those of unknown age with those of known age and/or order the progression of environments, organisms, and climatic and geological activity within or between regions.

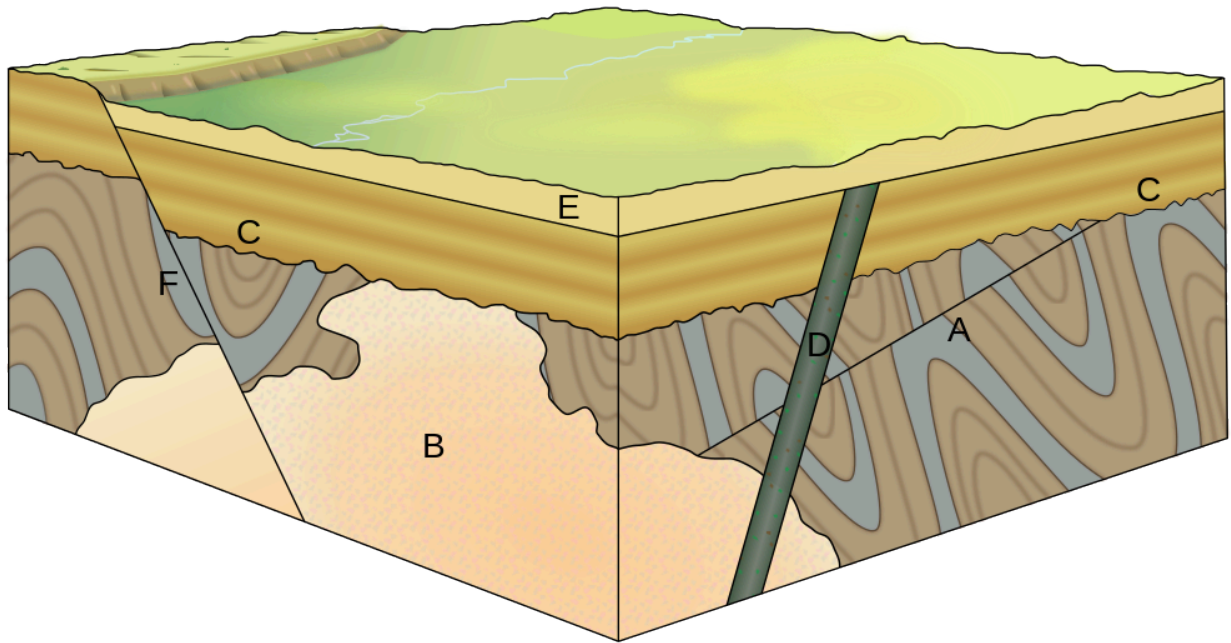


Diagram illustrating cross-cutting relations in geology. These relations can be used to give structures a relative age. Explanations: A – folded rock strata cut by a thrust fault; B – large intrusion (cutting through A); C – erosional angular unconformity (cutting off A & B) on which rock strata were deposited; D – volcanic dyke (cutting through A, B & C); E – even younger rock strata (overlying C & D); F – normal fault (cutting through A, B, C & E). Cross-cutting relations by Woudloper is licensed CC-BY-SA.

Absolute or chronometric dating techniques yield approximate dates in years **BP** (before the present) or **BCE** (before the Common Era). BCE and CE (Common Era) retain the BC/AD system of dating without the religious connotation. An abbreviated way to refer to a certain number of years ago, especially when considering the fossil record, is kya or mya (thousands or millions of years ago, respectively), thus eliminating all of those ungainly zeroes! While BP makes more sense in that you do not need to add 2,000+ years to the date, most people are accustomed to the BC/AD system, thus explaining the common use of BCE. The best-known absolute dating techniques are **radiometric dating methods**, for example, Carbon-14 (^{14}C). They are used to measure the half-life or replacement of radioactive elements in organic or fossil material or the layers in which they are found. Since those methods are time-limited and/or context-specific, the most appropriate technique(s) must be chosen based on a variety of parameters. The following techniques use radioactive decay for dating purposes:

[NOTE: For more information on the following methods, consult Henke and Tattersall (2006), *Handbook of Paleoanthropology*; and/or Davis (2009), “Other Dating Methods”: <http://www.geo.arizona.edu/palynology/geos462/11datingmeth.html>.]

Carbon-14 dating (≤ 60 kya) measures the remaining ^{14}C in organic materials (i.e., carbon-containing). Since plants use carbon dioxide for photosynthesis, they contain all three isotopes of carbon (^{12}C , ^{13}C , and ^{14}C) in the approximate ratios present in the atmosphere. Animals eat plants and thus, at any particular time, they will all have approximately the same amount of ^{14}C . Once they die, they no longer accumulate carbon. The level of the more stable ^{12}C can then be compared to the remaining ^{14}C in organic remains to determine when they died. The half-life of ^{14}C is $\sim 5,700$ years, that is, half of the ^{14}C will have been lost in a specimen in that amount of time.

Uranium series dating (≤ 500 kya) examines the relative levels of two elements, Uranium-234 and Thorium-230, resulting from the former’s decay into the latter. It is used to date calcium carbonate in coral and shells.

Potassium-Argon (K/Ar) and Argon-Argon (Ar/Ar) dating both measure the ratio of one isotope to another via the process of radioactive decay, Potassium-40 \rightarrow Argon-40 and Argon-40 \rightarrow Argon-39, respectively. They are often used to date volcanic layers but can also be used on other soil components, such as clay. While the age range for both methods may be reported to be unlimited, K/Ar dating is not useful for “young” materials because the half-life of potassium is so long—1.26 billion years.

Other methods that also rely on radioactivity are:

Electron spin resonance (ESR) (up to “a few” mya) examines the pattern of electrons that have “spun” out of their original location in mineral compounds (e.g., calcium compounds), leaving empty spaces behind, due to exposure to environmental radiation. Tooth enamel is the most useful application of ESR in paleoanthropology, but ESR can also be used to date quartz particles in sediments (Wagner 2006).

Fission track dating (20 mya— >10 kya) measures the number of “tracks” (pitting) in mineral compounds that result from the energy released when Uranium-238 spontaneously fissions over time. This method can be used to date a variety of minerals, such as mica, as well as products of volcanic (e.g., obsidian) and meteoric activities (Davis 2009; Wagner 2006).



Apatite crystals can be used in fission-track dating. “Apatite crystals” by OG59 is in the public domain.

Thermoluminescence (300–1 kya) measures radioactive decay particles in mineral compounds. It is useful for compounds that were exposed to intense heat (e.g., volcanic eruption) at some known point in time, when the “radioactive clock” was reset to zero and decay began anew. Thermoluminescence can be used to date artifacts (e.g., ceramics) and features (e.g., hearths), as well as products of sedimentation (e.g., speleothems, which are mineral deposits that form in caves) and volcanic activities (e.g., tephra, which are fragments from volcanic eruptions) (Davis 2009).

The following methods do not rely on radioactive activity but rather organic processes:

Dendrochronology uses tree rings in fossil or charred wood to date artifacts or fossils found in association with the wood. Each year, trees produce a new layer of peripheral tissue. When climatic conditions are favorable, more tissue is deposited and a thicker ring results, and vice versa. A cross-section of the tree tells the history of its growth (see Figure 1.8). However, in order to use dendrochronology as a dating method, a **chronology** (temporal record) needs to be constructed for a given region, in this case a map of the annual growth rate back through time. Living trees and dead wood can be used as long as there is overlap in ring patterns between them.



Dendrochronology: tree ring dating. “Dendrochronologie” by Stefan Kühn is licensed under CC BY-SA 3.0.

Amino acid racemization (2 mya–2 kya \pm 15%) measures the ratio of two forms of an amino acid, one produced while an organism is alive and the accumulation of a second form after death. If the ambient temperature at the time of death can be approximated, the specimen can be dated and vice versa (Davis 2009).

Paleomagnetism (hundreds of thousands–millions of years, Fagan 2000) measures past changes in the earth’s paleomagnetic fields that are preserved in some common minerals found in rocks and sediments. Since scientists have established a chronology of those changes, the materials can then be given approximate dates as to when they formed. When paleomagnetism is used to date archaeological materials, it is termed archaeomagnetic dating.

Obsidian hydration (100–1 mya) is used to date volcanic glass, that is, obsidian, by examining the amount of hydration that has occurred due to exposure to the elements. It is useful in dating obsidian artifacts as well as glacial and volcanic activities (Davis 2009).

Surface or Cosmogenic Nuclide Exposure Dating measures the amount of time that rocks have been exposed to the elements. It can be used to date glacial, lava, and rockslide movements and damage from extraterrestrial activities (e.g., solar flare-ups or meteorites) (Davis 2009; Wikipedia contributors 2015i).

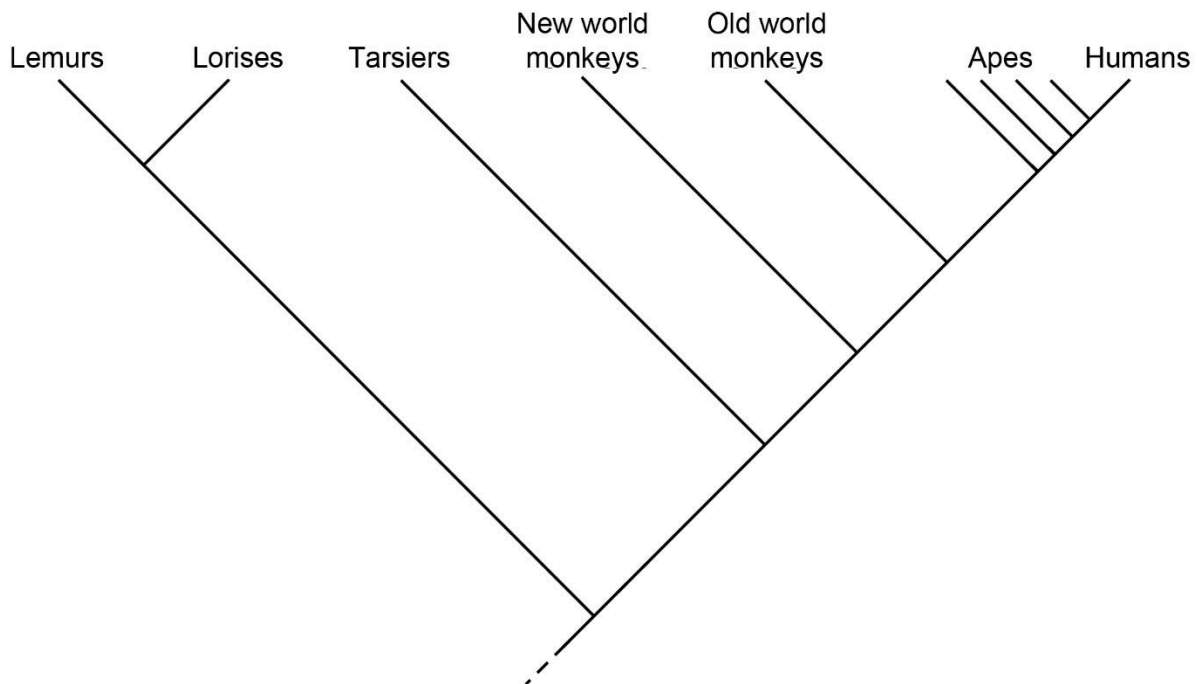
ADDITIONAL STUDENT RESOURCES

Henke W, Tattersall I, editors. 2006. *Handbook of paleoanthropology*. New York (NY): Springer; [accessed 2015 Aug 15]. http://www.evolbiol.ru/large_files/handbook_paleoanthropology.pdf.

2. Primate Classification

SYSTEMATICS: THE SCIENCE OF CLASSIFICATION

There are two means by which scientists classify organisms, **classic taxonomy** and **cladistics**. Paleoanthropologists are trained in evolutionary theory, and both biologists and paleontologists rely principally upon cladistics. There is definite utility in using a combination of both systems, that is, the binomial nomenclature (genus and species) of classic taxonomy combined with the cladistic arrangement of species in terms of shared characteristics. Classic taxonomy is based on the system begun by John Ray and elaborated by Carolus Linnaeus: kingdom, phylum, class, order, family, genus, species, etc. It classifies organisms based on descent from a common ancestor, using similarities in physical characteristics. We are *Homo sapiens*, as distinct from other members of our genus, such as *Homo neanderthalensis* (i.e. Neandertals). Note that since the “h” in *neanderthalensis* is silent, it is sometimes omitted from the common name. Cladistics refines classic taxonomy by linking organisms, based on the presence or absence of unique characteristics, into “grades.” For example, if three species share a suite of characteristics but only two of them have a particular trait that is not present in more distantly related species, those two are more closely related and would be depicted as a separate grade. Figure 2.1 depicts five primate grade.



Cladogram of Primates

“Cladogram of Primates” by Petter Bøckman, CC BY-SA 3.0.

The following terms are used to delineate characteristics in cladistics:

- **Plesiomorphy**—a primitive trait that is present in the ancestor as well as descendent species, for example, **pentadactyly** (five digits) in primates is an ancient trait seen in amphibians and reptiles.
- **Apomorphy**—a derived trait that is not found in the ancestor but is present in descendent species, for example, nails in primates.
- **Autapomorphy**—a unique derived trait present in member species of a particular grade, for example, the lack of a tail in apes.
- **Synapomorphy**—a trait inherited by members of two or more grades from their common ancestor, wherein the trait was an apomorphy, for example, **bipedalism** in the various grades within our tribe, **Hominini**.
- **Homoplasy**—a trait in more than one grade that evolved independently, for example, **brachiation** (swinging by one's arms) in some New World monkeys and apes.

PRIMATE CLASSIFICATION

We are primates, that is, members of the order **Primates** (prī-mā'-tēz). The pie chart in Figure 2.2 shows the various orders of animals within the class **Mammalia**. We are most closely related to **tree shrews** (order: Scandentia) and **colugos** (order: Dermoptera, also known as flying lemurs). Primates are distinguished by a suite of characteristics known as **evolutionary trends** (see table below). However, we do not exhibit all of them to the same degree, and some are absent in certain species or lineages. For example, **prosimians** retain a claw on the second digit of their feet, whereas **anthropoids** do not (more about the two primate groups later). These trends were first proposed by Napier and Napier (1967) and Le Gros Clark (1959), and more recently primatologists have refined and added to the list.

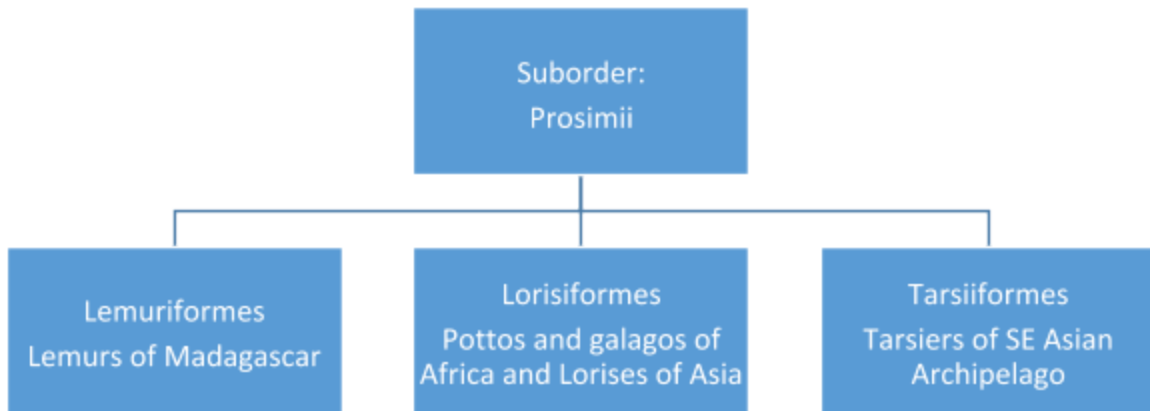


Orders within the class Mammalia. "Mammal species pie chart" by Aranae is in the public domain.

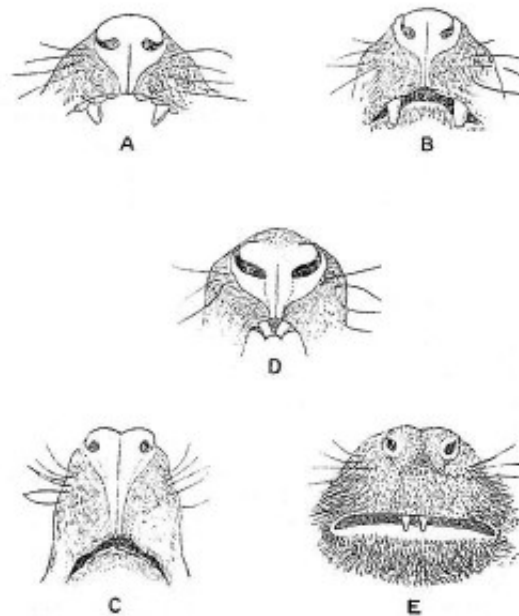
PRIMATE EVOLUTIONARY TRENDS

- Generalized, unspecialized skeleton:
 - No loss of limb bones from the ancestral condition.
 - Presence of a clavicle that allows greater mobility.
 - Capable of varied movement and locomotion.
- Large, complex brain (relative to body size), especially cerebral cortex.
- Decreased reliance on olfaction:
 - Reduction of snout and olfactory bulb in frontal cortex.
- Increased reliance on vision:
 - Enlarged visual cortex, greater visual acuity, and color vision.
 - Forward-oriented, overlapping fields (**binocular**) of vision, and excellent depth perception.
- **Prehensile** (grasping) hands and feet and **opposable** thumb and big toe.
 - Nails instead of claws.
- Long pre- and post-natal life periods with greater reliance on learning.
- Tendency toward diurnality.

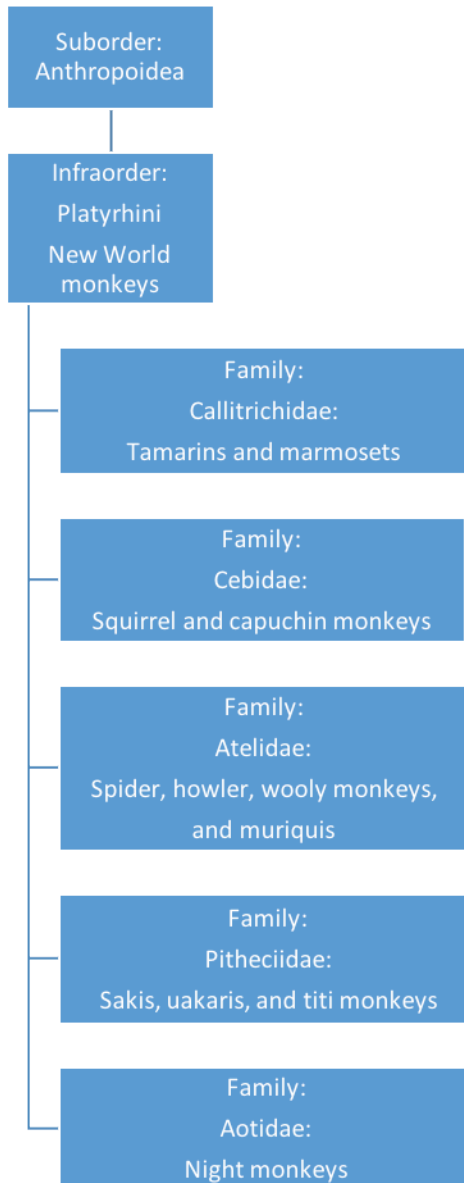
Taxonomic charts of the living primates can be found below. The primates are divided into two major taxonomic groups: strepsirrhines, which retain **primitive** characteristics, such as the lemurs of Madagascar and the bushbabies of Africa, and the more derived haplorrhines, that is, the tarsier, monkeys, and apes. The older terms for the suborders that are still in popular use are **Prosimii** (see figure 2.3) and **Anthropoidea**. However, tarsiers (small, nocturnal prosimian from the islands of the Southeast Asian archipelago) have characteristics of both groups. The strepsirrhine primates have more typical mammalian noses or rhinaria (see Figure 2.4) that are moist and more complex. They have a larger olfactory bulb in the frontal cortex of their brains and scent glands in various locations on their bodies. They use those glands to communicate to other members of their species. We haplorhines have simpler, dry noses and do not smell as good!



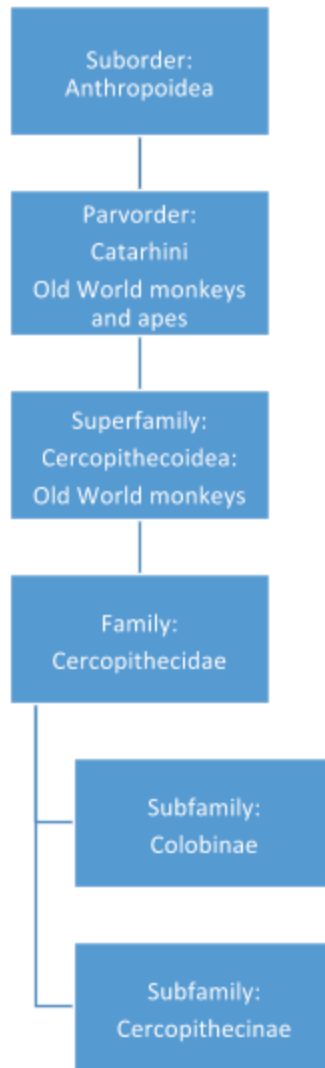
Prosimian classification.



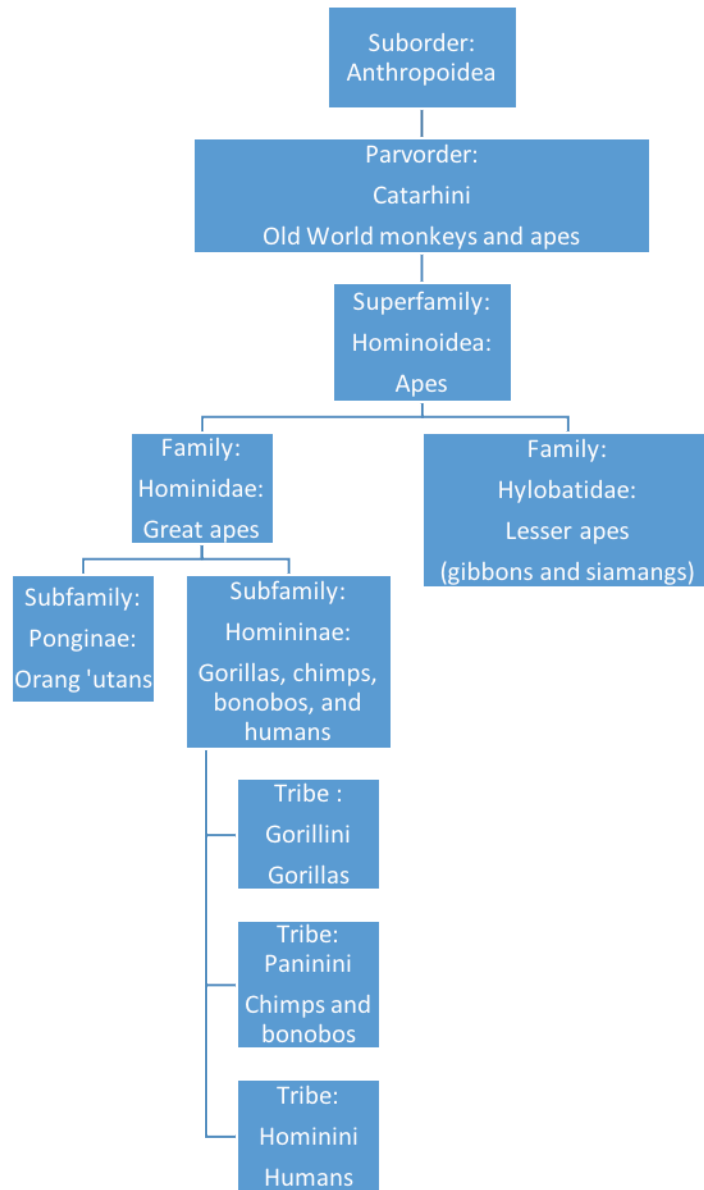
Prosimian noses (A through D) and the nose of a New World monkey (E). "Prosimian noses" by Reginald Innes Pocock is in the public domain.



New World anthropoid classification.



Old World monkey classification.



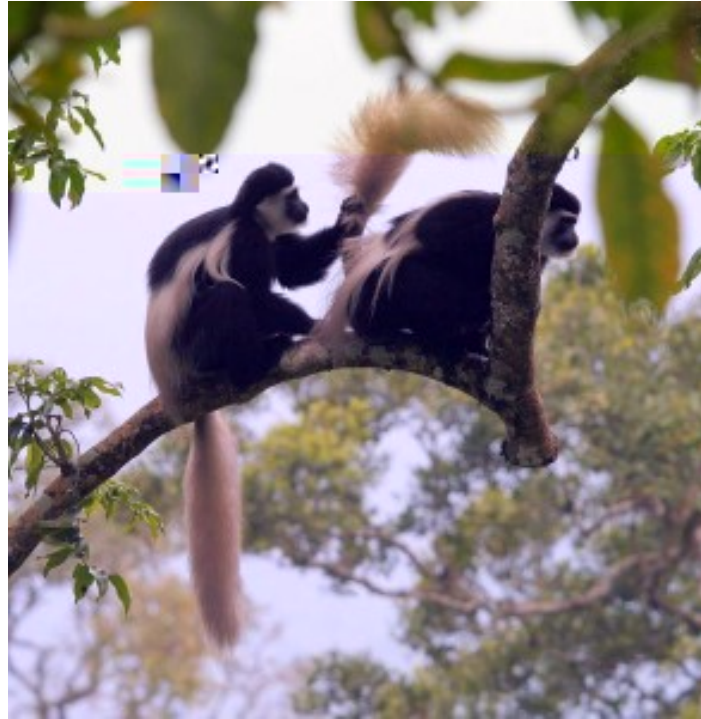
Ape classification.

As we learn more about biochemical and evolutionary relationships among the various groups of primates, primate taxonomy is changing. The **New World monkeys** (see Figure 2.5) have changed substantially in recent years, with the creation of multiple families that were formerly grouped into two or three.

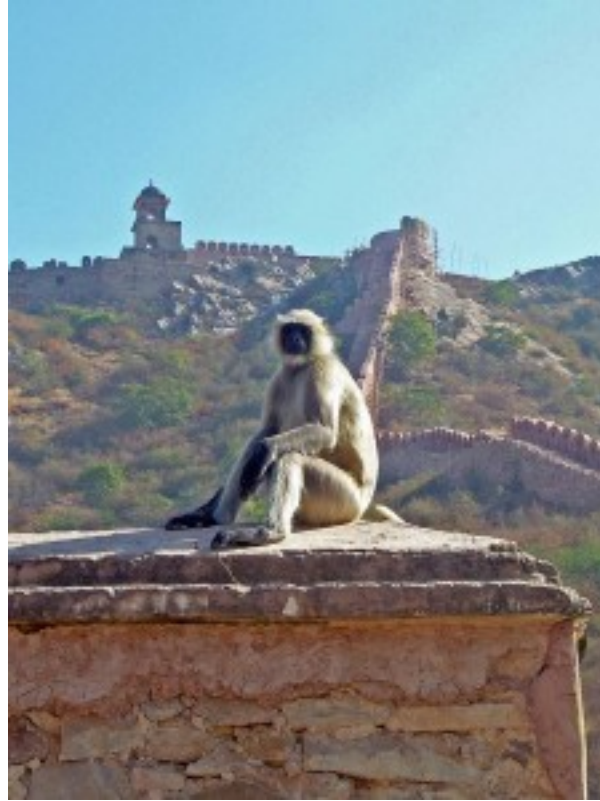
The Old World anthropoids (monkeys and apes) and New World monkeys are also distinguished by our noses. Old World anthropoids have more ovoid, downward-facing nostrils, whereas New World monkeys' nostrils are round and forward-facing.

The Old World monkeys (see figure 2.6) are divided into the **cercopithecines**, with their cheek pouches and more generalized diet, and the leaf-eating **colobines**, with their complex guts. Think baboon (Africa) or snow monkey (Japan) for the former and black-and-white colobus (Africa) or Hanuman langur (primarily Indian

subcontinent) for the latter. When asked, most people are more familiar with the cercopithecines, but if they see a picture of a black-and-white colobus (also known as a guereza) leaping through the air with its white mantle of fur and tail flying (or not...see Figure 2.8! I couldn't find an action shot!) or a Hanuman langur sitting on the steps of a temple (OK, a fort . . . see Figure 2.9!) in India, they usually recognize them.



Black-and-white colobus monkey. "Colobus guereza Mantelaffen" by Yoky is licensed under CC BY-SA 3.0.



Hanuman langur. “Langur-Amber Fort” by McKay Savage is licensed under CC BY 2.0.

The taxonomy of the apes (see Figure 2.7) has finally been updated. Until recently, humans were separated from the other great apes at the “family” level. All great apes are too closely related to be separated into different families. The **lesser apes**, i.e. the gibbons and siamangs of Southeast Asia, are still separated into their own family, the Hylobatidae. All of the **great apes** are now in the family **Hominidae**, formerly our exclusive domain. The orangutans come out at the subfamily level, leaving the African great apes in the subfamily **Homininae**. The gorillas have their own tribe, Gorillini (using the genus *Gorilla* to form the name) and if the chimps (genus *Pan*) are taken out of our tribe (**Hominini**), they are assigned the tribe **Panini**! I did not make that up! Some experts suggest that chimps and humans should be included in the same genus.

APE CHARACTERISTICS

“Why are sleeves always too short for me?”

We apes share a suite of characteristics (in varying degrees), and we humans have radically changed as we abandoned a more typical ape habitat and adapted to a more open terrestrial landscape. The table below lists great ape characteristics.

Great Ape Characteristics

- Relatively large brains.
- Y-5 molar—apes have a characteristic pattern of cusps and fissures on one or more mandibular molars.
- **Honing complex** consisting of large canines that are sharpened (honed) on the first lower premolar, termed a **sectorial premolar**.
- Upright trunk posture.
- Short, shallow, wide rib cage.
- High degree of mobility in joints of shoulders and wrists, termed the “**suspensory hanging adaptation**.”
- Long arms and short legs.
- Long, curved hand and foot bones.
- Variable degree of sexual dimorphism (i.e., differences between male and female morphology) in body size.
 - Low in humans, moderate in chimps, high in gorillas and orangutans.
 - Pronounced male prognathism (jutting jaws or muzzle) and large canines, depending on species.
- Long life stages, especially the juvenile dependency period.
- Build nests.
- Capable of learning and using symbols.
- Tool use with some modification (e.g. chimps and orangutans preparing a stick for probing).

The ancestor of the great apes was an arboreal climber. At some point, apes deviated from the more quadrupedal monkey-like morphology, in favor of (1) a more upright, shorter, broader, shallower trunk (just think of our thorax versus a dog's); (2) elongated upper limbs; and (3) more mobile shoulder and wrist joints. While we cannot swing by our arms as well as the lesser apes (brachiation is the technical term), we great apes retain the **suspensory hanging adaptation** and can swing to varying degrees, as long as the tree will support us. Adult male gorillas do not swing because they are too massive!

As hominins, or bipedal apes, came to rely less on an arboreal environment, the bones of our ancestors' hands and some foot bones became shorter and straighter and our legs became longer and more efficient for covering long distances on African landscapes. Beginning with the emergence of our own genus: *Homo* (~2 mya), we became increasingly **encephalized** (i.e. an increase in brain size relative to body size), leaving our fellow great apes behind. While all great apes are **sexually dimorphic** in terms of body size (i.e., males are larger than females), humans are less so and the trend began even prior to our own genus. Depending on which fossil hominins we include in our lineage, male canines were either monomorphic (i.e., male and female canines were the same size) or became less dimorphic over time. This is significant because male canine dimorphism is associated with competition for females, i.e. males bite one another! If we accept, for example, that we are descended from the **ardipiths** (see Chapter 8) that lived over 4 mya, ancestral males did not have large canines. However, there is better evidence that we are descended from the **australopiths** and within that lineage, male canines were initially larger than females' and became smaller over time.

Apes live a relatively long time and consequently all of our life stages are prolonged as well, especially our juvenile dependency period. Of the nonhuman primates, orangutans win. Female orangutans have an interbirth interval (i.e. a period of time in between births) of eight years and juveniles do not even start wandering off until they are seven. That is not good news from a conservation perspective!

All great apes build nests and scientists speculate that our ancestors likely did as well, at least until they left the trees. We also use tools. Chimps are the champs when it comes to tool use, e.g. nut cracking, ant fishing, etc. Orangutans are very adept at tool use as well, but their thumbs are short and more distant from their fingers, so that their opposability is poor. Consequently, they use their mouths to trim sticks and manipulate them for the desired task. In captivity, they also use their mouths to draw and paint. While gorilla tool use had been known from observations of gorillas in captivity, the use of a tool in the wild was finally recorded in 2005 when a female used a stick to test water depth. Of course, we humans are on a whole different level and we can trace the development of hominin technology in the archaeological record to over 3 mya.

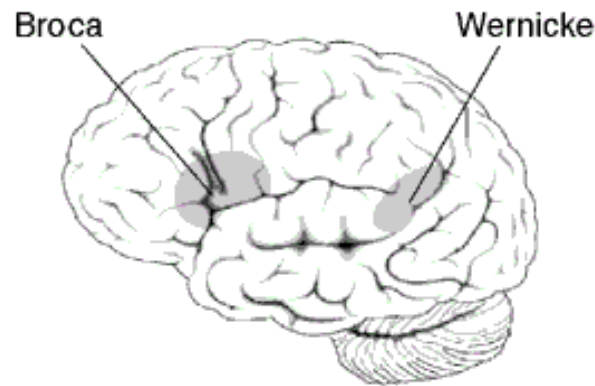
We have two language centers in our brain, **Broca's** and **Wernicke's areas** (see Figure 2.10). Broca's area is found in all Old World monkeys and apes; it plays a role in the motor control involved with speech production. As we well know from language studies, all nonhuman great apes are capable of learning and using symbols and have even made up a few. Washoe, the famous chimp that was taught American Sign Language, strung together the signs for "water" and "bird," when she saw a duck for the first time. Where they fall short is in using syntax; they are poor at correctly stringing symbols together into meaningful sentences. However, Kanzi, the super bonobo at Sue Savage Rumbaugh's lab, does pretty well. Check him out in the video below.



Kanzi and Novel Sentences by Iowa Primate Learning Sanctuary <https://youtu.be/2Dhc2zePJFE>

It is pretty convincing that he understands some syntax with following her commands, such as putting the pickles inside the vacuum cleaner versus the vacuum cleaner inside the pickles! Okay, I made that one up

but the things she has him do, in order to convince us that he understands, are amusing and amazing! We and our ancestors, beginning with the genus *Homo*, also have Wernicke's area. While a homologous area is present in monkeys and apes, ours has much broader interconnections and is uniquely involved with speech comprehension. At what point our ancestors began to speak is a highly contested topic but the archaeological record provides some clues (see Chapters 23 and 28).



Broca's and Wernicke's areas (left side of brain).
"BrocasAreaSmall" by the National Institutes of Health is in the public domain.

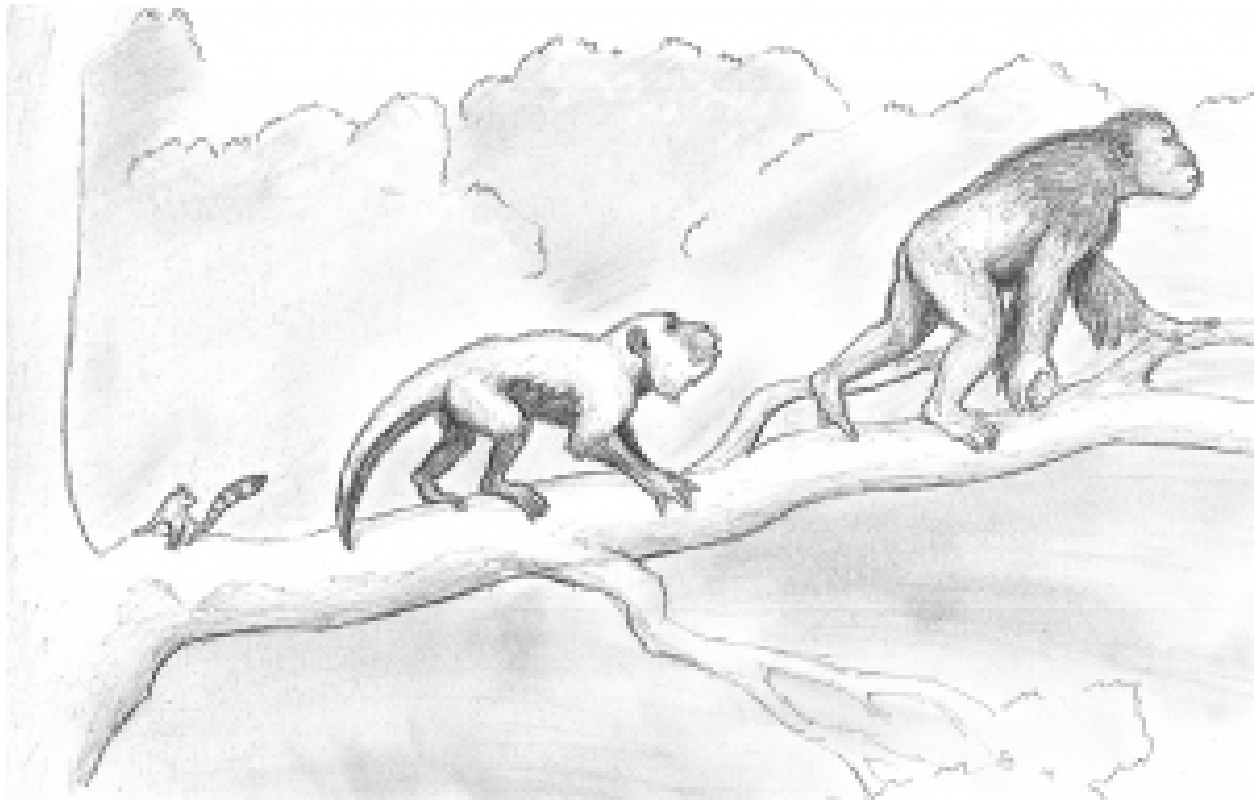
Great ape social organization varies by species. The chimps and bonobos (genus: *Pan*) are most like the majority of human traditional societies in that they live in **male philopatric**, multi-male/multi-female communities. **Philopatry** refers to the sex that remains in their **natal group**, i.e. the group into which they were born. This type of social organization is seen in some ripe fruit specialists, such as the chimps and bonobos of Africa and the New World spider monkeys. Since fruit is an ephemeral resource, females cannot cooperatively defend it. Groups of related males cooperatively defend a home range against outsider males. Females emigrate from their natal community and join a different community when they reach sexual maturity. Group members come together intermittently into larger aggregations wherein they may interact. This grouping pattern is termed **fission-fusion**. Since males patrol and protect the area and females are relatively large and powerful and can climb, the danger of predation is relatively low and they therefore have less of a need to congregate. The **mating pattern** is termed **polygynandry**, meaning that males and females are promiscuous and may have multiple sexual partners. Males may attempt to monopolize and coerce females to mate but females are adept at getting around bullying males and may even mate with males outside of their group.

Orangutans are considered to be solitary foragers and their prominent mating pattern is **polygyny** (males have multiple mates), wherein females in a given area usually mate with the resident, large, dominant male. Smaller males who are sexually mature but lacking the pronounced secondary sexual characteristics, such as facial pads (termed flanges) and an enlarged throat sac for loud calls, may try to forcibly copulate with females. Females are thought to monitor the dominant male's location so that they can stay within calling distance if they are being harassed by subordinate males.

Gorillas live in one-male groups, except for the mountain gorillas, where two males may reside, an older dominant and younger subordinate. Both sexes tend to leave their natal group. Females join a male who may or may not already have other female mates. Thus the mating system is also polygynous. Males defend their females and offspring from outsider males who may be infanticidal. In mountain gorillas, females are thought to prefer groups with two males as they provide better protection for her offspring.

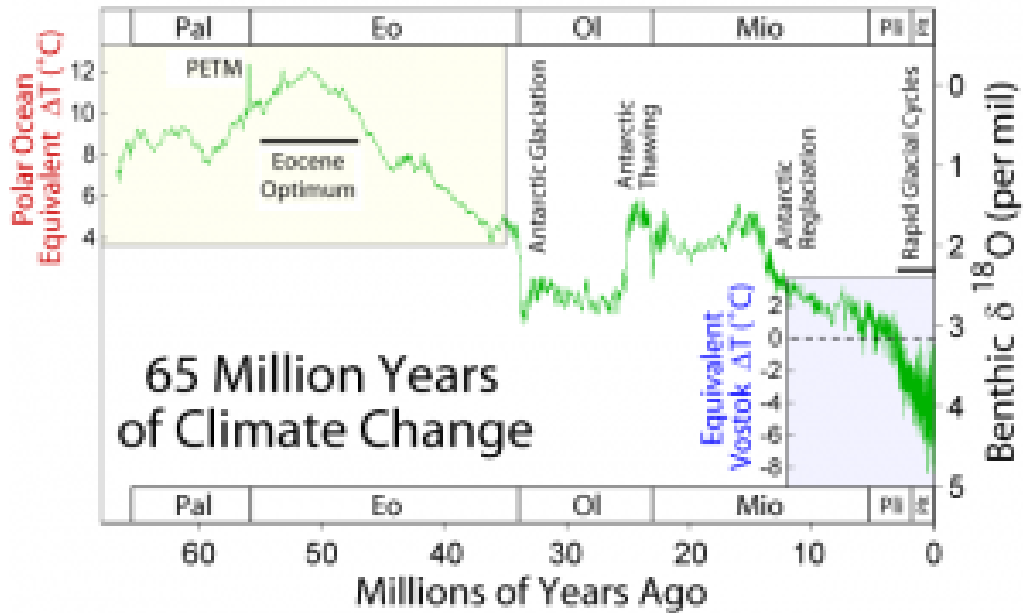
It can thus be seen that there are characteristics of the human sexes in all three great ape **genera** (plural of genus): male defense and mate-guarding, female choice for dominant males and good genes, male philopatry with females maximizing resources for themselves and offspring in chimps and bonobos, etc.

3. Primate Evolution

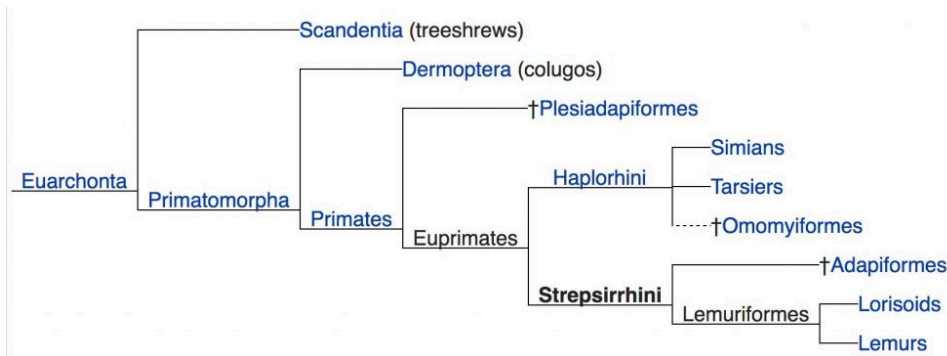


Anthropoid Evolution by Keenan Taylor.

While we have no primate fossil material prior to the Eocene Epoch, the first primates are thought to have evolved prior to the **Paleocene Epoch** (66–56 mya), possibly as far back as 90 mya, during the Late **Cretaceous Period**. With the extinction of the dinosaurs at the end of the Cretaceous, many terrestrial niches became available and predation pressures were somewhat relaxed. In addition, temperatures were higher than in the recent past (see Figure 3.2) and the **angiosperms** (flowering plants) were undergoing an **adaptive radiation**, i.e. relatively rapid speciation, and spreading globally. The spread of flowering plants resulted in an adaptive radiation of insect pollinators and herbivores (plant-eaters), as well as insectivorous and herbivorous arboreal vertebrates.



Temperature change over time. “65 Myr Climate Change” by Robert A. Rohde is licensed under CC BY-SA 3.0. Notes: Pal = Paleocene, Eo = Eocene, Ol = Oligocene, Mio = Miocene, Pli = Pliocene, and Plt = Pleistocene

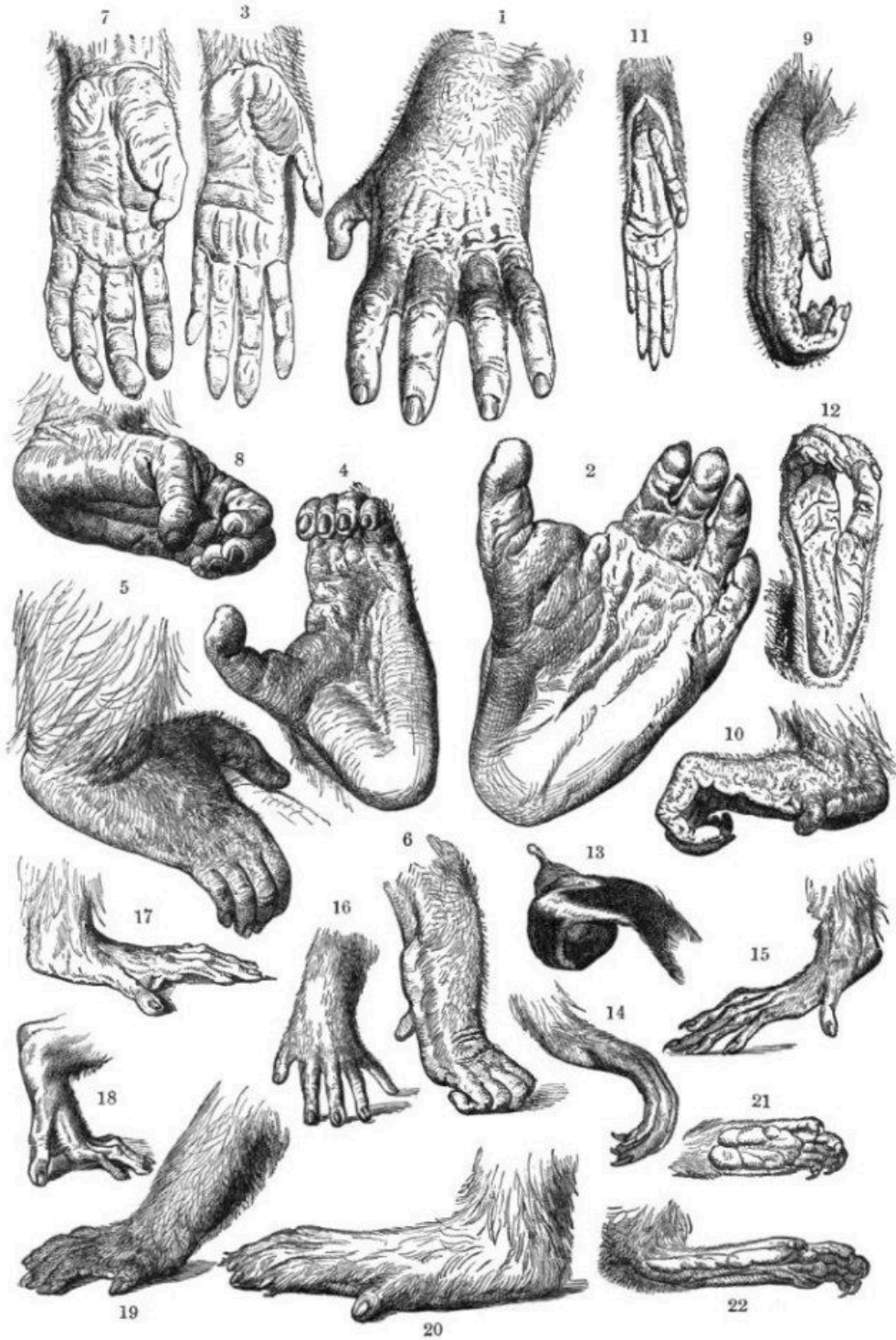


Primate phylogeny. “Primate phylogeny” from “Strepsirrhini” in Wikipedia is licensed CC-BY-SA

The earliest primates likely descended from a small, nocturnal, insectivorous mammal. The **tree shrews** and **colugos** (also known as flying lemurs) are the closest living relatives to primates. The tree shrew is used as a living model for what the earliest primates, or primate predecessors, might have been like. At some point, primates or their ancestors moved into the trees and adapted to an arboreal environment. Two theories regarding the evolution of some primate characteristics, such as grasping or prehensile hands, forward-oriented eyes, and depth perception, are the Arboreal and Visual Predation Theories. The **Arboreal Theory** posits that primate characteristics, such as grasping hands and feet and the presence of nails instead of claws, are the result of moving into and adapting to an arboreal environment. (Imagine the casualties!) The **Visual Predation Theory** asserts that characteristics that were well-suited to scurrying around in trees and visual features in particular, such as convergent orbits, are adaptations to insect predation. Short of a butterfly net, grasping hands, visual acuity, and depth perception are essential for catching insects, but I guess they would be kind of *handy* for using a butterfly net as well!



Tree shrew. "Tupaia cf javanica 050917 manc" by W. Djatmiko is licensed under CC BY-SA 3.0.

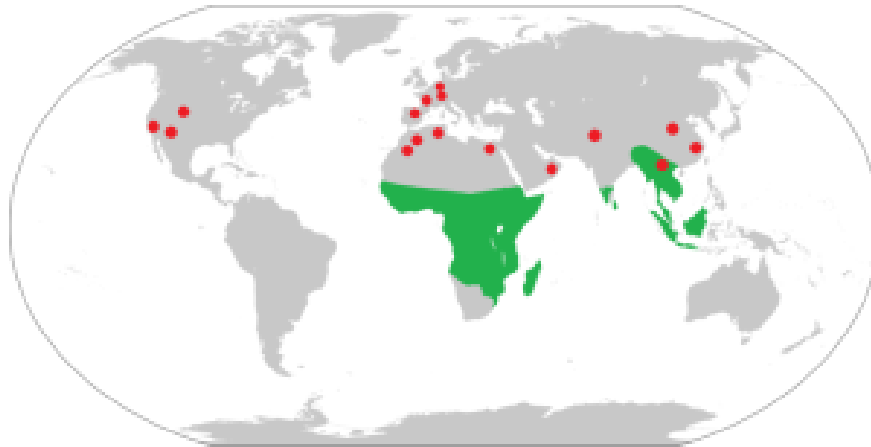


HANDS AND FEET OF APES AND MONKEYS.

1, 2, Gorilla ; 3-8, Chimpanzee ; 9, 10, Orang ; 11, 13, Gibbon ; 14, 15, Guereza ; 16-18, Macaque ; 19, 20, Baboon ; 21, 22, Marmoset.

Hands and feet of apes and monkeys. "Hands and Feet of Apes and Monkeys" by Richard Lydekker is in the public domain.

While primates are thought to have evolved in Asia, the majority of the early fossil material is found in North America and Europe, dating to the **Eocene Epoch** (~56–34 mya). The map in Figure 3.6 indicates both living and fossil strepsirrhine sites. They are divided into two superfamilies, **Adapoidea** and **Omomyoidea**. In general, the adapoids were diurnal, lemur-like animals that are thought to be the ancestors of the strepsirrhine primates, i.e. the lemurs of Madagascar and the lorises of Africa and Southeast Asia (i.e. bushbabies and pottos of Africa and lorises of Southeast Asia) (see Figure 3.7). The smaller, nocturnal omomyoids are good candidates for the ancestors of modern-day tarsiers. However, due to the early dates for ancestral tarsiers, it is possible that the omomyoids and tarsiers were sister lineages.



Range of living strepsirrhine primates (green) and Eocene-Miocene fossil sites (red). “Extant strepsirrhine range with fossil sites,” a derivative work by Maky, is in the public domain.

During the Eocene Epoch, the early strepsirrhine-like primates experienced an adaptive radiation and expanded into numerous niches over a broad geographic area. The northern expansion of early primates into Europe and North America was possible because Eurasia and North America were joined as the large landmass known as **Laurasia** and, as mentioned, it was warm enough for tropical animals to move into northern latitudes. Due to subsequent global cooling, the early primates in North America and Europe eventually went extinct. Strepsirrhine primates spread into Africa after it docked with Laurasia. They are also hypothesized to have “rafted” on floating mats of vegetation to Madagascar, where they evolved into the great diversity of extinct and extant lemur species.



Strepsirrhini. Notes: Top left: ring-tailed lemurs (Madagascar); top right: diademed sifaka (Madagascar); top middle left: aye-aye (Madagascar); top middle right: ruffed lemur (Madagascar); bottom middle left: mouse lemur (Madagascar); bottom middle right: slow loris (Asia); bottom left: slender loris (Asia); bottom right: greater bushbaby (Africa).

By at least the late Eocene, the first anthropoid primates had evolved. There is debate over the origin of the anthropoids, i.e. the ancestor of the monkeys and apes. There are four different theories of our ancestry, each with its share of supporters: (1) adapoid, (2) omomyoid, (3) tarsier, or (4) independent origin as yet undiscovered. Remains of early anthropoids dating to the late Eocene are found in Africa and Asia. A possible **stem** or **basal anthropoid**, meaning the original ancestor of all monkeys and apes, comes from the Shanghuang deposits of China. Termed genus: *Eosimias* (see Figure 3.8), it was as small as the smallest living anthropoid, the pygmy marmoset monkey of South America. While ring-tailed lemurs have striped tails, I do not know of any other striped primates so am not sure why the artist gave them stripes ... but it sure is an intriguing little creature! Other late Eocene fossils have been discovered in Myanmar (genus: *Pondaungia*), Thailand (genus: *Siamopithecus*), Libya (genus: *Biretia*), Algeria, and the **Fayum Beds** of Egypt.



Eosimias sinesis. Illustration by Keenan Taylor.

During the **Oligocene Epoch** (~34–23 mya), the anthropoid primates underwent a great adaptive radiation. The

richest location for Oligocene anthropoid fossils is the Fayum Beds of Egypt. Oligocene anthropoids are divided into three families: Parapithecidae, Oligopithecidae, and Propliopithecidae, from most primitive to most derived over time. The New World monkeys are thought to have branched off from the parapithecids, with which they share some characteristics. Genus: *Apidium* is a prime contender for a possible ancestor. Once again, a rafting hypothesis is proposed for the migration of that ancestor from Africa to South America.

The ancestors of the Old World monkeys and apes diverged from the family: **Propliopithecidae**. The propliopithecid, *Aegyptopithecus zeuxis* (also known as *Propliopithecus zeuxis*) is thought to be a common ancestor of the ape and Old World monkey lineages (see Figure 3.9). While the earliest anthropoids were more monkey- than ape-like, the apes (or hominoids) were the first to successfully adapt to changing environmental conditions in Africa.



Aegyptopithecus or *Propliopithecus zeuxis*. “*Aegyptopithecus NT*” by Nobu Tamura is licensed under CC BY-SA 3.0.

For years, people have asked me, “Barbara, you don’t really believe that we came from monkeys, do you?” and I always answered, “No, we came from apes!” However, our common anthropoid ancestor was more monkey- than ape-like.... So, “YEAH, I suppose I do!”

During the **Miocene Epoch** (~23–5.3 mya), the adaptive radiation of the apes or hominoids can be observed in the fossil record. The earliest fossils are from Kenya and Uganda. There were 20 or more genera of apes during the Miocene and they exhibited a wide range of body sizes and adaptive strategies. *Proconsul* is a possible stem ape, dating to ~18 mya (see Figure 3.10 and 3.11). The ancestry of the lesser apes is unclear but they are thought to have branched off 18–16 mya. The great apes diversified and spread from Africa to Asia and Europe. The ancestors of the orangutans, the **sivapithecines**, moved into western and subsequently eastern Asia. Remains in Turkey have been dated to 14 mya. The largest primate that ever lived, i.e. the now extinct genus: *Gigantopithecus* (known only from isolated dental and mandibular fragments), also had a sivapithecine ancestry. **Dryopithecine** apes moved into Europe during the late Miocene. Generally referred to as “dental apes,” due to the scanty remains of jaws and teeth, that evolutionary side branch eventually went extinct due to global cooling, as with the earlier strepsirrhines in the northern latitudes.

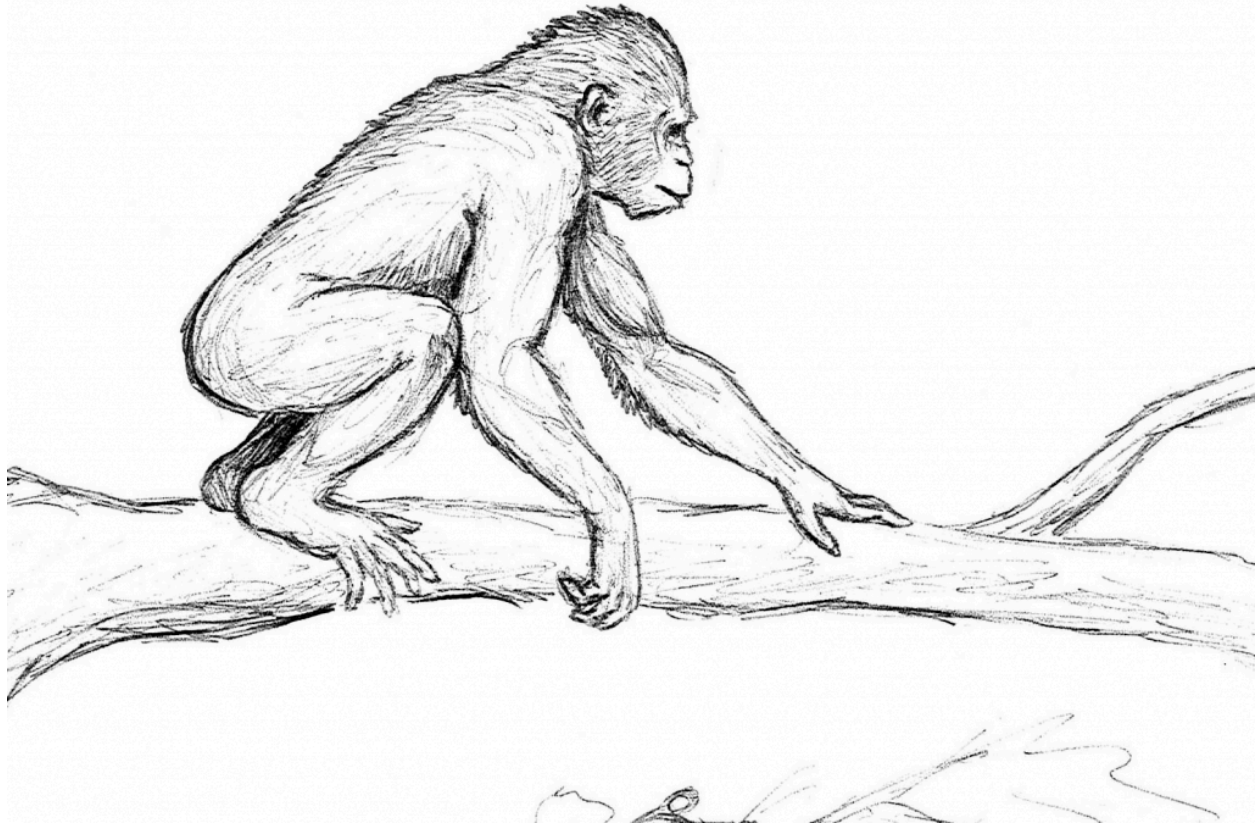


“Proconsul NT” by Nobu Tamura is licensed under CC BY-SA 3.0.

While there were Old World monkeys in the Miocene Epoch, such as genus: *Victoriapithecus* from Kenya, the adaptive radiation of the Old World monkeys lagged behind the hominoids. However, the same environmental conditions that drove most ape genera to extinction in Africa led to an explosion of monkey species. Monkeys could more quickly adapt due to their shorter life stages and greater number of offspring. A baboon can give birth every two years versus four or five years for gorillas and chimps, respectively. While the leaf-eating ancestor of the colobines stayed in the trees, the ancestor of the cercopithecine or cheek pouch monkeys, such as macaques and baboons, adapted to traveling on the ground as well as in the trees. The ability to exploit both arboreal and terrestrial resources expanded their niche and they survived and thrived in Africa and Asia. With only two extant genera, the African colobines did not diversify to the same extent, having been confined to forests. However, the Asian colobines did not experience the same forest loss as their African cousins did and are thus much more diverse. When African forests later expanded, the ancestors of some cercopithecine species, such as the colorful arboreal guenons, went back to the trees.

It has been difficult to trace the origin of the human/chimp/gorilla lineage during the mid-Miocene due to a paucity of fossils from that time and many conflicting viewpoints. Some of the contenders for the stem African great ape are *Nakalipithecus* (10 mya) and *Samburupithecus* (9.5 mya) from Kenya. Other possible ancestors or related species are *Afropithecus* (18–16 mya) and *Nacholapithecus* (15 mya) from Kenya and *Otavianpithecus* (13 mya) from Namibia.

The chimp and human lineages are thought to have diverged by the late Miocene. Global cooling in the latter part of the Miocene led to the extinction of all ape genera in northern latitudes. Forest cover in Africa was vastly reduced over time due to climatic fluctuations and while most apes went extinct, the newly emerged hominins thrived. Hominins experienced an adaptive radiation during the Pliocene Epoch (~5.3–2.6 mya), and late in the Pleistocene Epoch (~2.6 mya–11.7 kya) our own species, *Homo sapiens*, evolved (≤ 200 kya).



Proconsul africanus by Keenan Taylor.

4. Primate Social Organization



Stump-tailed macaques. “*Macaca arctoides*” by Frans de Waal is licensed under CC BY 2.5.

Most primates live in groups. The best explanation for why animals form groups and endure the costs of feeding competition is to minimize the risk of predation. Grouping patterns are tied to diet and the defensibility of resources. Females are out to maximize resources for themselves and their offspring, so as to maximize their reproductive success. If a species eats grass or leaves, it does not make sense to defend those resources. However, there is safety in numbers and those species (especially arboreal species) will normally be found living or foraging in small groups. If a species specializes on ripe fruit, they cannot defend them because of the patchy nature of fruit in geographic space and time. In the case of the few primate ripe fruit specialists, such as chimps and spider monkeys, males defend a home range that contains resources that females need, and thus females are attracted to join them. While orangutans are also preferentially frugivorous, they are solitary due to their large size and strict arboreality, which limits resources to those that are accessible from supporting branches. Finally, if a species can eat a variety of things that come in variable-sized patches, they can band together and defend those resources as they come across them in their daily ranging. In that case, females stay together in their natal group (termed female philopatry) and cooperate in resource defense.

Social organization involves several aspects of group life, such as (1) the average numbers of individuals in terms of age and sex; (2) whether group members remain in their natal group at maturity or leave, and hence whether individuals have relatives in the group; (3) whether those animals that join a group in adulthood stay permanently or tend to leave after a period of time; (4) the pattern of interactions between individuals, e.g. whether there is a dominance hierarchy and if so, if an individual's position in the hierarchy is permanent or temporary; and (5) the number of potential mates to which an individual has access. While we tend to categorize species by their grouping pattern or social organization, it is increasingly apparent that there is variability within primate species. Some species share our pattern of living in **multi-male/multi-female** groups. Other categories of primate social organization are **solitary**, **male-female pairs**, and **one-male/multi-female** groups.

