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Fossils and the Mosaic Nature of Human Evolution

Studies of Plio-Pleistocene hominids refine the early idea that bipedalism preceded encephalization.

Henry M. McHenry

As early as 1809 a broad outline of human evolution had been predicted with Lamarck's (*1*) arboreal quadrumanous animals descending to the ground, adapting to bipedalism, and eventually evolving into large-brained *Homo sapiens*. Soon after Darwin's (*2*) *Origin of Species* made evolution widely acceptable, Haeckel (*3*) refined the sequence of human evolution into three distinct stages: upright walking, articulate speech, and perfecting and differentiating of the brain. Darwin (*4*) soon followed with a similar scheme but with greater caution as to the exact order of the sequence.

Paleontological proof that bipedal walking evolved before brain expansion came in 1892 with Dubois' (*5*) discovery of Java Man (*Pithecanthropus erectus*, now classified as *Homo erectus*). This discovery of a perfectly modern human femur in the same stratigraphic layer as a small-brained skull seemed like confirmation of the early evolutionists' scheme. But there were doubts about the stratigraphic association of the skull and thigh, and recent research shows that these doubts were well-founded (*6*). There were also many who did not believe that the Java fossils were on the main phylogenetic line to *Homo sapiens* [for example, see (*7–9*)].

Further paleontological evidence weakened acceptance of this mosaic theory of human evolution—that is, body preceding brain in development. Some early 20th-century descriptions of the European Neanderthals characterized them as having big brains but many simian characteristics of the skull and skeleton, and even an incomplete adaptation to bipedalism (*7, 10*). The discovery in 1912 of *Eoanthropus dawsoni*, the Piltdown forgery with the fraudulent association of Pliocene fauna, a subfossil human skull, and an orangutan jaw, also led many to doubt the sequence before the fraud was exposed in 1953 (*11*). The large-brained Piltdown skull proved to some that the big brain was an early human adaptation, perhaps even preceding bipedalism (*8, 9, 12, 13*).

The notion that the brain expanded early in human evolution certainly detracted from acceptance of the very small-brained *Australopithecus africanus* announced by Dart in 1925 (*14*). The fossil was regarded by most as an ape or as a collateral off the mainstream of human evolution (*13, 15, 16*), despite the human nature of its teeth, the shape of the brain, and Dart's claim that the position of the foramen magnum was enough forward to indicate habitual upright posture (*14*). The latter point was disputed and dismissed by many (*16, 17*) although more evidence for upright posture came in 1938 when Broom (*18*) announced the discovery of a fragmentary arm and thigh bone of other australopithecines which were very human looking. By the late 1940's enough fossils of these creatures had been found to convince most skeptics that they were members of the human family (*19, 20*). They possessed just the mosaic of features predicted by the evolutionary models of Haeckel and Darwin: small brains but skeletons adapted for bipedalism (*21*).

This broad outline of the mosaic nature of human evolution is widely agreed upon today, but the specifics are not. One issue is the completeness of the mosaic: did the body evolve its modern form completely before the brain reshaped and expanded? The question involves the nature of the late Pliocene and early Pleistocene hominids of Africa dating between about 5 and 1.6 million years (*22*). Opinions vary widely on their taxonomy, phylogenetic position, and basic adaptations. Some investigators propose that the fossil skeletons are fundamentally different from modern human skeletons (*23, 24*) but others argue that at least one (*25*) or all (*26*) early hominid species had a postcranial anatomy which was essentially similar to that of *Homo sapiens*. In relative brain size, according to different authors, these fossil forms are either just above the apes (*27, 28*), intermediate (*29, 30*), or within the range of variation of modern humans (*31*). The purpose of this article is to review new fossils and recent analyses of these fossils which help to resolve some of these controversies.

Early Hominid Hip

Most agree today that at least one species of early hominid, the gracile *Australopithecus africanus*, had a skeleton similar to that of modern *Homo sapiens* [(*21, 25, 26*); for a dissenting view see (*23, 24*)]. The Sts 14 partial skeleton from Sterkfontein, South Africa, discovered by Broom and Robinson in 1947 showed how human these creatures were (*21, 25*). The low and broad iliac blades, the anteriorly directed sacrum, the shape of the vertebral column, and numerous other distinctively human traits are present (see Fig. 1). But there are some differences between this fossil and modern *Homo sapiens*, especially in pelvic morphology. For example, the iliac fossa is relatively very large compared to the sacral articular surface and the acetabulum (*32*). The iliac blades are oriented some-

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The author is an assistant professor in the Department of Anthropology at the University of California, Davis 95616.

what differently, and this trait, combined with some reconstructions of the pubis, yields an arrangement of muscles somewhat different from that of the *Homo sapiens* hip (*33*). The lateral support system seems to have been essentially human, however, so that bipedalism may not have involved excessive swaying of the hips (*26*). Small body size and small birth canal size may account for some of these differences (*26*).

