A Review of Current Research on Human Evolution

by

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Abstract

In this paper we discuss the importance of teaching human evolution to all public school students. To promote the teaching of human origins, we review current research in the field and include a list of recommended books and web sites on the subject. This material supplies the reliable resources necessary for teaching human evolution that are either missing or outdated in most secondary biology textbooks.

Keywords

Teaching Evolution, Human Evolution, Hominin Evolution, Paleoanthropology, Review

Introduction

As science educators, we have two goals in writing this paper. The first goal is to show the importance of teaching human evolution to all students. The second goal is to provide up-to-date resources for classroom teachers to use in teaching the subject. Secondary biology textbooks suffer from the inherent limitations of mass produced books making it difficult for them to stay current with rapidly changing scientific fields such as paleoanthropology. One of our motives for writing this paper is to compensate for this inherent limitation of textbooks.

The most important resource we provide is a review of current scientific research on human evolution that stresses the broad framework of what is reliably known about our origins. To this we have included a list of recommended books taken from our research that we feel are the most useful and accessible. In addition to text resources, we have added web links on human evolution that provide an increasingly sophisticated source of information. Together, this material should provide teachers with a variety of up-to-date resources for teaching human evolution.

Why Teach Human Evolution?

Modern science has reached the point where the broad outline of our origin is known. For each of us this scientific knowledge of human origins and evolution has a special significance, because central to each of our individual views of the world is a concept of who and what we are. The beliefs we hold about ourselves drive our attitudes and our actions and, as such, determine the kind of people we are and ultimately the kind of society we have. In the past we have answered the questions about our origins with the myths and creation stories unique to the culture of our birth. But today we live in a world where scientific answers to these questions are available. All of us can share these answers because they are based on public scientific knowledge instead of private beliefs. It is the knowledge of who and what we are that we can hold in common in our increasingly pluralistic society. This scientific knowledge of human origins need not replace faith in the moral teachings of any belief system. But if self knowledge is the most valuable knowledge we can possess, then what modern science can tell us about who and what we are is the most valuable knowledge we can teach our students.

Current Research on Human Evolution

We have confined our review of human evolution to the period between the late Miocene eight million years ago (m.y.a.) and 100,000 years ago. This period marks the evolutionary transition from our last common ancestor with modern chimpanzees to the first fully modern humans. Because of limited space, and to do proper justice to the subject, we have not included the last hundred thousand years of human evolution and history. Our knowledge of this period is growing daily and is best left as a story in itself.

(For an overview of the evolution of modern humans see Klein (2002) and Olson (2002) in recommended books, and Mellars (2006b) in recent articles of interest.)

Setting the Stage

To fully understand human evolution it should be seen as a recent installment in the much larger story of the evolution of life on Earth. Human evolution can then be understood as only one chapter in the larger story of vertebrate and mammalian evolution. Having said this, we must confine ourselves in this paper to setting the stage with those events just prior to the evolution of the last common ancestor of chimpanzees and humans.

By 22 million years ago, in the early Miocene, apes had diversified throughout the Old World, as many a 40 genera of fossil apes have been identified to date. Fourteen genera are known to have inhabited Africa alone during the early Miocene between 22 and 17 million years ago (Begun, 2003). In contrast, only 5 genera of apes are alive today worldwide.

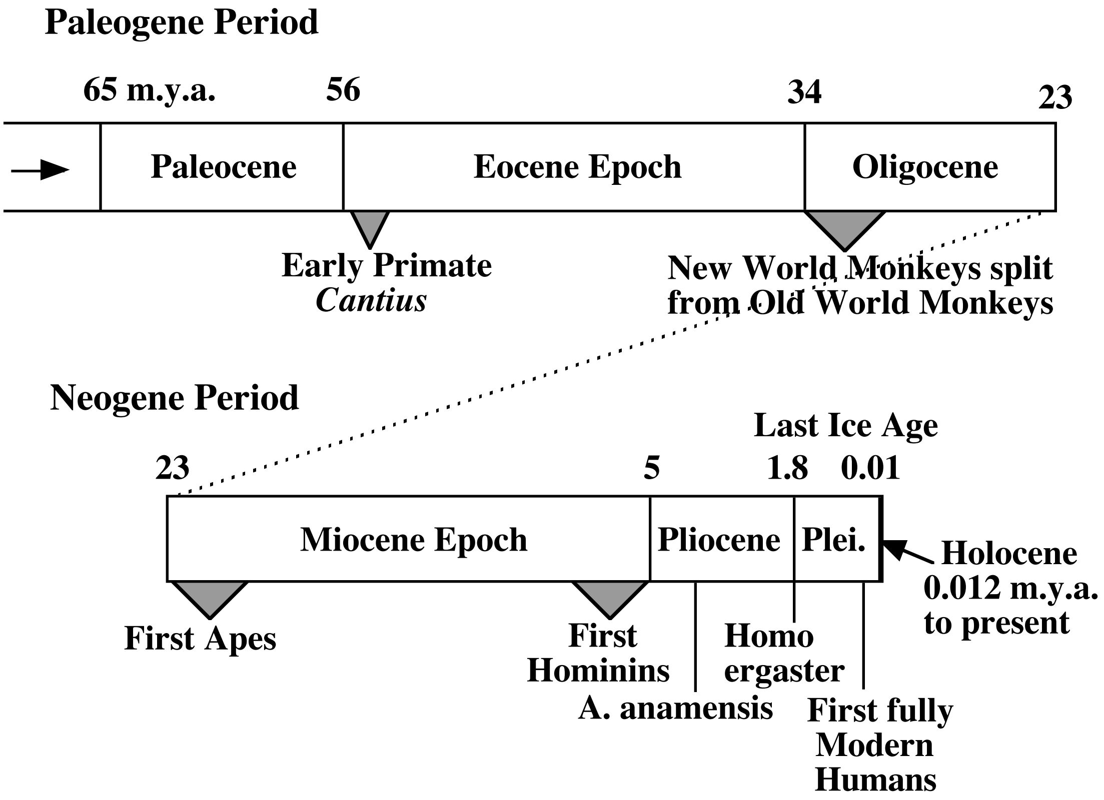
Early to mid-Miocene Africa had a much wetter climate than today (Coppens, 1999). Tropical rainforests near the equator extended across unbroken lowlands from the Atlantic to the Indian oceans. Starting eight million years ago, tectonic forces caused uplift on the west side of the east African rift preventing the easterly flow of rain clouds and creating a rain shadow over east Africa. The resulting climate change was compounded by a simultaneous global cooling and drying trend (Potts, 1998; Cane & Molnar, 2001; Sepulchre, et al., 2006). East Africa began to dry out.

These geological events split the common ancestors of modern chimpanzees and ourselves into two geographically separate populations. One population remained in the tropical rain forests of west Africa and gave rise to modern chimpanzees. The other population slowly began to adapt to the increasingly open, dry habitats of east, and perhaps north central, Africa and eventually gave rise to modern humans. The story of human evolution follows the complex history of changing climate followed by evolutionary adaptation and radiation in east African hominins, the group to which all the direct ancestors of modern humans belong.

Hominid or Hominin?

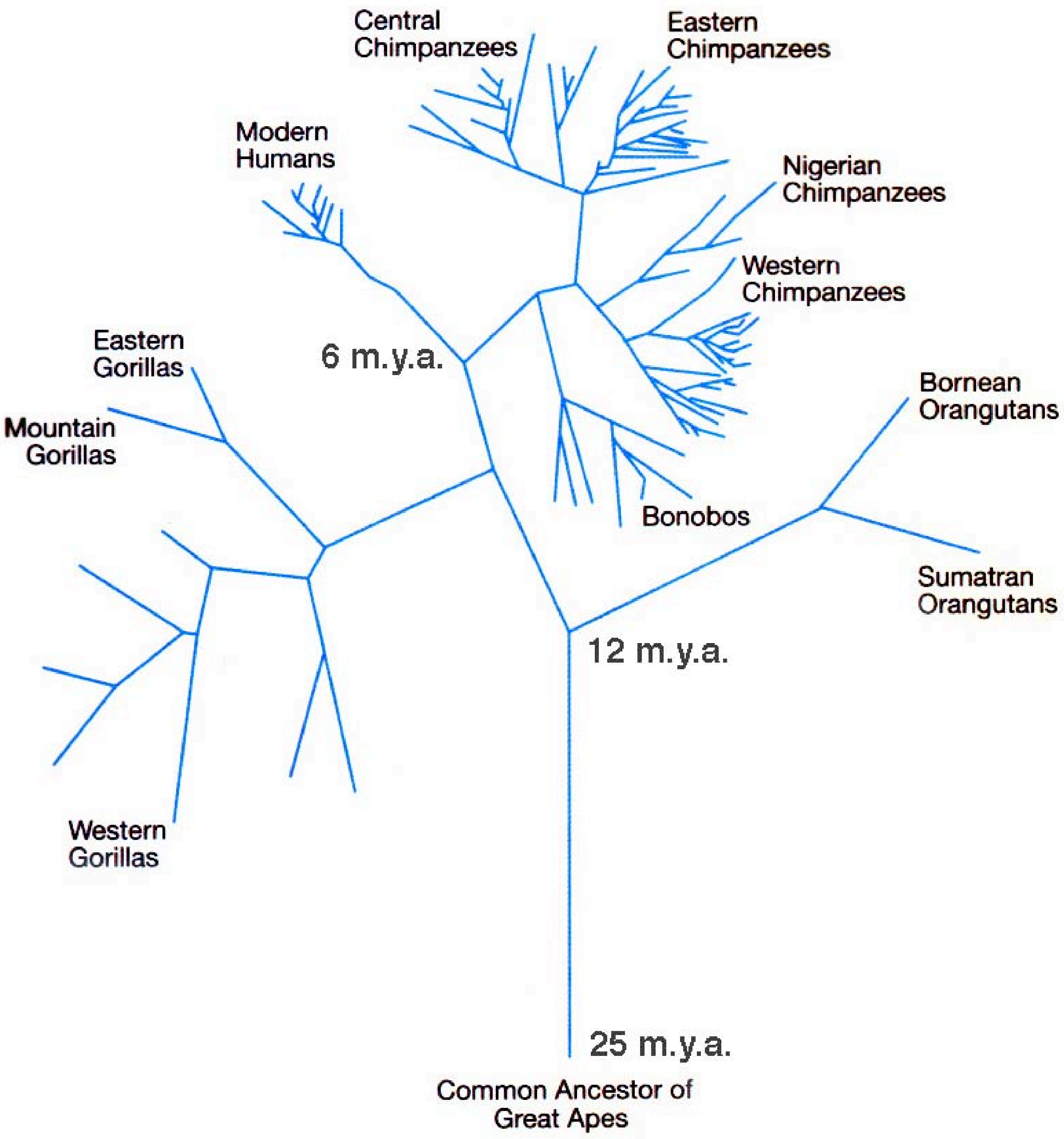
"A 'hominid' is a member of the family Hominidae, which classically includes all creatures, living and extinct, that are more closely related to *Homo sapiens* than to the extant chimpanzees (*Pan troglodytes* and *P. paniscus*), the closest living sister taxon to *Homo*. This classical solution is, however, more problematic for the great apes—chimpanzees, gorillas (Gorilla) and orangutans (Pongo)—which are lumped together in the family Pongidae. The problem is that some of these creatures (chimps and gorillas) are more closely related to humans than others (orangutans), in which case Pongidae is not a 'natural' group. One solution is to elevate chimps, gorillas and orangutans each to their own families. Another is to extend the family Hominidae to include great apes as well as humans and their immediate, extinct relatives, classifying humans and chimps in a subfamily (Homininae) and demoting hominids (in the old sense) to the subcategory of tribe (the Hominini). This is why Leakey, et al. (2001), using this new terminology, describe as 'hominins' what others continue to refer to as 'hominids'. 'Hominin', therefore, is not a misprint or a gratuitous attempt to bemuse the unwary. It is, rather, a way of acknowledging the close evolutionary relationship between gorillas, chimps, and ourselves." (Gee, 2001)

The Cenozoic Era



The First Catarrhine Primates

The first catarrhine primates evolved sometime after 50 million years ago and before 33 million years ago when it's estimated the New World monkeys split from the Old World monkeys. Most primate fossils from this period have been found in a region of northern Egypt known as Al Fayyum (or the Fayum). A primate group known as *Propliopithecus*, one lineage of which is sometimes called *Aegyptopithecus*, had primitive catarrhine features—that is, it had many of the basic features that Old World monkeys, apes, and humans share today. Scientists believe, therefore, that *Propliopithecus* resembles the common ancestor of all later Old World monkeys and apes. Thus, *Propliopithecus* may be considered an ancestor or a close relative of the common ancestor of the great apes.



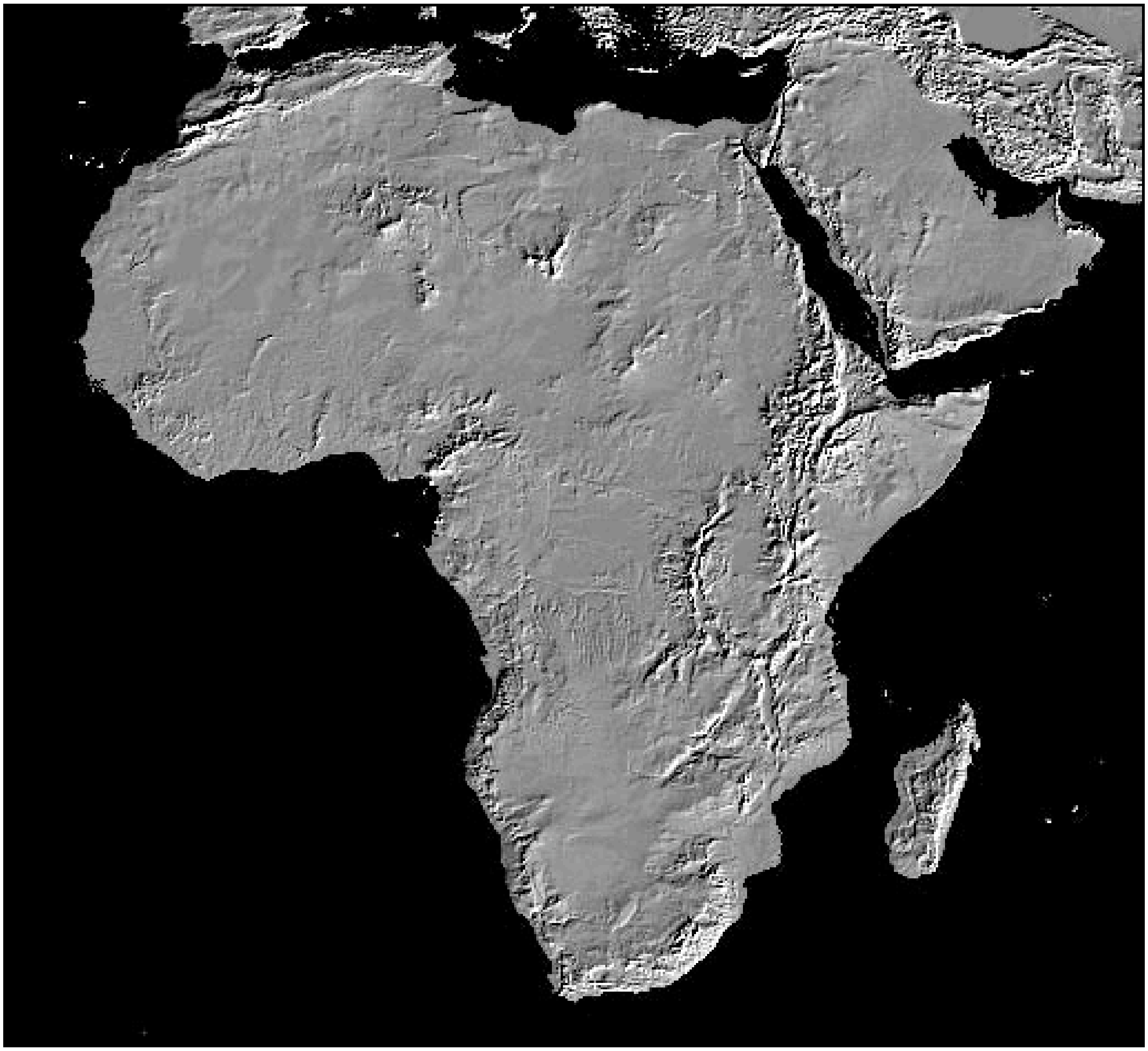
This evolutionary tree, based on genetic studies, shows how an ancestral ape gave rise to orangutans, gorillas, chimpanzees, and humans. The length of the branches reflects how far each population has genetically diverged from its relatives. The tree reveals that humans are barely distinguishable on a genetic level from bonobos and chimpanzees (Zimmer, 2001).

