

THE HISTORY OF OUR TRIBE - HOMININI



Barbara Welker
SUNY Geneseo

The History of Our Tribe - Hominini

Barbara Welker

SUNY Geneseo

This text is disseminated via the Open Education Resource (OER) LibreTexts Project (<https://LibreTexts.org>) and like the thousands of other texts available within this powerful platform, it is freely available for reading, printing, and "consuming."

The LibreTexts mission is to bring together students, faculty, and scholars in a collaborative effort to provide an accessible, and comprehensive platform that empowers our community to develop, curate, adapt, and adopt openly licensed resources and technologies; through these efforts we can reduce the financial burden born from traditional educational resource costs, ensuring education is more accessible for students and communities worldwide.

Most, but not all, pages in the library have licenses that may allow individuals to make changes, save, and print this book. Carefully consult the applicable license(s) before pursuing such effects. Instructors can adopt existing LibreTexts texts or Remix them to quickly build course-specific resources to meet the needs of their students. Unlike traditional textbooks, LibreTexts' web based origins allow powerful integration of advanced features and new technologies to support learning.



LibreTexts is the adaptable, user-friendly non-profit open education resource platform that educators trust for creating, customizing, and sharing accessible, interactive textbooks, adaptive homework, and ancillary materials. We collaborate with individuals and organizations to champion open education initiatives, support institutional publishing programs, drive curriculum development projects, and more.

The LibreTexts libraries are Powered by [NICE CXone Expert](#) and was supported by the Department of Education Open Textbook Pilot Project, the California Education Learning Lab, the UC Davis Office of the Provost, the UC Davis Library, the California State University Affordable Learning Solutions Program, and Merlot. This material is based upon work supported by the National Science Foundation under Grant No. 1246120, 1525057, and 1413739.

Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation nor the US Department of Education.

Have questions or comments? For information about adoptions or adaptations contact info@LibreTexts.org or visit our main website at <https://LibreTexts.org>.

This text was compiled on 06/13/2026

TABLE OF CONTENTS

Licensing

About the Author

1: Introduction to Paleoanthropology

- 1.1: Paleoanthropology
- 1.2: Primate Classification
- 1.3: Primate Evolution
- 1.4: Primate Social Organization
- 1.5: What is a Hominin

2: Miocene Epoch

- 2.1: Introduction to the Miocene Epoch
- 2.2: Sahelanthropus tchadensis
- 2.3: Orrorin tugenensis
- 2.4: Ardipithecus ramidus and Ardipithecus kadabba

3: Pliocene Epoch

- 3.1: Introduction to the Pliocene Epoch
- 3.2: Australopithecus anamensis
- 3.3: Gracile Australopiths
- 3.4: Australopithecus afarensis
- 3.5: Australopithecus bahrelghazali
- 3.6: Kenyanthropus platyops
- 3.7: Australopithecus prometheus or africanus
- 3.8: Australopithecus africanus

4: Pleistocene Epoch

- 4.1: Introduction to the Pleistocene Epoch
- 4.2: Paranthropines
- 4.3: Australopithecus/Paranthropus aethiopicus
- 4.4: Paranthropus boisei
- 4.5: Paranthropus robustus
- 4.6: Australopithecus garhi
- 4.7: Australopithecus sediba
- 4.8: Genus Homo
- 4.9: Homo habilis
- 4.10: Homo rudolfensis
- 4.11: Homo species indeterminate
- 4.12: Homo naledi
- 4.13: The "erectus Grade"
- 4.14: Homo ergaster
- 4.15: Homo erectus
- 4.16: Homo georgicus
- 4.17: Homo antecessor
- 4.18: Homo floresiensis

- [4.19: Homo heidelbergensis](#)
- [4.20: The Denisovans](#)
- [4.21: Homo neanderthalensis](#)
- [4.22: Homo sapiens](#)

[Bibliography](#)

[Postscript](#)

[Index](#)

[Detailed Licensing](#)

Licensing

A detailed breakdown of this resource's licensing can be found in [Back Matter/Detailed Licensing](#).

About the Author

Barbara Welker is Associate Professor of Anthropology at SUNY Geneseo. She received her Ph.D. in 2004 from SUNY Buffalo. She is a biological anthropologist, anatomist, primatologist, and behavioral ecologist. She teaches courses in biological anthropology, e.g. “Human Evolution”, “Human Ecology”, and “Primates”, and anatomy, e.g. “Human Osteology”. Her research involves feeding ecology and color vision genetics in mantled howler monkeys in Costa Rica.

CHAPTER OVERVIEW

1: Introduction to Paleoanthropology

[1.1: Paleoanthropology](#)

[1.2: Primate Classification](#)

[1.3: Primate Evolution](#)

[1.4: Primate Social Organization](#)

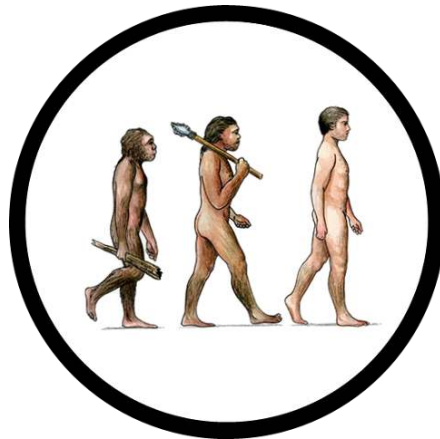
[1.5: What is a Hominin](#)

This page titled [1: Introduction to Paleoanthropology](#) is shared under a [CC BY-NC-SA 4.0](#) license and was authored, remixed, and/or curated by [Barbara Welker](#) via [source content](#) that was edited to the style and standards of the LibreTexts platform.

1.1: Paleoanthropology

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.



Human evolution. “[Human Evolution Icon](#)” by [Magnetic Hyena](#) is licensed under [CC BY-SA 3.0](#).

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).



