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AUSTRALOPITHECUS TO *HOMO*: Transformations in Body and Mind

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■ **Abstract** Significant changes occurred in human evolution between 2.5 and 1.8 million years ago. Stone tools first appeared, brains expanded, bodies enlarged, sexual dimorphism in body size decreased, limb proportions changed, cheek teeth reduced in size, and crania began to share more unique features with later *Homo*. Although the two earliest species of *Homo, H. habilis* and *H. rudolfensis,* retained many primitive features in common with australopithecine species, they both shared key unique features with later species of *Homo*. Two of the most conspicuous shared derived characters were the sizes of the brain and masticatory apparatus relative to body weight. Despite the shared derived characters of *H. habilis* and *H. rudolfensis,* one unexpected complication in the transition from australopithecine to *Homo* was that the postcranial anatomy of *H. habilis* retained many australopithecine characteristics. *H. rudolfensis*, however, seems to have had a more human-like body plan, similar to later species of *Homo*. *H. rudolfensis* may therefore represent a link between *Australopithecus* and *Homo*.

INTRODUCTION

When Kamoya Kimeu discovered the early *Homo* skeleton KNM-WT 15000 in 1984, something that had been vaguely understood before snapped into sharper focus: The evolutionary transition from australopithecine to *Homo* involved not only an expansion of the brain and a reduction of the cheek teeth, but a change in walking and climbing behavior (Walker & Leakey 1993a). Arguments remain about which early *Homo* species gave rise to later *Homo*, but the origin of the genus is becoming of greater interest.

New discoveries and new analyses of *Homo* include three major monographs (Tobias 1991, Walker & Leakey 1993a, Wood 1991). Most paleoanthropologists (e.g. Groves 1989; Tobias 1991; Wood 1991, 1992; Skelton & McHenry 1992; Walker & Leakey 1993a; McHenry 1994c; Strait et al 1997; Asfaw et al 1999a; Klein 1999; Wolpoff 1999; Wood & Collard 1999), but not all (e.g. Oxnard 1975), agree that *Homo* evolved from *Australopithecus*, but there is less consensus on

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which species of *Australopithecus* is the most likely ancestor and which fossils are the earliest members of *Homo*.

The search for the immediate ancestor of *Homo* among known species of *Australopithecus* may be fruitless because all the possible candidates have unique specializations (i.e. autapomorphies). It is more useful to search for the species whose unknown ancestor most recently branched off from the stem leading to *Homo*. The closeness of two species can be determined on the basis of morphological resemblances that are unique relative to other species (shared derived characters or synapomorphies). The closest branches in the evolutionary tree are referred to as sister clades. Unfortunately, there is little consensus on which species of *Australopithecus* is the closest to *Homo*. An analysis using most of the information on craniodental morphology of early hominids available in 1999 found that the sister clade to *Homo* was that containing the "robust" australopithecines (in their terminology, *Paranthropus aethiopicus*, *Paranthropus robustus*, and *Paranthropus boisei*), with *Australopithecus africanus* and *Australopithecus garhi* more distantly related to *Homo* (Strait & Grine 1999). Not all agree (Asfaw et al 1999b, McCollum 1999). Nor is there agreement on who are the earliest members of the genus *Homo* (Grine et al 1996) or whether the species known as *Homo habilis* and *Homo rudolfensis* should be put into Australopithecus (Wood & Collard 1999).

Even without unanimity of opinion on hominid taxonomy and phylogeny, there are some important generalizations that can be made about the origin of the genus *Homo*. Between 2.5 and 1.8 million years ago (mya) stone tools first appeared, brains expanded, bodies enlarged, sexual dimorphism in body size decreased, limb proportions changed, cheek teeth reduced in size, and crania began to share more unique features with later *Homo*. This paper reviews what can be said, and with what level of certainty, about these transformations.

CAST OF CHARACTERS

Table 1 presents one version of who's who in the early Plio-Pleistocene. The taxonomy is mostly from Klein (1999), who provides discussions of alternative views that are beyond the scope of this review. This taxonomic scheme recognizes three genera of hominid. *Australopithecus* and *Paranthropus* are often referred to informally as australopithecines, in contrast to members of the genus *Homo*. The body sizes, brain volumes, tooth dimensions, and other variables derive from sources given in the footnotes to the table.

TRANSFORMATIONS OF BODY

All species of hominid appear to be accomplished bipeds, but there are noticeable differences in body plan. Bipedal adaptations have so profoundly altered the general body plan of hominids away from that seen in other members of the

TABLE 1 Species, dates, body size, brain size, and posterior tooth size in early hominids[a]

Taxon	Dates (mya)	Mass (kg)		Stature (cm^3)		ECV (cc)	Brain weight (g)	Postcanine tooth area	EQ	MQ
		Male	Female	Male	Female					
Pan troglodytes	Extant	49	41	—	—	—	395	294	2.0	0.9
Australopithecus anamensis	4.2–3.9	51	33	—	—	—	—	428	—	1.4
Australopithecus afarensis	3.9–3.0	45	29	151	105	438	434	460	2.5	1.7
Australopithecus africanus	3.0–2.4	41	30	138	115	452	448	516	2.7	2.0
Australopithecus aethiopicus	2.7–2.2	—	—	—	—	—	—	688	—	—
Paranthropus boisei	2.3–1.4	49	34	137	124	521	514	756	2.7	2.7
Paranthropus robustus	1.9–1.4	40	32	132	110	530	523	588	3.0	2.2
Australopithecus garhi	2.5–?	—	—	—	—	450	446	—	—	—
Homo habilis	1.9–1.6	37	32	131	100	612	601	478	3.6	1.9
Homo rudolfensis	2.4–1.6	60	51	160	150	752	736	572	3.1	1.5
Homo ergaster	1.9–1.7	66	56	180	160	871	849	377	3.3	0.9
Homo sapiens	Extant	58	49	175	161	—	1350	334	5.8	0.9

[a] Taxonomy is based on Klein (1999). *Ardipithecus* and later extinct species of *Homo* are beyond the scope of this paper. Dates are from Klein (1999). mya, Million years ago. Body mass estimates are from McHenry (1992), except for the following: *A. anamensis* male is from Leakey et al (1995), *A. anamensis* female is calculated from the ratio of male and female in *A. afarensis*, and *H. ergaster* is from Ruff et al (1998). Statures are from McHenry (1991), except *H. ergaster*, which is from Ruff & Walker (1993). ECV is cranial capacity from sources listed in McHenry (1994), with the addition of A.L. 444-2 (540 cc) to *A. afarensis* (WH Kimbel, personal communication), Stw 505 (515 cc) to *A. africanus* (Conroy et al 1998), KGA 10-525 (545 cc) to *P. boisei* (Suwa et al 1997), and BOU-VP-12/130 (450 cc) to *A. garhi* (Asfaw et al 1999a). Brain weight is calculated from Ruff et al (1998). Postcanine tooth area (in square millimeters) is the sum of products of the mesiodistal and buccolingual dimensions lengths of P_4, M_1, and M_2 and is taken from McHenry (1994), with the addition of *A. anamensis* from Leakey et al (1995). Encephalization quotient (EQ) is calculated as brain mass divided by ($11.22 \times$ body mass$^{0.76}$), from Martin (1981). Megadontia quotient (MQ) is the postcanine tooth area divided by ($12.15 \times$ body mass$^{0.86}$), from McHenry (1988).

superfamily Hominoidea (apes and people) that differences between species of hominid are often not emphasized (e.g. Lovejoy 1988, Latimer 1991). By most accounts there are important differences in postcranial anatomy between australopithecine species, and especially between australopithecines and *Homo ergaster* (McHenry 1994b, Stern 2000). Some of the most conspicuous changes between the australopithecines and *H. ergaster* include a sharp increase in body size (especially among females), a reduction in relative forelimb size, a lengthening of the thigh, a narrowing of the pelvis, a side-to-side expansion of the femoral shaft, and the development of a more barrel-shaped chest.

