

EARLY HOMINID EVOLUTION

A Minimalist Approach - Part 1

INTRODUCTION

Our knowledge and understanding of the evolutionary past has changed dramatically over the past decade. In addition to the important insights added by molecular biology (genetics), recent fossil finds continue to add new pieces to the puzzle of the past. Up until just the turn of this century, the hominid fossil record only extended back to nearly 4 million years ago. Within the last 15 years, however, a number of significant discoveries have been “rewriting” our evolutionary theories, pushing back the appearance of our very earliest bipedal ancestors nearly 2-3 million years---close to the time that DNA evidence suggests the hominid lineage split from the common ancestral population we shared with the apes. A key theme in our evolutionary story is that of **DIVERSITY**. That diversity stems from the molecule of life—DNA---which continually gives species a chance to adapt and survive in ever changing environments.

As we survey some of the ancestors and relatives that make up our ever expanding family tree, it’s useful to think of **HOMINID EVOLUTION** as consisting of a series of **SEQUENTIAL ADAPTIVE RADIATIONS**. All of these radiations (or *punctuated* bursts of evolutionary activity) coincide with major changes in climate. Not surprisingly, these selective pressures appear to be producing lots of *variation* for natural selection to experiment with.

Classification and Evolutionary Trends

It was established in the early 20th century that the defining characteristic of the hominid lineage was **bipedalism**. Larger brains and cultural adaptations occur much later in our evolutionary history, so distinguishing between early bipedal ancestors and our nearest primate relative, the great apes, becomes increasingly challenging the further back in time we go. However, in addition to key skeletal adaptations for bipedalism (Building Bodies Reading), there are skull and dental features that help to make this distinction. Any fossil that possesses a more human like condition of these traits is generally classified as a hominid. Important diagnostic features include:

1. Reduction in canine tooth size, including a reduction in the CP₃ or honing complex (see illustration) and premolars.
2. Thicker tooth enamel (apes have thin enamel).
3. Smaller front teeth.
4. Broader dental arcade (tooth columns or palate shape)

Behaviorally, the earliest members of the hominid lineage most likely resembled the behaviors we have observed in modern chimp populations. Yet, the bipedal adaptation enabled these early family members to exploit the environment and interact with each other in a much different and more flexible way than any of the apes.

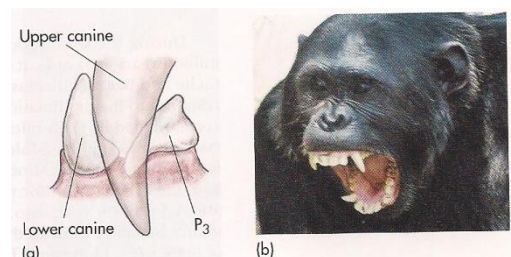


FIGURE 10.10 (a) A canine/premolar or CP₃ honing complex consists of a large, projecting upper canine passing across the blade-like edge of the lower premolar. Hominins lose this complex as the anterior teeth decrease in size. (b) Monkeys and apes such as this chimpanzee can be recognized in the fossil record by the anatomy of their teeth.

THE FIRST ADAPTIVE RADIATION was precipitated by the Terminal Miocene Event (around 7-6 million years ago) and produced an array of potential/possible **LAST COMMON ANCESTORS** for hominids and the apes, or the **EARLIEST HOMINIDS**. Among these late Miocene species, two have elicited some excitement:

Early Hominids

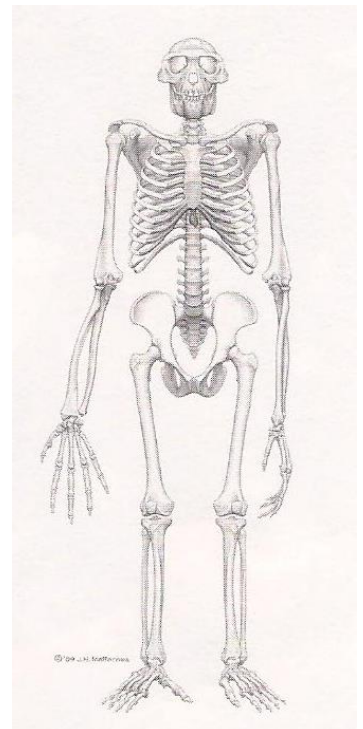
- **Sahelanthropus tchadensis** – a 6-7 million year old species from the north central African country of Chad. At present the species is known only from fragmentary skull, mandible, and dental remains. While some paleoanthropologists believe *S. tchadensis* walked upright, others disagree and contend that it may be a form of ape. The fossil remains do, however, exhibit a mix of ape-like and more later hominid-like traits, including a flat face and reduced canine. Dentition suggests a very generalized plant based diet that most likely included fruit, leaves, nuts, seeds, and roots and possibly insects. Only the postcranial bones of this specimen will allow us to establish its bipedal, and therefore, hominid status. *Sahelanthropus* is still an extremely important addition as it fills in a gap in the early hominid evolutionary fossil record at a key point in time--the split from the common ancestral population.
- **Orrorin tugenensis** – a 6 million year old species from the Tugen Hills region in Kenya, east Africa, nicknamed “Millenium Man” because it was discovered in the year 2000. At present, the species is known only from fragmentary postcranial remains, including the femur (although the knee portion--an important feature for determining if the femur angled inward, and was thus used in bipedal locomotion—is missing). As with *S. tchadensis*, there’s disagreement on whether this species was a habitual upright biped or an opportunistic biped. Orrorin’s discoverers claim that this species more closely resembles humans than Lucy’s species, *Aus. afarensis*, in both the post-cranial bones and dentition, including smaller teeth with thick enamel, but more remains will need to be found to make conclusive statements.

