"Robust" Australopithecines, Our Family Tree, and Homoplasy

Henry M. McHenry

Darwin never predicted the existence of the "robust" australopithecines.[1] In his 1872 book *The Descent of Man* he foretold the discovery of fossils linking the evolutionary lineages of apes and people in Africa.[2] He speculated that bipedal walking probably evolved before brain expansion, and fossil evidence for that sequence was eventually discovered. But he did not set the stage for what a school boy would hammer out of the rocks at a site called Kromdraai in South Africa in 1938. That discovery was so unexpected that even after more than half a century and the discovery of hundreds of similar fossils, the robust australopithecines remain a mystery.

The mystery stems from the fact that they are so unlike anything living today. They walked erect on hindlimbs remodeled from the common pattern seen in other primates to the unique configuration typical of only the human family. They had relatively larger brains than did apes or earlier humans. But they had what an experienced portrait artist would call bizarre faces, with no foreheads, ridiculously flat cheeks, and enormous mouths. They had quite small canine teeth but huge molars. General consensus has them on a side branch of the human evolutionary tree, as implied by the original name given to them, "Paranthropus." They are often portrayed as our herbivorous cousins who made no tools and who became extinct at least a million years ago. But now there are new clues to the mystery that are bringing some surprises.

Discovery

The school boy at Kromdraai gave his fossil to the foreman of a nearby mine, who sold it to Robert Broom on a Wednesday in June, 1938. Broom was one of the most colorful heroes in the drama of human origins research. He was a physician by training but his real love was paleontology. He was particularly well known for his work with the mammal-like reptiles from the Karoo of South Africa. He was an early defender of Raymond Dart's claim that *Australopithecus africanus* had human affinities, and in 1936 he discovered more of these human-like fossils. By this time he had written several books, including *The Coming of Man: Was It Accident or Design?* When he bought the Kromdraai fossil he was seventy-one years old, but still full of youthful vigor and mischief. His mischievousness included playing tricks on the press: He once advised a young apprentice to "publish only part of what you know, so

when critics harp you can devastate them with new information." It is said that he always wore a stiff collar and tie on the off chance that photographers would show up. Sometimes when he found important fossils he would cover them up again, invite the press out to the site for a routine interview, and "discover" the fossils before their eyes (and cameras). One story tells of an assistant who grew tired of these antics and painted a museum catalogue number on one of these "rediscovered" fossils, which somewhat reduced the spontaneity of Broom's feigned astonishment at the moment of discovery.

It is interesting to look up Broom's original announcements of discoveries.[3] He did not waste time. A new find would appear in the British science journal *Nature* very soon after its discovery. Accompanying the announcement would be Broom's remarkable sketches, which captured the essential details of the fragmentary and distorted fossils. Broom would distill the essential importance of a discovery without paying much attention to previous scientific literature. Often he sent casts of fossils to various other scientists. Most of these scientists did not realize the significance of the Kromdraai hominid. But Broom, who was one of the wild men of Africa along with Raymond Dart and Louis Leakey, did.

The strangeness of the Kromdraai hominid haunted the writers of human evolution for years. From the point of view of comparative anatomy at the time, it had a mix of human and ape characteristics. It was an ape by the fact that its brain was so small (502 cc by recent measures, although Broom gave various estimates that were higher). It was gorilla-like in that it had a crest of bone on the top of the skull for the attachment of powerful chewing muscles. If one measured humanness by brain size (as Broom did), this was an ape. But why did it have so many human attributes? Between 1938 and 1947 Broom had the chance to reflect on what he had found. He considered the advice of various sympathetic colleagues, particularly Franz Weidenreich. Ultimately he kept to his original opinion that it belonged to the human family. In the textbooks of the time, the Kromdraai hominid and its kin were still considered of the human lineage.

Close to his eightieth birthday in 1948, Broom and his young assistant John Robinson began excavations at Swartkrans. Swartkrans proved to be the most important site for understanding the robust australopithecines.[4] Their method of excavation was speeded by the liberal use of TNT. The results were spectacular in fossil hominids but, inevitably, problematic to those who came later

to determine geological age. What they found were Kromdraai-like fossils different enough to warrant separate species names according to some (Broom, Howell, Grine), but most paleontologists refer them to *Australopithecus robustus*. The richness of Swartkrans was astounding. Whole skulls, complete dentitions, and a few bits of the rest of the skeleton came to light. Among the skeletal remains were remains of a hip. The hip of these robust australopithecines appeared to have the fundamental reorganization for bipedalism that characterized other early hominids. Unfortunately, the site was owned by a mining company that took over when the paleontologists uncovered commercially valuable minerals. The mess left by the miners took decades to sort out. Fortunately, a highly competent and persistent geologist, C. K. Brain (who became director of the Transvaal Museum), sorted out the jumble left by the miners and by Broom's rapid excavations so that Swartkrans is now one of the best understood early hominid sites.