For more on the evolutionary relationship between chimps and bonobos go to: http://www.pbs.org/wgbh/evolution/library/07/3/l_073_03.html

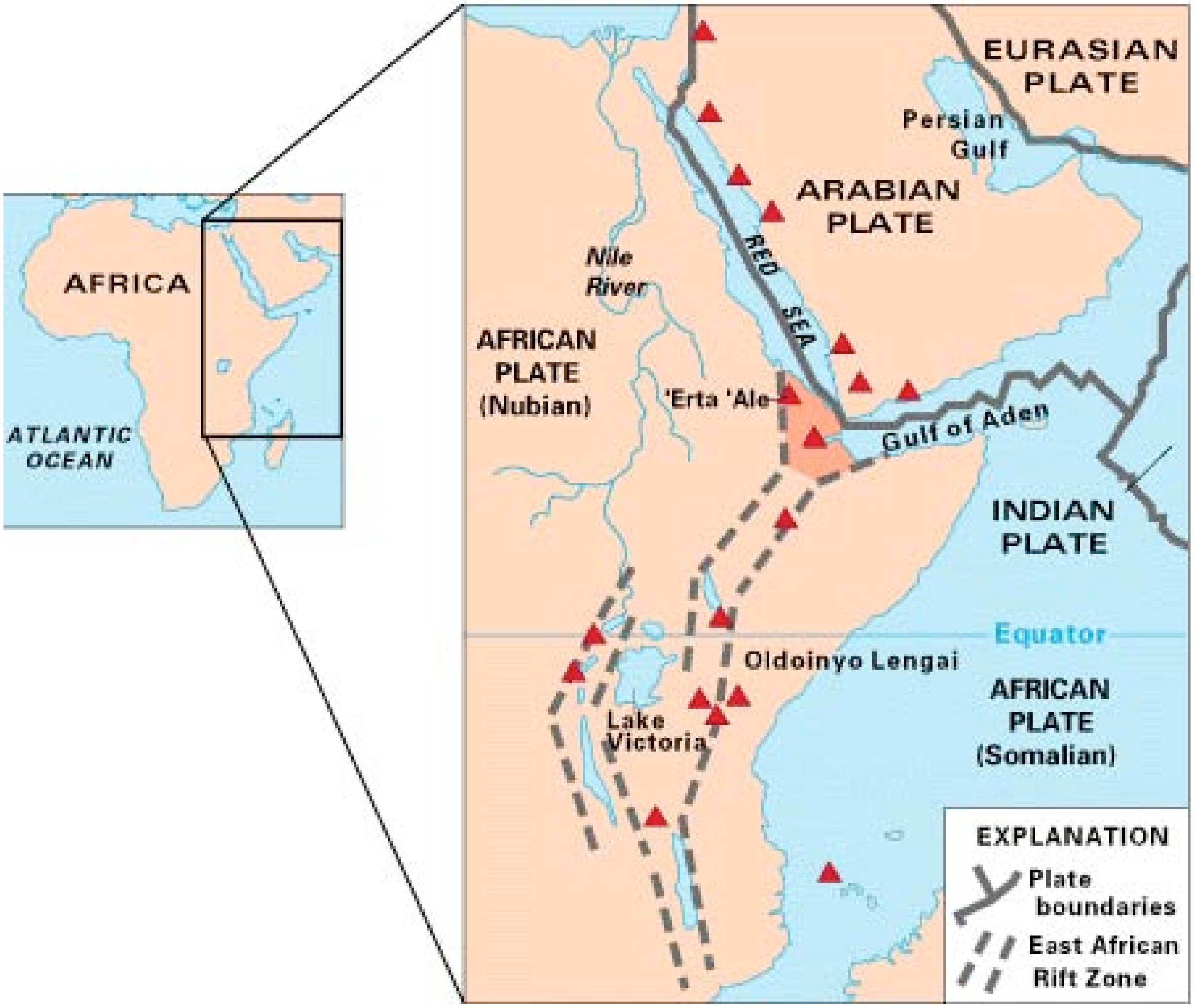
Map No. 4045 Rev. 2 UNITED NATIONS, March 2001

Department of Public Information, Cartographic Seciton

This map can be enlarged for greater detail.



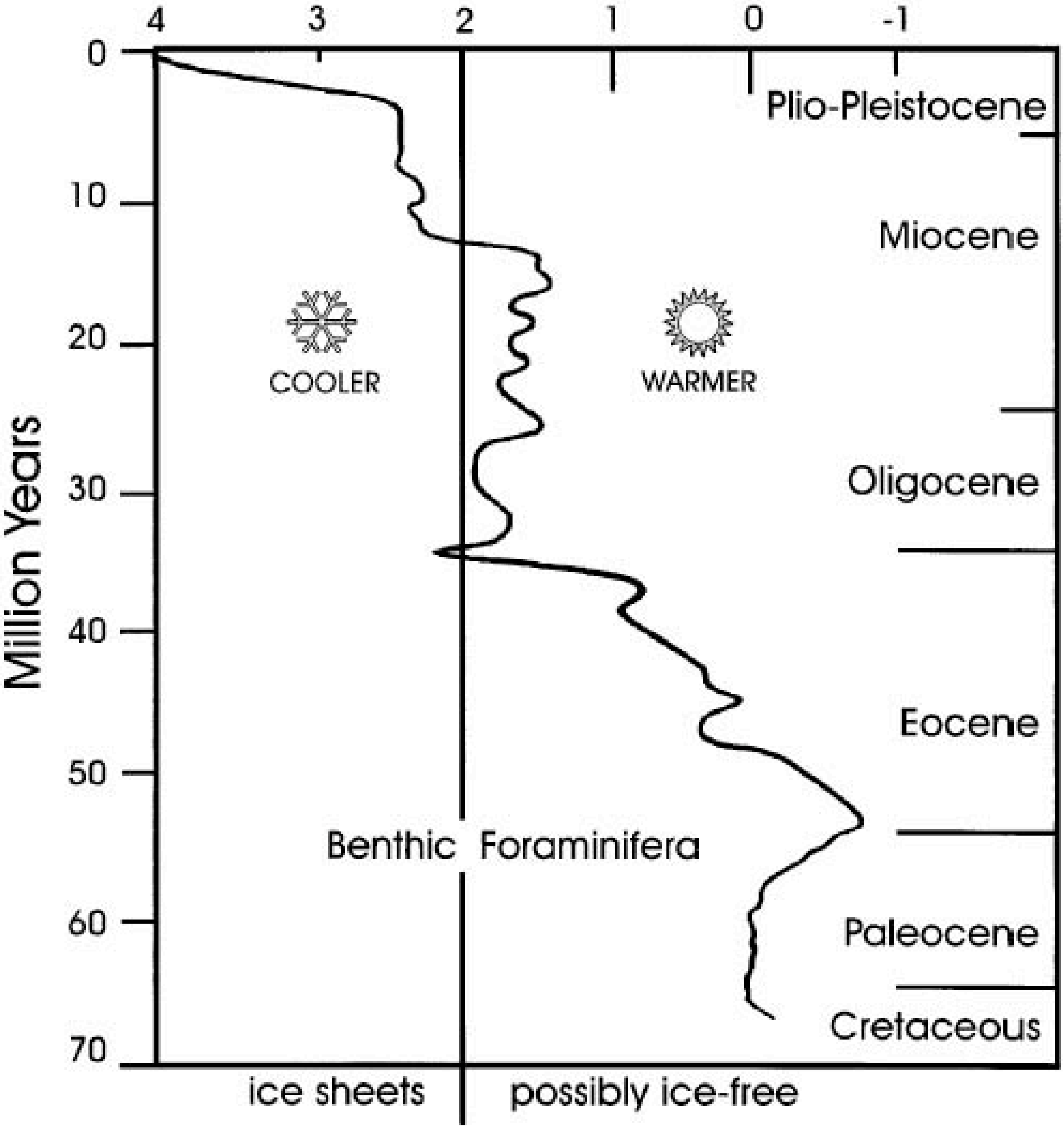
Above is a relief map of Africa and the Arabian peninsula showing the East African Rift System running north-south just right of center. The East African Rift System extends from Jordan in the Middle East south to Mozambique in southern Africa. It is some 4,000 mi (6,400 km) long and averages 30–40 mi (48–64 km) wide. The rift has been forming for some 30 million years, as Africa and the Arabian Peninsula separate. The system's main branch, the Eastern Rift Valley, is occupied in the north by the Jordan River, the Dead Sea, and the Gulf of Aqaba. It continues south along the Red Sea to several lakes in Kenya. Less obvious in Tanzania, with its eastern rim eroded, it continues south to the Indian Ocean near Beira, Mozambique. The western branch of the system, the Western Rift Valley, extends north from the northern end of Lake Malawi in an arc that includes lakes Rukwa, Tanganyika, Kivu, Edward, and Albert. Lake Victoria does not lie in the Great Rift Valley but between its main and western branches.



Above is a map of east Africa showing some of the historically active volcanoes (red triangles) and the Afar Triangle (shaded, center)—a so-called triple junction (or triple point)—where three plates are pulling away from one another: the Arabian Plate, and the two parts of the African Plate (the Nubian and the Somalian) splitting along the East African Rift Zone.

Web Reference
http://pubs.usgs.gov/publications/text/East_Africa.html

This vegetation map of Africa (courtesy of NASA) shows the dark green of equatorial western rainforests changing to the tan of savannah and desert in east Africa.



Climate Cooling in the Cenozoic (Potts, 1998)

Global climate change of the past 4 million years includes the end of the early Pliocene warm period (5-3 m.y.a.) and significant intensification of Northern Hemisphere glaciation, 2.7 to 2.4 m.y.a.. This can be restated as the current Ice Age began approximately 2.5 million years ago (Balco, 2005; Ravelo, et al. 2004).

An Overview

The following elements provide a framework for the broad patterns of hominin evolution (modified from Foley, 1999).

1. The Late Miocene (8-5 m.y.a.) witnessed the diversification of the African apes as the east African climate shifted from tropical rain forest to dryer conditions.

2. Bipedalism developed in late Miocene to early Pliocene hominins (6-4 m.y.a.) on the eastern side of the African continent, possibly in response to more open habitats.

3. An adaptive radiation of African hominins took place between 4 and 1.7 m.y.a., as east Africa again experienced further climate shifts to the dryer conditions of the current Ice Age.

4. The period between 1.7 m.y.a. to the present, which spans over two thirds of the current Ice Age, saw a dramatic increase in the cranial capacity of our ancestors effectively doubling brain size.

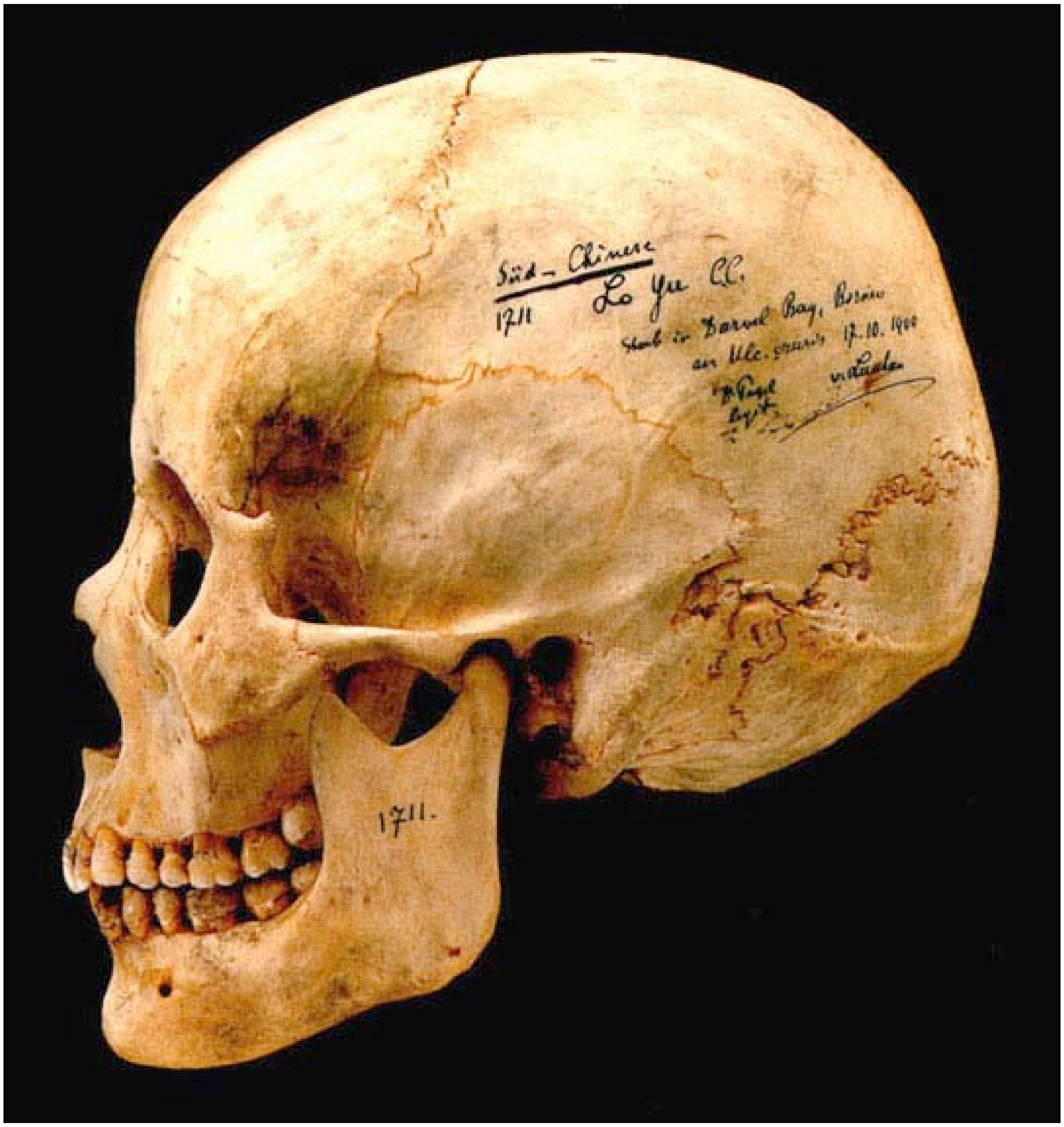
5. This same period includes the explosive geographical expansion and rapid divergence of the genus *Homo*.