Interestingly, all of the **mating systems** seen in primates, i.e. **monogamy**, **polygyny** (one male mates with multiple females), **polyandry** (one female mates with multiple males), and **polygynandry** (both males and females are promiscuous), are also seen in humans. Some men and women marry or mate for life; some men have multiple wives or partners, and the same goes for some women. I will discuss each type of social organization and mating pattern seen in the primates, along with example species.

SOLITARY AND DISPERSED POLYGYNY

Except for the orangutans, **solitary foragers** are small nocturnal prosimians that forage primarily for insects and fruit. Examples of solitary foragers are the bushbabies (see Figure 4.2) and pottos of Africa, most of the nocturnal lemurs of Madagascar, and the lorises of Asia. I am going out on a limb (too much?) to suggest that our earliest primate ancestors were as well, since we are thought to be descended from a small, insectivorous, nocturnal mammal. Prosimian solitary foragers either avoid predation by stealth (i.e. the **slow climbers**, such as pottos and slow lorises) or a form of locomotion termed **vertical clinging and leaping** (e.g., bushbabies) that allows for quick getaways. Females usually forage alone and either park their young nearby or leave them in a “nest,” such as a tree hole. Sleeping groups may consist of female relatives and their young and/or females, young, and males, depending on the species and female-female tolerance. Male home ranges often overlap multiple female home ranges, and males monitor female sexual cycles by “making the rounds” and monitoring their scent, hence the use of the term “**dispersed polygyny**,” i.e. one male and multiple dispersed females. One male may dominate other smaller or less dominant males in an area and may suppress them from breeding, via pheromonal activity.



Bushbaby of Africa. “Bushbabies” by Wegmann is licensed under CC BY-SA 3.0.

As mentioned, orangutans are the odd man out. They are large and arboreal so they do not need to group for protection. They need a lot of resources to support them and at some sites, they suffer periodic food shortages, so that grouping would hinder foraging. Females and their dependent offspring forage together. Females maintain proximity and mate with a dominant male with developed **secondary sexual characteristics**, i.e. large size, a throat sac for loud calls, and facial flanges. Until there is an opportunity for males to acquire

females, such as when a large male dies, males stay small and mate opportunistically. Scientists are stymied at how they can delay maturation and then facultatively develop into the larger morph.

TERRITORIAL PAIRS AND MONOGAMY

While a few species of primates are commonly referred to as monogamous, **extrapair copulations** have been observed in every one of them. The last primate to have lost the title of true monogamist was the night monkey of Central and South America. Prior to that revelation, it was always fun to ask my students who the only true monogamous primate species is and see if they answered, “humans.”



Gibbon of Southeast Asia. “Gibbon Hoolock de l’ouest” by Programme HURO is licensed under CC BY-SA 3.0.

Monogamy begs the question, “why?” While females may benefit from a monogamous relationship, if their mate supports them or their offspring in some way, it is difficult to understand why males would tie themselves to one mate when mating is not costly for them. There are several theories regarding the adaptive significance of pairing in primates. First is the idea that the female needs help defending a territory in order to obtain enough resources for herself and her offspring. Couples may actively and/or passively defend their territories (hence the more appropriate term “**territorial pair**”) via threats, fighting, and/or **duetting**, i.e. calling together to indicate that the territory is occupied by a bonded pair. In the majority of species, males help by carrying offspring. The second theory suggests that monogamy is a way for males to protect their offspring from **infanticide**. In those species that form one-male groups (see next section), when a new male takes over, he may kill nursing infants. Once nursing is interrupted, a female undergoes hormonal changes and may return to **estrus** (fertile period). It is in the new male’s best interest to impregnate females as soon as possible, in the “hope” that some of his offspring will make it to the juvenile stage before the next male comes in and wipes out the infants. Why would females mate with a homicidal maniac, you ask? It is not in their best interest to wait to reproduce either. That is the way natural selection works! Those traits that maximize **fitness**, i.e. reproductive success, are favored. In addition, a male offspring that grows up to be infanticidal will be in a better position to reproduce, if he has what it takes to take over a group.

There are territorial paired species within the prosimians (indris and wooly lemurs of Madagascar and the

tarsiers of the Southeast Asian archipelago), New World monkeys (night, titi, saki, and some marmoset monkeys of Central and/or South America), and the lesser apes (gibbons and siamangs of Southeast Asia—see Figure 4.3). We are learning that the lesser apes are much less monogamous than was previously thought. Females of some gibbon species tend toward polyandry and thus males are polygynous, making those species polygynandrous. We are the only great ape to have a *tendency* for monogamy, in that we tend to “fall in love” with one person at a time.

ONE-MALE GROUPS AND POLYGYNY

In some species, one male with one or a few females is the grouping pattern. However in other species (Hamadryas baboons, geladas, mandrills, drills, and some odd-nosed monkeys, such as snub-nosed monkeys), one-male units (OMUs) congregate into larger and larger groupings, in a multi-tiered or nested fashion, depending on their current activity. I will discuss this more complex grouping pattern after the discussion of one-male groups (OMGs). Except for the gorillas, all OMG species are Old World monkeys. The majority of the colobines form OMGs, e.g. African colobus monkeys of the genus: *Colobus* and Asian langurs and leaf monkeys. Cercopithecines of the genus: *Cercopithecus* (commonly known as guenons—see figure 4.4) and patas monkeys (*Erythrocebus*) are also OMG species.



De Brazza's monkey, a type of guenon of Africa. “Lightmatter guenon” by Aaron Logan is licensed under CC BY 1.0.

In the majority of OMG species, females are related but as groups get larger, they split along **matrilines**, meaning that a group of closely related females may splinter when competition increases. In addition, females may move between groups, especially in the colobines. Males fiercely compete for access to groups and infanticide occurs during takeovers. In those species that are seasonal breeders, it is difficult for the male to monitor and mate with all of the females and outsider males may sire some of the offspring. One guy can only do so much and females only have a small window of opportunity.

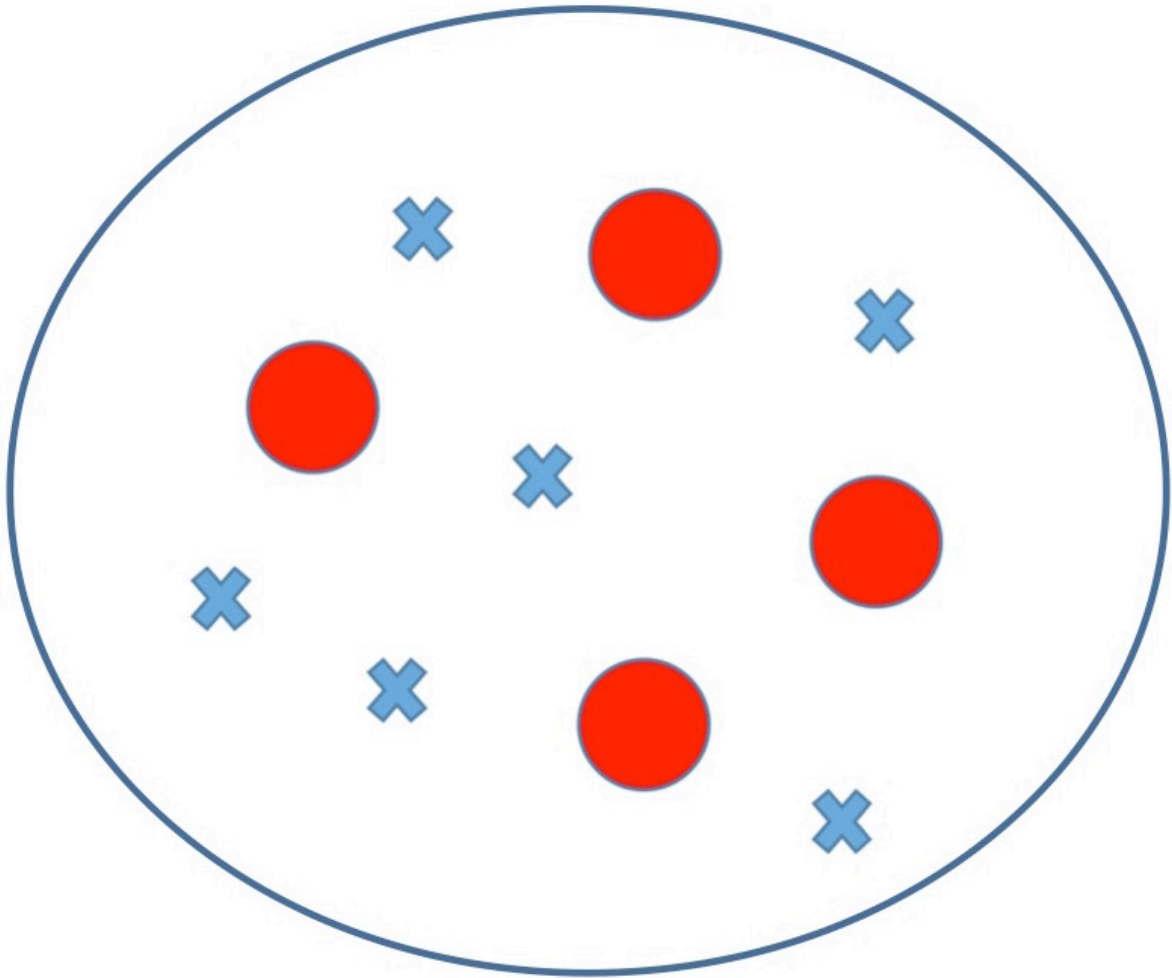
While the OMG makes sense for the colobines and their high leaf diet, it is not as clear why the more generalist guenons exhibit the same pattern. Like the colobine monkeys of Africa and Asia, it is possible that the ancestor of the extant arboreal guenons never left the trees and thus did not evolve the tendency for a larger grouping

pattern in response to terrestrial predators. In addition, if they remained arboreal in relict forests, they may have enjoyed a more stable resource base. They are small- to medium-sized monkeys and thus can subsist on a variety of foods, primarily insects and fruit, both of which are indefensible food items, from a female perspective. Thus while a group is beneficial, it does not need to be large. It may be a bit of an oversimplification that female resources drive primate social organization, but it is a useful model with demonstrated heuristic value.



Hamadryas baboons of East Africa and the Arabian Peninsula. "Hamadryas harems" by Brian Jeffery Beggerly is licensed under CC BY 2.0.

For those species with a nested grouping pattern of OMUs, I will describe the system in Hamadryas baboons (see Figure 4.5) and contrast it with geladas (see Figure 4.7). Both species consist of OMUs that congregate into three larger group levels. For some strange reason (as if there are not enough terms in a primate course), some primatologists use different terms for the levels in each of the species. The basic unit is the OMU. The next level is termed the clan; it consists of several OMUs, along with bachelor males, and the members tend to forage together (see Figure 4.6). The third level is the band, and that is the result of several clans congregating to forage over a large area. While Hamadryas bands are somewhat stable, gelada bands are not. Finally the troop (Hamadryas) or herd (gelada) is a combination of multiple bands that come together to sleep on cliffs in the mainly treeless regions where both species live, primarily in Ethiopia. Troops consist of hundreds of animals, over 700 in the Hamadryas and slightly fewer in the geladas. This odd grouping pattern is related to their harsh environment. Hamadryas live in subdesert conditions in Ethiopia and the Arabian Peninsula. They are generalists that eat whatever they can find. They fission and fuse (i.e. come together and separate again) into the various grouping levels as resources allow, but predators abound and shelter is scarce, so there is safety in numbers via vigilance. The geladas' situation is a bit different. They live in high-altitude conditions in Ethiopia and eat a lot of grass and grass products, such as seeds and corms. Again, there is safety in numbers but resources are ubiquitous so they spread out a bit and mooch and munch (new foraging category!), i.e. sit-eat-move, along the ground. The strangest aspect of the two species (other than their bizarre faces!) is that Hamadryas are male philopatric and geladas are female philopatric. While the gelada pattern makes sense, considering their relatedness to female-philopatric baboon species, Hamadryas are even more closely related to those baboons yet appear to deviate from the pattern. However, the females do not go far; they transfer at the clan or band level and thus are not far from kin. Thus the real question is why do male Hamadryas stay?



A depiction of a gelada or Hamadryas baboon clan. Note: OMUs =red circles and bachelors = blue Xs.



Grazing geladas. "Geladas" by Alastair Rae is licensed under CC BY-SA 2.0.

While there are regular takeovers in gelada OMUs, as would be expected, they are not as frequent in Hamadryas, primarily due to the facts that males have control over their small group of females and OMUs are surrounded by male relatives. Hamadryas females are usually coerced away from their mothers when they are young and then herded and punished by their new male leader until they learn to obey and not stray. Female geladas have a say in male takeovers; they either side with the resident male and help keep the new male out or they do not and the resident male is on his own. It is interesting that if a new male becomes established in the group, the former male may stay and help defend his offspring from becoming the victims of infanticide, but he can no longer breed.

ONE-FEMALE GROUPS AND POLYANDRY



Emperor tamarin. "Emperor Tamarin SF ZOO" by Brocken Inaglory is licensed under CC BY-SA 3.0.

This type of social organization is seen only in the callitrichids, i.e. the tamarins (see Figure 4.8) and marmosets of Central and South America. Within those groups, there is usually only one breeding female and one or two breeding males. Females gestate as many as five fetuses but on average, only two survive. Hence we talk about “**twinning**” in the callitrichids. Those groups with an extra male have better offspring survival. At birth, the offspring average one-fourth of the female’s weight and thus foraging to support them is a full-time job for the females. The females nurse the young and the males carry and nurture them.

Females pheromonally suppress cycling in their daughters and while sons become fertile, they have no mating options in the group. Mature daughters and sons also help with the care of their younger siblings. Helping behavior, while delaying their **direct fitness** (genes they pass on via reproduction), increases their **inclusive fitness** (genes they share with relatives). Full siblings share half of their genes (the same as between parents and offspring) and half siblings share one-fourth, on average. While the **proximate causation** (current stimulus or condition favoring the behavior, versus **ultimate causation**, i.e. the behavior was favored by natural selection due to its fitness benefits) for older siblings to stay is unclear, it is likely adaptive in some situations to delay reproduction. For example, it may be difficult for young animals to compete for territory or mates, and they are small and inexperienced and thus easy prey.

MULTI-MALE/FEMALE GROUPS AND POLYGYNANDRY

There are two types of multi-male/female groups (MMF). The first is the more common. They are medium to large groups of related females (female philopatric) with a sex ratio skewed in favor of females. Outsider males may congregate in all-male bands. Females and males are promiscuous, the mating pattern known as polygynandry. Many New World monkey species and most of the Old World cercopithecines (e.g. macaques—see Figures 4.1 and 4.9) exhibit this type of social organization. Females cooperate in resource defense and males may have a more peripheral position within the group, except during the mating season in seasonal breeders. Many semi-terrestrial species exhibit this type of social organization, e.g. baboons (Hamadryas are the exception)

and macaques. Terrestriality is associated with larger body and group size, likely for predation avoidance. With more females, come more males and with more males, females can benefit from seasonal breeding. There are enough males to go around and the glut of offspring that are then born reduces the probability that any one of them is eaten; i.e. the dilution effect. In addition, related females help keep watch over the young that then have playmates. Seasonal breeding is tied to environmental conditions, so that females benefit by timing events to coordinate with resource availability.



Long-tailed (also known as crab-eating) macaque. "Ngarai Sianok Sumatran monkey" by Sakurai Midori is licensed under CC BY-SA 3.0.

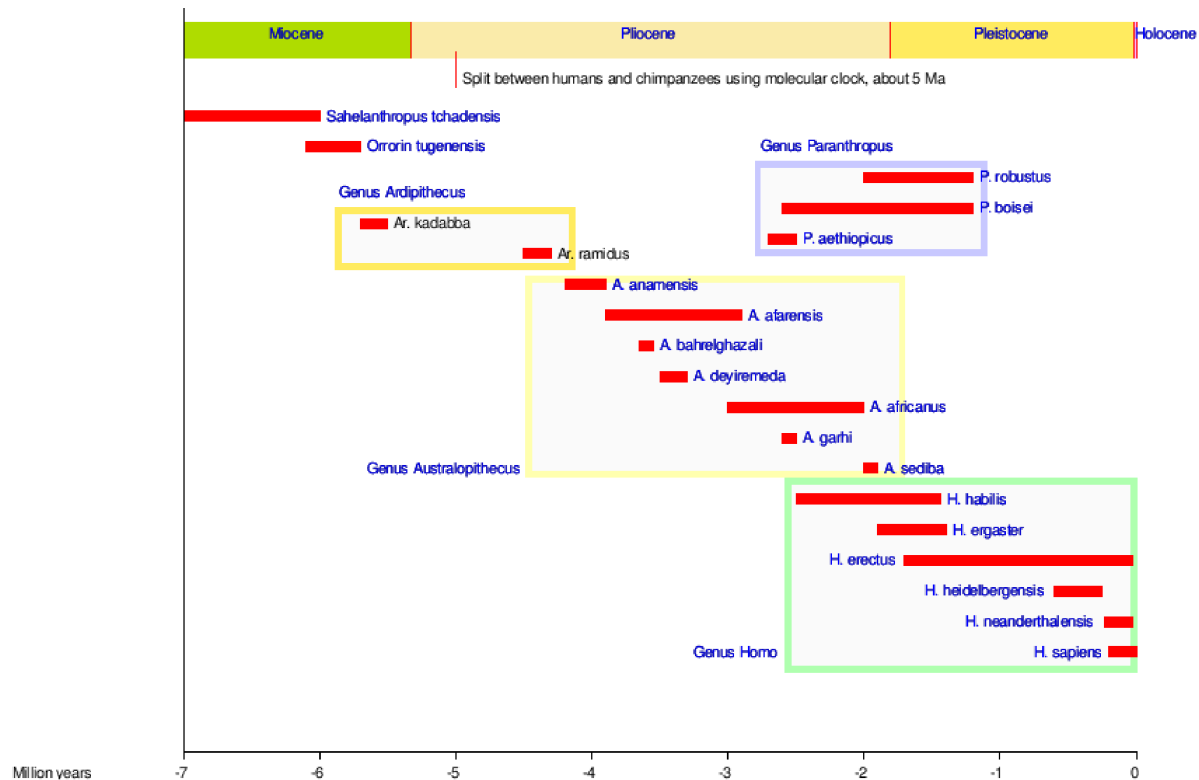
The second type of MMF is commonly called a **community** social organization. Species that exhibit this type of social organization are **male philopatric** ripe fruit specialists. As mentioned, females cannot defend fruit, so they do not band together into matriline. Related males defend a territory that contains enough resources to attract females. Females and their offspring forage independently but group members come together periodically into larger aggregations, hence the other term for this type of social organization, **fission-fusion**. New World spider and marmoset monkeys and the chimps and bonobos of Africa (see figure 4.10) are all categorized as community species.



“Bonobo group hug.” “Bonobo group hug” by Magnus Manske is licensed under CC BY-SA 2.0.

5. What is a Hominim

We are hominins, as are all those bipedal apes that came before us. Figure 5.1 shows most of the hominin species through time, some of which we are descended from and some that are side branches in our tribal tree!



Hominin species through time. "Hominin species distributed through time" from "Paleoanthropology" in Wikipedia is licensed CC-BY-SA

ANATOMICAL TERMS

In order to adequately understand a discussion of hominin evolution and appreciate changes over time, some basic anatomical information is necessary. It is also necessary in order to distinguish **primitive** or ape-like skeletal characteristics from those that are **derived**, i.e. those that arose later in time.

Any discussion of anatomy assumes that one is speaking of a body in **anatomical position**, i.e. facing forward if standing or supine (face up) if lying down, with palms forward or up (see Figure 5.2–5.4). When referencing particular structures or regions of the body, we make use of the following terms:

- **Superior**—closer to the top of the head.
- **Inferior**—closer to the soles (or plantar surfaces) of the feet.
- **Medial**—closer to the midline of the body.
- **Lateral**—closer to the far right or left of the body, relative to the midline.

The following two terms are used in reference to the limbs:

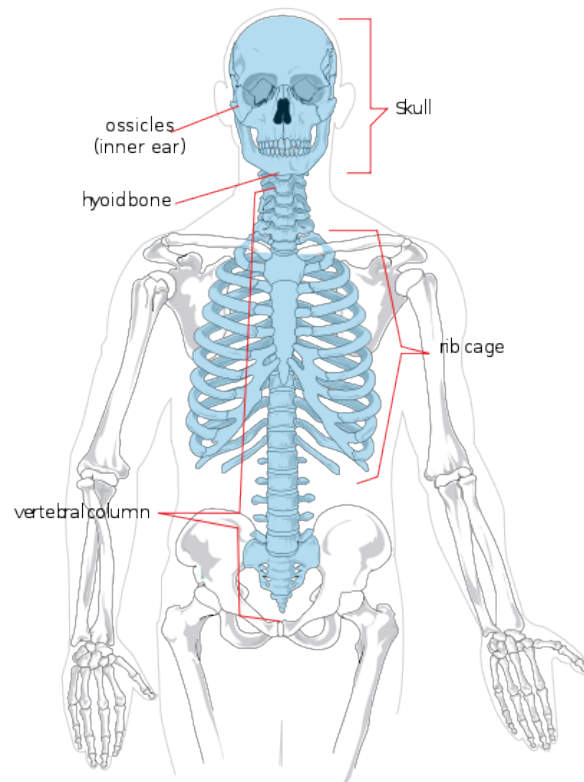
- **Proximal**—closer to the base of a limb.
- **Distal**—closer to the end of a limb.

You may hear your professor use the above terms when describing aspects of human or fossil specimen anatomy.

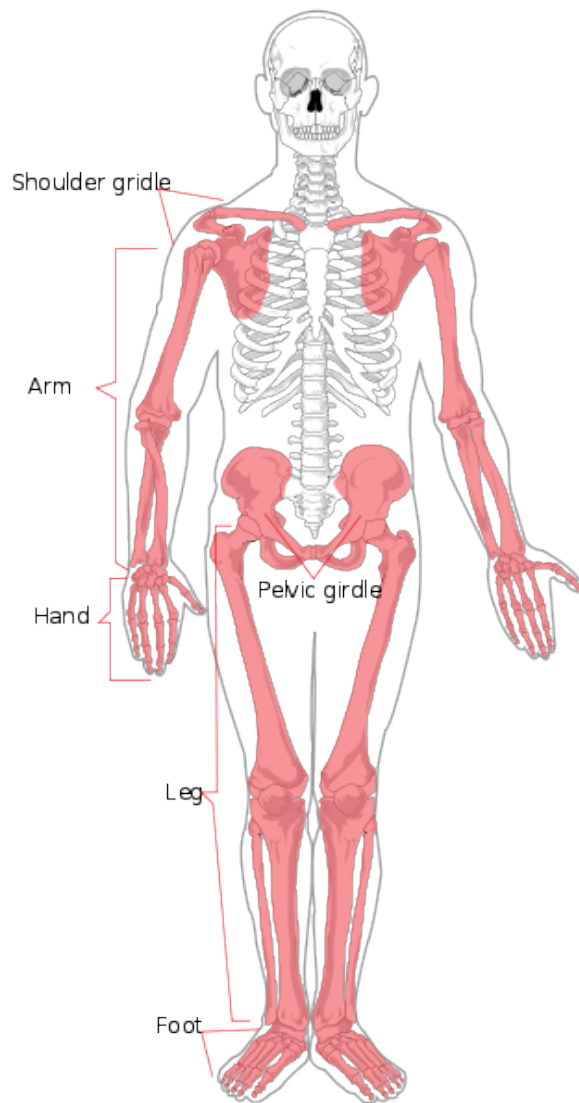
Note: If you are thinking about a career in paleoanthropology, get as much training in anatomy as possible, even while an undergraduate. Anthropology and biology departments may offer courses in human anatomy, human osteology, forensic anthropology, and the like. Finds like “Lucy” (*Australopithecus afarensis*, see Chapter 11) come along once in a lifetime. Most discoveries consist of little pieces of fossilized bone or teeth and thus knowledge of human anatomy is crucial for recognizing possible landmarks on the remains.

HUMAN GROSS SKELETAL ANATOMY

The terms *gross anatomy* and *macroscopic anatomy* refer to the study of structures that are visible to the naked eye. In this section, we will consider whole bones versus the individual parts of bones and only those bones that are external, as those are most relevant in a discussion of bipedalism and human evolution. While the anatomy of the lower limb takes precedence in a discussion of bipedalism, other parts of the body also changed over time. The anatomy of the skull is particularly important because the skulls and faces of hominin species changed over time and geographic space.



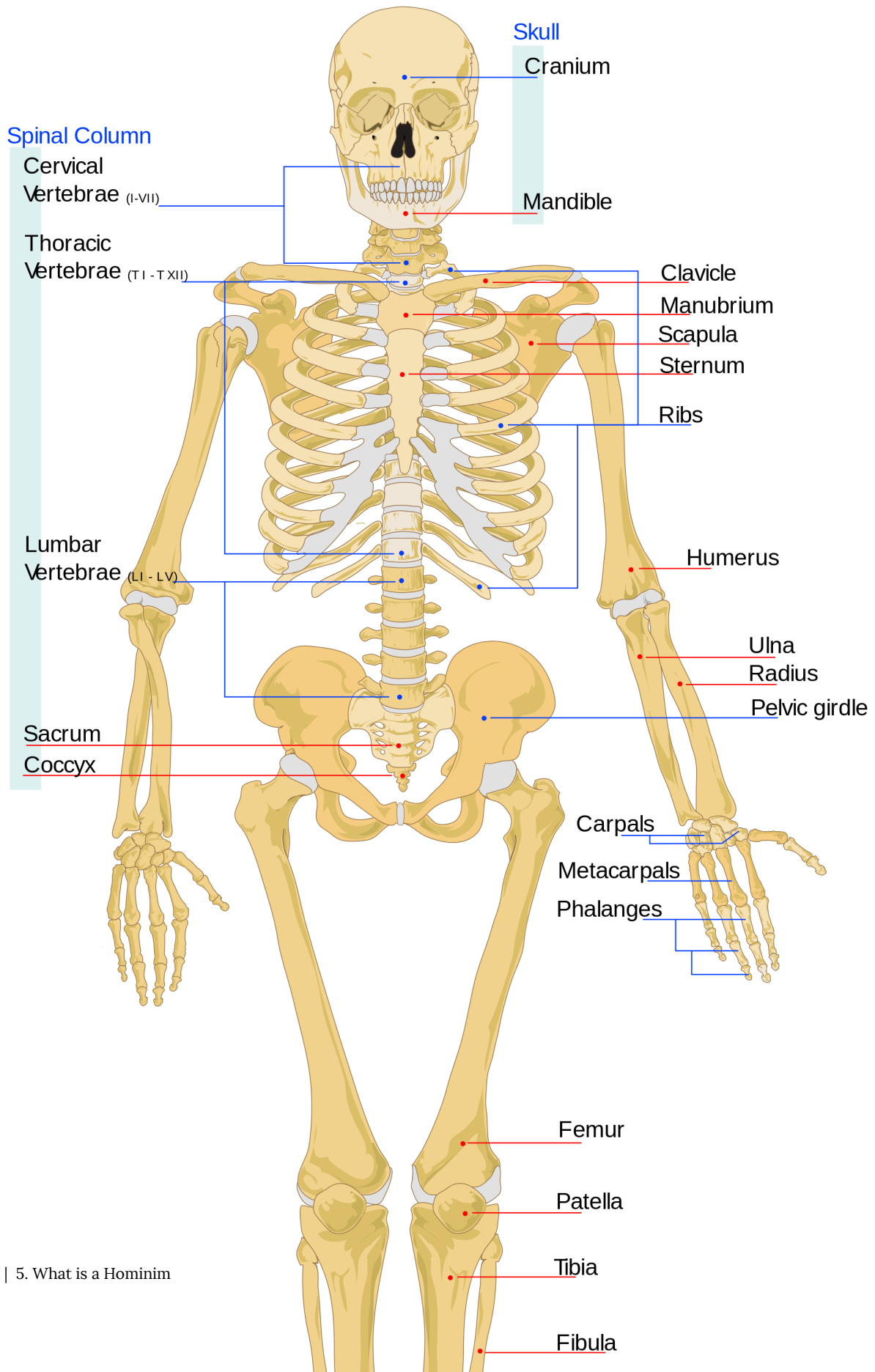
Human axial skeleton (shaded). “Axial skeleton diagram” by Mariana Ruiz Villarreal is in the public domain.



Human appendicular skeleton (shaded). "Appendicular skeleton diagram" by Mariana Ruiz Villarreal is in the public domain.

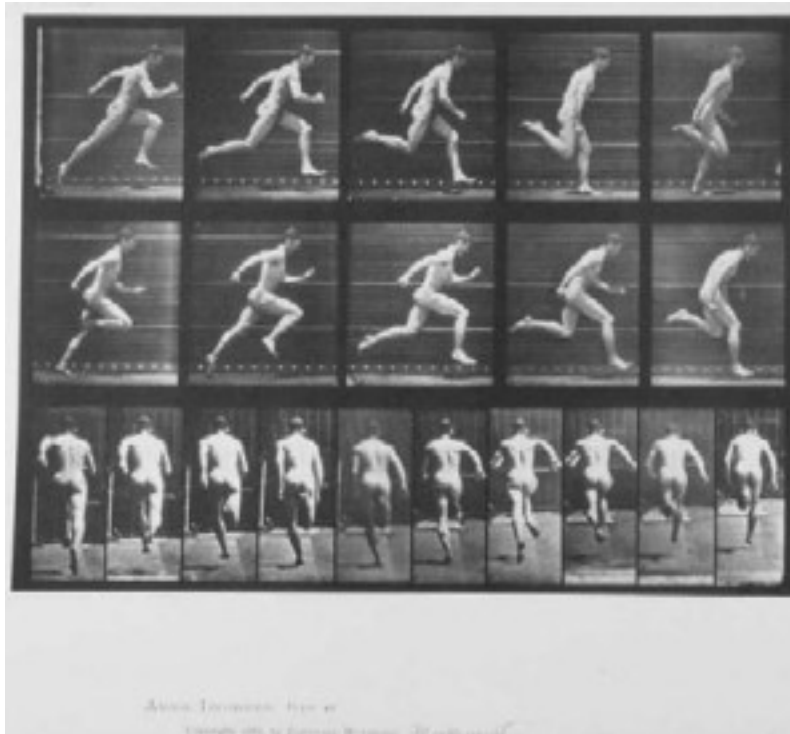
We will begin with regional anatomy. The **axial skeleton** consists of the head and torso. Regionally it is divided into the skull, thorax, and spinal column. The spinal column is divided into the seven cervical (neck), twelve thoracic (thorax/chest), five lumbar (lower back), five sacral (also known as sacrum), and four coccygeal (also known as coccyx or tailbone, they may also number three or five) vertebrae. The limbs and shoulder and hip regions make up the **appendicular skeleton**. The upper limb is also known as the arm or forelimb. It is divided into the arm (upper arm), forearm, wrist, and hand and fingers. The lower limb is also known as the leg or hindlimb and is made up of the thigh, leg (equivalent of forearm), ankle, and foot and toes.

Individual bones of the axial and appendicular skeletons are labeled in Figure 5.4. They will not be discussed here.



Human skeleton. "Human skeleton front en" by Mariana Ruiz Villarreal is in the public domain.

THE EVOLUTION OF BIPEDALISM



Running man. "Nude Man Running" by Eadweard Muybridge is in the public domain.

There are a variety of theories as to how bipedalism evolved and why it proved to be so successful for early hominins. One early idea suggested that by standing up, our ancestors would have been able to see above the grass and thus avoid predation. Baboons and patas monkeys provided living models for hypothesizing the environmental stresses early hominins might have faced on the open plains of Africa. While they likely traveled through open areas, we now know that the earliest hominins were exploiting forest resources, as evidenced by their thinner molar enamel, relative to later hominins. There were also theories that involved the freeing up of the hands to make and use tools and for carrying resources to a safe place or home base. C. Owen Lovejoy believes that bipedalism allowed males to provision mates with resources (Lovejoy, 1981). Those males with the most advanced bipedal capabilities would have had an increased chance of mating and possibly offspring survival, and thus bipedalism would have spread throughout the population. While Lovejoy makes a good case for how a trait could be favored in a population, it is not clear why females would have needed to be provisioned unless their offspring had already lost their ability to hang on with their feet, and hence became a burden to foraging. We now know that arthropods, while bipedal on the ground, had a divergent hallux, so that young animals could likely have hung on to their mothers in trees like modern primates. Although we cannot know for sure whether they were covered with hair, I can only speculate that when on the ground, young infants may have hung by clasping the fur on their mother's ventrum (anterior aspect of the trunk) while the mother supported their bottom. As the baby matured, it may have clasped its hands around the mother's neck or chest and hung on

to her fur with its feet and later ridden “piggy-back” like modern quadrupedal monkeys and apes. Eventually, it would have walked beside her from place to place. However, if resources had become extremely scarce, bipedal males may have ventured out onto dangerous ground for resources with which to provision their mates. Another theory that sees males as being the impetus for bipedalism suggests that males may have been more terrestrial and females more arboreal, i.e. a case of niche partitioning, like gorillas and the mandrill and drill monkeys, where males forage on the ground and females and young spend more time in the trees. Other theories also suggest that bipedalism was a response to the changing nature of the resource base. For example, Meave Leakey and Kevin Hunt (a theory known as Hunt’s Postural Feeding Hypothesis, Hunt 1996) believe that the ability to stand on two legs for long periods of time would have facilitated picking fruit from the terminal branches of low, scrubby trees in the increasingly open habitats of East Africa. While the aforementioned theories are not mutually exclusive and there was likely a synergistic effect that resulted from our ancestors’ changing locomotor capabilities, a highly plausible model suggests that it was our ability to break out of the “ape habitat” that facilitated our evolutionary success.

The following items will help us to better understand this great “step” in our ancestry:

- Apes are descended from an arboreal climber from the early Miocene of Africa.
- The ancestor of the African great apes possessed a suspensory hanging adaptation and thus had an upright trunk that was wide and shallow; mobile shoulder and wrist joints; long arms relative to leg length; long, curved hand and foot bones; and an opposable big toe (hallux). The next section explains how that thoracic morphology facilitated our ancestors’ bipedalism.
- The common ancestor of chimps and hominins was likely a semi-terrestrial quadruped that was adapted to climbing, feeding, and sleeping in trees, as well as moving and foraging on the ground.
- The late Miocene of Africa was marked by climatic change that spurred floral and hence faunal changes. Equatorial Africa was cooler and increasingly drier than in earlier times. The Indian subcontinent continued to move north, resulting in the uplifting of the Himalayan mountain chain that produced a rain shadow, i.e. moisture-laden clouds that would have previously drifted down into Africa now lost their moisture on the mountains. Drying winds and cooler temperatures resulted in forest reduction and fragmentation in Africa, splitting and isolating resident faunal populations.
- The majority of African ape species went extinct due to loss of habitat.
- Bipedalism is an efficient means of locomotion for covering distance on fairly level ground.
- A more vertical posture reduces the surface area exposed to solar radiation in a more open environment. It also raises a large percentage of the body away from the hot ground, where it is exposed to cooling breezes.
- The ancestors of the hominins adapted to the changing environment by becoming bipedal on the ground. Over time they developed a more efficient heat exchange system for their bodies (sweating) and brains (large venous sinuses for rapid blood movement) and lost much of their body hair.
- Based upon early hominin teeth, they were generalists like chimps, likely getting the majority of their carbohydrates and fats from fruit, protein from young leaves, and possibly fat and protein from animal matter, e.g. social insects (chimps and gorillas eat a lot of ants and termites) and

animals caught opportunistically. No early hominins exhibit the same degree of canine size or sharpness as chimp and gorilla males. Their canines stay sharp via a honing (sharpening) action with the first lower premolar, termed a **sectorial premolar** due to its unicuspid morphology. The combination of the action and morphology of the two teeth is termed a “**honing complex**”. Males’ canines are exceptionally large and, in combination with their high degree of sexual dimorphism, are used to compete with other males for access to females. Of course, they are also useful for predator defense. Thus, if the common ancestor of chimps, gorillas, and hominins possessed a premolar honing complex, as seems likely, the early hominin fossil evidence suggests that they were losing their fighting teeth. In addition, fossil hominins do not exhibit the same degree of sexual dimorphism as seen in chimps and especially gorillas. Later chapters contain more information on hominin socioecology.

Most apes went extinct as their habitats dwindled and they competed for limited resources. However, with an efficient means of locomotion to move between forest patches when resources became depleted, hominins could continue to exploit those resources to which they were adapted. They also likely evolved new capabilities for exploiting newly encountered food items as they moved through and between ecozones. Loss of habitat and resources often leads to local extinctions. By expanding their home ranges and dietary niches, hominins survived while the majority of their close relatives did not.

BIPEDAL ANATOMY

See Figure 5.4 for individual bones.

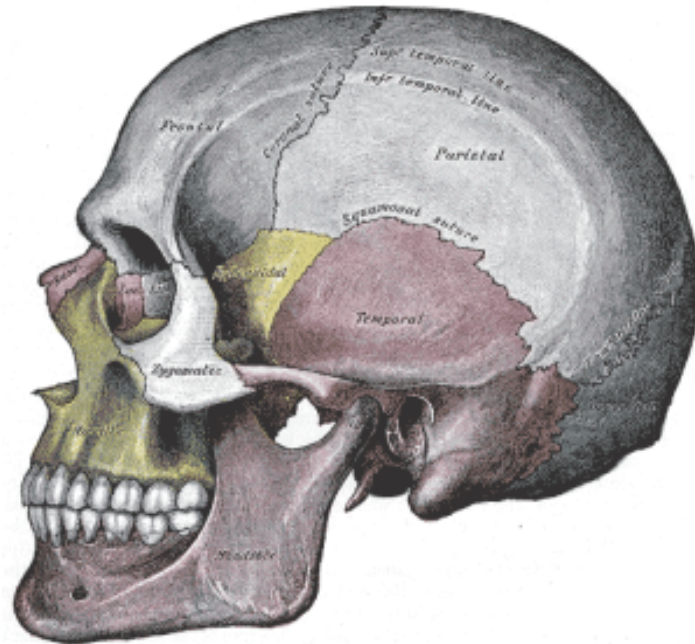
The majority of bipedal characteristics involve the hip (or pelvic girdle) and lower limb. However, as will be seen below, certain skull and trunk characteristics are also adaptations for bipedal locomotion. In addition, we have inherited many aspects of our upper bodies from our ape ancestors and those will all be discussed in the following sections.

SKULL

The skull consists of the bones of the braincase and face and the mandible (lower jaw). The **foramen magnum** is the hole in the occipital bone situated in the base of our skulls (see Figure 5.6). It is where our spinal cord exits the cranial vault. In hominins, the foramen magnum is positioned more anteriorly than in the other apes because our head sits on top of our vertebral column. Thus while the earliest hominins had very ape-like faces, the position of the foramen magnum shows that they were bipeds.



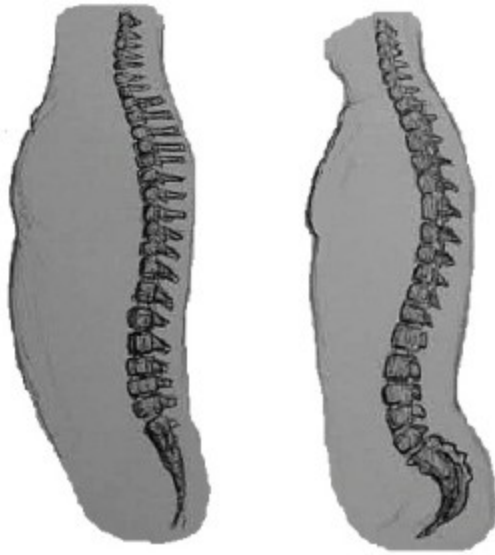
Foramen magnum indicated from inside skull vault. "Crane4 Foramen magnum" by Didier Descouens is licensed under CC BY-SA 3.0.



Bones of the skull. Plate 188 from Gray's Anatomy. "Side view of the skull" by Henry Vandyke Carter is in the public domain.

VERTEBRAE

Ape spines are not as flexible as monkeys' spines, giving us better upper body support since we are more upright than most other primates. Our vertebrae increase in size and robusticity from top to bottom so that our lumbar vertebrae are very large; they sit on the fused vertebrae of the sacrum, which is firmly attached to the hip bones. The sacrum is large and broad and curves inward (as does the coccyx) to help support the organs. Thus our spinal column is a strong supporting structure for the upper body. We hominins have two larger curves in our backs relative to the other apes, the **cervical curve** and the **lumbar curve**. The fact that our heads are more upright than nonhuman apes means that the cervical vertebrae must form a more concave curve, i.e. the superior aspect of our neck is arched back relative to theirs (see Figure 5.8). The more pronounced lumbar curve forms when we stand up and begin toddling about. The joints between the lumbar vertebrae are easily strained and it is thus important to maintain strong back and abdominal muscles throughout life, to aid in the stability of the region.



Chimp (left) vs. human spine (right). Illustration by Keenan Taylor

THORAX

The thorax consists of the sternum, ribs, and thoracic vertebrae. The ape **thorax** is adapted to climbing and swinging in trees. It is wide (right to left) and shallow (front to back) relative to quadrupedal monkeys, which have a narrow and deep thorax like those of dogs. While the morphology of the thorax was originally adapted to arboreal climbing, the upright trunk also allowed for bipedal locomotion. In addition, the shallow nature of the thorax brings the center of gravity closer to the vertebral column for better weight concentration and transfer. Apes are better bipeds than most nonhuman primates. They can walk bipedally for short to moderate distances, depending on the species, but it is not efficient and they cannot maintain it for very long.

SHOULDER GIRDLE

The shoulder girdle consists of the clavicle, scapula, and humerus. The shoulder joint of extant nonhuman apes and early hominins is and was angled upward, demonstrating the arboreal ancestry of those hominins and, in combination with their long, curved fingers, it suggested that they could ascend and climb about in trees. Our **clavicles** stabilize our shoulder joints for swinging and hanging. The triangular shape of the **scapula** (shoulder blade) is more equilateral than that of a quadrupedal monkey's, which is more elongated. Our scapulae are more mobile than those of a typical quadruped and the articular surface of the scapula, i.e. where the round head of the humerus articulates (makes contact), is shallow and allows us to rotate our arms at the shoulder. This **suspensory hanging complex** of clavicle, scapula, and humerus morphology (also elbow and wrist adaptations—see below), along with the muscles and connective tissue involved, allows us to climb, hang, and swing by our arms.

UPPER LIMB

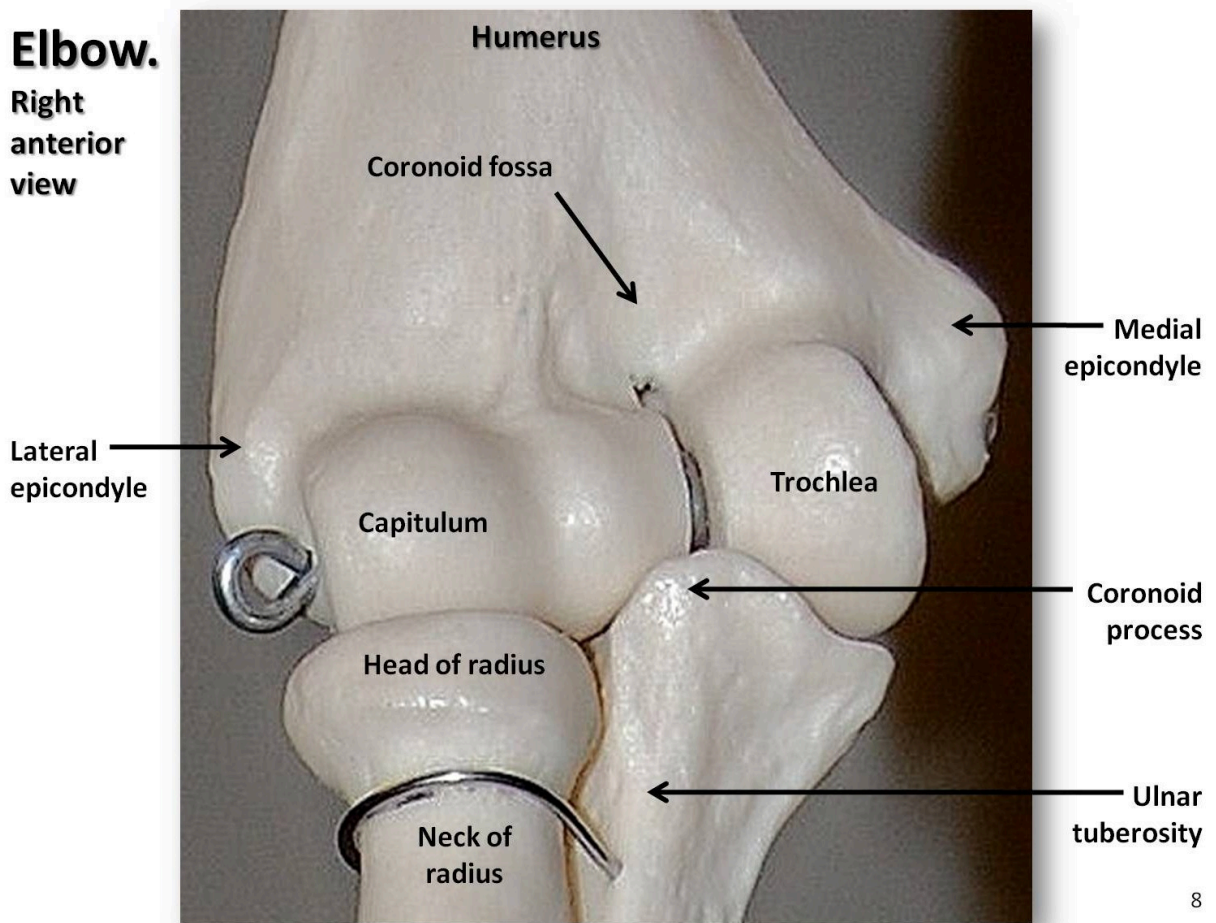
The upper limb consists of the humerus of the arm, the radius and ulna of the forearm, the eight carpal bones of

the wrist, the five metacarpals of the body of the hand, and the phalanges of the digits (three per finger and two per thumb, or pollex). As mentioned, the head of the ape **humerus** is round, resulting in a very mobile shoulder joint. We can fully extend our arms at the **elbow** in order to hang or swing, whereas quadrupeds cannot. In addition, we can supinate and pronate our **forearm**, i.e. move our hand palm up or palm down. This movement is possible because the head of the radius is a concave disk that rotates on a ball-like structure termed the capitulum on the **distal** humerus (see Figure 5.9). Our **wrist** joints are very flexible, allowing us to rotate and twist our hands in a variety of ways. Early hominins had short legs, long arms, and curved fingers. Over time, hominin legs lengthened so that their **intermembral index** (IMI) became reduced. The intermembral index is the ratio of armlength to leglength, calculated by the following equation:

$$IMI = \left(\frac{\text{armlength}}{\text{leglength}} \right) 100$$

If an animal has long legs and short arms (like us), they have a low IMI and vice versa; if fore- and hindlimbs are approximately equal in length, such as in terrestrial quadrupeds, the IMI will be close to 100.

Elbow.
Right
anterior
view



8

Human elbow. "Bones of the elbow" by Rob Swatski is licensed CC-BY-NC.

HIP OR PELVIC GIRDLE

Our shoulders are somewhat analogous to our butts! This is because muscles originating from outside the limbs

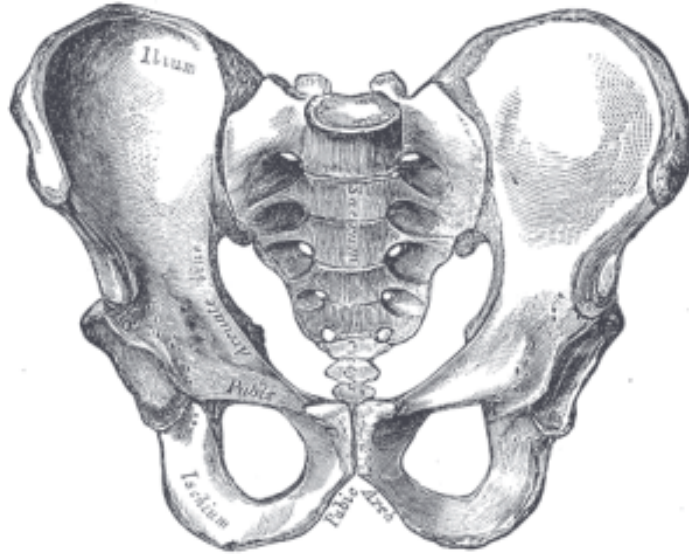
are crossing the joints to insert upon and move the limbs. Because we are bipeds, it is not as apparent as it is in quadrupeds, whose fore- and hindlimbs move similarly. However, if you compare the humerus and femur and the muscles that cross the respective joints (deltoids and gluteal muscles, respectively), you will definitely see similarities.

Our pelvis is very unique and interesting. It has changed significantly from an ape pelvis (see Figure 5.10). The pelvis is made up of three bones: the two lateral bones, termed innominate or os coxae, and the sacrum. Collectively, they form a basin-like structure that holds our internal organs while providing support for our upper bodies. Each **innominate** consists of three bones that fuse during development: the **ilium**, **ischium**, and **pubis** (see Figure 5.13). They meet at the hip joint. Hominin innominates became shorter and broader, so that the ilium wraps around laterally from an earlier, more posterior position. This changed the orientation and action of our hip muscles, allowing for our striding gait and the ability to balance our weight on one fully extended leg while the other leg is in the swing phase. A portion of the *gluteus maximus* muscle inserts behind the hip joint in hominins (versus lateral in chimps), and thus instead of abducting the femur (moving it out laterally, as when doing jumping jacks), it changed to a powerful hip extensor (backward motion) for running.



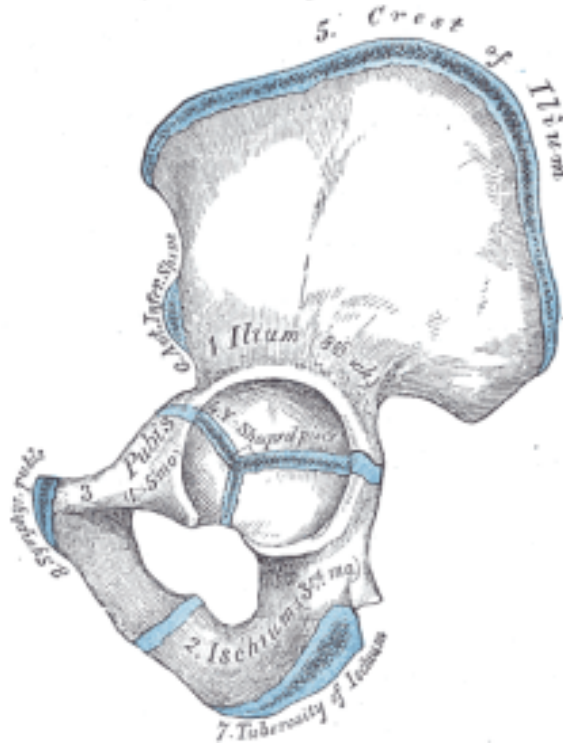
Left innominates of chimp (left), australopith (center), and human (right). Illustration by Keenan Taylor.

Figures 5.11 and 5.12 illustrate the landmarks that are adaptations to bipedalism. The **iliac crest** is long and curved, as the bone wraps around laterally. The **iliac blade** is short but expanded horizontally. The iliac blades are buttressed or reinforced to handle the stress of our upper body weight. The thick section of bone, termed the **iliac pillar**, can be seen running from the iliac crest (at the iliac tubercle) down behind the hip joint. The articular area, termed the **acetabulum**, is large and deep, providing a stable socket for the ball-like head of the femur. The joints of the pelvis are very strong and relatively immobile (compared to the shoulder joint). The **sacroiliac joint** (between the ilium and the sacrum) is large and more posterior and proximal to the hip joint than in quadrupedal apes. Together with the strong **pubic symphysis** (anterior joint where the pubis portions of the two innominates meet), these characteristics make for a very stable supporting structure.



Human pelvic morphology: The three fused bones of the innominates (ilium, ischium, and pubis), sacrum, and coccyx. Plate 241 from Gray's Anatomy. "Male pelvis" by Henry Vandyke Carter is in the public domain.

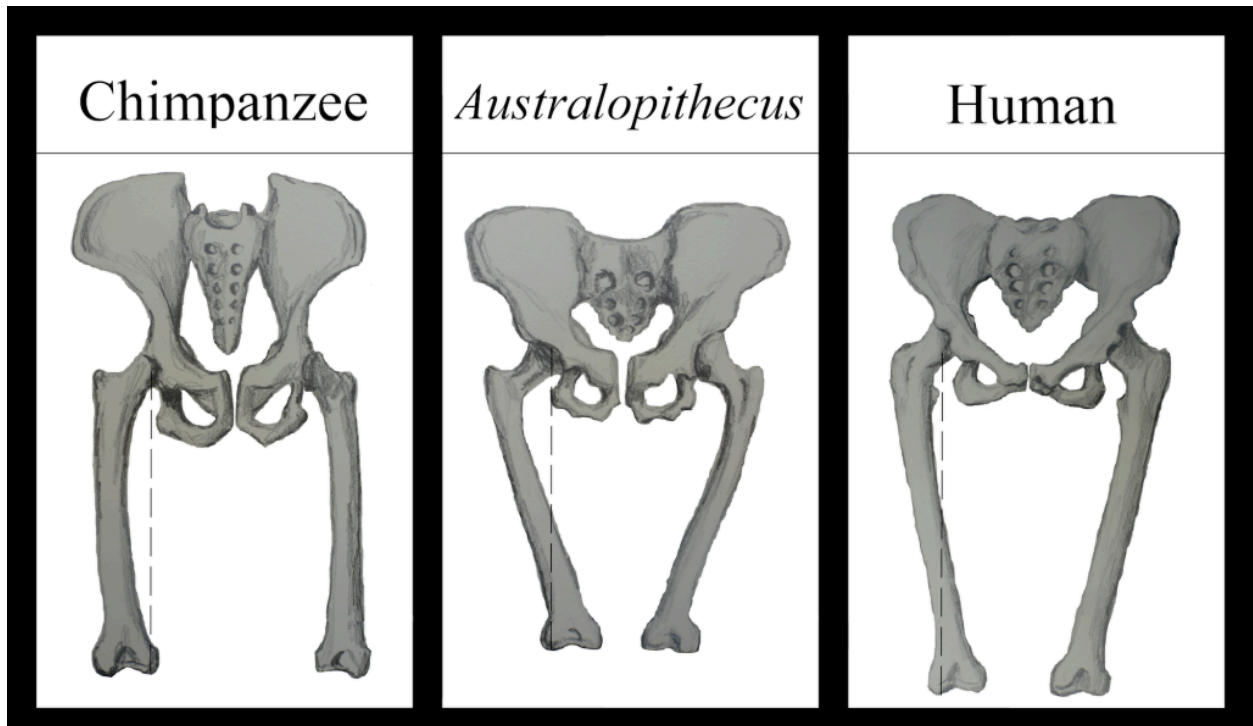
By eight centers { Three primary (Ilium, Ischium, and Pubis)
 { Five secondary



Ossified joints of the bones of a left innominate (lateral view). Plate 237 from Gray's Anatomy. Note where the ilium, ischium, and pubis articulate at the acetabulum. "Plan of ossification of the hip bone" by Henry Vandyke Carter is in the public domain.

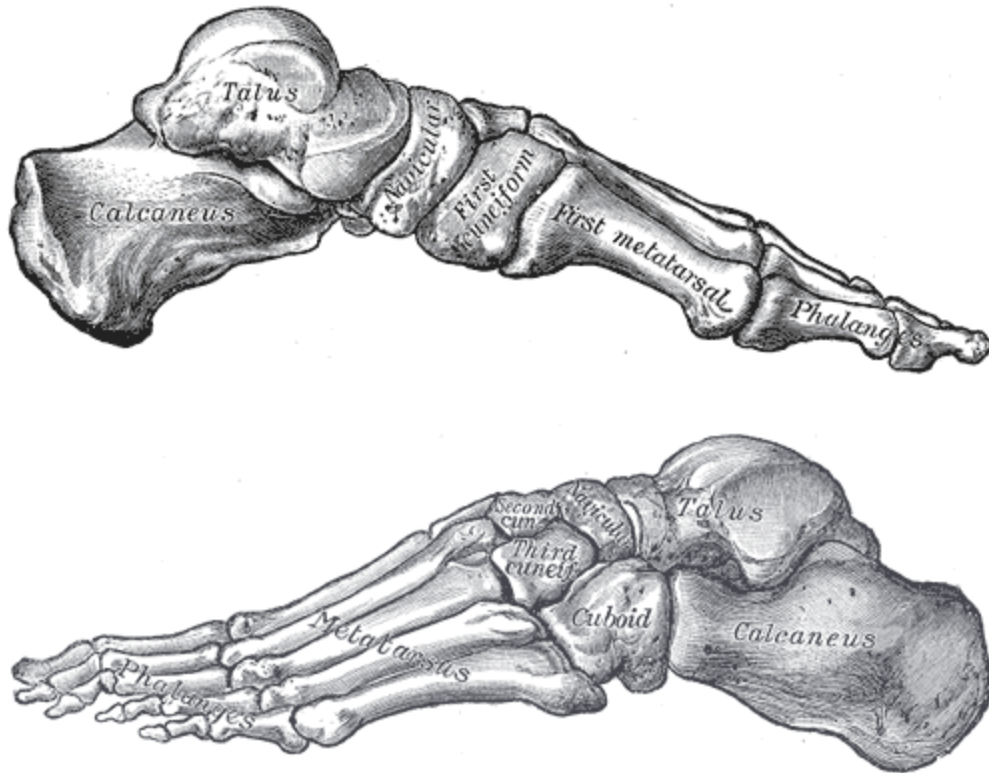
LOWER LIMB

The lower limb consists of the femur of the thigh, the tibia and fibula of the leg, seven tarsal bones of the ankle, five metatarsals of the body of the foot, and phalanges of the digits (three per toe and two per big toe or hallux). The head (proximal ball-like structure) of the hominin **femur** is large. The femur angles medially (inward) from hip to knee, so that our upper body weight is transferred down through our hip joints to our knees. This is termed the **carrying** or **bicondylar angle**. The knees of quadrupedal apes are directly below the hip joint, so there is more strain on the knee joints when they walk bipedally (see Figure 5.13). We have two bulbous structures on the bottom of each femur, termed condyles. The innermost condyle, the **medial condyle**, has lengthened in hominins so that the femur sits on top of the flat tibial surface. If this were not the case, the medial condyle would not make contact with the **tibial plateau**, due to the bicondylar angle. Weight is transferred through our innominate, hip joint, and **lateral condyle** of the femur (see Figure 5.13, "Human"). Unlike apes' knees that are chronically flexed, our knees are capable of full extension; each locks into place when the other leg is in swing phase, giving us a stable supporting leg. Each *gluteus medius* muscle alternately supports the opposite side of the torso and pelvis, so that it does not slump on the unsupported side.



Pelvic girdle and weight loading on knee joint. Illustration by Keenan Taylor.

Our feet (see Figure 5.14) have changed dramatically from a mobile, grasping structure to a rigid, supporting one. The tarsal bones of the human ankle are large and robust for support. The joint between the distal tibia and fibula is fairly immobile, so that the two bones are firmly lashed together. Together, they articulate with the **talus** (most superior tarsal bone) in a hinge joint. We have lost much of the mobility of an ape foot and thus have become less agile in climbing over time. The calcaneus or heel bone is very large and robust and, along with the ball of the foot (distal end of the first metatarsal) and the area below the baby toe (fifth metatarsophalangeal joint), forms a tripod structure. Our feet have three arches for support, shock absorption, and forward propulsion; they are the medial and lateral longitudinal arches and the transverse arch. Hominin toes became shorter and less curved over time. While shorter, the hallux became more robust and lost its degree of divergence and opposability, by coming into alignment with the lateral four toes, i.e. digits II through V.



Human foot bones. Plates 290 and 291 from Gray's Anatomy. "Skeleton of foot. Medial aspect" and "Skeleton of foot. Lateral aspect" by Henry Vandyke Carter are in the public domain.

HOMININ EVOLUTIONARY TRENDS

Just as there are evolutionary trends that characterize primates, there are also trends that characterize the hominins, i.e. traits that developed over time and occur to varying degrees in the various hominin species (see Table 5.1). While all of the morphological changes involved with bipedalism are hominin trends, there are also relevant characteristics in other parts of the body.

Table 5.1 HOMININ EVOLUTIONARY TRENDS

Bipedalism and related morphological adaptations.

Encephalization and corresponding prolonged juvenile dependency.

Loss of craniofacial robusticity and muscle attachments.

Reduced prognathism.

Reduction in size of dentition.

Molarization of premolars.

Increased manual dexterity.

Elongated legs and increased stature.

Increased reliance on culture, technology, and language.

Increased reliance on meat in the diet.

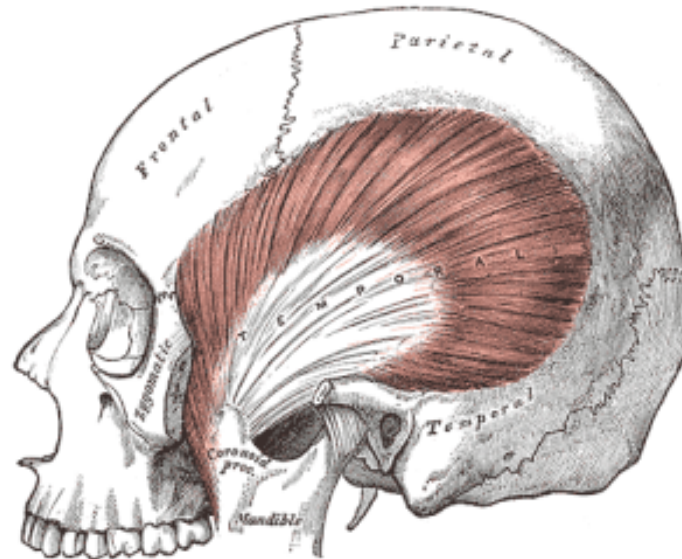
Most notable, our ancestors and their relatives became increasingly more intelligent. Our brains have increased in size more than four-fold, from a more chimp-sized brain (<400 cc) in the earliest hominins to a mean of ~1400 cc. This likely occurred in response to environmental stresses as well as competition with other hominins for resources. Skull size and shape changed in response to **encephalization**, i.e. increasing brain size.