The nature of the other South African form of early hominid, the robust *Australopithecus robustus*, is much more difficult to reconstruct because of the scarcity and fragmentary nature of postcranial fossils. Reconstructions have relied heavily on the badly distorted and fragmentary SK 50 pelvic bone from Swartkrans (*25*). Opinions on the gait of this species range from waddling and shuffling bipedalism (*34*) to tree climbing combined with inefficient bipedalism (*25*) to essentially modern human bipedalism (*26*). Fortunately, a new pelvic fossil was discovered in 1970, SK 3155 from Swartkrans (see Fig. 1), which is in a much better state of preservation (*32, 35, 36*). The new specimen permits a more reliable reconstruction than was possible with SK 50 and allows better assessment of the nature of the *A. robustus* skeleton (*37*).

This new fossil pelvic fragment shows that *A. robustus* has a basically hominid hip structure since it has the suite of diagnostic characteristics, including the low and broad iliac blade, the sciatic notch, a well-developed anterior inferior iliac spine, a groove for the iliopsoas muscle tendon, a thick iliac blade in the region of attachment for the gluteus minimus and medius muscles, an oblique angle between the iliac blade and the acetabulum, and many other human traits (*32*). It also has several characteristics which are unique to the australopithecines, such as a relatively small acetabulum and sacral articular surface and a relatively large iliac fossa (*32*).

A more detailed assessment of the *A. robustus* pelvic architecture requires further analysis. By describing the shape of the bone metrically, comparisons can be made which take into consideration the enormous morphological variability found in modern hominoids. Metrical data can be treated so as to account for the overall shape of the bone by combining all measurements into a single multivariate analysis. One such analysis uses 18 measurements on 144 hominoid pelvic bones (41 *Homo*, 24 *Pan*, 28 *Gorilla*, 28 *Pongo*, and 23 *Hylobates*) and the two best preserved australopithecines, Sts 14 and SK 3155 (*38*). The complexity of the resulting 18 × 144 matrix can be reduced to a small number of uncorrelated, nonredundant discriminant functions which retain most of the information and act to separate maximally the known groups (*38, 39*). There are problems in applying such multiple discriminant analysis to these data, however, such as the assumption that the fossils actually do belong to one of the groups, and the many possible violations of statistical assumptions such as multivariate normality and homogeneity of variables within groups (*40*). The results are consistent with many other lines of evidence, however (*41*). The first discriminant function accounts for 72 percent of the total variance and separates the hominids from the other hominoids (see Fig. 2a). Variables with high correlations with this axis are those which describe the uniqueness of the human pelvis. The two fossils project among the hominids and are far removed from any other hominoid. The second discriminant function is dominated by the effects of size, and the third picks up only minor differences. The placement of the fossils is closer to modern *Homo* than to the other hominoids when all three functions are plotted. Very similar results occur when ratios of the original measurements are used to partially eliminate size differences (*38*).

But size still affects the results in analyses using ratios instead of original measurements because of allometric distortions. One solution is to calculate a gen-