6. This expansion was followed by a subsequent reduction in species richness first with the extinction of the robust hominins and later of regional species of *Homo*. These extinctions resulted, finally, in the survival of only one *Homo* lineage, ourselves.

Skull of a Modern Chimpanzee Male
Average cranial capacity is ~ 410 cubic centimeters (cc).

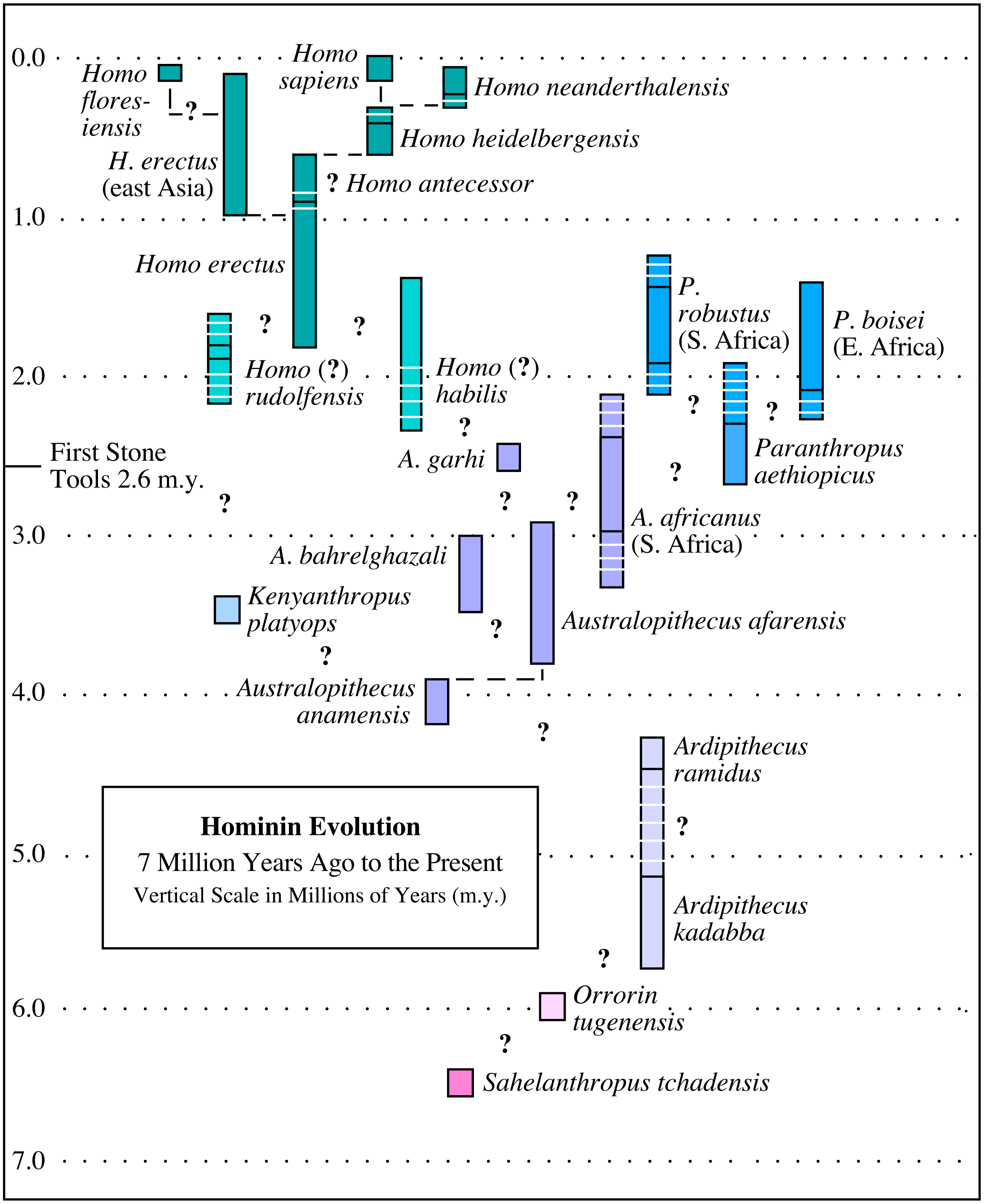
(Photograph by David L. Brill)

(Unless otherwise noted all photographs by David L. Brill
are from Johanson & Edgar 1996)



Skull of a Modern Human
Average cranial capacity is ~ 1350 to 1400 cc.

(Photograph by David L. Brill)



Rectangles represent approximate first and last dates for species.
Shading and relative horizontal position separate genera.

The Current Cast of Characters

The Earliest Hominins

Modern apes and humans differ greatly, but the earliest hominins contrasted in subtle ways from living apes primarily in their increasing reliance on walking upright known as bipedalism. The skeletal indicators of bipedalism include a forward placement of the hole at base of skull where the spinal column enters (the foramen magnum), and a shortening and broadening of the pelvis to make it "bowl-shaped". These changes were accompanied by shifts in muscle groups particularly the gluteal and hamstring muscles, a lengthening of the lower limbs particularly the femur in the genus *Homo*, and changes in the feet to become weight-bearing structures (Poirier & McKee, 1999).

The earliest possible hominin to date is *Sahelanthropus tchadensis* from Chad in the Sahel region of sub-Saharan Africa, which has tentatively been dated to between 6 and 7 million years old (Brunet, 2002). The fossils include an almost complete cranium with a mosaic of ape and hominin features but no post-cranial skeletal material that could confirm whether *Sahelanthropus tchadensis* was bipedal.

The earliest hominin bipeds may have appeared between 7 to 5 m.y.a.. An example of these early bipeds may be the fossils of *Orrorin tugenensis* found in the Tugen Hills of Kenya and dated to 6 m.y.a. (Senut, et al., 2001). Thick-enameled although relatively small molars and a human-like femur link it with later hominins. It also exhibits muscle attachments on the humerus and curved finger bones that are consistent with arboreal activity linking it to the apes. Based on associated plant and faunal remains, *Orrorin tugenensis* probably preferred open woodlands near forests.

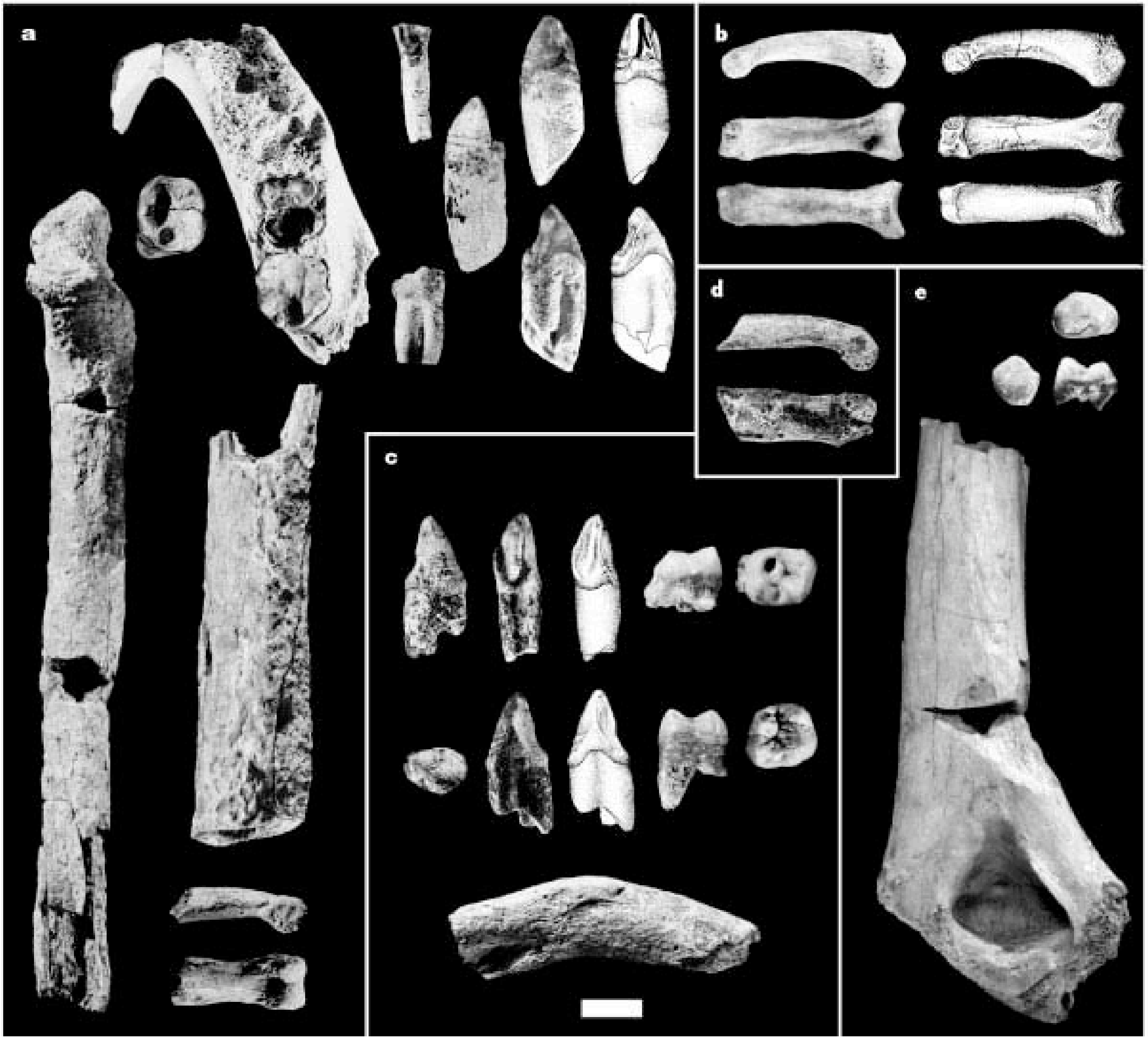
In addition to *Orrorin tugenensis* there are 11 specimens representing at least 5 individuals of *Ardipithecus kadabba* from the Middle Awash area of Ethiopia dating to 5.8-5.2 m.y.a. (Haile-Selassie, 2001). Another 50 partial individuals, representing a separate species, or possibly subspecies, *Ardipithecus ramidus*, were recovered at the 4.4 m.y. old site near Aramis, Ethiopia (Klein, 1999). The oldest specimens exhibit derived dental features that are only shared with later hominins (Haile-Selassie, 2001). The fossils from the Aramis site exhibit a forwardly placed foramen magnum and apparently free upper arms, traits consistent with bipedalism (Klein, 1999). However, the association with high altitude, closed canopy woodland habitat and thin enamel on the molar crowns are characteristics not found in later hominins. This suggests a species at or close to the shared ancestor of humans and modern chimpanzees.

Cranium of *Sahelanthropus tchadensis*

(Photograph courtesy of the journal *Science*)

Upper Femur of *Orrorin tugenensis*

(Photograph by Marc Deville courtesy of the journal *Science*)



Fossil hominin remains from the Late Miocene Middle Awash deposits assigned to *Ardipithecus ramidus*

(Photographs from Haile-Selassie, 2001).

Australopiths

All later hominins, including members of the genus *Australopithecus*, are characterized by bipedal locomotion, and the numerous species reflect differences in diet and presumed ecological specialization. In general, the older species share more primitive traits with their Miocene forebears. Among these older species are *Australopithecus anamensis* (4.2-3.9 m.y.a.) from Kenya (Leakey, et al., 1998) and Ethiopia (White, et al., 2006), and another closely related species, *Australopithecus afarensis* (3.8-2.9 m.y.a.), from Hadar, Ethiopia and Laetoli, Tanzania (Wood & Richmond, 2000). Hadar and Laetoli combined provide at least 60 to a100 partial individuals of *Australopithecus afarensis*. Adding to these species, a mandible and first upper premolar of *Australopithecus bahrelghazali* were discovered at Koro Toro, in Chad and dated to 3.5-3.0 m.y.a.. Although initially placed in *Australopithecus afarensis*, it may remain assigned to its own species because of an apparently flatter face evident from the chin.

Australopithecus anamensis and *Australopithecus afarensis* exhibit thicker enamel and broader molars indicating a dependence on nuts, grains or hard fruit. *Australopithecus anamensis* is found in deposits of former riverine woodlands and gallery forests of the Turkana Basin, Kenya. *Australopithecus afarensis* may have occupied more varied habitats from dry bushland to woodlands or riverine forests (Ward et al., 1999). The foramen magnum and tibia of *Australopithecus anamensis* are typical of habitual bipeds and the elbow and knee joints may be more humanlike than in *Australopithecus afarensis* (Tattersall & Schwartz, 2000). As in later hominins *Australopithecus anamensis* had relatively small upper incisors and less projecting canines. Large, projecting canine teeth are characteristic of our ape ancestors. *Australopithecus anamensis* shares with *Australopithecus afarensis* curved fingers and a relatively long radius; both traits would have been useful in the trees. Presumably their bipedalism was intermediate between apes and humans (Stern, 2000).

The better known *Australopithecus afarensis* includes many partial bones, a skull, and also almost half of an adult female skeleton known as “Lucy” (Wood & Collard, 1999; Wood & Richmond, 2000). The skulls, jaws and teeth are very ape-like except for reduced canines, larger postcanine teeth, and a reduced snout. The body trunks are “inverted funnels”, as in the great apes, and the upper limbs are relatively shorter than in apes but longer than in humans. Finger lengths are intermediate but the tips of the fingers are narrow and finger bones are longitudinally curved as in chimpanzees. The feet are also intermediate but include shortened toes and a robust heel characteristic of later hominins. Footprints at Laetoli, possibly made by *Australopithecus afarensis*, also support a picture of a habitual biped that stood 1 to 1.5 meters tall and walked fully upright 3.5 m.y.a. (Agnew & Demas, 1998).

