Climbing to the Top: A Personal Memoir of *Australopithecus afarensis*

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Last autumn marked the 25th anniversary of the discovery of "Lucy." While that certainly was a momentous event in paleoanthropology, it had no less profound an effect on my academic life, for it presaged my eventual seduction into the arena of hominid fossil interpretation. My friend John Fleagle, editor of Evolutionary Anthropology, says I may introduce this paper with a history of that experience. He assures me this is appropriate because I have now reached the age when young people in the field have no idea who I am.

DOWN THE GARDEN PATH

Just a few months before the A.L. 288-1 partial skeleton was found, I had seen the first published picture of the A.L. 129 knee.[1] It was obviously valgus, a trait expressed most markedly in bipedal hominids, and the discoverers described the morphology of the distal femur as "tres humaine." The following year yielded a published photograph of Lucy.[2] While it was difficult to discern from the picture what she would tell us about the origins of bipedalism, the authors commented that the pelvis had some similarities to that of Sts 14 (*Australopithecus africanus*), and that the knee bones were virtually identical to the A.L. 129 specimens. Like many other physical anthropologists, I looked forward to what future analyses of the Hadar finds would reveal. In January 1976 there appeared an abstract stating that the high bicondylar angle, deep patellar groove, and elliptical lateral femoral condyle of the A.L. 129 knee indicated mechanical features that characterize the modern human knee, including "the capacity of hyperextension."[3] The following year came the first abstract of potential interest for reconstructing Lucy's locomotor behavior.[4] It reported that "the degree of medial rotation of the tibia on the talus during dorsiflexion was 3 to 4 times greater than that of modern humans."

The 1979 meeting of the American Association of Physical Anthropologists contained a special session devoted to the Hadar finds. Owen Lovejoy[5] presented his reconstruction of the A.L. 288-1 pelvis, concluding that it "exhibits adaptation to full bipedality," and making special note of the broad iliac blade and the mechanically advantageous position of the anterior gluteals. That same year, Leakey and Hay[6] formally presented the discovery of the Laetoli hominid footprints, which they said evinced a "fully upright, bipedal and free striding gait." In 1980 Lovejoy's[7] abstract on the role of reproductive-behavioral adaptations in hominid evolution referred to the "fully developed adaptation to bipedality" of *A. afarensis,* and two analyses of the Laetoli footprints found them to be indicative of a modern human-like form of bipedalism.[8,9]

Meanwhile, other workers were making some rather different observations. While not disputing that the Hadar hominids were bipedal, Senut[10,11] noted traits of the upper limb (the narrow, deep intertubercular sulcus of the humerus, the well-developed lateral margin of the humeral trochlea, the relatively proximal origin of the lateral epicondyle of the humerus, the relatively distal position of the ulnar tuberosity, and the long and narrow neck of the radius) that were so similar to those of apes as to "signify a certain ability and possible propensity on the part of these hominids to climb trees."[11] Tardieu's[12,13] thorough analysis of the knee identified traits of the A.L. 129 and/or A.L. 288-1 specimens that suggested to her a shorter stride, less frequent total extension of the knee, absence of terminal locking rotation of the knee, and freer voluntary rotation of the tibia. These included modest development of the lateral lip of the patellar groove on the femur, an incipiently elliptical lateral femoral condyle, anteroposteriorly short femoral condyles, the relatively narrow anterior region of the medial femoral condyle, the incipient development of a human-shaped femoral intercondylar notch, narrowness of the tibial intercondylar eminence relative to the width of the femoral intercondylar notch, and the convex articular surface of the lateral tibial condyle. Tardieu concluded that the smaller of the Hadar hominids represented an early stage in the development of hominid bipedality and that it

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probably maintained a certain aptitude for arboreal locomotion.

This was the state of affairs in December 1980, six years after Lucy's discovery, when my colleague Randy Susman walked into my office to proclaim his opinion that we were as well qualified as anyone to perform a comprehensive functional analysis of the Hadar postcranial material. I immediately realized that Randy was half right. He further suggested that we should visit Ethiopia to look at the fossils. Not being able to find Ethiopia on a map of Long Island, I was reluctant, but eventually agreed. A trip was planned for the summer of 1981. Randy thought it would be wise to prepare for our study of the original fossils by taking a look at casts of the *A. afarensis* material in the Cleveland Museum of Natural History. Bill Jungers asked to come along so he could take some measurements of Lucy's body proportions. In May of 1981, the Stony Brook contingent of three arrived at the Cleveland Museum of Natural History, where Don Johanson graciously gave us complete access to all the casts of the Hadar material and the original specimen of the A.L. 333-115 foot. We collected many measurements, made extensive notes, and took numerous photographs, most of which were overexposed because Randy was not the excellent photographer he had claimed to be. (Randy redeemed himself on a 1992 visit to Addis during which he studied the original fossils and took fairly good pictures.) We left Cleveland with the tentative conclusion that the portrayals of *A. afarensis* locomotion by Senut and Tardieu were not far off the mark.