When did the body transform from the patterns seen in australopithecine species to the one manifest in *H. ergaster*? The first evidence of an *H. ergaster*–like body occurred at 1.95 mya with the pelvic bone KNM-ER 3228. About 60,000 years later there were several hindlimb specimens that were more like KNM-WT 15000 than like any australopithecine. These include the two well-preserved femora, KNM-ER 1472 and 1481, and the proximal and distal tibia and distal fibula of 1481. These derive from the Upper Burgi Member of Area 131 in Koobi Fora at the same time and place as the KNM-ER 1470 cranium of *H. rudolfensis*. It has always seemed reasonable to assume that these legs go with that head (Leakey 1973, Wood 1992), but the postcrania are not directly associated with the cranium. Wood & Collard (1999) reject Wood's (1992) earlier attribution of these femora to *H. rudolfensis*. However, the assumption that these femora do belong to the same species as *H. rudolfensis* is strengthened by the fact that there is no other *Homo* species at that site, although there are two *P. boisei* mandibles there (Wood 1991). The most common hominid craniodental specimens at the site are those that Wood refers to as *H. rudolfensis* (i.e. KNM-ER 1470, 1482, 1483, 1801, and 1802). The legs (KNM-ER 1472 and 1481) might belong to *P. boisei*, but that appears unlikely because they are unlike the one known *P. boisei* partial skeleton, KNM-ER 1500 (Grausz et al 1988). If it is true that these femora belong to *H. rudolfensis*, then it becomes more likely that the KNM-ER 3228 pelvic bone also belongs to that species. It is morphologically compatible with the femora. *H. rudolfensis* appears in the fossil record before 1.95 mya, but *H. ergaster* does not. The specimen comes from the earliest hominid-bearing levels in Area 102 and no other hominids have been found in those levels at that site.

As is discussed below, however, what is known of the body of *H. habilis* is much more like that of *Australopithecus* than *H. rudolfensis* or later *Homo*. The primitiveness of the *H. habilis* postcranium was one of the reasons Wood & Collard (1999) suggested transferring that species to the genus *Australopithecus*.

Hands and Tools

It has long been assumed that the morphology of the hand will reveal something about the manual dexterity required to make stone tools (Napier 1962, Leakey et al 1964), but interpretation of the hominid fossils is not simple (Marzke 1997). The earliest known stone tools appeared between 2.6 and 2.5 mya from

Kada Gona, Hadar (Semaw et al 1997), which predates the first known appearance of *Homo*. Evidence of tool use comes from 2.5-million-year-old sediments at Bouri on the Middle Awash River, with cut and percussion marks on mammalian bones made by stone tools (de Heinzelin et al 1999). These sediments also contained remains of only one species of hominid, *A. garhi* (Asfaw et al 1999a). Slightly later in time (2.4–2.3 mya) stone tools appeared at Afar Locality 666 (Kimbel et al 1996) associated with a maxilla of a hominid resembling some of the *H. habilis* specimens at Olduvai (i.e. specimens O.H. 16 and 39). Tools also made their earliest known appearance in the lower Omo River valley [Member F of the Shungura Formation (Howell et al 1987)] and at West Turkana [Kalochoro Member of the Nachukui Formation (Roche et al 1999)] at about that time. The richest collection of early stone tools occurred between 2 and 1.6 mya at Olduvai (Leakey 1971) and Koobi Fora (Harris & Isaac 1976). All of these are part of the Oldowan Industrial Complex, but those from before about 2 mya are more crudely flaked than the later Oldowan tools (Kibunjia 1994). Perhaps by 1.6 mya, but certainly by 1.4 mya, the Acheulean Industrial Complex appears in the record with more sophisticated tools, such as hand axes and cleavers (Asfaw et al 1992).

Is there a detectable change in hand morphology at the time tools first appeared or when they become more sophisticated? Hand bones are known for most species of *Australopithecus*. Within the collection of the earliest species, *Australopithecus anamensis*, is a proximal hand phalanx that is curved and has strong ridges for the attachment of the flexor sheath (Leakey et al 1998). Both features are present in *Australopithecus afarensis* and are considered primitive and possibly indicative of climbing ability (Stern & Susman 1983, Susman et al 1984). The capitate of *A. anamensis* is even more primitive than *A. afarensis* in that it has an ape-like, laterally facing metacarpal II facet (Leakey et al 1998). The hands of *A. afarensis* have many primitive features that are associated with arborealism, including strongly curved proximal phalanges, strong ridges for the flexor sheath, an elongated and rod-shaped pisiform, and expanded heads and bases of the metacarpals (Tuttle 1981, 1988; Stern & Susman 1983; Susman et al 1984, 1985; Susman & Stern 1991; Susman 1994, 1998). *A. afarensis* also possessed several derived features that would allow two distinctively human precision grips important to stone tool manufacture but it lacked the human mobility of the thumb. This lack may have limited its tool-making ability (Marzke 1997). *A. africanus* also combined primitive characteristics [e.g. its capitate had a dorsally placed trapezoid facet, mediolaterally constricted metacarpal III facet, prominent palmar beak, and reduced area for the styloid process of metacarpal III (McHenry 1983)], with derived features associated with the human pad-to-side precision pinch and handling grips (Marzke 1997). Remains of both of these species have been found in sediments that are distinctly lacking in stone tools.

At Olduvai, Koobi Fora, and elsewhere, stone tools are abundant in sediments containing *H. habilis*, yet in many respects the hand bones attributed to the type specimen of this species (O.H. 7) retain numerous primitive features (Susman & Creel 1979; Susman & Stern 1982; Susman 1994, 1998). That hand did have some key features associated with the firm precision pinch and handling grips used in making stone tools (Marzke 1983, 1986, 1997; Marzke & Shackley 1986; Marzke & Marzke 1987; Marzke et al 1992). A partial skeleton of *H. habilis*, KNM-ER 3735, has two fragments of proximal phalanges that are curved and strongly built (Leakey & Walker 1985). Stone and bone tools are also abundant at Swartkrans, and the hand bones there have traits associated with the ability to make tools (Susman 1988a–c, 1989, 1993, 1994, 1998; Marzke 1997). This may imply that *P. robustus*, by far the most common hominid at that site, was a toolmaker. However, a species of *Homo* is also present in Members 1 and 2 (but not 3), Swartkrans, and it is possible that the tools were made by it (Clark 1993).

There are few hand bones of *H. ergaster* and none that can be attributed with any certainty to *H. rudolfensis*. There are two phalanges (one proximal pollex, 15000 BQ, and one middle that is not from the thumb, 15000 BO) associated with KNM-WT 15000 (Walker & Leakey 1993b). Neither shows curvature. There are two juvenile thumb metacarpals that probably belong to KNM-WT 15000, but their association is uncertain (Walker & Leakey 1993b). If part of the skeleton, they are significant in that they are long and straight like those of modern humans and one of the Swartkrans specimens (SKW 5020), although the 15000 specimens have palmar beaks on their distal end formed by the diaphysis, not by the epiphysis, as it is in SK 84. There are two proximal phalanges of KNM-ER 164, a specimen that also has enough of a skull bone to allow Wood (1991) to classify it as *Homo* sp. *indet*. The phalanges do not have the strong curvature and markings for the flexor sheath that characterize *A. afarensis*. The KNM-ER 803 partial skeleton of *H. ergaster* preserves the proximal end of a metacarpal V, but it is not complete enough to show whether its hand had shed arboreal features. The lack of hand bones in early species of *Homo* is especially frustrating because other evidence points to important changes between australopithecines + habilines and later *Homo*.

Forelimb Transformations

The evidence from the hand is confusing and incomplete, but the forelimb as a whole shows profound modification between *Australopithecus* + *habilis* and later *Homo*: The former had big, robust arms and the latter was relatively petite. There are no associated limb bones of *A. anamensis*, but the well-preserved radius KNM-ER 20419 is very long [265–275 mm (Heinrich et al 1993)]. The humeri of *A. afarensis* are not exceptionally long but are exceptionally robust (Johanson et al 1982a; Jungers 1982, 1991, 1994; Lovejoy et al 1982; Jungers & Stern 1983; Susman et al 1984, 1985; White et al 1993; Kimbel et al 1994; White 1994). Forearms of *A. afarensis* appear to be very long relative to humeral length, however. Kimbel et al (1994) estimate an ulnar/femoral index of 91% for A.L. 438-1/137-50 and 92.5% for A.L. 288-1 that is closer to that of chimps (95%) than humans (80%). *H. ergaster* is closer to the human condition [85% (Ruff & Walker 1993)]. *A. garhi* also has a long forearm relative to humeral length. For BOU-VP 12/1, Asfaw et al (1999a) estimate a radial length of 231 mm and a humeral length of 236 mm, which makes a ratio of 98, more similar to chimps [87–100 (Napier & Napier 1967)] than modern tropical people (76–79) or *H. ergaster* [80 (Ruff & Walker 1993)].

The limbs of *A. africanus* are too fragmentary to be able to reconstruct total lengths with accuracy, but judging from the sizes of the articular ends, forelimb length is probably greater relative to hindlimb length than is true for modern people (McHenry & Berger 1998b). Joint breadths of the forelimbs are much larger than expected from human proportions relative to the joints of the hindlimb (McHenry & Berger 1998a). In fact, *A. africanus* had relatively larger forelimb breadths than did *A. afarensis* (McHenry & Berger 1998a).

Relatively large forelimbs characterize *H. habilis* as well. This is certainly true comparing shaft breadths, and according to some (Johanson et al 1987, Hartwig-Scherer & Martin 1991), but not all (Korey 1990, Asfaw et al 1999a), is probably true of estimated humeral and femoral lengths.