Above is a mandible and upper tibia of ***Australopithecus anamensis***. The tibia shows the articulation surface of the knee joint expanded front to back as in a biped.

(Photographs by Robert I. M. Campbell)

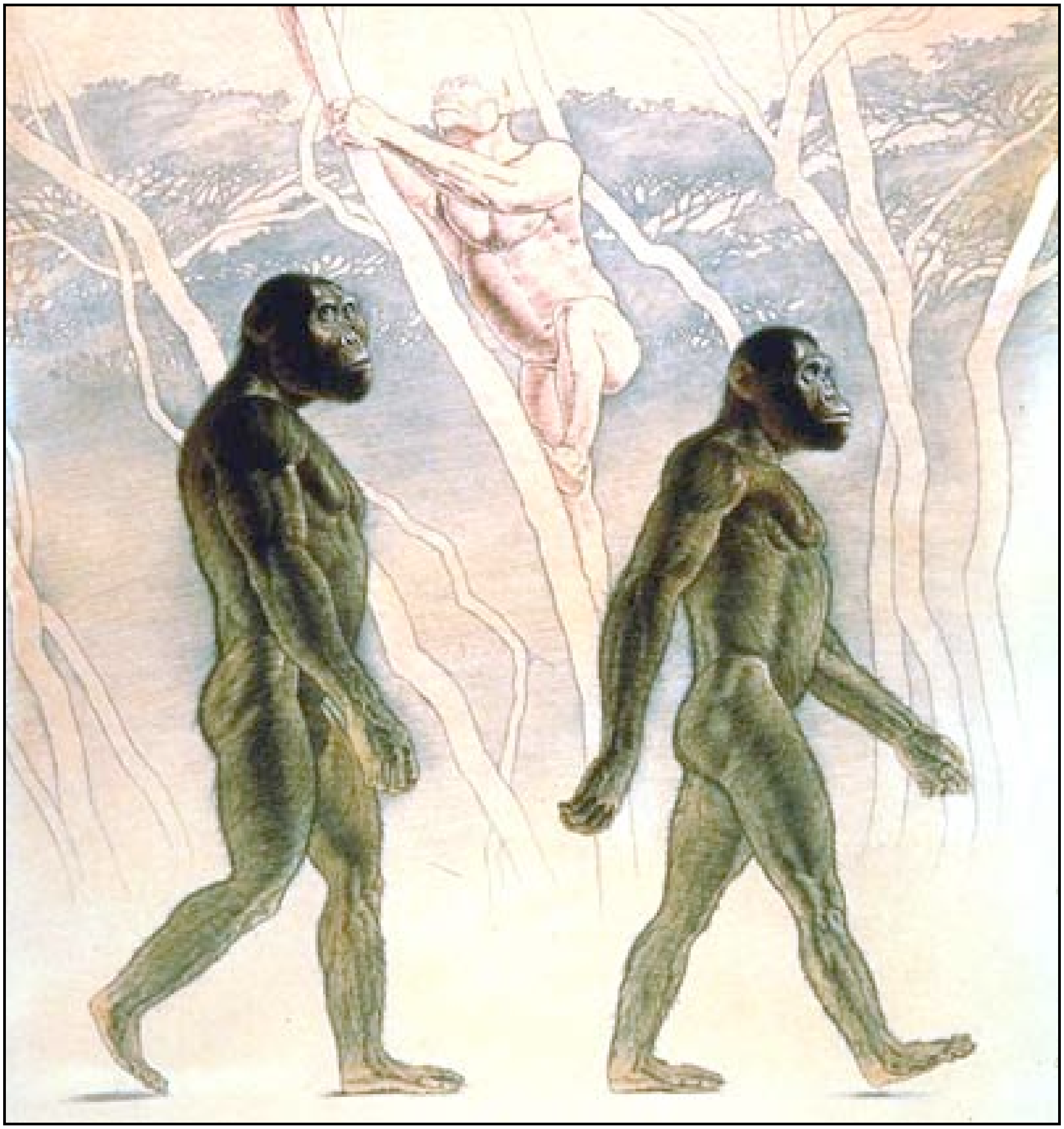
Cranium of *Australopithecus afarensis*

(Photograph by David L. Brill)

The teeth of ***Australopithecus afarensis*** **(left)** resemble those of its possible ancestor, ***Australopithecus anamensis*** **(center)**, compared to a **modern chimp (right).**

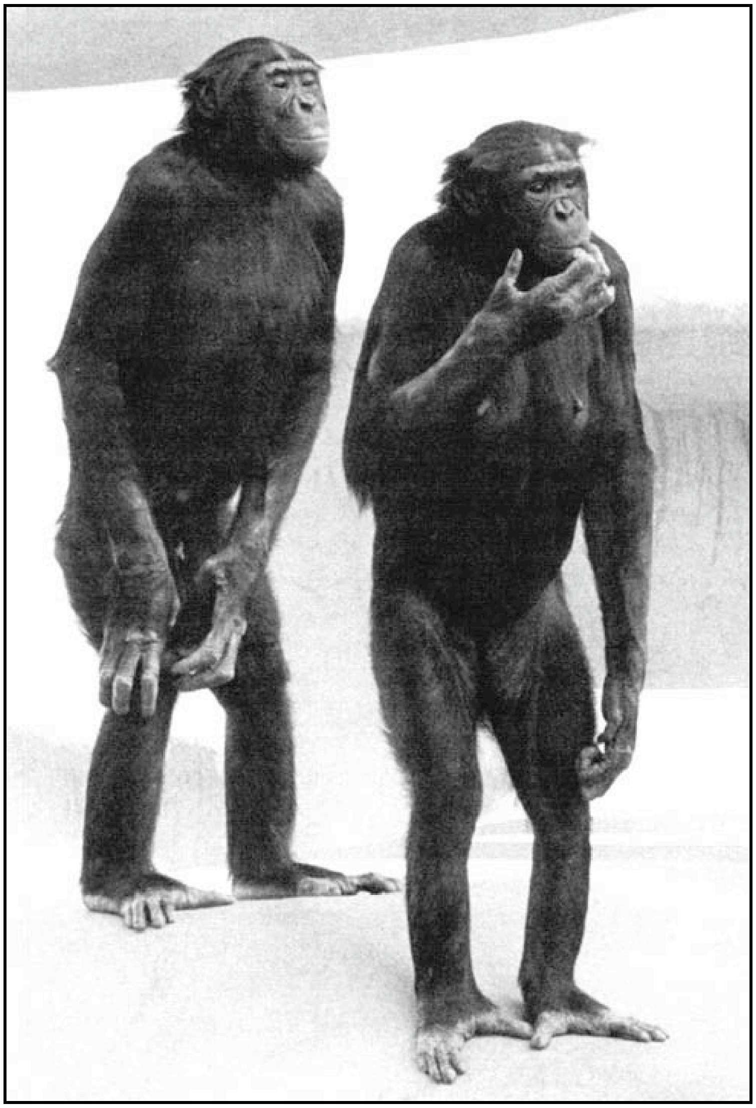
With the publication of discoveries of *Australopithecus anamensis* in Ethiopia (White, et al., 2006), many researchers now believe that *A. anamensis* was ancestral to *A. afarensis* (Gibbon, 2006).

(Photograph by David L. Brill)



***Australopithecus afarensis* was ~ 1 to 1.5 meters tall (3 to 4.5 feet).**

(Painting by John Gurche http://www.gurche.com/)



Bonobo (bo-no´-bo) chimpanzees, like this female (on the right) and male, are often seen walking bipedally, especially when carrying food (de Wall, 2001). Note the resemblance to John Gurche's painting of *Australopithecus afarensis*. But also note the relative proportions of the arms and legs, with the legs being shorter and the arms much longer in bonobos than in *Australopithecus afarensis*. Note as well the extreme splay for grasping between the big and little toes of the bonobo.

(Photograph by Frans de Waal)

In this photograph of a 3.5 million year old **hominin footprint from Laetoli, Tanzania**, notice the very human configuration of the big and little toes.

(Photograph by John Reader)

Lucy's Child

If Lucy, the most famous fossils of *Australopithecus afarensis*, had a child, it might have looked like the bundle of skull and bones shown above, which was discovered in 2000, in the desert region of northeastern Ethiopia known as Dikika .

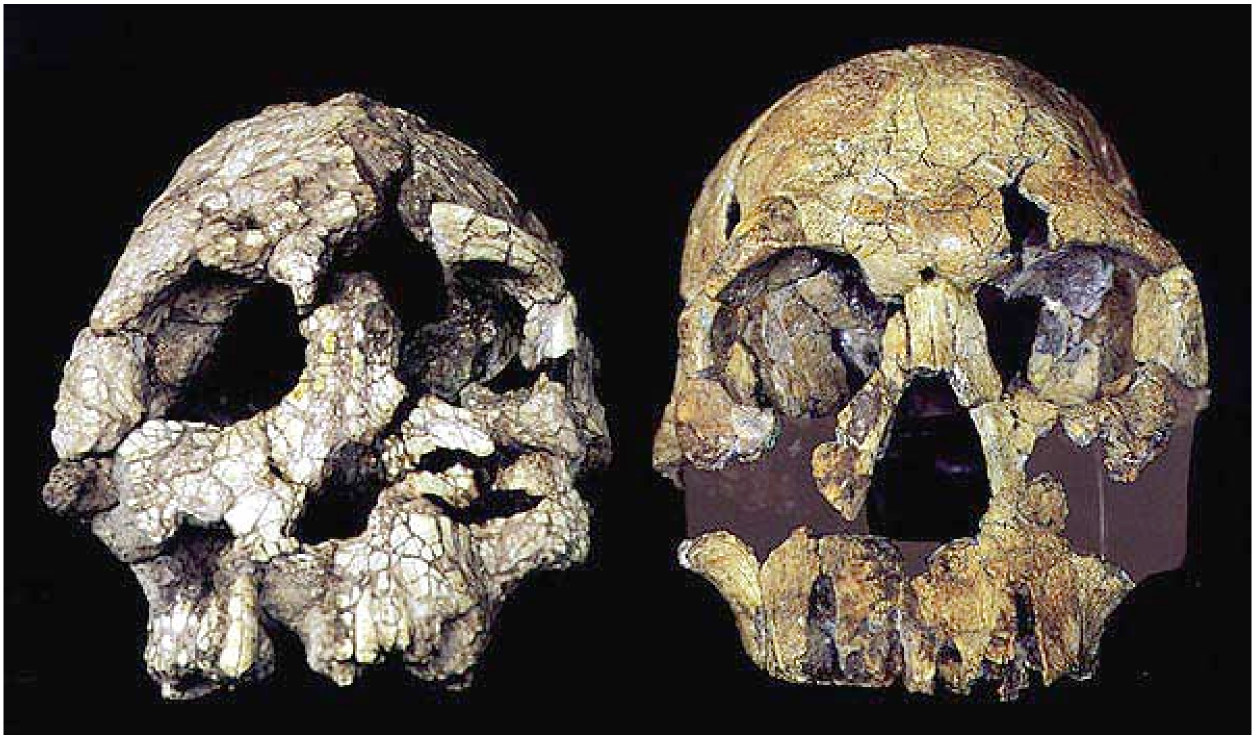
(Photograph by Zeresenay Alemseged / Dikika Research Project)

The team of researchers who made the discovery was led by Zeresenay Alemseged, Ethiopian leader of the team and a researcher at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. After the discovery, the team spent almost five years extracting the specimen from the surrounding sandstone with dentist's drills and picks (Wood, 2006). The tedious work exposed the full cranium and jaws, the torso and spinal column, limbs and the left foot. The child's one complete finger was curled in a tiny grasp, much like a young chimpanzee's. Because the skeleton is so complete, the 3.3-million-year-old fossils represents the earliest well-preserved child ever found in the human lineage. It was estimated to be about 3 years old at death, probably female, and a member of the species *Australopithecus afarensis*. The largely intact condition of the fossils indicated that the child was presumably buried shortly after death in sand and rocks during a flood (Wynn, et al., 2006).

Analysis of the skeleton revealed evidence of a species in transition. The lower limbs supported earlier findings that afarensis walked upright, like modern humans. But gorilla like arms and shoulders suggested that it possibly retained an ancestral ability to climb and swing through the trees. In the journal report announcing the discovery, Dr. Alemseged and his team wrote that "the functional interpretation of these features is highly debated, with some arguing that the upper limb features are nonfunctional retentions from a common ancestor only, whereas others proposed that they were preserved because *A. afarensis* maintained, to some degree, an arboreal component in its locomotor repertoire." (Alemseged, et al., 2006)

Later Australopiths and related Genera

Specimens of the 3.5-3.3 m.y. old ***Kenyanthropus platyops,*** recovered from the Turkana Lake region of Kenya, include a temporal bone, two partial upper jaws, isolated teeth and most of a cranium (Leakey et al., 2001). The 3.5 m.y. old site includes both former grassland and wooded habitats. *Kenyanthropus platyops* had a small ear hole, like *Australopithecus anamensis*, and thick enameled cheek teeth, small brains and flat nasal margins like *Australopithecus afarensis* and *Australopithecus anamensis* (Lieberman, 2001). It shares few cranial features with the "robust" hominins (see text below), and is distinguished from other australopithecines by derived features of the lower face. The species' unique combination of features, perhaps partly shared with the later *Homo rudolfensis,* may justify assigning it to the new genus *Kenyanthropus.*