We know very little about the lifeways of either of these species. We do know, however, that they were **FOREST ADAPTED**. This is intriguing because, it may suggest that bipedalism emerged in a more arboreal context than previously hypothesized. What has been established though, is that upright posture does appear to have developed as a “pre-adaptation” to bipedalism, and so, the trees, rather than the open grasslands may have been the cradle of bipedality.

THE SECOND ADAPTIVE RADIATION occurred around 4-5 million years ago and produced a number of true hominid genera and species (What ONE feature would define a true hominid?) Among these early Pliocene period species, two stand out (pun intended!):

- **Ardipithecus ramidus** – a 4.5 million year old species from Ethiopia. Nicknamed “Ardi,” paleoanthropologists worked for 3 years to excavate the skeleton at a place called Aramis in the Afar Rift of Ethiopia. The team recovered more than 125 pieces of one individual – a 4.4 million year old female, the oldest hominid skeleton yet found. The skeleton includes many important bones of the hands, feet, limbs and pelvis. Most of the skull with its teeth was preserved. Ardi’s skeleton demonstrates that she was a creature capable of both walking upright and clambering through the trees with a grasping big toe, in a way unlike any other creature known to science. This makes Ardi the most ape-like true hominid yet to be found.

Key skeletal features that distinguish *Ardipithecus* from other hominids are in her hands and feet. The bones in the palm of her hand are short, but her finger bones are long. This is neither an ape hand nor a human hand, but something unique. Her wrist bones show that she did NOT walk on her knuckles like chimps and gorillas, while her foot bones reveal that Ardi had a foot with a **DIVERGENT BIG TOE**, like most primates (but NOT like hominids). This allowed her to grasp branches while moving through the trees. The pelvis was clearly & substantially adapted for upright walking. Ardi’s skeleton suggests that early hominids utilized both the trees and the ground in search of food



and safety. Unlike apes, however, the canine teeth are small in both males and females of this species and there is a relatively small degree of sexual dimorphism as well. The remains of *Ardipithecus ramidus* have been extremely important for understanding both the environmental and anatomical context of early hominid bipedalism.

THE THIRD ADAPTIVE RADIATION occurred between 3 and 4 million years ago and produced a number of hominid species and at least one new genus. Among these middle Pliocene period hominids, several are important (both in terms of hominid evolution and in terms of the evolution of *our understanding* of hominid evolution):

The Lucy Show

- Australopithecus afarensis*** – dates to between 3 and 4 million years ago and was first discovered in the early 1970s by Don Johanson in Hadar, Ethiopia. This discovery made headlines around the world due to its nearly 40% complete skeleton and affectionately nicknamed “Lucy” (after the Beatles song, “Lucy in the Sky with Diamonds”). Nothing of this antiquity and completeness had yet been found at the time, so *Aus. afarensis* was considered to be the root or ancestral species to all other australopithecines. This species is well documented in the fossil record and includes the remains of males, females, juveniles and even a very young, three-year old child. *Aus. afarensis* species exhibits sexual dimorphism. Males were slightly larger than females (4-5 feet vs. 3 ½ - 4 feet; 65 lbs. vs. 45-50 lbs.) and possessed a small sagittal crest along the top of the skull (for the attachment of chewing muscles). Brain size was about the same as a modern chimpanzee.