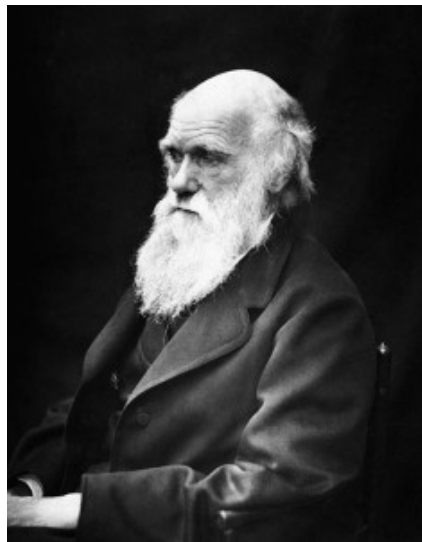
Pollen grains under scanning electron microscope. “[Misc pollen colorized](#)” by [Dartmouth Electron Microscope Facility](#), [Dartmouth College](#) is in the public domain.

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 PALEOENVIRONMENTS

A 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.

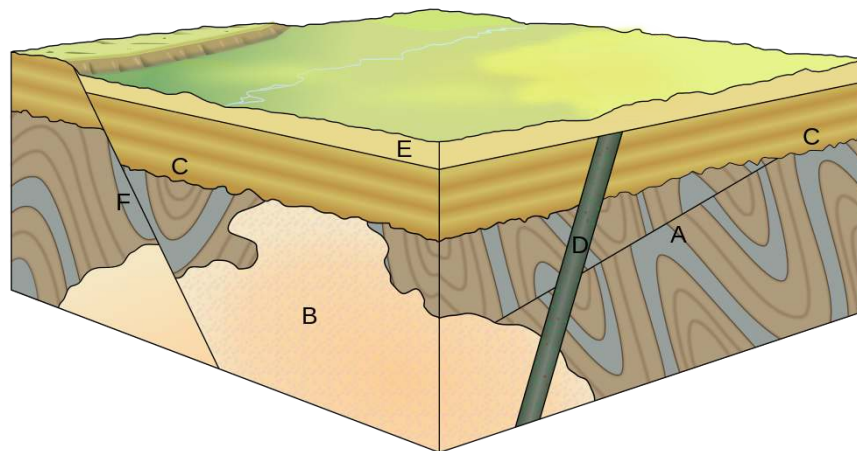


Diagram illustrating cross-cutting relations in geology. These relations can be used to give structures a relative age. Explanations: A – folded rock strata cut by a thrust fault; B – large intrusion (cutting through A); C – erosional angular unconformity (cutting off A & B) on which rock strata were 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”: 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 → Argon-40 and Argon-40 → 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

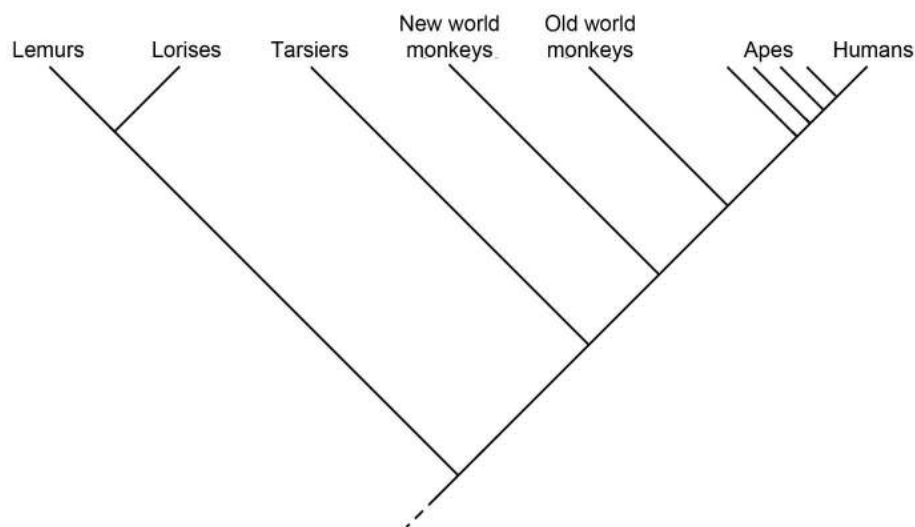
1. Henke W, Tattersall I, editors. 2006. *Handbook of paleoanthropology*. New York (NY): Springer; [accessed 2015 Aug 15].
http://www.evolbiol.ru/large_files/handbook_paleoanthropology.pdf.

This page titled [1.1: Paleoanthropology](#) is shared under a [CC BY-NC-SA 4.0](#) license and was authored, remixed, and/or curated by [Barbara Welker](#) via [source content](#) that was edited to the style and standards of the LibreTexts platform.

1.2: Primate Classification

SYSTEMATICS: THE SCIENCE OF CLASSIFICATION

There are two means by which scientists classify organisms, **classic taxonomy** and **cladistics**. Paleanthropologists 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 Bockman, CC BY-SA 3.0.

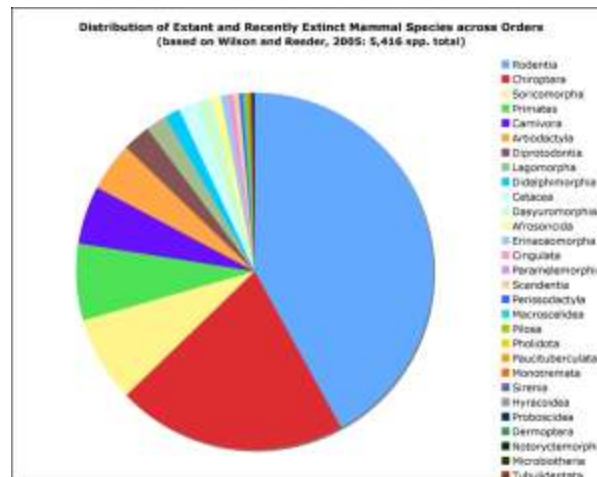
The following terms are used to delineate characteristics in cladistics:

- **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.