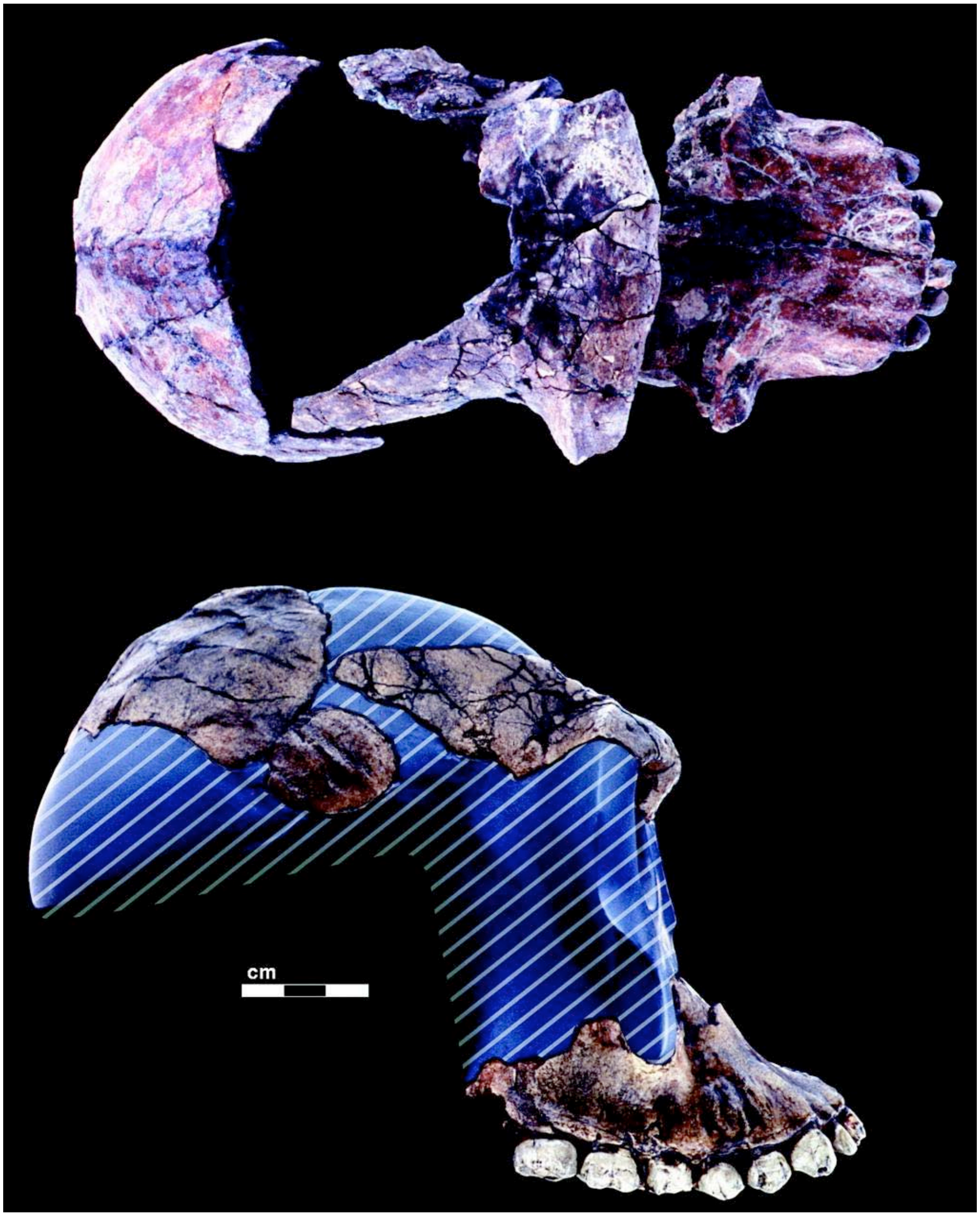


Left is the cranium of ***Kenyanthropus platyops***. Right is **KNM-ER1470**. This skull was formerly attributed to ***Homo rudolfensis***, but might best be reassigned to the genus *Kenyanthropus*—the two skulls share many similarities, such as the flatness of the face and the shape of the brow. However, they are clearly different species, as *Kenyanthropus platyops* had a significantly smaller brain (Lieberman, 2001).

Cranium of *Australopithecus africanus* from South Africa

Several cave sites in South Africa discovered in the 1920s and 1930s revealed the remains of *Australopithecus africanus* (Wolpoff, 1999). Dating these fossils has traditionally been done by comparing mammal fossils from these sites to fossil mammals from radiometrically dated sites in east African. They suggest that the breccia containing *A. africanus* remains may be 3 to 2.4 m.y. old. Relative to the preceding australopithecine species the face of *Australopithecus africanus* is broader and less projecting. The brain is slightly larger but the body is much the same. Their hands had broader tips presumably associated with larger, sensitive finger pads, a feature found in later species of *Homo*.

(Photograph by David L. Brill)



***Australopithecus garhi* Cranium**

Australopithecus garhi was discovered at Bouri, Ethiopia, (2.5 m.y. old) and includes the remains of at least 5 hominins found in ancient lake margin sediments (Asfaw et al., 1999; de Heinzelin et al., 1999). Its chewing muscles must have been large judging by the teeth and conspicuous postorbital constriction. *Australopithecus garhi* also exhibits a relatively longer femur reminiscent of *Homo*, but a relatively long forearm is consistent with australopith anatomy.

(Photographs from Asfaw et al., 1999)

Cranium of *Paranthropus aethiopicus*

The “robust” Hominins

The term “robust” in paleoanthropology has come to refer to the massive jaws and teeth of a group of later hominins. Robust species exhibit a number of unique and, therefore, derived features including greatly enlarged molars and premolars (Klein 1999). Some investigators emphasize the unique anatomy of these robust forms by placing them in their own genus, *Paranthropus*.

The earliest member of this group is *Paranthropus aethiopicus* whose fossils include the famous **“Black skull” (**above) discovered at West Turkana, Kenya (2.5 m.y. old) and mandibles and teeth recovered from the Omo region of Ethiopia (2.3 m.y. old). *Paranthropus aethiopicus* is similar to *Australopithecus afarensis* but differs in its forward placed cheek bones and teeth dimensions that anticipate later robust species.

(Photograph by David L. Brill)

Remains of ***Paranthropus boisei*** (above), one of the later robust species, have been discovered at many sites throughout east Africa. ***Paranthropus robustus*** (below) has been found in many of the cave sites of South Africa. The two species differ only in degree, with *Paranthropus boisei* considered “hyperrobust”. They seem to be geographical variants of closely related forms. These later robust species date from 2 to 1.2 m.y.a.. Both exhibit the cranial traits that allowed tremendous force to be applied by the cheek teeth (premolars and molars) during chewing. Their mandibles were large and, like *Paranthropus aethiopicus*, they had extensive attachments for chewing muscles (e.g., the sagittal crest). The large cheek teeth and skull bones contrast with their stout but small bodies. There are few limb bones for these forms, but in body proportions they were similar to *Australopithecus afarensis*. They are found mainly in deposits of former open, bushy grasslands.

(Photograph by David L. Brill)

Cranium of *Paranthropus robustus* from South Africa

(Photograph by David L. Brill)

Homo habilis **Cranium KNM-ER 1813**

Early *Homo*

Homo habilis remains have been found in Tanzania, Ethiopia, and Kenya, from deposits dated to 2.4-1.4 m.y.a. (Wood & Richmond, 2000; Spoor, et al., 2007). *Homo habilis*, which means "handy man", was originally assumed to be the first stone tool maker as the name implies. There is, however, no unequivocal evidence that habilis made stone tools. There is also some question as to which genus habilis should be assigned to, either *Homo* or *Australopithecus*. In general this species has a slightly larger cranium and narrower teeth. But its long arms and short legs resemble australopiths and, thus, it may not belong in the genus *Homo*.

(Photograph by David L. Brill)

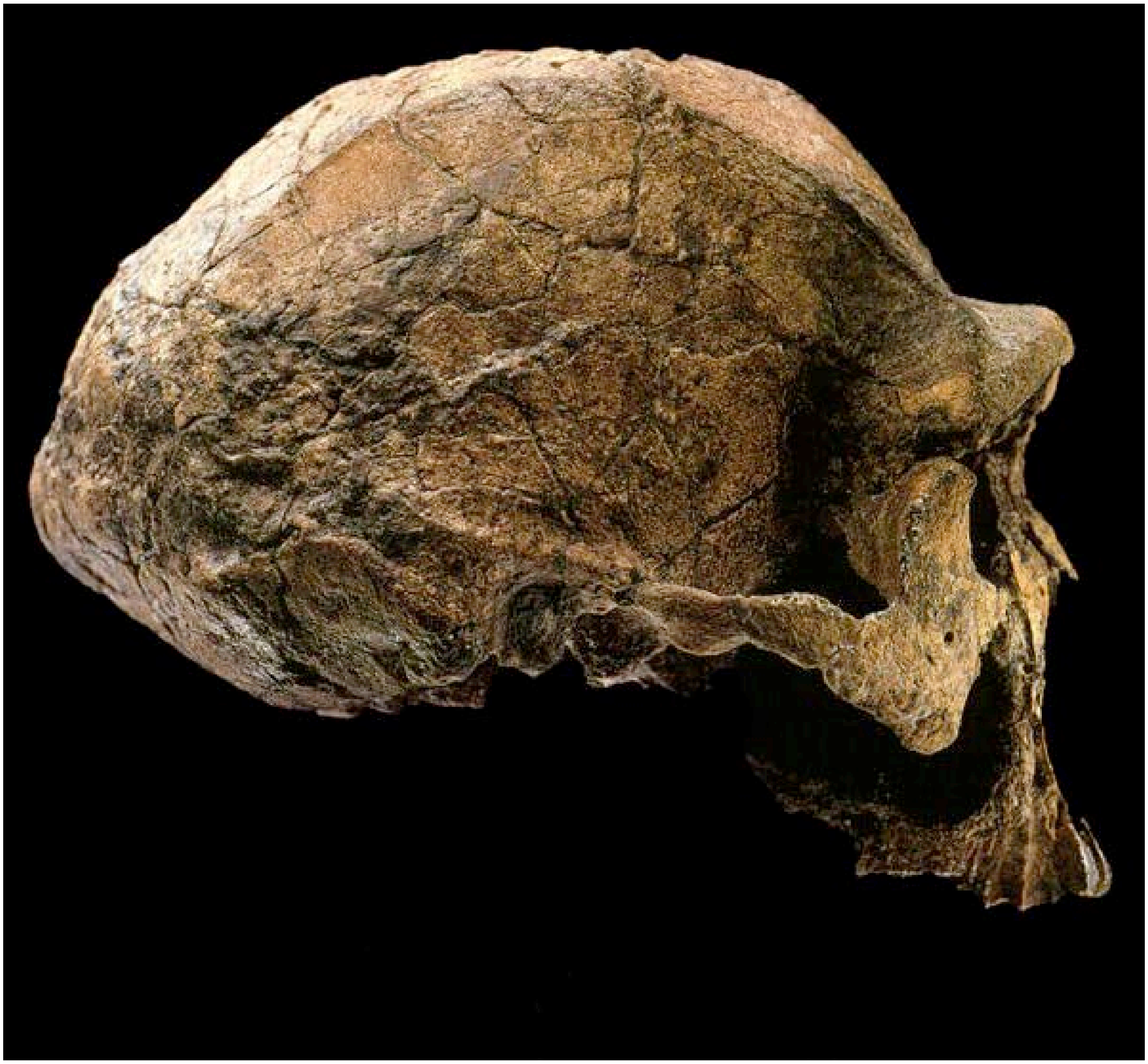
***Homo habilis* is shown on the left with *Homo rudolfensis* on the right.**

In addition, variation in the fossils assigned to *Homo habilis* may be too great to comprise a single species and a subgroup of these specimens has been identified as ***Homo rudolfensis***. Again it is unclear to which genus this new species will eventually be assigned. Some authorities suggest that it be assigned to the new genus *Kenyanthropus* based on similarities to *Kenyanthropus platyops*. *Homo rudolfensi*s remains have been found in Tanzania, Kenya, and Malawi.

Homo rudolfensis **Cranium KNM-ER 1470**

KNM-ER 1470, the code number of the most famous *Homo rudolfensis* cranium, is the best known of these fossils, and, like *Homo habilis*, is intermediate in form between australopiths and later humans. It has a large brain, but the enlarged cheek teeth and some facial features are typical of robust hominins. There are no limb bones for this species nor has a specific habitat been identified for either *Homo habilis* or *Homo rudolfensis*.

(Photograph by David L. Brill)



***Homo erectus* (*ergaster*) Cranium KNM-ER 3733 from Africa**

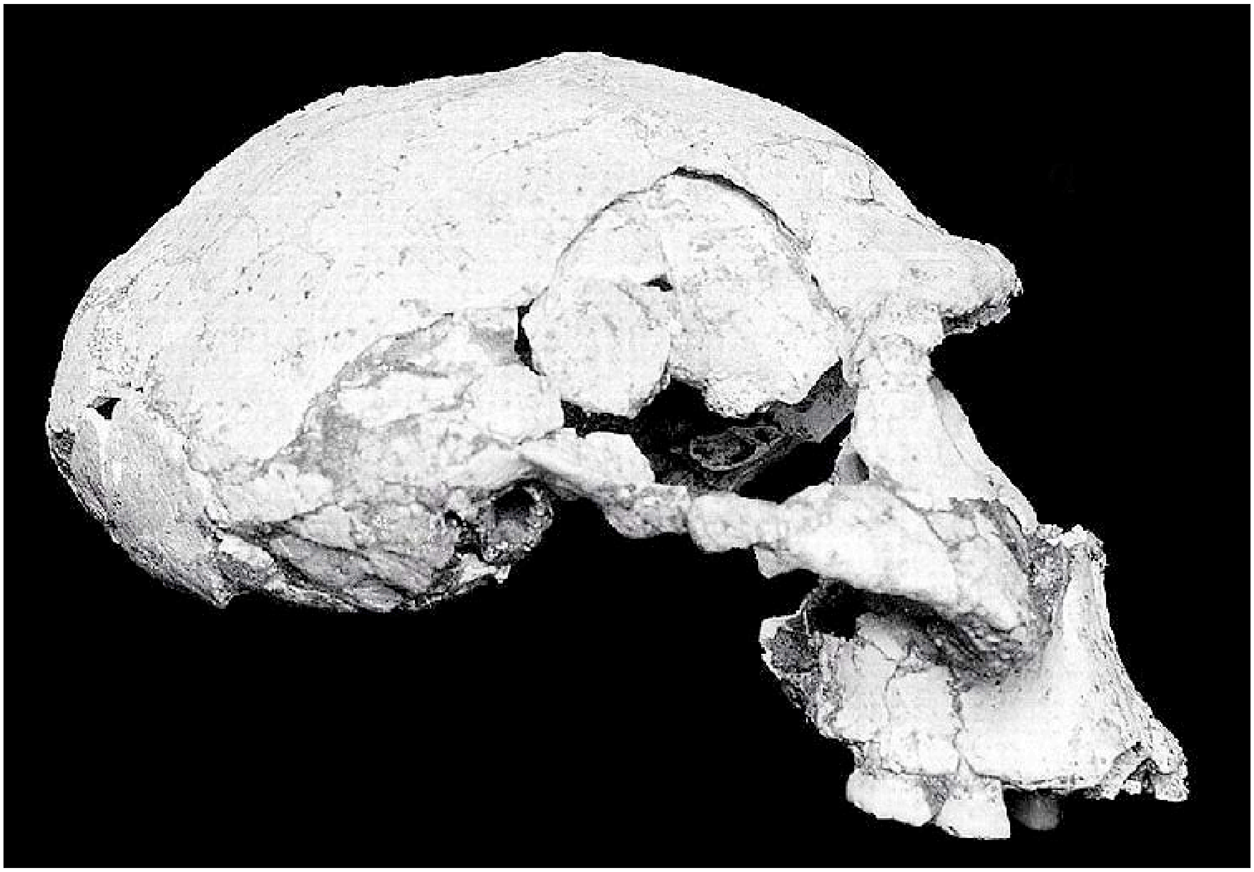
The first species to have approximately the same size and limb proportions as modern humans is *Homo erectus* (*ergaster*). The morphology of this species reflects a long-range bipedal adaptation to dryer, open grasslands and variable habitats. *H. erectus* (*sensu lato* = in the broad sense) in Africa dates from 1.9 m.y.a. to 1.0 m.y.a..