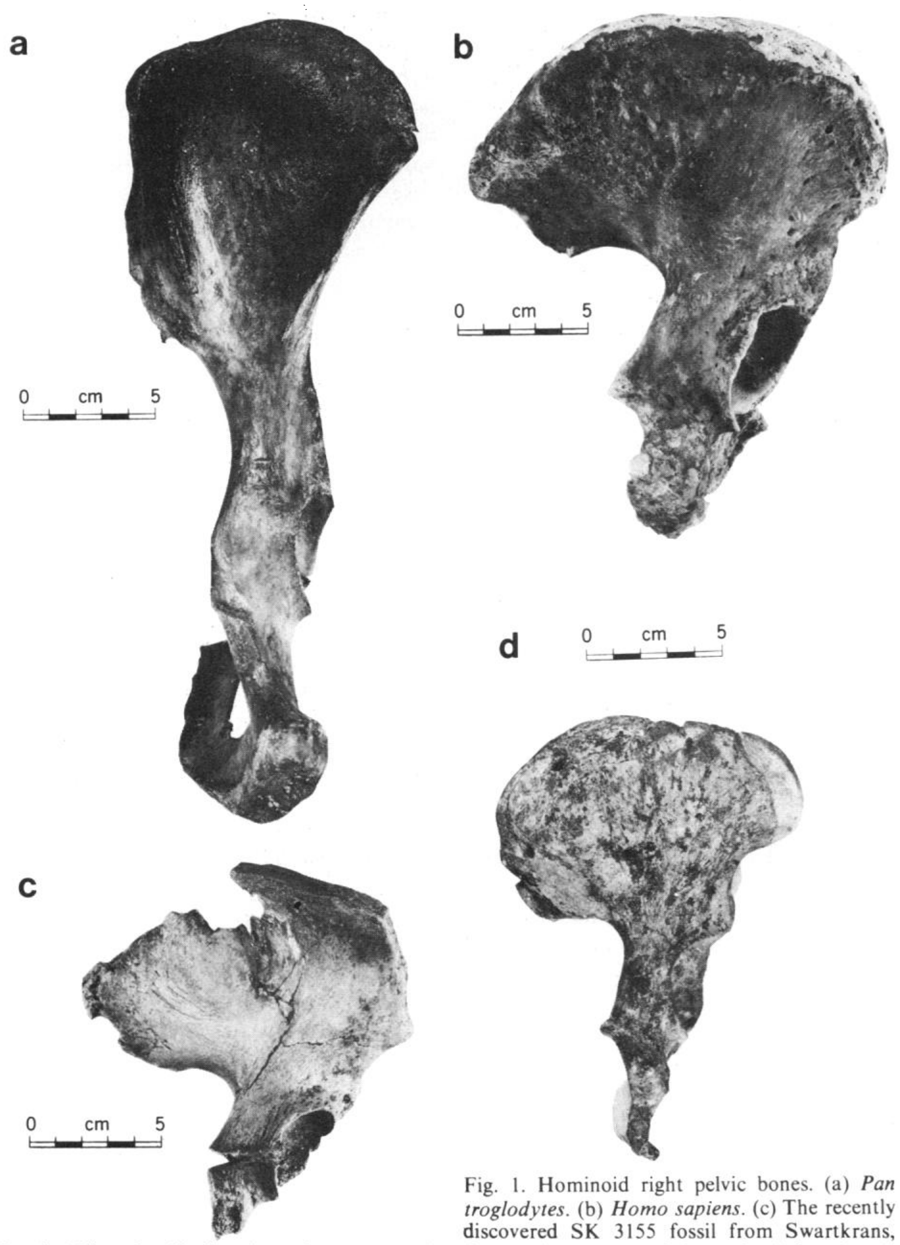

Fig. 1. Hominoid right pelvic bones. (a) *Pan troglodytes*. (b) *Homo sapiens*. (c) The recently discovered SK 3155 fossil from Swartkrans, South Africa, classified by the author as *Australopithecus robustus* (*32*). (d) Sts 14 fossil from Sterkfontein, South Africa, a representative of *Australopithecus africanus* (*25*). The shape of the iliac blades shows the typical human pattern in the two fossils which is quite distinct from the morphology of *Pan*. The large size of the iliac blade in proportion to the hip joint is a unique characteristic of both of these forms of early hominid.

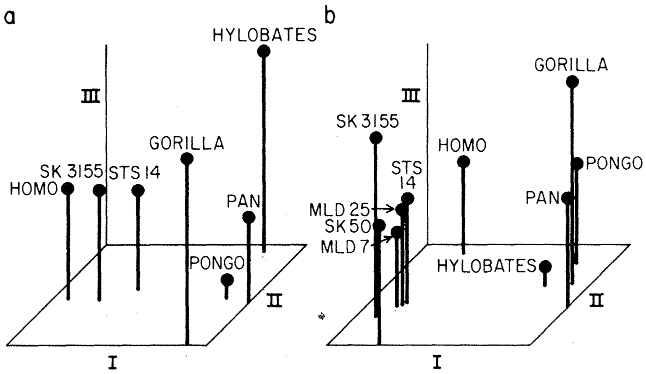

Fig. 2 (left). Results of multivariate analyses of the iliac blade and acetabulum. (a) Multiple discriminant analysis (*38, 39*). (b) Principal coordinates analysis (*43*).

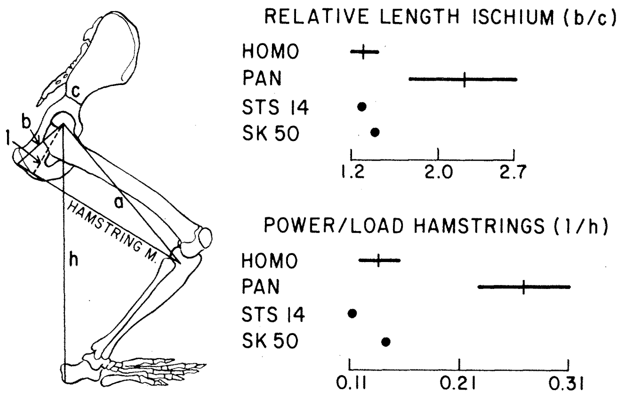

Fig. 3 (right). Relative length of the ischium and the ratio of power arm to load arm length of the hamstring muscles.

eral size vector for each specimen, find the coefficient of allometry between it and every variable, and correct each variable by raising it to the power of its allometric coefficient (*42*). The method was developed by Corruccini (*42*) and applied to the same data by McHenry and Corruccini (*43*) using principal coordinates analysis. Principal coordinates analysis has the advantage of not requiring the same statistical assumptions as multiple discriminant analysis. It also has the advantage of accommodating small amounts of missing data so that more fragmentary fossils such as the two *A. africanus* ilia from Makapansgat, MLD 7 and MLD 25 (*44*), could be entered. And it allows the incorporation of the fossils into the original calculations of the coordinates so that the uniqueness of the specimens can be evaluated.