Unfortunately, no forelimb specimens are definitely attributed to *H. rudolfensis*, although the proximal humerus KNM-ER 1473 is from the Upper Burgi Member of Area 131 and may belong to that species. The ratio of its head diameter to the femoral head diameters of KNM-ER 1471 and 1481a are 1.07 and 0.99, respectively, which is at the upper range of variation seen in modern humans and well below the ratio in any modern apes.

As noted above, the size of the arm relative to the forearm in the *H. ergaster* skeleton KNM-WT 15000 is very human-like and not at all similar to any species of *Australopithecus* (Ruff & Walker 1993). This is a conspicuous change and adds weight to the argument favoring a dramatic alteration in locomotor behavior between the australopithecines + *H. habilis* and later *Homo*. Both the humerus-to-femur length index (74%) and the ulnar-to-humeral length ratio (85%) of this specimen are human-like. Other partial skeletons of *H. ergaster* confirm the observation that forelimbs dramatically decreased in relative size. The clavicle and humerus of the KNM-ER 1808 partial skeleton are approximately the same size as those of KNM-WT 15000, but the KNM-ER 1808 femur is much larger. The KNM-ER 803 fore-to-hindlimb proportions are also very human-like (McHenry 1978).

Shoulders and Trunks

What many would consider climbing features are also retained in the shoulder and trunk of *Australopithecus* + *H. habilis* but not in later *Homo*. The shoulder joint appears to be directed more superiorly in *A. afarensis* (Jungers & Stern 1983; Stern & Susman 1983, 1991; Susman et al 1984, 1985; Susman & Stern 1991), but this appearance may not be related to locomotor behavior (Inouye & Shea 1997). The thorax of *A. afarensis* is distinctly pongid-like in its funnel shape (Schmid 1983, 1989, 1991; Berge et al 1984), but the thorax is barrel shaped in *H. ergaster* and later humans (Jellema et al 1993). Perhaps the more pongid shape of the *A. afarensis* thorax is simply an artifact of its wider hips, but it is also interpreted as an indication that this species' back muscles were specially adapted to climbing (Schmid 1983).

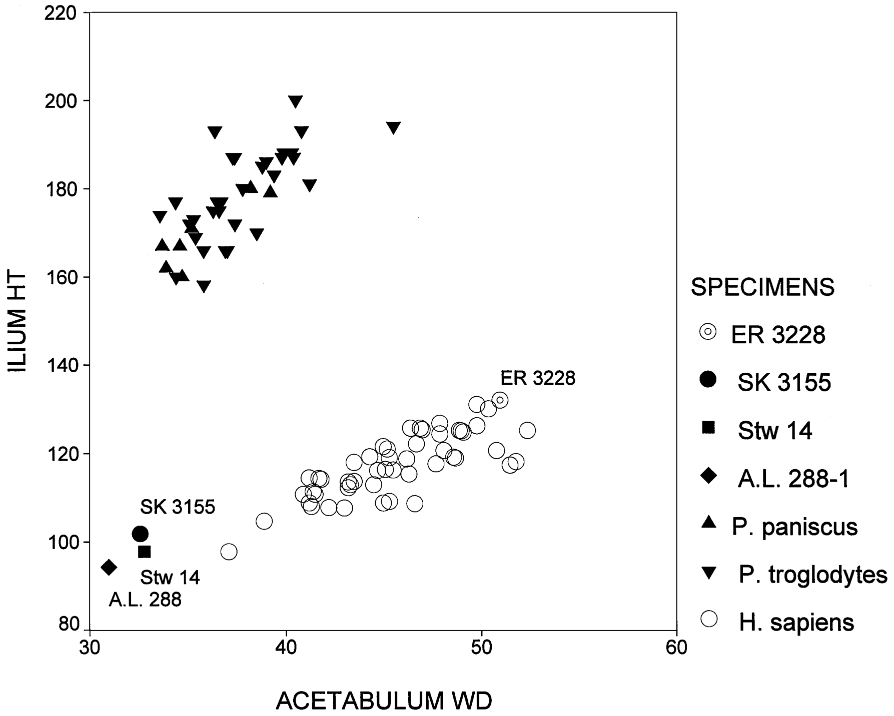

Figure 1 Scatter plot of hip-joint size against height of the pelvic blade. Measurements and samples are from McHenry (1975b). Like most mammals, the pelvic girdle of bonobos (*Pan paniscus*) and common chimps (*Pan troglodytes*) have small acetabulae and long iliac blades relative to the conditions seen in humans. The australopithecines are represented by the pelvic bones of *Australpithecus afarensis* (A.L. 288-1), *Australpithecus africanus* (Sts 14), and *Paranthropus robustus* (SK 3155) and are smaller in size than modern humans but decidedly human in shape. The specimen referred to, *Homo rudolfensis* (KNM-ER 3228), is indistinguishable from modern humans in this regard. Unfortunately, this part of the anatomy has not yet been recovered for *Homo habilis.*

Hips

Hips transform dramatically between *Australopithecus* and *Homo*. Here, the fossil sample includes a rich collection of pelvic and femoral specimens, including those that we argue belong to *H. rudolfensis* (i.e. the KNM-ER 3228 pelvic bone and the KNM-ER 1472 and 1481a femora). The pelvic girdles show key bipedal adaptations, such as shortening of the pelvic blades and anterior rotation of the sacrum. The big alterations from the pongid condition resulted from changes in the morphogenesis of the limb (Lovejoy et al 1999). Still, there are conspicuous differences between *Australopithecus* and *Homo* that are important but harder to explain in terms of genetic alterations.

The most obvious change from *Australopithecus* to *Homo* is in relative hip-joint size. Figure 1 plots pelvic height against acetabular width to illustrate how very small the hips were in *Australopithecus* and how human-like *H. rudolfensis* was in this respect. But there were interesting changes between the hips of early *Homo* and later *Homo* as well. Changes in the pattern of gait explain most of the changes in pelvic morphology between the last common ancestor of African apes and humans, but changes within the human lineage also involve birth. The shortening of the pelvic blades to make bipedalism possible reduced the front-to-back dimension of the birth canal. This may (Berge et al 1984, Tague & Lovejoy 1986, Berge 1991) or may not (Leutenegger 1987) have affected the birth process of small-brained australopithecines, but it became a painful reality to *Homo*. It probably explains the difference between early and late *Homo* hips.

Unfortunately, no pelvic remains are known for *H. habilis* except for a very eroded sacrum associated with KNM-ER 3735 (Leakey et al 1989). Something can be discerned about the *H. habilis* hip on the basis of its femoral shafts. Analyses using engineering principles show interesting contrasts between the proximal femora attributed to australopithecines + *H. habilis* and *H. rudolfensis* + later species of archaic *Homo* (Ruff 1995, 1998). The ratio of mediolateral bending strength to the anteroposterior bending strength is much higher in *H. rudolfensis* and later species of archaic *Homo* than in the australopithecines. The one femoral shaft that can definitely be attributed to *H. habilis*, O.H. 62, is australopithecine-like in this regard. Ruff (1995) provides one explanation for this difference that involves femoral neck length and the shape of the pelvic inlet. In australopithecine hips, long femoral necks compensate for the high hip-joint reaction forces generated by the abductor muscles. These high forces are due to the relatively wide mediolateral dimension of the birth canal. In *H. rudolfensis* and later archaic members of the genus *Homo*, the hip-joint reaction force increased, as indicated by relatively large joints, and so did the mediolateral strain of the femoral shafts. This implies, according to Ruff (1995), that early *Homo* retained the platypelloid pelvic outlet of *Australopithecus* and compensated by increasing the abductor force and mediolateral strain on the femoral shafts. Only by Middle Pleistocene times did the rounder pelvic inlet typical of modern humans evolve, a change that was made possible by the rotation during birth of the infant's head.

Femoral Length

It is known with certainty that relative to humeral length, the femur of *A. afarensis* was short (Johanson & Taeib 1976; Johanson et al 1982a,b; Jungers 1982, 1988a; Jungers & Stern 1983; Susman et al 1984, 1985) and that of *H. ergaster* was long (Ruff & Walker 1993). There is less certainty about relative femoral length in other early hominid species because of the fragmentary nature of the fossils, but enough is preserved to indicate that *A. africanus* (McHenry & Berger 1998b) and *H. habilis* (Johanson 1989, Leakey et al 1989, Korey 1990, Hartwig-Scherer & Martin 1991) also had relatively short femora. Associated fore- and hindlimbs from the Hata beds of Ethiopia's Middle Awash probably belong to *A. garhi* and appear to show femoral lengthening relative to humeral length (Asfaw et al 1999a). Relative to radial length, however, the length of this femur is intermediate between humans and apes.