Brains are very costly organs and researchers believe that in order for brain size to have increased, there would have had to have been a corresponding decrease in some other costly organ system. It is hypothesized that a higher quality diet allowed the hominin gut to shrink and, in turn, the brain to expand. Marked encephalization in the hominin lineage began with the first members of our own genus: *Homo*. While there is some evidence that earlier species (e.g. australopiths) manufactured tools, there is solid evidence that early *Homo* did, and the archaeological record suggests an increasing reliance on meat in their diet. While the dimensions of the thorax remained wide and shallow, the shape of the rib cage changed from a more conical, ape-like thorax that could accommodate a large gut, to our more barrel shape. As our brains became bigger, our ancestors gave birth to increasingly **altricial** (helpless) young that continued their development outside of the womb. Our offspring require protection and care for a much longer period than those of the other great apes, i.e. we have a prolonged juvenile dependency period. At least by the time of the earliest members of the *erectus* grade at 1.8 mya (see Chapter 27 and subsequent chapters), it is thought that infant requirements necessitated assistance from mates and/or relatives.

Many of the early hominins had pronounced, forward-oriented jaws, termed **prognathism** (*pro* = forward; *gnath* = jaw). Over time, hominins became more flat-faced, or **orthognathic**. While extant African apes retain primitive prognathism and the shearing/honing dental complex, hominins lost those pronounced canines, as well as the gaps in the corresponding tooth rows—termed **canine diastema** (singular) or diastemata (plural)—that allow apes to close their jaws. The hominin first lower/mandibular premolar developed into the characteristic **bicuspid** (two-cusped) morphology over time, as opposed to the apes' unicuspid sectorial premolar. The loss of the honing complex may have been in response to reduced competition for females as a result of male-female

pair-bonding. Once the jaws no longer locked into place, our ancestors were free to grind their food, aiding in its digestion.

The size of jaw and neck muscle attachment sites on the skull became reduced in the hominin lineage over time, along with a reduction in the size of the teeth and craniofacial robusticity. The action of the powerful *temporalis* muscle (a muscle of **mastication**) changed from primarily acting on the front of the jaw, allowing apes to clamp their jaws powerfully shut during fighting, to acting on the molar region for grinding food (see Figure 5.15). The origin of the *temporalis* muscle moved over time from the midline of the top of the skull to a more inferior position on the lateral aspect of the frontal and parietal bones (see Figure 5.15), due to the reduction of the sagittal crest and decrease in *temporalis* power in hominins.



Temporalis muscle: Originates on frontal, parietal, and temporal bones and inserts on mandible. (Zygomatic is shown as having been cut to reveal underlying muscle. Plate 382 from Gray's Anatomy. "The temporalis" by Henry Vandyke Carter is in the public domain.

Leglength increased as our hominin ancestors came to rely less on an arboreal environment and became primarily terrestrial. The pronounced increase in leglength and stature seen in the *erectus* grade (see Chapter 27), relative to past species, allowed them to cover vast distances efficiently and they moved from Africa to Asia in a relatively short period of time.

Hominin fingers became shorter and lost their curvature over time. By the time of the australopiths, hands had become more dexterous. There is evidence that *Australopithecus africanus* possessed a **"power" thumb**, giving them increased abilities for holding objects in one hand while manipulating or working them with the other hand. This was necessary for our ancestors to have made and efficiently used tools. The first metacarpal was adapted for such activity, and the **intrinsic thumb muscles** (within the hand versus extending from the forearm into the hand) were well-developed. There is some controversial evidence that by the time of the later robust australopiths, or paranthropines, expanded fingertips had appeared. Thus they may also have possessed the enlarged tactile pads and increased sensitivity and vascularization that allows for modern humans' fine degree of manual dexterity.

Finally there is the cultural side of things. We are like no other species that has ever lived. We are unique in our ability to practice, produce, and pass on culture. Our brains are predisposed to the acquisition of language and

culture. Thus, the final evolutionary trend seen in the hominins is an increased reliance on culture and language over time.

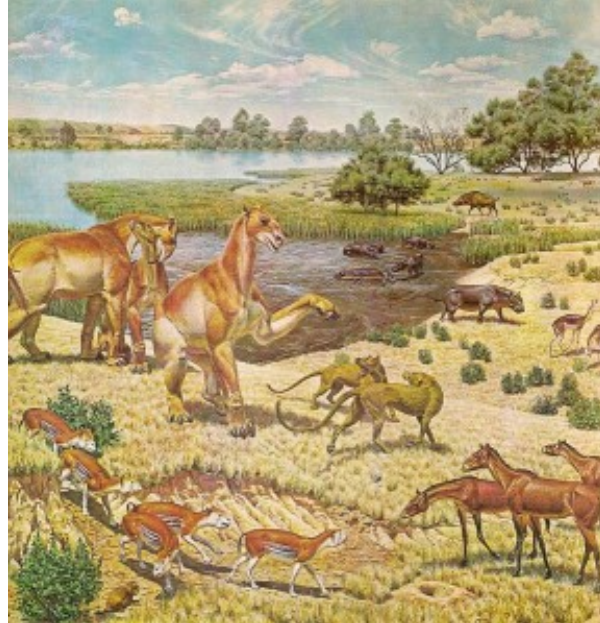
HOMININ GROUPS

The hominins can be divided into five groups that will be covered in subsequent chapters, based on shared characteristics and/or phylogenetic affinity:

1. Earliest bipeds: *Orrorin* and possibly *Sahelanthropus*.
2. Forest-adapted bipeds with relatively thin molar enamel: arthropiths.
3. Bipeds that exploited a more open and drier niche with thick molar enamel: gracile australopiths, such as *Australopithecus anamensis* and *afarensis*.
4. Descendants of gracile australopiths with heavy masticatory apparatus, adapted to exploit tough or hard foods when necessary: paranthropines, also known as robust australopiths.
5. Hominins that retained the gracile masticatory apparatus of their australopith ancestors and exhibited a trend for encephalization and increasingly complex culture: *Homo* species.

PART II: MIOCENE EPOCH

THE MIOCENE EPOCH (-23–5.3 mya)



And, on this side of “the pond”: Miocene North American fauna. “Miocene” by Jay Matternes is in the public domain.

Relative to the Oligocene Epoch, the Miocene was initially warmer and by the mid-Miocene, primates had once again ventured into the northern latitudes. This time they were apes, versus the prosimians of the Eocene. However, like those earlier primates, the northern apes would eventually go extinct due to global cooling that began ~14 mya.

Whenever there is climatic change, floral and faunal changes follow. Much of the dense equatorial forests became more open, and grasslands and deserts expanded so that the African landscape became more of a **mosaic environment**, versus deep, dark jungle. Initially the apes were very successful at diversifying and expanding into new niches; as mentioned in Chapter 3, this was the time of the **hominoid adaptive radiation**. Over time, however, as the landscape continued to change and forests became increasingly fragmented, the majority of ape species went extinct, leaving only a handful of species in Africa.

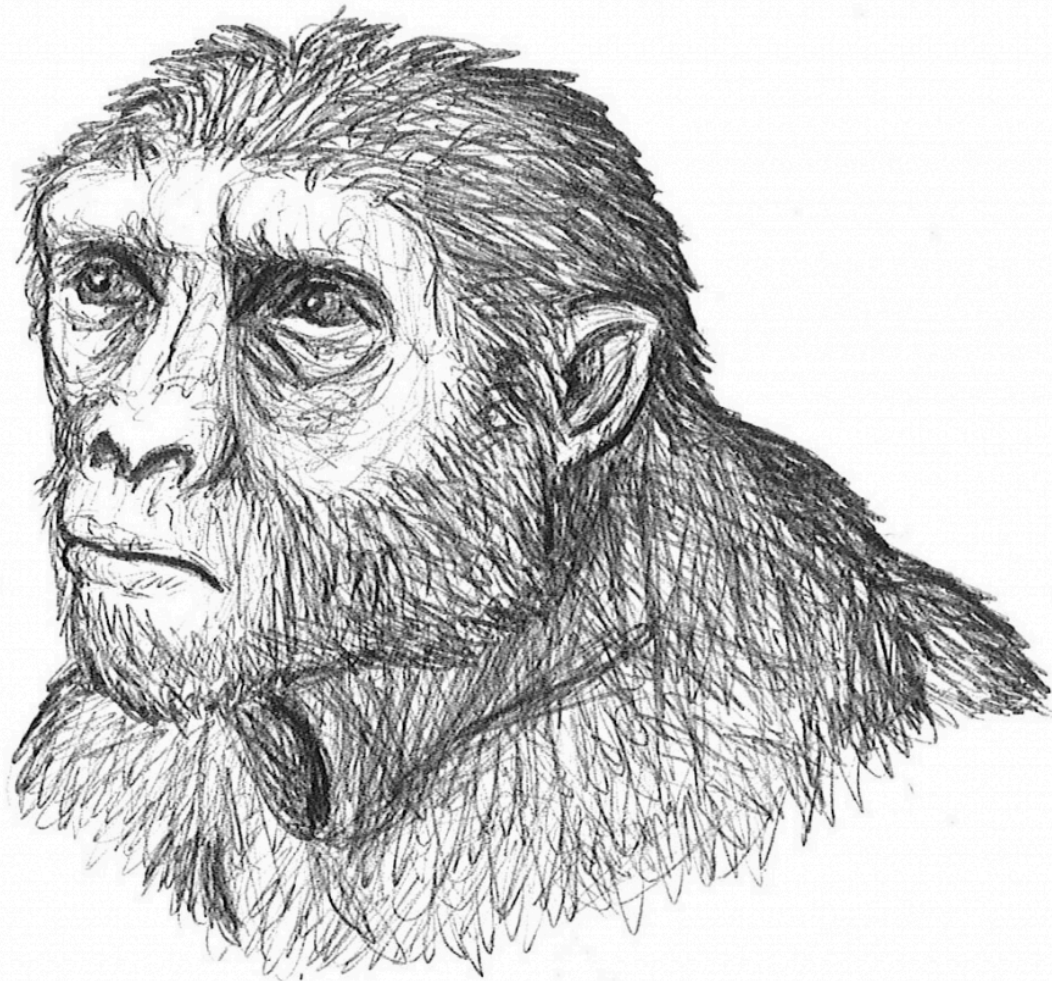
In recent years, three new genera of hominoids have been discovered in Africa. While there is debate as to whether the oldest, i.e. *Sahelanthropus*, is a true hominin, *Orrorin* and *Ardipithecus* are generally accepted as true hominins.

Caution must be exercised in the interpretation of the fossil record. It is tempting to formulate a linear history for our species, e.g. species A gave rise to Species B which gave rise to Species C, etc. The fossil record is extremely incomplete and we may get only a glimpse of the species that lived at a particular time and place. Paleoanthropologists are continually revising their theories as new discoveries are made and old material is reinterpreted in light of new discoveries, methodologies, and working hypotheses.

6. Sahelanthropus tchadensis

Sahelanthropus tchadensis (<7mya)

("human from the sahel" / Chad)



Sahelanthropus tchadensis by Keenan Taylor.

SITES

Toros-Menalla, Chad

PEOPLE

Michel Brunet

INTRODUCTION

The *Sahelanthropus tchadensis* specimen (see Figure 6.2) was discovered in 2001 at the site of **Toros-Menalla**, in the Djurab Desert of northern Chad, by **Michel Brunet** and associates. Brunet's incredible years-long quest for hominins in that area is documented in the NOVA series, *Becoming Human* (www.pbs.org/wgbh/nova/evolution/becoming-human.html). The species name translates to “human from the **sahel** of Chad.” The sahel is the region of dry grasslands south of the Sahara desert. The skull has been nicknamed “**Toumai**” in the Dazaga language, meaning “hope of life.”



Cast of the *Sahelanthropus tchadensis* holotype cranium. “*Sahelanthropus tchadensis* – TM 266-01-060-1” by Didier Descouens is licensed under CC BY-SA 4.0.

The location of the fossil material came as a surprise in that only one species of hominin had ever been discovered west of the Great Rift Valley of East Africa, i.e. *Australopithecus bahrelghazali* (see Chapter 12).

However in 1998, Noel Boaz speculated that, contrary to the Rift theory for the origin of the hominins, a portion of the ancestral stock that gave rise to the chimp and human lineages became isolated in a riparian (i.e. riverine or gallery) forest zone in Chad that was surrounded by arid, open land. At a later point in time, a forest corridor allowed their movement into East Africa. Part of the problem at that point in paleoanthropology was that no species of hominins, prior to the australopiths, had been discovered in East Africa. They seemingly appeared *de novo* in the fossil record, beginning about 3.5 mya, with no intervening stages or “missing links” in evidence. We now have much older hominin species from Kenya and Ethiopia, i.e. *Orrorin tugenensis* and *Ardipiths*, respectively.

PHYLOGENY

While the phylogeny of *S. tchadensis* is unknown, some researchers believe that it may represent a **stem** or **basal hominin**, i.e. one of the earliest members of our tribal tree. (**Note:** Once a genus is used the first time in a document, it can subsequently be abbreviated.) Just as we do not know the ancestry of the species, we do not have any species that are good contenders for its descendants.

DISCOVERY AND GEOGRAPHIC RANGE

As mentioned, the holotype (the fossil(s) from a particular individual that are assigned to **and** used to define the characteristics of a species) was discovered at the desert site of Toros Menalla (see Figure 6.3). Unless fossils are discovered elsewhere, it is impossible to speculate about the extent of the geographic range of the species.



Toros Menalla site, Chad. “Sahelanthropus tchadensis – TM 266 location” by 120 is in the public domain.

PHYSICAL CHARACTERISTICS

The skull of *S. tchadensis* is very robust, with a chimp-sized brain and pronounced ape-like muscle attachments. While only fragmentary postcranial material has been discovered, some researchers claim that the foramen magnum is anteriorly oriented, suggesting an upright and bipedal hominin. Pronounced brow ridges are also concordant with early hominin status. The facial profile is surprisingly orthognathic and the jaws lack the honing complex, leading some researchers to speculate that *S. tchadensis* may lie near the base of our family tree, versus other phylogenetic scenarios. However, the pronounced posterior neck muscle attachments have led others to suggest that *S. tchadensis* may have been quadrupedal.



Sculpture of *S. tchadensis* by Élisabeth Daynès.

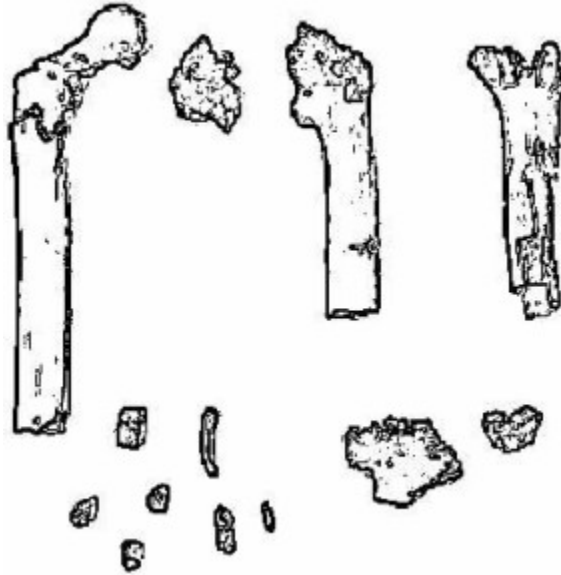
ENVIRONMENT AND WAY OF LIFE

Based upon fossilized faunal remains at the site, such as freshwater fish, rodents, and monkeys, it is likely that *S. tchadensis* inhabited a forest environment in close proximity to an ancient lake (Wayman 2012). Their way of life was likely that of a forest-dwelling ape. Like ardiipiths (see Chapter 8), their molar enamel was thinner than that of the later australopiths and they thus likely had a chimp-like diet consisting of fruit, young leaves, and tender shoots.

7. *Orrorin tugenensis*

Orrorin tugenensis (~6 mya)

(“original” / Tugen hills)



Drawing of *Orrorin tugenensis* fossil material. “*Orrorin tugenensis*” by Lucius is licensed under CC BY-SA 3.0.

SITES

Aragai and Kapsomin in the Tugen Hills of Kenya

PEOPLE

Brigitte Senut and Martin Pickford

INTRODUCTION

In 2000, the team of **Brigitte Senut** and **Martin Pickford** discovered fossil material (see Figure 7.1) from the

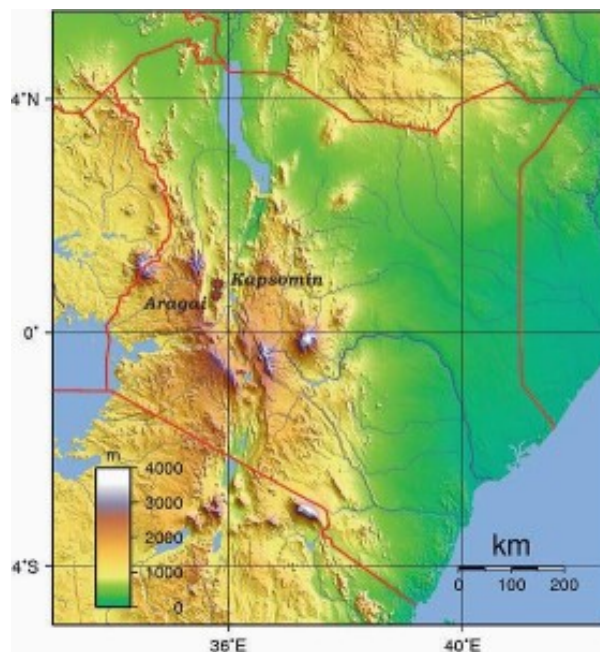
Lukeino Formation in the **Tugen Hills of Kenya**. Nicknamed “**Millenium Man**” due to its timely discovery, the fossils were dated to ~6 mya and given the taxonomic classification, *Orrorin tugenensis* (“original man from the Tugen hills”). Initially many paleoanthropologists were skeptical, especially since the fossils were not made available to the scientific community. While there is still debate, *O. tugenensis* is increasingly presented in published texts as a hominin.

PHYLOGENY

The ancestry of *O. tugenensis* is unknown. Senut and Pickford believe that *Orrorin* is ancestral to humans. They suggest that the hominin tribe split prior to 6 mya with *Orrorin* and some species of australopiths (specifically *Australopithecus anamensis* and *Australopithecus afarensis*, which they place in the genus *Preanthropus*) in the human lineage and ardpiths and robust australopiths, or paranthropines (including *Australopithecus africanus*), on another branch that died out.

DISCOVERY AND GEOGRAPHIC RANGE

There are only two known sites for the species, Aragai and Kapsomin, both of which are in the Tugen Hills of Kenya (see Figure 7.2).



Orrorin tugenensis sites, Kenya. “*Orrorin* localities” by Chartep is licensed under CC BY-SA 3.0.

PHYSICAL CHARACTERISTICS

Few body parts have been recovered. The fossils consist of a partial humerus, femur, and mandible; a distal thumb bone (phalanx); and some teeth. Primitive characteristics include remnants of a honing complex, with large canines and a “**semi-sectorial**” premolar. The molars were covered with **thick enamel** like those of later hominins, and while they were small like our own, they were not as laterally expanded. Senut and Pickford assert

that the femur of *O. tugenensis* is very human-like, with its large head and hominin-like carrying/bicondylar angle, and thus is part of the human lineage.

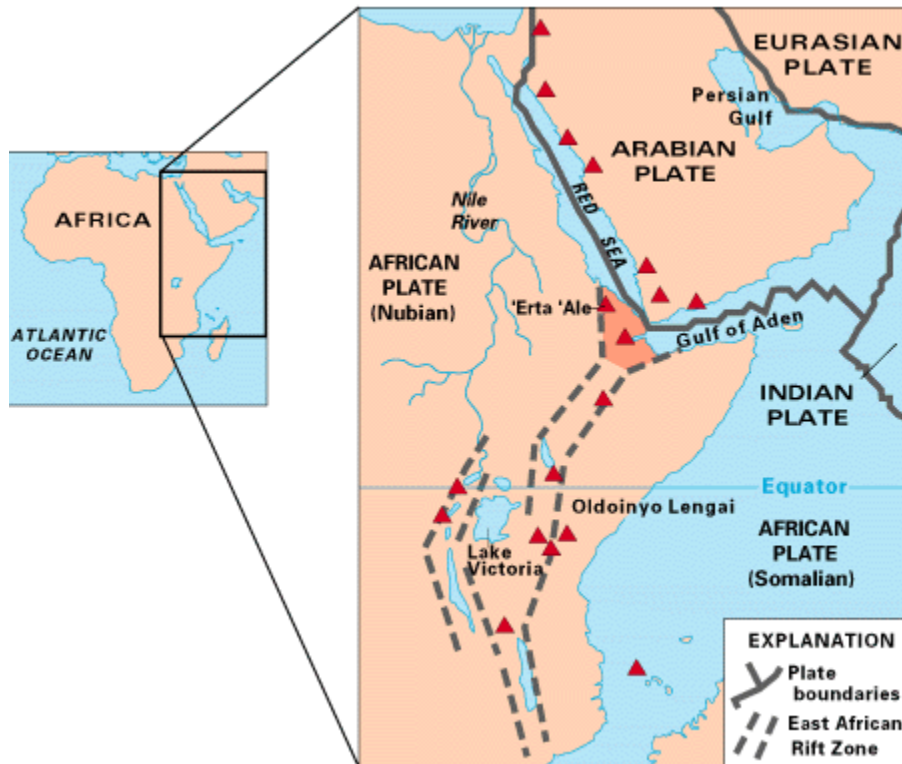
ENVIRONMENT AND WAY OF LIFE

It is generally accepted that *O. tugenensis* was bipedal, and that they likely practiced a similar way of life as the ardipiths and australopiths. Thus, they were likely semi-terrestrial, foraging both in trees and on the ground and using trees for sleep and safety. However, their more human-like femur and thick molar enamel allies them more with the australopiths and they thus likely spent more time on the ground than the ardipiths and exploited a greater percentage of terrestrial resources that cause more tooth wear. In addition, like *Australopithecus afarensis*, *O. tugenensis* exhibits vestiges of the honing complex and thus may be ancestral to australopiths.

8. *Ardipithecus ramidus*, *Ardipithecus kadabba*

GENUS: *Ardipithecus* (“ground ape”)

Deposits within the **Afar triangle/depression** of Ethiopia (see Figure 8.2) have yielded multiple hominin species within the genera *Ardipithecus* and *Australopithecus*. This hotbed of hominin fossils is the northern limit of the **East African Rift Zone**, where the Arabian and African plates converge. The first species of ar dipith to be discovered in the area was *Ar. ramidus* (4.4 mya), and the second and even older species was *Ar. kadabba* (5.8 mya). When *Ar. kadabba* was discovered by **Yohannes Haile-Selassie**, he believed that it was similar enough to *Ar. ramidus* that he included it in the same genus and species, thus warranting subspecies classification. Since *Ar. ramidus* was already named, its classification became *Ar. ramidus ramidus*, in the same manner that we became *Homo sapiens sapiens* when it was decided that Neandertals should be included in our species and they became *Homo sapiens neanderthalensis*. The original name is always preserved for the original fossil(s). It becomes known as the “**type specimen**” or “**holotype**” and is used to describe the characteristics that define the species. The older subspecies then became *Ar. ramidus kadabba*. Since that time, they have been split into two species within the genus: *Ardipithecus*. Each will be discussed below.



The East African Rift Zone. The Afar triangle is featured in darker pink at the most northerly limit (see 'Erta 'Ale site). “EAfrica” by the USGS is in the public domain.

Some paleoanthropologists have suggested that *Ardipithecus* may be a better candidate for our ancestry than one or more of the australopiths. It has also been suggested that australopiths are descended from *Ardipithecus* or that the ar dipiths are a separate but related branch.

Ardipithecus ramidus (4.4 mya)
("ground ape" / "at the root" in Afar language)



Map showing the fossil sites of the earliest hominids. "Map of the fossil sites of the earliest hominids (35.8-3.3M BP)" by Kameraad Pjotr and Sting is licensed under CC BY-SA 3.0.

SITES

Aramis, Ethiopia

PEOPLE

Tim White and colleagues

PHYLOGENY

The phylogeny of the ardiapithecids is unknown. We do not know if they left any descendants, but it is thought that *Ardipithecus ramidus* is likely descended from *Ardipithecus kadabba*.

DISCOVERY AND GEOGRAPHIC RANGE

During the early 1990s, fossils were unearthed at the site of **Aramis** in the **Middle Awash region** of the Afar Triangle of Ethiopia (see Figure 8.3). Since that time, material from more than 50 individuals has been recovered, in particular the famous “**Ardi**” skeleton (see Figures 8.4 and 8.5) that is ~50% complete. Prior to the discovery, all or most early African hominin fossils were considered to be australopiths. Tim White and his colleagues determined that the material was distinctive enough to warrant new genus classification.



Digital reconstruction of Ardipithecus ramidus specimen. “Ardi” by T. Michael Keesey is licensed under CC BY 2.0.

Fifteen years after its discovery, **Ardi** was presented to the world in a frenzy of media coverage. She shook the world, not just within paleoanthropology, but for anyone interested in our past. She was an upright ape! Yes, we are all apes, but Ardi looked like what we think of as an ape. She had an ape face, small brain, long and strong arms and fingers, and ape-like feet. However, she stood upright with straight rather than flexed legs. The film *Discovering Ardi* (2009, Discovery Communications) showcases her discovery, fossil processing and analyses, the artist’s skeletal and full-body reconstructions, biomechanical computer-generated graphics, etc.—everything for the modern tech-appreciative student!



Artist's representation of *Ardipithecus ramidus*. "Ardipithecus Gesamt!" by Ori- is licensed under CC BY-SA 3.0.

PHYSICAL CHARACTERISTICS

Ardipiths were likely arboreal climbers, like the ancient "basal" proconsulids. However, when they were on the ground, they walked bipedally, albeit with rather clumsy-looking feet. Characteristics that were initially used to designate hominin status were an anteriorly placed foramen magnum, aspects of the innominate and ulna, and especially the morphology of the humerus that suggested that it was not weight-bearing and therefore not involved in terrestrial locomotion.

Primitive characteristics of ardipiths can be seen in many body regions. Their brains were small. Depending on the source, their cranial base (the inferior portion of the occipital bone) was either flat like chimps and gorillas, or angled and tucked under the upper part of the cranium (termed **flexed cranial base** or **basiscranial flexion**). The enamel on their molars was thin like that of chimps and other extinct forest-dwelling apes. They retained several primitive characteristics that are related to arboreal climbing:

- Elevated shoulder joints for reaching up for branches, etc.
- Long arms and long, curved fingers.
- Mobile wrists.
- Poorly differentiated thumb, meaning that they had poor opposability.

Orangutans are the only great ape with a similar thumb morphology and hence have poor manual dexterity. Ardipiths' **divergent hallux** (i.e. the big toe diverges away from the lateral four digits, like our thumbs) would also have been adaptive for climbing.

Derived postcranial characteristics of ardipiths are all in the hip and lower limb. While Ardi's species had short legs and long arms (i.e. high intermembral index), the morphology of their hip and leg bones reflect bipedality, according to Tim White, Owen Lovejoy, and other members of their team. The innominate and foot morphology combine adaptations for climbing and bipedalism. They were capable of full extension at the knee, unlike the flexed knee seen in extant apes. Their feet were stable and supported their body weight and the divergent hallux facilitated grasping and climbing.

Body mass is estimated from Ardi's skeleton and thus no estimate for males of the species is possible. Ardi is estimated to have been 3'11" (120 cm) tall and weighed about 110 lb (50 kg) (Gibbons 2009). The absence of both a honing complex and pronounced prognathism suggests to some researchers, such as C. Owen Lovejoy, that males were not competing for females and may have formed pair-bonds with them.

Review of Primitive Characteristics

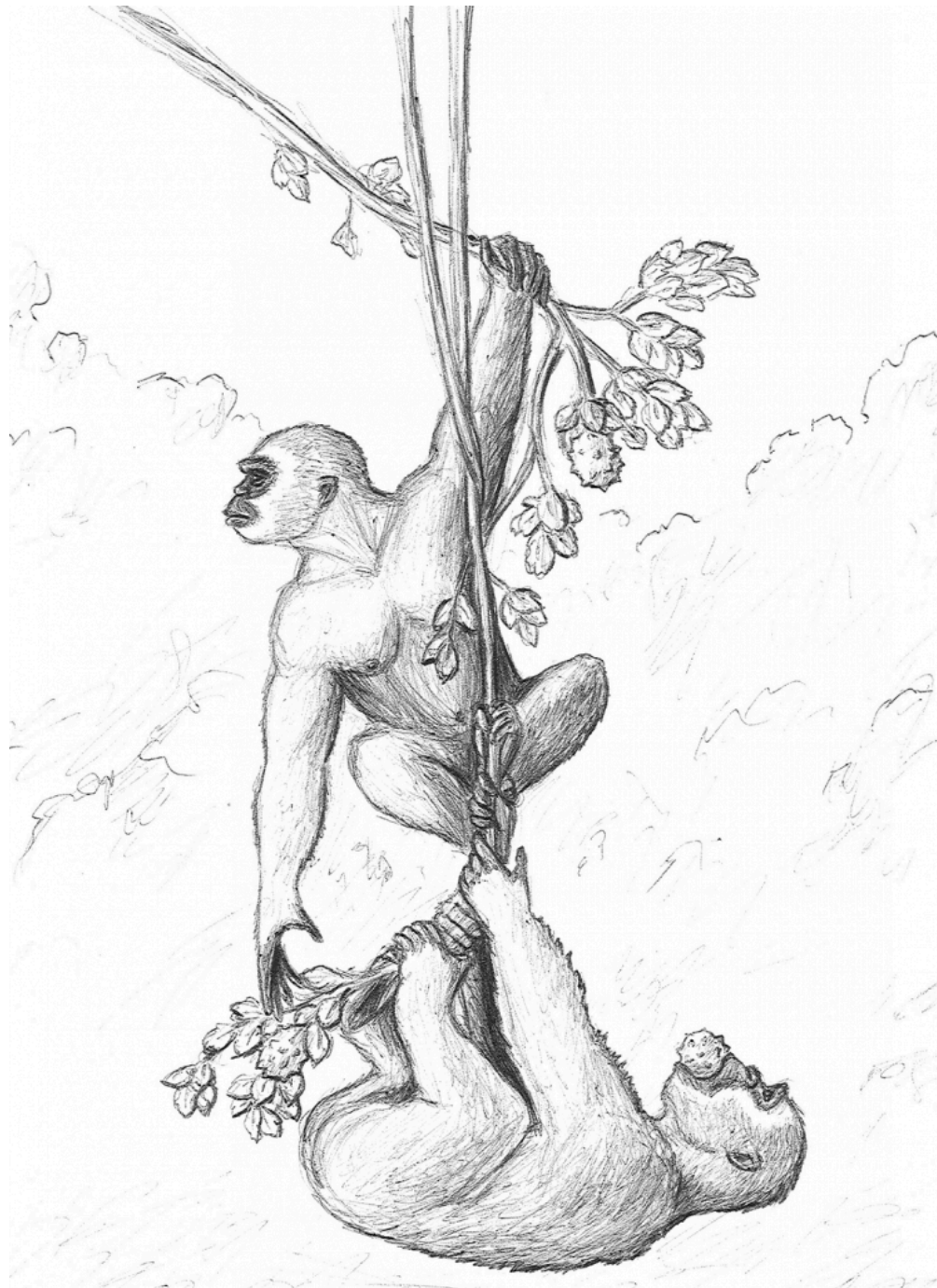
- Small brain and flat cranial base.
- Thin molar enamel.
- Climbing complex of upper limb:
 - Elevated shoulder joint.
 - Long arms.
 - Long and curved fingers.
- Low manual dexterity.
- Divergent hallux.

Review of Derived Characteristics

- Anteriorly oriented foramen magnum.
- Bipedal hip, leg, and foot characteristics.

ENVIRONMENT AND WAY OF LIFE

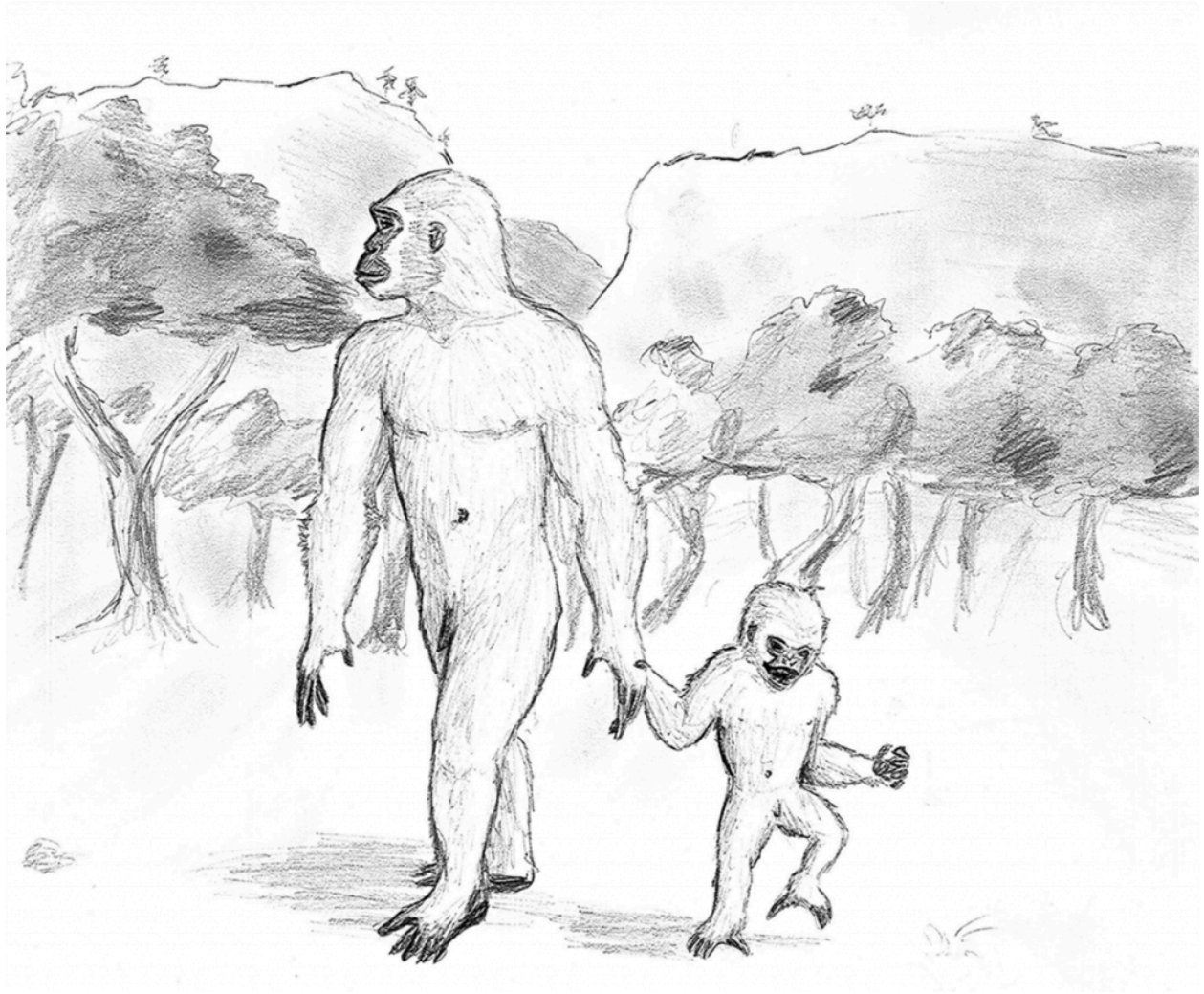
The sites where ar dipith fossils have been recovered were a mosaic environment consisting of wood- and grasslands during the late Miocene and early Pliocene. Those ancient apes likely subsisted on a combination of arboreal and terrestrial forest resources. Their thin molar enamel suggests that, like chimps and orangutans, their diet consisted of relatively soft food items, such as fruit, young leaves, and shoots and possibly ants and termites. They could locomote within and between trees when foraging, or climb down and travel between trees or forested areas. Since all great apes build nests, ar dipiths may have made a new arboreal nest every night.



Ardipith by Keenan Taylor.

Some scientists see the lack of canine sexual dimorphism and honing complex as evidence for **pair-bonding**. There is good evidence from the animal literature to relate sexual **monomorphism** (no difference in size between males and females) and pair-bonding. As mentioned in Chapter 4, while there are several groups of primates that exhibit that grouping and mating strategy, they are all arboreal. The lesser apes are arboreal, medium-sized (<6 kg) primates that form territorial pairs. Their mode of locomotion is brachiation, i.e. swinging under branches. While that is a more efficient means by which to avoid predation relative to arthropods climbing around in the trees, the latter were larger and heavier and thus were likely fairly safe. When they descended to the ground, however, pairs would have been fair game for predators.

The idea that male provisioning, in combination with pair-bonding, was the evolutionary stimulus for bipedalism is also problematic. As I discussed in Chapter 5, I do not understand why females would need to be provisioned unless their babies could no longer hang on. I just do not see males risking life and limb to bring food back to females. I know of no examples in nature of a mammalian male provisioning his mate. It is more likely that resources became fragmented to the point that upright locomotion was the most efficient way to move between trees and forest patches. Bipedalism was an adaptation to enable continued reliance on forest resources while minimizing competition. Arthropods could move to another forest patch when resources became scarce. I think of them as being semi-terrestrial apes like chimps and gorillas but, unlike those extant species, they had less of a stable resource base. They thus evolved a more efficient locomotor strategy for expanding their home range.

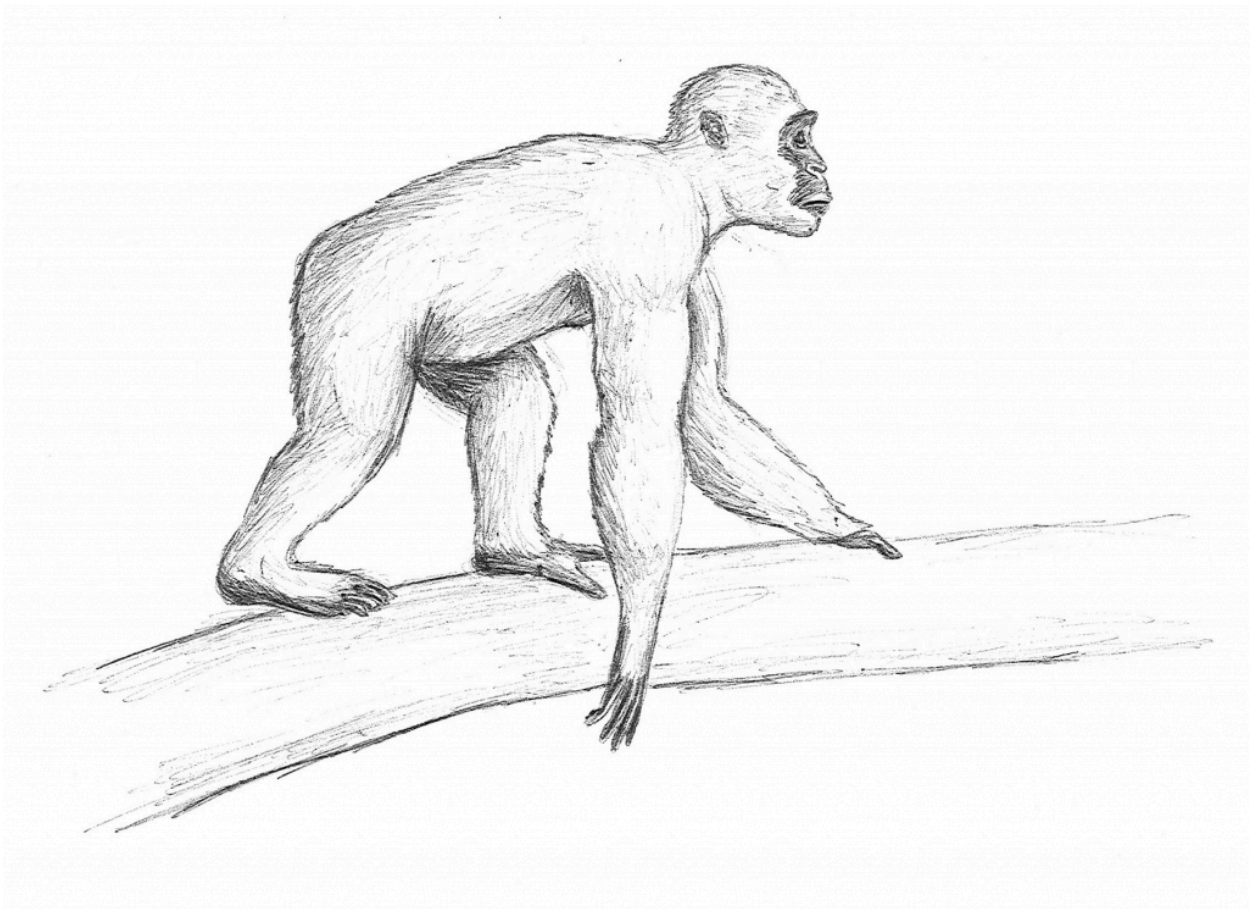


Ardipith Parenting by Keenan Taylor.

Ardipithecus kadabba (5.8 mya)

(“ground ape” / “oldest ancestor” in Afar language)

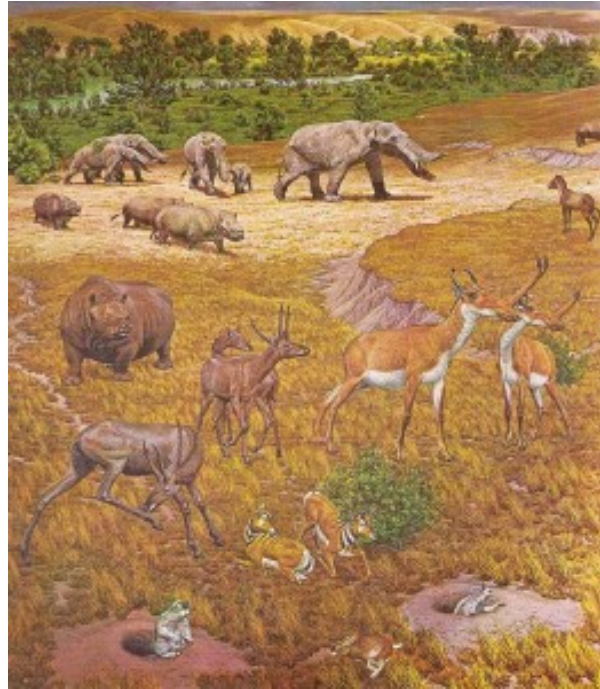
Yohannes Haile-Selassie discovered the second ar dipith species in the Middle Awash region of the Afar Depression (see Figure 8.3). The species is thought to be ancestral to *Ar. ramidus*. Dental characteristics are more ape-like than those of *Ar. ramidus*. While the fossils are very fragmentary, a toe bone suggests bipedal foot movement involving the “toe-off” motion, i.e. when we push off with the toes of one foot as we plant our other foot following its “swing” phase.



Ardipith by Keenan Taylor.

PART III: PLIOCENE EPOCH

THE PLIOCENE EPOCH (5.3–2.6 mya)



Pliocene fauna of North America. “Pliocene” by Jay Matternes is in the public domain.

The Pliocene Epoch (~5.3–2.6 mya) was characterized by global cooling and weather disruptions due to the formation of the Panama land bridge and resultant changes in ocean currents. The polar ice caps were expanding and sea levels had already begun to drop, as the Pleistocene Epoch (~2.6 mya–11.7 kya) approached. The geologic record shows us that Africa was subject to cooling and drying trends, with seasons becoming more pronounced. Grasslands were expanding and thus forest cover was shrinking. Intermittent wet and dry periods changed the African landscape. Lakes formed and dried and filled once again. All of the arthropods and most australopithecids went extinct during this epoch and by ~2.0 mya genus *Homo* appeared in the fossil record. The most tantalizing question with regard to the earliest members of our genus is what drove the encephalization process. By the time of the more derived paranthropines [*Paranthropus boisei* (2.5–1.4 mya) and *robustus* (1.9–1.3 mya)] and genus: *Homo* (≥ 2 mya), cranial capacity had increased ~100 cc and 200 cc, respectively, from the earlier hominins. It has generally been hypothesized that competition for resources was the driving force, and while that may be so, recent research has illuminated just how radical climatic changes were in East Africa. The film *Becoming Human* (2009, Discovery Communications) provides a nice overview of how scientists have pieced together the Pliocene environment of that region of the world from the local geology.

PLIOCENE HOMININS



Foraging paranthropines in South African grasslands. Artwork by Walter Voigt.

The Pliocene Epoch can be considered the time of the great **adaptive radiation of the hominins**, when more than a dozen species evolved in the **hominin corridor** from Ethiopia to South Africa. While the arthropods died out, concurrent with the reduction in forest cover during the late Miocene and early Pliocene, many australopiths came and went over the course of almost 3 mya of the Pliocene. The australopith lineage may pre-date the Pliocene; there is possible australopith material (possibly *Australopithecus anamensis* or *afarensis*) from the late Miocene from several Kenyan sites (e.g. Lothagam and Tabarin) for which no taxonomic designation has been established. While there is debate as to how much time australopiths spent outside of forested environments, they certainly filled distinctive niches, as evidenced by changing craniofaciodental morphology as well as more versatile hands that afforded them greater manipulative abilities. As we discover more about australopith limb morphology, it is apparent that some were more adapted to an arboreal environment whereas others were less so. Of even greater interest is that the East African australopiths (i.e. *Australopithecus anamensis*, *afarensis*, and *garhi*) may represent a different clade than those from South Africa (i.e. *Australopithecus africanus* and *sediba*). The East African species may have been more adapted to a terrestrial environment, while the South African forms may have retained or reverted to more primitive climbing adaptations. The various species may have walked differently as well.

The question remains: from which group are we descended? Some researchers have suggested that *Au. sediba* from South Africa may be part of our lineage; this confounds matters for some researchers as to how the older East African species were seemingly less primitive in some ways than the more recent South African forms. We need to realize that we are only seeing part of the picture. Just as the ape population levels exploded on three continents in the Miocene, the same was apparently true for African hominins in the Plio-Pleistocene. Discoveries of new species of African apes and hominins are accelerating. We need to break out of our linear mindset and realize that there were numerous species adapting to localized conditions, so we should not expect to see uniform changes across time and geographic space. In addition, the same may hold true for grouping and mating practices. We should not jump to conclusions or get too caught up in how the various species were

related and who begat whom! While everyone would like to be the person who found one of our long lost relatives, the history of paleoanthropology is fraught with those claims and debunks.



Modern landscape of Olduvai Gorge. "Panoramic view of Olduvai Gorge" by רגות is licensed under CC BY-SA 3.0.

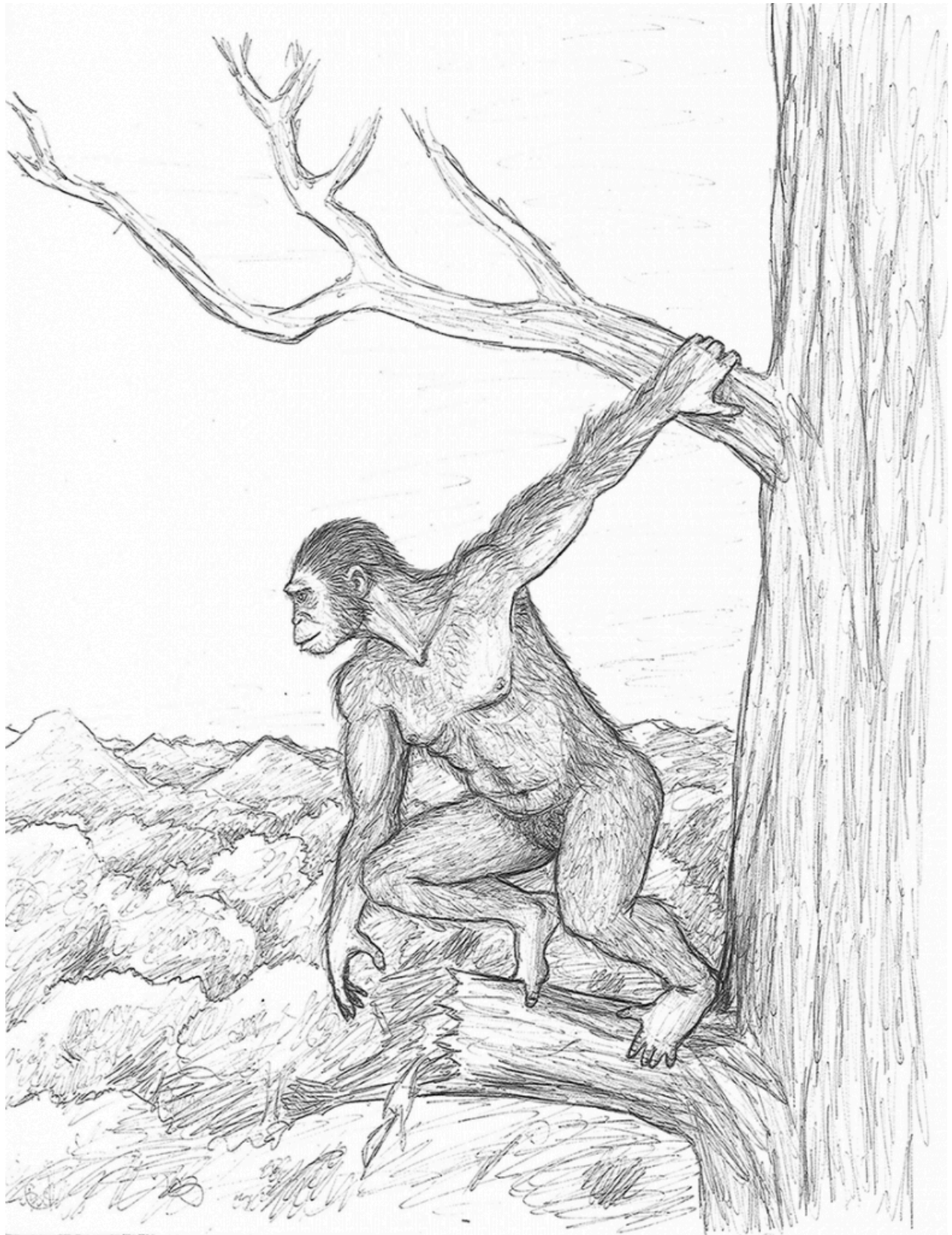
Upper limb morphology suggests that australopiths retained adaptations for climbing trees that were likely used for food and safety. However, when on the ground, they were habitual bipeds, albeit with some differences from ourselves.

9. Gracile Australopiths



Australopith fossil sites. “Map of the fossil sites of the early hominids (4.4-1M BP)” by Kameraad Pjotr and Sting is licensed under CC BY-SA 3.0.

Genus *Australopithecus* (“southern ape”) was first used in 1924 by Raymond Dart for the “Taung Child,” a juvenile *Au. africanus* specimen from the quarry site of Taung, in South Africa. *Au. anamensis*, *afarensis*, *africanus*, and *sediba* (depending on the evolutionary schema of individual paleoanthropologists) are popularly known as gracile australopiths, due to their more gracile masticatory apparatus relative to the robust paranthropines.



An australopith outlook. By Keenan Taylor, CC-BY-NC-SA.

10. Australopithecus anamensis

Australopithecus anamensis (4.2 mya)

(“southern ape” / from the “lake” in the Turkana language)



Distal humerus of *Australopithecus anamensis*. “*Australopithecus anamensis* bone (University of Zurich)” by Nicolas Guérin is licensed under CC BY-SA 3.0.

SITES

Allia Bay and Kanapoi, Kenya

PEOPLE

Meave Leakey and Alan Walker

INTRODUCTION

Australopithecus anamensis is the earliest known australopith. We do not know nearly as much about the species as about other australopiths due to a paucity of fossil material.

PHYLOGENY

Au. anamensis may be descended from the ardiopith lineage or a heretofore undiscovered group. Lucy's species, *Au. afarensis*, may be descended from *Au. anamensis*.

DISCOVERY AND GEOGRAPHIC RANGE

Multiple paleoanthropologists (most notably Meave Leakey and Alan Walker) are credited with the discovery of *Au. anamensis* material. The species name refers to the Lake Turkana area of Kenya where the fossil sites of Kanapoi and Allia Bay are located (see Figure 10.2). There are also newer fossils from the Middle Awash area of the Afar Depression of Ethiopia (see Figure 10.2). The Ethiopian material is close in time and geographic space to an *Ardipithecus ramidus* site, lending some support to the possibility of their phylogenetic relatedness. There is some controversy over the lumping together of material from different levels and locations in Kenya that could have confounded the description of the species' characteristics.



Australopithecus anamensis sites. "Anamensis localities" by Chartep is licensed under CC BY-SA 4.0.

PHYSICAL CHARACTERISTICS

The species is thought to have been highly sexually dimorphic in body and canine size.

Much of the morphology is ape-like, and hence primitive. The jaws and teeth are the most primitive of any australopith, which is not surprising since it is the oldest. Unlike the parabolic tooth arrangement in the jaws of later hominins, *Au. anamensis* had an apelike, U-shaped dental arcade wherein the cheek teeth are nearly parallel (see Figure 10.3). Their jaws were also prognathic and their **canines** were **larger** than descendent species. However, the molars were expanded with **thick enamel** and low cusps like later hominins. In addition, aspects of the elbow, knee, and tibia were more derived, indicating its bipedal mode of locomotion.



Jaw of extinct ape illustrating U-shaped dental arcade. "Rangwapithecus gordonii jaw" by Ghedoghedo is licensed under CC BY-SA 3.0.

Review of Primitive Characteristics

- High degree of sexual dimorphism.
- Prognathic jaws with ape-like parallel cheek teeth.
- Larger canines than subsequent species.

Review of Derived Characteristics

- Expanded molars, low cusp relief, and thick enamel.
- Bipedal adaptations of elbow, knee, and tibia.

ENVIRONMENT AND WAY OF LIFE

Fossils have been found in a variety of paleoenvironmental settings, such as lakeside, woodland, and more open areas. The species likely slept in trees and foraged both in trees and on the ground, as they moved bipedally around their home range in search of resources and mates. The high degree of sexual dimorphism and the presence of the honing complex suggest a polygynous or polygynandrous mating system. The former may have

involved a one-male/multi-female social organization and the latter, a multi-male/female pattern. A one-male system may have looked more like that of gorillas, where both males and females tend to leave their natal group. However, if we use chimps and bonobos as a model of our ancestral social organization, it was more likely a multi-male/female social organization, with males staying in their natal group (i.e. male-philopatric) and females leaving at sexual maturity to join another. While it is easy to use our more closely related relatives to reconstruct our past behavior, we must remember that social organization is a function of both phylogeny and ecology. Taking both into consideration, in combination with their anatomy, it is more likely that *Au. anamensis* were more chimp-like. Their teeth do not have the higher cusps of the more folivorous gorilla, so their diet was likely more chimp-like and hence a combination of fruit, tender greens, and opportunistic animal matter. As mentioned in Chapter 5, that type of diet is harder to come by and females may have needed males to defend a territory for their nutritional needs and those of their offspring. Interestingly, isotopic analyses of *Paranthropus robustus* (robust australopith from South Africa) fossil material show that while males were from the area where the fossils were found, females were not. Thus we now have a fourth line of evidence favoring male philopatry.

II. Australopithecus afarensis

Australopithecus afarensis (4.2 mya)

(“southern ape” / Afar region of Ethiopia)



Forensic facial reconstruction of *Australopithecus afarensis*.
“*Australopithecus afarensis*” by Cicero Moraes is licensed under CC BY-SA 3.0.

SITES

Ethiopia: Afar Depression (e.g., Hadar and Dikika)

Tanzania: Laetoli

Chad: Bahr el Ghazal

PEOPLE

Donald Johanson, Mary Leakey, Zeresenay Alemseged

INTRODUCTION

Australopithecus afarensis, or the “southern ape from Afar,” is a well-known species due to the famous “Lucy” specimen. It has been extensively studied by numerous famous paleoanthropologists. As mentioned, it is categorized as a gracile form of australopith. The species survived for over a million years in the changing East African landscape, covering a broad geographic range. The famous Laetoli footprints are attributed to *Au. afarensis* (see Figures 11.5 and 11.6). They provided support for the then controversial idea of habitual bipedalism, as well as the species’ presence in a more open environment.

PHYLOGENY

The most logical ancestor for *Au. afarensis* is *Au. anamensis*. The two species overlapped in time and geographic space. Some paleoanthropologists have always believed that genus: *Homo* is descended from *Au. afarensis*. Over time, others have changed their taxonomic scenarios from *Au. africanus* to *Au. afarensis* (which would formerly have been a sister lineage to *Au. africanus*) as our ancestor, and made *Au. africanus* a side branch of the robust forms. Part of the argument for classifying *Au. afarensis* outside of our lineage had to do with aspects of their anatomy being more derived than our own, e.g. the lateral flare of their ilia (the plural of ilium). Since the discovery of *Au. sediba* (Chapter 21), some scholars are back to favoring *Au. africanus* in our ancestry.

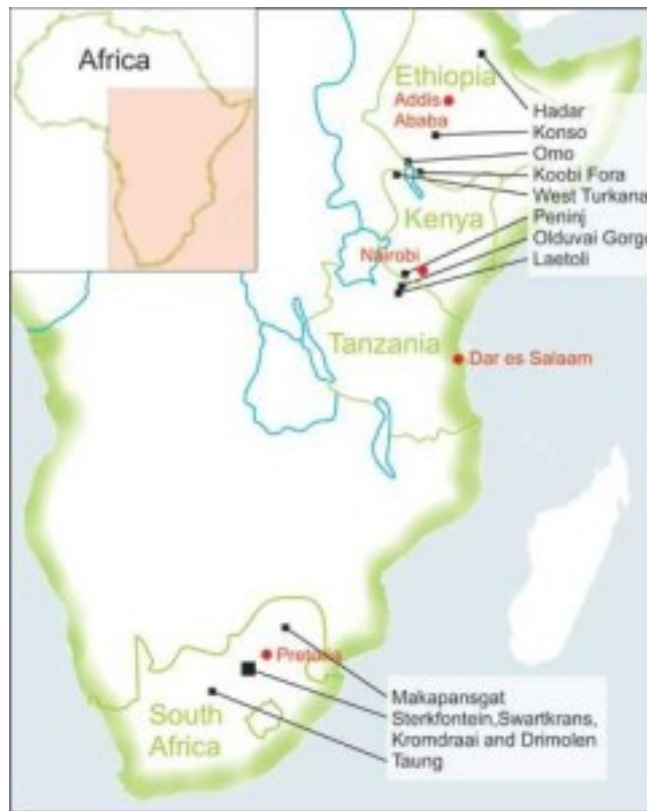


“Laetoli recreation.” “Laetoli recreated” by Wapondaponda is licensed under CC BY-SA 3.0.

DISCOVERY AND GEOGRAPHIC RANGE

The geographic range of *Au. afarensis* extends over 1,600 km from the site of Hadar in the Afar Depression of Ethiopia to the Laetoli site in Tanzania (see Figure 11.3). The **holotype** comes from Laetoli. There is conjecture as to whether the Ethiopian and Tanzanian material should be attributed to the same species, since the sites are distant from one another and separated in time by 800 kya. In addition, if *Au. bahrelghazali* is included as a

geographic variant of the species, their range expands 2,500 km westward into Chad (McHenry 2015). Thus this species was very successful at exploiting a variety of environments.



Map showing the major fossil sites where specimens of *Australopithecus* and *Paranthropus* have been found. From Clement and Hillson (2013), licensed under CC BY 3.0.

With the discovery of “**Lucy**” (3.2 mya) (see Figure 11.7) in 1974 by **Donald Johanson’s** crew at the site of **Hadar** in the Afar Depression of Ethiopia, paleoanthropology gained momentum and the rush was on in East Africa to find more evidence of human origins. Certainly **Louis** and **Mary Leakey** recognized the importance of the Great Rift Valley, but Johanson “upped the ante” with his 3.2 mya find. In addition, since Lucy’s skeleton was almost 40% complete (making it one of the six most complete fossilized hominin skeletons older than 100 kya), much could be said about her anatomy and locomotor capabilities.

Site **AL 333** at Hadar yielded remains of 13 individuals, referred to as the “**First Family**.” Some researchers speculated that they may have died together and thus possibly represent a social group. However, recent examination of the deposition pattern at the site suggests otherwise (see Behrensmeyer 2008).



Dikika Baby. "SelamAustralopithecus" by Jlorenz1 is licensed under CC BY-SA 3.0.

The more recently discovered "**Dikika Baby**" (3.3 mya) (see Figure 11.4), also known as "Selam" (meaning "peace" in the Afar language) has contributed greatly to our knowledge of development in early hominins. Dikika, meaning "nipple" in the Afar language, is the name of the nipple-shaped hill at the site of her discovery. Discovered by Zeresenay Alemseged in 2000, the three-year-old female has also been dubbed "Lucy's Baby" due to its proximity to Hadar where Lucy was discovered. Selam is now the oldest, most complete fossil hominin. It took five years to extract the fossils from the surrounding sandstone matrix in which they were embedded. Thus we can see that not only is there difficulty in locating fossils, along with their living conditions in the desert environments of East Africa, the fossils may take years to process before all of their secrets can be revealed.



Laetoli footprint cast. "Australopithecus afarensis footprint" by Tim Evanson is licensed under CC BY-SA 2.0.

Even more recent material from the Woranso Mille site in the Afar region has some scientists questioning whether the the *Au. afarensis* hypodigm (all fossil material attributed to a particular species) might represent at least two species. *Australopithecus deyiremeda* has been suggested for the newer material.

Mary Leakey discovered the first and oldest (4.2 mya) *Au. afarensis* material at Laetoli, Tanzania, and the holotype (type specimen) comes from that site. Her team recovered fossil material from 23 individuals, as well as the famous Laetoli footprints. The trail of footprints extends for almost 25 m. They were made by two individuals walking side by side, with a possible third, smaller individual hopping within tracks already made by one of the adults. The prints were formed when the hominins walked through wet ash that had erupted from a nearby volcano.

PHYSICAL CHARACTERISTICS

Note: Distinguishing primitive versus derived characteristics is difficult because we do not have all body parts to compare from one species to the next. In order to determine what changed, I am considering those aspects that are more *Homo*-like as derived characteristics, regardless of whether predecessors possessed them. In other words, it is not perfect science!

All body parts are represented in the **hypodigm**, i.e. all fossils assigned to a particular species. While some debate surrounds the gait and locomotor efficiency of the species, it is fairly well accepted that they were habitual bipeds that retained some arboreal characteristics in the form of upward-oriented shoulder joints, an ape-like scapula, a high intermembral index, and curved finger bones. Their innominates and lower limbs were

unquestionably those of a biped, and the big toe, while slightly divergent from the other four digits, was not nearly the grasping digit seen in apes. The buttressing of their ilium, in the form of the iliac pillar, shows that weight was being transferred through the bone in the same manner as our own. While there is evidence of the bicondylar or carrying angle of the femur, the femoral head was small and the neck (narrowing below the head) was longer in australopiths and paranthropines (i.e. robust australopiths—see Chapters 16–19), relative to *Homo* species. Lovejoy believes that the degree of lateral iliac flare and long femoral neck in australopiths were associated with increased leverage of the deep gluteal muscles so that they were more biomechanically efficient than modern humans (Lovejoy 1988). As we gave birth to larger-brained infants, our pelvic aperture had to expand laterally so that the femoral neck became shorter and the deep gluteal muscles became less biomechanically stable relative to australopiths. The bony elements of the *Homo* pelvis and hip had to become more robust to handle the increased force that the gluteal muscles generated on the bones (discussed in Lovejoy 1988 and Cartmill and Smith 2009). Based upon the Laetoli footprints, it appears that the feet of *Au. afarensis* were slightly inverted, which would have helped with climbing.