Evaluation of the uniqueness of the fossils is very important, as can be seen by the results of the principal coordinates analysis (Fig. 2b). The first axis again separates modern and fossil hominids from all of the hominoids, but the second axis is dominated by the uniqueness of the fossils with the two *A. robustus* fossils (SK 50 and SK 3155) at one extreme, the three *A. africanus* pelvic bones (Sts 14, MLD 7, and MLD 25) intermediate, and *Homo sapiens* at the other extreme. Traits with high correlations with this coordinate are those that describe the uniqueness of the early hominid hip: the broad iliac fossa, the small sacral articular surface, and the relatively small acetabulum.

Biomechanics of the Hip

The meaning of these differences can be interpreted in terms of the biomechanics of the bipedal hip, although this requires subjectively reconstructing the entire hip from fragmentary fossils (*26, 45*). Many of the differences can be explained by one interpretation of the lateral support system, in which the abductor muscles pull on the side of the supporting leg during the swing phase of walking to keep the body from having to sway over the supporting limb. Biomechanical analysis depends on finding the length of the abductor lever arms and the angle of pull of these muscles. The ratio of load arm to power arm in the reconstructed SK 3155 hip is very similar to that in Sts 14 and modern *Homo sapiens* (1.90, 2.14, and 2.01, respectively). Judging from the size of the bone, SK 3155 probably weighed about 32 kg (70 pounds) (*45*). If this estimate is at all correct, then the torque developed at the hip joint due to the medial position of the center of gravity during one-legged stance is extraordinarily small in SK 3155 compared to modern humans, about three times less. The force of the abductors to counteract this torque is therefore much smaller, perhaps one-third that in *Homo sapiens*. This explains why the femoral head and acetabulum are so small: there is much less abductor force needed for lateral balance and therefore less force going through the hip joint.

One of the major locomotor differences between *A. africanus* and *A. robustus* cited by Robinson (*25*) is the part of the hip extensor mechanism which involves the hamstring muscles. According to this theory, the ischium (from which the hamstrings originate) is relatively long and apelike in the robust australopithecine and thus supplies a relatively long power arm for these muscles. The long power arm implies a power-oriented extensor mechanism in the hip, an adaptation which may have allowed more efficient tree climbing. The *A. robustus* hip is thus seen as a compromise between the demands of bipedalism and the retention of ancestral tree-climbing adaptation.

My own studies do not support this view (*32*). The *A. robustus* ischium (as represented by SK 50) is not significantly longer than the *Homo sapiens* ischium (see Fig. 3) when measured from the approximate center of rotation in the hip to the end of the ischium (*46*). The relationship between the power arm and load arm of the hamstrings (see Fig. 3) can be estimated by predicting the length of the lower limb. With the knee flexed at 90° (which is close to the position of maximum power of the hamstrings) the ratio of power arm to load arm in both fossil forms is like that in *Homo sapiens* and about half the value found in apes (13 in SK 50, 11 in Sts 14, 14 in *Homo*, and 27 in *Pan* and *Gorilla*).

In sum, then, the available pelvic fossils indicate that both *A. africanus* and *A. robustus* were morphologically and biomechanically most similar to one another and to *Homo sapiens*, but with certain unique features which are difficult to interpret functionally. The basic morphological similarity between the early and modern hominids implies that bipedalism was well established by late Pliocene–early Pleistocene times. The differences that do exist may be related to birth canal size (*26*) and to subtle differences in hip function, but the unique features of the fossils are in no way more simian than human and therefore the fossils cannot be considered transitional.

Fossil Thighs

Fewer differences exist between some of the recently discovered fossil femora and those of *Homo sapiens*. These fossils from the Lower Member of the Koobi Fora formation east of Lake Rudolf, Kenya (KNM-ER 1472 and KNM-ER 1481c) appear to be much more like modern human bones than do the other early hominid femora of the same age and of even more recent data (*47–50*). The differences between these modern-looking East Rudolf bones and the other early hominid femora suggest that they belong to the same taxon as the relatively large-brained KNM-ER 1470 skull [*Homo* sp. indet. (*47–50*)].