Broom worked quickly in the last decades of his life. He did not worry too much about convention. Nor did Louis Leakey, a contemporary of Broom's who also made great strides in hominid discovery. Leakey was a Kenyan by birth, steeped in Kikuyu tradition and language and formally educated in the British system, complete with a Ph.D. from Cambridge University. With his wife Mary he began working at Olduvai Gorge in Tanzania in the mid-1930s. The site yielded much ancient fauna and archaic stone tools, but unlike the spectacularly hominid-rich sites of South Africa (especially Swartkrans), it contained almost no hominid fossils. There were many hominid tools there, however, and Mary became the foremost authority on the earliest material culture of our ancestors. The big event happened in 1959 with Mary's discovery of Olduvai Hominid 5.

O.H. 5 was discovered in 1959 and proved to have its closest affinities with the robust australopithecine of South Africa.[5] But it was quite different in many respects. Most conspicuously it had enormous cheek teeth that were way above the size seen in even the largest specimen of the robust australopithecines of South Africa. Leakey gave it the name *Zinjanthropus boisei*, but that name was changed to *Australopithecus boisei* by Phillip Tobias, who wrote the definitive monograph on the specimen. Hundreds of additional specimens of *A. boisei* are now known thanks to the efforts of a host of skillful collectors at various sites in Tanzania, Kenya, and Ethiopia.

A third species of robust australopithecine, *A. aethiopicus*, is

earlier and more primitive than *A. boisei*. A few jaws and teeth have been discovered since the late 1960s. In 1985 a complete skull of *A. aethiopicus* came to light from west of Lake Turkana in Kenya in beds as old as 2.5 million years.[6]

SPECIES OF "ROBUST" AUSTRALOPITHECINE

We will never know precisely what happened in history even if we have written records because those records will be one author's version of events. But we do have the paleontological record of mammals in the past and the geochronology. We are blessed with thousands of specimens from East and South Africa and we can begin to understand what these near-humans were like. Let us turn to look at the three species of "robust" australopithecine: *A. robustus*, *A. boisei*, and *A. aethiopicus*.

Australopithecus robustus is known only from two cave sites in South Africa: Kromdraai and Swartkrans. Neither site can be dated with precision but the associated fossil animals fit with animals between 1.8 and 1.0 million years ago. The habitat in which they lived was a dry and open grassland. Their skulls and teeth are designed for heavy chewing. The cheek teeth are quite large, especially relative to the size of their bodies. The roots of these teeth are fit into heavily built jaws. The chewing muscles were apparently very large, as can be seen by the attachment areas on their robust cheek bones and sagittal crest. The face is buttressed against the chewing forces as well.

Heavy chewing left such a conspicuous mark on the skulls and teeth of *A. robustus* that it is easy to overlook features that are *Homo*-like and unlike *Australopithecus*. The face is more tucked under the braincase, for example. The brain is larger. The base of the skull is more flexed. The jaw joint is deeper. The thumb is relatively longer and its tip is broad and flat like later *Homo* and unlike earlier *Australopithecus*.

Although the term *robustus* implies a large and powerfully built body, newly discovered skeletal parts show that *A. robustus* ranged in body weight from quite small (perhaps as little as 62 pounds) to only moderately heavy (120 pounds) compared to modern humans. The average female may have been about seventy

pounds and the average male about eighty-eight pounds. The fossil material is too fragmentary to make precise estimates of stature, but the available evidence suggests the female stood at about three feet seven inches and the male stood at about four feet four inches. The small size of the body implies that the relative size of the brain was larger than may be apparent from its absolute size. In fact, its relative brain size is very close to that seen in the earliest species of *Homo*.

In the last years of his life Broom was assisted by John Robinson. Upon Broom's death in 1951, Robinson took on the task of excavation and fossil description. He developed what came to be known as the dietary hypothesis. According to this theory there were fundamentally two kinds of hominids in the Plio-Pleistocene. One was the "robust" australopithecine (which he called *Paranthropus*) that was specialized for herbivory, and the other was the "gracile" australopithecine (*A. africanus*, which he later referred to as *Homo africanus*) that was an omnivore/carnivore. By this theory the former became extinct while the latter evolved into *H. erectus*. The specialization for herbivory in *A. robustus* includes the suite of traits listed earlier as adaptations for heavy chewing.

Like most generalizations about human evolution, Robinson's dietary hypothesis was controversial, but it stood as a useful model for several decades. Detailed analyses of the tooth surface using the scanning electron microscope appeared to confirm that the diet of *A. robustus* consisted primarily of plants, particularly small and hard objects like seeds, nuts, and tubers, while early *Homo* was more omnivorous. But as new fossil hominid species were discovered in East Africa and new analyses were done on the old fossils, the usefulness of the model diminished. Now there is a new understanding of how similar the two South African species—*A. africanus* and *A. robustus*—are when compared to other early hominid species. They share a suite of traits that are absent in earlier species of *Australopithecus*, including expanded cheek teeth and faces remodeled to withstand forces generated from heavy chewing. There is also new evidence that *A. robustus* was not a strict vegetarian.