It's felt by some authorities that a separate mainly African species *Homo ergaster* is ancestral to *Homo erectus*. In this paper "*Homo erectus* (*ergaster*)" is used to draw a distinction between older African fossils, and younger (<1.4 m.y.a.) African and Asian fossils assigned to *Homo erectus* (*sensu stricto* = in the strict sense).

(Photograph by David L. Brill)

***Homo erectus* (*ergaster*) from Nariokotome, West Turkana, Kenya**

One of the more amazing fossil discoveries in the history of paleoanthropology is the Nariokotome Boy. This find represents a nearly full skeleton of a hominin youth dated to ~1.50 m.y.a.. (Photograph by David L. Brill)



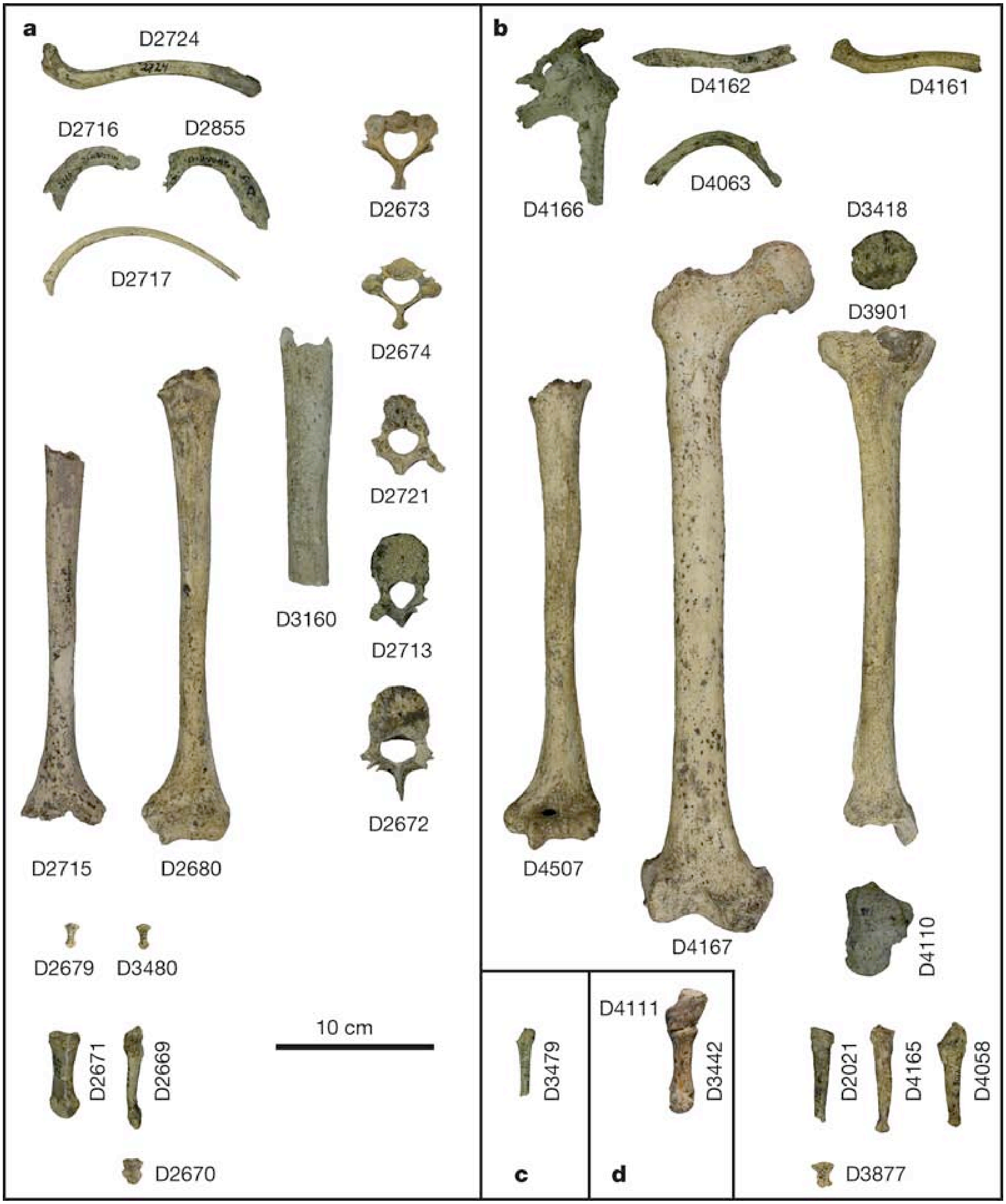
***Homo erectus* (*ergaster* or *georgicus*) Cranium from Dmanisi, Georgia**

Homo erectus (*ergaster*) presumably migrated from Africa soon after its origin (the Dmanisi fossil above is dated to 1.75 m.y.a.). Fossils of *Homo erectus* (*sensu lato*) have been found at numerous sites in Africa, Asia, and the edge of Europe as shown by two discoveries near Dmanisi, Georgia (Gabunia, et al., 2000; Vekua, et al., 2002).

"Two sets of discoveries [published in 2007] now help us to look more closely at the complex transition from *Australopithecus* to *Homo*. One of the papers is by Lordkipanidze, et al. deals with postcranial bones from Georgia, Eurasia (Lordkipanidze, et al., 2007). The other, by Spoor and colleagues, describes cranial material from Kenya (Spoor, et al., 2007).

In terms of the big picture, the transition to *Homo* was one of the most substantial in human evolution. When viewed up close, however, the *Australopithecus–Homo* transition has always been murky. One problem is that we don't know enough about *Homo habilis*, the putative ancestor of *H. erectus*. In addition, early *H. erectus* fossils are quite variable, and the more we look, the more we find contrasts with later hominins. These new discoveries, therefore, serve to further highlight the transitional and variable nature of early *Homo*." (excerpts from Lieberman, 2007)

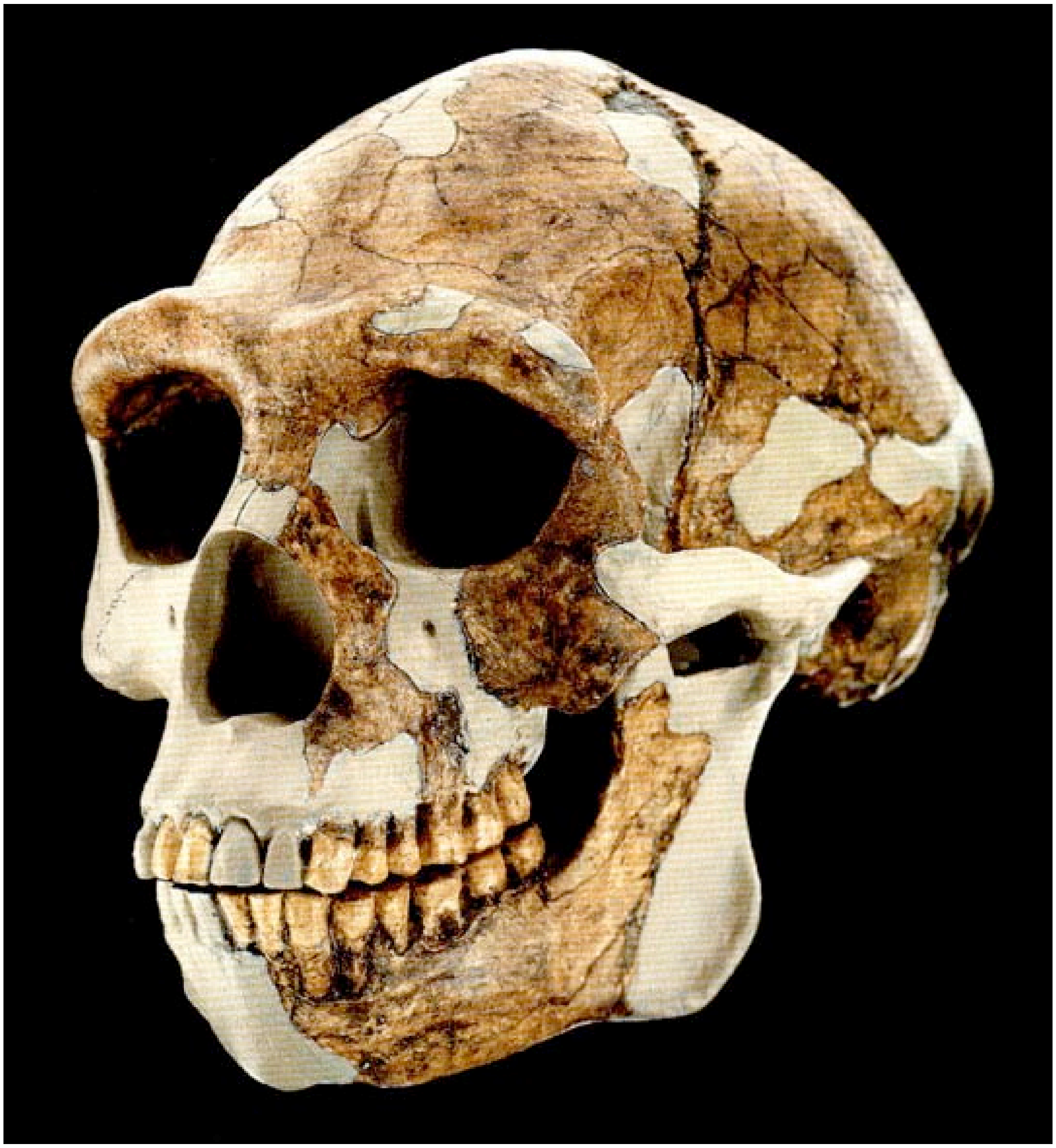
(Photograph from Gabunia, et al., 2000)



"The well-preserved postcranial remains recovered from block 2 [Dmanisi, Georgia] provide an insight into previously unknown aspects of early *Homo* morphology and also offer a new comparative perspective on key elements of the postcranial skeleton of the Nariokotome KNM-WT15000 sub-adult specimen..." (Lordkipanidze, et al., 2007)

This image from the August 9, 2007, issue of the journal *Nature* shows a new ***Homo erectus*** fossil, a partial skull known as **KNM-ER 42700**, dated to 1.55 m.y.a., with a cranial capacity of ~ 690 cc (Spoor, et al., 2007). It is shown above the largest African *H. erectus* specimen, OH 9 with a cranial capacity of ~1060 cc. The composite image is by Fred Spoor. The original image of OH 9 is by John Reader.

"The skull [KNM-ER 42700] also shows features that had previously been seen only in Asian fossils of *H. erectus*, such as a keeling (or ridge) on its frontal and parietal bones. These traits had persuaded a growing number of researchers in recent years to split the fossils of *H. erectus* into two species, with *H. erectus* from Asia and *H. ergaster* from Africa. But the skull's mix of traits shows *H. erectus* cannot be 'easily divided between two species from Africa and Asia,' says Spoor. [William] Kimbel and Arizona State graduate student Claire Terhune reached a similar conclusion after studying the temporal bones of 15 *H. erectus* skulls, in a paper published in the July issue of the *Journal of Human Evolution*." (Gibbons, 2007; Terhune, et al., 2007).



Skull of Peking Man, a *Homo erectus* from China

Homo erectus pekinensis remains were first discovered in 1923-27, during excavations at Zhoukoudian cave near Beijing (Peking), China. The fossils have been dated to 550,000-300,000 years ago.

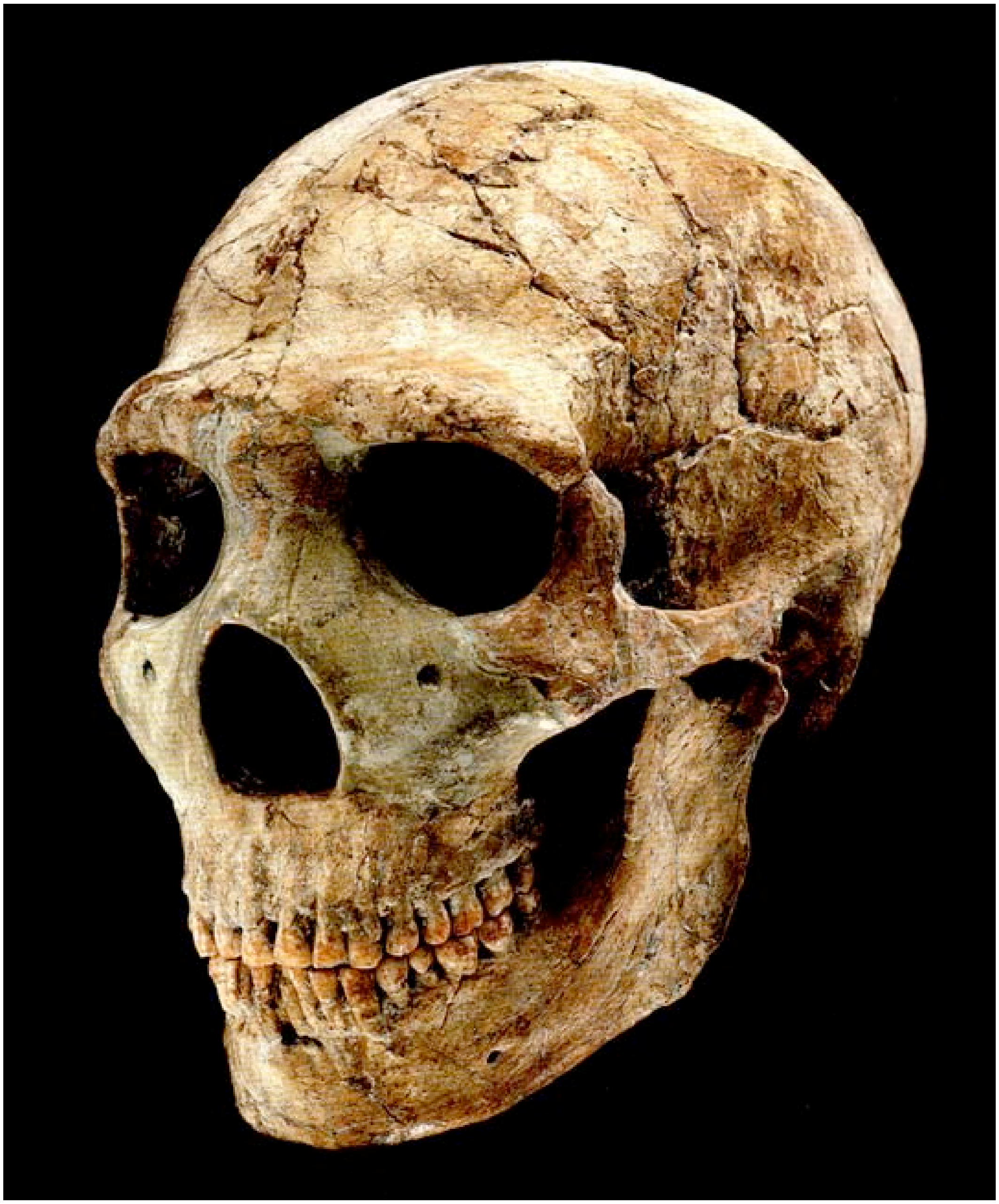
(Photograph by David L. Brill)

Cranium of *Homo heidelbergensis* from Petralona, Greece

Later *Homo*

Discoveries in Italy and Spain tentatively assigned to ***Homo antecessor*** are dated to 700,000 and 600,000 years ago, respectively. They provide evidence of an early entry into Europe of people intermediate in form between *Homo erectus* and later *Homo heidelbergensis*. The species ***Homo heidelbergensis*** (above)**,** sometimes referred to as Archaic *Homo sapiens*, describes hominins less than 600,000 years old in Africa, Europe, and Asia (Wood & Richmond, 2000). This group of fossils differs from *Homo sapiens* in the body and cranium being more heavily built.