Although we did not learn so until several months later, it turned out that some of our observations we thought to be novel had also been made by Russell Tuttle.[14] While we were in Cleveland, he published a paper noting the markedly curved pedal proximal phalanges of Hadar foot specimens, the broad peroneal groove on the fibula, and somewhat laterally oriented iliac blades. Such features caused him to conclude that the Hadar hominids were rather recently derived from arboreal bipeds and may have engaged in a notable degree of tree climbing. Because Tuttle found the shapes of the Laetoli footprints to be indistinguishable from those made by striding humans who habitually go barefoot, he found it difficult to assign their maker to the same species as that represented by the A.L. 333-115 foot.

We arrived in Ethiopia in August of 1981. British Airways lost my luggage. I was not only anxious about being in a country that had street signs preaching the evils of Uncle Sam, but also was not adjusting well to having only one of each clothing item. (I absolutely refused Randy's offer to share his underwear.) To make a long story short, Randy and I were denied permission to look at the Hadar fossils and, while Randy was sleeping, I received a phone call from an Ethiopian government official advising us to leave the country immediately.

There is no real dispute that *A. afarensis* progressed bipedally when on the ground (but see Sarmiento for the sole contrasting view) nor that this was such an important part of its overall locomotor repertoire as to have engendered anatomic changes promoting its performance.

Upon our return, we decided to complete our work on reconstructing *A. afarensis* locomotor behavior using casts instead of original material. Don Johanson saw to it that the material we needed was sent to Stony Brook. As we were completing our analysis of the Hadar postcrania, Johanson's and Edey's[15] book *Lucy* was published. Here it was stated that the Hadar hominid was not a climber, despite having slightly long arms for its size, a tendency for the fingers to curl a bit more, some ape-like wrist bones, arched and relatively long pedal phalanges, and metatarsal heads having a shape intermediate between those of apes and humans. Rather, as shown by the pelvis, knee, hallux, and joints of the toes, *A. afarensis* was said to be a fully erect bipedal creature that could walk at least as well as a modern human, a conclusion said to be confirmed by the Laetoli footprints. Lucy's ability to run as fast as a modern human was considered debatable.

The April 1982 the issue of the American Journal of Physical Anthropology was devoted to detailed descriptions of the Hadar hominids, but it contained no functional interpretations of the postcranial material. That summer, Bill Jungers' paper on the proportions of Lucy's limbs was published.[16] He showed that Lucy's humerus, compared to that of a modern human, was not relatively long, but that her femur was relatively short. Bill concluded that Lucy's ability to climb was less than an ape's, and that her relatively short stride length suggested a greater cost and lower maximum speed of bipedal locomotion. In September 1982, Marc Feldesman published a multivariate study of distal humeral dimensions showing that the Hadar specimens are "quite primitive, and may be close to the point where hominids and pongids diverged."[17]

Mine and Randy's paper on the locomotor anatomy of *A. afarensis* was published in March of 1983.[18] One month later, three of us from Stony Brook went west to participate in Don Johanson's symposium on *A. afarensis* locomotion. There began a change in my career that I had not anticipated. Virtually overnight, I was transformed from an obscure electromyographer into someone being quoted in the New York Times and featured in Discover magazine. Over the course of the next few years, four separate television crews visited Stony Brook to tape us (mainly Randy) talking about the origin of bipedalism. I became alienated from Owen Lovejoy, a person whom I have always considered one of the most creative and insightful workers in our field. I became such a staunch advocate for one position that I am no longer certain of my objectivity.