The possibility that *A. robustus* was omnivorous is suggested by the distribution of plants and animals and their availability for consumption by creatures such as this large primate. Omnivory is also suggested by studies of the stable carbon isotopes and strontium-calcium ratios in their teeth and bones. Simply put, they have the chemical signal associated with animals whose diet is omnivo-

rous and not specialized herbivory. In fact, there is some direct evidence of animal butchering associated with the cave deposits containing *A. robustus*. Distinctive cut marks made by stone tools occur on animal bones in Member 3 of Swartkrans as well as evidence of controlled use of fire. *A. robustus* is the only hominid recovered from this layer of the cave, but *Homo* was around earlier (in Member 1 and 2) and may have been in the area during Member 3 times and simply escaped preservation.

Australopithecus boisei is known from East African deposits from northern Tanzania to southern Ethiopia. It spans the time between approximately 2.2 and 1.3 million years ago. It is distinguished by its huge chewing apparatus. The architecture of the skull and teeth of this species is dominated by the stresses of heavy chewing. The molar teeth are enormous, even relative to the size seen in *A. robustus*. The premolars have expanded so much that they take on the look of molars. The jaw is massively thick and deep. The attachment areas for the muscles that move the jaw are powerfully built, including a strong sagittal crest on top of the skull and thick cheek bones. The cheek bones are pulled forward so that the sides of the face project ahead of the root of the nose. The skull and jaw are arranged to maximize biting force at the level of the cheek teeth.

Like its cousin to the south, *A. boisei* shares many features with *Homo* that are not seen in earlier species of *Australopithecus*. The face tends to be tucked in under the braincase more, although this is variable. The base of the skull is strongly flexed. The jaw joint is deep. The brain is expanded with an average size of 488 cc compared to the 384 cc of *A. afarensis*. The variation in size of the jaws and faces is considerable, which suggests that sexual dimorphism in size was greater than that in recent *Homo*.

Until recently, it was assumed that *A. boisei* had a large body to match its huge teeth, but no postcranial bones were directly associated with the crania or teeth of this species. This created a problem because the deposits that contained diagnostic craniodental fossils of *A. boisei* also contained early *Homo* fossils. The isolated pieces of postcrania could not be sorted by species with any confidence because no one knew what the skeleton of *A. boisei* should look like. Fortunately, a fragmentary skeleton has come to light that is associated with an identifiable piece of *A. boisei* jaw. There are also bits of isolated postcrania at one site that contains only *A. boisei* craniodental material, so it is likely that all of it is *A. boisei*. From these comes the surprising fact that *A. boisei*, like *A. robustus*, had a

relatively petite body, with females weighing approximately seventy pounds and standing at approximately four feet one inch. Males may have weighed approximately 108 pounds and stood at four feet six inches.

These small body weight estimates imply that the relative brain size of *A. boisei* was larger than that of *A. afarensis*. They also show just how relatively enormous the cheek teeth were: One estimate is that the area of these teeth was at least 2.5 times larger than expected from that seen in modern great apes or humans.

Tools and other archaeological indications of hominid activity in East African sites are relatively abundant throughout the time span of *A. boisei*. Authorship of these cultural relics is usually attributed to species of *Homo*, however, because *Homo* was present during this time, and after the extinction of *A. boisei* the tools continue.

Australopithecus aethiopicus is the least well known of the "robust" australopithecines. The name *aethiopicus* comes from the 1967 discovery of a 2.6-million-year-old jaw from Omo. The Omo sediments have yielded a substantial number of these "robust" australopithecines. Careful study of the lower premolars shows that *A. boisei* can be identified by many distinctive features in teeth dated from between 2.2 and 1.8 million years. There also are isolated teeth dated from between 2.7 and 2.2 million years ago that are "robust" australopithecine but not *A. boisei*. These may be referred to *A. aethiopicus*. Such tenuous attribution erodes confidence in the reality of this species; but whatever it is, we do have one great jewel, the Black Skull (KNM-WT 17000).

The Black Skull is nearly complete except for the crown of its teeth. It lay in sediments known to be 2.5 million years old until Alan Walker (a member of the team led by Louis and Mary Leakey's middle son, Richard) picked it up in 1985. A glance at its face brings quick recognition followed by doubt. It has many superficial resemblances to *A. boisei*. There are wide cheeks with a deeply set root of the nose made even deeper by the forward projection of the cheeks. The huge cheek teeth are there and also the sagittal crest. But look further.

Behind the superficial resemblances to *A. boisei* lie some real surprises: The sagittal crest peaks way back on the skull, not forward as in *A. boisei*; the muzzle protrudes way forward; the skull base is unflexed; the jaw joint is shallow. The brain case housed almost one hundred cc less brain than did that of *A. boisei*. All of these are traits of the early and primitive species, *A. afarensis*, of "Lucy" fame.