Except for these East Rudolf fossils, all of the early hominid femora have a unique combination of traits not seen in any living primate (*25, 38, 51, 52*). The most distinctive feature is the combination of a long femoral neck and a small femoral head, but there are many other more subtle characteristics. The shape is so unusual that the first two of these femora discovered (SK 82 and SK 97 from Swartkrans) were not described with the other hominid specimens from the same site for more than two decades (*25*).

The basic difference between the two East Rudolf fossils and the other early hominids is the large size of their femoral heads, which gives the entire proximal end of the bones a modern human appearance. Subtle differences do exist between these bones and most modern human femora, however, as shown by a multivariate analysis performed by McHenry and Corruccini (*51*). Using ten dimensions of the proximal end, adjusting them for size and allometric differences, and applying multiple discriminant analysis yields results which show that all of the early hominid femora are most similar to ***Homo sapiens*** and not at all like any ape, although they all have a distinct morphological pattern (see Fig. 4a). The two fossils from East Rudolf approach more closely the modern human form, although they share certain unique features with the other early hominids, such as the long femoral neck and several other more subtle characteristics.

One biomechanical explanation for the long femoral neck involves the same argument as that explaining the lateral support system during bipedal walking mentioned above (*26*). The longer neck provides a longer power arm for the abductor muscles, which implies that less abductor force is necessary to stabilize the hip from side-to-side swaying. Less abductor force would mean less pressure transmitted through the hip joint to the femoral head and would explain why the femoral heads are so small in these early hominids. The relatively larger femoral head in the East Rudolf specimens might be due to a greater body weight and longer abductor load arm, which would be related in part to the larger birth canal size concomitant with the larger brain evident in that species of early hominid.

Fossil Legs, Feet, and Backbones

The same pattern can be seen in the leg and foot of these early hominids: all fossils are basically human, but some have a unique combination of characteristics. The tibia is well represented in the hominid fossil record, but unfortunately conclusions about morphological affinities, biomechanics, and taxonomy are difficult to make (*47, 48, 53–55*). None of the tibial fossils deviate substantially out of the range of variation seen in modern human tibia. Biomechanical analysis of the Olduvai hominid 35 (OH 35) fossil shows that its shape is well adapted for the stresses typical in a biped (*56*).

The OH 8 foot shows the characteristics typical of the bipedal human organ with an adducted hallux, a relatively large fifth metatarsal, arches, and several other features (*57*). The shape of the big toe (OH 10) is just what would be expected in a biped (*58*) although there is some controversy over interpretation (*59*). The talus is more human than pongid (*18, 20, 21, 47, 48, 53–55*) although subtle differences in architecture have led some to argue that its adaptation to bipedalism is either incomplete or at least different from that of the typical modern human (*25, 60*). What vertebrae exist in the fossil record do not suggest an adaptation substantially different from that of modern ***Homo sapiens*** (*25*).

Forelimb Fossils

There is considerable diversity in the morphology of early hominid forelimbs. Certainly not all of the fossils are equally close to modern ***Homo sapiens***, and the overall structure and function of some forms still remain elusive. The shoulder is represented by a few fragmentary clavicles, scapulae, and proximal humeri, which have led to conflicting opinions by those who have studied them (*21, 25, 61*). The distal humerus is represented by four very complete fossils, however, and three of them have been the subject of extensive multivariate analyses (*38, 62, 63*).

The hominoid distal humerus is ideal for multivariate analysis because there are such subtle shape differences between species, particularly between ***Homo*** and ***Pan***, which are difficult to distinguish in a trait by trait (univariate) analysis (*64*). Multivariate analysis shows that although chimpanzee and human humeri overlap in almost all metrical characteristics taken one at a time, they differ when all traits are treated together in a single analysis where the bones are treated as integrated complexes. The study is still piecemeal, however, in that the distal humerus is not a separate unit but part of the larger complex of the forelimb and the total adaptation of the animal. Unfortunately, the fossil record is not complete enough to allow precise reconstructions of entire limbs and animals of all species of early hominids. With 16 measurements and over 300 comparative specimens, the multiple discriminant functions are able to separate all hominoid species very effectively (see Fig. 4b) (*38*). The results show that the Kanapoi specimen, which is 4 to 4.5 million years old, is indistinguishable from modern ***Homo sapiens***, the Kromdraai ***A. robustus*** fossil is about equally distant between ***Pan*** and ***Homo***, and the large specimen from East Rudolf (KNM-ER 739) is unique among all of the hominoids tested (*62, 63*). None of these fossils bear a special relationship to the combined sample of knuckle-walking apes (chimpanzee and gorilla). Nor do any of the fossils have a lateral ridge on the posterior surface of the trochlea and olecranon fossa, which is present in all of the 124 knuckle-walking apes sampled.