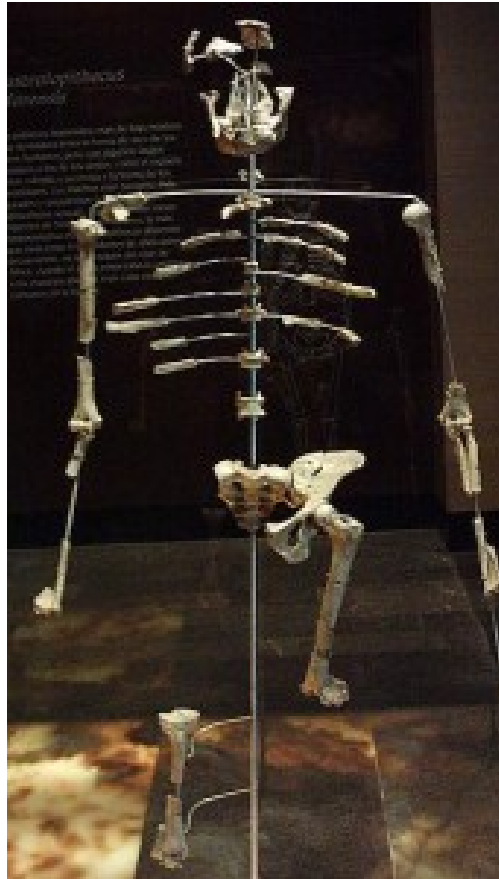


Replica of Laetoli footprints. “Laetoli footprints replica” by Momotarou2012 is licensed under CC BY-SA 3.0.

Au. afarensis had a prognathic, ape-like face (see Figure 11.8), a primitive skull morphology, and a small brain averaging 420 cc. They exhibited a slight sagittal crest for attachment of the temporalis muscle and a more pronounced nuchal crest, where their nuchal (posterior neck) muscles inserted on the posterior skull. The two crests were compound—a compound sagittal-nuchal crest—meaning that the sagittal crest converged at the center of the nuchal crest. Their teeth were large and their dental arcade was U-shaped, and thus more ape-like. The lower first premolar suggests a transitional phase, termed **semisectorial**, between the honing, sectorial (single-cusped) premolar of the apes and our more bicuspid premolars. The canines were monomorphic. Like *Au. anamensis*, their molars were expanded.

While their hands were capable of a precision grip, they did not have the same degree of mobility in their

thumbs as later species of australopiths and paranthropines. The conical thorax is linked to climbing and a large gut, and possibly the degree of lateral flare of the iliac blades.



“Lucy.” “Lucy Mexico” by danrha is in the public domain.

The Dikika Baby (see Figure 11.4) revealed inner ear adaptations that allowed them to distinguish their head from their torso; this is important for running. Her brain was of similar size to that of a same-aged chimp. This indicates that they had a more prolonged developmental period, since the adult brain was, for the most part, larger than those of chimps. While chimps’ brains are ~380 cc, *Au. afarensis*’ were on average 434 cc, and ranged from 342 to 540 cc. She had both deciduous and developing permanent teeth in her jaws. Finally, her ribs were in anatomical position, which confirmed the conical thorax.



Australopithecus afarensis reconstruction.
“*Australopithecus afarensis* reconstruction” by Durova is licensed under CC BY-SA 4.0

Au. afarensis exhibited pronounced sexual dimorphism, with males and females averaging 4’11” and 3’5” tall, respectively. Weights ranged from 64 to 99 lb. While the differences in size and morphology between the sexes might suggest that they were promiscuous and that males competed for females, their canines were monomorphic, suggesting pair-bonding. This is also supported by the change in the first mandibular premolar to being semi-sectorial.

Review of Primitive Characteristics

- High degree of sexual dimorphism.
- Low cranial capacity.
- Compound sagittal-nuchal crests:
 - Slight sagittal crest.
 - Pronounced nuchal crest.
- Flat cranial base.
- Prognathic jaws with U-shaped dental arcade and large ape-like incisors.
- Arboreal characteristics:
 - Upward-oriented shoulder joints.
 - Ape-like scapula.
 - Long arms relative to legs.

- Curved finger bones.
- Conical thorax.
- Some divergence of hallux.

Review of Derived Characteristics

- Inner ear adaptations allowed for more efficient running.
- Low cusp relief and thick enamel on molars.
- Loss of honing complex:
 - Semi-sectorial premolar.
 - Monomorphic canines.
- Precision grip adaptation in hands.
- Bipedal hips and lower limbs.
- Prolonged juvenile dependency and brain growth.

ENVIRONMENT AND WAY OF LIFE

This species inhabited a mixed woodland environment that is thought to have been more open than previous hominin habitats. They could thus have exploited arboreal resources and moved between trees and forested areas in a fairly efficient manner. They are considered to have been scavenger-foragers, collecting wild plant foods, opportunistically hunting animals, and scavenging large game from carnivore kills. There is evidence of stone tool use at the Dikika, Ethiopia, site. Since *Au. afarensis* are the only known hominin from that time and location, the tool use has been attributed to them. Researchers found cut marks on bones of two large animals that were dated to 3.4 mya. Even more exciting is the recent discovery of 3.3 mya tools in association with hominin fossil material at the West Lake Turkana, Kenya, site of Lomekwi 3. While it was commonly accepted that australopiths used tools, this is the first evidence that they made them. The tools have been designated as the **Lomekwian** industry and have displaced the Oldowan as the earliest tool industry, preceding it by 700,000 years (Harmund et al. 2015). The tools consist of anvils, cores (stones from which flakes for cutting are removed), and flakes (see *Homo habilis*: “Environment and Way of Life” for more information on stone tools and their production). Like extant great apes, they also would almost certainly have used biodegradable materials for tools, such as wooden, ivory, or antler digging sticks.

Au. afarensis exhibited premolar molarization and thick molar enamel for masticating a tougher, more dry-adapted diet, such as tubers (large edible roots, e.g. yams). However, they were not yet able to grind their food as well as later hominins whose jaws could move laterally due to the reduction in canine size.

The brain of Selam shows that the juvenile dependency period was prolonged relative to chimps and hence the chimp/hominin ancestor. In addition, once infants could not hang on with their feet, mothers would have had to

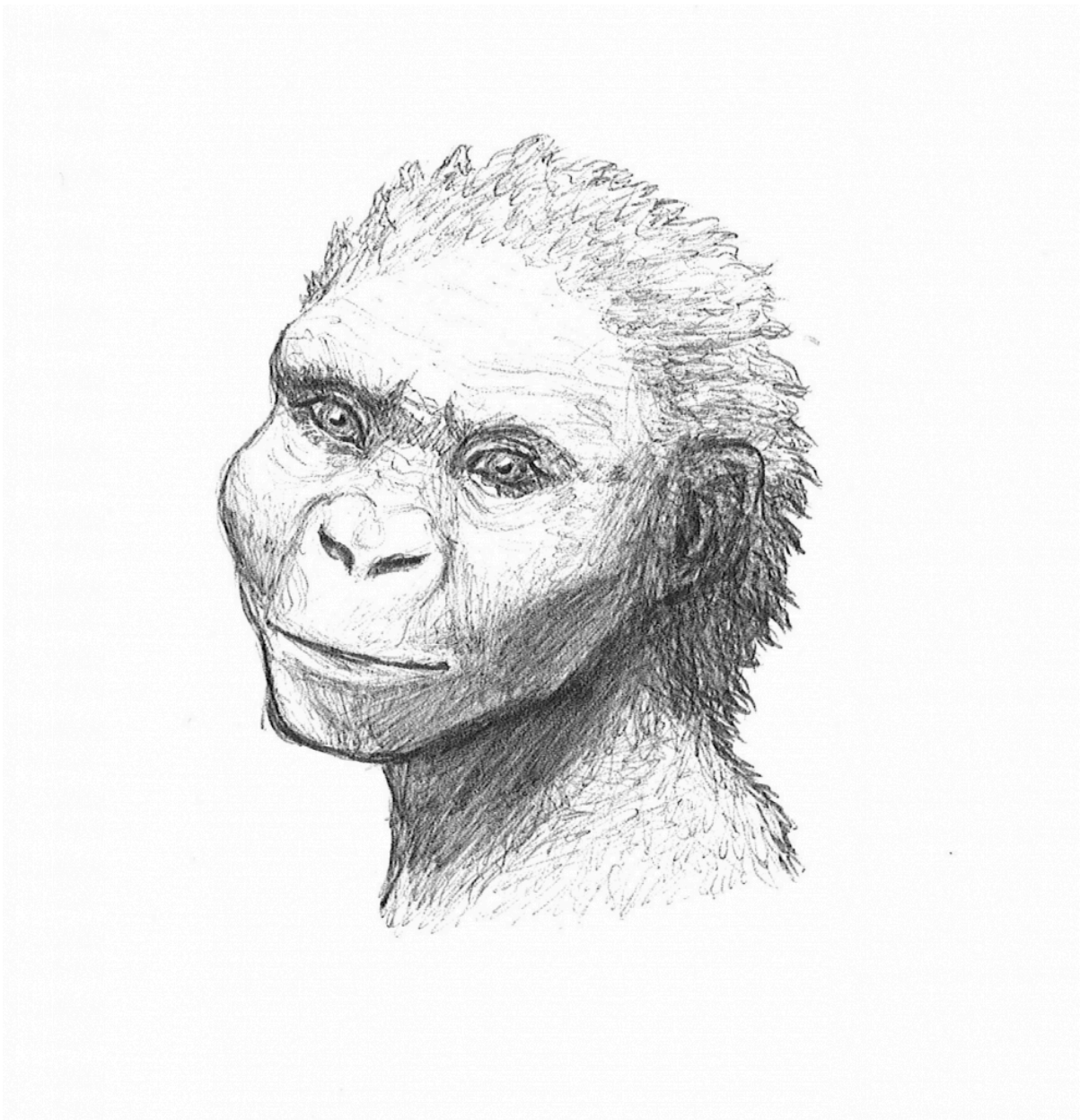
put their babies down periodically. Dean Falk has suggested that this pattern of mother-infant care may have led to language, in the form of what she refers to as “motherese” (Falk 2009).

It is interesting that female chimps use tools more often than do males. In addition, “woman the gatherer” should share the limelight with “man the hunter,” as women in most traditional societies collected a larger share of their family’s food. Is it possible that women invented tools? How about language? For how long have we heard about the male provisioning model for the evolution of bipedalism, “man the toolmaker,” “man the hunter,” men romancing women with the first language? Let’s stir up that cooking pot!!!



Selam reconstruction at the National Museum of Addis Ababa, Ethiopia.
“*Selam*” by Highrey is licensed under CC BY-SA 3.0.

As mentioned, we are unsure of their mating and thus grouping pattern. Regardless of whether the First Family died together and represented a social group, *Au. afarensis* likely lived in groups for protection and possibly cooperation. Males were much larger than females but had lost the large canines and honing complex of *Au. anamensis*. Thus while the degree of sexual dimorphism was much greater than in our own species, their monomorphic teeth suggest that they were transitioning toward pair-bonding while retaining polygynous tendencies. While females may have mated polyandrously, like a fair proportion of females in our own species, it may have been in their best interest to stick with their mate for help in raising their offspring, and not jeopardizing their safety with extra-pair copulations.



Lucy by Keenan Taylor.

12. Australopithecus bahrelghazali

Australopithecus bahrelghazali (<3.4 mya)

(“southern ape” / Bahr el Ghazal [Arabic: river of gazelles], Chad)

Note: *Au. bahrelghazali* is out of order here, in terms of date, because of its affinity to *Au. afarensis*.



Bahr el Ghazal site, Chad. “Bahr el Ghazal, Chad; Australopithecus bahrelghazali 1995 discovery map” by En rouge is licensed under CC BY-SA 3.0.

SITES

Bahr el Ghazal, Chad

PEOPLE

Michel Brunet

INTRODUCTION

While it is possible that *Au. bahrelghazali* was a distinct species, the majority view is that it was a geographic variant of *Au. afarensis*. If that is the case, one can see how far the species ranged, from the horn of Africa, south to Tanzania, and west to Chad (see Figure 12.1). The Chad population was close in time to the material from the Afar Depression in Ethiopia, e.g. Lucy at 3.2 mya and Selam at 3.3 mya, versus the older material from Laetoli, Tanzania, that is dated to as old as 4.2 mya. Remember also that some researchers believe that the Ethiopian and Tanzanian populations were too far removed in geographic space and time to be considered the same species and/or to be using the holotype from Laetoli for the other populations. The partial mandible that was discovered by Michel Brunet at Bahr el Ghazal differed from *Au. afarensis* only in having been less prognathic. A premolar was also found at the site. The ancient environment has been compared with that of Hadar (Lucy's site), i.e. a mosaic environment consisting of wood- and grasslands.

13. Kenyanthropus platyops

Kenyanthropus platyops (3,5 mya)

(“Kenyan human” / “flat-faced”)



Kenyanthropus platyops reconstruction. “*Kenyanthropus platyops* IMG 2946” by Rama is in the public domain.

SITES

Lake Turkana, Kenya

PEOPLE

Meave Leakey

INTRODUCTION

A surprisingly “flat-faced” hominin came to light with **Meave Leakey**’s discovery and naming of *Kenyanthropus platyops* (“flat-faced human from Kenya”) in 1999. The degree of orthognathism was surprising for such an early hominin.

PHYLOGENY

Since the skull was crushed and reconstructed (see Figure 13.1), some paleoanthropologists discount the degree of orthognathism and would like to see the specimen assigned to genus: *Australopithecus*, and possibly to species: *afarensis*. Others feel that it is the base of our lineage, believing that a cladistic event occurred at *Au. afarensis*, leading on the one hand to the robust forms (including *Au. africanus*) and on the other hand toward humans. In the latter case, some would like to see *K. platyops* assigned to genus: *Homo*, believing it to be the ancestor of *Homo rudolfensis*, with which it shares a similar orthognathic profile. Of interest is that some have speculated that the species may have made the Laetoli footprints. However, if the *platyops* fossils really belong in *Au. afarensis*, it would not be news!



Lake Turkana, Kenya. “Kenya relief location map” by Uwe Dederig is licensed under CC BY-SA 3.0.

DISCOVERY AND GEOGRAPHIC RANGE

K. platyops is known only from a site in the West Lake Turkana region of Kenya (see Figures 13.2 and 13.3), where Meave Leakey’s team found the crushed skull in 1999. The **hypodigm** consists of a reconstructed skull, plus two partial maxillae and a temporal bone from other individuals.



Lake Turkana, Kenya. "LakeTurkanaSouthIsland" by Doron is licensed under CC BY-SA 3.0.

PHYSICAL CHARACTERISTICS

While possessing primitive ape-like molars (elongated mesiodistally, i.e. front to back) and sharing similarities with *Au. anamensis* and *afarensis*, the lower face of *K. platyops* is surprisingly (and possibly mistakenly) orthognathic for its early date. The cranial capacity of *K. platyops* is also suspect due to the reconstruction but if accurate, it was fairly high relative to other species of the time, at 400–500 cc.

Review of Primitive Characteristics

- Elongated ape-like molars.

Review of Derived Characteristics

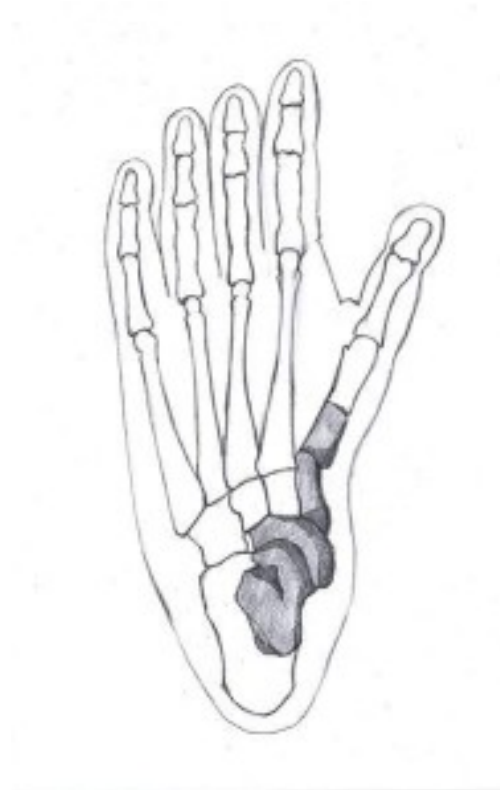
- Possibly more orthognathic.
- Possibly encephalized relative to previous and contemporary species.

14. Australopithecus prometheus or africanus

Australopithecus prometheus or africanus

“Little Foot” (-3.6–3.2 mya)

(“southern ape” / Prometheus / Africa)



Tarsals and metatarsal portion of “Little Foot.” “Little Foot 01” by Tobias Fluegel is licensed under CC BY-SA 3.0.

SITES

Sterkfontein and possibly Makapansgat, South Africa

PEOPLE

Ronald Clarke

INTRODUCTION

The controversial material that has come to be known as “Little Foot” is an almost complete skeleton from the site of Sterkfontein (see *Au. africanus* for more information on Sterkfontein). The story is remarkable in that the skeletal components were discovered at two different times. The earlier material was catalogued and stored as “cercopithecoid” (Old World monkey) remains. Fifteen years later, the rest of the skeleton was found at the same location at Sterkfontein (Silberburg Grotto) and matched to the previous material. The only other case that I know of where something like that happened was at the Swanscombe, England, site where three skull bones from a *Homo heidelbergensis* individual were found in three different years.

PHYLOGENY

Ronald Clarke believes that there were two species of australopith at Sterkfontein. He has assigned the species name *Australopithecus prometheus* to the Little Foot material, as well as two individuals that others assign to *Au. africanus*, one from Sterkfontein and the other from Makapansgat. While the phylogeny is unknown, Little Foot precedes and may be the ancestor of *Au. africanus*.

DISCOVERY AND GEOGRAPHIC RANGE

The “cercopithecoid” material was discovered by Ronald Clarke in a storeroom at the University of the Witwatersrand. Once he realized that the bones were hominin and had thus been miscatalogued, he sent his two assistants, Stephen Motsumi and Nkwane Molefe, out to the original site to see if they could find more ... and they did! The species’ geographic range is presently limited to the Sterkfontein area of South Africa (Duke 1998).

PHYSICAL CHARACTERISTICS

Little Foot is characterized as a climbing biped, as it had both arboreal and bipedal characteristics. Arboreal characteristics consisted of upward-oriented shoulder joints; ape-like arms that were, however, shorter than those of other southern australopiths; and curved hand and foot bones. Surprisingly, the few foot bones that were recovered are more complete than in any previous australopith specimen (see Figure 14.1). The morphology is transitional in that they retained some ape-like morphology. The hallux displayed the same degree of divergence as other australopiths. The upper limb combined both ape- and human-like characteristics. While the upper limb was shorter relative to australopiths, the hand bones remained curved. While the Little Foot specimen was ~4’ tall, males and females are estimated to have been 3’6” and 4’6” tall and 60–120 lb in weight, respectively.

ENVIRONMENT AND WAY OF LIFE

The environment of Sterkfontein is discussed in the section on *Au. africanus*.

Review of Primitive Characteristics

- Climbing adaptations:
 - Upward-oriented shoulder girdle.
 - Ape-like arms.
 - Curved hand and foot bones.

Review of Derived Characteristics

- Shorter arms relative to australopiths.

15. Australopithecus africanus

Australopithecus africanus (3–2 mya)

(“southern ape” / Africa)



Cast of Taung Child fossils. “*Australopithecus africanus* – Cast of taung child” by Didier Descouens is licensed under CC BY-SA 4.0.

SITES

Taung, Makapansgat, Sterkfontein, Drimolen, and Gladysvale, South Africa

PEOPLE

Raymond Dart, Robert Broom, and C. K. Brain

INTRODUCTION

Australopithecus africanus was the first fossil hominin discovered in Africa. In 1924, Raymond Dart (see his biographical sketch this chapter) identified the face, mandible, and **endocast** as being that of a juvenile bipedal ape (see Figure 15.1). Eugène Dubois’s discovery of the Javanese *Homo erectus* fossils in 1891 refuted the reigning belief that “we got smart before we stood up.” Once Dart’s claims were accepted, the world realized the extent

to which that idea was false. The small-brained *Au. africanus* showed that early hominins were bipedal apes as opposed to quadrupedal humans.

Unlike East African material that can be dated using a variety of techniques, primarily due to past volcanic activity, South African fossils and sites are much more difficult to date. Most dates can only be represented as ranges; hence the date for the earliest *Au. africanus* specimens falls between 3 and 2 mya.

PHYLOGENY

Au. africanus is considered to be a gracile australopith by some and a robust australopith by others. Traditionally, the species was favored as the immediate ancestor of the *Homo* lineage, specifically of *Homo habilis*. However, some researchers have always believed that *Au. afarensis* was the common ancestor of both *Au. africanus* and the *Homo* lineage, suggesting a cladistic event had occurred at *Au. afarensis*. This schema has gained popularity in recent years. However, with the new evidence being put forth for *Au. sediba*, it seems that the *Au. africanus* → *Homo* scenario was closer to the truth in that *Au. africanus* and *Au. sediba* are undoubtedly related and *Au. sediba* shares many characteristics with genus *Homo*. While there is some support for *Au. africanus* as ancestral to the more derived robust forms, that still leaves unresolved those characteristics shared between *Au. aethiopicus* and both *P. boisei* and *Au. afarensis* (see *Au. aethiopicus*, Chapter 17).

DISCOVERY AND GEOGRAPHIC RANGE

Au. africanus is known only from sites in South Africa (see map showing the major fossil sites in Chapter 11, Figure 11.3). Material from more than 200 individuals has been collected over more than 80 years. Most of the fossils came from caves, some of which were discovered during mining and blasting activities. Those caves formed via underground water activity. Fossilization was facilitated by water dripping on bones and calcifying, just as stalagmites form. Over millennia, many of the caves filled in with mineralized deposits and as the ground surfaces eroded, the underlying deposits were exposed and mined and then later excavated for fossils.

BIOGRAPHICAL SKETCH: RAYMOND DART (1893–1988) and the “TAUNG CHILD”

Raymond Dart was the first to recognize a fossil hominin in Africa. While his claim to have discovered a human ancestor was not initially accepted by the scientific community, he was vindicated when Robert Broom began finding similar material at other South African sites. The work of Dart and Broom played a pivotal role in directing attention to Africa as the birthplace of humanity, as Charles Darwin had earlier predicted.

Raymond Dart was a renowned Australian anatomist who was teaching at the University of Witwatersrand in South Africa at the time of the discovery. I have read several accounts over the years of the fateful day when the fossil material landed in Dart's hands. The Taung material was brought to him by either quarry workers or a colleague while he was dressing for the wedding of his daughter or friend, depending on the source you read. He is said to have attempted to use his wife's knitting needles to extract the fossils from the surrounding matrix. I am not sure why we need to know what he was doing when he got his hands on the goods. We certainly do not know what most

paleoanthropologists were doing when they were presented with fossil finds. However, it conjures up amusing possibilities in my mind!

The fossilized remains came from the **Taung Quarry** in the process of blasting for lime. When presented with the material, Dart established that it was the face, mandible, and **endocranium** (fossilized interior of the cranial vault) of a juvenile hominin. He based this on the anterior position of the foramen magnum and aspects of brain morphology reflected on the interior of the skull vault. Dart named his find *Australopithecus africanus*, meaning “southern ape of Africa,” and the specimen became known as the “**Taung Child.**”



Raymond Dart. “Smithsonian Institution Archives – SIA-SIA2008-0845” from the Smithsonian Institution Archives is in the public domain.

The Taung child was two to three years old when it died. We now know that the caves of South Africa were formed by underground water activity and hominins that dropped or were dragged into those subterranean caves became fossilized during the process of speleothem formation. Over millennia, the caves filled with mineral deposits, and via erosion, the mineralized contents and underground cavities surfaced. Many fossils were likely destroyed during quarrying activities, but we are lucky that many were preserved.

Raymond Dart is also renowned for his “**Killer Ape**” theory and the **osteodontokeratic** (bone-tooth-antler) culture. Dart believed that animal long bones and carnivore mandibles that were found with australopith remains had been used as weapons to fight and kill one another. We now know that was not the case. They were most likely opportunistically hunting small prey and scavenging larger kills, and they were prey for larger animals.

Raymond Dart is credited with the 1924 discovery and naming of *Au. africanus*. His now famous “Taung Child”

came from the Taung quarry site. The two- to three-year-old juvenile is represented by its face, skull fragments, and mandible, and an endocast of its brain. Dart also worked at the site of Makapansgat. His contemporary, Robert Broom (see biographical sketch below), worked at the caves at Sterkfontein (see Figure 15.4), where he discovered a complete, female cranium known as “Mrs. Ples”, along with other *Au. africanus* material. Broom also worked at the sites of Kromdraai and Swartkrans; the latter is where he discovered the first paranthropine, *Paranthropus robustus*. C. K. Brain, a famous taphonomist, also worked at Sterkfontein. He discounted Dart’s views of the australopiths as “killer apes”. He believed that bones either dropped into caves as part of large cats’ prey or were dragged in by rodents for gnawing. Some individuals are thought to have accidentally been trapped in underground caverns. Some speculate that those individuals that show no evidence of having been preyed upon, due to their degree of completeness (e.g. Sts 573 from Sterkfontein and the *Au. sediba* party from the Malapa site), surely became trapped. The six *Au. sediba* individuals are thought to have possibly been attracted to the cave by water. Drimolen, a more recently discovered site, has yielded an almost complete cranium as well as material from approximately 80 individuals. A fifth site associated with the species is Gladysvale.

BIOGRAPHICAL SKETCH: ROBERT BROOM (1866–1951)



Robert Broom. “Robert Broom00” from the American Museum of Natural History is in the public domain.

Robert Broom was a Scottish medical doctor and paleontologist who subsequently made a name for himself as a paleoanthropologist, even though the term did not exist at the time. He taught

geology and zoology at a South African college until he was let go for his controversial beliefs in evolution that were contrary to the religious teachings at the college. Subsequent to his termination, his finances went downhill until Raymond Dart's influence secured him a position at the Transvaal Museum. While his specialty was mammalian-like reptiles, he became increasingly involved with fossil hominins. Together, Dart and Broom made paleoanthropological history, discovering the first and second species of African hominins, respectively. Broom worked at the *Au. africanus* sites of Sterkfontein and the *P. robustus* sites of Swartkrans and Kromdraai. All of those sites are now contained within the **Cradle of Humankind World Heritage Site**. He was the first to discover and name *Paranthropus robustus*, and his work with *Au. africanus* helped to support Dart's claims to have discovered a bipedal ape and human ancestor. Broom's most famous *Au. africanus* find was "Mrs. Ples" (possibly a male), which he originally named *Plesianthropus transvaalensis* or "primitive human" of the Transvaal.

If accounts of Robert Broom are to be believed, he was a colorful character. He is said to have worn semi-formal attire while excavating and when media were present, he conveniently happened upon important discoveries. Supposedly, one of his team buried an artifact that was already labeled with a catalog number. Oh, to have been on the scene and witnessed what must have been an embarrassing situation! Not to mention that, according to numerous online sources, he thought nothing of stripping naked when it became "Africa Hot"! (I picked up that term from a couple of comedy movies but it is now in the Urban Dictionary.)

It is interesting that Broom did not believe in Darwinian evolution but rather, what we would now call Intelligent Design (Wikipedia contributors 2015h).

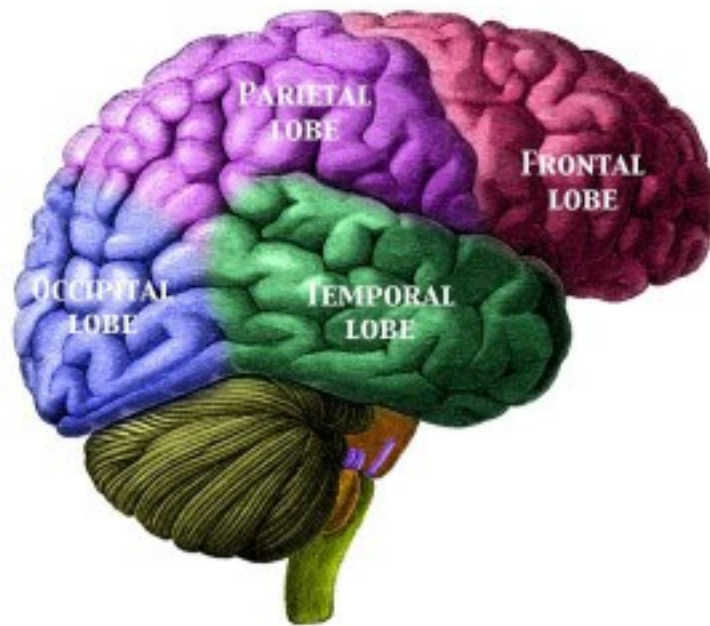


Sterkfontein Cave. "Sterkfontein Caves 16," photograph by Mike Peel (www.mikepeel.net), is licensed under CC BY-SA 4.0.

PHYSICAL CHARACTERISTICS

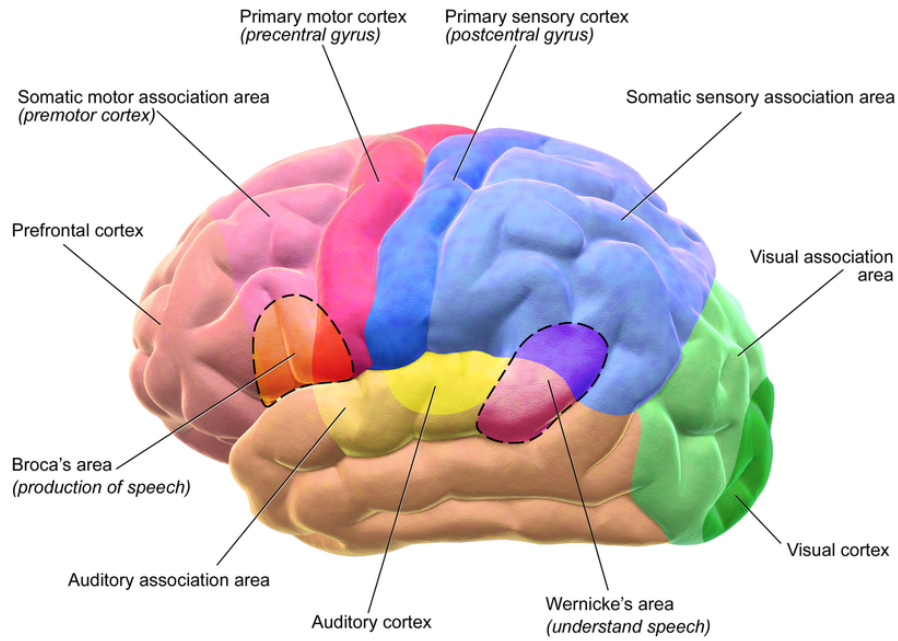
Au. africanus was more derived than *Au. afarensis*. This is not surprising considering that they lived at least one million years later, as well as the trend within the hominin lineage to become more encephalized and manually dexterous over time. *Au. africanus* were habitual bipeds with all of the corresponding lower limb adaptations. They also retained climbing characteristics, such as upward-oriented shoulder joints; long arms relative to legs; and long, curved hand and finger bones. However, in general their hands were more human-like than those of *Au. afarensis*.

While the brain was small relative to later species, *Au. africanus* was not only more encephalized than past species, with a cranial capacity of 450 cc (range = 424–508 cc), but also possessed an enlarged cerebral cortex in the frontal and parietal regions (see Figure 15.5). Their **encephalization quotient (EQ)** was 2.7. The quotient is a method for comparing brain size among species. Anything greater than 1.0 means that the brain is larger than would be expected based on body size (FYI: our EQ is ~7.6). Broca's area is an area of the left lateral frontal cortex that is involved with the production of language (see Figure 15.6). It is present in all Old World monkeys and apes, but it is enlarged in *Au. africanus* relative to previous species. These are all important developments, in that they herald the appearance of more complex thought processing and likely communication skills. There is debate over whether the lunate sulcus (see Figure 15.7), a fissure on both sides of the occipital lobe that is involved with vision, was more ape- or human-like. The sulcus is smaller in humans than in monkeys and apes.

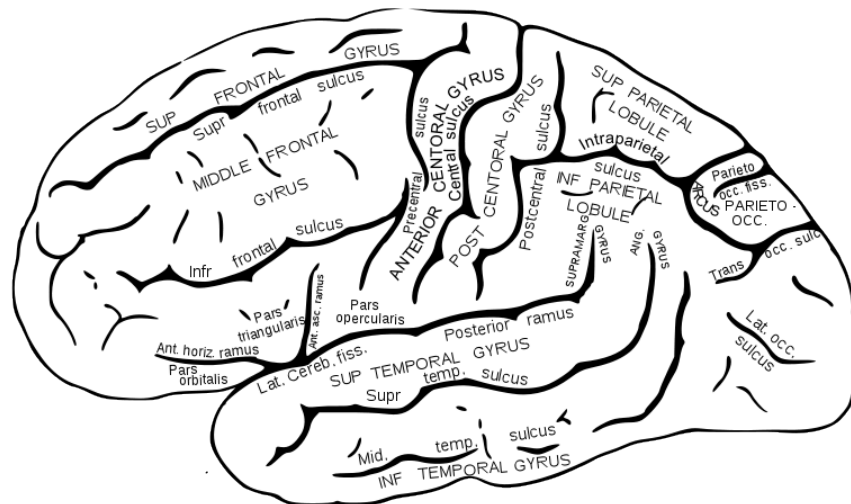


Lobes of the brain. "BrainLobesLabelled" by Camazine is licensed under CC BY 3.0.

Motor and Sensory Regions of the Cerebral Cortex

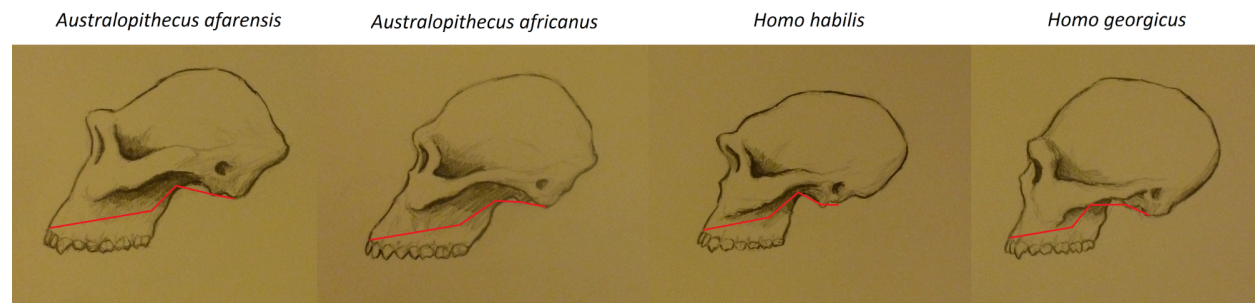


Broca's and Wernicke's areas (see areas surrounded by dotted lines). "Blausen 0102 Brain Motor&Sensory" by Blausen Medical Communications, Inc. is licensed under CC BY 3.0. Blausen.com staff. "Blausen gallery 2014." Wikiversity Journal of Medicine. doi:10.15347/wjm/2014.010. ISSN 20018762.



Lunate sulcus, also known as the simian or lateral occipital sulcus, outlined in red. "Gray726" vectorized by was_a_bee based on drawing by Henry Vandyke Carter is in the public domain.

The external skull reflected the cerebral expansion by becoming more rounded and exhibiting more of a forehead. In addition, the sagittal and pronounced nuchal muscle crests seen in *Au. afarensis* were not present. However, some males had convergent temporal lines that suggest that they may have had a slight sagittal crest. There is debate over whether the cranial base was flexed (see Figure 15.8), or whether that was a development seen only in more derived forms of *Homo*.



Basicranial flexion in four hominin species. Illustration by Keenan Taylor.

The species' face was prognathic with a distinctive concavity in the midfacial region (see Figure 15.9). The dental arcade was more parabolic, and the teeth were smaller than those of *Au. afarensis*. The first premolar is considered to have been bicuspid, versus semi-sectorial in *Au. afarensis*. However, their faces were more heavily buttressed for chewing a tougher diet, and some researchers thus consider them to be "robust" australopiths.



Concave facial profile of Mrs. Ples (*Au. africanus*).
 "Australopithecus_africanus_STS_5-side_3204" by NCSSM is licensed
 CC-BY-NC-SA

They retained the primitive condition of long arms and their finger bones were somewhat curved. However, their hands were more human-like and they possessed our "power" thumb, giving them increased pinching and gripping capabilities. This was accomplished via better developed intrinsic thumb muscles, i.e. within the hand versus coming from the forearm to act on the thumb, and a specialized first metacarpal.

While they were considered to be habitual and very likely obligate bipeds, they still retained a divergent hallux. According to McHenry and Berger (1998) and Green et al. (2007) they may have been more arboreal than *Au. afarensis*.

Au. africanus were less sexually dimorphic than *Au. afarensis*, with males averaging 4'6" (138 cm) tall and 90 lb (41 kg) and females at 3'9" (115 cm) and 67 lb (29 kg).

Review of Primitive Characteristics

- Somewhat prognathic.
- Arboreal characteristics:
 - Upward-oriented shoulder joints.
 - Long arms relative to legs.
 - Long, curved metacarpals and phalanges.

Review of Derived Characteristics

- Skull changes:
 - More rounded skull vault.
 - Increased encephalization.
 - Frontal and parietal expansion.
 - More of a forehead.
 - Loss of sagittal crest and less pronounced nuchal crest.
- Facial buttressing.
- More of a parabolic dental arcade and reduced anterior dentition.
- Power thumb:
 - Well-developed intrinsic thumb muscles.
 - Specialized first metacarpal.
- Reduced sexual dimorphism.

ENVIRONMENT AND WAY OF LIFE

While there is some controversy as to how much time *Au. africanus* spent in open versus closed (forest) environments, their facial robusticity and molars reflect a greater reliance on tougher, more dry-adapted plant foods than earlier hominins. They retained climbing adaptations and thus could have used trees for safety, sleeping, and food. When on the ground, it is thought that they were scavenger-foragers, foraging for plant

foods and small prey and scavenging remains of carnivore kills. Crude stone tools have been found at the sites of Sterkfontein and Makapansgat, and while there is no evidence of tool manufacture, it appears that they were using stones for hammering and cutting. They are thought to have relied on tubers for part of their diet and they likely used digging sticks to unearth them, in much the same way as modern African peoples, such as the San-speaking groups of the Kalahari Desert.

As mentioned, it is thought that hominins may have fallen through the surface into subterranean caves and/or bones were dragged in by rodents for gnawing. While it is possible that they used open caves for shelter from sun and rain, there is no evidence that they lived in caves.

In nature, extractive foragers have relatively large brains. Examples within the primate world include the aye-aye (a prosimian of Madagascar) that hunts insects via a combination of audition (hearing) and extraction (see www.arkive.org for multiple videos); New World capuchin monkeys that steal young animals from tree holes and rip bark from trees to get at insects; open-country baboons that dig for tubers; and the brainy orangutans and chimps that use a variety of tools to extract a range of foods, from ants to honey (see Figures 15.10 and 15.11 for videos of chimps and orangutan). Chimps have even been observed using sticks to spear bushbabies (small nocturnal African prosimians) in tree holes (e.g. see “How Smart Are Planet’s Apes?” on NationalGeographic.com). The same can be seen in some bird species, most notably tool-using crows and nut-burying nuthatches. Since our last common ancestor with chimps and bonobos was already relatively smart, I believe that while bipedalism was in response to diminishing habitat and resources, encephalization was in response to having to locate and learn to process new foods. Beginning with *Au. africanus* and the subsequent paranthropines, we see an upward trend for encephalization and expansion of those portions of the brain involved with association, i.e. complex thought processing, as well as increasing manual strength and dexterity for manipulating tools and objects. Thus we stepped out and then had to find and fix dinner!

We tend to think of “evolution by means of natural selection” as being a positive aspect of life, i.e. “**survival** of the fittest.” However, when there is a “rapid” response to a changing environment, many individuals die out while those few survive.

Videos



Ant dipping 1 by TheFriendsAndAi, <https://youtu.be/ScqG54B4KtE>



Orangutan using tool by Alain Compost, <https://youtu.be/pXOTAgq-eiY>

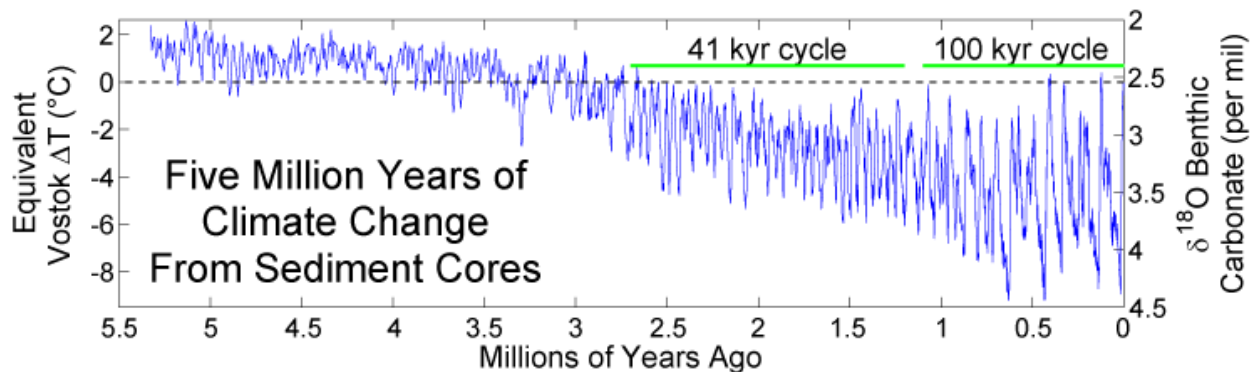
PART IV: PLEISTOCENE EPOCH

THE PLEISTOCENE EPOCH (-2.6 mya – 11.7 kya)



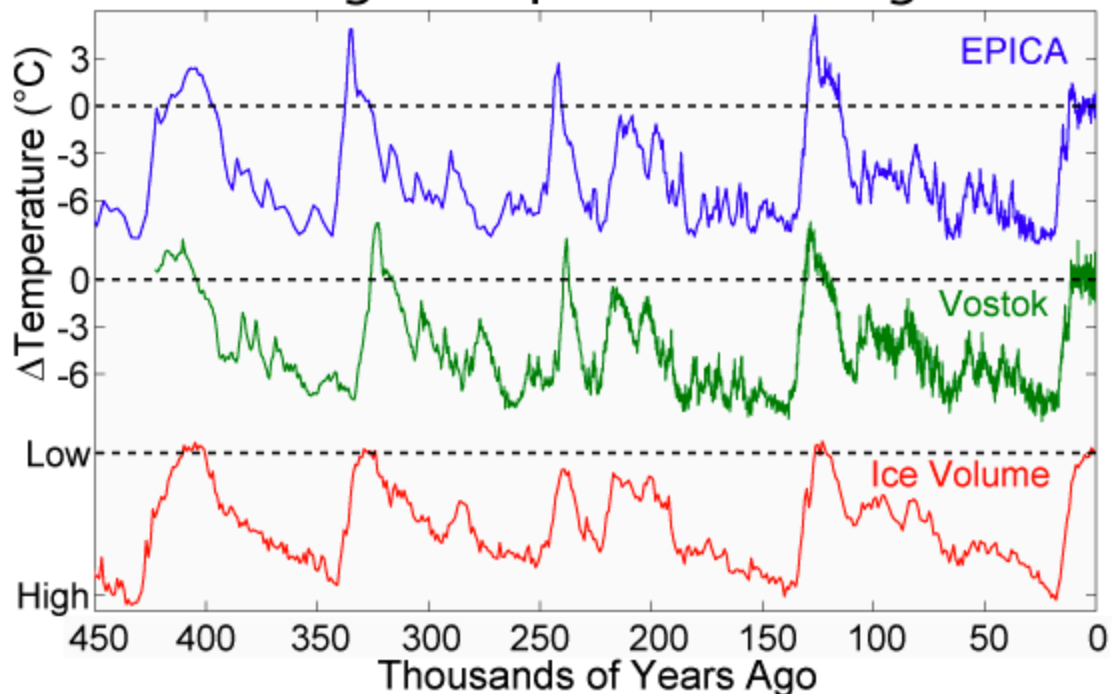
East African grassland and a local. Photo by the author.

The Pleistocene Epoch is commonly known as the Ice Age. The climate of Africa continued on the trajectory that began in the late Miocene and continued throughout the Pliocene (see Figures IV.2 and IV.3). While the Pleistocene was characterized as a period of global cooling, glacial advances, and dropping sea levels, the cold periods were interspersed with interglacial periods when the ice retreated and sea levels rose (see Figures IV.2, IV.3, and IV.4). Even within glacial periods, the climate varied. Animals in northern areas that were not adapted to arctic conditions went extinct or moved south when temperatures dropped and vice versa. They pushed in and out of Africa, in response to those climatic pulses.



Global temperature fluctuations from Pliocene (5–1.8 mya), through Pleistocene (1.8–0.1 mya), to present. “Five Myr Climate Change” by Robert A. Rohde is licensed under CC BY-SA 3.0.

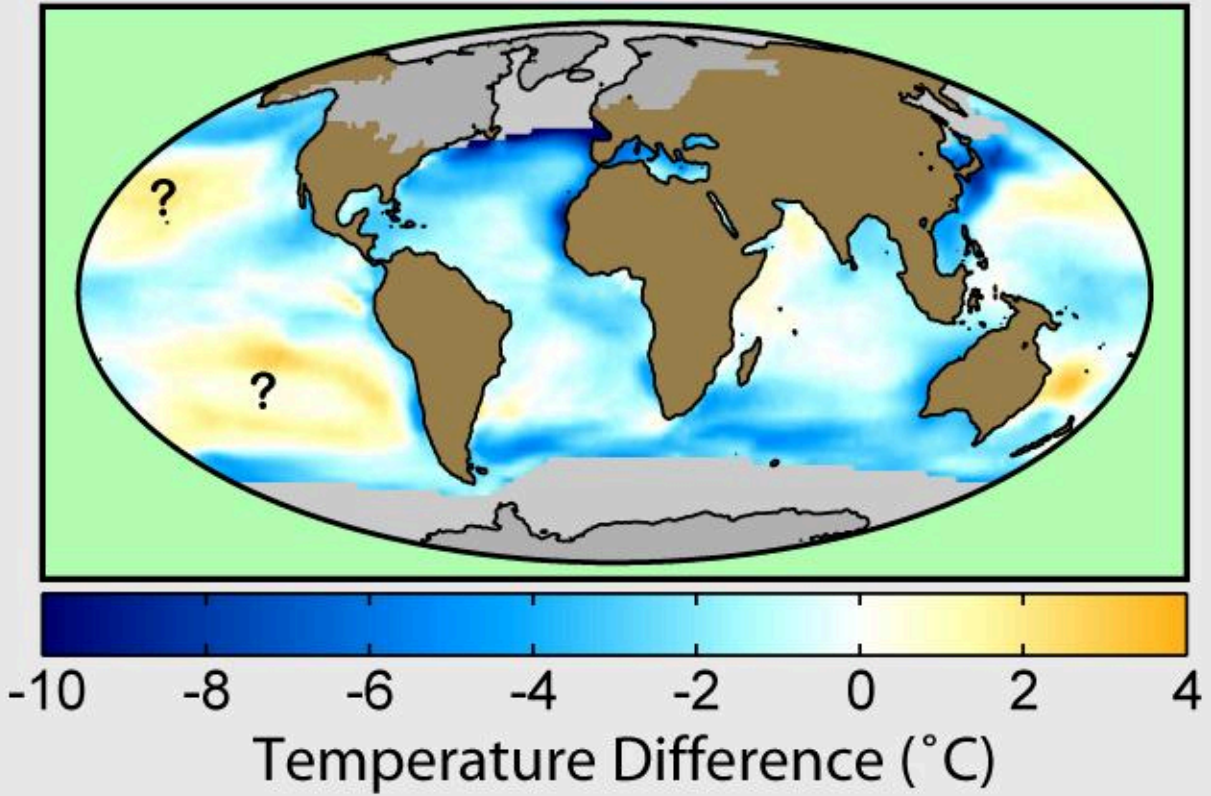
Ice Age Temperature Changes



Antarctic temperature changes during the last several glacial and interglacial cycles of the present ice age and a comparison to changes in global ice volume. "Ice Age Temperature" by Robert A. Rohde is licensed under CC BY-SA 3.0.

Elizabeth Vrba claims that there was a pulse-like turnover in faunal populations in East Africa at ~2.5 mya, in response to climatic change. Termed her "Turnover Pulse Hypothesis," she finds evidence of an increase in bovids (cow-like animals like wildebeests and water buffalo) and their predators and a decrease in forest-dwelling ungulates, corresponding to an increase in dry savanna environment (see Vrba 1985 and subsequent publications). Based on deep sea cores, we know that by 1.8 mya, there was a definite increase in the sahel-type of environment. Thus evidence from past flora and fauna supports the more robust craniofaciodental anatomy of species that lived during the early Pleistocene, e.g., *Au. garhi*, *Au. aethiopicus*, *P. boisei* and *P. robustus*. They would have needed stronger chewing abilities and thicker molar enamel to process more dry-adapted vegetation. Once the more gracile (in term of their masticatory apparatus) *Homo* species came on the scene, the East African hominins would come to represent an example of niche partitioning. Fossil sites suggest that *P. boisei*, *H. habilis*, and *H. egaster* could have been **sympatric** (i.e. overlapping geographic ranges). Thus while *Au. aethiopicus* and *P. boisei* survived by what might be termed masticatory brawn, the more encephalized *Homo* species used their brains and tools to consume a higher-quality diet. We can thus see that hominins were some of the colonizing species of the African savanna.

CLIMAP: The Last Glacial Maximum



Temperature reductions during last glacial maximum 18 kya. "CLIMAP" Robert A. Rohde is licensed under CC BY-SA 3.0.

18. Paranthropus boisei

Paranthropus boisei (2.5 mya)

(“beside human” / Boise: surname of one of the Leakey’s financiers)



Paranthropus boisei. “*Paranthropus boisei* side (University of Zurich)” by Nicolas Guérin is licensed under CC BY-SA 3.0.

SITES

Ethiopia: Shungura Deposits and Konso

Kenya: Chesowanja, West Lake Turkana, and Koobi Fora

Tanzania: Olduvai and Peninj

PEOPLE

Mary and Richard Leakey

INTRODUCTION

In the first course that I took in physical anthropology, I was most fascinated by the *Paranthropus boisei* face from Olduvai Gorge (see Figures 18.1 and 18.5) and the Natron/Peninj mandible from the Peninj site near Lake Natron. I still remember the first time I saw them, and the species has always been for me one of the more interesting discoveries in paleoanthropology. Their faces, jaws, and cheek teeth were massive and truly unforgettable. While

the Olduvai material is attributed to Mary Leakey, it was her husband Louis who announced to the world that he had his “man.” He had been finding tools of what are now termed the Oldowan tradition and was hoping to discover who had made them when Mary discovered the first *P. boisei* fossils. They were assigned to a new genus and species: *Zinjanthropus boisei*, or “human from East Africa.” “Zinj” is a derivation of the archaic term “Zanj” for an area of the East African coast, and Boise was the surname of one of the Leakeys’ financial supporters (Wikipedia contributors 2015g). Louis claimed that they had their toolmaker, but many did not agree with his conclusion. They thought he had found a big, dumb, herbivorous, bipedal ape that would not have had the cognitive abilities to produce stone tools. Hand bones have been attributed to the species by some researchers. If they are correct in their assignment, the species may have been capable of tool manufacture and efficient use. However, while their brains were somewhat larger than earlier species, we still do not know if they had the cognitive abilities and thus whether tools from East African sites can be attributed to them.



Olduvai Gorge, by David Berkowitz, CC BY 2.0

Fossils from more than 100 individuals have been recovered in the last 55 years. Over time, the genus has changed from *Zinjanthropus* to *Australopithecus* to *Paranthropus*, but some researchers are still using genus: *Australopithecus*.

PHYLOGENY

Support for *P. boisei* being descended from *Au. aethiopicus* has steadily increased. However, some still group *P. boisei* as a sister species of *P. robustus* and believe that they descended from *Au. africanus*. The two more derived forms share a molar trait with *Au. africanus*, in that the second molar (M2) is larger than the third (M3). Members of the latter group, such as Henry McHenry, contend that the more primitive *Au. aethiopicus* is an example of

homoplasy or convergent evolution, making the robust traits homoplasies. Paleoanthropologists have tended to be conservative in their acceptance of homoplasies; common ancestry is more parsimonious.

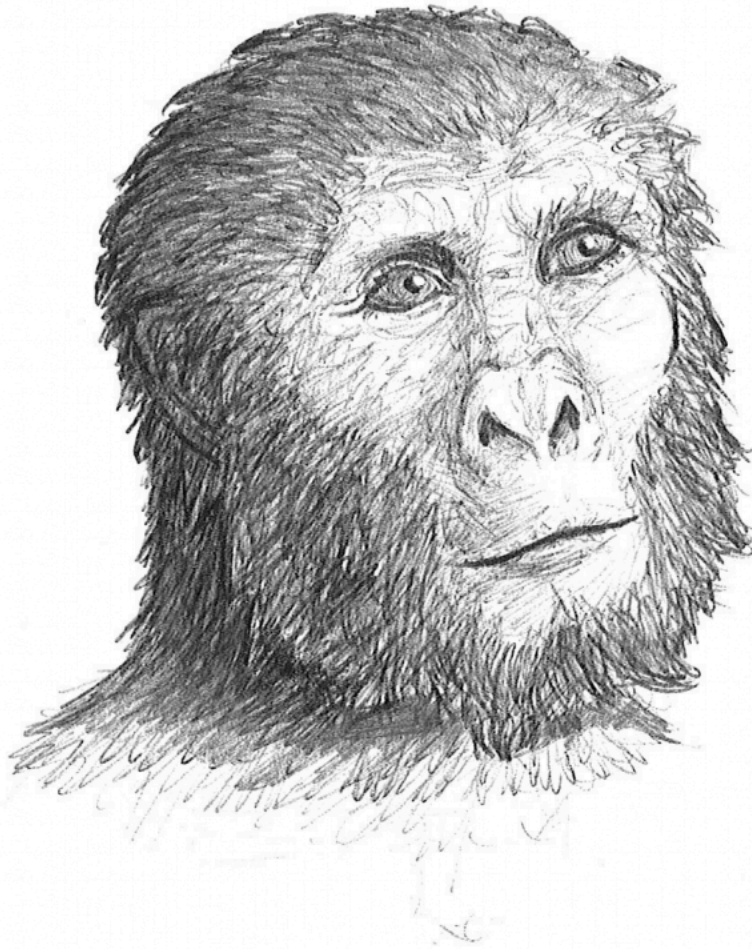
Except for the possible *Au. aethiopicus* → *P. boisei* scenario, the robust australopiths were evolutionary dead-ends as far as we know.



Scientific reconstruction of *Paranthropus boisei*. “*Paranthropus boisei*” by Lillyundfrey is licensed under CC BY-SA 3.0.

DISCOVERY AND GEOGRAPHIC RANGE

Mary Leakey discovered the first material in 1959 at Olduvai Gorge, Tanzania (see Figure 18.2). Nicknamed “Nutcracker Man,” “Zinj,” or “Dear Boy,” the skull and face were dated to 1.7 mya. Fossils attributed to the species have since been found at other sites in Tanzania (Peninj), Kenya (Chesowanja, West Lake Turkana, and Koobi Fora in the East Lake Turkana area), and Ethiopia (the Shungura Deposits and Konso). Richard Leakey discovered the Koobi Fora fossils. Thus, like *Au. afarensis*, the species had a broad geographic range and survived for over a million years.



Paranthropus boisei by Keenan Taylor.

PHYSICAL CHARACTERISTICS

While the robust forms are somewhat larger than the gracile forms, they do not differ much postcranially. It is their skulls that set them apart; *P. boisei* had the most pronounced masticatory adaptations, so that relative to the other two species, they are termed “hyper-robust.” Along with the other robust forms, they shared a buttressed

skull, face, and mandible; large molars and premolars; a compound sagittal-nuchal crest (not compound in *P. robustus*); large muscles of mastication and nuchal muscles to support their heavy skulls; large, flared zygomatic arches; and a supraorbital torus to absorb the stress generated by chewing. According to some researchers, they shared the following with *P. robustus* and *Homo*: flexed skull base; more orthognathic face; lower face tucked under the braincase, thus increasing chewing force on the molars; a more parabolic dental arcade; and a longer thumb with broad, flat, distal phalanges that gave them better opposition and gripping power. The sagittal crest in *P. boisei* and *P. robustus* was more anteriorly positioned relative to *Au. aethiopicus*. In combination with less prognathism and the fact that their face was tucked under the braincase, the action and strength of the temporalis muscle was concentrated on the cheek teeth. The degree of robusticity and the size of craniofaciodental characteristics were unique to *P. boisei*. The zygomatics were large, heavy, and widely flared, making their faces very broad and the temporal fossa (the space between the zygomatic and the temporal bone) very deep. Again, this facilitated the passage of the temporalis muscle to insert on the mandible and expanded the attachment and anchoring of the masseter muscle. The mandible was massive, with a very robust and deep body and tall rami (vertical side portions), and the temporomandibular (jaw) joint was exceptionally large. Their front teeth were so dwarfed by their enormous cheek teeth, they almost look juvenile. Their premolars were molarized, and some had a third root. The third molar exhibited a unique wrinkling pattern. Their **megadontia quotient** (MQ) was 2.7, meaning that their teeth were 2.7 times larger than would be expected. *P. boisei* had the largest supraorbital torus of the robust forms. They were somewhat more encephalized than past species, with a cranial capacity of 514 cc (range = 494–537 cc). Like all australopiths, the species was sexually dimorphic, with males at 4'6" (137 cm) tall and 108 lb (49 kg) and with more pronounced sagittal-nuchal crests and females at 4'1" (124 cm) and 70 lb (34 kg).



Natron mandible. "Peninj mandible. *Paranthropus boisei*" by Matt Celaskey is licensed under CC BY-SA 2.0.

Review of Derived Characteristics

- Same robust characteristics as seen in *Au. aethiopicus* with the following differences:
 - More robust craniofaciodental characteristics.
 - Sagittal crest more anteriorly placed.
 - Large supraorbital torus.
 - Huge molars and premolars.
 - Large, heavier mandible.
- Encephalized.
- Flexed skull base.
- More orthognathic face.
- Molarized premolars.
- Lower face tucked under braincase, maximizing chewing force on molars and premolars.
- More parabolic dental arcade.
- Longer thumb with broad, flat distal phalanges.

ENVIRONMENT AND WAY OF LIFE

While they still had relatively long arms, one seldom hears anything about the arboreal habits of the robust forms. In East Africa, that is not too surprising since the forests had receded and the grasslands had expanded. By 1.8 mya, deep sea cores reveal an increase in the **sahel** type of environment, i.e. the area south of the Sahara that consists of dry grasslands and scrub forest. Based on **microwear** evidence from their molars, all or most of which are ground flat, *P. boisei* likely subsisted on open, dry-adapted plants. Silt on terrestrial foods would have contributed to the wear patterns. The availability of high-quality foods must have gotten even worse by the time of *P. boisei*, because their chewing and bite-force capabilities were increased relative to *Au. aethiopicus*. They ate a high proportion of C₄ plants, i.e. open and more dry-adapted grasses and shrubs. It is thought that they likely survived on hard, tough, and brittle fallback foods during periods of preferred resource scarcity. This is another possible example of niche partitioning, in that sympatric *Homo* species may not have been able to utilize or digest either food category. Isotopic analyses to calculate the strontium-to-calcium ratio in fossilized bones of *Au. africanus* and *P. robustus* have determined that they ate some animal matter. It is possible that *P. boisei* did as well. While we do not know if they were scavenging or hunting animals, it is very possible that early hominins ate insects and insect larvae. All extant great apes consume social insects (ants and termites), and they derive a surprising degree of nutritional value from them. In traditional human societies, larvae are a favored resource.



Paranthropus boisei: "King of the termite mound" by Keenan Taylor.

It seems likely that *P. boisei* lived in small groups ... or did they? Living in a more open environment in equatorial Africa, there would seemingly have been safety in numbers. Since they were adapted to low-quality savanna resources and could fall back on food items that were unavailable to other sympatric species, they may have avoided strong within- and between-group feeding competition. We also know that pair-bonding may have been necessary, as females were not as self-sufficient as their quadrupedal ancestors. They had babies that could not hold on and were surrounded by males that could rape or commit infanticide. There is an argument that monogamy is a male adaptation that increases paternity assurance while reducing the risk of infanticide. We know that males compete for mates, and the high degree of sexual dimorphism in *P. boisei* supports that fact.

With all of the preceding arguments in mind, is it possible for apes with a tendency toward monogamy to live together without all of the rules and laws seen in modern humans to keep male competition and jealousy in check? While we could argue that they also could have lived in pairs with their dependent offspring and never ventured far from trees, how did females climb with their infants? We still have many unanswered questions about hominin behavioral ecology!

19. Paranthropus robustus

Paranthropus robustus (2.3 mya)

(“beside human” / robust)



Paranthropus robustus. “Sterkfontein Caves 66,” photograph by Mike Peel (www.mikepeel.net), is licensed under CC BY-SA 4.0.

SITES

Swartkrans, Kromdraai, Drimolen, Gondolin, and Coopers Cave, South Africa

PEOPLE

Robert Broom and Andre Keyser

INTRODUCTION

In 1938, Robert Broom discovered the first *Paranthropus robustus* material at the site of Swartkrans, South Africa. He later found material at Kromdraai, and because the molar teeth were more primitive at that site, he changed the species name at Swartkrans to *P. crassidens* but used *P. robustus* for the Kromdraai material. Molar characteristics from the more recent material from the Drimolen site are thought to be intermediate between the Swartkrans and Kromdraai molars, and most researchers now consider the material from all three sites to be species: *robustus*.

PHYLOGENY

Au. africanus is the favored ancestor of *P. robustus*. However, others believe that *P. boisei* and *robustus* are descended from *Au. aethiopicus*. Of the former school, some believe that *P. boisei* is also descended from *Au. africanus* and thus a sister species to *P. robustus*. The two species would then have inherited their flexed skull base from *Au. africanus*. Like *P. boisei*, *P. robustus* appears to be an evolutionary dead end.

DISCOVERY AND GEOGRAPHIC RANGE

The species is known only from sites within the Cradle of Humankind World Heritage Site in South Africa. As mentioned in the introduction, Robert Broom discovered the first material at Swartkrans and subsequent specimens at the site of Kromdraai. Andre Keyser discovered the jaw and dental material at Drimolen in 1994.