HOMOPLASY AND THE "ROBUST" AUSTRALOPITHECINES

One of the most interesting aspects of the "robust" australopithecines is what they reveal about homoplasy. Homoplasy is the independent appearance of similar structures in two or more lines of descent. The term *independent* is the key here. It applies to resemblances between organisms that are not attributable to inheritance from a shared ancestor. Homoplastic resemblance comes about because lineages often change through time in similar ways. In Darwin's words, "…animals belonging to two most distinct lines of descent may readily become adapted to similar conditions, and thus assume a close external resemblance."[7] He went on to warn, "…but such resemblances will not reveal—will rather tend to conceal their blood-relationship to their proper line of descent." The fin-like limbs of whales and fishes, he observed, resembled each other not because of common descent but as adaptations for swimming. The resemblance is due to convergent or parallel evolution, not to inheritance from a common ancestor. The wings of birds, bats, and butterflies are due to homoplasy. The opposable big toes of lemurs, monkeys, and apes, on the other hand, are due to inheritance from an ancestor who also had this trait.

The idea is simple, but subtleties can obscure the distinction between resemblances due to homoplasy and those due to common inheritance. In the sixth edition of *On the Origin of Species* Darwin pointed out one reason for the obscuration. Closely related organisms, he observed, "…have inherited so much in common in their constitution that they are apt to vary under similar exciting causes in a similar manner; and this would obviously aid in the acquirement through natural selection of parts or organs strikingly like each other, independently of their direct inheritance from a common progenitor."[8]

Among species of fossil hominids, some resemblances are due to homoplasy and some are inherited from a shared ancestor. Homoplastic resemblances occur when species are so closely related that they evolve similarities in parallel as they adapt to the same environments. Homoplasy obscures attempts to find phylogenetic relationships. An excellent example of this obscuration is the problem of interpreting the Black Skull (KNM-WT 17000).

When Alan Walker found the Black Skull there was little doubt that it belonged to the "robust" australopithecines. It shared with *A. robustus* and *A. boisei* a suite of traits related to heavy chewing, including huge cheek teeth, massive jaws, and a heavily buttressed skull to withstand the chewing forces. These resemblances imply close phylogenetic affinity among these hominids *if* these traits are due to descent from a shared ancestor. However, most authors agree that the "robust" australopithecines form a branch of our family tree that is quite separate from the lineage leading to *Homo*. The black skull and other "robust" hominids from between 2.7 and 2.3 million years ago form the base of this branch as the species *A. aethiopicus*. The species from South Africa, *A. robustus* (1.8–1.0 million years ago), and from East Africa, *A. boisei* (2.2–1.3 million years ago), are the terminal parts of the "robust" branch. Relative to other contemporary hominid species, they form one branch, or, more precisely, they are monophyletic. They share a similar complex of features related to heavy chewing. Their faces, cranial vaults, jaws, and teeth are strikingly similar in many specific ways. Presumably they inherited these similarities from a common ancestor, making these resemblances homologous.

But the view that the robust australopithecines are quite separate from the *Homo* line presents a problem. If the "robusts" are monophyletic with *A. aethiopicus* at the base, and *A. robustus* and *A. boisei* arise out of this common stem, then why do these two later species resemble early *Homo* in so many ways? Early *Homo* and the later "robust" species share numerous traits that are not present in *A. aethiopicus*. These resemblances include brain expansion, flexion of the cranial base, reduction of prognathism, deepening of the jaw joint (TMJ), and a host of other features. In fact, in many ways *A. robustus* and *A. boisei* resemble early *Homo* more than any of these resembles *A. africanus* (the 2.4- to 3-million-year-old South African "gracile" australopithecine). Perhaps these resemblances are due to homoplasy. On the other hand, perhaps the resemblances between *A. aethiopicus* and the later "robust" australopithecines are due to homoplasy and the "robust" species are not monophyletic.

It is a difficult paradox to resolve. Some of these resemblances are concealing the true "…blood-relationships to their proper lines of descent," to use Darwin's words. Clearly, some procedure needs to be applied to partial out homoplasy in a way that makes assumptions and biases clearly visible. Many procedures are avail-

able, but those developed by Willi Hennig have evolved into an approach that has been effectively applied to this problem.[9] Although there are many extreme views that have developed out of Hennig's system, some fundamental features of what is commonly referred to as cladistic, or phylogenetic, analysis have proved to be very useful.

CLADISTIC ANALYSIS

One useful feature of cladistic analysis is that when it is properly applied, assumptions and biases are clearly revealed. At each step one has to expose one's thinking to critical analysis. This exposure safeguards against the corrupting desire to advocate a fixed position.

There are many ways to proceed in a cladistic analysis, but it is helpful to follow a few basic steps. First, traits and species must be defined clearly. This step exposes a weak flank for critics to attack but ensures that the practitioner has some depth of defense. Paleospecies are hard to define, of course, and traits must be selected with special care. Care means that the traits are selected without the bias of a preconceived desire to advocate a fixed position. Care must also be given to the functional meaning of the trait. A paradox arises here because the interpreter of the functional meaning of a feature may have a bias about how the overall scheme of phylogenetic relationships ought to be.

A second step involves following the sequence of changes in the trait in the species under study without regard to preconceived notions about the direction. Brain size in human evolution increases through time and there is no problem with bias in that. The chewing surface area of cheek-teeth is medium in the earliest species of hominid (*A. afarensis*), large in one of the next oldest species (*A. africanus*), huge in the "robust" australopithecines that came after *A. africanus*, and medium again in the earliest *Homo*. This second step disregards time and preconception. The sequence of changes in cheek-tooth size places *A. afarensis* and the earliest *Homo* together.