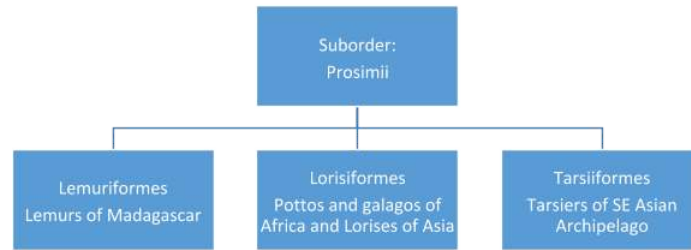


Orders within the class Mammalia. “[Mammal species pie chart](#)” by [Aranæ](#) is in the public domain.

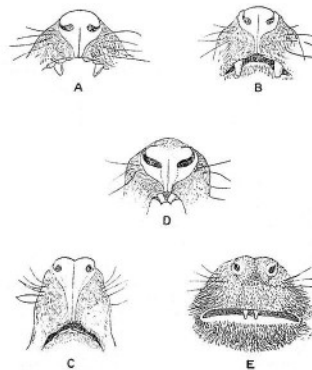
PRIMATE EVOLUTIONARY TRENDS

- 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.

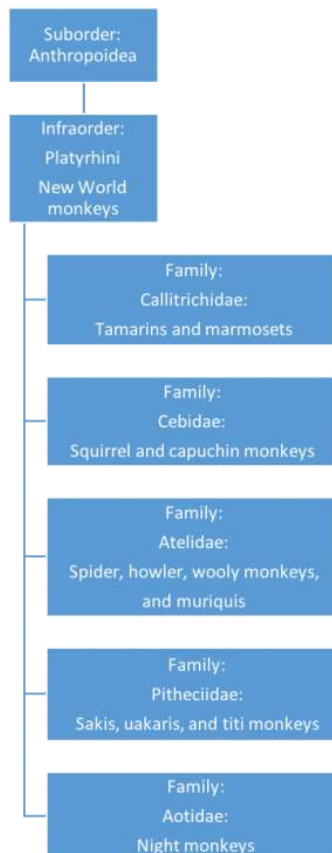
Taxonomic charts of the living primates can be found below. The primates are divided into two major taxonomic groups: strepsirrhines, which retain **primitive** characteristics, such as the lemurs of Madagascar and the bushbabies of Africa, and the more derived haplorrhines, that is, the tarsier, monkeys, 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 haplorrhines have simpler, dry noses and do not smell as good!



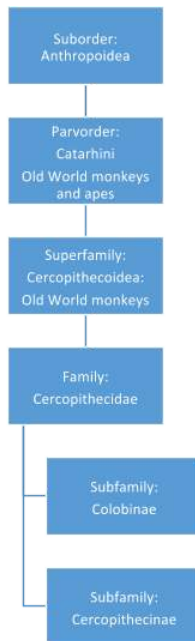
Prosimian classification.



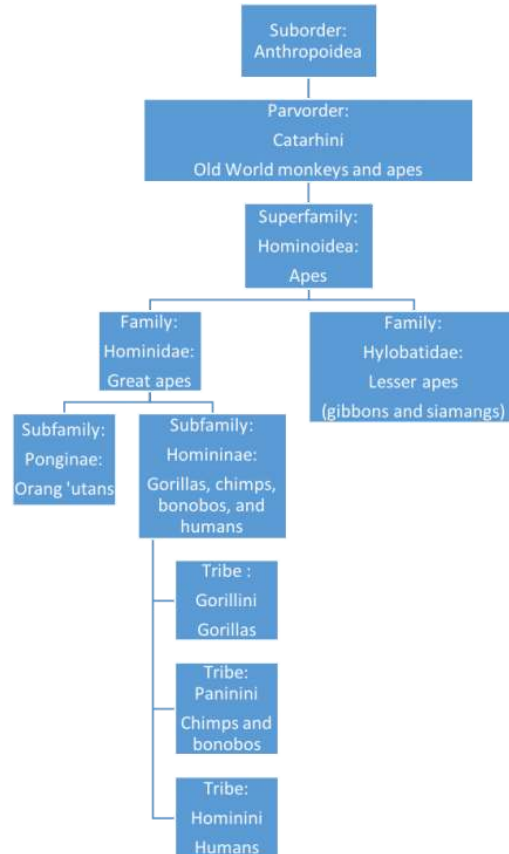
Prosimian noses (A through D) and the nose of a New World monkey (E). “[Prosimian noses](#)” by [Reginald Innes Pocock](#) is in the public domain.



New World anthropoid classification.



Old World monkey classification.

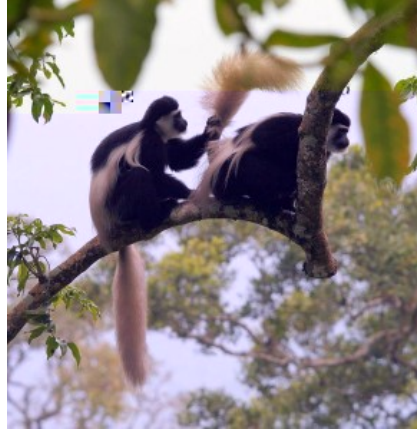


Ape classification.

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.

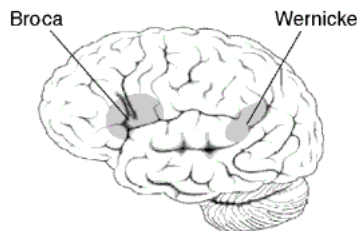
Apes live a relatively long time and consequently all of our life stages are prolonged as well, especially our juvenile dependency period. Of the nonhuman primates, orangutans win. Female orangutans have an interbirth interval (i.e. a period of time in between births) of eight years and juveniles do 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.



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.