(Photograph by David L. Brill)



***Homo neanderthalensis* from Amud Cave, Israel**

(Photograph by David L. Brill)

H. neanderthalensis **is shown on the left, with** ***H. sapiens*** **on the right.**

Homo neanderthalensis is a relatively homogeneous group dating between 250,000 and 29,000 years ago. It is represented by many fossils from all over Europe (excluding Scandinavia), and in southwestern and western Asia (Hoss, 2000; Klein, 2003). *Homo neanderthalensis* had large double-arched brow ridges, a projecting face, especially large nose, a weak chin, and brains larger than modern humans. Their bodies were thickset, hands and feet broad, and their limbs exhibited large muscle attachments. The analysis of mitochondrial DNA (mtDNA) recovered from Neanderthal bones and compared to mtDNA of living *Homo sapiens* supports the conclusion that *Homo neanderthalensis* was a distinct species from modern humans (Krings et al., 1997; Ovchinnikov et al., 2000).

(Photographs by Jeffrey H. Schwartz)

Homo floresiensis ***Homo sapiens***

In 2003, a new human-like species named *Homo floresiensis* was discovered in Indonesia. Skeletal remains show that the hominins were only one meter tall (~3 ft), and had a brain one-third the size of that of modern humans. They may have lived just 18,000 years ago on an isolated island long after *Homo sapiens* had migrated through the South Pacific region (Brown, et al., 2004; Lahr & Foley, 2004; Morwood, et al., 2004).

The new species was found by Australian and Indonesian scientists in a rock shelter called Liang Bua on the island of Flores. The team unearthed a near complete skeleton, thought to be a female, including the skull, jaw and most teeth, along with bones and teeth from at least seven other individuals. In the same site they also found bones from Komodo dragons and an extinct pygmy elephant called *Stegodon*.

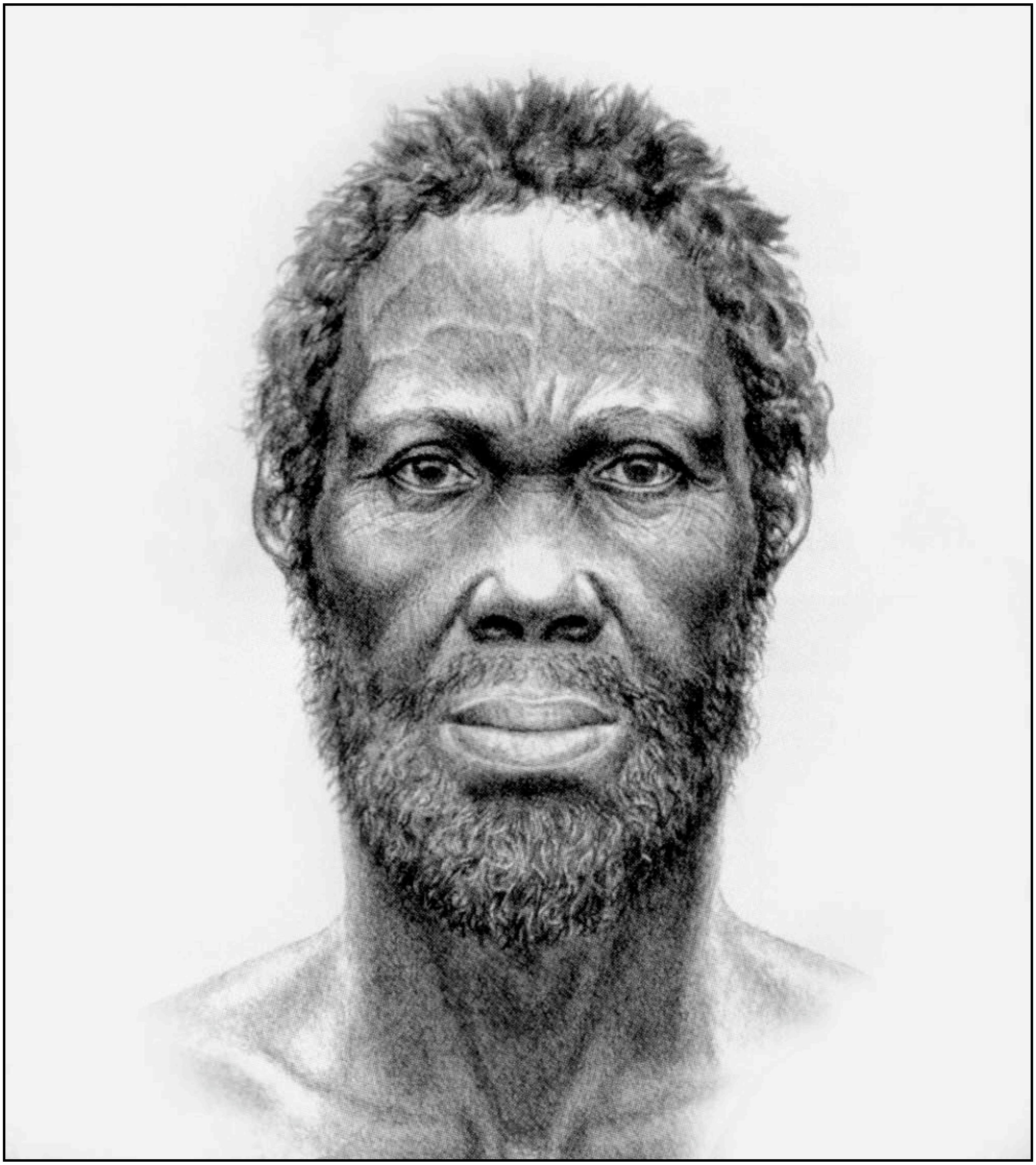
Since the publication of this discovery in the journal *Nature* in 2004, *Homo floresiensis* has been the subject of intense controversy. The debate, however, has had a positive side effect by inadvertently showcasing the very nature of scientific inquiry itself.

(Photograph by Peter Brown)

Homo sapiens idaltu

The origin of anatomically modern humans and the fate of Neanderthals have been fundamental questions about human evolution for over a century. A key barrier to the resolution of these questions has been the lack of substantial and accurately dated African hominin fossils from between 100,000 and 300,000 years ago. The published description of *Homo sapiens idaltu* from Herto, Middle Awash, Ethiopia, dated to between 160,000 and 154,000 years ago, fills this gap and provides crucial evidence on the emergence of *Homo sapiens*. The Herto hominins are morphologically and chronologically intermediate between archaic African fossils and later anatomically modern humans. They therefore represent the probable immediate ancestors of anatomically modern humans (White, et al., 2003).

(Photograph by David L. Brill)



This portrait of *Homo sapiens idaltu* is from the cover of the June 12, 2003, issue of the journal *Nature*. The portrait represents what the ancestor of all living human beings may have looked like, a black man from Ethiopia.

The Moderns

At some point between 200,000 and 100,000 years ago a population of early humans in Africa crossed the morphological threshold to fully modern humans. The timing of this watershed event is supported by a variety of genetic studies (Cavalli-Sforza 1998). These same studies estimate the number of individuals in this population to be from 20,000 to as few as 2,000 individuals (Harpending, 1998).

A population of two thousand individuals is about the size of a large high school in America today. It challenges the imagination, then, to understand that a population of just two thousand individuals may have been the common ancestors of all six billion plus living human beings. What a stunning moment in time to think of those two thousand individuals poised on the brink of a brave new world. But in looking back to that moment, we can only wonder what our small band of ancestors might think of our world today.

Because of limited space and the accelerating growth of information about the origin of fully modern humans, we stop our review of the fossil record here, at the threshold of our species.

(For an overview of the evolution of modern humans see Klein (2002) and Olson (2002) in recommended books, and Mellars (2006b) in recent articles of interest.)

A Note about Species Names

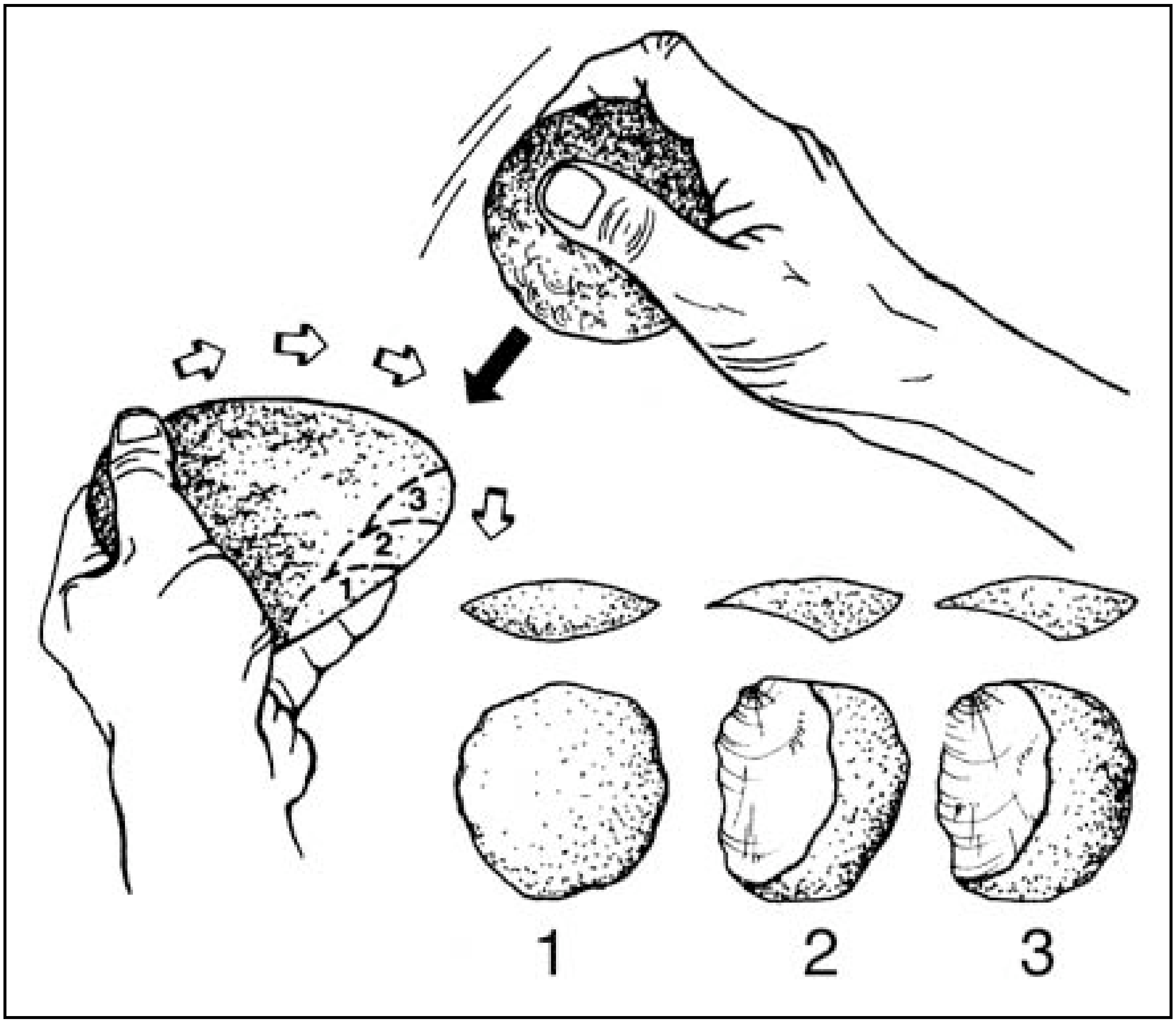
New fossil discoveries of our early ancestors are occurring at an increasing rate, each with new names and claims of direct ancestry to modern humans. But even as paleoanthropologists shuffle species names to accommodate these new discoveries the general outline of human evolution remains sturdy. The astrophysicists James E. Peebles has suggested that rapidly changing sciences, like astronomy and paleoanthropology, are a sign of healthy activity. Shifts in opinion are not a reflection of some inherent weakness, "… rather it shows the subject in a healthy state of chaos around a slowly growing fixed framework. Confusion is a sign that we are doing something right; it is the fertile commotion of a construction site." (Peebles, 2001)

Major Trends in Hominin Evolution

Cultural Evolution

Bipedalism appeared 5 to 6 m.y.a. and it is likely that these earliest hominins achieved a level of technology consistent with contemporary chimpanzee tool use (Ambrose, 2001). The earliest stone tools date to ~ 2.6 m.y.a. from Gona, Ethiopia (Semaw, et al., 2003). Sites in Ethiopia provide evidence of the disarticulation and defleshing of large mammals and of long bones that were smashed open presumably to obtain the marrow. These early stone tools are lumped with the slightly later tools at Olduvai Gorge into the **Oldowan Industry** that lasted until 1.7-1.6 m.y.a.. Their shapes are mostly a function of the characteristics of the raw material used but represent skilled percussion flaking (well beyond the capacity of chimpanzees) that maximizes the production of sharp edges (Ambrose, 2001).