The beauty of this formal procedure is that the practitioner is exposed at every step to corrections kindly provided by colleagues. A third step, exposing even greater vulnerability, consists of arranging the species according to where they fall—from most

primitive to most derived. There are formal procedures for such ordering. Time provides an imperfect clue; usually the most primitive is the earliest, but not always. A check is provided by comparing the expression of the trait in closely related species that are not part of the analysis (outgroups that for hominid studies consist of nonhominid members of the ape and human superfamily, *Hominoidea*). A variety of other methods exist for finding the direction of change for each trait, but usually time and outgroup tell a consistent tale.

At this point one has a trait list with the expression of each trait in a list of species and a direction of change for each trait. From this one can derive a branching tree of relationships (cladogram) for each trait. The procedure further exposes the practitioner to scrutiny by doubting colleagues, although drawing a cladogram is quite lock-step. One simply takes each trait individually, joins the two most derived species by two intersecting lines, connects the next most derived species, and so on. The simple diagram for each trait is meaningful. When the two lines join from the two most derived species, the resulting mutual line means that these species are united by descent from a common ancestor (the joined line) who also expressed the trait. It is so simple, but so easily missed.

The final step is to compile all the cladograms for all the traits and look for patterns. Usually there are many different cladograms. Brain size and cheek-tooth area in hominid species are two quite distinct patterns. Here again the cladist exposes the weaknesses and strengths of the analysis for all to judge. The most common way to resolve this conflict between cladograms is to choose the one that requires the least amount of homoplasy and is the most consistent with the data (i.e., the most parsimonious).

OTHER SPECIES OF EARLY HOMINID

There are many ways to divide the hominid bone pile into genera and species. In what follows, early hominids are divided into six species of *Australopithecus*. Early *Homo* is treated as a single species in this analysis. The three "robust" australopithecines, *A. robustus*, *A. boisei*, and *A. aethiopicus* have already been described. The remaining species are as follows:

Australopithecus ramidus is the earliest well-defined species of hominid, and it is best known from deposits in Ethiopia dated to

4.4 million years ago. Overall, it is quite ape-like, but it does share a few unique features with later hominids, such as a broader, less projecting canine, a shorter cranial base, and some details of the elbow. It had thinner molar enamel than did later hominids, perhaps implying a diet more similar to that of African apes. Its habitat was closed woodland. Unfortunately, as of yet there are no hindlimb fossils to ascertain its locomotion.

Australopithecus afarensis is the next oldest (3.9–2.8 million years old). It is difficult to appreciate fully because it has such a wonderful mixture of ape-like and human-like qualities. Its skull is close to what one might expect in the common ancestor of apes and people, with an ape-sized brain (384 cc of endocranial volume, roughly the same as that of a chimp and not at all like that of a modern human, which averages about 1350 cc), big muzzle, flat cranial base, flat jaw-joint, and sagittal crest that is highest in the back. Its teeth bridge the gap between ape and people, with large central and small lateral upper incisors (ape-like), reduced upper canine (human-like) but still large with shear facets formed against the lower premolar (ape-like), variable lower first premolar, with some individuals having only one strong cusp (ape-like), and others having some development of a tongue-sided (metaconid) cusp (between modern ape and human), and parallel or convergent tooth rows (ape-like). Their cheek teeth were quite large relative to their body weight. Below the head (postcranially), *A. afarensis* is mostly human-like in having a hip, thigh, knee, ankle, and foot adapted to bipedality. But superimposed on this human-like body are many traits reminiscent of the common ancestor, such as somewhat elongated and curved fingers and toes, a relatively short thigh, and backwardly facing pelvic blades. Sexual dimorphism in body size is higher than in modern humans, but not as high as in *Gorilla* or *Pongo*. Males weighed approximately one hundred pounds and females weighed approximately sixty-five pounds. They lived in a mixed habitat, with some in well-watered woodland conditions and others in more open environments.

Relative to *A. afarensis* and *A. aethiopicus*, *Australopithecus africanus* has more *Homo*-like craniodental features. It is known only in South Africa and its age is only approximately established (three to two million years ago). Its vault is higher and more rounded than that of the earlier species, its face is less prognathic, and its jaw-joint is deeper. The lower first premolars are bicuspid. Cranial capacity is larger (442 cc). Although the skeleton below the

head is much like that of *A. afarensis*, the hand bones are more *Homo*-like. Body size resembles that of *A. afarensis*, although sexual dimorphism appears to be slightly reduced, with males weighing approximately ninety pounds and females weighing approximately sixty-seven pounds. The cheek-teeth are larger than those of *A. afarensis*.

There is evidence that there may be two species represented among specimens attributed to *Homo habilis*, although some authors make a strong case for just one. For the purposes of this study, it is appropriate to regard specimens from 2.4 to 1.6 million years ago that have been referred to as *Homo* as a single unit. Variability is high, but some consistent differences from *Australopithecus* are apparent. Brain-size is higher (597 cc average), vaults are more rounded and higher, and cheek-teeth are smaller. Body size for males may have been approximately 144 pounds, and females may have weighed approximately 70 pounds.