The forearm of the hyperrobust ***Australopithecus boisei*** is represented by the nearly complete ulna from the Omo River Basin in Ethiopia (*65*). A multivariate analysis of 14 linear measurements taken on 222 hominoids indicates that this fossil is unique in shape among the extant hominoids, although it is most similar to ***Pan*** and ***Homo*** and very unlike ***Pongo*** (*66*). The same general results were found by Rightmire (*67*) for an ***A. robustus*** thumb metacarpal from Swartkrans. Detailed studies of an ***A. africanus*** wrist bone from Sterkfontein by Lewis (*68*) led to similar conclusions. A complete description of the Olduvai hand bones (OH 7) has not been published yet, but preliminary studies show that they do not differ fundamentally from the human pattern (*69*). Certainly no definite evidence of knuckle-walking traits in the fossil hand and wrist is apparent (*70*).

Fore- and Hindlimb Proportions

Further evidence that the postcranium of some forms of early hominids differed from that of modern ***Homo sapiens*** comes from comparing body proportions. Modern humans are unique hominoids in having relatively large and especially long hindlimbs in proportion to their forelimbs, and there is some evidence that early hominid body proportions differed from this modern human condition. Individuals with associated fore- and hindlimb fossils are rare in the record, but a few are present. The type specimen of the South African robust australopithecine (TM 1519 from Kromdraai) has a talus smaller than would be expected from the size of its humerus, but the proportions are only slightly out of the human range of variation (*71*). Two individuals from East Rudolf have proportions similar to those of Kromdraai: KNM-ER 1500 and KNM-ER 1503-4 (*48*) have associated fore- and hindlimb parts which indicate proportions different from modern human ones (*72*). None of these fossils approach the range of proportions seen in modern apes, however. Their ratio

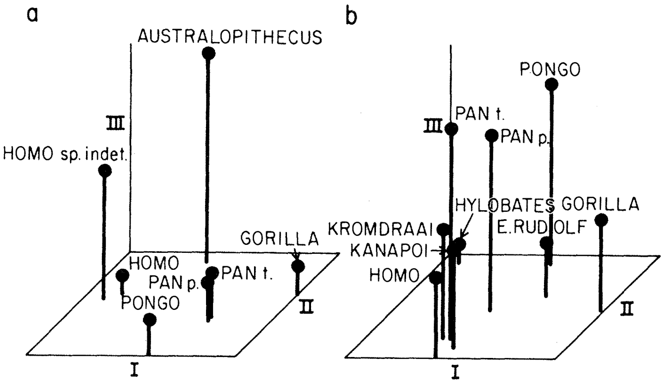

Fig. 4. Multivariate analysis of the proximal femur and distal humerus. (a) Multiple discriminant analysis of ten allometrically adjusted shape variables describing the proximal end of the femur. Although the fossils were entered as one group, they are plotted here as two: *Australopithecus* referring to specimens SK 82, SK 97, and KNM-ER 1503, and *Homo* sp. indet. to KNM-ER 1472 and KNM-ER 1481c (*51*). (b) Multiple discriminant analysis of the distal humerus (*38, 39*). *Pan t.* and *Pan p.* stand for *Pan troglodytes* and *Pan paniscus*.

of forelimb to hindlimb size is just above the range of variation in a sample of humans. These differences in proportions are probably of minor importance to basic locomotor adaptation, however. A partial skeleton from East Rudolf higher up in the geological sequence, about 1.5 million years old (KNM-ER 803) has proportions within the human range of variation (*54, 72, 73*).

Although some of these forelimb fossils deviate from the human morphology, they do conform to the basic hominoid pattern, and their deviations from the *Homo* pattern may not be of great significance to locomotor behavior. The forelimbs of all hominoids are basically similar, especially in the light of the fundamental differences between human and nonhuman hominoid hindlimbs. The fossil hindlimbs are much more like those of *Homo sapiens* than of any pongid, which indicates that habitual upright posture was well established. The forelimbs were probably freed, therefore, from their role in terrestrial locomotion. Thus, the unique features of the early hominid forelimbs may be evolutionary retentions of ancestral characteristics which have gradually been eliminated in the subsequent several million years of evolution.

Fossils Before 5 Million Years Ago

Overall, then, these early hominids had fundamentally human bodies, but some forms had many unique characteristics. The actual origin of bipedalism must have occurred earlier in time since these fossils are not really intermediate between a generalized hominoid and a bipedal human. Hominoid postcranial fossils are very sparse before about 3 million years ago, however. A single hominoid distal humerus is known from the beds at Fort Ternan, Kenya, which date at about 14 million years, but multivariate analyses show that this fossil resembles cercopithecoid monkeys more than extant hominoids (*63, 74*). Most studies of the fossil remains attributed to the Tertiary hominoid genus *Dryopithecus* show that they are also more similar to cercopithecoids than to hominoids in their postcrania, even in key hominoid features such as the wrist (*63, 75*). The same is true for the gibbinoid fossils such as *Pliopithecus* and *Limnopithecus* (*63, 75, 76*). From the fossil evidence one might conclude that the hominoid locomotor specializations such as brachiation, knuckle walking, and bipedalism arose later in time than these Tertiary fossils, perhaps between 10 and 5 million years ago, fitting the molecular clocks of Sarich and Wilson (*77*). The fossil samples are undoubtedly biased, however, particularly in the low number of forest specimens preserved. The remains of Lamarck's hypothetical arboreal quadrumanous creatures which descended to the ground and first adapted to bipedalism have not yet been found.