PHYSICAL CHARACTERISTICS

Like *P. boisei*, *P. robustus* exhibited buttressing of the skull, face, and mandible; orthognathism in that the teeth were tucked under the cranial base; small anterior dentition; molarized premolars; large muscles of mastication; large zygomatic arches for passage of the temporalis muscle; sagittal crests in males and a nuchal crest that did not converge with the sagittal crest; tall mandibular rami to increase the strength of the masseter and medial pterygoid (another muscle of mastication) muscles for their tough, fibrous diet and a large mandibular body; and a high degree of postorbital constriction due to their large face (see skull cast in Figure 19.1).

Characteristics shared with *Au. africanus* are a flexed skull base, megadontia (*P. robustus*'s molars were 17% larger, but their MQ of 2.2 was lower), molarized premolars, a larger second than third molar, and facial buttressing. While *P. robustus* appears to have been more orthognathic than *Au. africanus*, they were not. Their anteriorly oriented orbits and zygomatics reduced the distance between their midface and jaws, making it appear so. The nasal bones were recessed relative to the forward-oriented zygomatics, so that they too had a somewhat dish-shaped midface like *Au. africanus*. They had less of a forehead than *Au. africanus* because of the forward-oriented orbits. Finally, unlike *Au. africanus*, where maximum force was on the molars, the maximum force was on the premolars due to a combination of the forward placement of the zygomatics and an enlarged anterior portion of the temporalis muscle that was offset by the positioning of the dental arcade under the braincase (Cartmill and Smith 2009).

Average cranial capacity is estimated to have been 530 cc, giving them the highest EQ, 3.0, of any australopith (Cartmill and Smith 2009).

The postcranial morphology of *P. robustus* shares some similarities with *Homo*, such as broad distal finger phalanges that are thought to indicate enlarged tactile pads and increased vascularization, sensitivity, and motor control, as well as a large attachment for the *flexor pollicis longus* muscle that acts as a powerful thumb flexor. They thus are thought to have had a great degree of manual dexterity and were likely capable of making and

certainly using tools. However, they retained some primitive australopith characteristics, including long arms; small vertebral bodies, especially inferiorly; small sacroiliac and hip joints; more posteriorly oriented ilia; and a long femoral neck. Males of the species are thought to have stood 4' (1.2 m) tall and weighed 120 lb (54 kg) and females, 3'2" (<1.0 m) and 90 lb (40 kg).

Review of Primitive Characteristics

Retain prognathism, concave facial profile, long arms, small vertebral bodies, small sacroiliac joints, posteriorly-oriented ilia, and long femoral neck of *Au. africanus*.

Review of Derived Characteristics

- Same characteristics as *P. boisei*, except not as robust and large.
- Maximum bite force on premolars.
- Encephalized.

ENVIRONMENT AND WAY OF LIFE

Like *P. boisei*, *P. robustus* are thought to have been generalist herbivores that may have consumed some animal matter and could fall back on hard and brittle items, such as nuts, seeds, and hard-skinned fruits, when preferred items were not available. C. K. Brain found wooden digging sticks in association with *P. robustus* remains. In addition, polish on bone and horn cores (bone interior of animal horns) attributed to *P. robustus* is consistent with repeated digging, such as for tubers.

Of interest is recent research that indicates that they were more male- than female-philopatric, supporting the notion that we have inherited the chimp and bonobo pattern of females relocating to join and range with a group of males. Amazingly, isotopic analyses of strontium in their teeth indicates that females did not grow up where their fossils are found (Copeland et al. 2011).

20. Australopithecus garhi

Australopithecus garhi (2.5 mya)

(“southern ape” / “surprise” in the Afar language)



Reconstructed *Australopithecus garhi* skull. “Musée national d’Ethiopie-Australopithecus garhi (2)” by Ji-Elle is licensed under CC BY-SA 3.0.

SITES

Bouri site in the Middle Awash area of the Afar Depression, Ethiopia

PEOPLE

Tim White and Berhane Asfaw

INTRODUCTION

In 1996, researchers recovered portions of the frontal and parietal bones as well as a maxilla that contained teeth (see Figure 20.1). These materials were attributed to *Australopithecus garhi*. While nearby limb bones could not be attributed to the species with absolute certainty, they have been used by some paleoanthropologists to

describe the species' characteristics. Thus there is very little useful material to “reconstruct” this species. Fossil-containing sediments also contained bones with cut marks and a few surface cores (shaped and modified rock) and flakes (sharp pieces of rock struck from a core) were found, suggesting that *Au. garhi* butchered animal remains and possibly made tools. However, tools in fossil-bearing layers would be better evidence. Some believe that the manufactured stone tools at the nearby Gona, Ethiopia, site may have been manufactured by *Au. garhi*.

PHYLOGENY

The species is likely descended from *Au. afarensis*, possibly directly so. Like *Au. afarensis*, *Au. garhi* is thought to have been more terrestrial than the South African australopiths. As is the case for the rest of the australopiths, some researchers believe them to be ancestral to genus *Homo*, and what little evidence there is for tool manufacture accords with our lineage.

DISCOVERY AND GEOGRAPHIC RANGE

The species was discovered in 1996 by Tim White's crew, and later Berhane Asfaw became involved. The only fossil material comes from the Bouri site in the Middle Awash region of the Afar Depression in Ethiopia.

PHYSICAL CHARACTERISTICS

The maxilla and teeth are larger and more robust than those of *Au. afarensis*, and some researchers lump them with the paranthropines. Thus like *Au. aethiopicus* and *P. boisei*, *Au. garhi* were adapted to a broader dietary niche in response to environmental changes, particularly expanding grasslands. If the limb bones are rightfully attributed to the species, they had longer, more humanlike legs than other australopiths. Their arms were still apelike, based on the ratio of the arm to forearm length. The cranial capacity was 446 cc, falling midrange within that of *Au. afarensis*.

Review of Primitive Characteristics

- Ape-like arms.
- Small brain.

Review of Derived Characteristics

- Robust craniofaciodental characteristics.
- Possibly longer, more human-like legs.

21. Australopithecus sediba

Australopithecus sediba (-2.0 mya)

(“Southern ape / “fountain or wellspring” in the Sotho language)



Australopithecus sediba holotype. “*Australopithecus sediba*” by Brett Eloff is licensed under CC BY-SA 4.0.

SITES

Malapa, South Africa

PEOPLE

Lee and Matthew Berger and subsequent colleagues

INTRODUCTION

My research on this interesting species showed me how little I knew! Since (1) many biological anthropologists who teach human evolution are not paleoanthropologists, (2) *Au. sediba* is a fairly recent discovery, and (3) many

textbooks have not as yet included much information about it, I have provided a more in-depth overview of this species.

Six well-preserved individuals of a new species of *Australopithecus* were discovered, beginning in 2008, at the cave site of Malapa, South Africa. Lee Berger's crew is credited with the discovery after Berger's nine-year-old son Matthew (see Figure 21.2) happened upon the fossils of a juvenile male (MH1) that became the holotype for the species (see Figure 21.1). The other five individuals were an adult male, an adult female (MH2) and, remarkably, an infant. It is of great utility in terms of interpreting morphology that much of the fossil material was found *in situ* (i.e. where the body settled versus missing or scattered about), demonstrating that they became buried and began fossilizing fairly rapidly. It is thought that they fell into a cavern, possibly lured by the presence of water in that then dry environment.



Nine-year-old Matthew Berger with fossil discovery. "Matthew Berger with Malapa Hominin 1" by Lee R. Berger is licensed under CC BY-SA 3.0.

PHYLOGENY

Since *Au. sediba* shares characteristics with both *Au. africanus* and *Homo*, it is thought to possibly be intermediate between the two species. That scenario, of course, disagrees with *Au. afarensis* as being our direct ancestor, with *Au. africanus* as a side branch. According to Berger et al. (2010), *Au. sediba* is more distinct from *Au. africanus* than the latter is from *Au. afarensis* in hand, pelvis, foot, and ankle morphology. However, the team working with the material believe it should stay within the genus *Australopithecus* because it lacks the *Homo* encephalization trend. Surprisingly, *Au. sediba* is more similar to *Homo erectus* in some respects than to Early *Homo* (*H. habilis* or *rudolfensis*). There has also been speculation that *Au. sediba* is a derived form of *Au. africanus*, but it is problematic in that the Malapa specimens are only 100 kya more recent than the youngest *Au. africanus* material. Furthermore, because the Malapa material is contemporary with Early *Homo* material (*H. habilis* and *rudolfensis*), some insist that they cannot be ancestral to those species. However, Pickering et al. (2011) dispute that claim, since Early *Homo* material is still problematic, both taxonomically and spatiotemporally. Berger et

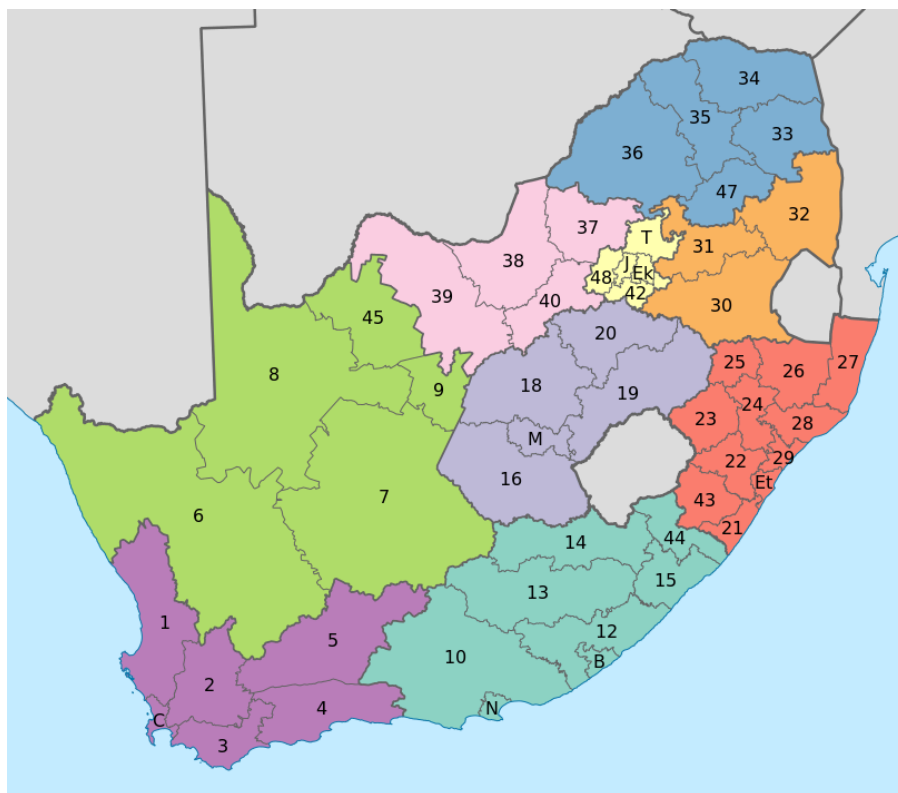
al. (2010) have proposed four phylogenetic scenarios—that *Au. sediba* was the ancestor of *Homo habilis*, *Homo rudolfensis*, or *Homo erectus*, or was a sister species to the ancestor of the *Homo* lineage.



Malapa site. “Malapa fossil site, August 2011 site of discovery of *Australopithecus sediba* – view North” by Lee R. Berger is licensed under CC BY-SA 3.0.

DISCOVERY AND GEOGRAPHIC RANGE

Because the “Malapa Party” (my term) discovery is such a great story, I used it to introduce the species and will not repeat it here. Malapa (see Figure 21.3) is 9.3 km northeast of Sterkfontein and 45 km north-northwest of Johannesburg in the Cradle of Humankind World Heritage Site (see Figure 21.4) (Wikipedia contributors 2015f). No fossil material has been found elsewhere.

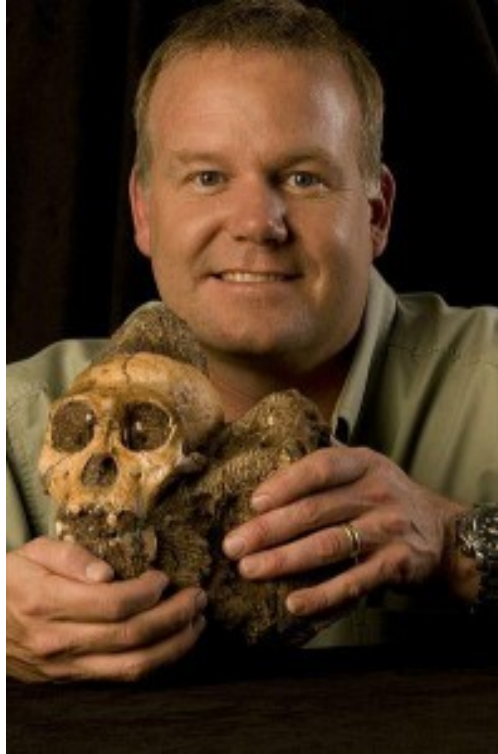


Malapa area indicated on map of South African provinces. “Map of South Africa with provinces shaded and districts numbered (2011)” by Htonl is licensed under CC BY-SA 3.0.

PHYSICAL CHARACTERISTICS

In general, the species’ morphology is a mosaic of australopith- (especially *Au. africanus*) and *Homo*-like characteristics, but there are multiple lines of evidence to support its classification as a separate species (Berger et al. 2010). Since the Malapa material provides some of the best *in situ* evidence for many body parts, relative to other contemporary and previous species, I will spend more time discussing the physical and biomechanical significance.

The brain of *Au. sediba* was australopith-like in its size and “convolucional patterns” (Carlson et al. 2011). However, derived aspects of the frontal lobe show that *Homo*-like reorganization preceded pronounced encephalization (Carlson et al. 2011). This is an exciting discovery, in that we do not see so much of a gradual increase in size but rather that the hominin brain evolved in a mosaic fashion and that an increase in the association region was favored at the time. If cranial capacity alone was all that was available to infer cognition in *Au. sediba*, that important fact would be missed.



Lee Berger with MH1. “Lee Berger and the Cranium of *Australopithecus sediba* MH1” by Brett Eloff is licensed under CC BY-SA 3.0.

Like most areas of the body, the cranial morphology reflects australopith- (especially *Au. africanus*) and *Homo*-like characteristics (Berger et al. 2010). Relative to *Au. africanus*, *Au. sediba* had smaller teeth and a less robust face (see Figure 21.5). Of interest is that they are described as having an “incipient” nose, i.e. the beginnings of a protruding nose (Berger et al. 2010). They share various mandibular and dental characteristics with *Au. africanus*, Early *Homo*, and *Homo erectus* (Irish et al. 2013; de Ruiter et al. 2013). Mandibular size and shape and tooth size most closely resemble Early *Homo*, and while some tooth measures and growth pattern are most similar to *H. erectus*, the overall growth trajectory is unique compared to other fossil hominins (de Ruiter et al. 2013). Analysis of tooth shape, molar cusp patterns, and root number of the various teeth shows that *Au. sediba* and *Au. africanus* share five synapomorphies (shared traits among related species), thus supporting a South African australopith clade. In addition, *Au. sediba* shares five synapomorphies with *H. habilis/rudolfensis/erectus*, suggesting a South African australopith ancestry for our lineage (Irish et al. 2013).

Au. sediba retained relatively long arms and elevated shoulder joints for climbing (see Figure 21.6) (Kivell et al. 2011; Schmid et al. 2013). Except for three wrist bones and the distal phalanges of the four fingers, the right distal forearm, wrist, and hand have been recovered intact for the adult female MH2. While the morphology of the hand is unique in some ways and they were still capable of strong flexion for climbing, some traits are associated with tool production in *Homo* species, especially the longer, more dexterous thumb and shorter fingers that facilitate our strong precision pinching. The only other hand that is well preserved from the late Pliocene is that of OH 7, attributed to *Homo habilis*. However, the Malapa hand was better suited to tool production and there is still speculation that OH 7 was actually *P. boisei*, a robust australopith not in our lineage. Thus, *Au. sediba* may have been responsible for the tools that have been recovered at South African sites (Kivell et al. 2011).



Australopithecus sediba compared with Lucy. From left to right: MH1, Lucy, MH2. “*Australopithecus sediba* and Lucy” by Peter Schmid is licensed under CC BY-SA 3.0.

While determining the thoracic shape of fossil hominins has been a problem due to the lack of intact specimens, it is generally thought that australopiths had a conical thorax like extant great apes. A conical thorax is involved with arboreal locomotion, whereas our barrel-shaped thorax is (1) adapted for endurance walking and running, (2) related to shoulder breadth and arm-swinging to counter trunk rotation and facilitate our greater respiratory abilities, and (3) facilitated by a decrease in gut volume related to encephalization and a less herbaceous diet (first reviewed in Bramble and Lieberman 2004 and later in Schmid et al. 2013). The *Au. sediba* specimens support the notion of a conical shape to the upper thorax, but surprisingly, the lower thorax is not as flared as was previously thought, being more human-like. Schmid et al. (2013) assert that the “uncoupling” of the upper and lower trunk morphology in *Au. sediba* argues against a physiological response, in favor of a biomechanical one. The conical upper thorax would have been useful for climbing but would not have allowed for effective arm-swinging or heavy breathing and thus they were likely not capable of exertive walking and running. Their gut must have been smaller than a typical ape’s, suggesting a less herbaceous diet and setting the stage for the expensive tissue trade-off allowing for encephalization in our lineage (Schmid et al. 2013).

Au. sediba likely possessed the modern number of regional vertebrae. While the vertebrae of all hominoids increase in size from superior to inferior, earlier hominins lacked enlarged lumbar and sacral vertebral bodies and our pronounced sacral curve (see Williams et al. 2013 for references). *Au. sediba* is the earliest hominin to exhibit those characteristics, which are present in *Homo erectus* and all subsequent species. While the vertebrae in the five regions of our vertebral column have distinctive characteristics, they morphologically grade into one another so that there are transitional vertebrae, e.g. the seventh cervical vertebra resembles the first thoracic vertebra and so on. Unlike humans, the transitional thoracolumbar vertebra in *Au. sediba*, *H. erectus* (based on the Nariokotome specimen), and possibly *Au. africanus* is 11 versus 12. Thus while vertebra 12 is rib-bearing, it also likely functioned to elongate the lumbar region, increasing lower back flexibility (Williams et al. 2013).

The innominates were australopith-like in dimensions involved with childbirth but exhibited buttressing and other characteristics of *Homo*, such as iliac shape and vertical positioning, shortened ischium, and so forth (Kibii et al. 2011). The proximal femur was australopith-like with a small head and long neck, but the bicondylar/

carrying angle and insertion of the gluteus maximus were humanlike. The knee exhibits both australopith- and human-like characteristics. Like us, they were capable of fully extending their knees during the swing phase of walking (DeSilva et al. 2013).

The partially articulated ankle and foot elements present a unique combination of primitive and derived traits. Humanlike characteristics include the morphology of the distal tibia, Achilles tendon insertion (calcaneal tuberosity), possible valgus (medially inverted) knee indicative of the bicondylar angle, probable arched foot, etc. Some aspects of the bones are more australopith-like, e.g. more gracile calcaneus; and some are more ape-like, e.g. robust medial malleolus (distal fibula, what we think of as our medial ankle “bone”) and some joints and muscle attachment sites (Zipfel et al. 2011).

Like in apes, initial ground contact was via the heel and lateral aspect of the foot, so that the foot was inverted. They then hyperpronated the foot by transferring weight medially so that the ankle was inverted and the plantar surface of the foot rolled medially and became everted. Modern humans with hyperpronation have problems with increased stress and wear on the joints, and the same is evident in *Au. sediba* remains (DeSilva et al. 2013). Hyperpronation, along with a robust medial malleolus, flexible midfoot, and upper limb adaptations, was apparently an adaptive response to bipedal terrestrial locomotion and retention of arboreal climbing abilities (J.M. DeSilva, personal communication with author, 2014). As in the ardipiths, the divergent hallux likely aided in climbing and would have given them more of a tripod foundation to stabilize their upright stance when standing and walking (Lovejoy et al. 2009).

Taken together, the mosaic of lower limb characteristics suggest that *Au. sediba* may have practiced a form of bipedalism unique from australopiths, or that they were descended from a more terrestrial ancestor and they then reverted to a more semi-arboreal lifestyle (DeSilva et al. 2013).

Review of Primitive Characteristics

- Brain size and convolutions.
- Australopith-like growth trajectory of teeth and jaws.
- Climbing adaptations: elevated shoulder joint, long arms, and strong hand flexion.
- Conical upper thorax.
- Australopith-like femoral head and neck.
- Some primitive aspects of ankle and foot.
- Retention of semi-divergent hallux.

Review of Derived Characteristics

- Reorganization of the frontal cortex.
- Small teeth and jaws and less robust face.
- *Homo*-like tooth shape and growth pattern.
- Humanlike lower thorax.

- Increased manual dexterity and precision grip.
- Longer, more dexterous thumb.
- Shorter fingers.
- Enlarged lumbar and sacral bodies and sacral curve.
- Buttressed and more vertical ilium.
- *Homo*-like carrying angle and *gluteus maximus* insertion.
- Full knee extension.
- Humanlike aspects of tibia, ankle, and foot.
- Possibly unique form of bipedalism, e.g. hyperpronation.

ENVIRONMENT AND WAY OF LIFE

The habitat of *Au. sediba* is thought to have been a mosaic environment of wood- and grasslands. Phytoliths from their tooth enamel indicate that they had access to forest products. Phytoliths are species-specific silica bodies in plants that can be used to identify what plant species were consumed. Fruit, leaves, wood, and bark were identified, with the latter being a first for fossil hominins (Henry et al. 2012).

Unlike other australopiths and paranthropines, the diet of *Au. sediba* most closely resembled savanna-dwelling chimps and secondarily *Ar. ramidus*, in that they specialized on C₃ plants, such as herbaceous plants, shrub and tree plant products, and grasses, and possibly animals that consumed those items. We know that C₄ plants were available at the time because remains of those more open, dry-adapted plants have been recovered in the same layers within which the Malapa material was found. In addition, C₄-consuming rodents, horses, and bovids were resident at the time. Their diet was thus less “carbonically” (I made that up for fun!) varied than contemporary hominin species inhabiting similar environments, such as *Au. africanus* and *Paranthropus robustus*, as well as *Homo* species that had an even broader diet. Microwear analyses show that the two Malapa individuals (MH1 and MH2) under study ate a greater percentage of hard food items relative to other australopiths, being more similar to *P. robustus* or *H. erectus* (Henry et al. 2012).

Being C₃ specialists in a C₄-dominated environment may have involved more time invested in foraging, or they may have favored a more closed environment for feeding. It is thus likely that there were enough woodland or riverine environments to have supported the population. Additionally, they could have consumed hard items when available or as fallback foods.

22. Genus Homo

It is generally thought that by 2.5 mya, there were at least two species of *Homo* in East Africa, *Homo habilis* and *Homo rudolfensis*. The inclusion of those fossils in our genus is not accepted by all and is somewhat arbitrary. Some argue that *H. habilis* does not differ enough from australopiths to warrant different genus designation. Its inclusion in *Homo* was prompted by the fact that they are thought to have made and used tools and thus to have been cognitively advanced. *H. habilis* was more encephalized than the australopiths, and the skull vault is flexed as in *Au. africanus*, *P. boisei*, *P. robustus*, and later species of *Homo*.

There is debate as to whether *H. habilis* or *H. rudolfensis* gave rise to *Homo ergaster* (African form of the *erectus*-grade) and hence should be included in our lineage. Both species overlap the more derived *H. ergaster* in time and geographic space. The size and architecture of the brain of *H. habilis* make it a contender in the minds of some researchers. However, their limb proportions, i.e. retention of long arms and short legs, do not resemble *H. ergaster*. According to some researchers, *H. rudolfensis* possessed more modern femora (plural of femur), limb proportions, and a more orthognathic face, thus making them a better candidate for the ancestor of *H. ergaster*. However, it has not been determined that postcranial remains can be definitively assigned to the species, because postcrania are rarely found in association with cranial material (from which species designation derives). In addition, the claim to a more orthognathic face has been called into question based upon biometric impossibilities—the reconstruction of the face is impossible in terms of the relative positioning of key features (Bromage et al. 2008). While some claim that *H. rudolfensis* were more encephalized than *H. habilis*, others believe that their relative brain size (i.e. brain size taking into account body size) was lower and the temporal region, which is a conservative region of the skull, was more primitive. They also had more robust faces and teeth, unlike *H. ergaster*.

23. Homo habilis

Homo habilis (2.3 mya)

(“same” / “handy,” “able,” etc.)

SITES

Ethiopia: Hadar (and possibly Omo)

Kenya: Koobi Fora

Tanzania: Olduvai Gorge

South Africa: Swartkrans and Sterkfontein

PEOPLE

Mary and Louis Leakey, Donald Johanson, Tim White, and others



Scientific reconstruction of *Homo habilis*.
“*Homo habilis*” by Lillyundreya is licensed under
CC BY-SA 3.0.

Of the two species of Early *Homo*, *Homo habilis* is the favored ancestor of *Homo ergaster* and all subsequent hominin species.

PHYLOGENY

While the origin of *Homo habilis* has been in a state of flux in recent years, the discovery of *Au. sediba* has raised more questions about the origin of our genus. The discovery of Lucy in the early 1970s led some researchers to turn away from *Au. africanus* in favor of *Au. afarensis* as the ancestor of genus: *Homo*. In recent years, the idea that a cladistic event had occurred with *Au. afarensis*, leading to *Au. africanus* and the more derived robust forms on the one hand and genus *Homo* on the other, gained in popularity. *Au. sediba* now seems to have bridged the gap between the australopiths and genus *Homo*, sharing characteristics with *Au. africanus*, *H. habilis*, and *H. ergaster*. The similarities with the two *Homo* species may help resolve the problem as to which of the two species of “Early *Homo*” gave rise to *H. ergaster*. There are proponents in support of each of the evolutionary scenarios, with their share of pros and cons.



KNM-ER 1813, Koobi Fora, Kenya. “*Homo habilis*-KNM ER 1813” by Locutus Borg is in the public domain.

DISCOVERY AND GEOGRAPHIC RANGE

Louis and Mary Leakey discovered the first fossil material in 1960 at their site in Olduvai Gorge, Tanzania. Louis had been recovering stone tools from the site for years, but the manufacturer of those tools had previously eluded him. He named the species *Homo habilis* or “handy-man.” Fossils attributed to *H. habilis* have also been found at Hadar (and possibly Omo), Ethiopia; Koobi Fora, Kenya (see Figure 23.2); and the South African sites of Swartkrans and Sterkfontein.

PHYSICAL CHARACTERISTICS

H. habilis exhibited a high degree of sexual dimorphism, with males and females weighing 114 and 70 lb and standing 5'2" and 4'1", respectively. Their skull, face, and dentition were more gracile than the australopiths. Their teeth and dental arcades were very human-like. The skull base was flexed, as seen in *Au. africanus* and the more derived robust australopiths and, relative to past species, the skull was rounder and higher, reflecting architectural changes in the brain. Cranial capacity ranged from 500 to 800 cc with a mean of 631 cc. This gave them an EQ of 3.1–3.5. At this point in hominin evolutionary history, we see increased asymmetry in the two hemispheres of the brain, termed lateralization or left hemispheric dominance. The left side of our brain is involved with language and analytical processes. Like all Old World monkeys and apes, *H. habilis* possessed Broca's area, which is involved with language production. However, it was larger than in past hominin species, and they also possessed Wernicke's area, which plays a role in language comprehension. They thus had the neural capacity for language. The left hemisphere is also related to right-handedness. They may have exhibited our tendency to hold objects with our left hand while working on them with our right. The frontal lobe, important in association processes, was expanded and resulted in more of a vertical forehead. The enlarged brain may have been facilitated by a decrease in gut volume, combined with a higher-quality diet that resulted from increased cognitive capabilities and an expanded technology base.

H. habilis had a smaller supraorbital torus and its face was more orthognathic than its supposed ancestor, *Au. africanus*, but they retained some prognathism in the lower face. They had fairly large ape-like incisors, but their canines, premolars, and molars were reduced in size. The mandible was more gracile, reflecting their reduced masticatory capabilities.

Like the majority of the australopiths, *H. habilis* possessed elongated arms, possibly suggesting continued reliance on an arboreal environment. While the digits were still curved, they had increased gripping capabilities for tool manufacture and use, as evidenced by the pronounced attachment site for the *flexor pollicis longus* muscle, which acts to flex the thumb.

The femoral head was enlarged and the neck shortened. Those changes are thought to have been the result of increased strain generated by an expanded pelvis for birthing larger-brained infants. However, no fossilized pelvic fossils have been found. Their foot was more modern, in that the hallux was no longer divergent but rather aligned with the lateral four digits, and the toes were shorter. They had less mobility in their feet, in that the foot had become more of a support structure like our own. The metatarsals were thick relative to modern feet, and the morphology of the third metatarsal suggests that they did not yet exhibit the degree of weight transfer and propulsive capabilities seen in modern humans.

Review of Primitive Characteristics

- Some prognathism.
- Large incisors.
- Curved phalanges.
- Long arms and short legs.
- Thick metatarsals.

Review of Derived Characteristics

- Gracile craniofaciodental characteristics:
 - Thin skull vault.
- More globular cranium.
- Expanded frontal lobe.
- Left hemispheric dominance.
- Enlarged Broca's and Wernicke's areas.
- Reduced supraorbital torus.
- Smaller mandible, canines, and cheek teeth.
- Parabolic dental arcade.
- Increased manual dexterity.
- Larger femoral head (and hence acetabulum) and shorter neck.
- More stable foot:
 - Loss of divergent hallux.
 - Shorter toes.

ENVIRONMENT AND WAY OF LIFE

Certainly one of the most interesting things about *H. habilis* is the appearance of a much more extensive archaeological record. The cultural period at that time, and extending through *Homo erectus*, is termed the **Early Paleolithic**, or the early portion of the Old Stone Age. While other species apparently preceded *H. habilis* in the manufacture of tools, it was thought for many years that they were the first to do so. The **Oldowan** or **Olduwan tradition** (**industry** and **technology** are also used synonymously with “tradition”), named after Olduvai Gorge, consisted of simple core tools and flakes. The technique involved the selection of a **cobble** (a workable-sized rock), followed by the use of a **hammerstone** to remove the outer rough surface (see Figure 23.3) or “**cortex**” and then to shape it into a **core tool**, by the removal of **flakes**. The flakes that are removed may be suitable for cutting and slicing. The process is called hard percussion, and the shaping is known as lithic reduction. “**Lithic**” refers to stone and is also used to denote a stone tool. Stone resources for the manufacture of tools were chosen for their suitability and transported across the landscape. Of course, this indicates a level of cognitive complexity, but we must remember that chimps and orangutans choose sticks and grass of particular widths and strengths, trim them to the appropriate length, and transport them in their mouths to their site of intended use. Apes learn by trial and error, innovation and imitation, and cultural transmission, i.e. traits spread throughout a group by observation. Cultural transmission of innovations is even seen in monkeys, e.g. Japanese macaques washing sweet potatoes, skimming grain kernels floating on the surface to separate them from beach sand, and bathing in volcanic springs. While we do not know which species was the first to invent stone tools that were modified from their original form via lithic reduction and shaping, we can see the precursors of innovation and cultural transmission in our primate relatives. The real skill comes with having the manual dexterity to do so, making a tool that can accomplish a variety of uses, and the ability to teach others. I would argue that the earliest members of our genus had “**theory of mind**,” i.e. the realization of another’s thoughts. There is only one example

of teaching in nonhuman primates and that was a mother chimp in the Tai Forest of the Ivory Coast that helped her daughter crack a nut, using their unique hammer and anvil technique. Our closest relatives, with all of their intelligence, symbolic capabilities as demonstrated in language studies, and similarities to our own behavior, do not know enough to teach their children. They are not capable of realizing that “I know something that you don’t know” and vice versa. We go on and on about encephalization in the hominin lineage and technological advancements in the archaeological record over time, but what may have been the true dividing line between ourselves and the apes, whether bipeds or not, was the ability to teach our young, kin, and other group members and thus increase their chance of survival. The vehicle for developing a theory of mind is language. Human children develop a theory of mind at three or four years of age. Prior to that time, they do not realize that they or others may have incomplete information. Here is a fun anecdotal account that I always relay to my students:

My brother Michael was visiting my brother Jimmy. Jimmy was nowhere to be found when Michael realized that Jimmy’s 18-month-old son had messed his diaper. Jimmy’s older son must have been about three years old at the time. He helped Michael find everything that he needed to clean the baby. After Jimmy had reappeared and Michael had left for the day, the older boy remarked to his dad, “Uncle Mike is so dumb!” When asked what he meant by that, he replied, “He didn’t know where the towels were; he didn’t even know how to use the Diaper Genie® [a gizmo that turns dirty diapers into self-contained plastic coated links—truly magical!].”

This indicates that my nephew had not developed a theory of mind. He did not understand that Michael did not know things that he knew.



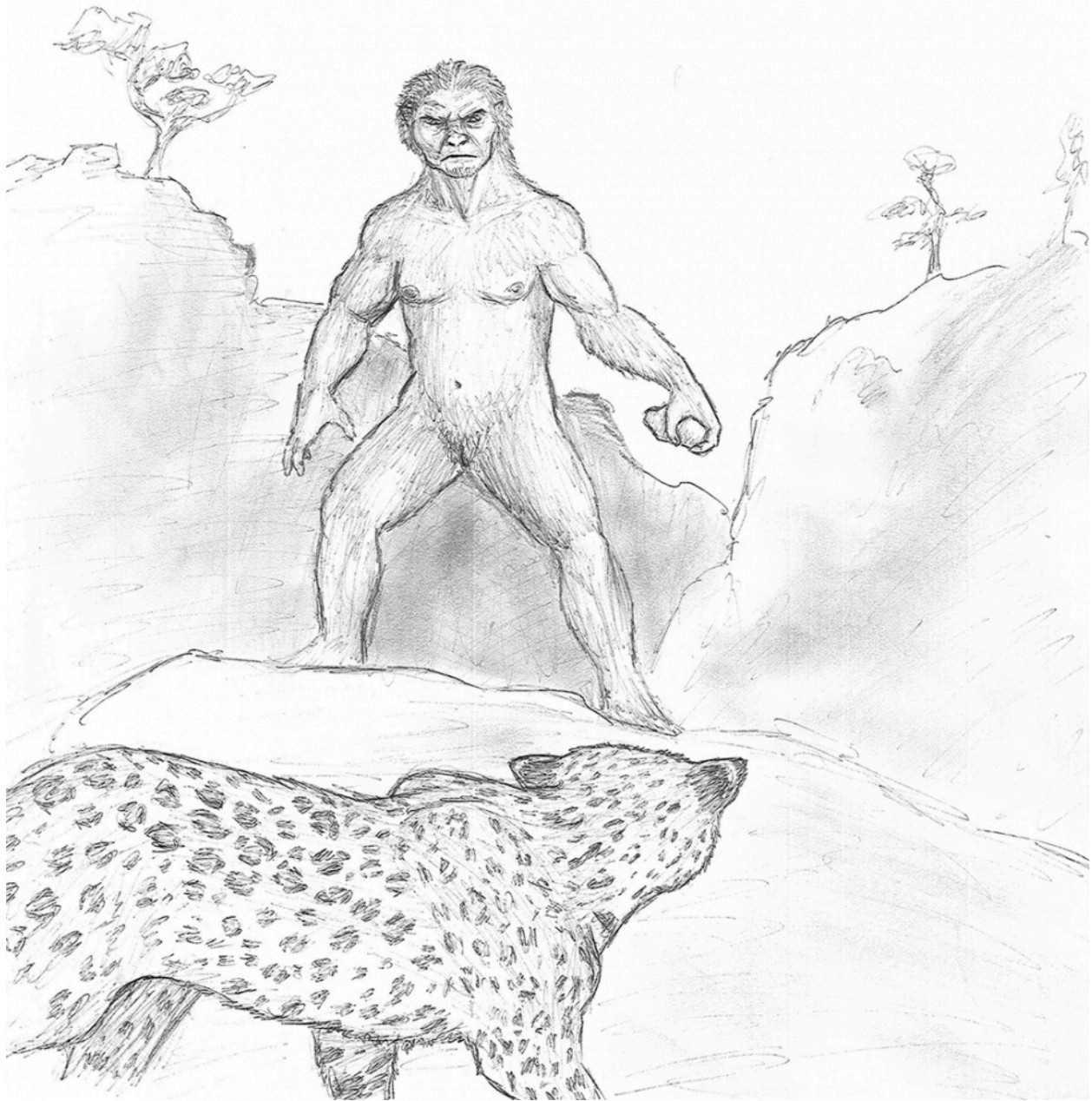
Hard hammer percussion. “Hard Hammer” by ZenTrowel is in the public domain.

Homo habilis was the first species to exhibit enlarged Broca’s and Wernicke’s areas. They thus may have had the motor control that allowed more lingual activity and the ability to comprehend the resulting sounds they could produce. Great apes can comprehend symbols, i.e. *this* stands for *that* even though *this* bears no resemblance to *that*. They have been taught American Sign Language, various computer languages, and spoken language. Where they fall short is in syntax—they cannot string together symbols into meaningful sentences. I firmly believe that the descendant species of Early *Homo*, i.e. *Homo ergaster*, had theory of mind, based on their stereotypical production of tools. There had to be teaching, learning, and training involved in order to produce an implement that is readily recognized as an Acheulian hand axe (see Figure 23.4). Thus, since we see an earlier stage of tool production in Early *Homo*, I would argue that they had rudimentary language and theory of mind.



Acheulian hand axe. "Bifaz en mano" by José-Manuel Benito Alvarez is licensed under CC BY-SA 2.5.

The Oldowan tradition lasted from approximately 2.5 to 1.5 mya but survived in some areas until 600 kya. Tools consisted of crude choppers (see Figure 23.6) and scrapers, as well as simple flake tools, some of which indicate that they were "retouched," i.e. secondarily shaped and/or sharpened. In addition, there is evidence of possible wooden digging sticks or spears at the site of Koobi Fora, in the East Lake Turkana region of Kenya and possible bone tools at Olduvai Gorge.



Homo habilis Leopard Confrontation by Keenan Taylor.

Tools were likely used for acquiring and processing both animal (scavenging, butchering, disarticulation, skinning, cutting flesh, chopping bones open, etc.) and plant (digging tubers, cutting stalks, pounding to break down fiber, etc.) foods. Indications of hominins having butchered and scavenged animals comes from several lines of evidence. First, tools have been found with *H. habilis* remains. Second, there are concentrations of tools and fossilized animal bones that exhibit signs of cutting, disarticulation, and marrow extraction. Mary Leakey mapped one such area with a high accumulation of stone tools and bones, known as site DK. Third, the high frequency of particular bones at some sites is indicative of the hominins having “brought back the good stuff”

i.e. skulls for brain and limb bones for meat and marrow. Fourth, microscopic analyses indicate that cut marks on some bones overlay predators' teeth marks, showing that the hominins arrived afterward. How they got meat away from scary scavengers is anyone's guess. Finally, experiments with modern-made stone tools in the Oldowan style reveal (1) that it is possible to butcher an elephant and (2) wear patterns that result from the butchering process match those found on ancient tools.

The following sites contain evidence of stone tools and their manufacture:

- Lomekwi 3, Lake Turkana region, Kenya (3.3 mya): cores, anvils, and flakes.
- Gona, Ethiopia (>2.5 mya): 3,000 stone artifacts.
- Hadar, Ethiopia (2.4 mya): tools were found with a *H. habilis* mandible.
- Olduvai Gorge, Tanzania (1.8 mya): numerous tools.
- Koobi Fora, Kenya: high concentration of flakes suggesting repeated use.



Oldowan choppers. “Pierre taillée Melka Kunture Éthiopie fond” by Didier Descouens is licensed under CC BY-SA 4.0.

H. habilis are thought to have been forager-scavengers that collected wild plant foods, hunted small animals opportunistically, and scavenged carcasses from large predators. While there is evidence of “**repeated-use**” sites, meaning that individuals returned to particular areas to meet, they are not thought to have settled in any one area but rather moved about the landscape in their quest for food. They may have made use of those sites for a variety of communal or individual activities, such as grouping for “central place foraging” activities (from the animal literature, meaning to move out from and possibly return to a particular place), making new and/or using cached tools, butchering carcasses, sharing food, etc. Mary Leakey believed that her Site DK was indicative of a home base. While it is a romantic notion to look to modern hunter-gatherers with modern intelligence and advanced weaponry as being able to stay in one place until resources became scarce, it is not likely that those primitive hominins were camped out on a lake shore. It would have been a very dangerous place to be for long periods of time.

While they could have climbed trees and made sleeping nests in trees or on the ground, we do not know how much time they spent in the two microenvironments.

THE FIRST FAMILY OF PALEOANTHROPOLOGY: THE LEAKEYS

Louis Leakey (1903–1972) was born to British missionary parents residing in Kenya. He and his wife Mary made names for themselves with their pioneering work, searching for and discovering fossil hominins in East Africa. Louis is credited with the discovery of three hominin species, the first of which is considered to be a possible **basal** or **stem** ape, *Proconsul africanus* (“before Consul” [a famous chimp at the London Zoo]/“from Africa”). Louis was an early believer in an African human origin (Cartmill and Smith 2009). He became interested in the search for ancient hominins after his discovery of stone tools that he attributed to human ancestors. The Leakeys worked at Olduvai Gorge in Tanzania for many years. When Mary discovered the robust australopith that she named *Zinjanthropus boisei* (later to be changed to *Australopithecus boisei* and later to *Paranthropus boisei*), Louis proclaimed to the world that they had found his predicted “man the toolmaker.” According to legend, he was ridiculed by some because they felt that “Zinj” (also known as “Dear Boy” or “Nutcracker Man”), as the specimen came to be known, was an herbivorous ape that would not have had the mental capabilities to manufacture the tools that became known as the **Oldowan technology**. Louis was later rewarded with the discovery of fossils of a more derived hominin with a larger cranial capacity. He named the species *Homo habilis* (“Handy man”) as the first tool makers. There was and still is some controversy surrounding the classification of the species. He and his colleagues were accused of using cultural versus physical attributes to justify their inclusion of the fossil material in our genus *Homo*. Some still believe the species should be assigned to genus: *Australopithecus*. Regardless of the controversies, Louis made a name for himself and added to our knowledge of human ancestry. At Olduvai, he also discovered the cranium (missing its face) of a 1.2 mya *H. ergaster* individual. Another great accomplishment was sending the three “grand dames” of ape primatology into the field. He correctly believed that we can learn about ourselves from our closest relatives. He thus funded Jane Goodall to study the chimps of Gombe, Tanzania; Dian Fossey for her work with mountain gorillas in the Virunga Volcano region of Rwanda; and Biruté Galdikas to study the orangutans of Borneo.

Mary Leakey (née Mary Douglas Nikol, 1913–1996) is described on the Leakey website (www.leakey.com) as “one of the world’s most distinguished fossil hunters.” She is credited with the discovery of two species of early hominins, *Au. afarensis* at Laetoli and *P. boisei* at Olduvai, as well as the Laetoli footprints. (Laetoli is also in Tanzania.) Mary had an early interest in archaeology and, like Louis, excavated stone tools; in her case in France as a mere child. By age 17, she was auditing university courses in archaeology and geology. She met Louis in 1933 and accompanied him to Kenya to illustrate stone tools for a book he was writing. They married several years later and had three sons, Jonathan, Richard, and Philip. Jonathan hunted fossils along with his parents and discovered the first *H. habilis* specimen, a mandible known as “Jonny’s Child.” Richard moved into Kenya to work at sites around Lake Turkana, and his team discovered the oldest *H. ergaster* specimen (1.75 mya)

in the West Lake Turkana region. In addition to his paleoanthropological work, he is a champion of wildlife conservation. His wife Meave is a renowned paleoanthropologist with several hominin species discoveries to her credit, and their daughter, Louise, is well on her way to making a name for herself (www.leakey.com).

24. Homo rudolfensis

Homo rudolfensis (2.4 mya)

(“same” / from Lake Rudolf)

SITES

Koobi Fora, Kenya; Chiwondo Beds, Malawi; possibly Olduvai Gorge, Tanzania

PEOPLE

Richard and Meave Leakey, Bernard Ngeneo



Homo rudolfensis holotype: KNM-ER 1470 from Koobi Fora, Kenya. “*Homo rudolfensis*” by Durova is licensed under CC BY-SA 4.0.

INTRODUCTION

The second species of Early *Homo* to be discovered is now known as *Homo rudolfensis*, since it was discovered at the site of Koobi Fora on the east side of Lake Turkana, which was formerly known as Lake Rudolf.

PHYLOGENY

Homo rudolfensis may be a descendent of *Kenyanthropus platyops*. Those who favor that scenario would either assign *rudolfensis* to genus: *Kenyanthropus* or move *platyops* into genus: *Homo*. There are proponents on both sides of the argument as to whether *H. habilis* or *H. rudolfensis* gave rise to the earliest member of the “erectus grade,” i.e. *Homo ergaster* in Africa, and its four descendent species: *erectus* in Asia, *antecessor* in Western Europe, *georgicus* in the Republic of Georgia, and *floresiensis* on the island of Flores.

DISCOVERY AND GEOGRAPHIC RANGE

The majority of *Homo rudolfensis* material comes from the Koobi Fora site where Richard Leakey discovered the type specimen, KNM-ER 1470 (see Figure 24.1) (Kenya National Museum – East Rudolf), as well as subsequent material. Material has also been recovered from the Chiwondo Beds of Malawi, and there is possible material at Olduvai Gorge. Thus, the species ranged from northern Kenya down through Tanzania and into Malawi, along the north-south hominin corridor.

Leakey originally called the material *Homo indet.* (“indeterminate”) because he did not know in what, if any, group to include it. The use of species: *rudolfensis* began to gain in popularity as researchers came to realize they were dealing with two distinct species. For a while, some were content with the two species being geographic species, i.e. *H. habilis* at Olduvai and *H. rudolfensis* at Koobi Fora. However, *habilis*-like material was discovered at Koobi Fora (KNM-ER 1813) and some material at Olduvai resembled *H. rudolfensis*. The two species went through a tumultuous period when the species names were abandoned by some, in favor of “Early *Homo*.” However, critics complained that it had become a “wastebasket” species. During that time, Richard Leakey visited SUNY Geneseo, and I had the opportunity to chat with him about the taxonomic problem. He was frustrated with the state of things and wished that paleoanthropologists would work out exactly what characterized the two species. Over time, paleoanthropologists have seemingly become more comfortable with the *habilis* designation for the majority of fossils from Olduvai Gorge, even if some of them prefer genus: *Australopithecus*. The same is true for the type specimen, KNM-ER 1470, as *H. rudolfensis*.

PHYSICAL CHARACTERISTICS

Relative to *H. habilis*, *H. rudolfensis* was larger and more robust, with a heavier face and jaws and larger dentition. Their faces were long, and the lower face was thought to be somewhat orthognathic based on the type specimen, KNM-ER 1470. New material discovered at Koobi Fora was thought to support the reconstructed facial morphology of KNM-ER 1470 and elucidate heretofore unknown aspects of the face and jaw. However, Bromage et al. (2008) have conducted architectural constraints analyses demonstrating that the degree of orthognathism would be biomechanically impossible. The molars were large with complex crowns and thick enamel like other contemporary and descendant species, but they were mesiodistally long and hence more primitive than *H. habilis*. The brain averaged 751 cc, but their encephalization quotient may have been only 3.0, versus the 3.1–3.5 range estimated for *H. habilis*. As mentioned, it is not known for certain that any of the postcranial material that some researchers assign to the species is justified. If the postcranial material belongs in the *H. rudolfensis* hypodigm, the following can be stated about the species: their innominate, femur (larger head, shorter neck, and robust shaft), and limb proportions were more modern, with longer legs and shorter arms, and the femoral robusticity corresponds to increased strain generated by a wider pelvic aperture.

Review of Primitive Characteristics

- Robust craniofaciodental characteristics.
- Primitive temporal region.
- Long molars (mesiodistally).

Review of Derived Characteristics

- Long orthognathic face?
- Large brain.
- Human-like limb proportions, innominate, and femora?

ENVIRONMENT AND WAY OF LIFE

While their environment did not differ from that of *H. habilis*, they may have been able to process tougher food items with their more robust masticatory apparatus. While tools are known from the time period and geographic region occupied by the species, tools have not been found in association with fossil material. It is possible that the more gracile masticatory apparatus of *H. habilis* could have resulted from tool use in food-processing activities and relaxed selection for robust features.

25. Homo species indeterminate

Homo species indeterminate (2.8 mya)

A possible new species of Early *Homo* was recently discovered. Villmoare et al. (2015) reported on what they are calling *Homo species indet.* (“indeterminate”). The half mandible (LD 350-1) was discovered by Chalachew Seyoum in 2013 at the Ledi-Geraru site in the Afar region of Ethiopia. If indeed the jaw is part of the *Homo* lineage, it extends the origin of our genus to 2.8 mya, 400 kya older than the oldest *H. habilis* specimen, i.e. AL 666-1 from the Hadar site in Ethiopia where Lucy was discovered. Villmoare et al. (2015) believe that the specimen represents a transitional form between *Au. afarensis* and *Homo habilis*. Support for their supposition includes the combination of australopith and *Homo*-like characteristics seen in the mandible and teeth, as well as the fact that it is from the same area as *Au. afarensis* that is known to have survived there until 3 mya. They report on a fragmentary mandible from the Koobi Fora site in Kenya (KNM-ER 5431) that exhibits a similar combination of australopith and *Homo* morphology (see Villmoare et al. 2015 for references).

The anterior of the mandible exhibits the most primitive characteristics, along with some *Homo*-like characteristics. *Homo* characteristics include narrower molars with more derived dimensions and cusp morphology, and the canine/first premolar configuration is less ape- or australopith-like, as evidenced by wear patterns. They conclude that deviation in the teeth and jaws, from the australopith condition, occurred early in the *Homo* lineage.

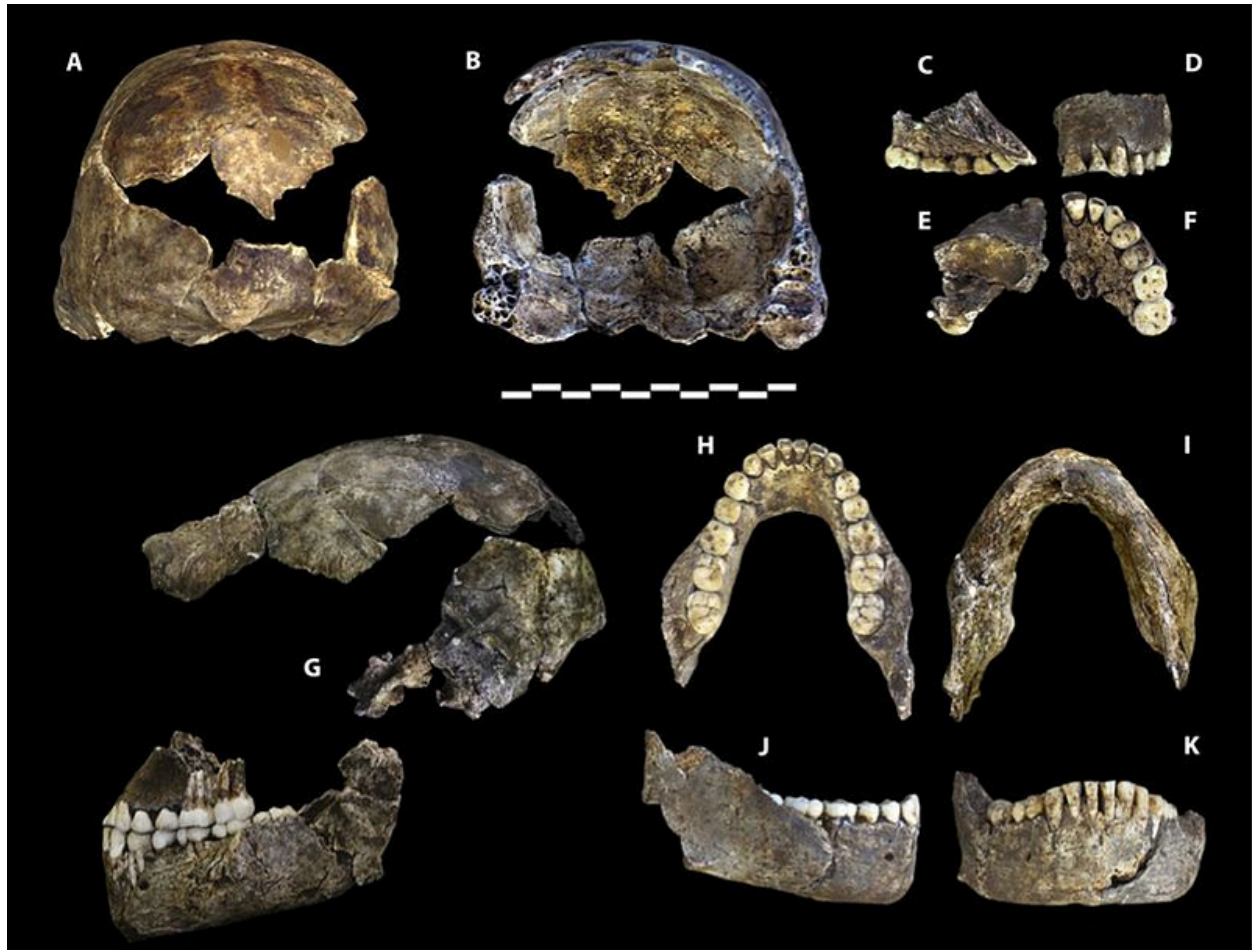
DiMaggio et al. (2015) reported on the paleoenvironment of the site. The area was a mosaic environment consisting of open grass- and scrubland, gallery forest, and lakes and/or rivers. They see a faunal turnover 2.8-2.6 mya in the strata, in accordance with the area becoming more open and likely arid with an increase in grazers. They cite evidence for climatic and vegetation shifts resulting from “rifting processes and extensive volcanism [that] altered the architecture of sedimentary basins” (see DiMaggio et al., p. 1, for references). Their work fills an important gap in the paleoenvironmental history of the region.

The fact that *Au. garhi* is younger and their teeth are more robust leads the researchers to conclude parsimoniously that *Au. garhi* is not part of our ancestry, as earlier and later forms of *Homo* had more gracile teeth and jaws. The same would also hold true for *Au. sediba* due to their much later appearance in the fossil record at ~2 mya. However, Hawks et al. (2015) argue that the **osteometrics** (bone measurements) and anatomical features do not support firm taxonomic placement in genus: *Homo*. They believe that they have ample evidence showing that *Au. sediba* is closely related to early species of *Homo* (see Chapter 21).

26. Homo naledi

Homo naledi (date unknown)

("same" / "star" in Sotho language)



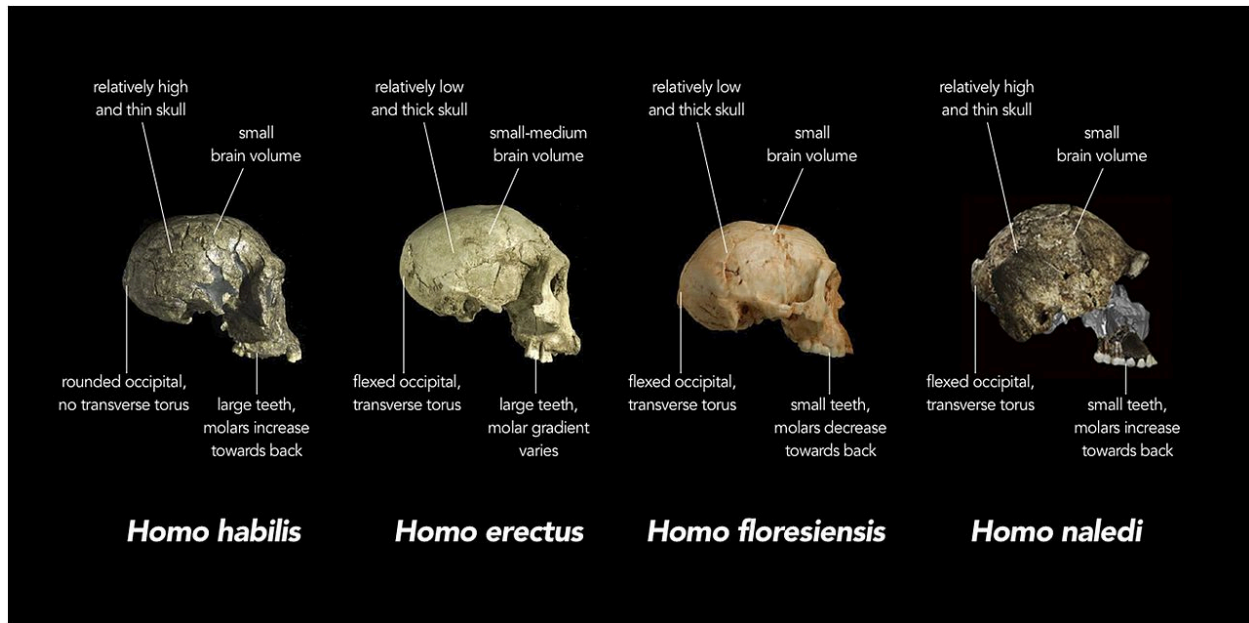
Skull and mandible of type specimen DH-1 by Lee Roger Berger research team is licensed under CC-BY-SA 4.0.

SITE

Rising Star cave system, South Africa

PEOPLE

Cavers Steven Tucker and Rick Hunter and investigated by Paul Dirks and Lee Berger and their associates



Comparison among *H. naledi*, *H. habilis*, “African *H. erectus*”, and *H. floresiensis*. By Chris Stringer, Natural History Museum, United Kingdom – Stringer, Chris (10september 2015). “The many mysteries of *Homo naledi*.” *eLife* 4: e10627. DOI:10.7554/eLife.10627. PMC: 4559885. ISSN 2050-084X. Licensed under CC-BY 4.0.

INTRODUCTION

This newest member of our genus has once again confounded the evolutionary history of the *Homo* lineage. The most exciting aspect is the nature of the remains suggests that they were intentionally deposited in the deep cavern where they were discovered. *H. heidelbergensis* was heretofore the earliest species thought to have practiced intentional body disposal. Attempts at dating the remains have not been successful. However, Thackeray (2015) has estimated that the species may date to 2.0 ± 0.5 mya, based on comparisons of date and anatomical characteristics among *H. naledi*, *H. habilis*, *H. rudolfensis*, and *H. erectus* (see Figure 26.2 and Chapter 27 for the *erectus* grade).

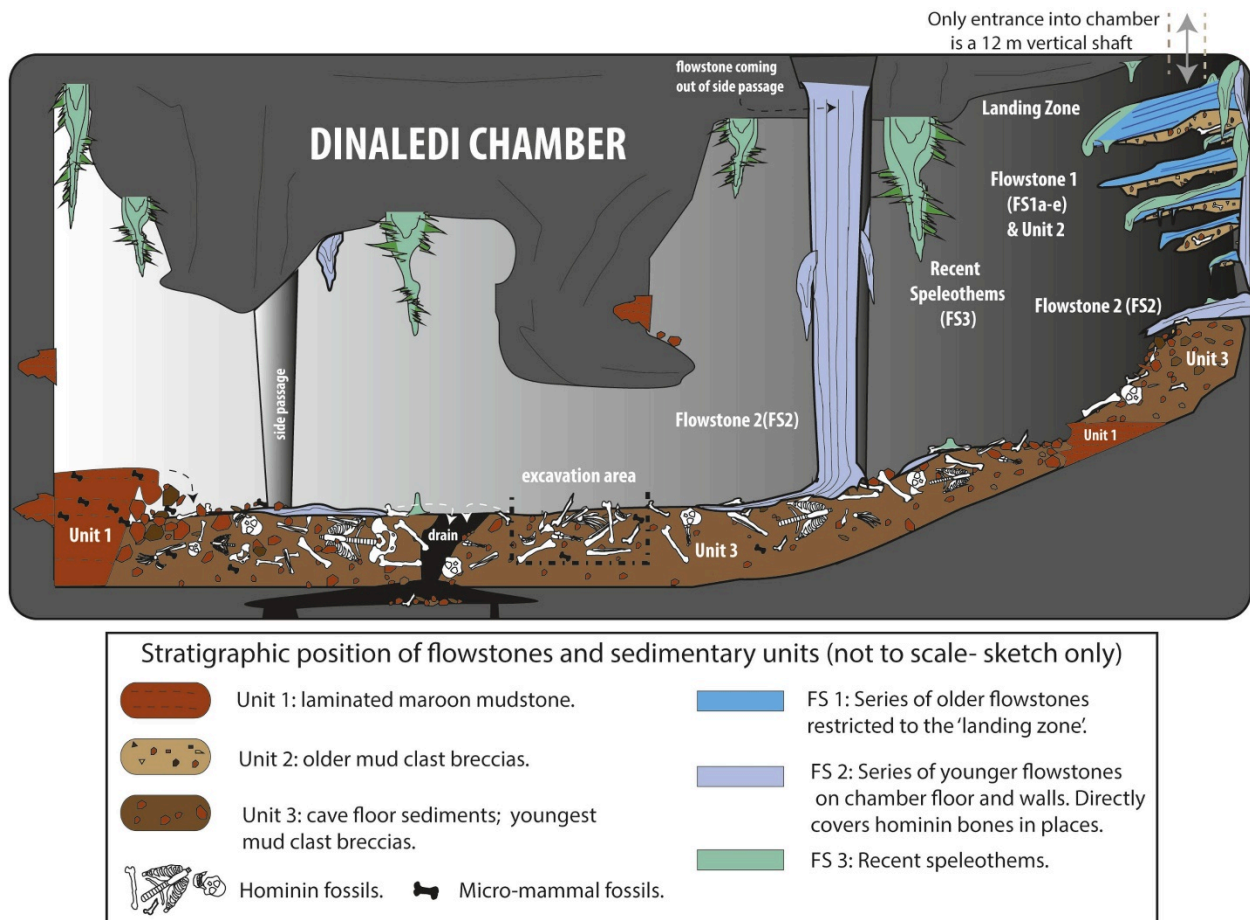
PHYLOGENY

It appears that the majority of researchers agree that the remains reflect a new hominin (see references this section, especially Randolph-Quinney 2015). Like most hominins, the phylogeny of the species is unknown but it likely descended from an australopith ancestry. What makes things even more difficult is that the species

shares characteristics with possible extant or near extant species of *Homo* (*H. habilis*, *H. rudolfensis*, and *H. erectus*), more derived forms (e.g. neandertals and humans), as well as various australopiths. The mosaic of traits is interesting and further supports the bushy nature of the hominin tree.

DISCOVERY AND GEOGRAPHIC RANGE

The remains of a minimum of 15 individuals, totaling 1550 fossils (see Figure 26.4), were excavated in 2013 and 2014 from the Dinaledi Chamber, located within the Rising Star cave system in the Cradle of Humankind World Heritage Site, Gauteng Province, South Africa (Berger et al. 2015). The fossils are the largest collection of a hominin species in Africa (Dirks et al. 2015). The chamber is 30 m below ground and is only accessible via a 12 m narrow shaft (Randolph-Quinney 2015 and see Figure 26.3 – top right). Based on depositional data, the bodies were deposited over time (Dirks et al. 2015).