TRAITS AND STATES

The next step in cladistic analysis is selecting traits and their expressions in each species. Randall Skelton's and my study uses seventy-seven variable morphological traits and their expression in all of these species (except *A. ramidus*) and in an outgroup (extant great apes).[10] The traits include twenty-two features of the face, palate, and zygomatic arch; twenty-five dental traits; seven mandible traits; ten features of the basicranium; and thirteen features of the cranial vault. These can be grouped into five functional complexes, including heavy chewing, front teeth, bending of the base of the skull, muzzle protrusion, and encephalization. We provide a further description and discussion of these traits and their functional meaning.

MORPHOCLINES AND CLADOGRAMS

The direction of evolutionary transformation for each trait (i.e., the polarity) flows from primitive to derived. The outgroup (i.e., great apes) determines the primitive pole unambiguously for all of the craniodental traits in this study. For example, brain size is 343 cc in

Pan paniscus (outgroup), 384 cc in *A. afarensis*, 399 cc in *A. aethiopicus*, 420 cc in *A. africanus*, 488 cc in *A. boisei*, 502 cc in *A. robustus*, and 597 cc in early *Homo*. This sequence is the polarized morphocline. It implies that early *Homo* and *A. robustus* are the most highly derived for this trait and can be joined as sister taxa relative to all other species. Their joint line connects next to *A. boisei* to form a group of three species who are derived relative to all other species. The process continues until all groups are connected into a cladogram, as shown in Figure 1a.

The simplicity and straightforwardness of this procedure allows for conflicting evidence. For example, unlike endocranial volume, cheek-tooth area goes from 227 mm^2 in the outgroup to 460 mm^2 in *A. afarensis* to 479 mm^2 in early *Homo* to 516 mm^2 in *A. africanus* to 588 mm^2 in *A. robustus* to 688 mm^2 in *A. aethiopicus* to 799 mm^2 in *A. boisei*. This results in the cladogram displayed in Figure 1b. It is incompatible with the cladogram in Figure 1a. To choose the one that most likely reflects the true evolutionary relationships, one must use the principle of parsimony.

PARSIMONY

The theory of parsimony is the subject of much discussion, but fundamentally it is quite straightforward. To deal with the conflicting evidence revealed by incompatible cladograms, parsimony assumes that the true phylogeny resulted from the fewest evolutionary steps. There are various measures of parsimony. The most commonly used measure is the consistency index, which is simply the minimum number of steps possible divided by the actual number of steps. If no homoplasy were present, then the consistency index would equal one.

The most parsimonious cladogram that can be constructed out of the seventy-seven traits described by Skelton and me is the one shown in Figure 2a. The two most derived taxa are *A. robustus* and *A. boisei*, whose stem joins *Homo* in forming the next most derived group relative to the other species. The *A. robustus/boisei/Homo* clade then joins *A. africanus* and that stem next joins *A. aethiopicus*. *A. afarensis* forms a sister clade to all other hominids. The consistency index is 0.722 when all 77 traits are used. This is also the most parsimonious cladogram when traits are grouped into anatomical regions or functional complexes.

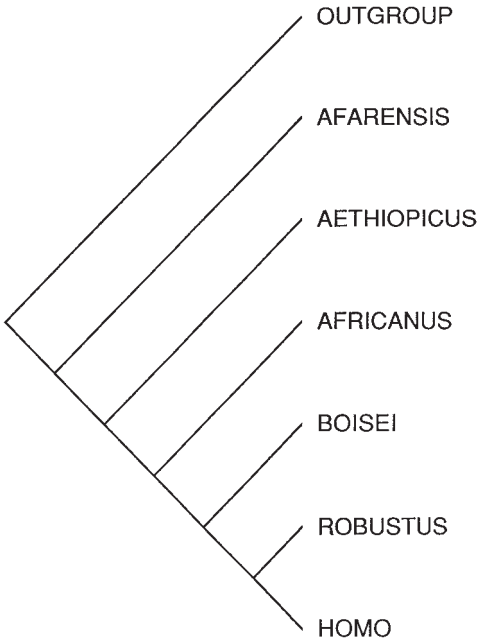

Figure 1a
Cladogram Implied by the Polarized Morphocline Based on Endocranial Volume

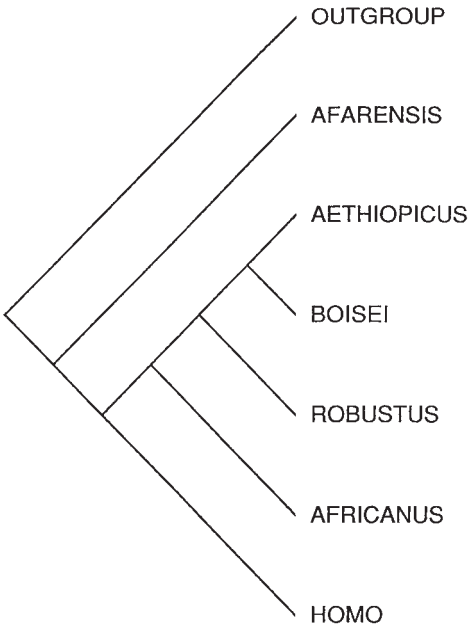

Figure 1b
Cladogram Implied by the Polarized Morphocline Based on Cheek-Tooth Area