Early Hominid Brain Size

Although the Plio-Pleistocene hominids had basically human-like bodies, the absolute size of their brains was definitely not human. The average brain size of the South African *A. africanus* is close to the mean for the great apes and about one-third of the *Homo sapiens* average, although the internal structure may have been reorganized to a more human pattern (*27–30, 78*). Some East African fossils have larger volumes, but still only about one-half the average for humans (*50*).

The significance of brain size is difficult to assess, however. In *Homo sapiens* it varies widely, and differences in brain size do not seem to be correlated directly with differences in behavior (*79*). Brains of normal humans range from less than 1000 to more than 2000 cm^3 in volume. The chimpanzee varies between 282 and 500 cm^3, the gorilla between 340 and 752 cm^3, and the orangutan between 276 and 540 cm^3 (*79*).

The existence of this wide range of variation in modern hominoid species makes classification of fossil hominids more difficult. The range is very narrow in South African *A. africanus* (428 to 485 cm^3), but the East African hominids range from 506 to 775 cm^3 (*50, 78*). Sorting the East African fossils into taxa on the basis of brain size is complicated by the nearly continuous series of endocranial volumes: 506, 510, 530, 590, 650, 687, and 775 cm^3 (*50, 78*). Classification has been done in numerous ways, ranging from lumping all fossils into a single evolving lineage (*80*) to dividing them into several taxa (*55, 81*). Part of the problem is where to draw the line on brain size. Several investigators (*55, 81*) feel that the larger-brained specimens should be placed in the genus *Homo* (either as *Homo* sp. indet. or *Homo habilis*) leaving the smaller-brained forms in the genus *Australopithecus*.

One issue in this debate is the relative size of the brain: Could the differences in body weight account for the differences in brain size? There is some indication that those specimens assigned to the genus *Homo* had larger bodies than the other early hominids (*50, 55, 81*).

Brain to Body Weight Ratios

Unfortunately, body weight is difficult to measure in fragmentary fossils. Until recently estimates have been quite subjective and have consequently varied between 40 (*82*) and 200 pounds (*25*). New efforts involve establishing the relationship between skeletal size and body weight in modern humans and great apes, calculating regression formulas, and predicting the weights of the fossils (*83*). The resulting equations show surprisingly high correlations between measures of the cross-sectional area of vertebral centra and body weight ($r = 0.69$) and measures of proximal femur size and body weight ($r = 0.68$) when proper allometric adjustments are made. Using the vertebral equation a weight of 27.6 kg (61 pounds) is estimated for one individual of the South African *A. africanus* (Sts 14) and 36.1 kg (79 pounds) for one individual of the South African *A. robustus* (SK 3981). These derive from fossils which are among the smallest from their taxa and are therefore minimal estimates. The maximum for *A. africanus* may have ranged as high as 43.0 kg (95 pounds) judging from a single large vertebra (Sts 73). The upper limit to the weight of *A. robustus* may have been 57.7 kg (116 pounds) based on size of the proximal femur (*83*). Body weight estimates from East

African fossils range from 43.1 kg (95 pounds) to 49.9 kg (110 pounds) for femora classified as *Australopithecus* sp. indet. and from 51.3 kg (113 pounds) to 54.3 kg (119 pounds) for femora classified as *Homo* sp. indet.

Using these body weight estimates, several indices of encephalization can be applied to test the possibility that the larger brains of the crania classified as *Homo* sp. indet. are merely the result of larger body sizes. Published endocranial volumes for *Homo* specimens include 775 cm^3 for KNM-ER 1470, 687 cm^3 for OH 7, and 650 cm^3 for OH 13 (*50, 78*). The OH 16 specimen is excluded because of its very fragmentary nature. The average brain size is 704 cm^3 and the average weight is 52.8 kg. The East African crania classified as *Australopithecus* include OH 5 with 530 cm^3, OH 24 with 590 cm^3, KNM-ER 406 with 510 cm^3, and KNM-ER 732 with 506 cm^3 (*78*). The average endocranial volume for East African australopithecines is 534 cm^3 and the average weight it 46.5 kg (102 pounds).