TABLE 1. POSTCRANIAL TRAITS IDENTIFIED BY STERN AND SUSMAN,[18] JUNGERS AND STERN,[21] AND SUSMAN AND COWORKERS[22] AS DISTINGUISHING *A. AFARENSIS* FROM MODERN HUMANS

Relatively short hindlimb (A*, N**)
Relatively long foot (N)
Elongated, rod-shaped pisiform (A)
Finger metacarpals with large heads and bases relative to parallel-sided and somewhat curved shafts (A)
Finger proximal phalanges slender and markedly curved, with a bilateral expansion of shaft correlated with strong expression of flexor sheath ridges (A)
Trochleae of finger proximal phalanges subtend large angles and are deeply grooved (A)
Strong impressions for insertion of flexor digitorum superficialis on finger middle phalanges (A)
Glenoid cavity of scapula faces more superiorly (A)
Relatively larger moment arm of hamstrings (A, N)
Relatively wide tuberoacetabular sulcus (N)
Hamstring surface of ischial tuberosity makes a sharp angle to adductor magnus surface (N)
Absence of falciform crest on medial aspect of ischial tuberosity (N)
Ventral concavity of sacrum slightly developed (N)
Sacrum lacks well developed upper lateral angles (N)
Acetabular lunate articular surface has a diminutive anterior horn (N)
Absence of iliopubic eminence (N)
Iliac blades more coronally oriented (N)
Superior articular margin of femoral head runs from posterolateral to anteromedial (A)
Lateral lip of patellar groove weakly developed for degree of valgus at knee (N)
Medial femoral condyle wider than lateral condyle (N)
Distal articular surface of Lucy's tibia angled to face posteriorly (N)
Proximal margin of talar facet on fibula is oblique (A)
Peroneal groove on fibula is wide, deep, and has prominent medial lip (A)
Anterior limit of lateral margin of talar trochlea is extended distally (A)
Calcaneus has large peroneal trochlea and small lateral plantar process (N)
Hallucal tarsometatarsal joint is curved (A)
Head of hallucal metatarsal is mediolaterally very curved (A, N)
Lack of mediolateral widening of dorsal region of metatarsal heads (N)
Pedal proximal phalanges II-V are slender, relatively long (N), and markedly curved (A)
Pedal proximal phalanges II-V have bilateral expansion in region of well developed flexor sheath attachments (A)
Trochleae of pedal proximal phalanges II-IV subtend large angles (A)
Lack of dorsoplantar expansion at base of pedal proximal phalanges II-V (N)
Proximal phalanx of toe II is shorter than that of toe III (A)
Pedal middle phalanges are relatively long compared to proximal phalanges (A, N)
Laetoli footprints have small impression or none for ball of big toe (N)
Laetoli footprints show variable length of impressions for lateral toes (N)

*A = interpreted as being related to an arboreal component of behavior.
**N = interpreted as being related to a novel form of bipedalism

Sometimes I hope we will be proven wrong, just so I won't feel aggravated when I see a paper by Owen, Bruce Latimer, or Jim Ohman. But this desire quickly passes, as will soon become evident.

JACK OF TWO TRADES, MASTER OF NEITHER

There is no real dispute that *A. afarensis* progressed bipedally when on the ground (but see Sarmiento[19, 20] for the sole contrasting view) nor that this was such an important part of its overall locomotor repertoire as to have engendered anatomic changes promoting its performance. The chief evidence for these conclusions comprises the shortened ilium, the posterior displacement of its auricular surface relative to the acetabulum, the presence of an iliac pillar, and a high bicondylar angle of the femur. However, while acknowledging this, our papers[18,21–25] claimed that:

1. *A. afarensis* also possessed anatomic adaptations for movement in trees (Table 1 and Fig. 1).
2. Certain anatomic traits long thought to be diagnostic of a completely human-like form of bipedalism are not truly diagnostic of such behavior or are not actually present on Hadar specimens. These include an iliopsoas groove on the os coxae, an anterior inferior iliac spine, a femoral intertrochanteric line, an obturator externus groove on the femoral neck, and thin superior cortical bone coupled with thick inferior cortical bone in the femoral neck.
3. *A. afarensis* possessed anatomic traits suggesting that its bipedalism lacked human-like extension at the hip and knee during stance phase (Table 1 and Fig. 1), and that early in the stance phase of bipedal walking the lesser gluteal muscles controlled side-to-side balance at the hip by acting as medial rotators of the partly flexed thigh.[26] Even if these particular claims are incorrect, the relatively short lower limb and relatively long foot of *A. afarensis* point to an energetically more costly form of bipedalism[16,21] and a kinematically distinctive swing phase.[27]