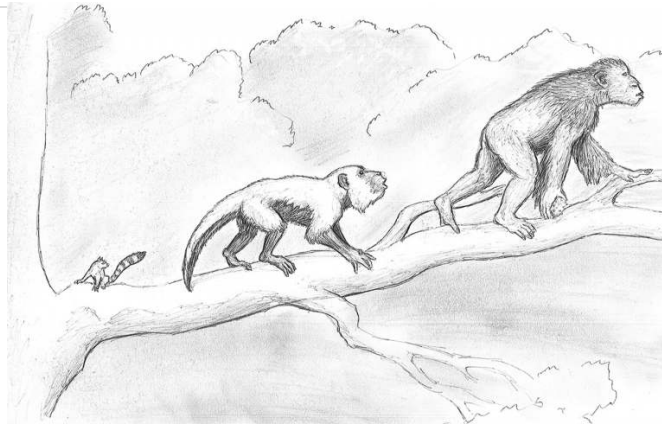
Gorillas live in one-male groups, except for the mountain gorillas, where two males may reside, an older dominant and younger subordinate. Both sexes tend to leave their natal group. Females join a male who may or may not already have other female mates.

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.

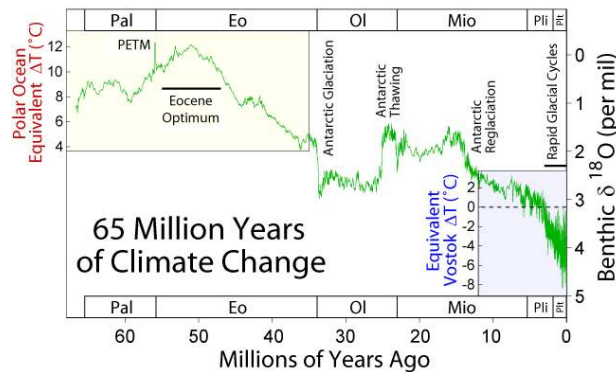
This page titled [1.2: Primate Classification](#) is shared under a [CC BY-NC-SA 4.0](#) license and was authored, remixed, and/or curated by [Barbara Welker](#) via [source content](#) that was edited to the style and standards of the LibreTexts platform.

1.3: Primate Evolution

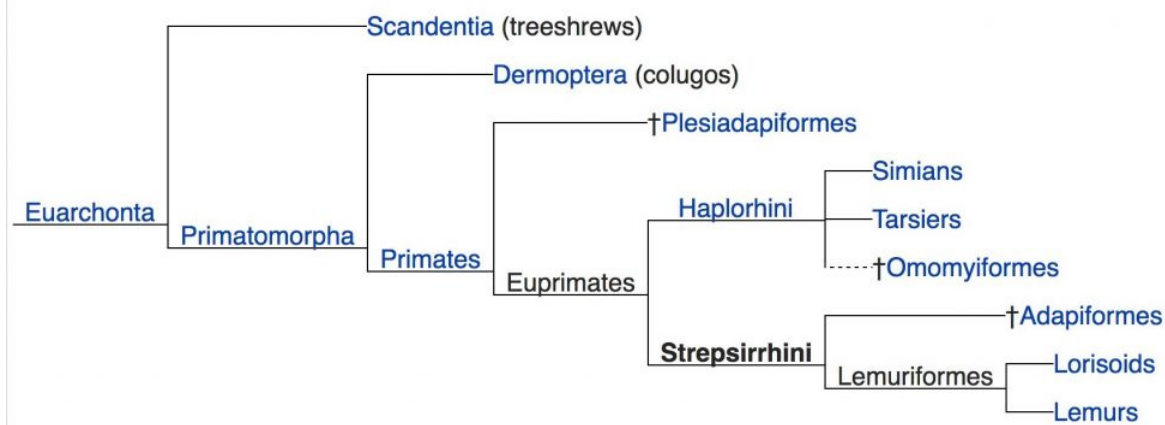


Anthropoid Evolution by Keenan Taylor.

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. “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 sinensis. 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](https://creativecommons.org/licenses/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.

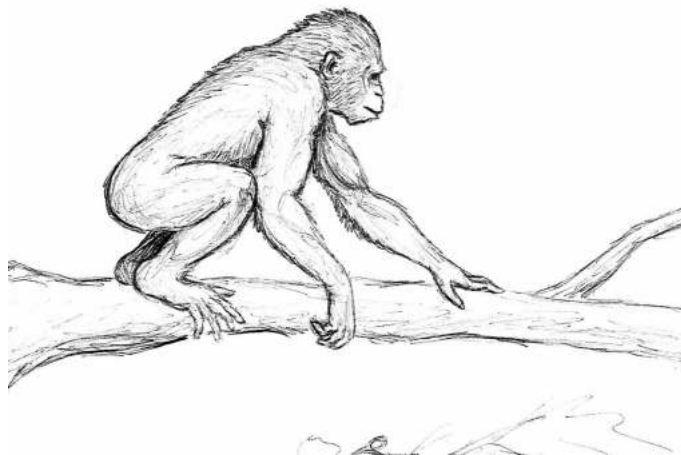


“Proconsul NT” by Nobu Tamura is licensed under [CC BY-SA 3.0](#).

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 *Otavipithecus* (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.

This page titled [1.3: Primate Evolution](#) is shared under a [CC BY-NC-SA 4.0](#) license and was authored, remixed, and/or curated by [Barbara Welker](#) via [source content](#) that was edited to the style and standards of the LibreTexts platform.

1.4: Primate Social Organization

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.



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

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 woolly 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.