Legs

The tibia and fibula of the australopithecines + *H. habilis* are variable, decidedly more human-like than ape-like, but there remains a debate as to the precise kinematics of the knee and ankle (Susman & Stern 1982, 1991; Stern & Susman 1983, 1991; Tardieu 1983, 1986, 1998; Susman et al 1985; Latimer et al 1987; Latimer 1988, 1991; Berger & Tobias 1996; Tardieu & Preuschoft 1996; Crompton et al 1998). These elements are variable in modern human populations, but all relevant specimens of australopithecines + *H. habilis* show the key adaptations to bipedalism, particularly a horizontally oriented talar facet.

Feet

There are numerous primitive features reported from the pedal remains of *A. afarensis*, including relatively long and curved toes and the lack of side-to-side widening of the dorsal region of the metatarsal heads (Johanson & Edey 1981; Tuttle 1981; Stern & Susman 1983; Susman et al 1984, 1985; Susman & Stern 1991). Primitive features have also been emphasized in the description of foot remains from Member 2 of Sterkfontein that might belong to *A. africanus* (Clarke & Tobias 1995, Clarke 1998). The primitive qualities of the Olduvai Hominid 8 foot have been noted (Oxnard 1972, 1973; Lisowski et al 1974, 1976; Oxnard & Lisowski 1978; Lewis 1980, 1989; Kidd et al 1996), and this foot probably belongs to *H. habilis* (Day & Napier 1964; Day & Wood 1968; Day 1973, 1976; Susman & Stern 1982). Unfortunately, there are no foot specimens that can be attributed to *H. rudolfensis* and only a few scraps to *H. ergaster*. A very human-looking talus from East Turkana, KNM-ER 813, derives from strata dated to 1.85 mya (Feibel et al 1989) and may belong to *H. ergaster*, but it is not directly associated with taxonomically diagnostic craniodental material (Wood 1974). There is evidence that the toes of *H. ergaster* were shorter and less curved than those of *A. afarensis*. One of the partial skeletons of *H. ergaster*, KNM-ER 803, preserves two intermediate toe phalanges (803k and 803l) that are relatively short and straight compared with the equivalent parts of *A. afarensis* [A.L. 333x-21a and 333-115k & l (Day & Leakey 1974, Latimer et al 1982)]. The footprints attributed to early *Homo* at Koobi Fora may be more human-like than those attributed to *A. afarensis* (Behrensmeyer & Laporte 1981), but given the controversy over the interpretation of the Laetoli footprints (Clarke 1979; Tuttle 1981, 1985, 1987, 1988, 1994; Jungers & Stern 1983; Stern & Susman 1983, 1991; Susman et al 1984, 1985; Deloison 1985; White & Suwa 1987; Susman & Stern 1991; Tuttle et al 1991a,b, 1992, 1998), such contrasts may not be important. A first metatarsal (KNM-WT 15000 BX) may belong to the Strapping Youth, but it is not closely associated with the rest of the skeleton, and it contains peculiarities that make the original describers doubt its attribution (Walker & Leakey 1993b).

Body Size

Table 1 presents estimates of body weights for males and females of each species. Most of these are based on the relationship between known body weight and hindlimb joint size in modern humans (McHenry 1992a). Many other estimates appear in the literature (e.g. McHenry 1974, 1975a, 1988, 1991a–c, 1992b, 1994a, 1996; Jungers 1988b, 1991; Hartwig-Scherer & Martin 1992; Hartwig-Scherer 1993, 1994; Ruff & Walker 1993; McHenry & Berger 1998a, b; Ruff et al 1998). Until the appearance of *H. rudolfensis*, the male averages are small by modern human standards (37–51 kg) and female averages are tiny (29–37 kg). By 1.95 mya, modern-sized hindlimbs appear in the record. Although it is still uncertain what isolated limb bones belong to *H. rudolfensis*, by 1.8 mya there are partial associated skeletons of *H. ergaster* that are from big-bodied individuals (i.e. KNM-ER 803 and 1808). What is particularly striking is the apparent increase in the size of the *H. ergaster* female compared with that seen in earlier species of hominid.

Craniodental

The high level of heterogeneity in craniodental morphology among australopithecine species and among specimens attributed to *H. habilis* and *H. rudolfensis* makes it difficult to generalize about specific transformations between the australopithecines and *Homo*. In a formal cladistic analysis of 60 craniodental characters, Strait et al (1997) found only four synapomorphies defining the *Homo*-clade, and two of these were reversals or parallelisms. Their most parsimonious cladogram placed *H. habilis* as the sister clade to all later species of *Homo*, including *H. rudolfensis*. Lieberman et al (1996) did a similar analysis and found *H. habilis* to be the closest clade to later *Homo* to the exclusion of *H. rudolfensis*. In one analysis, Chamberlain & Wood (1987) found *H. habilis* to be the sister of all other species of *Homo*, including *H. rudolfensis*. Wood (1991) preferred a cladogram in which *H. habilis* and *H. rudolfensis* are on sister clades and their combined branch is sister to other *Homo*. Wood & Collard (1999) reanalyzed these and other data sets and showed that four clades are equally close, including that of *Paranthropus* species, *H. habilis, H. rudolfensis,* and all later *Homo* species. If genus names were to be applied strictly on the basis of monophyly, their cladogram suggests that either all species of *Paranthropus* should be included in the genus *Homo* (because relative to other species of hominid, *Paranthropus, H. habilis, H. rudolfensis,* and all other *Homo* are monophyletic), or each of the four clades should be given different genus names.

For the purposes of this review, we assumed that *H. habilis, H. rudolfensis, H. ergaster*, and all later species of *Homo* are monophyletic relative to species of australopithecines. When scaled to body size, they all share two distinctive and fundamentally important characteristics not found in combination in any other hominid species: All species of *Homo* have both a relatively reduced masticatory system and an expanded brain.

The reduction in absolute size of the masticatory system is clearly evident in *H. habilis*. One measure of this reduction is given in Table 1 (postcanine tooth area). The absolute sizes of cheek teeth expand through successively younger species of australopithecine, from the oldest, *A. anamensis* (428 mm^2), to *A. afarensis* (460 mm^2), *A. africanus* (516 mm^2), *P. robustus* (588 mm^2), and *P. boisei* (756 mm^2). The trend is reversed in successively younger species of *Homo*, from *H. rudolfensis* (572 mm^2) to *H. habilis* (478 mm^2), *H. ergaster* (377 mm^2), and *Homo sapiens* (334 mm^2).

The absolute size of the cheek teeth is correlated to the morphology of much of the skull, including mandibular corpus robusticity, position and robusticity of the zygomatic arches, attachment areas and buttressing for the chewing muscles, and many features of the face. *H. rudolfensis* resembles some of the australopithecines in retaining absolutely larger cheek teeth and related features (Wood 1991), but when scaled to body weight, its teeth are relatively much smaller than any australopithecine.

The relative size of the cheek teeth can be estimated by comparing postcanine tooth area with body size. This can be done by comparing postcranial dimensions of associated skeletons with cheek-tooth size (McHenry 1984), but there are few specimens. Although there are methodological problems (Smith 1996), it is heuristically interesting to compare tooth area directly with estimated body weight to find a measure of relative tooth size. Table 1 presents one measure of relative cheek-tooth size by way of the ratio of actual postcanine tooth area to predicted tooth area based on scaled body weight [the megadontia quotient (MQ)]. By this measure, the average extant hominoid has an MQ of 1. Both modern chimps and humans are slightly below this average and have a value of 0.9. The australopithecine species expand through time from the earliest, *A. anamensis*, with 1.4, to *A. afarensis* with 1.7, *A. africanus* with 2.0, *P. robustus* with 2.2, and *P. boisei* with 2.7. This trend is reversed in the *Homo* lineage. The earliest species of *Homo* show some reduction from late *Australopithecus* (*H. habilis* has an MQ of 1.9 and *H. rudolfensis* one of 1.5). The values for *H. rudolfensis* depend on the assumption that the large hindlimbs of Area 103 at Koobi Fora belong to that species and thereby provide valid body weight estimates. Attempts have been made to estimate body weight directly from the skull (Aiello & Wood 1994, Kappelman 1996), and these range between 46 and 54 kg for the skull of *H. rudolfensis*. These are slightly smaller than the 60-kg estimate derived from the postcranium of the presumptive male of that species. The lower body weight estimates would raise the MQ value slightly. Because of its large body size, the relative size of the cheek teeth of *H. ergaster* is the same as that of modern humans (i.e. 0.9).

TRANSFORMATIONS OF MIND

There was probably significant internal reorganization of the brain between *Australopithecus* and *Homo*, but the fossil record preserves only the exterior shape.