Of the few indices of encephalization commonly used to compare brain and body weight ratios (illustrated in Fig. 5), all show the same pattern: the specimens classified as *Homo* sp. indet. have relatively larger brains than the australopithecines despite the larger body weight of the former. Thus, the constant of cephalization (*84*) is 45.1 in the australopithecines and 57.7 in *Homo* sp. indet.; the index of progression (*30, 85*) is 14.3 and 17.4, respectively; the encephalization quotient (*86*) is 3.7 and 4.2; and the extra neuron index (*28*) is 4.3 billion and 5.4 billion.

These results show that despite their possible larger body sizes, the fossils classified as *Homo* sp. indet. have relatively larger brains than the East African australopithecines. This does not solve the problem of dividing the brain size continuum into taxonomic groups, however, but it does show that some forms were closer to *Homo sapiens* in encephalization than were others.

The South African *A. africanus* samples have slightly lower encephalization values than the East African australopithecines. Assuming an average weight of 35.3 kg (78 pounds) and an average brain size of 442 cm^3, the constant of cephalization is 39.8, the index of progression is 14.1, the encephalization quotient is 3.4, and the extra neuron index is 3.8 billion. These values are very close to those in *Pan* and well below those in the East African *Homo* sp. indet. The South African *A. robustus* encephalization values are very similar to those of the East African australopithecines.

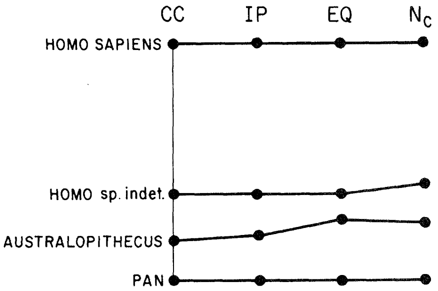

Fig. 5. Indices of encephalization expressed as percent deviation from *Homo*. *Homo* sp. indet. refers to specimens KNM-ER 1470, OH 7, and OH 13. *Australopithecus* includes only specimens from East Africa (that is, KNM-ER 406, KNM-ER 732, OH 5, and OH 24. *CC* is the constant of cephalization (*84*), *IP* is the index of progression (*30, 85*), *EQ* is the encephalization quotient (*86*), and N_c is the extra neuron index (*28*).

None of these early hominids had brains approaching the size of modern human ones. The indices of encephalization show that the australopithecines were only slightly above the great apes in relative brain size and even the largest cranium (KNM-ER 1470) is about as close to apes as it is to humans.

It appears, therefore, that brain expansion began not much before 2 million years ago in human evolution when, for a variety of reasons, the stabilizing selection maintaining smaller brain size was transformed into directional selection favoring larger brains. At approximately the same time evidence occurs for tool manufacture, meat eating, use of a home base, and probably food sharing, indicating a new adaptive strategy which becomes typical of later hominids (*87*).

The expansion of the brain probably involved a complicated complex of characters encompassing the reshaping not only of the cranium but also of the birth canal (*26*). Selection must have favored large pelvic inlets to accommodate larger-brained fetuses. This would lead to the reshaping of the pelvis by increasing the load arm of the abductor muscles, which would require greater abductor force, resulting in greater pressure through the hip and subsequently larger hip joints. Part of this architectural rearrangement would involve changes in the thickness of the buttress supporting the abductor muscular attachment on the iliac blades. It also may have involved shortening of the femoral neck to maintain the limb axis near the midline.

One might expect, therefore, to find hominid populations from dates earlier than about 2 million years ago to have relatively smaller brains and differently shaped pelvic architecture. The Sterkfontein and Makapansgat fossils may be samples from such such early populations if the recently derived dates of 3.0 to 2.5 million years are accurate (*88*). By about 2 million years ago relative brain size is greater in some populations in East Africa and the hip architecture has undergone some reshaping related to larger birth canal size for the larger-headed fetuses (*89*).

Summary

These new fossils, dates, analyses, and interpretations lead to confirmation and refinement of the mosaic scheme of human evolution as proposed by early evolutionists such as Lamarck, Haeckel, and Darwin. Evolutionary changes in the body adapting our ancestors to bipedalism occurred before 3 million years ago, judging by the completeness of the adaptation in the late Pliocene–early Pleistocene hominids. The skeletons of these early hominids were not identical to those of modern humans, but locomotor behavior was probably human. At about 3 million years ago their brains were relatively small, although internal reorganization may have been taking place. By 2 million years ago a wider range of variation in brain size appears in the fossil record, with an average size somewhat larger than that in earlier hominids. Concomitant with this beginning of brain size increase was the reshaping of the pelvic region, perhaps related to an increase in birth canal size to accommodate larger-brained fetuses. Evidence for tool manufacturing, meat eating, shelter building, and probably food sharing also occurs at about this time, which signals the coming of a new adaptive strategy.

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