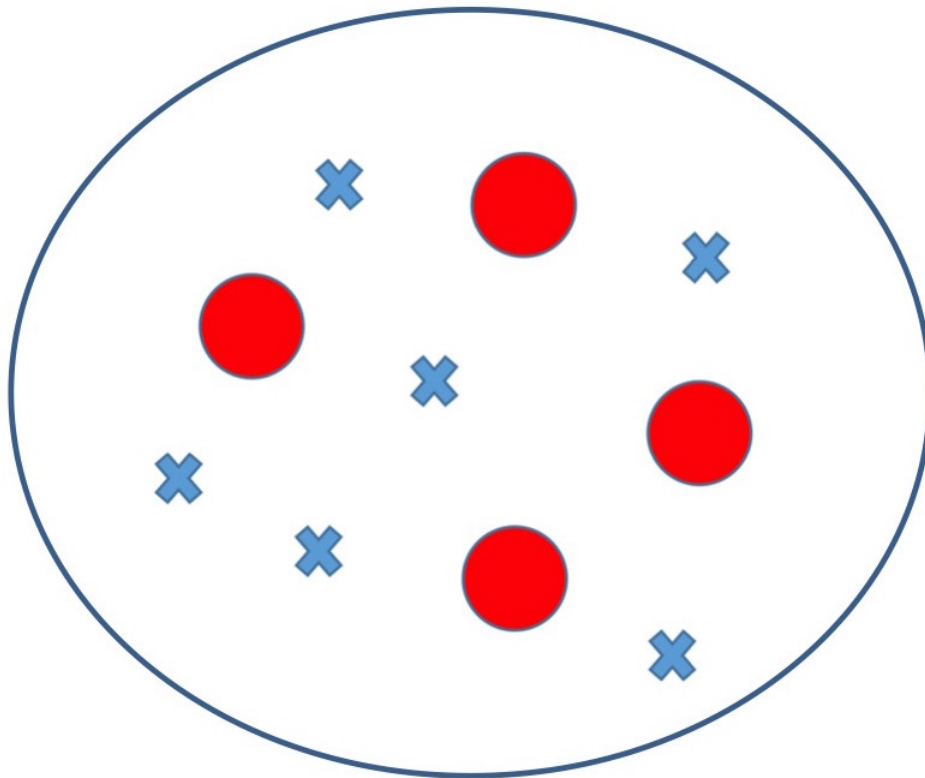
While the OMG makes sense for the colobines and their high leaf diet, it is not as clear why the more generalist guenons exhibit the same pattern. Like the colobine monkeys of Africa and Asia, it is possible that the ancestor of the extant arboreal guenons never left the trees and thus did not evolve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

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.



Emperor tamarin. “[Emperor Tamarin SF ZOO](#)” by [Brocken Inaglory](#) is licensed under [CC BY-SA 3.0](#).

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 muriqui 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](#)

This page titled [1.4: Primate Social Organization](#) is shared under a [CC BY-NC-SA 4.0](#) license and was authored, remixed, and/or curated by [Barbara Welker](#) via [source content](#) that was edited to the style and standards of the LibreTexts platform.

1.5: What is a Hominim

We are hominins, as are all those bipedal apes that came before us. Figure 1.5.1 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!

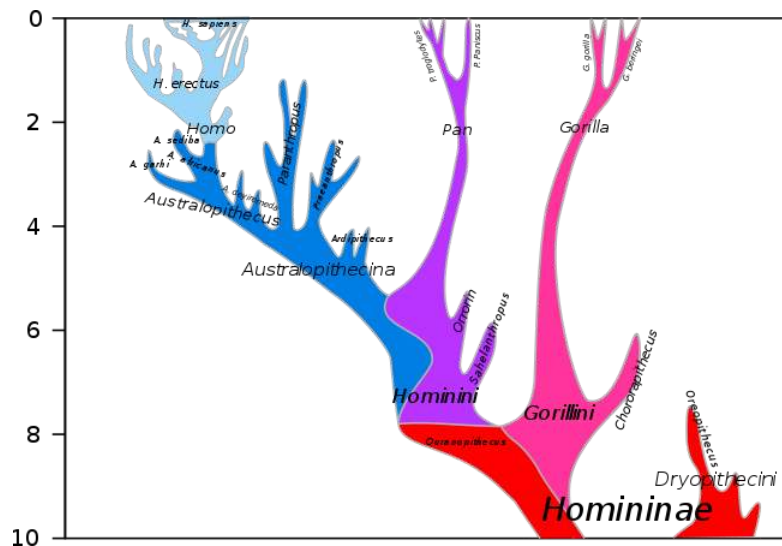


Figure 1.5.1: Hominin species through time. Model of the phylogeny of Hominini over the past 10 million years. (CC BY-SA 4.0; Dbachmann)

ANATOMICAL TERMS

To adequately understand a discussion of hominin evolution and appreciate changes over time, some basic anatomical information is necessary. It is also necessary 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*) 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.