The external morphology of the KNM-ER 1470 endocast appears to have a reorganized frontal lobe with a distinctively human-like Broca's area (Holloway 1995). The most conspicuous change in the human fossil record through time is in brain size. Table 1 gives the average endocranial volume for each species and provides the calculated brain size. The brain size of *A. afarensis* ranges from 342 to 540 cc and averages 434 cc, which is about that of modern chimpanzees and one third that of modern humans. The range for *A. africanus* is from 424 to 508 cc, with an average of 448 cc. The one endocast so far reported for *A. garhi* would predict a brain size of 446 cc, and the one for *Australopithecus aethiopicus* would predict 407 cc. There is, therefore, little difference between these representatives of early species (3.2–2.5 mya). The specimens recovered from slightly later than 2 mya are larger. There are four endocranial casts of *P. boisei*, ranging from 494 to 537 cc, with an average brain size of 514 cc. The one specimen of *P. robustus* is 523 cc. There are six specimens of *H. habilis* that range from 503 to 661 cc, with an average of 601 cc. The single representative of *H. rudolfensis*, KNM-ER 1470, is 736 cc. Brain size jumps to 849 cc with *H. ergaster*, although there is one specimen (O.H. 12) that is as small as 712 cc and one (O.H. 9) as large as 1035 cc.

These absolute values for brain weight are instructive, but they should be viewed in the context of body weight to determine relative size. Figure 2 is a plot of brain and body weight. The small body sizes of the australopithecines and *H. habilis* shift them strongly to the left of the plot, but within that group there are three distinct grades of brain size, with small-sized *A. afarensis* and *A. africanus*, medium-sized *P. robustus and P. boisei*, and larger-sized *H. habilis*. The larger body size of *H. rudolfensis* aligns it more with later *Homo*. There are four distinct grades of brain size among the later *Homo* and *H. rudolfensis* sample: (*a*) *H. rudolfensis* is distinctly smaller; (*b*) *H. ergaster* and other hominids from between 0.6 and 1.15 mya are a step larger; (*c*) those from between 0.2 and 0.55 mya are intermediate; and (*d*) the early late Pleistocene (0.1–0.15 mya) and Neanderthal samples are large brained like the anatomically modern *H. sapiens* samples (Skhul-Qafzeh and modern). A strong case can be made for separating the Neanderthals and other late Pleistocene archaics from the anatomically modern sample on the basis of brain size relative to body weight using encephalization quotients (EQ) (Ruff et al 1998).

The EQ is the ratio of actual brain weight divided by brain weight predicted from scaled body weight. The method has its limitations (Smith 1996) but is certainly a useful heuristic tool. Table 1 gives EQ values for the hominid species, and Figure 3 plots these values against time. The same pattern emerges except for the position of *H. habilis*. Because of its very small body size, the relative size of its brain is strikingly enlarged relative to its contemporaries. *H. rudolfensis* has a larger body, and therefore a smaller relative brain size. The contrast between anatomically modern *H. sapiens* and Neanderthals becomes clear with the use of EQ. Accompanying this expansion in brain through time is an ever-increasing complexity of material culture. Neither brain size nor material culture complexity increases at a gradual rate. The paleoanthropological record is dense enough now to

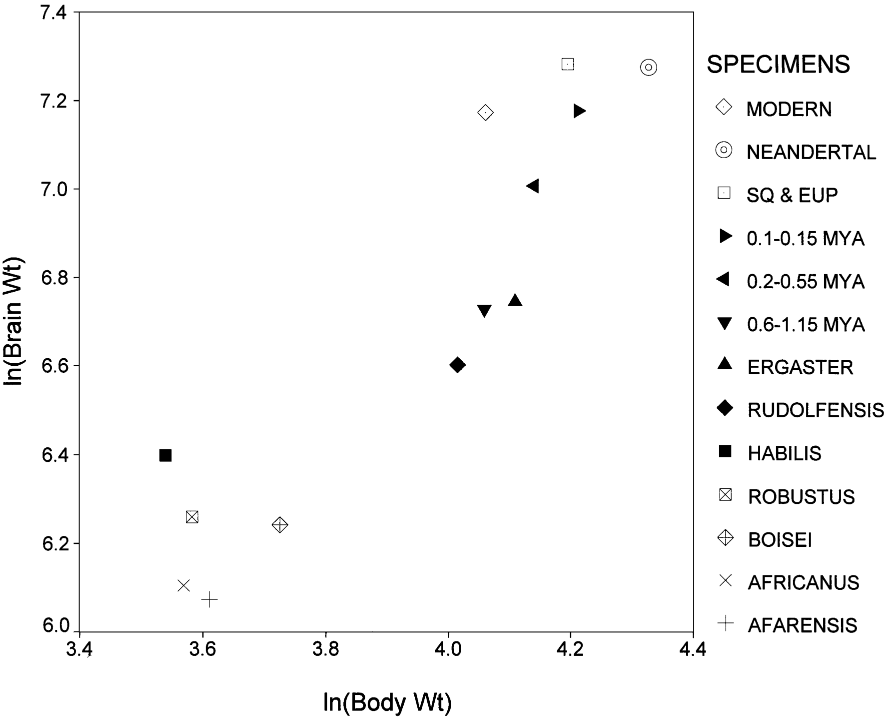

Figure 2 Scatter plot of brain and body size. This is an expanded version of Figure 3 of Ruff et al (1998), with data from Table 1. The two species of *Australopithecus*, *A. afarensis* and *A. africanus*, are similar to one another. The two species of *Paranthropus* are similar, but the one specimen representing *P. robustus* has a larger brain size than *P. boisei* relative to its diminutive body mass. *Homo habilis* combines a very small body with a brain larger than that seen in any australopithecine species. *Homo rudolfensis* has an absolutely larger brain than the australopithecines or *H. habilis*, but this may be due primarily to its larger body size. MYA, Million years ago; SQ, Skhul/Qafzeh; EUP, European Upper Paleolithic.

reveal a pattern of stasis in certain characteristics over long periods within species, as well as rapid shifts between species.

SUMMARY AND CONCLUSIONS

Before about 2.6 mya, stone tools were absent at sites containing hominid fossils, brain sizes were chimp-like, cheek teeth and supporting masticatory structures were enormous, numerous primitive traits were retained in all parts of the body, including the skull, bodies were small, there was strong sexual dimorphism in body size, and hindlimbs were small relative to forelimbs. By 1.8 mya, *H. ergaster* stepped into view with its more human-like body and behavior. What is known about this

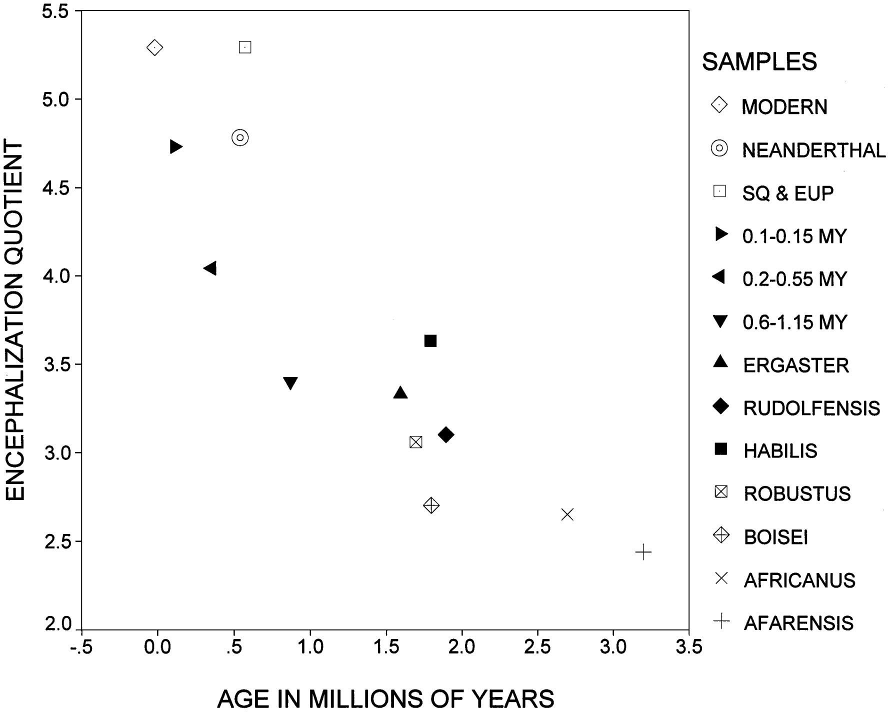

Figure 3 Scatter plot of relative brain size against time. Note the high level of variability around 1.8 million years ago (mya) and the apparent fact that *Homo ergaster* did not have a higher encephalization quotient than *Homo habilis*. MY, Million years ago; SQ, Skhuls/Qafzeh; EUP, European Upper Paleolithic.

transformation and with what certainty? Stone tool manufacture and the use of them on animal carcasses certainly appears in the record by about 2.6 mya. Perhaps brains expanded at that time, but specimens attributed to early *Homo* that are nearly that old do not preserve enough of the skull to show this. In *H. rudolfenisis*, by 1.9 mya, brains were significantly expanded and there was a more human-like form to their frontal lobes. Brain size relative to body weight expanded further in specimens attributed to *H. habilis*, which began to appear in the record by 1.8 mya. The size of the cheek teeth and other parts of the chewing apparatus reduced in *H. habilis* perhaps as early as 2.3 mya, but certainly by 1.8 mya. Although *H. rudolfensis* appeared to have retained the megadontia of its ancestor, scaled to body weight its cheek-tooth size is reduced and similar to that of *H. ergaster*.