Dinaledi Chamber by Paul H. G. M. Dirks, et al. is licensed under CC-BY 4.0.

PHYSICAL CHARACTERISTICS

The remains are especially valuable as all body regions are represented, and some bones are articulated, so that anatomical positions and arrangements are preserved, e.g. an almost complete leg of a child and an adult hand (Dirks et al. 2015). The low cranial capacity, elevated shoulder joints, curved phalanges, and trunk and

hip morphology are australopith-like. Crania, jaw and teeth morphology, and leg bones are, for the most part, *Homo*-like. The wrist is most similar to humans and neandertals. The foot is very human-like. (Berger et al. 2015, Harcourt-Smith et al. 2015, Kivell 2015, Thackeray 2015) Thus, we see an able terrestrial biped that could climb, forage, and take refuge in trees.



Homo naledi collection by Lee Roger Berger research team is licensed under CC-BY 4.0.

Cranial capacity falls within the range for the australopiths, with males averaging 560 cc and females, 465 cc (Berger et al. 2015). The base of skull vault is flexed like members of the *erectus* grade and subsequent species of *Homo* (see Figure 26.2 and 15.8). The vault bones are thin like those of *H. habilis*. *H. naledi* exhibits less postorbital constriction than the earliest australopiths, yet possesses a larger supraorbital torus than any gracile australopith (Berger et al. 2015). Taken together, it is an odd combination. A more gracile face would result in less postorbital constriction, yet the supraorbital torus is associated with chewing stress. Even more surprising, the teeth are smaller than those of *H. habilis*, *H. rudolfensis*, and the *erectus* grade, except for *H. floresiensis*

(Berger et al. 2015). The skull vault is pentagonal in cross-section like Asian *H. erectus* (see Figure 26.5), due to the presence of a sagittal keel, i.e. a thickening along the midline of the skull, from front to back (Berger et al. 2015). Since the trait is poorly understood in *H. erectus*, its presence in another species may shed more light on the adaptive significance or ontological processes involved. However, unlike *H. erectus*, the keel begins in the parietal versus the frontal region (again, see Figure 26.5). While not well developed, *H. naledi* exhibits a canine fossa, i.e. a depression above the canine tooth, as seen in *H. antecessor*, *H. heidelbergensis*, and humans.



A cast of Peking Man (*H. erectus*) to illustrate its sagittal keel – see ridge running across the top of the skull from front to back. By kevinzim. Licensed under CC-BY 2.0.

While the hand of *H. naledi* (see Figure 26.6) shares characteristics with other hominins, the combination of characteristics is unique. They had long fingers and the two more proximal digit phalanges are curved even more than those of australopiths, suggestive of arboreal activities. Yet their wrist morphology is most similar to neandertals and modern humans and, along with their long, robust thumb, they were thus capable of strong manipulatory activities (Berger et al. 2015, Kivell et al. 2015).



Hand of *H. naledi* by Lee Roger Berger research team is licensed under CC-BY 4.0.

The thorax and pelvis were flared like australopiths, but the vertebrae resemble those of the *erectus* grade and subsequent species of *Homo*.

While the combination of characteristics seen in the leg bones are distinctive, they are *Homo*-like, except that the femoral neck is long like that of australopiths. The foot (see Figure 26.7) is very human-like, with the primary differences being the curvature of their digits and less of a medial longitudinal arch (Harcourt-Smith 2015).



Foot of *H. naledi* by Lee Roger Berger research team is licensed under CC-BY 4.0.

The seemingly advanced bipedal morphology of the two most recent hominin discoveries, i.e. *Au. sediba* and *H. naledi* suggest that strong selective forces favored the ability to move through the landscape, in search of food and other resources.

Berger et al. (2015) have calculated the weight of the sexes as follows: males at 55.8 kg and females at 39.7 kg. The only bone that they could use for calculating height was a tibia that yielded an estimate of 144.5 – 147.8 mm. They state that the species falls within the height range of modern small-statured human populations, as well as estimates for the *H. georgicus* hypodigm from Dmanisi (Lordkipanidze et al. 2007, cited in Berger et al. 2015).

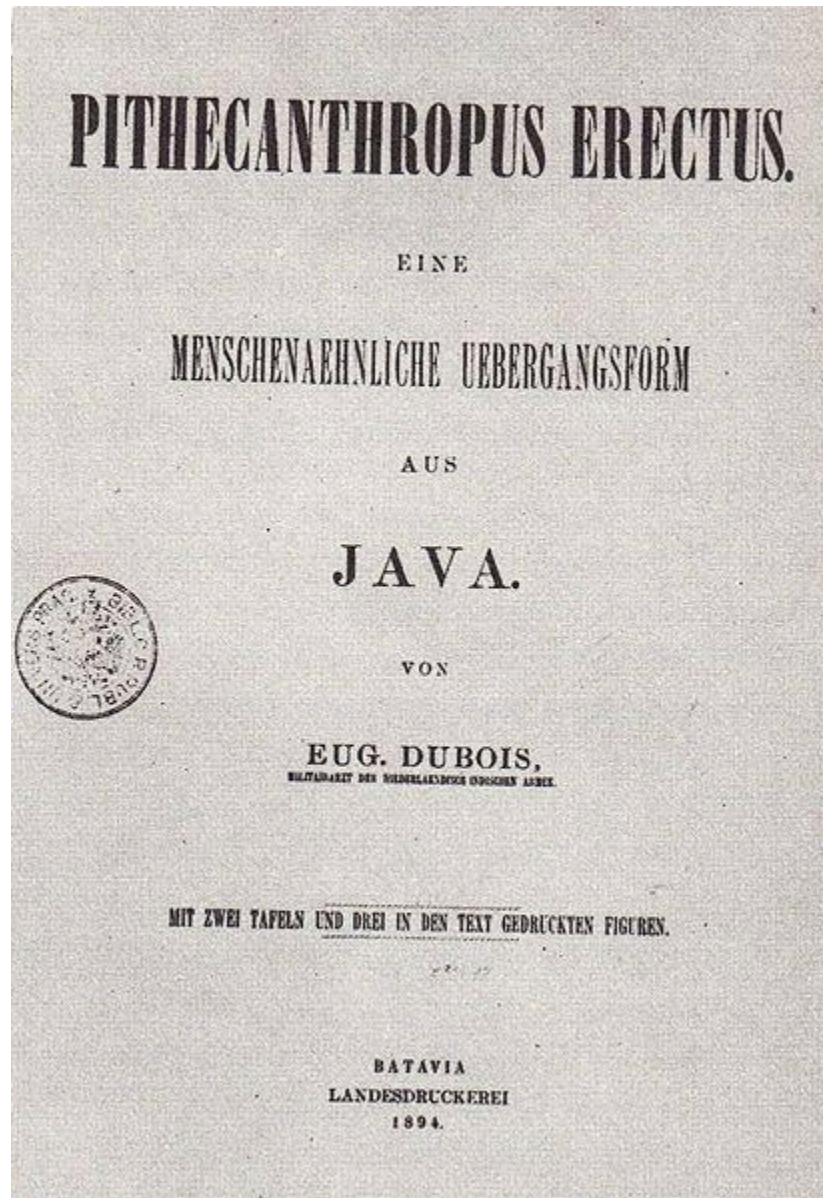
ENVIRONMENT AND WAY OF LIFE

The environment of the region, at around 2 mya, has already been described in the “ENVIRONMENT AND WAY OF LIFE” sections of *Au. sediba* and *P. robustus*. Interestingly, the Dinaledi site is 800 m southwest of the *P. robustus* site of Swartkrans. It was a hominin neighborhood!

The evidence is compelling that the remains could not have been deposited via natural forces, but rather were carried at least part of the way, through a dark and narrow passage. We thus need to reassess our image of the cognitive capabilities and awareness of earlier members of our genus.

27. The “erectus Grade”

The species that are collectively known as the *erectus* grade are believed to be descendants of the African “erectus” form, *Homo ergaster*, which in turn is thought to be descended from one of the two species of early *Homo*, *H. habilis* or *H. rudolfensis*. They lived in one form or another from 1.8 mya to as recently as 25–17 kya. *H. erectus* was first discovered by Eugène Dubois in 1891 (see Figure 27.1), at the Trinil site on the Solo River in Java. He had gone to Asia to find evidence of human ancestors, since the popular notion at the time was that we originated there.



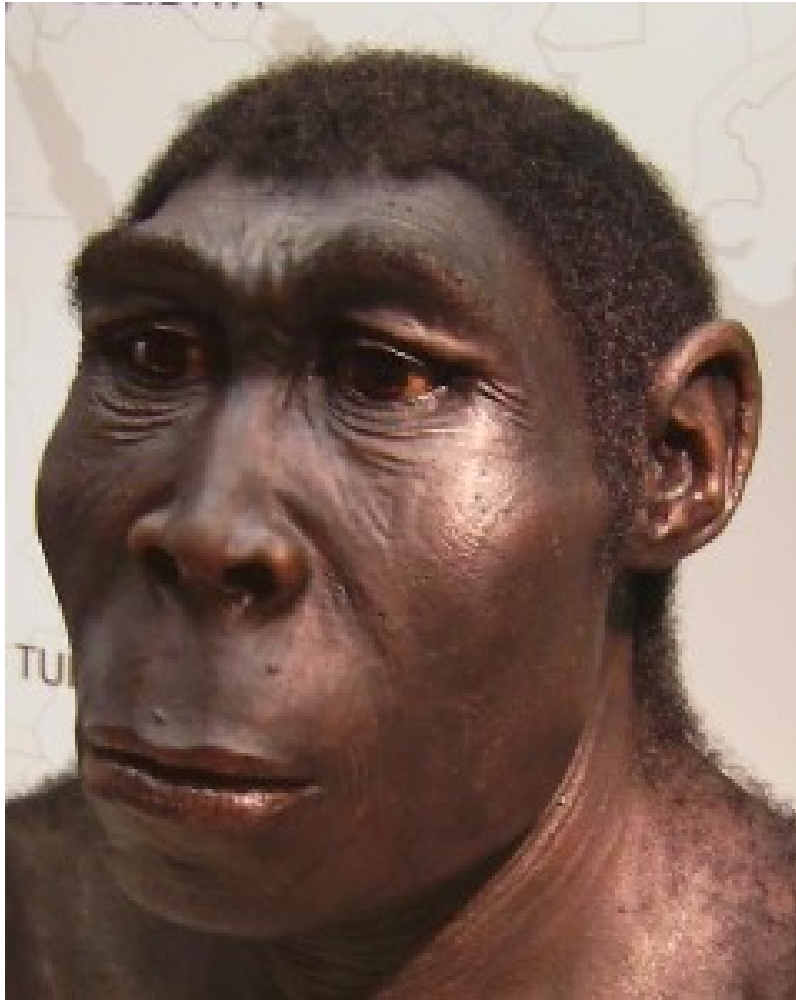
Title page from Dubois's monograph. “Eugene Dubois, book” is in the public domain.

The first genus and species combination he assigned to the material was *Anthropopithecus erectus* (“upright man-ape”). He then changed it to *Pithecanthropus erectus* (“upright ape-man”). It was only later, after much more material had been unearthed, that Franz Weidenreich persuaded researchers that the species did not differ enough from our own to warrant different genus status. In more recent years, researchers have argued that the material from different continents should be assigned to different species. While we cannot know if the different continental assemblages represent true biological species, i.e. incapable of interbreeding, they are now minimally classified as geographic species. Since the holotype or “type specimen” came from Asia (Java), the species designation “*erectus*” was retained for Asian material. The African material has come to be known as *H. ergaster*, contemporary material from Dmanisi (in the Republic of Georgia) is known as *H. georgicus*, material from Spain as *H. antecessor*. The strangely tiny and small-brained species from the island of Flores, *Homo floresiensis*, is thought to be a derived form of *H. erectus*. Some researchers place all of this material into the taxon *H. erectus*. Depending on which model people embrace for explaining the origin of our own species, one or more of those species would have evolved into archaic or premodern humans and, subsequently, **anatomically modern humans (AMH)**, i.e. *Homo sapiens sapiens*. The **Regional Continuity** or **Multiregional Model** supposes that whatever *erectus* forms were present in the various locations evolved through a premodern form, often termed Archaic *Homo sapiens* whether neandertal-like or otherwise, and then into AMH via gene flow between the populations. However with the more widely accepted “**Recent African Origin**” (**RAO**) theory, which holds that our ancestors arose in Africa ~200 kya and then moved out to populate the rest of the world, those “*erectus*” species that did not contribute to our lineage went extinct. The problem remains as to which of the later “*erectus*” forms gave rise to our premodern form, *Homo heidelbergensis*. At this point in time, the most plausible choices for the origin of *H. heidelbergensis*, the ancestor of both *Homo neanderthalensis* and AMH, are *Homo ergaster* or *Homo antecessor*.

28. Homo ergaster

Homo ergaster (1.8 mya)

(“same” / “working man”)



Reconstruction of *Homo erectus*. “*Homo erectus new*” by Lillyundfreyia is licensed under CC BY-SA 3.0.

SITES

Algeria: Tighenif

Morocco: Thomas Quarries and Sidi Abderrahman

Ethiopia: Konso Gardula and Omo

Kenya: Olorgesailie and Nariokotome

Tanzania: Olduvai Gorge

South Africa: possibly Swartkrans

PEOPLE

Richard Leakey, Kimoya Kimeu, Bernard Ngeneo

INTRODUCTION

As mentioned, the African form of the “*erectus* grade” is termed *Homo ergaster*.

PHYLOGENY

H. ergaster is thought to have evolved from either *H. habilis* or *H. rudolfensis* in East Africa. However, it is possible that *H. habilis* may have been the first to leave Africa, after which it may have evolved into a pre-*ergaster/erectus* form that then moved into Africa and Asia. If *H. habilis* was in our ancestry, the latter scenario might explain how the more modernly proportioned *H. ergaster* appeared in the fossil record contemporary with *H. habilis* in East Africa. Of course, the hit and miss nature of the fossil record and fossil and species discoveries could also explain that phenomenon, i.e. the seeming lack of transitional forms in Africa.

DISCOVERY AND GEOGRAPHIC RANGE

The earliest *H. ergaster* material is from the East Lake Turkana site of Koobi Fora in Kenya. Richard Leakey is credited with this 1.8 mya discovery. Other sites outside of Africa are contemporary with African sites, e.g. the 1.8 mya Dmanisi site in the Republic of Georgia and the 1.8–1.6 mya site of Modjokerto in Java. (Note: There are problems with the Javanese dates because the fossil-containing layers are not conducive to more reliable dating methods.) The almost complete Nariokotome or Turkana Boy (see Figure 28.2) from the West Lake Turkana region of Kenya was discovered in 1984 by Kamoya Kimeu and dated to 1.6 mya. The skeleton has been extremely important for reconstructing body morphology and limb proportions. The boy is thought to have been eight years old based upon tooth development patterns. He was formerly thought to be as old as 15, based on his height, stage of bone development, and hypothesized growth trajectories. However, dental calculations can accurately determine age due to the daily pattern of enamel deposition during tooth development. Scientists can count the microscopic, bead-like deposits that are laid down daily during the course of a tooth’s development. Once it was determined that he was only eight years old yet 5’3” tall, it was apparent that *H. ergaster* developed at a much faster rate, more like a chimp than a human. Had Turkana Boy lived to adulthood, he would have been over 6’ tall. His morphology was adapted to the hot, dry conditions in equatorial East Africa, i.e. tall and long-limbed, similar to modern peoples of the region.

Other African sites include the North African sites of Tighenif (formerly Ternifine and sometimes assigned to

Homo mauritanicus) in Algeria and Thomas Quarries and Sidi Abderrahman in Morocco; the East African sites of Konso Gardula and Omo in Ethiopia, Olorgesailie in Kenya, and Olduvai Gorge in Tanzania; and possibly the South African site of Swartkrans, although it is not universally accepted that *H. ergaster* was there.



PHYSICAL CHARACTERISTICS

H. ergaster exhibited robust craniofacial characteristics relative to modern humans, but overall we see the continued reduction in dentition and masticatory apparatus. Their brains were large, with a maximum cranial capacity of 1200 cc and a range of 800–1200 cc, based on the material from the three continents. However, the relative brain size of early specimens may not have been much greater than that seen in early *Homo*. They had fairly robust supraorbital and nuchal regions. The skull vault was long and low, termed **platycephalic**, with a low maximum width. Our vaults are much higher, and we have high maximum width, due to subsequent cerebral expansion. The shape of the vault in cross-section has been described as that of a turtle shell. *H. ergaster*, like all hominins before and especially the robust australopiths, exhibits postorbital constriction between the orbits and the cranial vault. Their temporal lines were more pronounced than ours (see Figure 28.4), indicating that they had more powerful jaw muscles and chewing capabilities. They did not have much of a forehead due to several of the aforementioned craniofacial characteristics. Their nasal bones suggest a human-like, projecting nose. This would have been adaptive in arid as well as cold conditions. In addition to warming and humidifying inhaled air, the moisture in warm exhaled air condenses on the cooler nasal membranes, resulting in water conservation. The jaws were somewhat prognathic in the alveolar region, i.e. the bone that houses the teeth, and the mandibles were robust. They lacked a chin, a characteristic seen only in anatomically modern humans.



Homo ergaster by Keenan Taylor.

Relative to *H. habilis*, long thought to be the species from which *H. ergaster* was derived, *H. ergaster* possessed a longer skull vault, a larger brain (however, see previous paragraph), a smaller temporal fossa (the opening formed by the zygomatic arch where jaw muscles pass through and/or attach), a shorter face, a larger nose, reduced dentition and jaw robusticity, and a heavier nuchal region.

Relative to Asian *H. erectus*, *H. ergaster* possessed a higher cranial vault, and the bones of the vault were thinner. They also did not exhibit the **sagittal keel** (see *Homo erectus*, Chapter 29) typical of the Asian form. However, the Koobi Fora specimen exhibits slight keeling (see Figure 28.4).



Koobi Fora *Homo ergaster*. Postorbital constriction. Slight keeling Temporal line. "Homo ergaster skull replica, World Museum Liverpool" by Reptonix is licensed under CC BY 3.0.

Postcranially, *H. ergaster* was very human-like. While the thorax may still have been somewhat conical, they had more of a waist, demonstrating an uncoupling of the lower limb from the torso. The small birth canal relative to adult brain size suggests a long period of postnatal brain growth, as seen in subsequent hominins, especially our own species. They were tall, achieving heights of over 6'. They were also more robust than premodern humans that, in turn, were more robust than modern humans. Males were 20–30% larger than females. While the lifespan tended to be short, some individuals lived to be 50 to 60 years of age. There was high infant mortality, with 40% of fossil remains estimated to be less than 14 years of age.

Review of Primitive Characteristics

Retain:

- Initially brain possibly no larger than early *Homo*.
- Some robusticity in cranium and face.
- Supraorbital and nuchal tori.
- Postorbital constriction.
- Low forehead.
- Conical thorax.

Relative to later hominins:

- Platycephalic skull vault with low maximum breadth.
- Pronounced temporal lines.
- Alveolar prognathism.
- Large teeth but smaller than previous species.
- No chin.

Review of Derived Characteristics

- Protruding nose.
- Postcranially robust.
- Tall with long legs.
- Development of waist (decoupling between torso and lower limb).

ENVIRONMENT AND WAY OF LIFE

The environment of East Africa during the Pleistocene was hot and arid. Savannas had expanded and forests had become increasingly fragmented. There was increased volcanic activity in the Great Rift zone, and that is one hypothesis as to why at least a portion of the population moved out of the area. It is of great interest as to how and why *H. ergaster* (or a predecessor) first left East Africa. The “how” is not as difficult as the “why.” While they may have crossed the Red Sea, they could also have come up through the Nile Valley and exited Africa across the Arabian land bridge that was exposed at the time. As to why they left, there are a variety of ideas that are not mutually exclusive. They may have ventured farther and farther due to (1) competition for resources with their own or other species of hominins or non-hominins; (2) local resource depletion; (3) similar environment (there is speculation that they were a grassland species that followed African grasslands into West Asian steppes, through the Indian subcontinent, and southeast to Indonesia); (4) following herd animals north and out of Africa; and/or (5) the aforementioned volcanic activity.

While there is debate as to whether the various “*erectus*” species hunted large game, it is not likely, since they lacked weaponry. It is generally accepted that they were mobile scavengers and foragers that hunted opportunistically. They certainly would have been capable of taking small prey and older and/or injured animals. Faunal remains at the Zhoukoudian, China, site consisted of deer, elephant, rhino, and beaver remains, but the bulk of the animal matter in their diet is thought to have come from smaller animals, such as rodents, hedgehogs, hares, and frogs, as well as ostrich eggs. However, Bunn and Gurtov (2014) have analyzed faunal remains at the Zinj FLK site in Olduvai Gorge, Tanzania (1.8 mya) and concluded that the high percentage (72%) of prime-aged large prey (especially bovids with weights of 250–750 lb) conforms solely to hominin hunting patterns, versus accidental deaths or carnivore kills. Thus at least some *H. ergaster* are thought to have been practicing ambush hunting and were therefore big-game hunters.



Acheulian hand axe. "Bifaz en mano" by José-Manuel Benito Álvarez is licensed under CC BY-SA 2.5.

While nomadic, they are thought to have stayed in an area for at least short periods of time, relative to past species. Early *H. ergaster* is associated with the Oldowan technology, and that is the technology that they took with them out of Africa. *H. ergaster* subsequently invented a tool tradition, termed **Acheulian**, that first appears in the archaeological record at 1.4 mya (newer data suggests possibly as early as 1.7 mya) and lasted to as late as 115 kya in some areas. The latter industry spread throughout Africa and as far east as the Indian subcontinent and west to Western Europe. It involved the use of better stone resources and tools that were more refined and standardized than in the Oldowan tradition. The most representative tool was a bifacially worked (shaped on both sides) hand axe in the shape of a teardrop (see Figure 28.5). The tool manifests what is called a "target design," in that the manufacturer knew what he or she was making and followed standardized steps in shaping the core into the resulting tool form. Once the core was prepared with the use of a stone hammer, the next step involved a "soft hammer" technique (see Figure 28.6). This required the use of a bone or antler hammer that could more carefully control the size and shape of the flakes to be removed on either side of the axe as it was shaped. Sharper and straighter edges resulted from the technique. The hominins had different tools for different purposes. The categories of tools included hand axes, smaller flake tools, choppers, picks, cleavers, and some bone tools. They would likely have been used to kill; butcher; scrape and cut hides; shape wood, bone, antler, and stone; and harvest and process plant foods.



Soft hammer percussion. “Soft Hammer” by ZenTrowel is in the public domain.

It would have been necessary for *H. erectus* to have had some sort of body covering prior to moving north into colder regions of Eurasia. There is some evidence to support *H. erectus*'s use of fire, but it is scant. However, even in later species wherein we know they had fire, such as *H. heidelbergensis* and *H. neanderthalensis*, there are fewer hearths apparent at archaeological sites than would be expected.

It was previously believed that the *erectus* grade lacked the technology to cross open water and therefore were limited to land travel. However, the discovery of a site dated to >8 kya on the island of Flores suggests that early *H. erectus* were capable of crossing fairly sizeable stretches of open sea. It is thus possible that *H. ergaster* may have rafted across the Red Sea to the Arabian Peninsula or across the Mediterranean to Gibraltar or Italy (via Sicily) during periods of lower sea levels when much of the earth's water was tied up in ice.

While it is likely that *H. ergaster* and related species had some complex form of communication, due to their advanced cultural achievements, it is not known whether they had speech or language similar to our own. They possessed the arched palate, flexed cranial base, and cerebral centers that are necessary for speech production and comprehension. However, Turkana Boy had small intervertebral foramina (the openings in between the vertebrae where the spinal nerves exit the spinal cord) in the thoracic region. It is thus thought that they may not have had the necessary motor function for controlled breathing and speech. However as mentioned in the section on *Homo habilis* (Chapter 23), I believe the standardized nature of the Acheulian tool industry demonstrates active teaching and thus theory of mind that in turn assumes some sort of language.

29. Homo erectus

Homo erectus (1.8 mya)

(“same” / “upright”)



Drawing of Trinil material. “*Pithecanthropus-erectus*” by 120 is in the public domain.

SITES

Java: Trinil, Modjokerto, Sangiran, Ngandong

China: Zhoukoudian, Taiwan, and sites in Yunxian, Hexian, and Lantian counties

India: Narmada

Turkey: Kocabas

PEOPLE

While there are many people associated with *Homo erectus*, I have listed a few of the historic names.

Java: Eugène Dubois

China: J. Gunnar Andersson, Davidson Black, Franz Weidenreich

INTRODUCTION

Homo erectus is the genus and species combination that was retained for all mainland Asian, Taiwanese, and Javanese fossil material.

PHYLOGENY

The most popularly held notion is that *Homo erectus* is derived from *H. ergaster* or a pre-*ergaster* form that “quickly” moved out of Africa into Eastern Europe and Southeast Asia. However, *H. georgicus* is another possibility for the ancestor of *H. erectus*.

DISCOVERY AND GEOGRAPHIC RANGE

Eugène Dubois discovered the first *H. erectus* material at the Trinil site (see Figure 29.1) on the Solo River in Java in 1891. While there are problems with the dates, the oldest material from the Javanese site of Modjokerto may be “contemporary” with African and Georgian material at 1.8 mya. Other famous Javanese sites are Sangiran, Ngandong, and Trinil. Java is part of the Sunda shelf, and when initially colonized by *H. erectus*, it was connected to mainland Asia (see Figure 29.2). After reaching Java and possibly other areas of Southeast Asia, later groups of *H. erectus* moved north into China. The earliest Chinese fossils are dated to 1 mya. First assigned to the genus *Sinanthropus* (“Chinese man”), the material was later included in our own genus after Franz Weidenreich pointed to the similarities between the various assemblages of *erectus*-like fossils and other extinct and modern humans. The first fossils were discovered at the now famous site of Zhoukoudian (formerly Choukoudian), near Beijing (formerly Peking and hence the term, “Peking Man”). The local people called them “dragon bones” and were using them for medicinal purposes. Material from Zhoukoudian spans a time period of over 200,000 years, from 460 to 230 kya, with three distinct cultural periods thought to be in evidence.

One of the great mysteries of paleoanthropology surrounds the Zhoukoudian material. Weidenreich and his predecessors, Davidson Black and J. Gunnar Andersson, had amassed an unprecedented amount of fossil material from the site. Due to the imminent Japanese invasion, Weidenreich packed up the fossil material in 1941 with the intent of having it shipped to the United States. However, the material disappeared, and all that remains are Weidenreich’s notes, drawings, and some casts of the original fossils.

Other Chinese sites are found in the counties of Lantian, Yunxian, and Hexian. A new discovery on the island of Taiwan has been linked to *H. erectus*, with the closest resemblance to the Hexian remains (Chang et al. 2015). Finally, the Narmada site in India has been a topic of debate for a long time but it has now been decided, at least by a portion of the paleoanthropological community, as being *Homo erectus*.



Sundaland (northwest of the Wallace Line). “Map of Sunda and Sahul” by Maximilian Dörrbecker is licensed under CC BY-SA 3.0.

PHYSICAL CHARACTERISTICS

While many of the physical characteristics of *H. erectus* are similar to *H. ergaster*, the Asian species is unique in a number of ways. Asian forms exhibit a thickening along the sagittal suture, termed a sagittal keel. The keel gives the skull a pentagonal shape in cross-section. It is unknown whether the keel served a function.



Homo erectus by Keenan Taylor.

Their incisors were shoveled, an adaptation that increases the stress resistance of teeth, especially when using them as tools. The molar enamel was characterized by a unique wrinkling pattern. Both of those dental characteristics are found in modern people of Asia and Asian ancestry and are interpreted by some scholars as evidence of regional continuity; in other words, there was a gradual evolution from *erectus*-like forms through archaic human populations and into modern populations in multiple areas via gene flow.



Homo erectus: Peking Man by Keenan Taylor.

Review of Derived Characteristics

- Sagittal keel.
- Shoveled incisors.
- Wrinkled molar enamel.

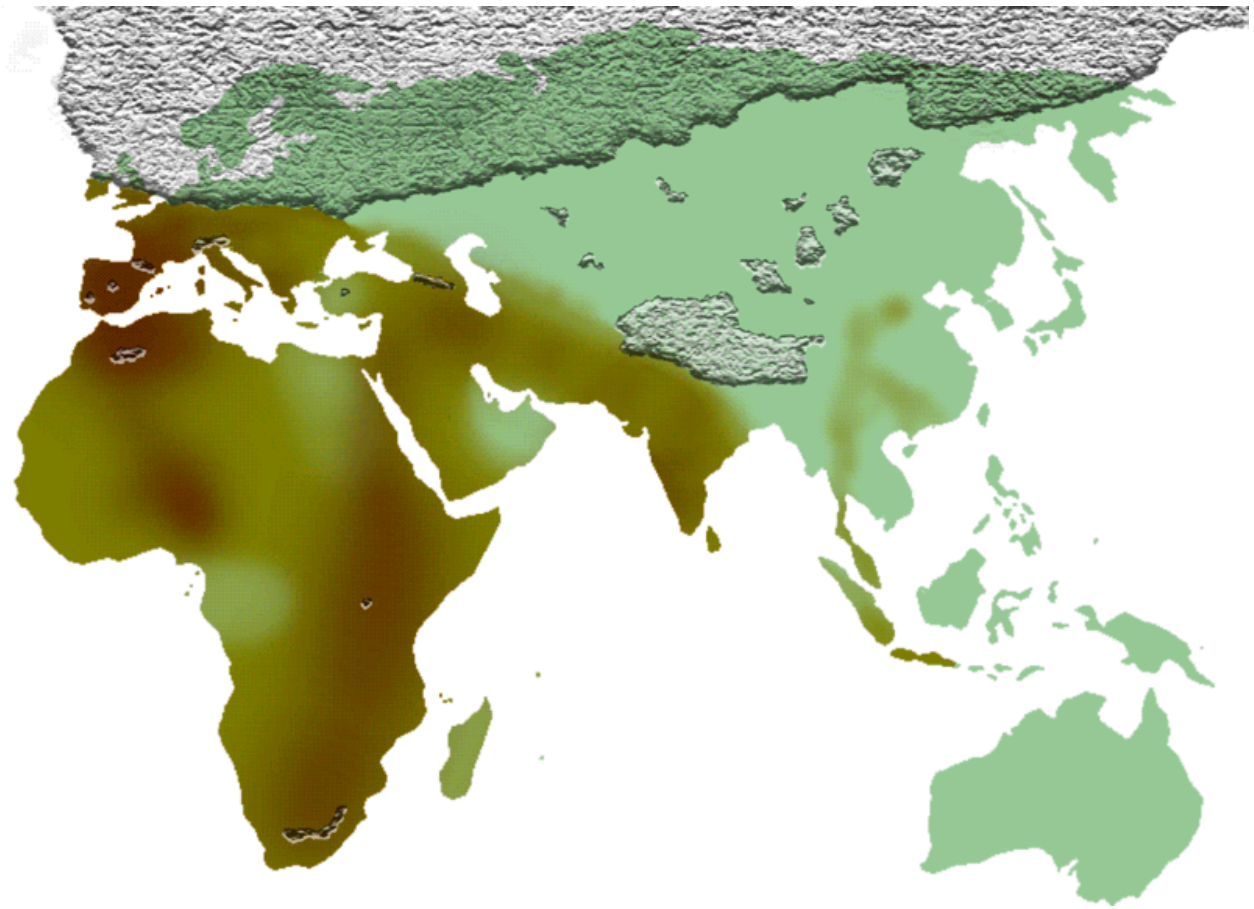
ENVIRONMENT AND WAY OF LIFE

Javanese sites in the early Pleistocene would have been conducive to tropical-adapted animals like *Homo erectus*. The area was part of the land bridge that was exposed beginning ~2.5 mya, making it accessible by land. Pleistocene Java was a mix of environments consisting of a variety of forest types, freshwater lakes and rivers, brackish marshes, and grasslands (Blain 2012).

At the time of *H. erectus* occupation, the site of Zhoukoudian, China, was in a transitional zone between temperate steppe and boreal forest. It would thus have been seasonally cold and would likely only have been habitable during the warmer months.

Culturally and technologically, Asian *H. erectus* are thought to have been somewhat similar to African *H. ergaster*. One of the key differences is the fact that the Acheulian industry never made it to Asia. The earliest inhabitants of Asia carried with them the Oldowan tool tradition, but the inventors of the Acheulian tradition apparently never followed. On maps, the **Movius Line** (see Figure 29.5) demarcates the border between the two tool traditions during the Pleistocene. It has been suggested that bamboo would have been a suitable material for making tools, which could explain the paucity of stone tools found.

Populations of *H. erectus* survived in Asia for much of the Pleistocene Epoch. Recent redating of the Javanese site of Ngandong has yielded dates as recent as 53–27 kya. Even more surprising is the recent discovery of dwarfed hominins on the island of Flores, termed *H. floresiensis*, that have been dated to 18 kya. *H. floresiensis* is thought to be descended from a population of *H. erectus* that adapted to limited island resources by becoming dwarfed in size.



Movius Line: color change delineation extending from Eastern Europe to northeast India. "Biface Extension" by José-Manuel Benito Álvarez is in the public domain.

30. Homo georgicus

Homo georgicus (1.8 mya)

(“same” / “Georgia”)



Reconstruction of *Homo georgicus*. “*Homo georgicus*” by 120 is licensed under CC BY-SA 3.0.

SITES

Dmanisi, Georgia

PEOPLE

Leo Gabunia, Yekva Abesalom, David Lordkipanidze

INTRODUCTION

Located in the southern Caucasus region of the Republic of Georgia (see Figure 30.2), Dmanisi is the only known site for the geographic species *Homo georgicus*, of the *erectus* grade. Some treat it as a subspecies of *Homo erectus*, *H. erectus georgicus*, while others attribute it to *H. erectus*.

PHYLOGENY

H. georgicus is dated to the same time as the earliest African material at 1.8 mya. It is thus thought to be (1) closely related to or possibly a descendent species of *Homo ergaster* or (2) possibly the ancestor of *H. ergaster* and Asian *Homo erectus*.

DISCOVERY AND GEOGRAPHIC RANGE

Leo Gabunia and Vekua Abesalom discovered the site and first reported on the hominin fossil material. Beginning in 1991 and continuing to the present, David Lordkipanidze and his team have recovered teeth, multiple skulls, and numerous postcranial remains. A partial skeleton that was discovered in 2001 was thought to be more primitive than other *erectus*-grade material, and there was speculation that *H. habilis* may have preceded *H. ergaster* out of Africa, where it then evolved into an intermediate form. Since that time, researchers have come to believe it to be a more a primitive form of the *erectus* grade versus *H. habilis*.

The site has an interesting history (see Figure 30.4). The area has been settled since the Bronze Age. In the 6th century, an orthodox Christian cathedral was built on the site. By the 9th century, the region was under Arab rule. Because of its location on two important trade routes, by medieval times it had become an important commercial center. It was conquered by the Seljuk Turks in the 11th century and later liberated by Georgian kings. The area was then attacked by the Turkomans in both the 14th and 15th centuries, from which it never fully recovered, in terms of its regional importance and economic development (Wikipedia contributors 2015b).



Dmanisi site. "GeorgieKaart met Dmanisi" by Rasbak is in the public domain.

PHYSICAL CHARACTERISTICS

H. georgicus exhibited a mix of primitive and *erectus*-like characteristics. They had small, robust skulls and habiline-like, prognathic faces (see Figure 30.3). Their upper limbs were australopith-like, while their spines and lower limbs were more modern. The cranial vault for one of the four adult skulls measured only 546 cc. Their

molars were large, and tooth microwear suggests that they ate tough, fibrous plant foods and thus had a low-quality diet. Their canines were surprisingly long.



Cast of *Homo georgicus*. "Homo Georgicus IMG 2921" by Rama is in the public domain.

Review of Primitive Characteristics

- Robust skull.
- Small brain.
- Prognathic face.
- Large molars and long canines.

Review of Derived Characteristics

- Human-like spine and lower limb.



Dmanisi castle ruins with archeological site in background (under the white roof). "Ruins of Dmanisi Castle" by Larry V. Dumlao is licensed under CC BY-SA 4.0.

ENVIRONMENT AND WAY OF LIFE

The environment at the time when *H. georgicus* lived in the area is thought to have been a mosaic of forest and steppes. A great many Oldowan tools and **debitage** (i.e. small chips of stone that are byproducts of tool manufacture) were found at the site, along with faunal remains. Due to their australopith-like upper limb morphology and the dangerous predators at the site, there is speculation that they may have slept and foraged in trees (de Lumley et al. 2005).

Of great interest is an older edentulous male. The tooth loss was antemortem because the alveolar bone had been resorbed, showing that he lived for quite a while after he began losing his teeth (de Lumley and Lordkipanidze 2006). He would likely have needed care during the intervening years, and his family or group-mates must have helped and supported him. This would be the earliest known evidence for **kin selection** and/or **reciprocal altruism**, respectively. Kin selection involves incurring a cost to oneself in order to benefit relatives, thus increasing their survival and propagating your genes because they share a portion of your genes in common. Reciprocal altruism is basically tit for tat. It explains why we will help nonrelatives. During our long hominin history prior to agriculture and sedentism, our ancestors lived in small bands. They were related to the members of their groups by blood or marriage. If Individual A incurred a cost to help a nonrelative, Individual B, there is a good chance that Individual B may have been around at a future point in time when Individual A needed help. Genes involved with those cooperative behaviors could thus have spread via natural selection. We are, and past hominins were, cooperative.

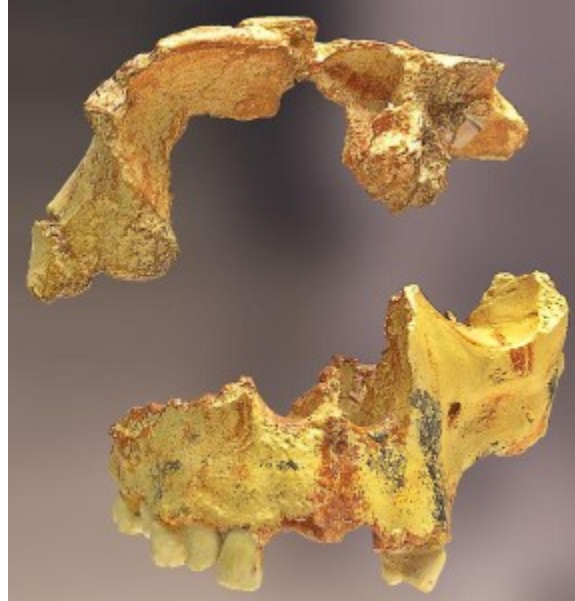


Homo georgicus by Keenan Taylor.

31. Homo antecessor

Homo antecessor (1.2 mya)

(“same” / “predecessor” or “pioneer”)



Incomplete Homo antecessor skull from Gran Dolina, Spain. “Homo antecessor” by José-Manuel Benito is in the public domain.

SITES

Gran Dolina and Sima del Elefante, Spain

PEOPLE

Eudald Carbonell, Juan Luis Arsuaga, and J. M. Bermúdez de Castro

INTRODUCTION

Until the recent discovery of hominin fossils dating to over 1.2 mya in the Atapuerca Mountains of Spain, the earliest known fossil material from the area was no more than 800 kya. The 800 kya material was assigned the

taxonomic designation of *Homo antecessor*, or “Pioneer Man,” as the first hominins to have ranged into Western Europe.

PHYLOGENY

Since its discovery, researchers have speculated that *Homo antecessor* was descended from a more derived form of *H. ergaster* that may have crossed the Mediterranean Sea from North Africa during a period of lowered sea levels. Now that the geological clock has been pushed back 300 kya, it is thought that they may have traveled through the Levant (i.e. the Eastern Mediterranean region). What is not known is whether the evolutionary event took place in Europe or North Africa. As far as descendant species, *Homo antecessor* is one contender for the ancestor of *Homo heidelbergensis* that in turn is thought to have given rise to neandertals and modern humans.



Homo antecessor by Keenan Taylor.

DISCOVERY AND GEOGRAPHIC RANGE

The species was discovered by Eudald Carbonell, Juan Luis Arsuaga, and J. M. Bermúdez de Castro. The first site to yield fossil material was the Gran Dolina site (see Figure 31.4) in the Atapuerca mountain range in Spain. Dated to 900 kya, the site has yielded both *H. antecessor* and *H. heidelbergensis* material. Eighty fossils from six

individuals were recovered. It is of interest that much of the fossil material is immature and exhibits cut marks that may indicate that they were victims of cannibalism.



“Homo antecessor moves to Spain” by Keenan Taylor.

The earliest *H. antecessor* site is Sima del Elefante (“Pit of the Elephant”). Dated to 1.2 mya, only a handful of fossils have been recovered from the site.

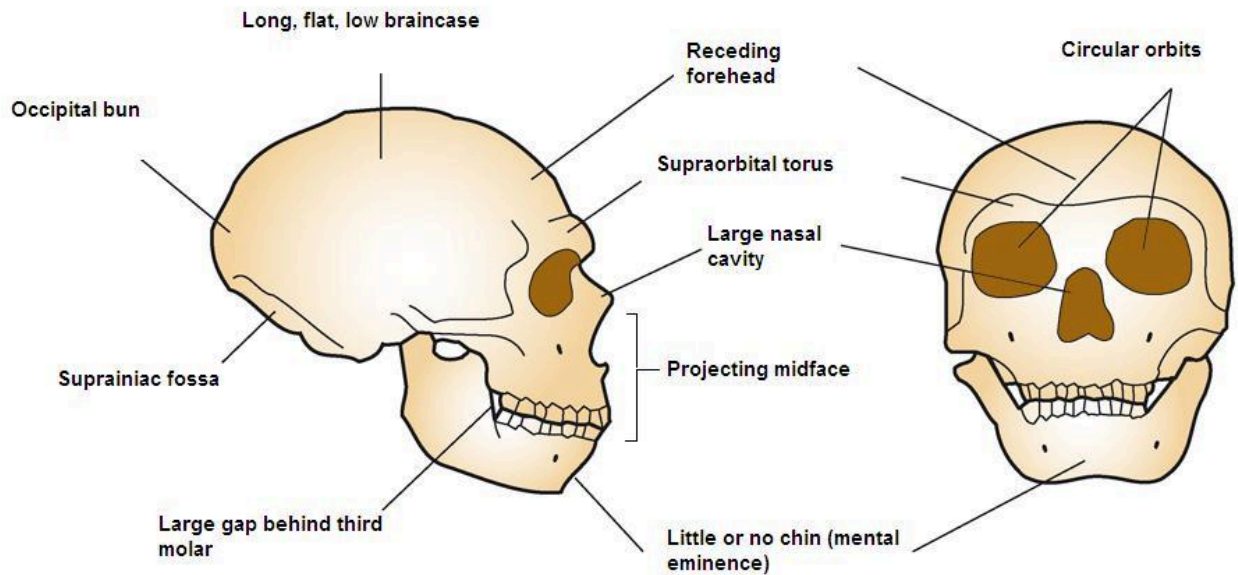
In addition to other sites in Spain, tools and footprints have been found in Happisburgh, England and Ceprano, Italy (also known as *Homo cepranensis*, some consider it more closely related to *H. heidelbergensis*).



Gran Dolina site. “Gran Dolina 2012 (Sierra de Atapuerca)” by Mario Modesto Mata is licensed under CC BY-SA 2.0.

PHYSICAL CHARACTERISTICS

The 800 kya *H. antecessor* material was more derived than earlier *erectus* forms, possessing a larger brain (1,000–1,150 cc) and a more modern skull and face. They had low foreheads and possessed an **occipital bun** (a bun or chignon is the hairstyle wherein one winds long hair into a doughnut shape on the top or back of the head), as did neandertals (see neandertal features in Figure 31.5). It has been suggested that the purpose of that posterior protrusion is to balance the weight of the anterior portion of the skull and face. Based upon cranial anatomy, they are thought to have been capable of detecting the same range of sounds as modern humans and were possibly right-handed. They were almost as tall as modern humans at 5.5–6' (1.6–1.8 m), with males weighing ~200 lb (90 kg).



Neandertal cranial characteristics. "Neanderthal cranial anatomy" by Jason Potter is licensed under CC BY-SA 2.5.

Review of Derived Characteristics

- Increased encephalization.
- Occipital bun.
- Tall like Turkana Boy.

32. Homo floresiensis

Homo floresiensis (74–12 kya)

(“same” / Flores)



By
Momotarou2012
http://commons.wikimedia.org/wiki/File:Homo_floresiensis_Restoration_model.jpg

SITES

Liang Bua cave, Flores, Indonesia

PEOPLE

Mike Morwood



Liang Bua Cave. “Homo floresiensis cave” by Rosino is licensed under CC BY-SA 2.0.

INTRODUCTION

The material assigned to the species *Homo floresiensis* comes only from the cave site of Liang Bua (see Figure 32.2) on the island of Flores in Indonesia (see Figure 32.3). Because of its diminutive size, the new species took the world by storm when it was discovered in 2003 by Mike Morwood and his team. While tools attributed to the species have been dated to almost 100 kya, skeletal remains are dated to as young as 18 kya and as old as 95–74 kya (Brown et al. 2004).

Morwood et al. (1998) had previously discovered a much older site (840 kya) that they attributed to *H. erectus*, but no associated skeletal material was found. Thus the ancestor of *H. floresiensis* may have arrived much earlier.

PHYLOGENY

While there is controversy (see PHYSICAL CHARACTERISTICS below) surrounding this strange species, *H. floresiensis* is thought to have descended from a group of *H. erectus* that traveled across the sea from mainland Asia. Once there, they adapted to the island via a process known as **insular** or **island dwarfism**. Large mammalian

species that become isolated on islands tend to decrease in size over time (as opposed to reptiles and small mammals that may increase in size), as smaller individuals require less food and thus have a better chance of survival and reproduction, when faced with limited space and resources and low risk of predation. (However, komodo dragons were present.) A dwarf stegodon (a relative of the Asian elephant) also inhabited the island and served as a prey species, as evidenced by juvenile bones with signs of butchering. In addition, modern “pygmy” human groups inhabit tropical rainforests where small body size is thought to possibly be adaptive for traveling through the tangled interior. Though short, they have low mass relative to surface area and relatively long limbs and extremities just like tall peoples of East Africa (e.g. the Maasai), to reduce metabolic heat and maximize cooling via sweating. The hominins may have survived until 12 kya when a volcanic eruption may have caused their extinction, as well as that of the dwarf stegodon. Since Flores was not inhabited when discovered by Portuguese traders in the 15th century, they may never have coexisted with modern humans (Wikipedia contributors 2015c, 2015d).



Flores Island in red. “ID – Flores” by M. Minderhoud is in the public domain.

DISCOVERY AND GEOGRAPHIC RANGE

As mentioned, there is only one site on Flores where *H. floresiensis* material has been found, Liang Bua cave. Mike Morwood and his colleagues are credited with the discovery of this species that is so recent in time, the skeletal elements are not even fossilized (Brown et al. 2004)! Material from nine individuals has been recovered. The only complete skull, LB1, is from a 30-year-old adult female for which they have postcranial material as well. Nicknamed “The little lady of Flores” or “Flo,” she serves as the **type specimen** for the species (Brown et al. 2004)



Homo floresiensis. “*Homo floresiensis*” by Ryan Somma is licensed under CC BY-SA 2.0.

PHYSICAL CHARACTERISTICS

At only ~3.5' (1.06 m) tall and 35–79 lb (16–36 kg), LB1 is very small relative to *H. erectus*, falling at the low end of *H. habilis*. Even more incredible is her brain size of 380 cc. Yet her encephalization quotient is estimated at 2.5–4.6. When compared with the brains of *H. erectus* and *H. ergaster* at 3.6–4.3 and *H. habilis* at 3.6–4.3, her brain is not as small as it first appears. Other aspects of *H. floresiensis*'s morphology are primitive relative to *Homo* species, such as its australopith-like hip and limb characteristics, especially in the shoulder and wrist. Craniofaciodental characteristics (see Figure 32.4) are consistent with *Homo* status, most closely aligning with *H. erectus*, including multiple mental foramina (i.e. small holes in the mandible through which multiple branches of the trigeminal nerve exit the bone to innervate the face), whereas we have only one (Brown et al. 2004; Morwood et al. 2005). Postcranially, the limb bones were robust and the feet were flat and relatively large (Jungers et al. 2008).

While body size is expected to decrease via insular dwarfism, brain size does not usually keep pace and thus can be used to support a case for dwarfism. Some researchers have argued that LB1 is a modern human with microcephaly, an ontogenetic disorder that results in an exceptionally small brain and cranium and greatly limited cognitive capabilities. However, primitive skeletal characteristics, the complexity of the cultural remains, and the size of an important association area of the prefrontal cortex (Falk et al. 2005) do not support the microcephaly argument.

Review of Primitive Characteristics

- Australopith-like hip and upper limb morphology, especially shoulder and wrist components.

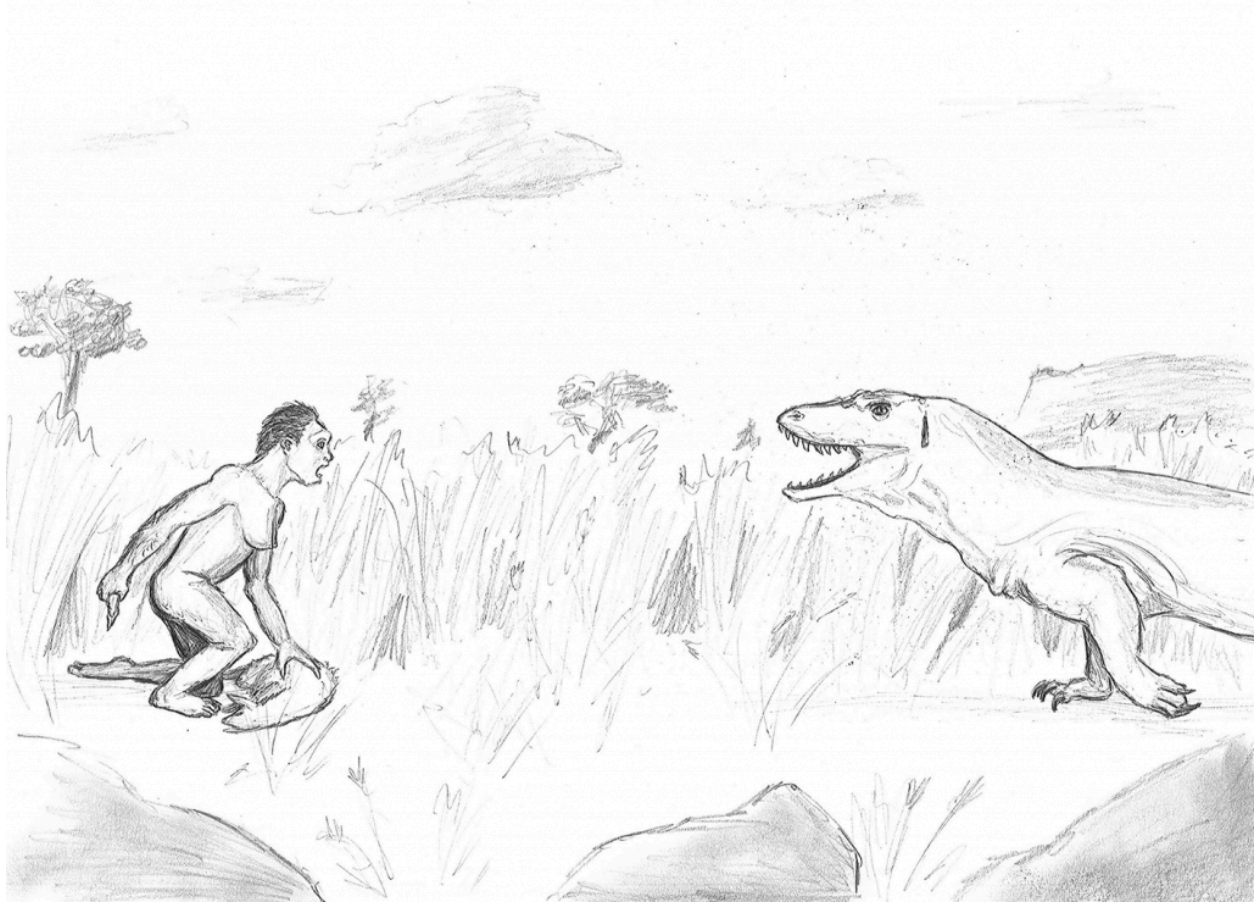
Review of Derived Characteristics

- Dwarfism.
- Brain reduction without apparent loss of cognition.

ENVIRONMENT AND WAY OF LIFE

Flores was primarily tropical forest during the time that *H. floresiensis* occupied the island. Tropical forests, while rich in biodiversity, are poor human habitats due to a low density of food species. In other words, on average you will find many different species of plants and animals per unit area but not very many of each. Compounded by the small area of the island, dwarfism and complex culture likely explain the survival of the species. They made and used tools, as evidenced by the presence of sharpened tools, prepared cores for the production of tools, debitage from their manufacture, anvils, etc., along with faunal remains from a variety of species, such as stegodon, komodo dragons, rats, and bats (Morwood et al. 2005). Their tools were small, compatible with their small body size. Burnt bones, fire-cracked rock, and a possible hearth consisting of a circle of fired rocks show that they made use of fire.

Large predators and scavengers like komodo dragons are known to “clean up” anything that dies, often without a trace. It is thus lucky that we have some remains of *H. floresiensis*.



Homo floresiensis: *Megalania* encounter by Keenan Taylor.

33. Homo heidelbergensis

Homo heidelbergensis (<600 kya)

(“same” / Heidelberg, Germany)



Model of *Homo heidelbergensis* head and shoulders. “*Homo heidelbergensis* adult male – head model – Smithsonian Museum of Natural History – 2012-05-17” by Tim Evanson is licensed under CC BY-SA 2.0<.

SITES

Europe:

Spain: Sima de los Huesos

France: Arago

Germany: Mauer, Steinheim, Ehringsdorf, Schöningen, Bilzingsleben

England: Boxgrove, Swanscombe

Italy: Ciampate del Diavolo (footprints)

Hungary: Vértesszöllös

Greece: Petralona, Apidima

Africa:

Morocco: Jebel Irhoud

Ethiopia: Bodo, Omo (Kibish Beds)

Zambia: Kabwe

Tanzania: Lake Eyasi, Laetoli (Ngaloba Beds)

South Africa: Florisbad, Elandsfontein

Asia:

China: Dali, Maba, Jinniushan

PEOPLE

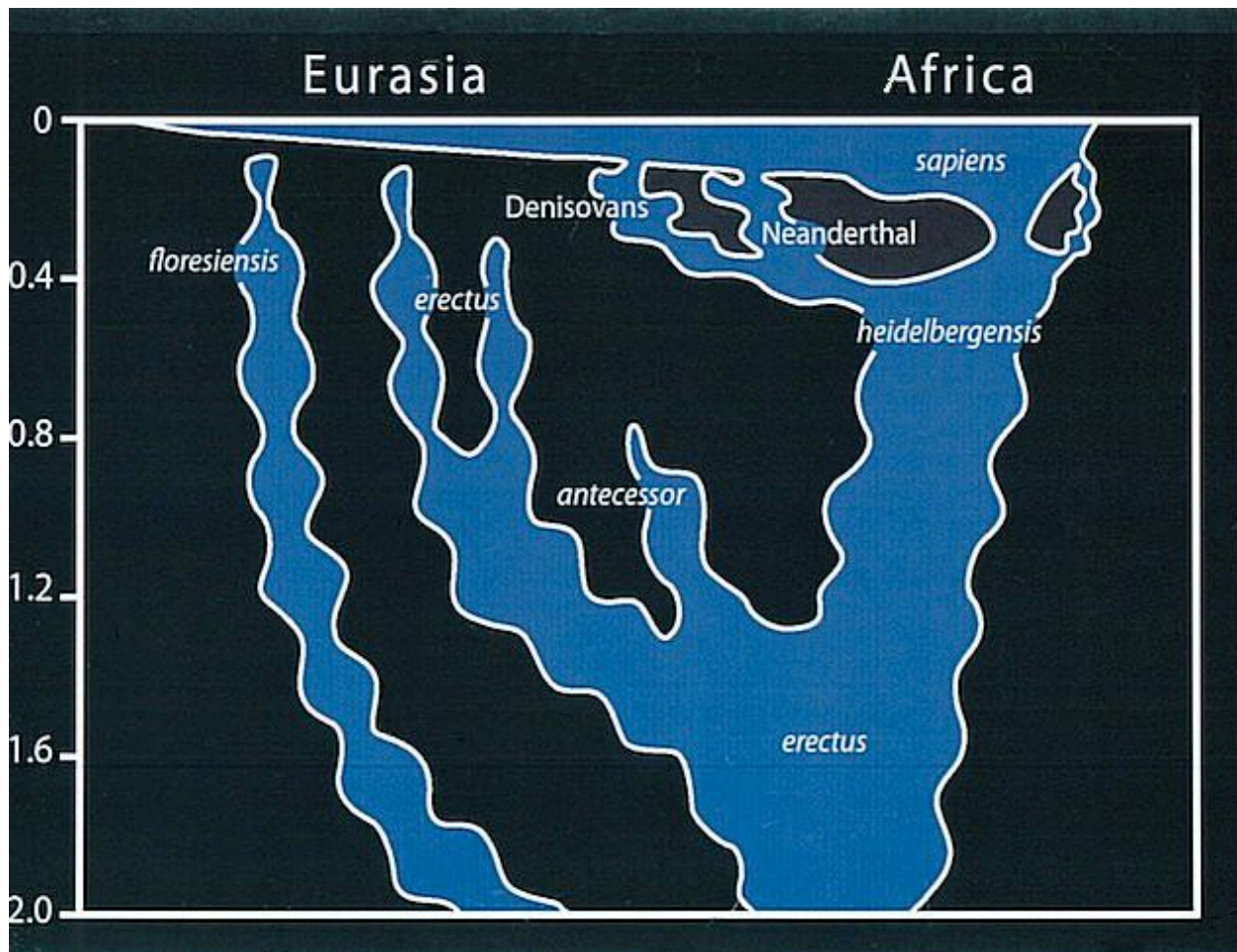
Otto Schoetensack and many more

INTRODUCTION

For many years, fossil material from ~500–200 kya from Africa, Asia, and Europe that was more human- or *sapiens*-like was included in our own genus and species but was distinguished as “Early Archaic” *Homo sapiens* (EAHS). There was much debate as to when to draw the line between more *erectus*-like forms and more *sapiens*-like forms. The prevailing view was that material on all three continents was descended from *H. erectus*. (The various geographic species distinctions for *H. erectus* had not yet come into use.) Again, this is referred to as the **Regional Continuity Model (RCM)** for the origin of modern humans. In this scenario, *erectus*-like forms on each of the continents slowly evolved into modern humans via gene flow between populations. This is in contrast to the **Recent African Origin (RAO)** model whereby modern humans evolved in Africa and moved out to eventually replace archaic forms elsewhere, e.g. *H. erectus* in Asia.

The RAO model has gained in popularity due to a combination of the reevaluation of fossil material and especially DNA methods aimed at evaluating genetic distance between species, in terms of number of years since divergence from a common ancestor. The material from Asia that had previously been assigned to EAHS has been relegated to *H. erectus*, with very little evidence for an intermediate form bridging the gap between *H. erectus* and AMH.

Fossil material from Europe and Africa that was formerly assigned to EAHS is now termed *Homo heidelbergensis*, with some researchers using *Homo rhodesiensis* for some of the African material. It is now well accepted that *H. heidelbergensis* was ancestral to both humans and neandertals (see Figure 33.2—note that in this scenario, *H. antecessor* is not considered to be ancestral to *H. heidelbergensis*).



Human phylogeny. "Homo-Stammbaum, Version Stringer" by Chris Stringer is licensed under CC BY-SA 3.0 DE.

PHYLOGENY

H. heidelbergensis is thought to have evolved from a more derived form of *H. ergaster*. Some researchers believe that the material from Tighenif (formerly Ternifine), Algeria, known by some as *Homo mauritanicus*, is a possible transitional form between the two species. Mandibles from Tighenif are very similar to the type specimen, the Mauer mandible (see Figure 33.3) from the Heidelberg area of Germany, from which the species name is derived. In addition to the material from North Africa, the oldest material is from the Bodo site in Ethiopia, dated to 600 kya. Thus while an African origin is favored, some believe that *H. heidelbergensis* is descended from *H. antecessor* in Europe. Whether *H. heidelbergensis* evolved in Europe or Africa, they had to have migrated from one continent to the other. Thus if *H. heidelbergensis* evolved in Europe from *H. antecessor*, a portion of the population migrated to Africa and evolved toward AMH, leaving some regional population of the remaining European stock to evolve into *H. neanderthalensis*. The other more popular scenario has *H. heidelbergensis* evolving in Africa from some descendant form of *Homo ergaster*. A portion of the population then emigrated to Europe and evolved into neandertals while a portion of the remaining African stock evolved toward AMH.

In addition, a new species of hominin is also thought to be descended from *H. heidelbergensis*. The **Denisovans** (see this chapter), as they have come to be known due to their discovery in the Denisova Cave in the Altai

Mountains of Russia, are thought to have branched off from the *H. heidelbergensis* lineage that led to neandertals. DNA analyses show that Denisovans interbred with neandertals, as well as the first wave of AMH that left Africa, possibly around 125 kya and subsequently settled Melanesia and Australia.



Type specimen: Mauer mandible. "Unterkiefer von Mauer (Replika)" by Gerbil is licensed under CC BY-SA 3.0.

Contrary new DNA evidence suggests that *H. heidelbergensis* branched off from some common ancestors prior to 800 kya and is thus not part of our recent lineage. *H. heidelbergensis* then divided into the neandertals and the Denisovan lineages, but interbreeding continued between them in areas of geographic overlap.

There is good evidence that *H. heidelbergensis* gave rise to neandertals. There are skulls from the sites of Erhingsdorf, Germany; Fontechavade, France; and Sima de los Huesos, Spain, that appear to be transitional in that they exhibit characteristics seen in neandertals, such as similar brow ridge morphology, enlarged facial sinuses, occipital bun, etc. It is rare in paleoanthropology to have such good support for continuity in physical characteristics between ancestor and descendent species. However, the fact that those species lived more recently in time and in developed and populated areas certainly helps, in terms of facilitating discoveries.



Homo heidelbergensis from Steinheim, Germany. “*Homo steinheimensis*, holotype” by Dr. Günter Bechly is licensed under CC BY-SA 3.0.

DISCOVERY AND GEOGRAPHIC RANGE

The earliest discoveries of *H. heidelbergensis* are from Germany. The type specimen was discovered in 1907 in Mauer, Germany. The oldest site is **Bodo**, Ethiopia (600 kya). There are numerous *H. heidelbergensis* sites in Europe (e.g. Steinheim, see Figure 33.4) that date from as early as 500 kya and range from Spain through Eastern Europe. The greatest number of individuals came from the **Sima de los Huesos (“Pit of Bones”)** (see Figure 33.5) site in the Atapuerca Mountains of Spain. Both *H. antecessor* and *H. heidelbergensis* sites in that area were discovered when a railway was built. The *H. heidelbergensis* remains were found in a deep chamber inside of a cave, hence the name, “Pit of Bones.” More than 32 individuals have been recovered, and most of them are juveniles. While there has been much speculation, the significance of this find in terms of cultural complexity (see ENVIRONMENT AND WAY OF LIFE below) remains elusive. There are a couple of sites in Asia that some researchers believe are also representative of *H. heidelbergensis*, including Dali, China. Sites in Africa (also referred to as *H. rhodesiensis*) include Jebel Irhoud in North Africa; Omo, Bodo, Nduetu, Eyasi, and Ngaloba in East Africa; Kabwe in Zambia; and Florisbad and Elandsfontein in South Africa.