OUR FAMILY PHYLOGENY

Figure 2b displays the phylogenetic tree implied by the most parsimonious cladogram. *A. ramidus* was not included in the analysis but its position is unequivocally at the root of the entire tree as the most primitive of all hominid species. These results imply that there was a large amount of parallel evolution in our family tree. The most conspicuous case of parallel evolution involves heavy chewing in *A. aethiopicus*, *A. robustus*, and *A. boisei*. This phylogeny implies that the specific resemblances between *A. aethiopicus* and the later "robust" australopithecines are due not to descent from a common ancestor who had these traits but to independent acquisition. This is a very surprising result. The Black Skull looks so much like *A. boisei* that its discoverers and original describers attribute it to that species and not to *A. aethiopicus*. For example, both have extreme forward projection of the cheek bone, huge cheek teeth, enormous lower jaw robusticity, a heart-shaped foramen magnum (the hole for the spinal cord), and similarity in how the vault bones articulate above the ear.

But all of these traits except for the heart-shaped foramen magnum are related to the functional complex of heavy chewing. The huge cheek-teeth and robust mandibles of both species are obviously part of masticatory heavy chewing. The forward projection of the cheek bones brings the masseter muscles into a position of maximum power. The encroachment by the root of the cheek bones obscures the expression of the pillars of the face. Even the way the vault bones fit together above the ear is related to the function of the forces generated by the chewing muscles.

Theoretically, it is understandable how such detailed similarity could be due to parallel evolution. This is an example of what Darwin referred to: These species are closely related and share "…so much in common in their constitution" that similar selective forces produce similar morphologies. The selective forces in this case are related to a feeding adaptation that is associated with a specialized ecological niche. As Ernst Mayr points out, "Most adaptations for special niches are far less revealing taxonomically than they are conspicuous.… Occupation of a special food niche and the correlated adaptations have a particularly low taxonomic value."[11] In fact, many of the same traits characteristic of *A. aethiopicus* and the other "robust" australopithecines reap-

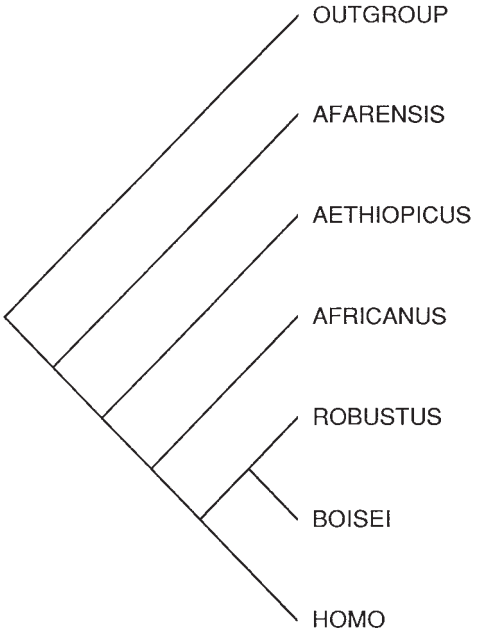

Figure 2a
The Most Parsimonious Cladogram

This cladogram uses all seventy-seven traits or summary scores from the analyses of five functional complexes or seven anatomical regions.

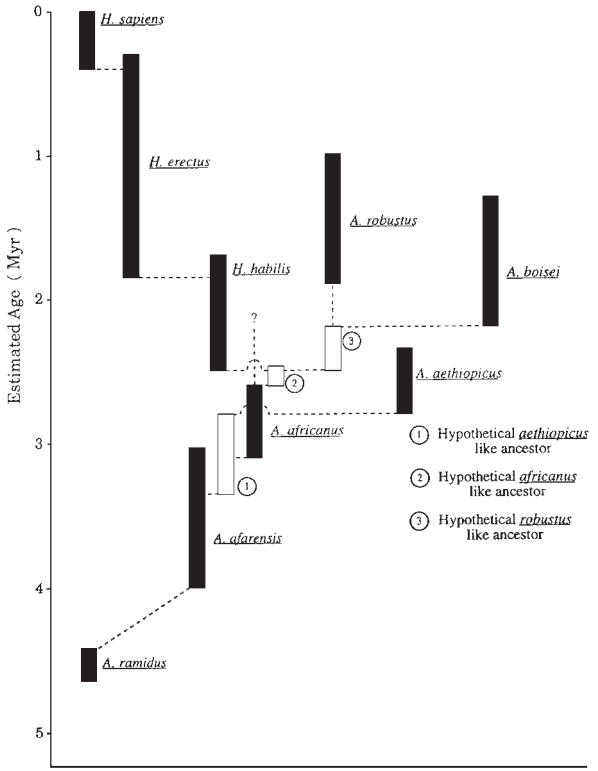

Figure 2b
Phylogeny Implied by the Most Parsimonious Cladogram

Three hypothetical ancestors are predicted. The horizontal axis is calibrated to the cheek-tooth area.

pear in distantly related species adapted to heavy chewing. Expansion of the cheek-teeth, shortening of the muzzle, and anterior migration of the attachment areas of the chewing muscles are seen in other primates whose diet requires heavy chewing (e.g., *Hadropithecus*, *Theropithecus*, probably *Gigantopithecus*, and *Ekmowechashala*).