The transformations of the body below the head are profound between the australopithecines and *H. ergaster*, but the intermediate stages are not well established. What is known of the body of *H. habilis* reveals a remarkably australopithecine morphology, including (*a*) small body size, (*b*) relatively small hindlimbs and large forelimbs, (*c*) an australopithecine-like femoral-shaft morphology that is probably related to a walking mechanism different from that seen in *H. ergaster* and later species of *Homo,* (*d*) hands lacking the morphology relating to some precision and power grips characteristic of later *Homo,* and (*e*) more flexible feet. If the fossil limbs discovered at the same geological area and time as the skull fragments of *H. rudolfensis* belong to that taxon, then the link between *Australopithecus* and *H. ergaster* becomes clearer. The size and morphology of these limbs are very much like that of *H. ergaster* and unlike the australopithecines and *H. habilis*.

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LITERATURE CITED

Aiello LC, Wood BA. 1994. Cranial variables as predictors of hominine body mass. *Am. J. Phys. Anthropol.* 95:409–26

Asfaw B, Beyene Y, Suwa G, Walter RC, White TD, et al. 1992. The earliest Acheulean from Konso-Gardula. *Nature* 360:732–35

Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. 1999a. *Australopithecus garhi*: a new species of early hominid from Ethiopia. *Science* 284:629–35

Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. 1999b. Cladistics and early hominid phylogeny. *Science* 285:1210–11

Behrensmeyer AK, Laporte LF. 1981. Footprints of a Pleistocene hominid in Northern Kenya. *Nature* 289:167–69

Berge C. 1991. Size- and locomotion-related aspects of hominid and anthropoid pelves: an osteometrical multivariate analysis. *Hum. Evol.* 6:365–76

Berge C, Orban-Segebarth R, Schmid P. 1984. Obstetrical interpretation of the australopithecine pelvic cavity. *J. Hum. Evol.* 13:573–87

Berger LR, Tobias PV. 1996. A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for the interpretation of bipedalism in *Australopithecus africanus. J. Hum. Evol.* 30(4):343–48

Brain CK, ed. 1993. *Swartkrans: A Cave's Chronicle of Early Man.* Pretoria: Transvaal Mus.

Chamberlain AT, Wood BA. 1987. Early hominid phylogeny. *J. Hum. Evol.* 16:119–33

Clark JD. 1993. Stone artefact assemblages from members 1–3, Swartkrans cave. See Brain 1993, pp. 167–94

Clarke RJ. 1979. Early hominid footprints from Tanzania. *S. Afr. J. Sci.* 75:148–49

Clarke RJ. 1998. First ever discovery of a well-preserved skull and associated skeleton of *Australopithecus*. *S. Afr. J. Sci.* 94(10):460–63

Clarke RJ, Tobias PV. 1995. Sterkfontein

Member 2 foot bones of the oldest South African hominid. *Science* 269:521–24

Conroy GC, Weber GW, et al. 1998. Endocranial capacity in an early hominid cranium from Sterkfontein, South Africa. *Science* 280:1730–31

Coppens Y, Senut B, eds. 1991. *Origine(s) de la bipedie chez les hominides.* Paris: Cah. Paleoanthropol., CNRS

Corruccini RS, Ciochon RL, eds. 1994. *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell.* Englewood Cliffs, NJ: Prentice Hall

Crompton RH, Yu L, Weijie W, Gunther M, Savage R. 1998. The mechanical effectiveness of erect and “bent-hip, bent-knee” bipedal walking in *Australopithecus afarensis. J. Hum. Evol.* 35(1):55–74

Day MH. 1973. Locomotor features of the lower limb in hominids. *Symp. Zool. Soc. London* 33:29–51

Day MH. 1976. Hominid postcranial material from Bed I, Olduvai Gorge. In *Human Origins: Louis Leakey and the East African Evidence*, ed. GL Isaac, ER McCown, pp. 363–74. Menlo Park, CA: Benjamin

Day MH, Leakey REF. 1974. New evidence of the genus *Homo* from East Rudolf, Kenya III. *Am. J. Phys. Anthropol.* 41:367–80

Day MH, Napier JR. 1964. Hominid fossils from Bed I, Olduvai Gorge, Tanganyika: fossil footbones. *Nature* 201:969–70

Day MH, Wood BA. 1968. Functional affinities of the Olduvai hominid 8 talus. *Man* 3:440–55

de Heinzelin J, Clark JD, White T, Hart W, Renne P, et al. 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* 284:625–29

Deloison Y. 1985. Comparative study of calcanei of primates and *Pan-Australopithecus-Homo* relationship. See Tobias, pp. 143–47

Else JG, Lee PC, eds. 1986. *Primate Evolution.* Cambridge, UK: Cambridge Univ. Press

Feibel CS, Brown FH, McDougall I. 1989. Stratigraphic context of fossil hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthropol.* 78:595–622

Giacobini G, ed. 1989. *Hominidae: Proc. 2nd Int. Congr. Hum. Paleontol., Turin, September 28–October 3, 1987.* Milan: Jaka

Grausz HM, Leakey REF, Walker AC, Ward CV. 1988. Associated cranial and postcranial bones of *Australopithecus boisei.* See Grine 1988, pp. 127– 32

Grine FE, ed. 1988. *Evolutionary History of the “Robust” Australopithecines.* New York: Gruyter

Grine FE, Jungers WL, Schultz J. 1996. Phenetic affinities among early *Homo* crania from East and South Africa. *J. Hum. Evol.* 30(3):189–225

Groves CP. 1989. *A Theory of Human and Primate Evolution.* Oxford, UK: Clarendon

Harris JWK, Isaac G. 1976. The Karari industry: early Pleistocene archaeological evidence from the terrain east of Lake Turkana, Kenya. *Nature* 262:102–7

Hartwig-Scherer S. 1993. Body weight prediction in early fossil hominids: towards a taxon-“independent” approach. *Am. J. Phys. Anthropol.* 92:17–36

Hartwig-Scherer S. 1994. Body weight prediction in fossil *Homo*. In *100 Years of Pithecanthropus: The Homo erectus Problem*, ed. JL Franzen, pp. 257–79. Frankfurt: Forschungsinst. Senckenberg

Hartwig-Scherer S, Martin RD. 1991. Was “Lucy” more human than her “child”? Observations on early hominid postcranial skeletons. *J. Hum. Evol.* 21:439–49

Hartwig-Scherer S, Martin RD. 1992. Allometry and prediction in hominoids: a solution to the problem of intervening variables. *Am. J. Phys. Anthropol.* 88:37–57

Heinrich RE, Rose MD, Leakey RE, Walker AC. 1993. Hominid radius from the middle Pliocene of Lake Turkana, Kenya. *Am. J. Phys. Anthropol.* 92:139–48

Holloway RL. 1995. Toward a synthetic theory of human brain evolution. In *Origins of the Human Brain*, ed. J-P Changeux, J Chavaillon, pp. 42– 60. Oxford, UK: Clarendon

Howell FC, Haesaerts P, de Heinzelin J. 1987. Depositional environments, archaeological occurrences and hominid from Members E and F of the Shungura Formation (Omo basin, Ethiopia). *J. Hum. Evol.* 16:665–700

Inouye SE, Shea BT. 1997. What's your angle? Size correction and bar-glenoid orientation in "Lucy" (A.L. 288–1). *Int. J. Primatol.* 18(4):629–50

Jellema LM, Latimer BM, Walker A. 1993. The rib cage. See Walker & Leakey 1993a, pp. 294–325

Johanson DC. 1989. A partial *Homo habilis* skeleton from Olduvai Gorge, Tanzania: a summary of preliminary results. See Giacobini 1989, pp. 155–66

Johanson DC, Edey M. 1981. *Lucy: The Beginnings of Humankind.* New York: Simon & Schuster

Johanson DC, Lovejoy CO, Kimbel WH, White TD, Ward SC, et al. 1982a. Morphology of the Pliocene partial hominid skeleton (A.L. 288–1) from the Hadar Formation, Ethiopia. *Am. J. Phys. Anthropol.* 57:403–52