Homo heidelbergensis from Sima de los Huesos, Spain. “*Homo heidelbergensis*-Cranium -5” by José-Manuel Benito Álvarez is licensed under CC BY-SA 2.5.

PHYSICAL CHARACTERISTICS

In general, *H. heidelbergensis* was less robust, both cranially and postcranially, than the *erectus* grade and more robust than AMH. There is intraspecific variability in craniofacial morphology, with some specimens being more robust and others more gracile. While this is not surprising, considering the temporal and geographic range for the species, it has led to disagreement as to how to define it.

H. heidelbergensis is primarily distinguished from *erectus*-like forms by its increased cranial capacity (1100–1400 cc—93% that of AMH) and more modern skull vault. Cerebral expansion, especially of the parietal lobes, led to increased cranial breadth in the superior aspect of the skull vault and thus a more vertically oriented skull. The occipital region is less angular due to reduced robusticity in the nuchal musculature. Some specimens have very pronounced brow ridges (see Figure 33.7) and some have speculated that those individuals represent males of the species. They share the presence of a canine fossa with AMH. The canine fossa is a depression above the canine on either side of the maxilla. The robusticity of their jaw morphology and tooth wear suggests that they were using their mouths and teeth as tools, for example, pulling meat off bones and working hides. Surprisingly, the middle ear bones were discovered for one specimen, and it could thus be determined that their hearing was comparable with our own (Martínez et al. 2004).



Homo heidelbergensis by Keenan Taylor.

Some *H. heidelbergensis* are considered to be transitional and exhibited characteristics seen in the subsequent neandertals. Their midfacial region was (1) prognathic with a corresponding large nose and (2) puffy due to large frontal and maxillary sinuses. Their zygomatics have a “swept back” appearance, and the posterior skull vault exhibited an occipital bun. The outer layer of their long bones (the cortical bone) was thick, and the interior medullary (marrow) cavity was narrow. The species was taller than neandertals, with males and females averaging 5' 9" (175 cm) and 5' 2" (157 cm), respectively. Average weights for males and females were 136 lb (62 kg) and 112 lb (51 kg), respectively (Smithsonian Institution 2015).

Review of Derived Characteristics

- Increase in brain size & complexity of skull architecture, and corresponding vault changes.
- Loss of angulation in occipital region.
- Canine fossa.

Review of Characteristics Inherited by Neandertals

- Midfacial prognathism and large nose.
- Puffy appearance to face due to large frontal and maxillary sinuses.
- “Swept back” zygomatics.
- Occipital bun.
- Thick cortical bone and narrow medullary cavity.



“Broken Hill Man” from Kabwe, Zambia (formerly “Rhodesian Man”). “Broken Hill Skull (Replica01)” by Gerbil is licensed under CC BY-SA 3.0.

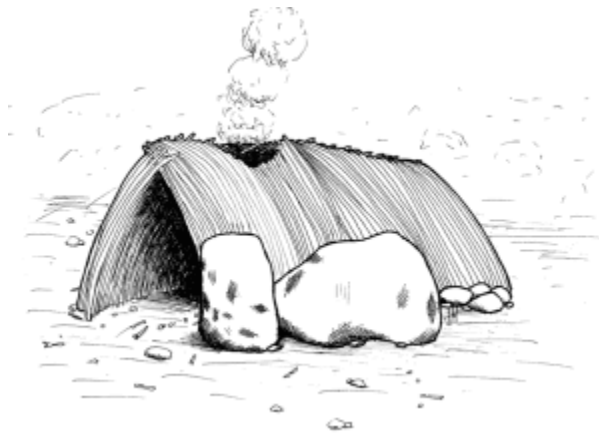
ENVIRONMENT AND WAY OF LIFE

The Bodo site was of course, close to the equator and hence warm. *H. heidelbergensis* moved into Europe during the Holstein interglacial period (400–300 kya) (Wikipedia contributors 2015e).



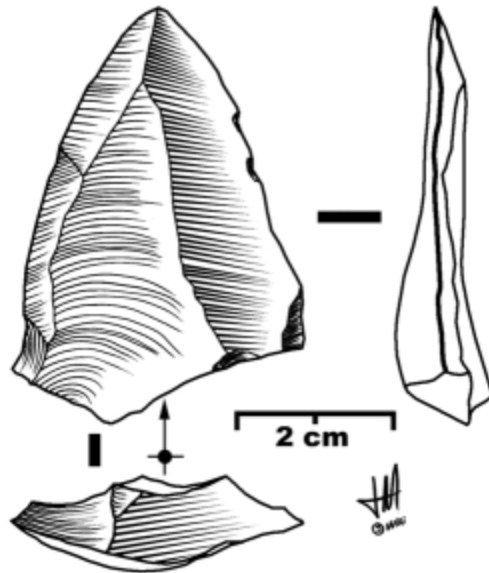
Homo heidelbergensis hunting by Keenan Taylor.

Like those species that preceded them, *H. heidelbergensis* were mobile foragers. They left evidence for both seasonal and differential use camps. In addition to using rock shelters and caves for shelter, they are the first species for which we have evidence of building free-standing structures. At the site of **Terra Amata** in the south of France, the living floors of free-standing structures have been excavated. It is thought that a group returned to the site annually for fishing and other subsistence activities and reconstructed their huts (up to 11 times) on the exact same site (see Figure 33.9). They are credited as having been the first to make the tools necessary for efficient fishing. Like past species, their big-game hunting capabilities are questionable. However, there is evidence that they may have ambushed large animals by forcing them off cliffs or cornering them in dead-end canyons. Support for ambush comes from faunal assemblages on the Channel Islands off the coast of France. The remains are from animals in prime condition, and the frequency of the various bones shows that the hominins were differentially removing the limbs and bringing them back to butcher at a home base. Javelin-type spears and thousands of faunal remains have been recovered at Schöningen, Germany. The spears were fire-hardened for strength and expertly weighted for flight, like modern javelins.



Hut design at Terra Amata. “Terra-Amata-Hut” by Locutus Borg is in the public domain.

While some tools from *H. heidelbergensis* are Oldowan-like, most are of the Acheulian tradition. The species is credited with inventing a more conservative method, termed the **Levallois technique**, for controlling flake shape and maximizing their yield from a core. Flakes could then be worked into a variety of tools. They could also shape the core in such a way that a point could be struck off that was sharp on all sides (see Figure 33.10). *H. heidelbergensis* were the first to make compound tools, i.e. tools with more than one component, such as hammers and stone-tipped spears. There is a great website demonstrating and describing tool production at <http://donsmaps.com/makingflinttools.html>, as well as an animated visual for the Levallois technique at http://en.wikipedia.org/wiki/Levallois_technique.



Levallois point. "Levallois point" by José-Manuel Benito Álvarez is licensed under CC BY-SA 2.5.

H. heidelbergensis is the first species for which there is ample evidence of the controlled use of fire, in that hearths have been found at several sites. In addition to the aforementioned inventions, a couple of novel cultural practices have been suggested for the species. They may have made and used furniture, such as seaweed beds and stone blocks, and there is some evidence of art or written communication in the form of arcs and angles and the use of ocher (mineral pigments). A fine pink quartz hand axe, nicknamed "Excalibur," was found among the bodies in the "Pit of Bones." Some researchers believe it is the earliest evidence of ritual associated with burial, in that the artifact was seemingly unused and manufactured from exotic stone. The seclusion of the bodies may also represent an attempt at keeping them from being ravaged by scavengers. All of these advancements and innovations are unequivocal support for the increase in cognition that resulted from the degree of encephalization and changes in brain architecture that are evident in the skull size and shape of *H. heidelbergensis*. Finally, if the new DNA evidence is correct and *H. heidelbergensis* branched off from our ancestry versus being our ancestor, the behavioral and cultural complexity apparent at *H. heidelbergensis* sites indicates that our common ancestor was cognitively advanced more than 800 kya!



Hand axe from Boxgrove, England. "Boxgrove handaxe" by Midnightblueowl is licensed under CC BY-SA 3.0.

34. The Denisovans

THE DENISOVANS

A New Species of Hominin

SITE

Denisova and Okladnikov Caves in the Altai Mountains of Russia

PEOPLE

Michael Shunkov and Anatoly Derevianko



Denisova Cave (approximate location indicated by arrow). “Russia edcp relief location map” by Uwe Dederling is licensed under CC BY-SA 3.0.

INTRODUCTION

In 2008, Russian scientists Michael Shunkov (paleontologist) and Anatoly Derevianko (archaeologist) discovered a terminal finger phalanx from a young girl, dubbed “X-woman,” in the Denisova Cave in the Altai Mountains of Russia (see Figures 34.1 and 34.2). The Denisovans, as they have come to be called, inhabited the cave by 50 kya.

PHYLOGENY

The phalanx was sequenced by Svante Pääbo’s lab at the Max Planck Institute, where it was determined to be from a new form of extinct hominin. Its ancestor is thought to have split from our own lineage by >800 kya, subsequently splitting into the Denisovan and neandertal lineages ~640 mya (Callaway 2013). The two resulting

lineages remained as genomically alike as two geographically distant modern human populations. Pääbo (2014) uses the example of Finns and the San people of South Africa. It is estimated that gene flow from neandertals to Denisovans was fairly low ($\geq 0.5\%$) and seemingly occurred only locally in the Altai region (Prüfer et al. 2013). What is even more interesting from our perspective is that Denisovans seem to have interbred with the first wave of AMH as they passed through southern Asia after leaving Africa. These humans already carried neandertal genes from having interbred with them. Thus modern human populations that have descended from those early humans (i.e. indigenous Melanesians, Polynesians, Australians, and some Filipinos) carry 4.8% Denisovan genes, along with the mean of 2.5% neandertal genes that all Eurasians possess, meaning that a total of $\sim 7\%$ of their genes are derived from extinct hominins! Genes for dark skin, hair, and eyes were present in the Denisovan genome and are present in modern Melanesians (Marshall 2013). This is fascinating from two perspectives. First, it is interesting that those ancestral characteristics survived in a modern population. Second, we now know something about what the Denisovans likely looked like. Wow!

The Denisovan-like genes that the rest of Eurasians possess may have been inherited from neandertals, due to their close genetic relationship with the Denisovans. It is of great interest that the genetic variability in one of our important immunological systems, the human leucocyte antigen (HLA) system, is probably due to interbreeding with neandertals. Half of the HLA variant genes, termed alleles, seen in Eurasian populations are derived from those two extinct species (Abi-Rached et al. 2011). What is fascinating is that those alleles likely conferred a selective advantage on some of our ancestors, and they thus survived in their descendants. It is likely that neandertals and Denisovans inherited the allele(s) from *H. heidelbergensis*, lending further support for the latter species having diverged from our lineage prior to the mutation(s) that led to the forms present in the former two species.

Finally, a variant of the EPAS1 gene in Tibetans has also been traced to the Denisovans. The allele is an adaptation to the hypoxic (i.e. low oxygen) conditions of high altitude. The allele affords those individuals with better oxygen metabolism capabilities (Huerta-Sanchez et al. 2014).

Mitochondrial DNA (mtDNA) from a 400 kya femur from the Sima de los Huesos site in Spain has been found to most closely resemble Denisovans (Callaway 2013). The site contains *Homo heidelbergensis* material, and if the leg bone is from an individual of that species, it will further muddy the phylogenetic waters. However, it must be remembered that mtDNA gives only maternal lineage information, and it is thus possible that the individual was not more closely related to Denisovans but that the mtDNA alleles were conserved in his or her lineage.

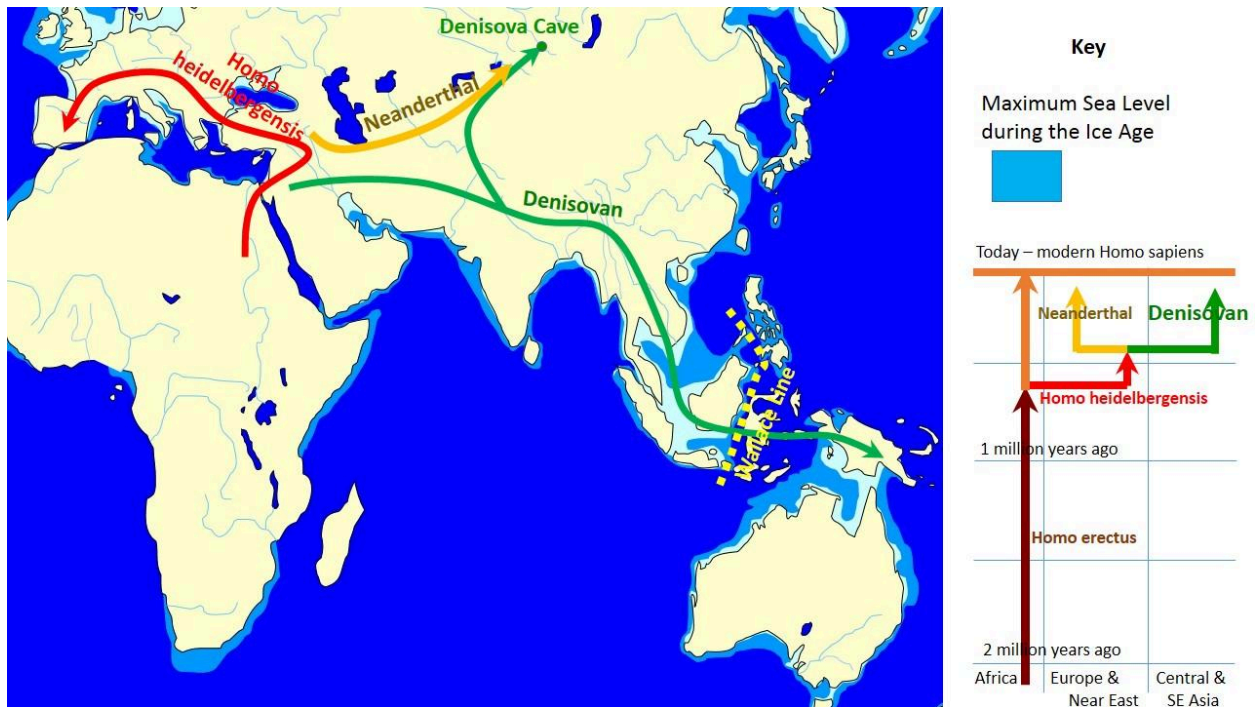


Denisova Cave. "Turist den-peschera" by ЧуваевНиколай at ru.wikipedia is licensed under CC BY-SA 3.0.

DISCOVERY AND GEOGRAPHIC RANGE

In addition to Denisova Cave, Shunkov and Derevianko also found bone fragments in the nearby Okladnikov Cave. They have since recovered two teeth and a toe bone.

The caves were also occupied by neandertals and humans at various times over the millennia. Prior to the discovery of neandertals in the area, it was thought that they ranged no farther east than Uzbekistan. This new discovery extends their geographic range by 2,000 km. The Denisovans also must have had a large geographic range, since they are thought to have bred with AMH as they passed through southern Asia (see Figure 34.3). It is amazing that for over 100 years, the only extinct hominins that we knew of in the northern hemisphere were the *erectus*-forms and neandertals and now, in just the last couple of years, we have two more, the Denisovans and the Red Deer Cave hominins. (Pääbo 2014, unless otherwise indicated.)



Possible routes taken by Late Pleistocene hominins. “Spread and evolution of Denisovans” by John D. Croft at English Wikipedia is licensed under CC BY-SA 3.0.

PHYSICAL CHARACTERISTICS

While there is not much to go on, the finger bone was broad and robust relative to modern humans and the molars were large with widely diverging roots, unlike the little or no space between neanderthal molar roots. The robusticity of the phalanges suggests that the Denisovans may have been morphologically similar to neanderthals (Reich et al. 2010).

ENVIRONMENT AND WAY OF LIFE

The environment of the area must have been at least seasonally cold. Mountains surrounding the area were covered with glacial ice during the Late Pleistocene (Lehmkuhl et al. 2011). However, it is possible that game may have been available year-round in the lower elevations. If large game migrated seasonally, then the hominins would have followed and thus would have only resided in the area when animals were on their northern grazing and birthing grounds.

Since *H. heidelbergensis* was cognitively and culturally advanced, the Denisovans were descended from them, and Denisovans interbred with neanderthals in the Altai region at some point(s) in time, it is likely that they all had similar behavior and culture. While complex tools and an ivory bracelet were found, it is not known whether they are attributable to the Denisovans. They are more likely AMH artifacts, as they are usually only found at AMH sites.

35. Homo neanderthalensis

Homo neanderthalensis (>300 kya)

("same" / Neander Valley, Germany)



Reconstruction of Neandertal at Neanderthal Museum. "Neandertaler reconst" by Stefan Scheer is licensed under CC BY-SA 3.0.

SITES

See "Neandertal sites" map, Figure 35.2

PEOPLE

Too many to mention (see text for some prominent researchers)

INTRODUCTION

One of the best known and most enigmatic of the archaic hominins were the neandertals, *Homo neanderthalensis*. Although *Homo neanderthalensis* was originally included in our own genus and species but

distinguished by subspecies status, i.e. *Homo sapiens neanderthalensis*, increasing evidence from DNA analysis suggests that the two lineages split sometime prior to 300 kya and, if new DNA evidence is correct, possibly prior to 800 kya. However, DNA evidence shows that they interbred, possibly as AMH migrated out of Africa one or more times or cohabited with neandertals in the Middle East. Eurasians and Australasians carry, on average, 2.5% neandertal genes. Thus while the RAO model for the origin of AMH is still favored and neandertals are considered a separate species, at least some populations were capable of interbreeding and thus were not true biological species at that point in time and geographic space.

The material that became the holotype for the species was discovered in the **Neander Valley** near Dusseldorf, Germany. The German word for valley is “thal,” and the “h” is silent. The “h” has been dropped for the common name in some sources. I can only imagine that someone got tired of people pronouncing the “th” and decided to head up a campaign to put a stop to it!

PHYLOGENY

There are two possible scenarios for the origin of neandertals and AMH. The first is based on fossil evidence and the second on DNA. The interpretation of the fossil record suggests that both species are derived from *H. heidelbergensis*, which in turn likely evolved from a derived form of *H. ergaster* (possibly *H. mauritanicus*) in Africa. At some point prior to 500 kya, *H. heidelbergensis* split into the AMH and neandertal lineages.

The latest genetic evidence supports a split between the AMH and neandertal lineages prior to 800 kya in Africa. The branch leading to neandertals and Denisovans is then considered *H. heidelbergensis*. The Denisovans and neandertals then split ~640 kya. However, localized groups continued to interbreed.

It is refreshing to learn that populations of hominins have been interbreeding and maintaining or forming genetic relationships since the beginning of “our” time. We modern humans are much more closely related to one another than were those ancient hominin “species” and yet some of us do not see ourselves in others due to physical differences that mean no more than that we went different ways at different times and adapted to different environments.

Regardless of the neandertal/human/Denisovan phylogeny, a group of *H. heidelbergensis* moved into Western Europe, where a localized group then evolved into the neandertal lineage <300 kya. Transitional forms can be seen in several locales in Western Europe, especially Spain, France, and Germany.

As Pleistocene Europe became colder, neandertals adapted to the harsher conditions. The neandertals from Western Europe, with their stunted and cold-adapted bodies, are known as the “Classic” neandertals, as distinct from those to the east and southeast that retained a more gracile morphology. Dates for the Classic neandertals range from 75 to <30 kya. Figure 35.2 shows neandertal sites in Eurasia.

DISCOVERY AND GEOGRAPHIC RANGE



Neanderthal sites. "Carte Neandertaliens" by 120 is licensed under CC BY-SA 3.0.

The earliest recognized discoveries were in Belgium and Gibraltar. The next discovery was the Neander Valley remains, which lent the name to the species. Fossil sites are ubiquitous in Western Europe, with the majority located in well-watered river valleys of France. More than 200 sites fall within a 20-mile radius of Les Eyzies, France. There are also sites in Germany, Belgium, Spain, Portugal, and Italy. Some of the more famous sites are La Chapelle-aux-Saints, La Ferrassie, and St. Césaire in France; the aforementioned Neander Valley in Germany; and Zafarraya Cave in Spain. The Chapelle-aux-Saints site has played a key role in the development of the myth of the neandertals as hulking, barbaric cavemen. The remains of an approximately 40-year-old male (see Figure 35.3) were excavated in 1908 and analyzed by Marcellin Boule, who characterized the individual as primitive, brutish, and hunched over. Researchers later realized that the adult was afflicted with arthritis, which accounted for his posture. While we cannot know how neandertals behaved relative to ourselves, they achieved a theretofore unprecedented level of cultural and technological complexity. The derogatory characterization stuck for many years until researchers realized just how much those ancient “peoples” had accomplished, such as intentional burial of their dead.



“Old Man” of La Chapelle-aux-Saints. “*Homo sapiens neanderthalensis*” by Luma04 is licensed under CC BY-SA 3.0.

From their supposed Western European origin, they spread east into the Middle East and as far east as Uzbekistan and northeast to Russia, in the area of the Denisovans. Some researchers do not accept that the nine-year-old boy at the site of Teshik Tash, Uzbekistan is neandertal, but rather they argue that he is AMH.

Non-classic neandertal sites are found in Croatia, the Czech Republic, Hungary, Syria, the Republic of Georgia, Russia, the Ukraine, Iraq, Uzbekistan, and Israel. Famous sites include Krapina and Vindija in Yugoslavia; the cave sites of Kebara, Amud, and Tabun in Israel; Shanidar in Iraq; and the aforementioned Teshik Tash in Uzbekistan.

The Israeli sites have been of interest for decades because they are seemingly contemporary with nearby AMH sites. There has been much speculation as to the nature of interactions between the two species. One theory is that when ice sheets blanketed much of Europe, the neandertals moved down into the Middle East along with other animals. The fact that AMH reached the Middle East by 120 kya but never entered Europe until after 40 kya suggested to some that the neandertals “held” Europe, preventing the encroachment of AMH. When moving down into the Middle East, neandertals may have pushed resident AMH out of the area. During subsequent warmer periods, AMH may have moved back into the area following the retreat of the neandertals to more northerly destinations. This idea of trading places has now been superseded by the idea of contemporaneity and interbreeding, at least by some groups at some point(s) in time.

Figure 35.2 illustrates the broad geographic range of the neandertals. It is likely that during glacial advances, populations moved south so that those in Western Europe were closer to the Mediterranean Sea and eastern neandertals may have pushed down into Israel and other warm areas, along with other animals. The fossil record indicates that animal herds moved up and down in latitude in accordance with climatic pulses, so it is very likely that hominin populations did as well. They were smart and may have inherited past cultural knowledge if they had language and theory of mind and, if for no other reason, they needed to eat and would have followed the game.

By the time that AMH moved into Western Europe ~35 kya, the neandertals had begun to die out. They likely succumbed to the increasingly harsh climate. They also went through an evolutionary bottleneck at some point

and lost some of their genetic diversity, possibly leaving them more vulnerable to disease. As in the Middle East, there has been much speculation about what went on when AMH arrived in Western Europe. While they likely carried neandertal genes (unless those western AMH left no modern descendants), they themselves may not have mated with neandertals, and certainly western populations would have appeared somewhat different than Middle Eastern neandertals. However, most eastern neandertals were gone by the time AMH passed through their former eastern geographic range, en route to Western Europe. It has been suggested that AMH outcompeted them either directly, which is known as contest competition, or indirectly, which is known as scramble competition, or possibly even killed them as they encountered them. Contest competition involves one group preventing another group from accessing resources, whereas scramble competition involves one group being better at gaining access to resources than the other. I always think of a bully defending a buffet table from others versus kids scrambling at an Easter egg hunt where some are better than others at getting to and/or finding eggs. It has also been widely accepted that the neandertals were marginalized as AMH encroached on their territory. Except for a more recent date from the Croatian site of Vindija (28 kya), the most recent dates are from the Iberian Peninsula, where it is thought they retreated and died out. Regardless of what transpired between the two species, since it appears that neandertals were on their way out, it is likely a moot point. It is rather fitting that after all of the years of thinking that humans played a role in the demise of the neandertals, it appears they made love not war (at least as far as we know)!

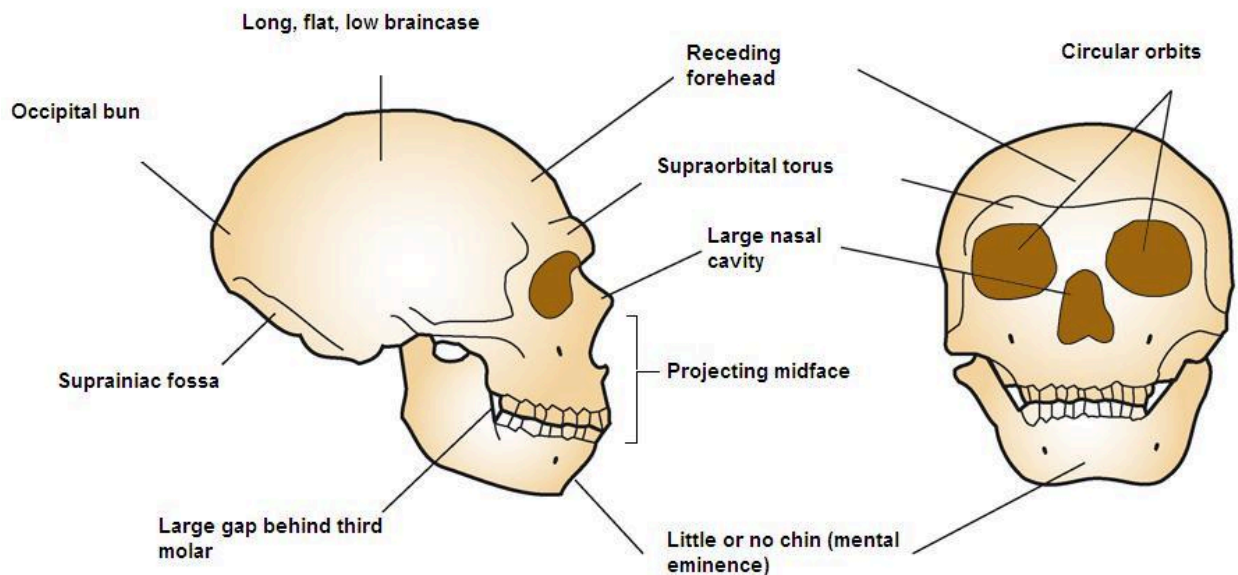
PHYSICAL CHARACTERISTICS



Neanderthal skeleton. "Neanderthalensis" by Claire Houck is licensed under CC BY-SA 2.0.

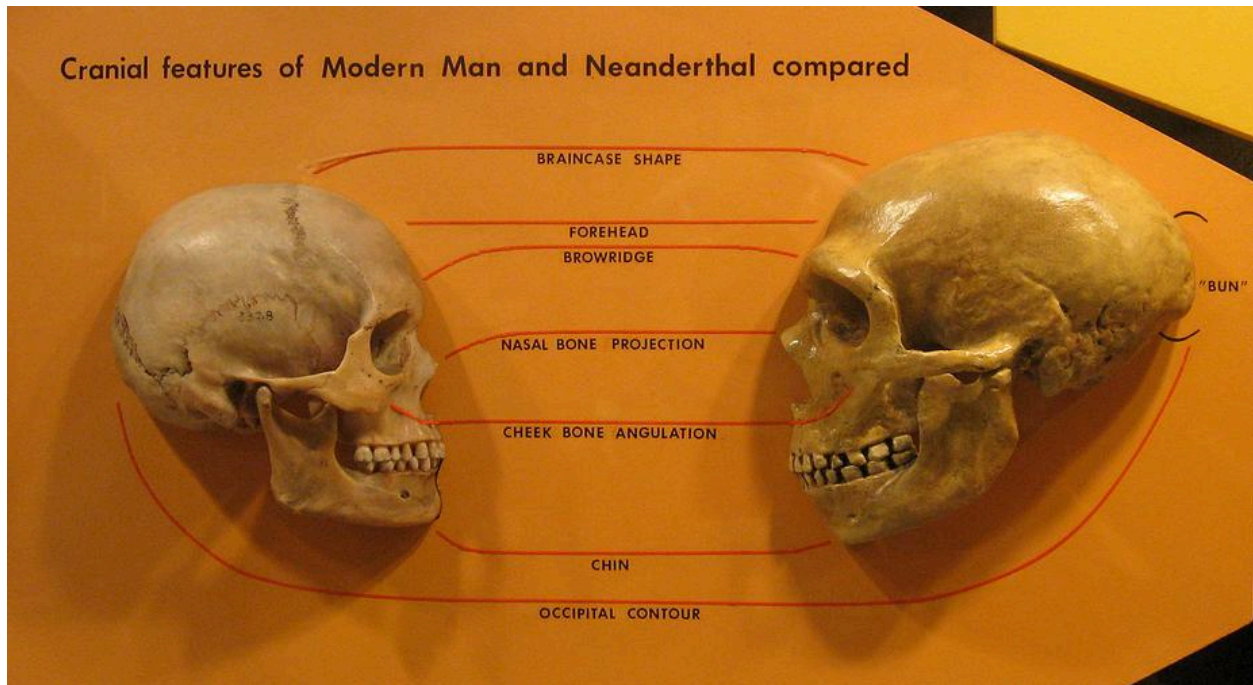
See Figure 35.4 for a full skeletal view of a neandertal. As mentioned, western and eastern neandertals diverged morphologically over time. That clinal variation, i.e. a graded change in physical characteristics over geographic space, is thought to have been the result of time, varying adaptation and exposure to chronically cold Ice Age conditions, and possibly gene flow with AMH in the Middle East. Populations in Western Europe lived at higher latitudes, and the Classic neandertals exhibited cold adaptations that conform to **Bergmann's and Allen's Rules**.

Bergmann's Rule states that as you move away from the equator, mass increases relative to surface area in order to conserve heat, as heat loss is a function of surface area. Allen's Rule pertains to limb or extremity length, so that organisms in colder environments exhibit shorter appendages. Thus in equatorial Africa, where people have adapted over the long term to hot and dry conditions, body morphology is long and gracile versus the short, stocky morphology of Arctic peoples. In addition to their stocky bodies, short appendages, and barrel chests, neandertals had facial adaptations to the cold. Like *H. heidelbergensis*, neandertals exhibited **midfacial prognathism**, large noses, and puffy faces due to enlarged sinuses. Due to their forward-oriented maxilla, the mandible also moved forward, leaving a space behind the third molar, termed a **retromolar space**. The internal nasal projections were large, thus increasing the internal surface area even further for warming and humidifying inspired air. In addition, unique projections extended from their internal nasal region, up into their orbits. Additional skull characteristics seen in both cold-adapted and eastern neandertals were large, smoothly rolled brow ridges above large, round, widely spaced orbits; "swept back" zygomatics; some unique inner ear characteristics; and, in the occipital region, an occipital bun and suprainiac fossae (two small depressions located above *inion*, or the external occipital protuberance; see Figure 35.5 for general area). While their skulls were longer and lower than those of AMH (see Figure 35.6), their absolute cranial capacity exceeded even that of modern humans. In accordance with Bergmann's Rule, a larger brain, while energetically costly in terms of calories, is more conservative from a heat generation and retention perspective. While the neandertal brain was larger, the frontal and parietal lobes (involved with higher thought processes) of AMH were expanded relative to those of neandertals. This may have given AMH an advantage in Ice Age Europe.



Neanderthal cranial anatomy. "Neanderthal cranial anatomy" by Jason Potter is licensed under CC BY-SA 2.5.

Postcranially, neandertals have been described as a cross between a marathon runner (in terms of their endurance) and a wrestler. They were built for chasing down and killing prey. Their upper body was heavily muscled.



Homo sapiens and neanderthal skulls compared. "Sapiens Neanderthal comparison" by hairy-museum-matt is licensed under CC BY-SA 2.0.

ENVIRONMENT AND WAY OF LIFE

The neandertals have traditionally been portrayed as having endured harsh climatic conditions. However, there is debate as to how much of a tolerance they had for conditions in Ice Age Europe. Tattersall (2009) presents an overview of research that suggests that during the coldest periods neandertals lived in more southerly regions and only moved into higher latitudes when temperatures were warmer. While their morphology reflects chronic exposure to cold, like traditional arctic peoples, they did not have the modern technology of those modern humans, such as better shelter, tailored clothes, weapons, and millennia of advanced cultural traditions. They thus had to biologically adapt to the cold. However, when conditions deteriorated as the last glacial maximum approached, they went extinct along with other ill-suited species in the northern latitudes.



Homo neanderthalensis by Keenan Taylor.

It has been known for many years that there were two different types of neandertal settlements, and discussions were often biased as though some inhabited prime real estate and others eked out a living on the open plains. Cave sites in southern France were often described as well-watered river valleys with plentiful caves for shelter, game, water, stone resources for tools, and so forth, and they were thought to have been inhabited for millennia. Open-air sites were apparently inhabited by more nomadic groups that lived out in the open in free-standing structures and followed herd animals. Cave sites and open-air sites are now thought to represent the seasonal shift in subsistence strategies practiced by the same peoples.

Thus while neandertal populations may have been able to live year-round in more temperate regions, the rest were likely semi-nomadic like their ancestors. During the cold of winter in Western Europe, they likely sheltered in southern caves and, in summer, ventured north in pursuit of migrating herds. In addition to caves, they used

rock shelters, whereby they built outward from a rock wall or overhang. They did the same inside of caves, building a shelter within a shelter. **Post molds** form when a wooden post inserted in the ground decays, so that a darker circle of humus is apparent. The pattern of post molds can be used to reconstruct the shape and size of houses and walls in the archaeological record. Based on post molds, neandertals are known to have covered cave entrances, probably during colder periods. Remains of constructed structures show that they used bones, posts, and rocks and likely covered them with skins and insulated with grass. At the Moldova site in the Ukraine, a 26 x 16' oval ring of mammoth bones was excavated. The bones were likely covered with hides, forming a hut that contained numerous hearths.

During the Pleistocene, European winters are described as having been long and cold and summers were short and cool. Because of the seasonality, plant foods would primarily have been available during warmer months. European neandertals ate a high proportion of meat, with reindeer and mammoth making up the majority of the diet, based upon faunal assemblages and isotopic analyses, respectively. However, dietary composition varied by region. Horses, bovids, and goats inhabited plains whereas at higher elevations, mountain sheep and ibex dominated. At the site of Shanidar, Iraq, faunal remains included goat, sheep, bovid, pig, tortoise, bear, deer, fox, marten, and gerbil bones. At the same site, there is evidence of plant consumption and cooking. Henry (2011) found phytoliths and starch grains in calcium deposits (calculus) on neandertal teeth. Some of the starch from grasses showed damage that is characteristic of cooking. While we know that neandertals used fire, as evidenced by hearths at their sites, and likely ate plants when they were available, it is valuable to finally have supporting evidence. Since Shanidar is south of most of Europe and thus more temperate, it is likely that the neandertals had greater access to such resources.



Restoration of Le Moustier Neanderthals by Charles R. Knight. "Le Moustier" by 1920 is in the public domain.

While debate has raged for some time over whether neandertals practiced cannibalism, fossil material, especially from the French site of Moula-Guercy, provides convincing evidence that at least some groups did eat their own. Neandertal bones at the site exhibit the same signs of processing as animal bones. Bones were disarticulated and hammered open for marrow, and exhibit cut marks from muscle removal.

It is interesting how abhorrent cannibalism is to us. We identify with the neandertals and may feel disappointed that they practiced cannibalism. While it is difficult to say why they ate one another, there is evidence of dietary stress in the form of enamel hypoplasia at some sites, such as Krapina, Croatia. Thus some groups suffered periodic food shortages that resulted in faulty enamel deposition in developing children. If people are starving and there is a dead body available, historic accounts show that they will eat it. Thus it should not be surprising

if neandertals consumed the dead, versus killing for consumption. There is no evidence that they practiced cannibalism in all times and places, and thus it could have been in response to extreme conditions.

Prior to the evidence from Moula Guercy, there was great reluctance anytime someone proposed cannibalism to explain damage to remains at particular sites. I think that the stimulus for many of us to feel an affinity for the neandertals is that they intentionally buried their dead. They seem so human. Now that we know that some of our ancestors interbred with them, we may feel an even greater connection to them and will have to accept the good along with possible acts of survival.



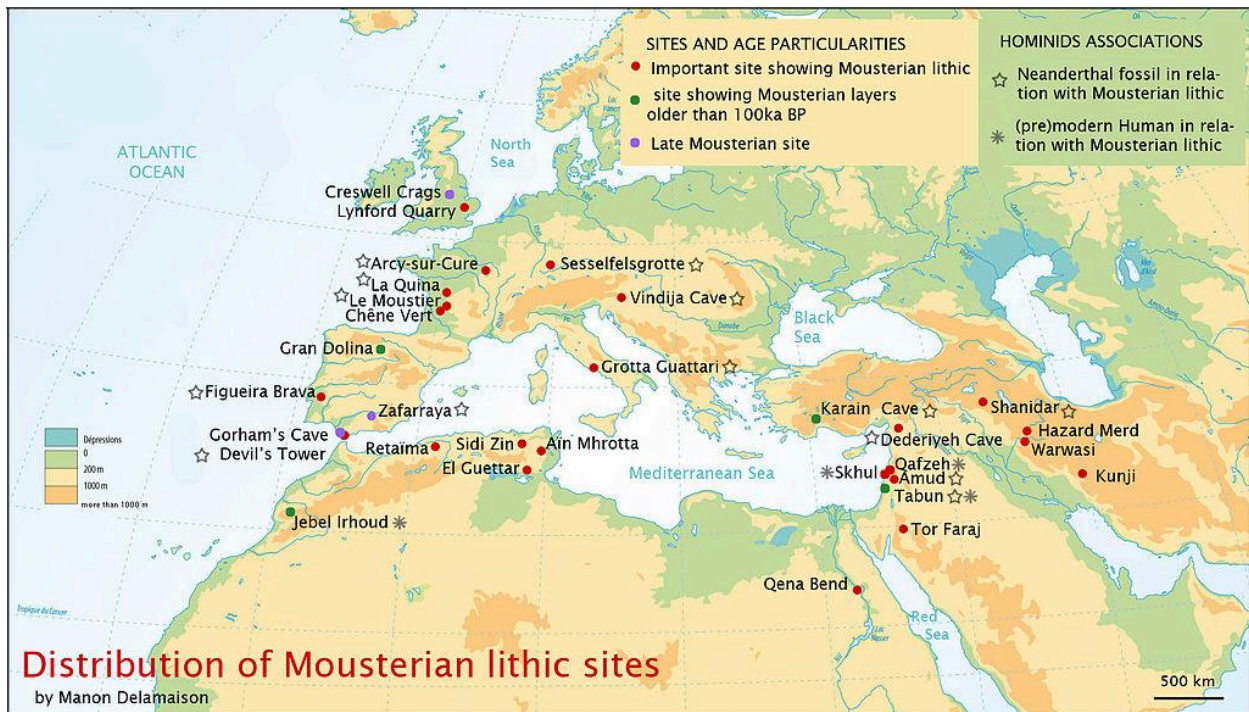
Discoid hand axe from Lyndford Quarry (near Mundford, Norfolk, UK), 60 kya. “Lyndford Hand axe-Discoid” by José-Manuel Benito Álvarez is licensed under CC BY-SA 4.0.

Neandertal culture falls within the period termed the **Middle Paleolithic**, i.e. the middle portion of the Old Stone Age. The neandertal tool tradition is termed the **Mousterian Industry** (see Figures 35.9 and 35.10 for examples of Mousterian tools), after the **Le Moustier** site in France (see Figure 35.8). While there are no known neandertal remains from North Africa, it is of interest that their tools have been found there (see Figure 35.11). The Mousterian method was an improvement on the Levallois technique that provided greater control over resulting flakes. Flakes were then modified into a variety of tools, such as scrapers and points, for various functions. Some of the tools were **denticulate**, meaning that they were saw-toothed. Like *H. heidelbergensis*, they made compound tools by hafting stone implements onto handles and shafts.

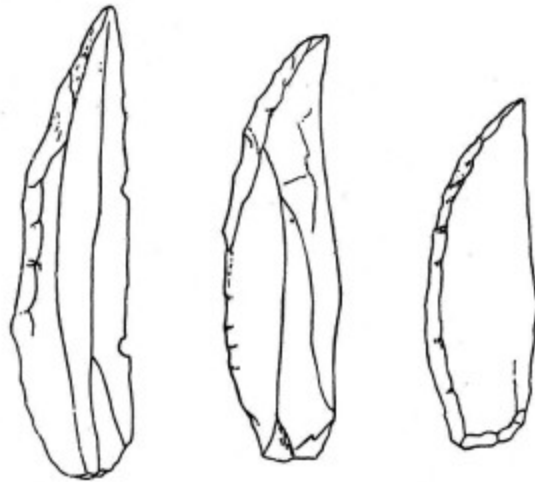


Mousterian flint artifacts. "Pointe levellois Beuzeville MHNT PRE.2009.0.203.2" by Didier Descouens is licensed under CC BY-SA 4.0.

A later tool tradition (35 kya) from the St. Cesaire site in France is categorized as an Upper Paleolithic industry, as the tools exhibit characteristics of AMH industries. Termed the Chatelperronian tradition (see Figure 35.12), it may be evidence of direct or indirect contact between neanderthals and AMH, meaning they obtained the technology via contact with AMH or found one or more tools and used their own methods to replicate them. Some scholars claim the latter versus learning AMH modes of production. Several items from the neanderthal site of Arcy-sur-Cure, France, have been interpreted as jewelry, another cultural achievement attributed solely to AMH.



Distribution of Mousterian lithic sites. "Distribution géographique des sites du Moustérien" by Manon Delamaison is licensed under CC BY-SA 3.0.



Chatelperronian tools. From *Manuel d'archéologie préhistorique, celtique et gallo-romaine* by Joseph Déchelette (1862–1914). “Pointes de chatelperron” by 120 is in the public domain.

While *H. naledi* and *H. heidelbergensis* deposited their dead in deep caves, the neandertals were the first species known to bury their dead in individual graves. Bodies are often found in a flexed position. There is very little evidence of ritual associated with neandertal burials. It appears that they dug a hole, folded the body into the hole, hence the flexed position, and possibly threw some other things in with it. Items are often interpreted as having some significance, but they are usually limited to animal bones and broken tools. However, at the site of Teshik Tash, Uzbekistan, a nine-year-old boy was buried with five sets of wild goat horns that may have adorned his body. While some have suggested that he was an AMH, if he was neandertal it appears to have been a ritualized burial.

The Shanidar site (see Figure 35.13) has always been the most romantic from my perspective. It is a cave site that experienced periodic cave-ins and has yielded the remains of several interesting individuals, some of which were intentionally buried. Shanidar 1 was an adult male. While ultimately the victim of a cave-in, he survived one or more earlier traumatic events in his life. He is thought to have been partially blind due to a head injury that involved one of his eyes. He was missing the end of one of his forearms and thus the hand as well. He suffered a leg injury that resulted in a permanent limp, and some of his teeth were completely worn down. The interesting question is, how did he survive? The oft-cited response is that his group mates helped him in life. He is thus heralded as another case of pre-human altruism or at least kin selection, if the care was provided by his relatives.

Shanidar 3 may be the earliest evidence for murder. Another adult male, he was possibly stabbed, as evidenced by a cut wound to one of his ribs. While the bone showed signs of healing, it is not known whether he died from the wound and was intentionally buried or died in a cave-in. Another interesting burial is Shanidar 4. He was also an adult male that was intentionally buried, and pollen from eight wildflower species was found in the grave. While highly controversial and possibly attributable to a seed-caching rodent species, many would like to think that neandertals not only buried their dead but also placed flowers on their remains.

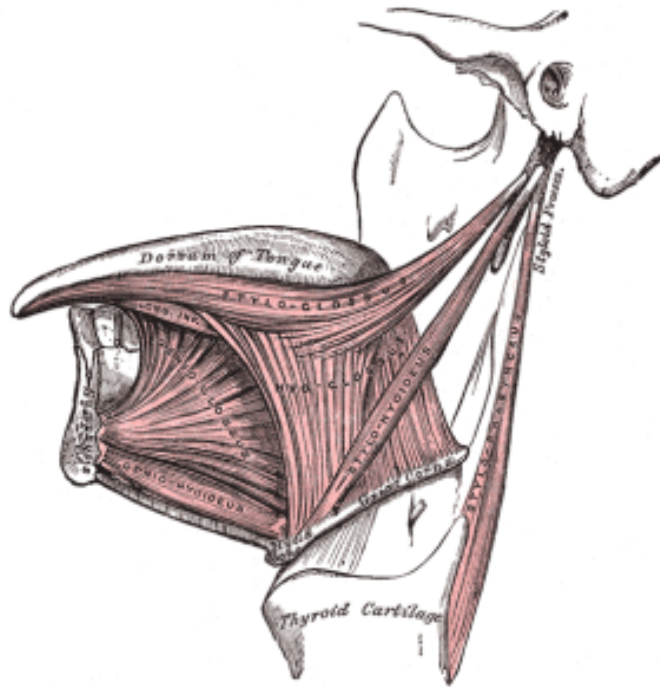
As I was writing the previous section, it occurred to me that males may have been differentially buried relative to females. While I do not know the answer to that question, it is interesting and food for thought.



Shanidar Cave, Iraq (see the two men in the cave entrance for scale). "Erbil governorate shanidar cave" by JosephV at the English language Wikipedia is licensed under CC BY-SA 3.0.

The debate as to whether the neandertals could speak has raged for decades. For many years, experts thought that their larynx was situated too high in their throats to have allowed for speech. Our larynx drops during the course of development. Early on it is positioned high in the throat to allow simultaneous drinking and breathing. Babies cannot talk until the larynx drops and they then begin to babble. Thus while they are not mechanically able to speak early on, they are cognitively capable of learning language. Of interest is that some parents now teach their infants sign language so that they can communicate earlier.

While some researchers still doubt the neandertals' ability to speak, many have accepted that they likely had spoken language but would have been unable to produce the full range of sounds that characterize our own speech. The discovery of a neandertal hyoid bone at the Kebara site in Israel led many to accept their ability to talk, since its morphology was similar to our own. The hyoid is an important attachment site for the ligaments and cartilages of the larynx and for some extrinsic muscles of the tongue (i.e., geniohyoid, hyoglossus). The most telling evidence in support of neandertal speech, in addition to all of my previous arguments, is the presence of the FOX P2 gene in their genome. We also possess the gene, and it plays an important role in the acquisition of language.



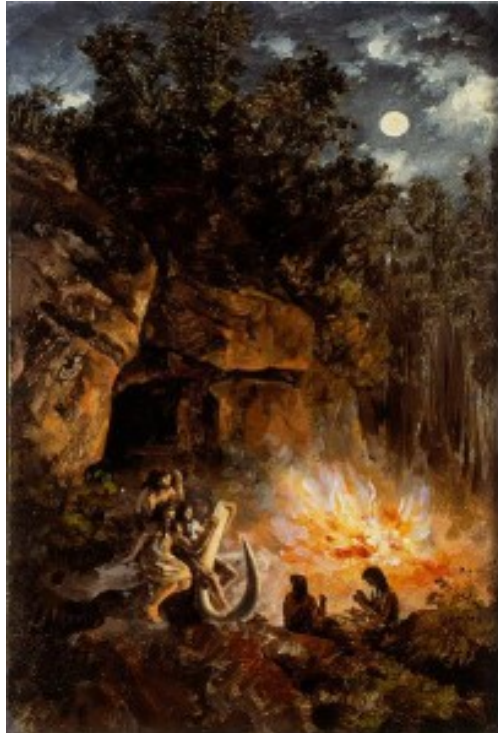
Muscles involved with speech. Plate 386 from Gray's Anatomy. "Gray1019" by Henry Vandyke Carter is in the public domain.

36. Homo sapiens

Early Anatomically Modern Humans

Homo sapiens (>200 kya)

(“same” / “capable of discerning”)



“Scene from the Upper Quaternary Paleolithic Period.” Painting by José María Velasco (1840–1912) (Mexican).“José María Velasco – Scene from the Quaternary upper Paleolithic Period – Google Art Project” by Google Cultural Institute is in the public domain.

SITES

Africa:

Tanzania: Ngaloba

Kenya: Guomde

Ethiopia: Omo Kibish and Herto

Democratic Republic of Congo: Katanda

South Africa: Border Cave and Klasies River Mouth

Asia (the following are earliest regional sites):

Israel: Skhul and Jebel Qafzeh

Mongolia: Ordos

Europe (the following are famous sites):

France: Cro Magnon (the most famous site in France)

Germany, Italy, Spain

Australia (the following are earliest regional sites):

Mungo Lake and Kow Swamp

New World (the earliest regional site):

Chile: Mesa Verde

PEOPLE

Too numerous to mention, as one or more individuals work at each site and sites are numerous, especially in Eurasia

INTRODUCTION

My discussion of early AMH will cover their existence and culture prior to the Mesolithic period (~12 kya) only and will focus primarily on European sites due to the paucity of information from earlier and non-European sites.

PHYLOGENY

The origin of our species is thought to have occurred in Africa sometime prior to 200 kya, based on fossil and genetic evidence. We may be descended from an African population of *Homo heidelbergensis* (sometimes referred to as *Homo rhodesiensis*) or an earlier common ancestor of *heidelbergensis*, based on recent genetic evidence. Fossils characteristic of a transitional form, termed *Homo helmei*, are found at the South African site of **Florisbad** and dated to 260 kya. Material from the **Herto** site in Ethiopia (Middle Awash area of the Afar Depression) is dated to 160 kya and sometimes referred to as *Homo idaltu* or *Homo sapiens idaltu*. *Homo idaltu* may be descended from the earlier South African form(s) and the most recent ancestor of AMH.

Groups of AMH made one or more exoduses out of Africa during the Late Pleistocene. The ancestors of some Southeast Asians and the earliest Australians (as well as inhabitants of surrounding islands and those that were used as “stepping stones”) may have left Africa ~125 kya. There are sites dating to ~120 kya in the Middle East.

A later group left prior to 50 kya and populated Eurasia and the New World, and made their way to the South Pacific as well, where they must have come into contact and interbred with the previously existing humans there.

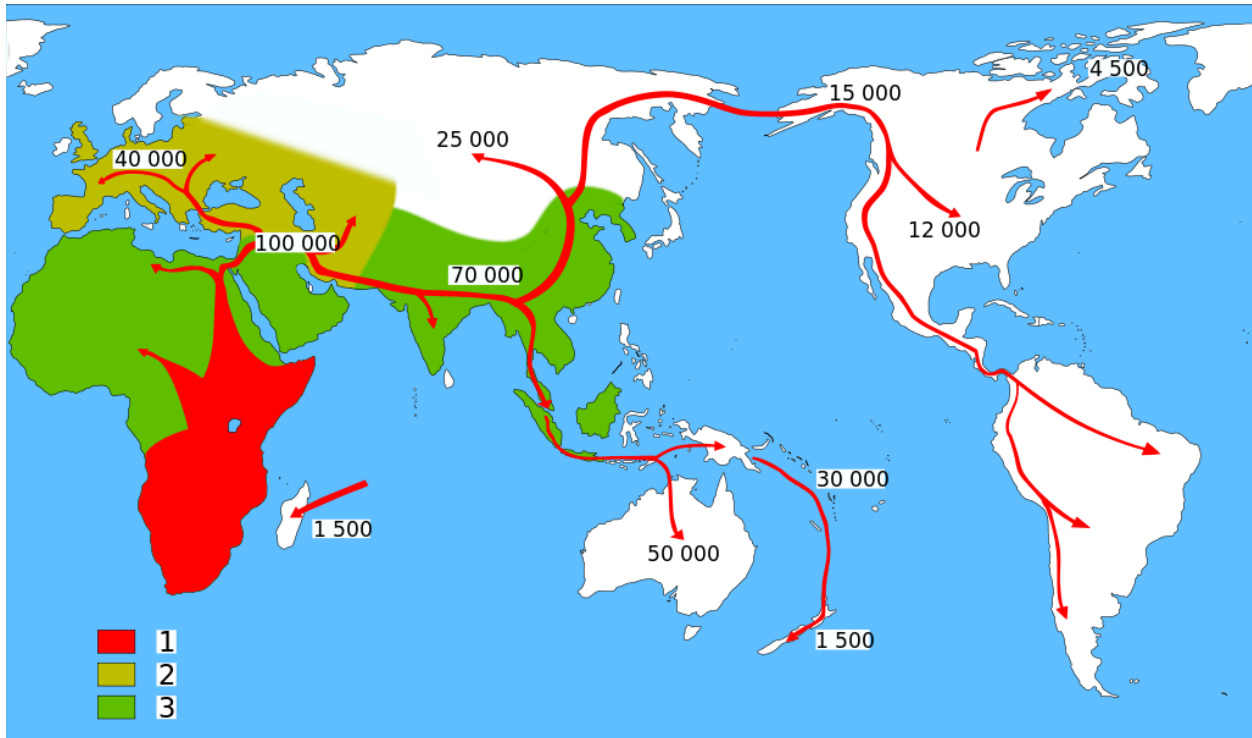
The AMH ancestors of Eurasians interbred with neandertals, so that living descendants have inherited an average of 2.5% of neandertal genes. Some Southeast Australasians inherited both neandertal and Denisovan genes, due to interbreeding, and they carry ~7% of genes from those two species.

DISCOVERY AND GEOGRAPHIC DISTRIBUTION

Most of the oldest AMH material has been discovered in more recent times, relative to early discoveries of Asian *Homo erectus* and neandertal remains. The earliest AMH material is dated to 200–150 kya in East Africa (e.g. Omo Kibish and Herto in Ethiopia, Guomde in Kenya, and Ngaloba in Tanzania), 180 kya in central Africa (Katanda in the Democratic Republic of Congo), and 160 kya in South Africa (e.g. Klasies River Mouth). Later sites dated to 115 kya are found in Israel (Skhul and Jebel Qafzeh caves) and South Africa (Border Cave).

Due to increasing aridification during the Late Pleistocene of sub-Saharan Africa, researchers speculate that there were few areas that would have been habitable for early AMH. South Africa and other coastal areas likely served as refugia during those times.

By 125 kya, it would have been possible for AMH to have left Africa during a short interglacial period (see Figure 36.2 for routes and dates of arrival throughout the world). Middle Eastern sites dated to <120 kya preserve evidence of AMH. The Arabian land bridge likely served as a corridor to Southeast Asia, just as it had for the ancestor of *Homo erectus*. By ~50 kya, that early wave of humans made it all the way to Australia. Archaeological sites dated to over 50 kya are found in Japan and Australia (with cave art possibly as old as 75 kya), and fossil material from Australia is dated to 40 kya. Some researchers see similarities between early Australians and early Africans, supporting the idea of at least two African exoduses and multiple human migrations into the South Pacific. The first wave left Africa first and arrived by 50 kya. Ancestors of AMH that left Africa during the “second” exodus followed at a later point in time. It is not known when they arrived in the various areas of Southeast Asia or whether they made it to the same destinations as the original colonizing group, prior to modern times.



Human arrival dates: 1 = Homo sapiens, 2 = neandertals, 3 = early hominins. "Spreading homo sapiens" by Magasjukur2 is licensed under CC BY-SA 2.5.

The earliest date for AMH in Eurasia is from the **Ordos** site in Mongolia at 50 kya. AMH reached Western Europe by 35 kya. Sites are found in Germany, France, Italy, and Spain, with the best-known site being the **Cro-Magnon** site in Les Ezies, France. The Cro-Magnon site gave the name to the earliest people of Western Europe and is the location where the "**Old Man of Cro-Magnon**" (see Figure 36.3) was found in 1868 by Louis Lartet.

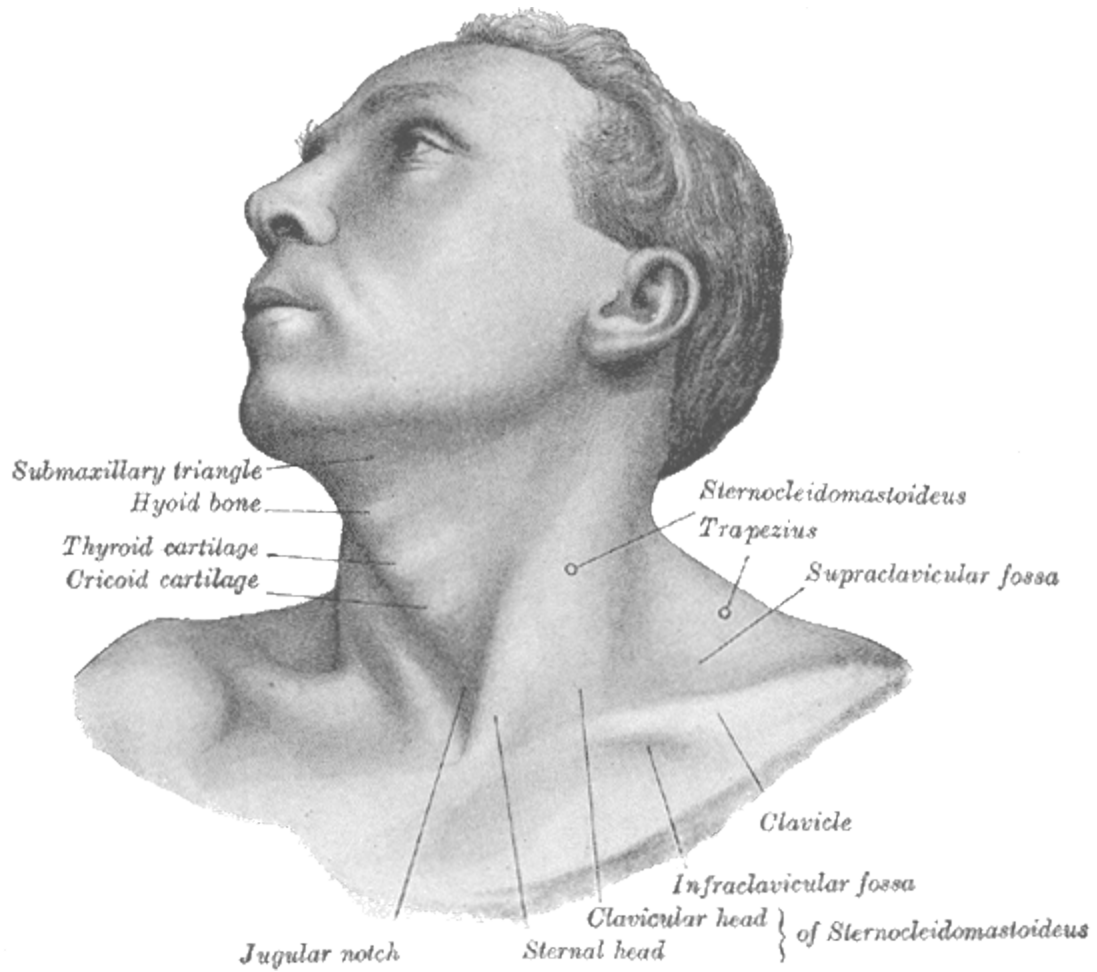
By 15 kya, humans had spread throughout the world. They reached the New World, either by rafting along the shoreline from Asia during extremely low sea levels that characterized the last glacial maximum (~17 kya) or by crossing the Bering Land Bridge at a later point in time. Dates in South America (~14 kya) are older than those in North America and represent the former mode of travel. Sea levels dropped by as much as 120 m during that time. Crossing **Beringea** involved traveling between two ice shields and was likely a difficult undertaking.

PHYSICAL CHARACTERISTICS

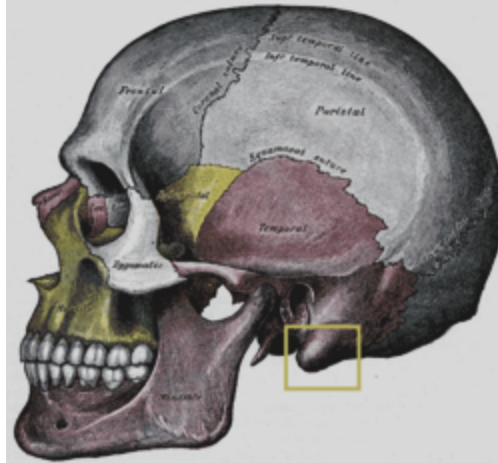


“The Old Man of Cro-Magnon.” “Cro-Magnon” by 120 is licensed under CC BY-SA 3.0.

AMH are distinguished from *Homo heidelbergensis* and *rhodesiensis* by a suite of cranial characteristics and continued loss of robusticity, both cranially and postcranially. AMH skulls were more vertically oriented with thinner bones. While the cranial capacity (mean = 1450 cc) was lower relative to neandertals, the brain was architecturally different, and corresponding behavior was more complex and indicative of greater lateralization. The parietal and frontal lobes were expanded, resulting in high maximum width and breadth and a more pronounced forehead. Those areas of the cerebrum are involved with higher thought-processing skills related to association, speech, and all of the other cognitive capabilities that make us unique relative to other species, past and present. The face was shorter, the orbits were more rectangular, and the brow ridges were less pronounced. The brows are termed **bipartite** in that they are characterized by a slight bulge on either side of the nose, with a break in between. While the nose may have been pronounced, the nasal opening was narrower, and the midfacial prognathism seen in earlier forms was absent. Jaw and dental robusticity became further reduced. AMH are characterized by a **chin**, or **mental eminence** (an autapomorphic, or unique, trait in AMH). While the mandible was less robust, the morphology (described as an inverted T-shape) was strong and stress resistant.



Sternocleidomastoid muscle. Plate 1194 from Gray's Anatomy. "Gray1194" by Henry Vandyke Carter is in the public domain.



Mastoid process. From Gray's Anatomy. "Processus mastoideus ossis temporalis" by Engusz is in the public domain.

Because they had more gracile and hence lighter faces, they needed stronger anterior neck muscles to flex the head from an extended position, i.e. from a back-tilted to a forward-tilted position. The **sternocleidomastoid** muscle (see Figure 36.4) accomplishes that action, along with some rotation. The muscle originates on the sternum and clavicle and inserts on the **mastoid process** (bony projections posterior to ears; see Figure 36.5). The mastoid process became more pronounced to handle the additional power that was necessary (Campbell 1998).

Postcranially, AMH exhibited narrow hips, long legs, and thinner long bones than *H. heidelbergensis* or *neanderthalensis*. While they were seemingly not as cold-adapted as neandertals, they moved into northern latitudes and survived through the last glacial maximum. It is strange that the seemingly more heat-adapted humans survived and the robust neandertals did not. However, their long legs and more gracile morphology were less energetically costly and afforded them greater endurance and a longer stride and hence greater speed. In addition, cultural adaptations to the climate must have occurred or they could not have survived. They are thought to have made better clothes, shelter, and weaponry and were skilled hunters.