Oldowan Stone Tool

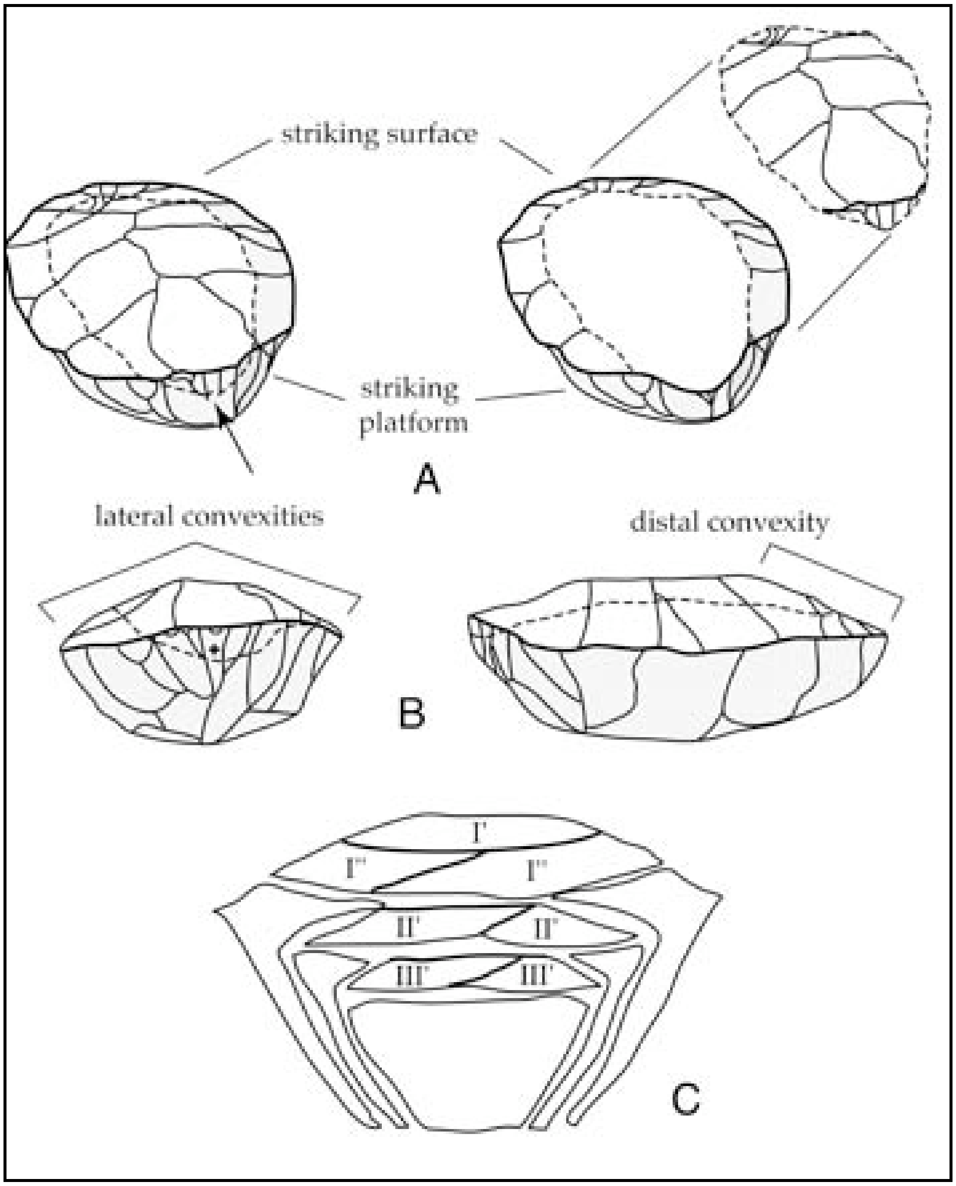


Manufacture of Oldowan Flake Tools

(Ambrose, 2001)

Acheulean Handaxe

Larger stone cutting tools 10-17 cm (~ 4-7 inches) in length of the **Acheulean Industry** appeared around 1.5 m.y.a. at approximately the same time as *Home ergaster* / *Homo erectus*. They represent a long lived tool association and were produced as recently as 300,000 years ago (y.a.) by *Homo heidelbergensis* (Ambrose, 2001). The Acheulean Industry is found only west and south of the “Movius Line” which curves from India-Bangladesh to northern England (with a few exceptions in China and Korea). This distribution may reflect the exit of the earliest migrants out of Africa at 1.8-1.6 m.y.a. thus predating the invention of Acheulean tools. The typical tools in this complex were bilaterally symmetrical with standard shapes suggesting a predetermined goal, a conceptual ability not evident in the Oldowan assemblages.



Levallois Technique

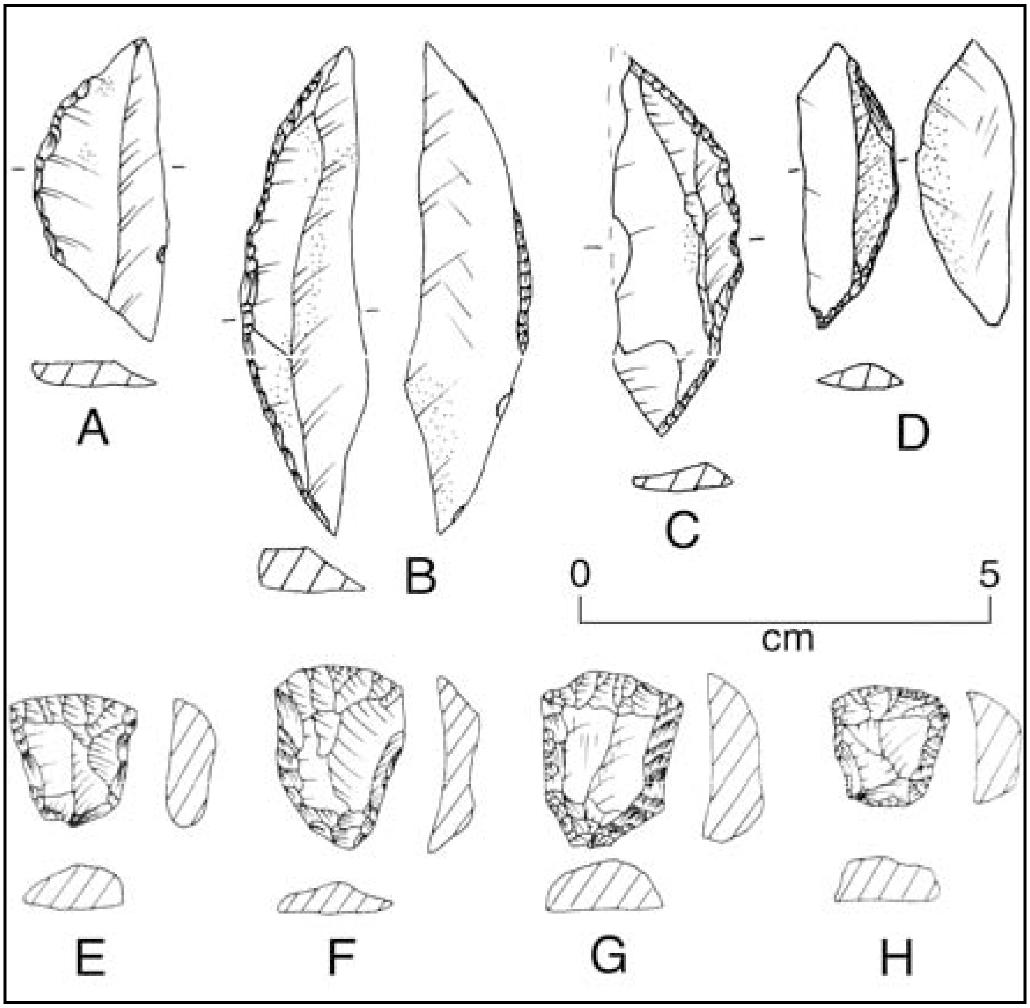
(Ambrose, 2001)

The shaping of later Acheulean tools became more sophisticated due to the use of soft hammers either of wood or bone to knock off flakes. The cores from which these flakes were struck were better-prepared, so that resulting flakes were large and nearly finished. The combined use of soft hammers and well prepared cores is known as the Levallois technique.

Schöningen, site 13 II-4: Recovery of a Wooden Spear

The oldest known wooden tools, 2 meter long (6-1/2 ft) spears ~ 400,000 years old, were discovered in deposits near Schöningen, Germany. Made from spruce and weighted for precision throwing much like a javelin, they are the oldest and most complete hunting weapons ever found. The spears were most likely made by the ancestors of the Neanderthals, *Homo heidelbergensis*.

(Photograph courtesy of NLD Hannover)



Examples of Upper Paleolithic Blade Tools

(Ambrose, 2000)

The Oldowan and Acheulean tool traditions are lumped into the Lower Paleolithic. After 300,000 y.a. tools become more complex and are labeled in Europe as the Middle Paleolithic or in Africa, as the Middle Stone Age (Ambrose, 2001). Regional variation is great enough that cultural traditions become evident. Tools composed of two or more materials that require complicated preparation become common and suggest increasingly complex brains. The tool tradition associated with the Neanderthals in western Europe is called the Mousterian (Klein, 1999). All are eventually replaced by the blade industries of the Upper Paleolithic which are associated with modern humans.

Diet

In addition to forcing changes in locomotion that led to walking upright, the increasingly dry climate of east Africa over the last six million years forced changes in the diet of early hominins from the soft fruits of the tropical rain forest to the increasingly fibrous and tough foods available in open habitats.

Early hominin diets are reconstructed partly based on the surface areas of the molars and the cross-sectional area of the body of the lower jaw (Collard & Wood, 1999). Tooth area reveals the efficiency of food processing; whereas, the mandibular body size reflects the amount of force applied during processing. Humans are omnivores that favor nuts, fruit and meat. The chimpanzee diet is not much different from that of humans except in a greater emphasis on fruit, stems and leaves and less on meat. Chimpanzees do not differ particularly from modern humans in the efficiency and force of their dentition. However, only *Homo ergaster* of the early hominins shared these dental dimensions with us. Australopithecines and the robust *Paranthropus* species, in particular, required more area for processing and more robust jaws. *Paranthropus* species especially relied on hard food items suggested by scratches on their teeth (Kay & Grine, 1988).

In general the earliest sites showing hominin activity are near lake margins where streams join or at rock outcrops, places with a variety of resources that can be exploited for longer periods (Larick & Ciochon, 1996). This pattern changes after 2.0 m.y.a. as landscapes became more open. Fewer resources are exploited at any one locale, and individuals probably used several locales simultaneously which would have required a wide-ranging scavenging behavior. This shift happens after the appearance of relatively longer lower limbs and coincides with the first exit from Africa. By 1.7 m.y.a. it is the most common pattern and is associated with *Homo ergaster* / *Homo erectus*, and Acheulean tools. The first use of fire may be represented by burnt bones (1.5-1.0 m.y. old) found at the Swartkrans Cave in South Africa. Although we do not know if they used fire for cooking, or at all, it is commonly believed that *Homo erectus* regularly ate meat. How they acquired it, however, whether by scavenging or hunting, is controversial (Klein, 1999; Tappen, 2001). It is more commonly accepted that *Homo heidelbergensis* hunted meat regularly.

Encephalization, Language and Speech

Brain sizes expressed as estimated cranial capacities are commonly reported for various species of hominin. *Australopithecus afarensis* and *Australopithecus africanus* have the smallest averages to date at 410 and 440 cubic centimeters (cc), respectively (Collard &Wood, 1999). Chimpanzee cranial capacity also averages 410 cc. But chimpanzees weigh about 24% more than the australopiths, thus complicating this simple comparison. The cranial volume of the robust hominins such as *Paranthropus robustus* and *boisei* were in the 500's and *Homo habilis, rudolfensis* and *ergaster* averaged 610, 750, 850 cc, respectively. *Homo erectus* range from 725 to 1250 cc, and all later forms had brains as large (or larger, e.g., Neanderthals) than modern humans (Wood & Richmond, 2000).

Although absolute brain size is a better predictor of the cognitive differences that distinguish apes from monkeys (Gibson, 2001), it is not considered as good an indicator of intelligence in hominins as measures that adjust for body size. An example is Jerison (1973), who expressed intelligence as an Encephalization Quotient (EQ) which represents the brain size of a specific mammal species that exceeds or is less than the brain size of typical mammals of similar body size. EQ only increases approximately 50% going from the australopiths to *H. habilis* or *H. erectus* (*ergaster*), but doubles when they, in turn, are compared to modern humans. Higher EQ's do correlate with high energy diets and the challenging search for high energy food that may have helped initiate brain enlargement.

Language ability must have developed as the brain enlarged. But there is only indirect evidence for this, including endocasts (molds of the skull's interior), the relative degree of curvature of the base of the skull (which has some relationship to the shape of the voice box), and the diameter of vertebral canals (reflecting the innervation of the rib cage for controlling movement of the diaphragm in conjunction with speech) (Klein, 1999). There is some evidence for early language, if not full speech, capabilities. One speech area of the brain, Broca's area, can be discerned on endocasts and is either missing or undeveloped in australopiths, but is developed in *Homo erectus* (*ergaster*).

Recent genetic studies of language ability (Enard, et al., 2002; Lai, et al., 2001) have supported the hypothesis, put forward by Richard Klein (Klein, 1999; Klein, 2002), that fully modern language ability did not appear in humans until after 50,000 years ago and represents a genetic rewiring of the brain. This hypothesis is also supported by, and helps explain the archeological record which shows a sudden appearance starting 50,000 years ago of representational art and sophisticated stone tools, an indication of conceptual thought characteristic of modern language ability.

Summary

It is highly unlikely that the general framework we have portrayed for human evolution will change in the near future. This in spite of the fact that the cast of characters will surely expand with new discoveries, and paleoanthropologists will surely readjust genus and species names to reflect our growing knowledge. And that is good news, for it reflects the healthy chaos of Peeble's busy construction site. By the same token, it is the broad framework of human evolution that all biology students should learn, not just a long list of species names. Learning the scientific story of our origin should leave students with a sense of anticipation for further discoveries that will fill in the missing gaps in our knowledge and, in so doing, add further supports to the already sturdy framework of our understanding of human evolution.

Recommended Books

Johanson, D., & Edgar, B. (1996). *From Lucy to Language*. New York: Simon & Schuster. (Although somewhat dated, this book includes David L. Brill's stunning photographs of the world's most important human fossils.)

Klein, R. G. (1999). *The Human Career: Human Biological and Cultural Origins, 2nd Edition*. Chicago: University of Chicago Press. (Klein's book is one of the most cited and important books on human evolution. It is somewhat technical but provides a complete and balanced view of human evolution.)

Klein, R. G., & Edgar, B. (2002). *The Dawn of Human Culture*. New York: Wiley. (This is an excellent updated, popular version of Klein's *The Human Career*, that provides a coherent view of human evolution for all interested readers.)

Olson, S. (2002). *Mapping Human History: Discovering the Past Through Our Genes*. Boston: Houghton Mifflin. (Olson gives an excellent account of recent genetic studies on human evolution. This book is highly recommended for all readers.)

Tattersall, I., & Schwartz, J. (2000). *Extinct Humans*. New York: Westview Press. (This book gives an overview of the complexity of human evolution and includes magnificent photographs of human fossils by Schwartz.)

Walker, A., & Shipman, P. (1996). *The Wisdom of the Bones*. New York: Knopf. (This is one of the best first hand popular accounts of paleoanthropology as a living science.)

Recommended Web Sites

Human evolution by Wikipedia, available at: http://en.wikipedia.org/wiki/Human_evolution Last accessed 8-30-07.

Becoming Human by The Institute for Human Origins, Arizona State University, Tempe, available at: http://www.becominghuman.org/ Last accessed 8-30-07.

Paleoanthropology by the University of California, Los Angeles, available at: http://cogweb.ucla.edu/ep/Paleoanthropology.html Last accessed 8-30-07.

Fossil Hominids: The Evidence for Human Evolution in The Talk Origins Archive, available at: http://www.talkorigins.org/faqs/homs/ Last accessed 8-30-07.

Human Evolution by MSN Encarta, available at: http://encarta.msn.com/encyclopedia_761566394_8/Human_Evolution.html Last accessed 8-30-07.

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