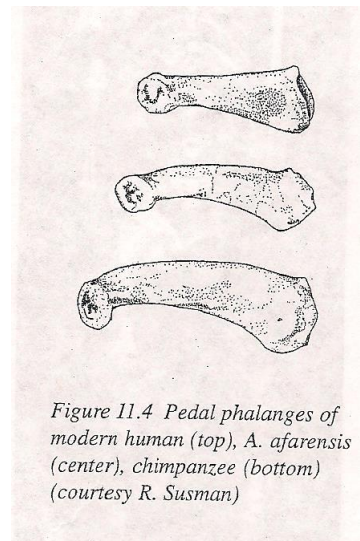
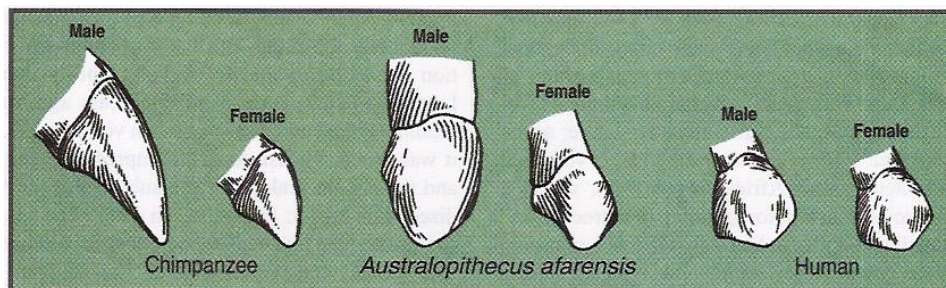


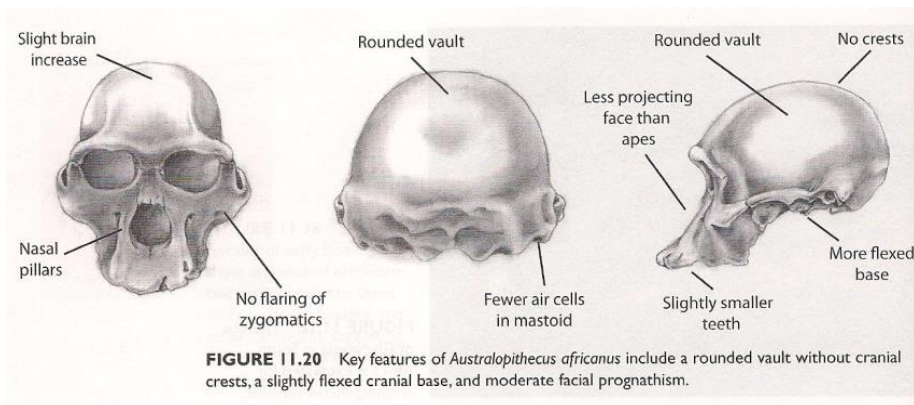
Figure 11.4 Pedal phalanges of modern human (top), *A. afarensis* (center), chimpanzee (bottom) (courtesy R. Susman)

Aus. afarensis has some ape-like physical features, especially in the face, but the hand bones, foot bones, pelvis and jaw bones all exhibit some intermediate features between later hominids and chimps. Very little is known about *Aus. afarensis* lifeways except that some of them lived in open woodlands and along wooded streams in the savannas. To date, all *Aus. afarensis* fossils come from east Africa. Although no tools have been found with this species, it's quite possible they possessed a tool-culture like that of modern day chimps. On the basis of dental wear, it seems their diet included large amounts of fruit and other soft, easily chewed foods.

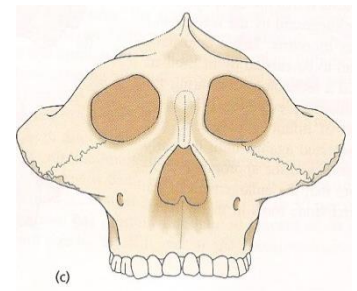
Comparison of chimpanzee, Au. afarensis and human canine teeth



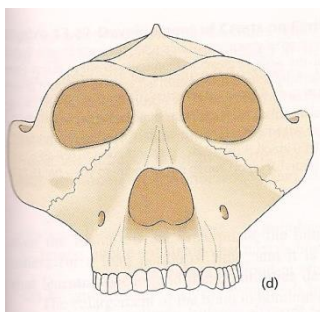
THE FOURTH ADAPTIVE RADIATION occurred between 2 and 3 million years ago and produced a number of hominid species and two new genera (including the genus *Homo*, which is covered in Part 2). Among these late Pliocene period hominids several are important:



- Australopithecus africanus*** – fossils of this species come primarily from south Africa (though at least one possible *Au. africanus* fossil has been found in east Africa) and date to between 2.5 to 3.5 million years ago. *Au. africanus* was the first australopithecine species to be discovered (in 1924 by Raymond Dart). Brain size was about the same as a modern chimp, so probably engaged in the same types of behaviors (such as tool use) observed in living chimps. Compared to *Au. afarensis*, *Au. africanus* is a more “gracile” species, exhibiting less robust features (for example, no sagittal crest), a more rounded cranial vault, and less projecting (prognathic) face. *Au. africanus* remains show clear skeletal adaptations to bipedalism in the spine, leg and foot and exhibit slightly shorter arms than *Au. afarensis*. Indeed, *Au. afarensis* is thought to be ancestral to *Au. africanus*. *Australopithecus africanus* had a similar diet to *afarensis* and foraged for fruits and soft, easily chewed foods.
- Paranthropus boisei* and *Paranthropus robustus*** – These two species were originally assigned to the genus *Australopithecus*, but through further analysis (although not with complete agreement among anthropologists), were later assigned to a new genus due to their specialized adaptations, namely their robust features. *P. robustus* was the first robust species discovered in South Africa in 1936 by Dr. Robert Broom. It existed between 2 – 1.5 mya. It was clearly different from the only other early hominid known at that time---*Au. africanus*---and was immediately given a new species name highlighting its robust features.



P. robustus



P. boisei

P. boisei was discovered by Mary Leakey in 1959 in Tanzania, East Africa. It existed between 2.1 – 1.1 mya. At first, the Leakeys thought they had found the maker of all the stone tools and fragments they had uncovered for decades in the area, but the extremely robust features exhibited by *P. boisei* were not consistent with a stone tool user, but rather, a specialized adaptation to a diet of hard food items such as nuts, roots, tubers, and seeds which required the teeth and jaws to be used as food processing tools. Also, considering the larger body size of these species, the cranial capacities (ranging from 400 – 550 cc) are not much more

than those of modern apes. Their faces are large, with flaring (wide) zygomatics, and a pronounced sagittal crest for muscle attachment of the chewing muscles.

IMPORTANT NOTE: The robust hominids, or Paranthropids, became extinct around 1 million years ago, meaning that their specialized, robust features are not seen in any other hominids dating from 1 million years and forward. It is hypothesized that they may have been pushed to the fringes by tool-making and using hominids who were better able to exploit their environment. These robust species, therefore, are true evolutionary dead ends, but, are yet another example of the *variations* present in hominid populations undergoing intense selective pressures.



Australopithecus sediba - One of the most recent hominid discoveries (2010) comes from the Malapa cave site in South Africa and dates to close to 2 my old. The find includes close to 220 bones from the cranial and post-cranial skeleton and include both an adult and a juvenile. Given an unusual mix of early and advanced hominid traits, paleoanthropologist, Lee Berger who discovered the Malapa fossils says that if the bones had not been found together in the same deposit, his team could have easily concluded that the bones came from different species. This is because *Aus. sediba* exhibits an interesting mix of characteristics some resembling the genus *Australopithecus* and other characteristics that are seen in later members of the genus *Homo*, specifically, *Homo erectus*, particularly in the pelvis, the dentition (broad

palate with relatively small pre-molars and molars) and a less prognathic lower face. Its small brain places it squarely within the australopithecine range (around 420-435 cc) as does its postcranial proportions with relatively long arms and a small body. The pelvis, indicating an upright posture, was adapted for bipedal walking and appears more human-like than the australopith pelvic pattern, however, the heel bones are more primitive than those of Lucy (*Aus. afarensis*, which is much older than *sediba*) while the ankle bones are more advanced as compared to *Aus. afarensis*.

The mixing of “old” and “new” features suggests that the traits that we have generally used to define the hominids that are classified in the genus *Homo* such as a larger brain, increased body size and more modern pelvis did not appear as a “package deal,” but rather, evolved at different rates (a mosaic or “patchwork” of characteristics). Given this species’ mosaic pattern of evolution and its place on the evolutionary timeline, *Aus. sediba* may reveal important clues about the origin of the genus *Homo* and could possibly be a direct ancestor to later *Homo* species, or represent an entirely different branch of lineage on the hominid family tree. More analysis and indeed, more fossils from the time period around which the earliest members of the genus *Homo* appear to have evolved will be needed to make solid conclusions about *sediba*’s place on the family tree.

CONCLUSION: There are numerous other fossil hominid species* which are not covered in this minimalist survey. The interpretations of the relationships between these various early hominid species vary and to date, there is no consensus. What is clear, however, is that there was A LOT of variation in early hominid populations which means, there was a lot of “raw material” for natural selection to work with. Which of these early hominid lineages are directly related to humans is still not clear. As more fossil remains are unearthed, the more complete picture we will have of our distant past, and the ancestral line that eventually led to *Homo sapiens*. Until then, the detective work in this millennial drama continues, as does the cast of characters. One thing is for certain, the frequent new discoveries being made suggest that there are many more species of hominids that remain to be found.

*Early hominid species not covered in this reading: *Aus. anamensis*, *Aus. bahrelghazali*, *Aus. garhi*, *Paranthropus aethiopicus*, *Kenyanthropus platyops*