ENVIRONMENT AND WAY OF LIFE

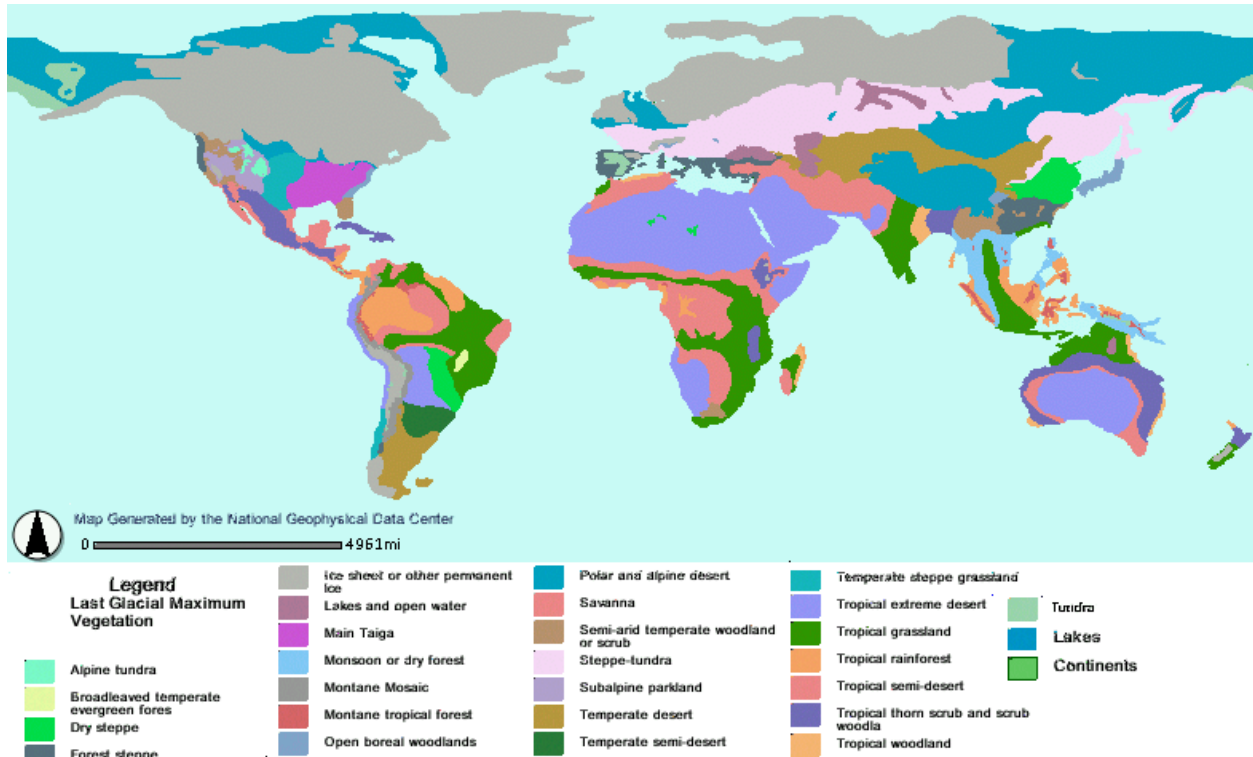
Early AMH arose and lived during the latter part of the Pleistocene Epoch, which was characterized by intermittent glacial and interglacial periods. They ventured into northern latitudes by ~50 kya and stayed and survived in extreme conditions during the period prior to, during, and after the last glacial maximum. Populations that stayed in Africa and other warm regions would certainly have continued with life as usual in the absence of climatic upheaval.



“Glyptodon old drawing” by Haplochromis is in the public domain. Paleolndians hunting a glyptodon in South America. Being large and slow-moving, they were hunted to extinction within two millennia. Painting by Heinrich Harder (1858–1935).

Until the advent of agriculture and the beginning of the modern geological epoch (i.e., the **Holocene**) approximately 10 kya, humans were mobile to semi-sedentary foragers. They exploited whatever flora and fauna were native and available in the various regions they inhabited and colonized, from mastodons in the far north to wallabies in the far south of the Old World. We really do not need to discuss much about how AMH made a living because we have living and historic examples in the ethnographic record to show us how people lived and adapted, even to environmental extremes, from the cold of the Arctic to the deserts of the world. We have a record of Stone Age populations whose way of life disappeared within my lifetime, such as Australian Aborigines and Amazonian Indians. Like modern foragers, population density would have been low, and life ranged from easy to hard, depending on the availability of resources, seasons, and climatic patterns and disasters. One estimate of mortality rates has 50% of people dying before 20 years of age, few females living beyond 30, and only 12% living beyond the age of 40.

Any discussion of early AMH culture is seemingly Eurocentric, because the majority of the known archaeological record falls between 30 and 20 kya in Western Europe. We know that ~30 kya, a warming trend occurred that lasted several thousand years. As glacial ice retreated, prime grazing land opened and spread from Spain to Siberia. As large game expanded their geographical range, so did humans and other predators. Human population numbers increased as groups spread throughout the habitable landmass. However, as the last glacial maximum approached, ice reclaimed the land and humans were once again restricted in their range and movements.



Vegetation map for last glacial maximum (zoom in for a better look). "Last glacial vegetation map" by Jrockley is in the public domain.

The vegetation map in Figure 36.7 shows what the world was like beginning about 20 kya, during the last glacial maximum. By that time, AMH were living in Africa, Eurasia, island chains southeast of Asia, and Australia and the surrounding islands. A short time later, they ventured into the New World.

We certainly know that early humans had spoken language, and it would have facilitated their survival via group memory and tradition as well as problem-solving. They were qualitatively different than the neandertals, and their modes of communication were likely more advanced. Modern languages can be traced, showing their spread and evolution over time and geographic space. Some of the symbols that have survived from Paleolithic times, such as dots, dashes, and hand-prints, may have conveyed information. The same may be said for depictions of animals, humans, and hunting on cave walls.



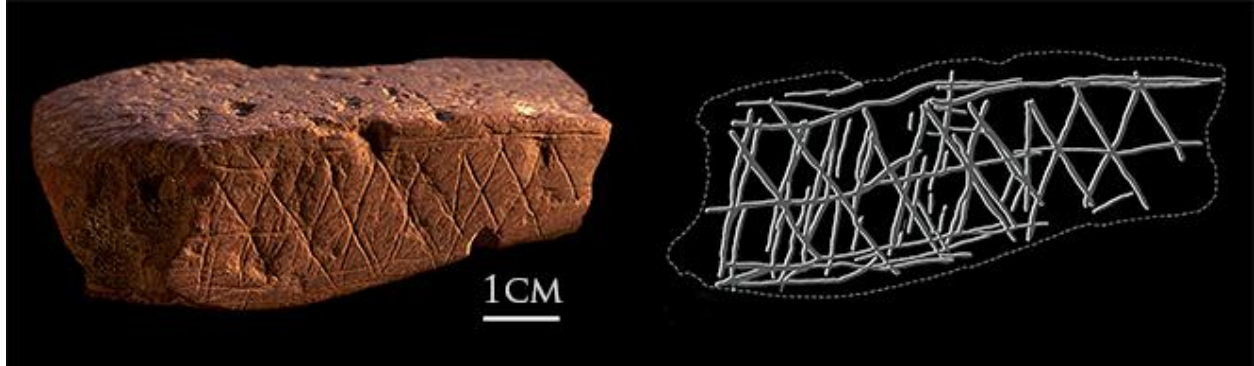
“Ice age fauna of northern Spain” by Mauricio Antón. “Ice age fauna of northern Spain – Mauricio Antón” by FunkMonk is licensed under CC BY 2.5.

Early AMH culture falls within the period termed the **Upper Paleolithic** (40–12 kya). Relative to prior Middle Paleolithic sites, AMH cultural achievements are much more impressive. Over time, they made great technological advances, inventing a great variety of new and useful objects and modes of production. People left Africa armed with language, religion, and cultural identity, as they are cultural universals and there is some evidence in the archaeological record that suggests religious practices and initiation rituals (see below). Greater individual expression is apparent in the wonderful representational art that has survived in cave paintings and sculptures, and body adornment in the form of clothing, jewelry, and pigmentation. Complex aspects of culture, such as rules regarding kinship and marriage, also may have preceded the African diaspora(s). They too are cultural universals, and while they likely changed over time in response to need and ecology, they certainly did not evolve independently in all places.

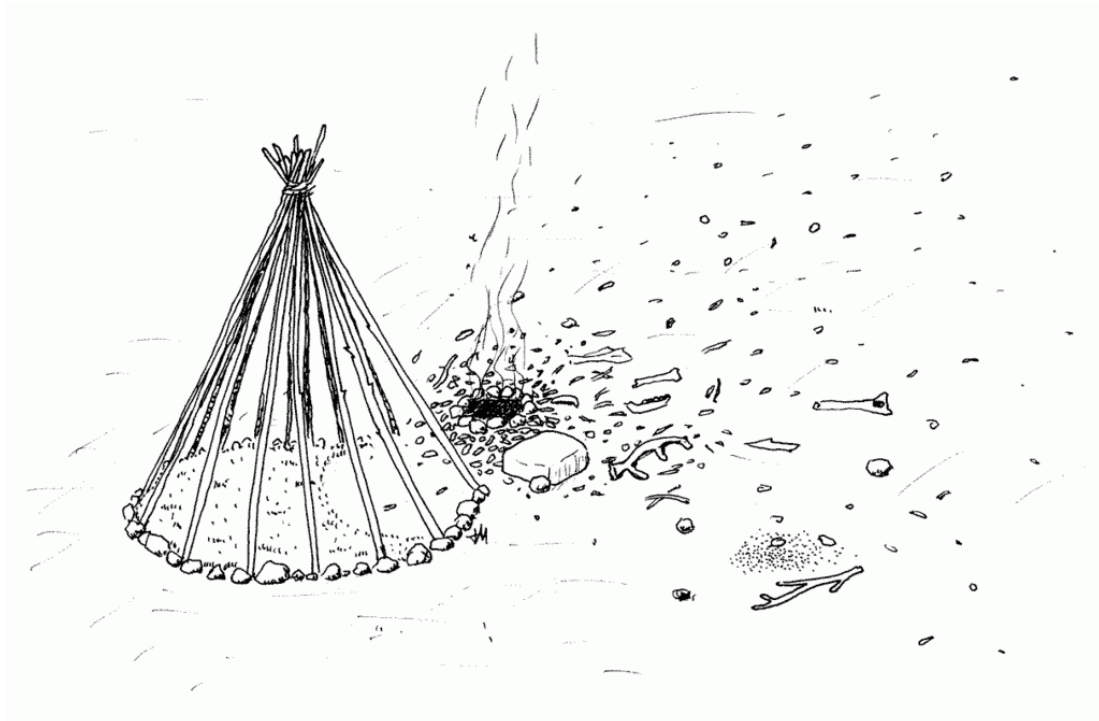
According to Stringer and Andrews (2005), cultural achievements in the various regions of the Old World were as follows:

- Europe ~40 kya:
 - All aspects of Upper Paleolithic culture.
 - Only early representational art.
- South Africa ~75 kya:
 - Blombos Cave.
 - Carved and decorated ocher crayons (see Figure 36.9).
- Australia ~30 kya:
 - Rafts.
 - Cremation.
 - Art.
 - Body adornment.

- Bone artifacts.



Blombos Cave, South Africa: engraved ochre. “Blombos Cave engrave ochre” by Chris S. Henshilwood is licensed under CC BY-SA 3.0.



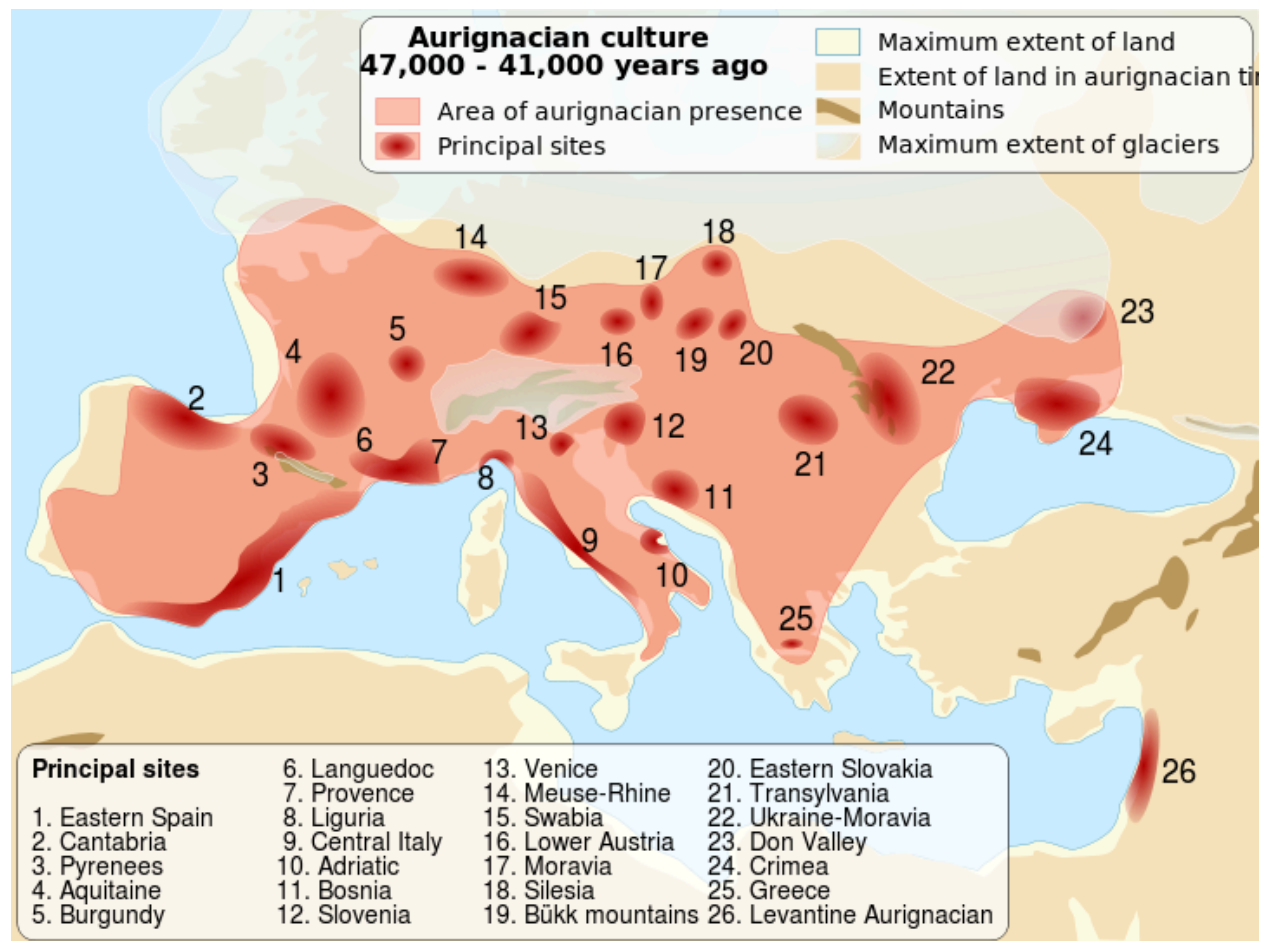
Reconstruction of tent from Magdalenian times at Pincevent, France. “Pincevent tent” by José-Manual Benito is in the public domain.

AMH settlements were larger and more permanent than those of neandertals and were often located on the tops of hills. Researchers have speculated that the view of the surrounding areas may have been beneficial for monitoring herd movements. They built better shelters, some of which had sunken and stone foundations. Materials that were utilized consisted of wooden posts and branches, stone, and hides, and where no wood was available, bones, tusks, and antlers. They also made tents (see Figure 36.10). The remains of a house in Russia

show that it was approximately 50 by 120' with multiple hearths along its length. That is four times the size of my house and architecturally impressive, considering their tool kit relative to ours. Cooking was done in stone-lined hearths and ovens. They dug storage pits to preserve and protect food stores from animals. Stone lamps consisted of a flat stone with a depression into which was placed animal fat that would have provided light for a couple of hours.

At the Sungir site near Moscow, clothes from 22 kya survived in permafrost. We thus know that Paleolithic peoples made tailored clothing like our own. Earlier hominins are thought to have worn ponchos and lashed skins onto their bodies. AMH tools of the trade that survive in the archaeological record are bone needles, pins, and awls for punching holes in the skins. In addition to animal hides, they used bark cloth and woven grass for insulation.

Upper Paleolithic tool industries were advanced relative to past traditions, with greater diversification and refinement. Tools consisted of knives, scrapers, chisels, borers, awls, needles, and a greater number of blade and compound tools. Stone, bone, ivory, and antler were used. Some of the more famous Upper Paleolithic industries are the **Aurignacian** (possibly <40 kya), **Gravettian** (~28-22 kya), **Solutrean** (~22-17 kya), and **Magdalenian** (~18-10 kya).



Map showing Aurignacian culture, 47-41 kya. "Aurignacian culture map-en" by Hughcharlesparker is licensed under CC BY-SA 3.0.

The Aurignacian industry (see Figure 36.11) may have originated in Asia, but it can be found throughout Europe

(Stringer and Andrews 2005). The Cro-Magnon people that produced the tools, art, and other cultural achievements from that time are thus known as the Aurignacian or Cro-Magnon culture. Aurignacian and subsequent tool industries were predominantly blade-based. Like the Levallois technique and the Mousterian industry, AMH could produce a variety of tools from a single core, but they used a new mode of production known as the **punch technique**. It involved using a hammerstone, a hammer and chisel, or a long wooden spear (using upper body weight and strength) to “punch” blades from the core. For illustrations on this technique see Dennis O’Neil’s Early Modern Human Culture at <http://anthro.palomar.edu/homo2/>.

The Gravettian industry had a more limited distribution in Eastern Europe and Western Asia (Stringer and Andrews 2005). Stereotypical tools of the industry were flat-end blades and burins (see Figure 36.12) that were used to work wood.



Brassempouy burins from the Gravettian culture. “Burin Brassempouy 213.3 Profil (3)” by Didier Descouens is licensed under CC BY 3.0.

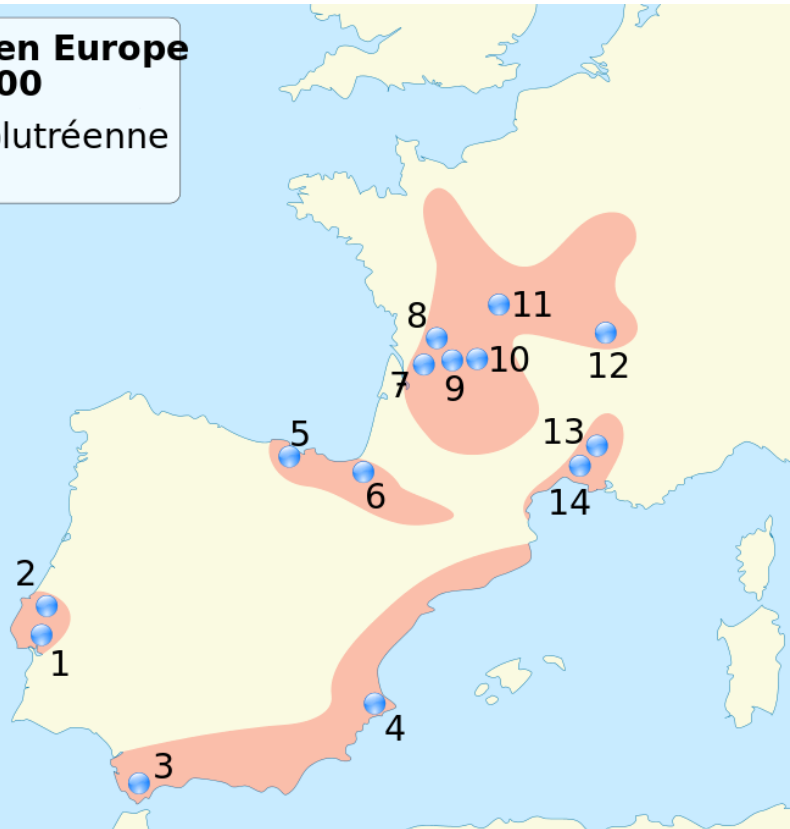
The Solutrean industry (see Figure 36.13) is most famous for its beautiful and refined laurel leaf blades (see Figure 36.14). A method known as **pressure flaking** was used to finely and bifacially shape the blade. Pressure flaking involves the use of a pointed tool, such as antler or bone, to force tiny flakes from the surface and edges of the tool (see Figure 36.15).

La culture solutréenne en Europe - 20 000 ~ - 15 000

- Zone de présence solutréenne
- Sites principaux

Principaux sites

1. Vale Comprido
2. Casa da Moura
3. La Pileta
4. El Parpallo
5. Grotte Chufin
6. Isturitz
7. Roc de Sers
8. Le Placard
9. Fourneau du Diable
10. Combe-Saunière
11. Les Maîtres
12. Solutré
13. Oulon
14. La Salpêtrière



Solutrean sites. "Homo Sapiens in Europe – solutrean distribution map-fr" by Sémhur is licensed under CC BY-SA 4.0.



Solutrean leaf blade. "Biface feuille de laurier" by Calame is in the public domain.

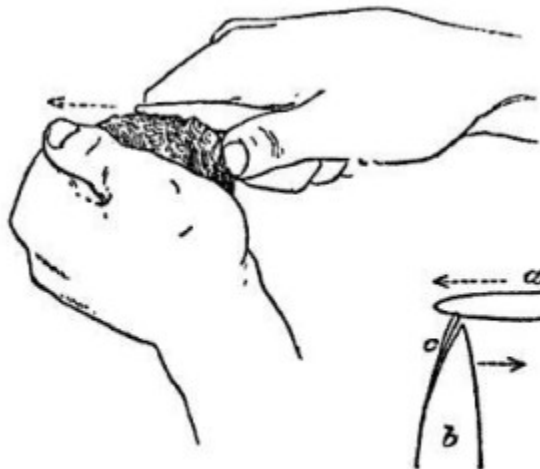


FIG. 22.—Flaking Stone by outward pressure.
(After Holmes.)

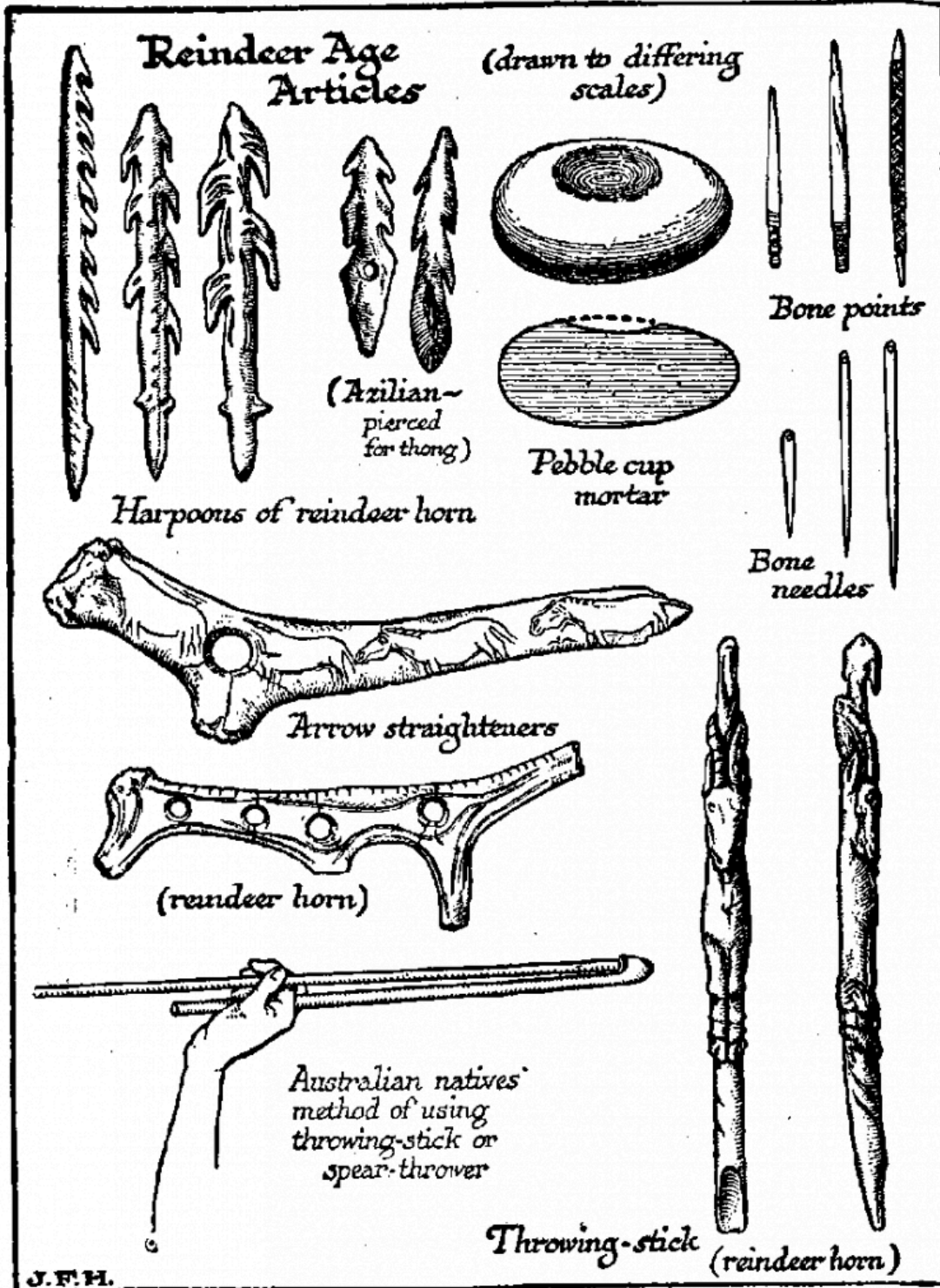
Flaking stone. From *The origins of invention: a study of industry among primitive peoples* by Otis Tufton Mason (1895). "19th century knowledge stone tools flaking stone by outward pressure" by Jonp154 is in the public domain.

Finally, the Magdalenian industry (see Figures 36.16, 36.17, and 36.18) is characterized by great advances in

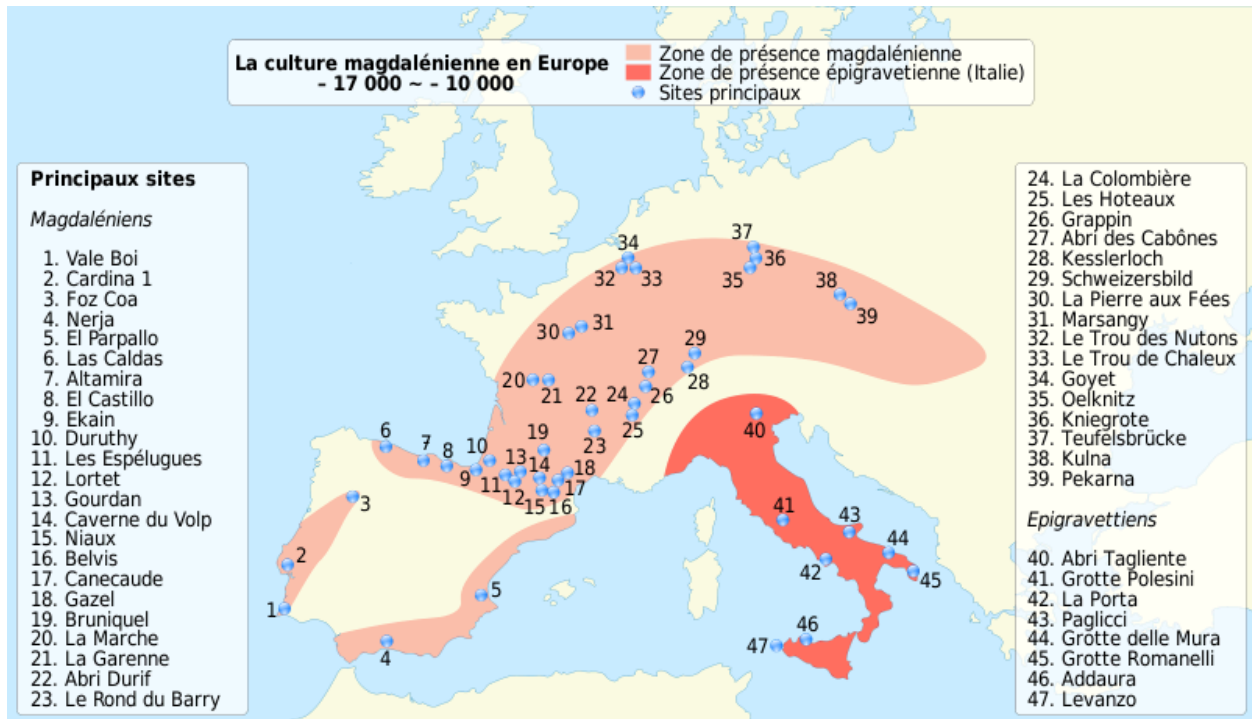
weaponry, such as the bow and arrow and the atlatl or spear thrower (see Figures 36.19 and 36.20), both of which allowed hunters to put distance between themselves and their prey.



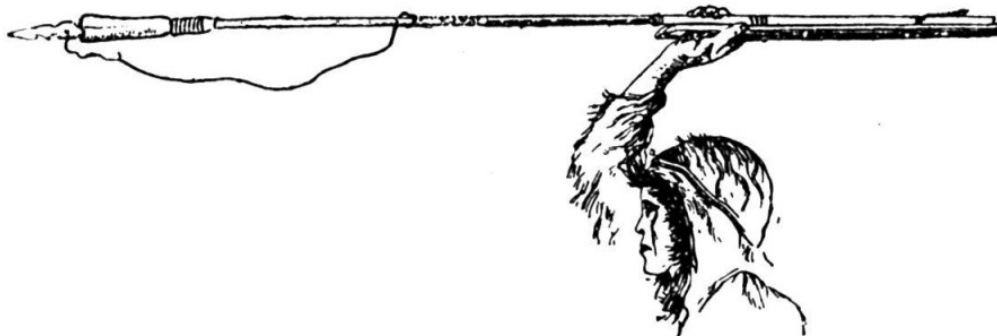
Magdalenian blades and burins. "Burins and blades – Bernifal – Meyrals – MNP" by Sémhur is licensed under CC BY-SA 4.0.



Examples of antler weapons. From *The Outline of History* by H. G. Wells (1920). "Wells Reindeer Age articles" by SEWilco is in the public domain.



Geographic range of Magdalenian culture (in pink). "Homo Sapiens in Europe – magdalenian distribution map-fr" by Sémhur is licensed under CC BY-SA 4.0.



Atlatl being used to throw a spear. From Manuel d'archéologie préhistorique, celtique et gallo-romaine by Joseph Déchelette (1862–1914). "Propulseur-2" by 120 is in the public domain.



Atlatl. "Atlatl" by Maxim Razin is in the public domain.

Other weapons from the Upper Paleolithic are **stone missiles** or **bolas** (see Figure 36.21), **boomerangs**, spears, javelins, and clubs. AMH had refined fishing techniques, rafts, and canoes. **Harpoons** appear very early in the archaeological record, e.g. the **Katanda** site in the Democratic Republic of Congo is dated to 180–75 kya. They also constructed **traps**, **rope**, and **baskets**.



Bola from the site of Sidi Abderrahman, Morocco. "Bolo-Sidi-Abderrahman" by 120 is licensed under CC BY-SA 3.0.

Beginning ~25 kya, a cultural and symbolic explosion is evident in the archaeological record of Western Europe, possibly in response to the increasingly cold temperatures, such as if they spent more time inside caves or were performing rituals aimed at increasing their survival. The Cro-Magnon/Aurignacian people are known for their cave art and sculptures (see Figures 36.23 and 36.24). Figure 36.22 illustrates the incredible number of sites where early AMH art has been found. There are 150 sites in southwest France alone.



Paleolithic art sites. Aqua lines indicate "limits of the main glaciations." "Upper Paleolithic Art in Europe" by Sugaar is in the public domain.

Common cave art themes are fauna; hunting; hands; dots and lines; some humans; and the occasional human costumed as an animal and sometimes dancing, such as "The Sorcerer" (see Figures 36.23 and 36.24). Men appear alone or in groups, but women are never pictured alone. Drawings of male and female genitalia are reported from multiple sites.



Half-bull/half-human etching. Cave site in Dordogne, France. “Gabillou Sorcier” by José-Manuel Benito is in the public domain.



Drawing by Breuil of the “Sorcerer” Cave painting. Trois-Frères, Ariège, France (15 kya). “Pintura Trois Freres” by Dcasawang1 is in the public domain.

Artists used charcoal and mineral pigments, such as ocher (see Figure 36.9 for a photo of an ocher crayon from Blombos Cave), and may have applied some of the shading by chewing the pigments and spitting them onto the

walls, resulting in an air-brushed effect. There is a great demonstration of that practice in the third segment of the public television series *In Search of Human Origins* (NOVA 1994).

The art may have served a variety of purposes. First, it is difficult not to imagine their aesthetic and emotional value, e.g. accompanying stories and myths. They may have been used for more utilitarian purposes, such as hunting strategies or keeping records. Some might have served a social function, such as communication within and between groups or education. Finally, of course, there is their proposed use in magic and ritual. Some art is found deep within caves in association with primitive stone lamps and children's footprints. Some of the caves were discovered by divers, and thus the archaeological record was not disturbed, i.e. they were not modern footprints. It is easy to see why this has been interpreted as possible evidence of initiation rituals.

While they drew and painted on outer walls as well as inside caves, the cave paintings survived better. The French site of **Lascaux Cave** (18 kya) (see Figures 36.25 and 36.26) is renowned for the color and beauty of its animal depictions, especially those seen in the "Great Hall of Bulls." At the cave site of **Grotte Chauvet**, France (~30 kya) (see Figure 36.27), more than 300 animals are depicted, many of which are not seen elsewhere, such as panthers and lions. Figures 36.29 and 36.30 show maps of the Spanish cave of La Pasiega (<20 kya), giving you some idea of the labyrinthine nature of some of the cave systems and richness of the galleries. Figures and forms in the cave number over 700 and consist of the following:

97 deer (69 females and 28 males), 80 horses, 32 ibex, 31 cattle (17 bison and 14 aurochs), two reindeer, a carnivorous animal, a chamois, a megaloceros, a bird and a fish; also there may be a mammoth and about 40 quadrupeds not clearly identified; also the ideomorphs, such as roof-shaped and other surprisingly varied symbols (more than 130), and very often including various anthropomorphs and hundreds of marks and partly erased traces. (Wikipedia contributors 2015a)

Another famous Spanish cave site is **Altamira** (15 kya) (see Figure 36.28). The cave is about one kilometer long (Chivers, 2004) and contains polychromatic renderings of large mammals, especially bison, and human hand prints.



Great Hall of Bulls, Lascaux Cave, France. "Lascaux painting" by Prof saxx is licensed under CC BY SA 3.0.



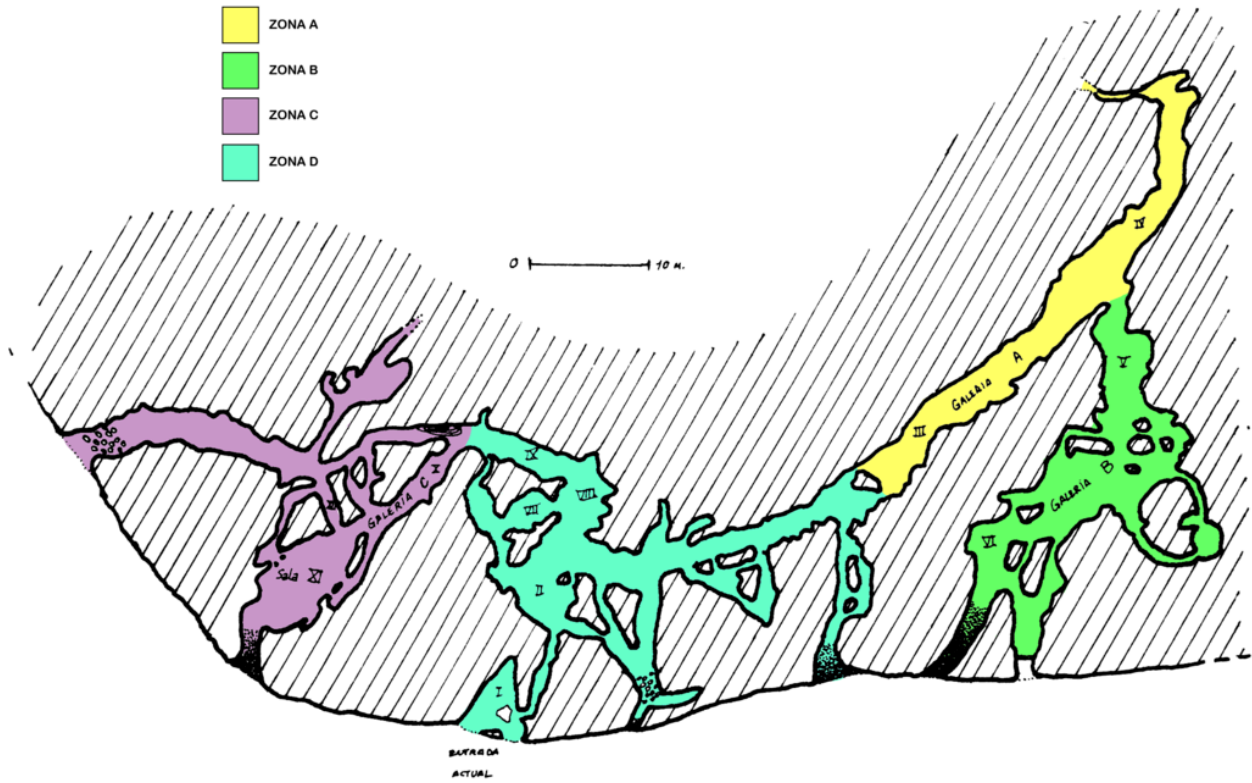
Great Hall of Bulls, Lascaux Cave, France. "Entrance to Lascaux Cave, France" by Thoreno is licensed under CC BY-NC-ND 3.0.



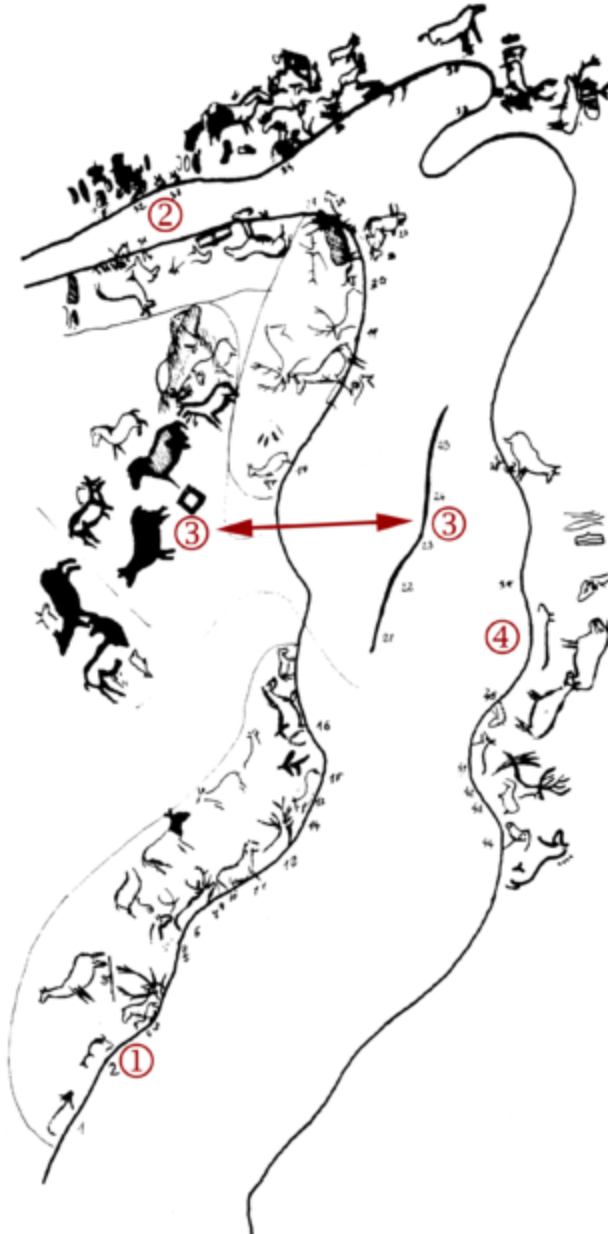
Grotte Chauvet cave, France. "Lions painting, Chauvet Cave (museum replica)" by HTO is in the public domain.



Altamira cave, Spain. "AltamiraBison" by Rameessos is in the public domain.



Map of Gallery Zones within La Pasiega Cave, Spain. "La Pasiega-Plano (Cantabria)" by Locutus Borg is licensed under CC BY-SA 3.0.



Map of art of Gallery A, La Pasiega Cave, Spain (also see map above). "La Pasiega-Galería A-1er Santuario" by Locutus Borg is licensed under CC BY-SA 3.0.

It is of interest that some of the most magnificent animal art is located in the most acoustically resonant areas within caves. It conjures images of our ancestors having special ceremonies or gatherings. Some musical instruments have survived in the form of bone flutes, percussion instruments, and a possible lithophone (a stone xylophone). Their music would have been amplified, and with the addition of flickering flames, the wall images would have seemingly come alive!

AMH invented pottery, with the earliest evidence being fired-clay animals from the Czech Republic. The most famous sculptures are the Venus figurines (i.e. fertility goddesses) that have been found from Western Europe to

Siberia. They are usually clay or stone depictions (also wood, bone, and ivory) of obese women with pronounced breasts and buttocks. They were originally thought to have been produced by men for fertility purposes. A more recent interpretation is that they were self-sculptures by women. That may explain why they were usually faceless and why body parts closest to the eyes were large and disproportionate compared with their tiny feet. Another idea suggests their use as obstetrical aids. Other sculptures were created via bas-relief on walls and rocks, which involves carving some dimensionality into the façade (see the Venus of Laussel, Figure 36.31), and there were also engraved tools, jewelry, and so forth.

The idea of fecund women as fertility goddesses is an example of sympathetic magic, i.e. depicting what one would like to happen. Obese women would have been better able to carry and nurse their babies so that they had better chances of survival. The same could be said for hunting scenes and game animals. Men may have been hoping for safe and successful hunting or an increase in the local game.

Other interesting sculptures came from the following sites or areas:

- Le Tuc d'Audoubert, France:
 - Footprints (see Figure 36.32).
 - Two 1 m clay bisons found propped up in the middle of a small chamber inside the cave.
- Grotte de Montespan, France:
 - Children's footprints.
 - Clay figures of a bear, a lion, and other animals propped up against the cave's walls.
- Czech Republic:
 - Fired animal figurines (27 kya).
 - "Oldest human portrait" (26 kya) carved from mammoth ivory and possibly attached to a staff or baton, showing great detail in the eyes, hair, mouth, and expression.
- El Juyo, Spain (14 kya):
 - Stone figure on which one side of the face is a smiling man and the other is a feline predator, discovered in a possible ceremonial sanctuary.



Venus sculptures from EuropeLeft: **Venus of Laussel**. “Venus-de-Laussel-vue-generale-noir” by 120 is licensed under CC BY 3.0. Top right: **Venus of Willendorf**. “A female Paleolithic figurine, Venus of Willendorf Wellcome M0000440” by Wellcome Images is licensed under CC BY 4.0. Bottom right: **Venus of Brassempouy**. “Venus of Brassempouy” by Jean-Gilles Berizzi is in the public domain.



Footprints in the Cave of Tuc d'Audoubert, France. "Upper Paleolithic period, view of gallery with heel prints, Wellcome M0015047" by Wellcome Images is licensed under CC BY 4.0.

In addition to murals and sculptures, early humans also decorated their tools and bodies. Ocher is found in burials and was likely used to color the body, just as seen in many modern indigenous groups. Depending on the mineral composition, ocher is found in a variety of colors: yellow, orange, rust, brown, etc. They also made and wore jewelry and decorated their clothes with beads. At the Sungir site near Moscow (see more in section on burial practices), two children and an old man were buried in garments that were covered with thousands of ivory beads, thought to have taken an hour each to produce.



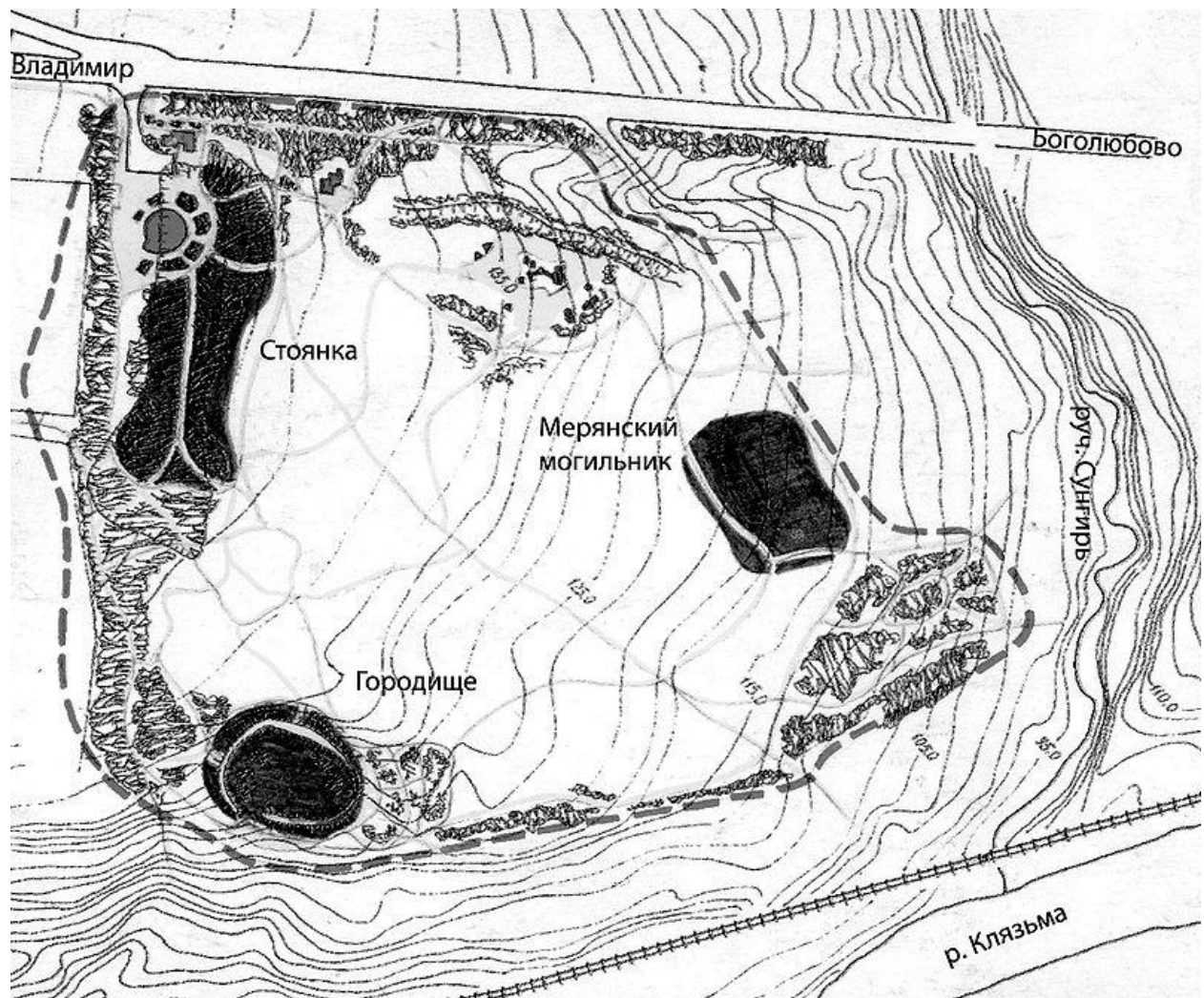
“Lion Man” Aurignacian artifact. Oldest known zoo-/anthropo-morphic figurine (40 kya) from Hohlenstein-Stadel cave, Germany. “Lion man photo” by JDuckeck is in the public domain.

The earliest intentional burials that have been discovered for AMH are from the Middle East and dated to 120–80 kya. As mentioned, they not only buried their dead but also included grave goods and decorated the bodies in ritual fashion. Some Paleolithic cultures cremated remains. Mass burials have been found at some sites. Burial practices included placing the body in a flexed position, as the neandertals did, or supine and, in a few instances, covered with a slab of rock. Two interesting burials were found at Italian and Russian sites. At the site of **Grotte des Enfants**, Italy, two youngsters were decorated with hundreds of shells and pierced animal teeth. At the famous site of **Sungir** (see Figures 36.34 and 36.35) near Moscow, three interesting burials were found. In one grave, a nine-year-old and a twelve- or thirteen-year-old were buried together. They were flanked by two mammoth bone spears. The tusks would have had to have been boiled in a pit of water, using hot rocks, in order to straighten them. Ten thousand beads were sewn to their clothes, and the bodies were decorated with

hundreds of perforated fox canines (remember that each fox has only four large canines!), carved ivory animals, pins, and pendants. They were placed on a bed of ocher. A 40-year-old man was also honored in death. His clothes were also decorated with thousands of beads, and he wore ivory bracelets. He too was placed on a bed of ocher.



Paleolithic burial at Sungir site, Russia. "Sungir-tumba paleolítica" by José-Manuel Benito Álvarez is in the public domain.



Map of Sungir site, Russia. "SungirMap" by ASekirin is licensed under CC BY-SA 3.0.

In conclusion, I found this great timeline of the Upper Paleolithic (Wikipedia contributors 2015):

Timeline of the Upper Paleolithic

45,000–43,000

- Earliest evidence of modern humans found in Europe, in Southern Italy.

43,000–41,000

- At Ksar Akil in Lebanon, ornaments and skeletal remains of modern humans are dated to this

period.

- Denisova hominin live in the Altai Mountains, Russia.

40,000–35,000 BC

- Early cultural center in the Swabian Alps.
- Earliest figurative art (Venus of Schelklingen, Germany).
- Beginning of the Aurignacian.
- The first flutes appear in Germany.
- Lion-Human created from Hohlenstein-Stadel.

39,000 BC

- Most of the giant vertebrates and megafauna in Australia became extinct, around the time of the arrival of humans.

38,000 BC

- Examples of cave art in Spain are dated to around 38,000 BC, making them the oldest examples of art yet discovered in Europe.

38,000 BC–29,000 BC

- Wall painting with horses, rhinoceroses, and aurochs, Chauvet Cave, Vallon-Pont-d'Arc, Ardèche gorge, France, is made.

35,000 BC

- Zar, Yataghyeri, Damjili and Taghlar caves in Azerbaijan
- First evidence of people inhabiting Japan.

32,000 BC

- Europeans understand how to harden clay figures by firing them in an oven at high temperatures.

30,000 BC

- First ground stone tools appear in Japan.
- Invention of the bow and arrow.

29,000–25,000 BC

- Venus of Dolní Věstonice, Czech Republic. It is the oldest known ceramic in the world.
- The “Red Lady of Paviland” lived around 29,000–26,000 years ago. Recent evidence has come to light that he was a tribal chief. (Note: it was a male skeleton dyed with red ocher.)

23,000 BC

- Venus of Petřkovice (*Petrkovická venuše* in Czech) from Petřkovice in Ostrava, Czech Republic, was made.

22,000 BC

- Last Glacial Maximum.
- Venus of Brassempouy, Grotte du Pape, Brassempouy, Landes, France, was made.
- Venus of Willendorf, Austria, was made.

20,000 BC

- Last Glacial Maximum. Mean sea levels are believed to be 110 to 120 meters (361 to 394 ft) *lower than present*, with the direct implication that many coastal and lower riverine valley archaeological sites of interest are today under water.

18,000 BC

- Spotted Horses, Pech Merle cave, Dordogne, France are painted.

18,000 BC–11,000 BC

- Ibex-headed spear thrower, from Le Mas d’Azil, Ariège, France.

18,000 BC–12,000 BC

- Mammoth-bone village in Mezhirich, Ukraine, is inhabited.

17,000 BC

- Spotted human hands, Pech Merle cave, Dordogne, France are painted.

17,000 BC–15,000 BC

- Hall of Bulls, Lascaux caves, France is painted.
- Bird-Headed man with bison and Rhinoceros, Lascaux caves, is painted.
- Lamp with ibex design, from La Mouthe cave, Dordogne, France, is made.

16,500 BC

- Paintings in Cosquer cave, where the cave mouth is now under water at Cap Margiou, France were made.

15,000 BC

- Bison, Le Tuc d’Audoubert, Ariège, France.

15,000 BC–12,000 BC

- Paleo-Indians move across North America, then southward through Central America.
- “Pregnant woman” from Laugerie-Basse, France was made.

14,000 BC

- Paleo-Indians searched for big game near what is now the Hovenweep National Monument in Colorado and Utah.

- Bison, on the ceiling of a cave at Altamira, Spain, is painted.
- Domestication of reindeer.

13,000 BC

- Beginning of the Holocene extinction.
- Earliest evidence of warfare (found in the Americas).

11,500 BC-10,000 BC

- Wooden buildings in South America (Chile), first pottery vessels (Japan).

11,000 BC

- First evidence of human settlement in Argentina.
- The “Arlington Springs Man” dies on the island of Santa Rosa, off the coast of California.
- Human remains deposited in caves which are now located off the coast of Yucatán.

10,500 BC

- Stone Age Creswellian culture settlement on Hengistbury Head, England, dates from around this year.

....And the rest, as they say, is “history”!

16. Paranthropines

The paranthropines are three species of fossil hominins that exhibited hyper-robust masticatory apparatus, as evidenced by their heavy faces and mandibles, huge molars, and muscle insertions. They were included in the genus *Australopithecus* for many years, but the original genus invented by Robert Broom for the South African form, *Paranthropus robustus*, has been revived for at least two of the species. Chronologically, the earliest species was *aethiopicus*, and some researchers still assign them to *Australopithecus*. The second oldest is *Paranthropus boisei*, and both *Au. aethiopicus* and *P. boisei* are from East African sites. The South African and youngest species is *P. robustus*. The last of the paranthropines died out ~1 mya, 1.7 mya after *Au. aethiopicus*'s first appearance in the fossil record. They were a very interesting and apparently successful group of animals that adapted to the changing African landscape by expanding their dietary niche. The geographic range of the eastern species stretched down the “**hominin corridor**” from Ethiopia to Malawi, whereas the South African form is known only from South Africa. While it is thought that their preferred foods were similar to the more gracile forms, they could fall back on tougher and harder foods when resources became scarce.

17. Australopithecus/Paranthropus aethiopicus

Australopithecus/Paranthropus aethiopicus (2.7–2.3 mya)

(“southern ape” / “beside human” / Ethiopia)



Model of *Paranthropus aethiopicus*. “*Paranthropus aethiopicus*” by Nrkpan is licensed under CC BY-SA 3.0.

SITES

Ethiopia: Shungura Deposits

Kenya: West Lake Turkana

PEOPLE

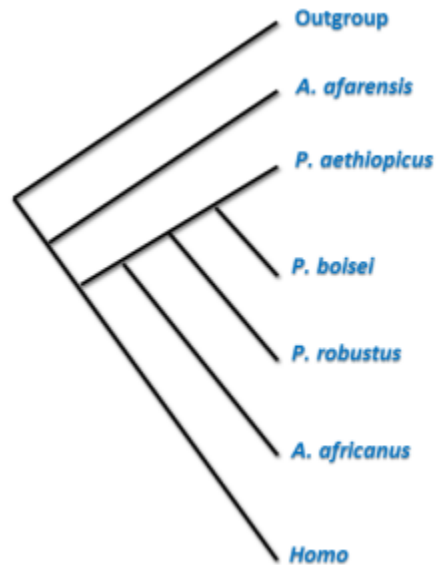
Yves Coppens, Camille Arambourg, and Alan Walker

INTRODUCTION

Australopithecus aethiopicus is the most primitive of the robust species. I use genus *Australopithecus* because it is thought to be descended from *Au. afarensis*. In addition, *Paranthropus* was the genus name assigned to the South African robust form, *P. robustus*, and questions remain as to whether the two species are related.

PHYLOGENY

There are multiple lines of evidence to support *Au. aethiopicus* as a descendent species of *Au. afarensis*. While some believe that *Au. aethiopicus* gave rise to *P. boisei*, others link *P. boisei* with *P. robustus* in a different clade, with *Au. africanus* as their common ancestor. More recently discovered material within the geographic range of *Au. aethiopicus* supports the *Au. aethiopicus* → *P. boisei* evolutionary scenario. The dates of the new fossils fall between the two species, and they possess intermediate or transitional characteristics. Figure 17.2 shows one cladistic schema that illustrates how some researchers suggest these species were related. This particular scenario shows the authors' belief that *Au. africanus* is a robust form.



Cladistic analysis of early hominins. "Cladistic analysis of early hominins" by Charles T. G. Clarke is licensed under CC BY-SA 3.0.

DISCOVERY AND GEOGRAPHIC RANGE

In 1967, the earliest *Au. aethiopicus* fossils were discovered by Yves Coppens and Camille Arambourg in the Shungura deposits at the site of Omo in southern Ethiopia. They assigned them to a new genus and species, *Paraustralopithecus aethiopicus*. While it was debatable as to whether they actually had a new species, the discovery of the "Black Skull" (see Figure 17.1) in the West Lake Turkana region of Kenya by Alan Walker in 1985 put any doubts to rest. At that time, the species was added to genus *Australopithecus* because it was thought to be descended from *Au. afarensis*. There were then three recognized species of robust australopiths in Africa, and efforts to determine their phylogenetic relationships began.

The Black Skull or KNM-WT (Kenya National Museum – West Turkana) 15000 was a magnificent find. The almost complete skull was stained from manganese, but it is always fun to sing scary movie music to my students when introducing ... THE BLACK SKULL! (Figure 17.3 ... for fun!)



Skull and crossbones. "Crossbones (PSF)" by Pearson Scott Foresman is in the public domain.

PHYSICAL CHARACTERISTICS

A unique characteristic that ties *Au. aethiopicus* to *P. boisei* is a heart-shaped foramen magnum, as opposed to the more ovoid form seen in *Au. africanus* and *P. robustus*. Primitive characteristics shared with *Au. afarensis* are the flat cranial base, small brain (~410 cc), long molars (mesiodistally, i.e. front to back versus side to side), and the degree of prognathism in the lower face. Because their faces were so broad and their brains so small, they exhibit a high degree of postorbital constriction (also known as waisting), i.e. the area between the face and braincase is narrow. Derived robust characteristics are buttressing of the skull, face, and mandible. Their muscles of mastication were incredibly strong, as evidenced by the sagittal crest running down the midline of their skull where the temporalis muscle originated. The sagittal crest was higher and more posteriorly placed than in the two more derived robust species. The zygomatics were large and flared to allow for passage of the temporalis muscle from the sagittal crest to insert on the mandible and to expand the attachment site for the masseter muscle, the other large muscle of mastication (see Figure 17.4). The zygomatics were more forwardly flared than in the other two robust species. They also had heavy nuchal (posterior neck) muscles to support the weight of their heavy face and skull, and the attachment sites of those muscles on the posterior skull was also an expanded crest that converged with the sagittal crest, i.e. a compound sagittal-nuchal crest. Large brow ridges in the robust species offset the stress generated by biting down on hard foods. However, *Au. aethiopicus*'s brows were smaller than the other two species. Their third maxillary molars were convergent, meaning they were positioned more medially than the first and second. While some researchers disagree, others find evidence for a more derived venous sinus system in the crania of the robust forms. The system consists of large collecting veins that ultimately empty into the jugular veins, allowing for rapid, gravity-fed blood drain from the brain, in order to keep fresh blood pumping in via several arterial systems. The largest and most superficial of those sinuses (see Figure 17.5) leave impressions on the inside of the skull vault. Dean Falk's "Radiator Theory" argues that our ancestors needed to keep their brains cool as they increased in size in a hot, open environment. The system became more complex after the time of the australopiths.

Review of Primitive Characteristics

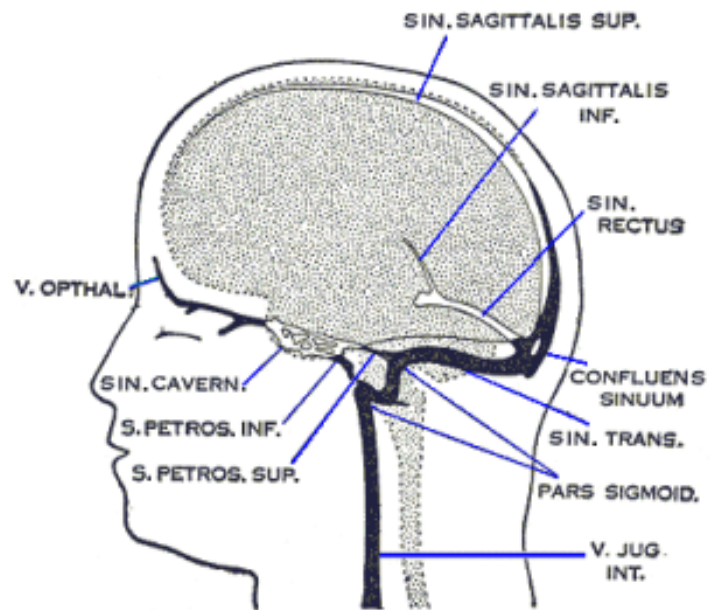
- Flat cranial base.
- Small brain.
- Long molars.
- Prognathic.

Review of Derived Characteristics

- Heart-shaped foramen magnum.
- Robust skull, face, and mandible.
- Large, compound sagittal-nuchal crest.
- Large brow ridges.
- Pronounced postorbital constriction.
- Large, powerful muscles of mastication.
- Large forwardly flared zygomatics with a large zygomatic arch.
- Convergent maxillary third molars.
- Possible derived venous sinus system.



Muscles of mastication (Red=temporalis and peach=masseter)
Illustration by Keenan Taylor



Cranial sinus system (SIN. = sinus). Based on Gray's Anatomy Plate 488.
"Gray488 blue" by Wikid77 is in the public domain.

ENVIRONMENT AND WAY OF LIFE

As mentioned, there is evidence that *Au. afarensis* was more terrestrial than the southern australopith clade, suggesting that the classic ape environment had diminished. We know that grasslands were expanding and woodlands were shrinking. Since it is assumed that *Au. aethiopicus* is descended from *Au. afarensis*, the environment was favoring species with dietary adaptations that allowed them to survive.



"Australopithecus aethiopicus tool use" by Keenan Taylor.

Postscript

It can certainly be said that we humans are special relative to past and present species. We have changed the world in both wonderful and terrible ways. Let us hope that (1) we can understand and appreciate our common origin as well as our cultural and physical differences so that we can live together as a global community; (2) we continue to advance technologically in order to correct the problems, afflictions, and mistakes of the past, present, and future; and (3) our time on earth will continue so that we do not become just another extinct hominin in the fossil record

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