Johanson DC, Massao FT, Eck GG, White TD, Walter RC, et al. 1987. New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. *Nature* 327:205–9

Johanson DC, Taeib M. 1976. Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature* 260:293–97

Johanson DC, Taieb M, Coppens Y. 1982b. Pliocene hominids from the Hadar Formation, Ethiopia (1973–1977): stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics. *Am. J. Phys. Anthropol.* 57:373–402

Jungers WL. 1982. Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis. Nature* 297:676–78

Jungers WL. 1988a. Lucy's length: stature reconstruction in *Australopithecus afarensis* (A.L.288–1) with implications for other small-bodied Hominids. *Am. J. Phys. Anthropol.* 76:227–32

Jungers WL. 1988b. New estimations of body size in australopithecines. See Grine 1988, pp. 115–26

Jungers WL. 1991. A pygmy perspective on body size and shape in *Australopithecus afarensis* (A.L. 288–1, "Lucy"). See Coppens & Senut, pp. 215–24

Jungers WL. 1994. Ape and hominid limb length. *Nature* 369:194

Jungers WL, Stern JT. 1983. Body proportions, skeletal allometry and locomotion in the Hadar hominids: a reply to Wolpoff. *J. Hum. Evol.* 12:673–84

Kappelman J. 1996. The evolution of body mass and relative brain size in fossil hominids. *J. Hum. Evol.* 30(3):243–76

Kibunjia M. 1994. Pliocene archaeological occurrences in the Lake Turkana basin. *J. Hum. Evol.* 27:159–71

Kidd RS, O'Higgins P, Oxnard CE. 1996. The OH8 foot: a reappraisal of the functional morphology of the hindfoot utilizing a multivariate analysis. *J. Hum. Evol.* 31(3):269–91

Kimbel WH, Johanson DC, Rak Y. 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* 368:449–51

Kimbel WH, Walter RC, Johanson DC, Reed KE, Aronson JL, et al. 1996. Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *J. Hum. Evol.* 31(6):549–61

Klein RG. 1999. *The Human Career: Human Biological and Cultural Origins.* Chicago: Univ. Chicago Press

Korey KA. 1990. Deconstructing reconstruction: the OH 62 humerofemoral index. *Am. J. Phys. Anthropol.* 83:25–33

Latimer BM. 1988. *Functional analysis of the Pliocene hominid ankle and pedal bones recovered from the Hadar Formation, Ethiopia: 1974–1977 collections.* Ann Harbor, MI: UMI Dissertat. Inf. Serv.

Latimer BM. 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. See Coppens & Senut 1991, pp. 169–76

Latimer BM, Lovejoy CO, Johanson DC, Yves Coppens. 1982. Hominid tarsal, metatarsal, and phalangeal bones recovered from the Hadar Formation: 1974–1977 collections. *Am. J. Phys. Anthropol.* 57:701–20

Latimer BM, Ohman JC, Lovejoy CO. 1987. Talocrural joint in African hominoids: implication for *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 74:155–75

Leakey LSB, Tobias PV, Napier JR. 1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202:7–9

Leakey MD. 1971. *Olduvai Gorge: Excavations in Beds I and II, 1960–1963*. Cambridge, UK: Cambridge Univ. Press

Leakey MG, Feibel CS, et al. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565–71

Leakey MG, Feibel CS, McDougall I, Ward C, Walker A. 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* 393:62–66

Leakey REF. 1973. Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. *Nature* 242:447–50

Leakey REF, Walker A, Ward CV, Grausz HM. 1989. A partial skeleton of a gracile Hominid from the Upper Burgi Member of the Koobi Fora Formation, East Lake Turkana, Kenya. See Giacobini 1989, pp. 167–74

Leakey REF, Walker AC. 1985. Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. *Am. J. Phys. Anthropol.* 67:135–63

Leutenegger W. 1987. Neonatal brain size and neurochemical dimensions in Pliocene hominids: implications for obstetrics. *J. Hum. Evol.* 16:291–96

Lewis OJ. 1980. The joints of the evolving foot. III: The fossil evidence. *J. Anat.* 131:275–98

Lewis OJ. 1989. *Functional Morphology of the Evolving Hand and Foot*. Oxford, UK: Clarendon

Lieberman DE, Wood BA, Pilbeam DR. 1996. Homoplasy and early *Homo*: an analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis*. *J. Hum. Evol.* 30(2):97–120

Lisowski FP, Albrecht GH, Oxnard CE. 1974. The form of the talus in some higher primates: a multivariate study. *Am. J. Phys. Anthropol.* 41:191–215

Lisowski FP, Albrecht GH, Oxnard CE. 1976. African fossil tali: further multivariate morphometric studies. *Am. J. Phys. Anthropol.* 45:5–18

Lovejoy CO. 1988. Evolution of human walking. *Sci. Am.* 259:118–26

Lovejoy CO, Cohn M, White TD. 1999. Morphological analysis of the mammalian postcranium: a developmental perspective. *Proc. Natl. Acad. Sci. USA* 96(23):13247–52

Lovejoy CO, Johanson DC, Coppens Y. 1982. Hominid upper limb bones recovered from the Hadar Formation: 1974–1977 collection. *Am. J. Phys. Anthropol.* 57:637–50

Martin RD. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293:57–60

Marzke MW. 1983. Joint functions and grips of the *Australopithecus afarensis* hand, with special reference to the region of the capitate. *J. Hum. Evol.* 12:197–211

Marzke MW. 1986. Tool use and the evolution of hominid hands and bipedality. See Else & Lee 1986, pp. 203–9

Marzke MW. 1997. Precision grips, hand morphology, and tools. *Am. J. Phys. Anthropol.* 102(1):91–110

Marzke MW, Marzke RF. 1987. The third metacarpal styloid process in humans: origin and function. *Am. J. Phys. Anthropol.* 73:415–31

Marzke MW, Shackley MS. 1986. Hominid hand use in the Pleistocene: evidence from experimental archaeology and comparative morphology. *J. Hum. Evol.* 15:439–60

Marzke MW, Wullstein KL, Viegas SF. 1992. Evolution of the power (“squeeze”) grip and its morphological correlates in hominids. *Am. J. Phys. Anthropol.* 89:283–98

McCollum M. 1999. Cladistics and early hominid phylogeny. *Science* 285:1211

McHenry H. 1991a. Femoral lengths and stature in Plio-Pleistocene hominids. *Am. J. Phys. Anthropol.* 85:149–58

McHenry HM. 1974. How large were the Australopithecines? *Am. J. Phys. Anthropol.* 40:329–40

McHenry HM. 1975a. Fossil hominid body weight and brain size. *Nature* 254:686–88

McHenry HM. 1975b. A new pelvic fragment from Swartkrans and the relationship between the robust and gracile australopithecines. *Am. J. Phys. Anthropol.* 43:245–62

McHenry HM. 1978. Fore- and hindlimb proportions in Plio-Pleistocene hominids. *Am. J. Phys. Anthropol.* 49:15–22

McHenry HM. 1983. The capitate of *Australopithecus afarensis* and *Australopithecus africanus*. *Am. J. Phys. Anthropol.* 62:187–98

McHenry HM. 1984. Relative cheek-tooth size in *Australopithecus*. *Am. J. Phys. Anthropol.* 64:297–306

McHenry HM. 1988. New estimates of body weights in early hominids and their significance to encephalization and megadontia in "robust" australopithecines. See Grine 1988, pp. 133–48

McHenry HM. 1991b. Petite bodies of the "robust" Australopithecines. *Am. J. Phys. Anthropol.* 86:445–54

McHenry HM. 1991c. Sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 20:21–32

McHenry HM. 1992a. Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 87:407–31

McHenry HM. 1992b. How big were early hominids? *Evol. Anthropol.* 1:15–19

McHenry HM. 1994a. Behavioral ecological implications of early hominid body size. *J. Hum. Evol.* 27:77–87

McHenry HM. 1994b. Early hominid postcrania: phylogeny and function. See Corruccini & Ciochon 1994, pp. 251–68

McHenry HM. 1994c. Tempo and mode in human evolution. *Proc. Natl. Acad. Sci. USA* 91:6780–86

McHenry HM. 1996. Sexual dimorphism in fossil hominids and its socioecological implications. In *The Archaeology of Human Ancestry Power, Sex, and Tradition*, ed. J Steele, S Shennan, pp. 91–109. London/New York: Routledge.