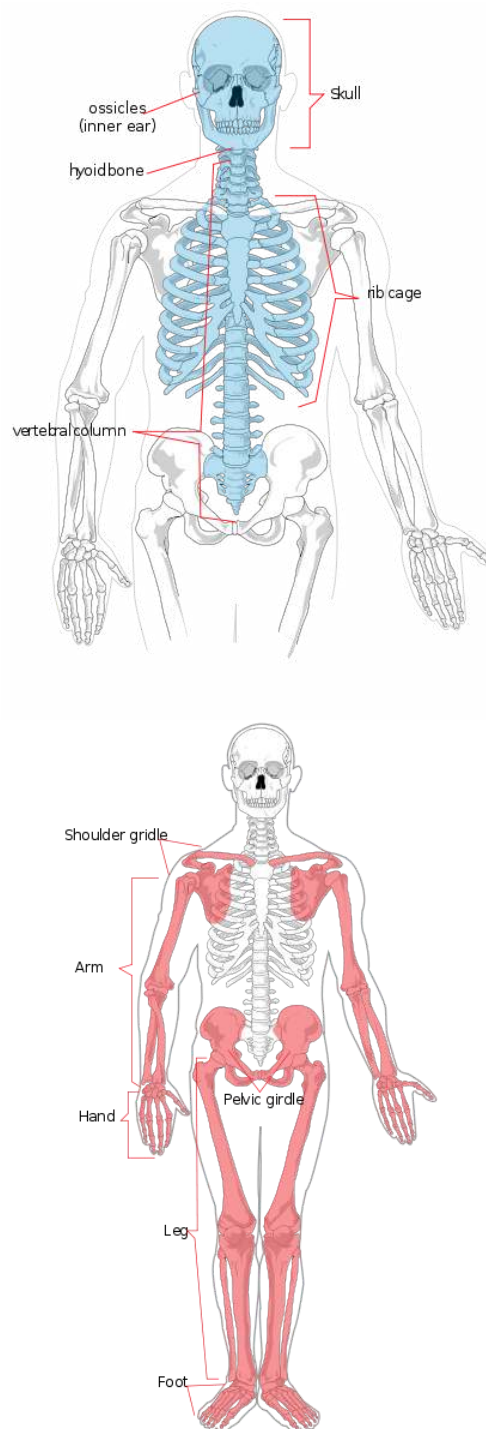


Figure 1.5.2: Human axial skeleton (shaded). “[Axial skeleton diagram](#)” by Mariana Ruiz Villarreal is in the public domain. Human appendicular skeleton (shaded). “[Appendicular skeleton diagram](#)” by Mariana Ruiz Villarreal is in the public domain.

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.

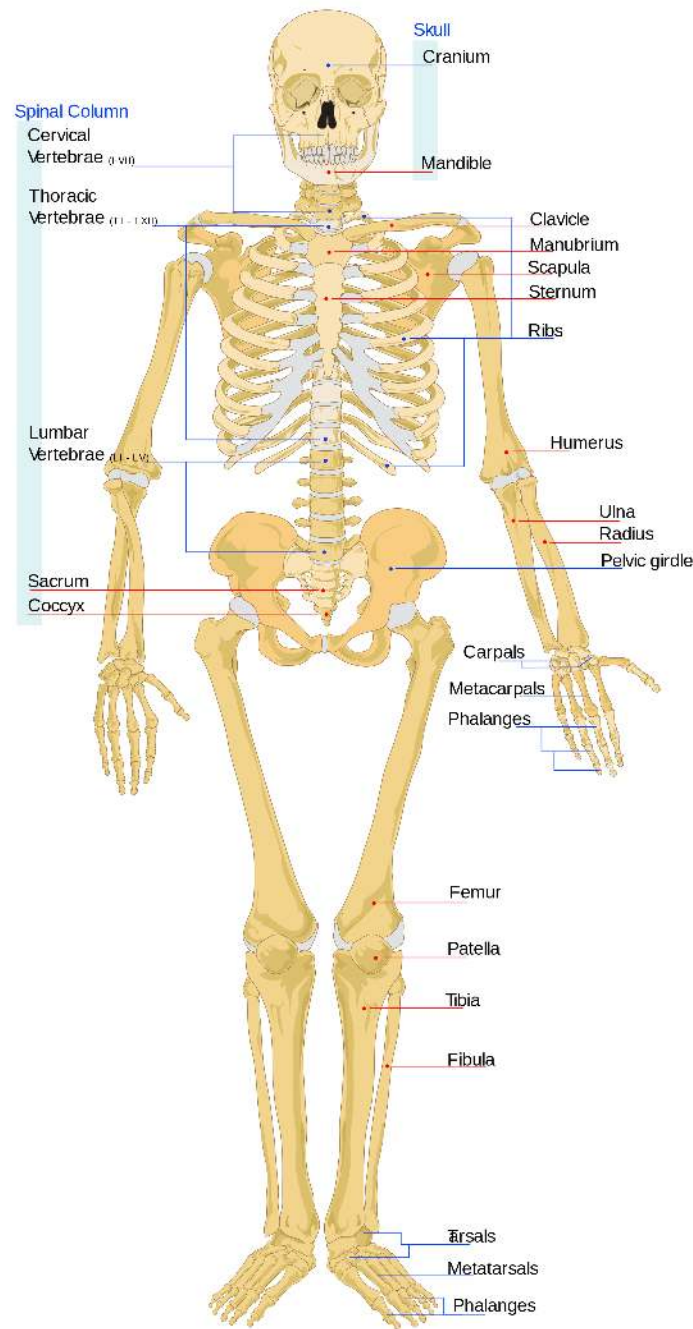


Figure 1.5.3: Human skeleton. “[Human skeleton front en](#)” by Mariana Ruiz Villarreal is in the public domain.

THE EVOLUTION OF BIPEDALISM

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 *ardipiths*, 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.

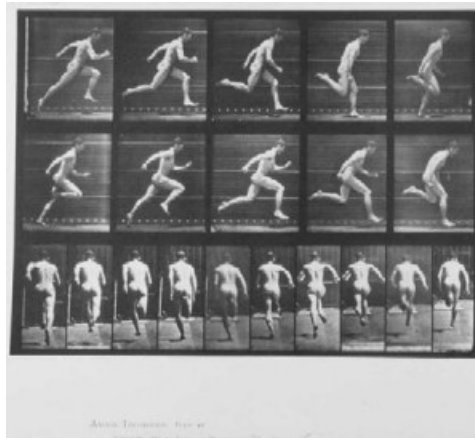


Figure 1.5.4: Running man. "Nude Man Running" by Eadweard Muybridge is in the public domain.

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 leglength; 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.