Although the most parsimonious cladogram implies this phylogeny, other cladograms are possible but less probable. A cladogram linking *A. aethiopicus* to *A. boisei* and *A. robustus* as one branch and *A. africanus*/early *Homo* as another requires more evolutionary steps because the later "robusts" resemble early *Homo* in so many features. These features include many aspects of bending of the base of the skull, loss of a muzzle, changes in the front teeth, and encephalization. The skeleton below the head, although not included in this analysis, supports the view that at least *A. robustus* and early *Homo* are monophyletic relative to other species of early hominid.

Whatever the true phylogeny is—and there can be only one—the fact remains that homoplasy is commonplace. There is just no avoiding it: Some resemblances appeared independently, not because of evolution from a common ancestor who possessed the same features. Either adaptations for heavy chewing evolved twice, or bending of the base of the skull, loss of a muzzle, reduction in the front teeth, and encephalization evolved more than once. Darwin's astute observations apply to our own family tree.

General Lessons

One general lesson from this approach to hominid evolutionary biology is how to deal with ambiguity. As the King of Siam said in Rodgers and Hammerstein's *The King and I*, "What was so was so; what was not was not," but now "some things nearly so, others nearly not." It's a common experience. Perhaps it is uncommon to have such a clear example of ambiguity as is provided by the hominid fossil record. Either heavy chewing resulted in the independent evolution of *A. aethiopicus* and *A. robustus/boisei* or other forces shaped *A. boisei*, *A. robustus*, and early *Homo* to resemble each other in encephalization, bending of the base of the skull, loss of a muzzle, and reduction in the front teeth.

From this point of view it is not particularly useful to advocate a fixed position. One needs to make the best of our tiny sample of life in the past, to remain open to new discoveries and ideas, and to enjoy the pleasure of learning and changing.

NOTES

1. The phrase "robust" australopithecines refers to early hominids that have specializations for heavy chewing. Various taxonomic names are associated with these fossils, including *Paranthropus robustus* (from the South African site of Kromdraai), *Paranthropus crassidens* (from Swartkrans of South Africa), *Zinjanthropus boisei* of Olduvai, and *Paraustralopithecus aethiopicus* from Member C of the Shunguru Formation of Omo. They are very similar to one another in features related to heavy chewing and many authors prefer to recognize their similarity by designating them as a separate genus, *Paranthropus*.
2. Charles Darwin, *The Descent of Man and Selection in Relation to Sex* (London: D. Appleton and Co., 1872).
3. Robert Broom, "The Pleistocene Anthropoid Apes of South Africa," *Nature* 142 (1938): 377–379.
4. Robert Broom, "Another New Type of Fossil Ape-man," *Nature* 163 (1949): 57.
5. Louis B. Leakey, "A New Fossil Skull from Olduvai," *Nature* 184 (1959): 491–493.
6. Alan Walker, Richard E. Leakey, John M. Harris, and Frank H. Brown, "2.5 Myr. *Australopithecus boisei* from West of Lake Turkana, Kenya," *Nature* 322 (1986): 517–522.
7. Charles Darwin, *On the Origin of Species by Means of Natural Selection* (London: John Murray, 1859), p. 427.
8. Charles Darwin, *The Origin of Species*, 6th ed. (New York: Random House, 1872), p. 328.
9. Willi Hennig, *Phylogenetic Systematics* (Urbana: University of Illinois Press, 1966).
10. Randall R. Skelton and Henry M. McHenry, "Evolutionary Relationships among Early Hominids," *Journal of Human Evolution* 23 (1992): 309–349.
11. Ernest Mayr, *Principles of Systematic Zoology* (New York: McGraw-Hill, 1969), p. 125.

SUGGESTED READINGS

Grine, Fredrick, ed. *The Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter, 1988. Thorough but technical discussions of all aspects of these creatures.

Jones, Steven, Robert Martin, and David Pilbeam, eds. *The Cambridge Encyclopedia of Human Evolution*. Cambridge: Cambridge University Press, 1992. This is a beautifully written and authoritative work on all aspects of human evolution.

Klein, Richard C. *The Human Career*. Chicago: University of Chicago Press, 1989. The best place to start for more information about hominid species, sites, archaeology, and much more.

Ridley, Marc. *Evolution*. Boston: Blackwell Scientific Publications, 1993. A very readable account of our current understanding of evolutionary processes.

Tattersall, Ian, Eric Delson, and John Van Couvering. *Encyclopedia of Human Evolution and Prehistory*. New York: Garland Publishing, 1988. This includes articles on early hominid species and has nice illustrations.

Research TOC