McHenry HM, Berger LR. 1998a. Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. *J. Hum. Evol.* 35(1):1–22

McHenry HM, Berger LR. 1998b. Limb lengths in *Australopithecus* and the origin of the genus *Homo*. *S. Afr. J. Sci.* 94:447–50

Napier JH. 1962. Fossil hand bones from Olduvai Gorge. *Nature* 196:409–11

Napier JR, Napier P. 1967. *A Handbook of Living Primates*. New York: Academic

Oxnard CE. 1972. Some African fossil foot bones; a note on the interpolation of fossils into a matrix of extant species. *Am. J. Phys. Anthropol.* 37:3–12

Oxnard CE, ed. 1973. *Form and Pattern in Human Evolution: Some Mathematical, Physical, and Engineering Approaches*. Chicago: Univ. Chicago Press

Oxnard CE. 1975. The place of the australopithecines in human evolution: grounds for doubt. *Nature* 258:389–95

Oxnard CE, Lisowski FP. 1978. The Olduvai foot. *Anat. Res.* 190:499–50

Roche H, Delagnes A, Brugal J-P, Feibel C, Kibunjia M, et al. 1999. Early hominid stone tool production and technical skill 2.34 myr ago in West Turkana, Kenya. *Nature* 399:57–60

Ruff C. 1995. Biomechanics of the hip and birth in early *Homo*. *Am. J. Phys. Anthropol.* 98(4):527–74

Ruff C. 1998. Evolution of the hominid hip. See Strasser et al 1998, pp. 449–69

Ruff CB, Trinkaus E, Holliday TW. 1998. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387:173–76

Ruff CB, Walker A. 1993. Body size and body shape. See Walker & Leakey 1993a, pp. 234–65

Schmid P. 1983. Eine Rekonstruktion des

skelettes von A.L. 288–1 (Hadar) und deren Konsequenzen. *Fol. Primatol.* 40:283–306

Schmid P. 1989. How different is Lucy? See Giacobini 1989, pp. 109–14

Schmid P. 1991. The trunk of the Australopithecines. See Coppens & Senut 1991, pp. 225–34

Semaw S, Renne P, Harris JWK, Feibel CS, Bernor RL, et al. 1997. 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* 385:333–36

Skelton RR, McHenry HM. 1992. Evolutionary relationships among early hominids. *J. Hum. Evol.* 23:309–49

Smith RJ. 1996. Biology and body size in human evolution: statistical inference misapplied. *Curr. Anthropol.* 37(3):451–60

Stern JT. 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis. Evol. Anthropol.* In press

Stern JT, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis. Am. J. Phys. Anthropol.* 60:279–318

Stern JT, Susman RL. 1991. "Total morphological pattern" versus the "magic trait": conflicting approaches to the study of early hominid bipedalism. See Coppens & Senut 1991, pp. 99–112

Strait DS, Grine FE. 1999. Cladistics and early hominid phylogeny. *Science* 285:1210

Strait DS, Grine FE, Moniz MA. 1997. A reappraisal of early hominid phylogeny. *J. Hum. Evol.* 32(1):17–82

Strasser E, Fleagle J, Rosenberger A, McHenry H, eds. 1998. *Primate Locomotion: Recent Advances.* New York: Plenum

Susman RL. 1988a. Hand of *Paranthropus robustus* from I, Swartkrans: fossil evidence for tool behavior. *Science* 240:781–82

Susman RL. 1988b. New postcranial fossils from Swartkrans Member 1: implications for the behavior of *Paranthropus robustus. Annu. Rev. Am. Assoc. Phys. Anthropol.* 75:77

Susman RL. 1988c. New postcranial remains from Swartkrans and their bearing on the functional morphology and behavior of *Paranthropus robustus.* See Grine 1988, pp. 149–74

Susman RL. 1989. New hominid fossils from the Swartkrans Formation (1979–1986 excavations): postcranial specimens. *Am. J. Phys. Anthropol.* 79:451–74

Susman RL. 1993. Hominid postcranial remains from Swartkrans. See Brain 1993, pp. 117–36

Susman RL. 1994. Fossil evidence for early hominid tool use. *Science* 265:1570–73

Susman RL. 1998. Hand function and tool behavior in early hominids. *J. Hum. Evol.* 35(1):23–46

Susman RL, Creel N. 1979. Functional and morphological affinities of the subadult hand (O.H. 7) from Olduvai Gorge. *Am. J. Phys. Anthropol.* 51:311–32

Susman RL, Stern JT. 1982. Functional morphology of *Homo habilis. Science* 217:931–34

Susman RL, Stern JT. 1991. Locomotor behavior of early hominids: epistemology and fossil evidence. See Coppens & Senut 1991, pp. 121–32

Susman RL, Stern JT, Jungers WL. 1984. Arboreality and bipedality in the Hadar hominids. *Fol. Primatol.* 43:113–56

Susman RL, Stern JT, Jungers WL. 1985. Locomotor adaptations in the Hadar hominids. In *Ancestors: The Hard Evidence,* ed. E Delson, pp. 184–92. New York: Liss

Suwa GB, Asfaw B, et al. 1997. The first skull of *Australopithecus boisei. Nature* 389:489–92

Tague RG, Lovejoy CO. 1986. The obstetric pelvis of A.L. 288–1 (Lucy). *J. Hum. Evol.* 15:237–55

Tardieu C. 1983. *L'articulation du genou. Analyse morpho-fonctionelle chez les primates et les hominides fossiles.* Paris: Cah. Paleoanthropol. 108 pp.

Tardieu C. 1986. Evolution of the knee intra-articular menisci in primates and some hominids. See Else & Lee 1986, pp. 183–90

Tardieu C. 1998. Short adolescence in early hominids: infantile and adolescent growth of the human femur. *Am. J. Phys. Anthropol.* 107(2):163–78

Tardieu C, Preuschoft H. 1996. Ontogeny of the knee joint in humans, great apes and fossil hominids: pelvi-femoral relationships during postnatal growth in humans. *Fol. Primatol.* 66:68–81

Tobias PV, ed. 1985. *Hominid Evolution: Past, Present and Future.* New York: Liss

Tobias PV. 1991. *Olduvai Gorge.* Vol. 4: *The Skulls, Endocasts and Teeth of Homo habilis*. Cambridge, UK: Cambridge Univ. Press

Tuttle RH. 1981. Evolution of hominid bipedalism and prehensile capabilities. *Philos. Trans. R. Soc. London Ser. B* 292:89–94

Tuttle RH. 1985. Ape footprints and Laetoli impressions: a response to SUNY claims. See Tobias 1985, pp. 129–34

Tuttle RH. 1987. Kinesiological inferences and evolutionary implications from Laetoli bipedal trails G-1,G-2/3 and A. In *Laetoli: A Pliocene Site in Northern Tanzania*, ed. MD Leakey, JM Harris, pp. 503– 23. Oxford, UK: Clarendon

Tuttle RH. 1988. What's new in African anthropology. *Annu. Rev. Anthropol.* 17:391–426

Tuttle RH. 1994. Up from electromyography: primate energetics and the evolution of human bipedalism. See Corruccini & Ciochon 1994, pp. 269–84

Tuttle RH, Hallgrimsson B, Stein T. 1998. Heel, squat, stand, stride: function and evolution of hominoid feet. See Strasser et al 1998, pp. 435–48

Tuttle RH, Webb DM, Baksh M. 1991a. Laetoli toes and *Australopithecus afarensis. Hum. Evol.* 6:193–200

Tuttle RH, Webb DM, Tuttle NI. 1991b. Laetoli footprint trails and the evolution of hominid bipedalism. See Coppens & Senut 1991, pp. 187–98

Tuttle RH, Webb DM, Tuttle NI, Baksh M. 1992. Footprints and gaits of bipedal apes, bears, and barefoot people: perspective on Pliocene tracks. In *Topics in Primatology*, ed. S Matano, RH Tuttle, H Ishida, M Goodman, 3:221–42. Tokyo: Univ. Tokyo Press

Walker A, Leakey R, eds. 1993a. *The Nariokotome Homo erectus Skeleton.* Cambridge, MA: Harvard Univ. Press

Walker A, Leakey R. 1993b. The postcranial bones. See Walker & Leakey 1993a, pp. 95–160

White TD. 1994. Ape and hominid limb length, reply. *Nature* 369:194

White TD, Suwa G. 1987. Hominid footprints at Laetoli: facts and interpretations. *Am. J. Phys. Anthropol.* 72:485–514

White TD, Suwa G, Hart WK, Walter RC, Wolde Gabriel G, et al. 1993. New discoveries of *Australopithecus* at Maka in Ethiopia. *Nature* 366:261–65

Wolpoff MH. 1999. *Paleoanthropology.* Boston: McGraw-Hill

Wood B, Collard M. 1999. The human genus. *Science* 284:65–71

Wood BA. 1974. Evidence on the locomotor pattern of *Homo* from early Pleistocene of Kenya. *Nature* 251:135–36

Wood BA, ed. 1991. *Koobi Fora Research Project IV: Hominid Cranial Remains From Koobi Fora.* Oxford, UK: Clarendon

Wood BA. 1992. Origin and evolution of the genus *Homo*. *Nature* 355:783–90