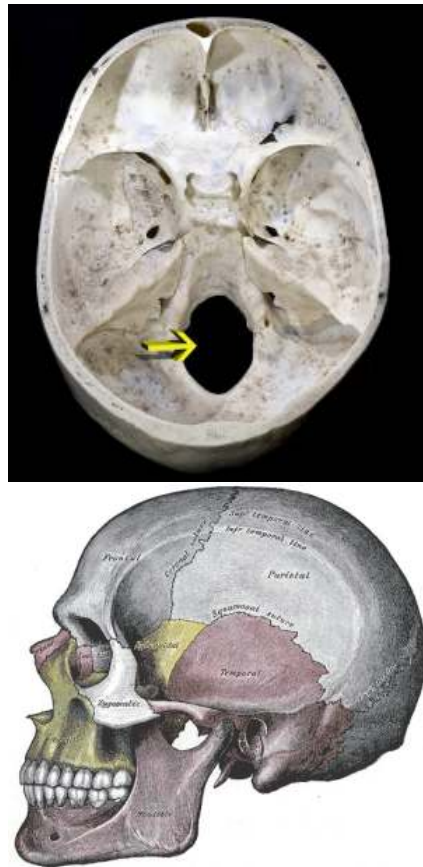


Figure 1.5.5: Foramen magnum indicated from inside skull vault. “Crane4 Foramen magnum” by Didier Descouens is licensed under [CC BY-SA 3.0](#). Bones of the skull. Plate 188 from Gray’s Anatomy. “Side view of the skull” by Henry Vandyke Carter is in the public domain.

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 (Figure 1.5.6). 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.

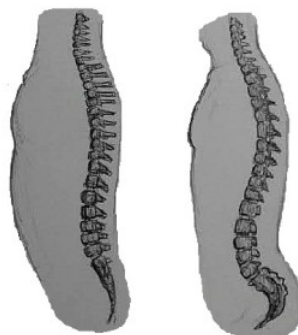


Figure 1.5.6: Chimp (left) vs. human spine (right). Illustration by Keenan Taylor

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 (Figure 1.5.6). 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:

$$IMI = \left(\frac{armlength}{leglength} \right) \times 100 \quad (1.5.1)$$

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.

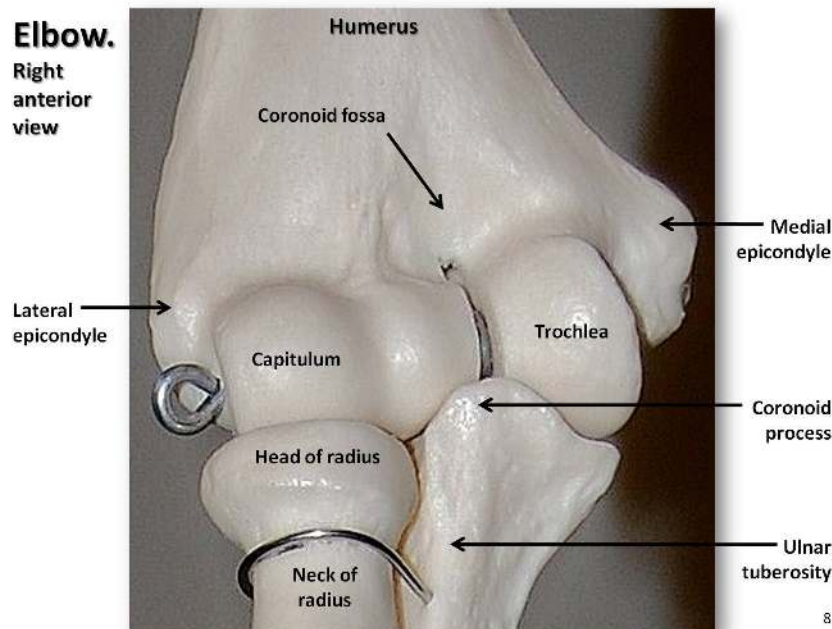


Figure 1.5.7: Human elbow. “*Bones of the elbow*” by Rob Swatski is licensed CC-BY-NC.

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 innominates 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** (Figure 1.5.6). 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.

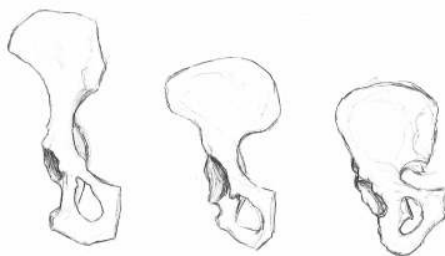


Figure 1.5.8: Left innominates of chimp (left), australopith (center), and human (right). Illustration by Keenan Taylor.

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.

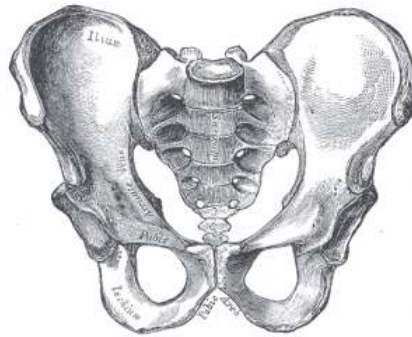


Figure 1.5.9: Human pelvic morphology: The three fused bones of the innominates (ilium, ischium, and pubis), sacrum, and coccyx. Plate 241 from Gray's Anatomy. "Male pelvis" by Henry Vandyke Carter is in the public domain.

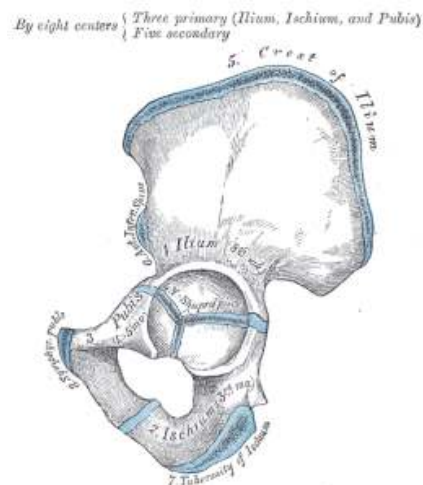


Figure 1.5.10: Ossified joints of the bones of a left innominate (lateral view). Plate 237 from Gray's Anatomy. Note where the ilium, ischium, and pubis articulate at the acetabulum.

"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 (Figure 1.5.11). 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 (Figure 1.5.11, "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.

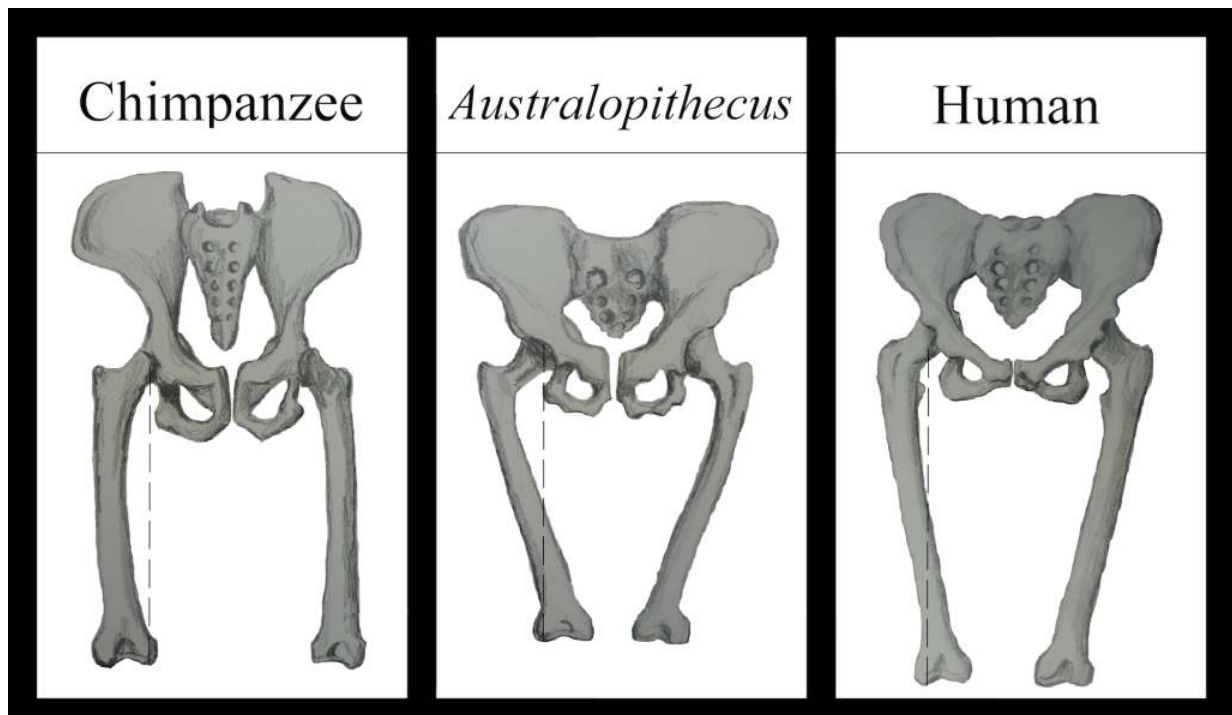


Figure 1.5.11: Pelvic girdle and weight loading on knee joint. Illustration by Keenan Taylor.

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.

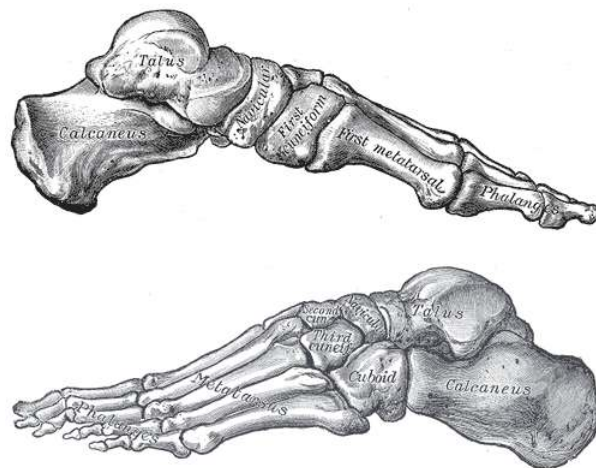


Figure 1.5.12: Human foot bones. Plates 290 and 291 from Gray's Anatomy. "Skeleton of foot. Medial aspect" and "Skeleton of foot. Lateral aspect" by Henry Vandyke Carter are in the public domain.

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 (Table 1.5.1). While all of the morphological changes involved with bipedalism are hominin trends, there are also relevant characteristics in other parts of the body.

Table 1.5.1: **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.

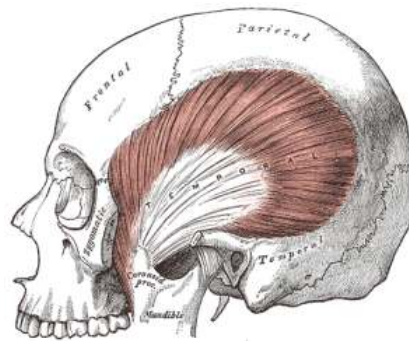


Figure 1.5.13: *Temporalis muscle: Originates on frontal, parietal, and temporal bones and inserts on mandible. (Zygomatic is shown as having been cut to reveal underlying muscle. Plate 382 from Gray's Anatomy. "The temporalis" by Henry Vandyke Carter is in the public domain.*

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: ardiipiths.
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.

This page titled 1.5: What is a Hominin is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Barbara Welker via source content that was edited to the style and standards of the LibreTexts platform.

CHAPTER OVERVIEW

2: Miocene Epoch

The Miocene epoch extends from about 23.03 to 5.333 million years ago (Ma). The Miocene was named by Charles Lyell and means "less recent" because it has 18% fewer modern sea invertebrates than the Pliocene. The Miocene follows the Oligocene and is followed by the Pliocene epoch.

[2.1: Introduction to the Miocene Epoch](#)

[2.2: Sahelanthropus tchadensis](#)

[2.3: Orrorin tugenensis](#)

[2.4: Ardipithecus ramidus and Ardipithecus kadabba](#)

This page titled [2: Miocene Epoch](#) is shared under a [CC BY-NC-SA 4.0](#) license and was authored, remixed, and/or curated by [Barbara Welker](#) via [source content](#) that was edited to the style and standards of the LibreTexts platform.