At the same time or shortly after the publication of our earliest papers on *A. afarensis* locomotion, there appeared a spate of other contributions reporting a mosaic of human-like and ape-like features in its postcranial anatomy. Clearly, these were based on work that had been done simultaneously with or even before our own. Marzke,[28] analyzing bones and joints of the wrist, and McHenry,[29] focusing on the capitate, seemed willing to recognize the possibility of some degree of arboreality in *A. afarensis* locomotor behavior but were reluctant to actually draw this conclusion. Rose,[30] who made many of the same observations on the Hadar feet and hands that we did, showed no such reluctance, nor did Schmid,[31] who focused on the ribs and pelvis. Deloison's[32] study of the Hadar calcanei led her to state explicitly that *A. afarensis* bipedalism must have been distinct from that of modern humans. In contrast, Wolpoff,[33,34] challenging Jungers's[16] claim that Lucy's lower limb was shorter than expected for a diminutive human-like biped, drew a picture of *A. afarensis* as an efficient terrestrial biped that also made extensive use of arboreal resources. Berge[35–37] seemed to have a difficult time deciding on the functional significance of her multivariate osteometric study of the A.L. 288-1 and Sts 14 innominates. She interpreted the lateral orientation of the iliac blade, the proximity of the iliac pillar to the anterior edge of the bone, and the beaked form of the anterior superior iliac spine as pointing to a type of bipedal adaptation differing from that of modern humans. Furthermore, she stated that the smallness of the acetabulum, auricular surface, and the portion of the ilium just above the hip joint indicate a limited adaptation for weight bearing. Yet Berge also stated that gracile australopithecines were "as bipedal as *Homo*," with an equally effective lateral balance mechanism and pelvic proportions that in no way provide evidence for an arboreal adaptation. Finally, the formal publication of Tardieu's[38] thesis contained a new section reporting that the knee of *A. afarensis* was distinctly nonhuman by virtue of having only a single attachment of the lateral meniscus anterior to the external tibial spine. Tardieu[39,40] linked this trait to an enhanced range of lateral tibial rotation and said it would be useful if the foot were used as a prehensile organ.

From 1982 to 1985 there seemed to be a growing consensus that not only favored an adaptively important role for arboreality in the life of the Hadar hominids, but even recognized the possibility that their manner of bipedalism was recognizably different from that practiced by modern humans. Tardieu joined Senut in expressing the belief that both *Homo* and *Australopithecus* were represented at Hadar, and that the anatomy of the Hadar postcranial material indicated two different locomotor profiles, one human-like and one not. (More recently, Tardieu has attributed all the Hadar specimens to *A. afarensis* and makes no mention of a type with human-like locomotion.) In 1984, we expressed our opinion that there was one hominid species at Hadar and that all its members were distinctly nonhuman-like in locomotion, but that sexual dimorphism in the degree of arboreality was possible.[22]

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During this period only one abstract was published portraying the Hadar hominid as a fully developed biped.[41] It dealt with the foot, reporting that metatarsophalangeal joint conformations provide evidence of the extreme dorsiflexion that occurs during toe-off in a habitual biped. Curved proximal phalanges were dismissed as "an adaptive response to large dorsoplantar bending moments," prehension as exhibited in the modern ape foot not being part of the *A. afarensis* locomotor repertoire. Longitudinal and transverse bony arches were said to exist and to indicate a bipedal foot. The arches were short-lived, however, for analysis of the navicular and cuboid from Hadar published a year later indicated that "*A. afarensis* possessed a more mobile transverse tarsal joint, and probably a wider and flatter

Figure 1. Some of the traits identified in Table 1 as indicating that *A. afarensis* either possessed anatomic adaptations for movement in the trees or was not entirely human-like in its manner of terrestrial bipedality. A = *A. afarensis,* B = bonobo, C = chimpanzee, G = gorilla, H = human, O = orangutan. 1. Outline drawings of body shapes illustrating the relatively short lower limb of *A. afarensis.* 2. Side views of manual proximal phalanges from ray IV showing the marked curvature of this bone in *A. afarensis.* 3. Radial views of pisiform bones illustrating the rod-like nature of this bone in *A. afarensis.* 4. Ventral views of scapulae illustrating that the glenoid cavity faces more cranially in *A. afarensis.* 5. Lateral views of hip bones illustrating in the fossil the relatively wide tuberoacetabular sulcus (1), the relatively large distance from the center of the hip joint to the hamstring origin (2), the sharp angle between the area for origin of the hamstrings (2) and the area for origin of the adductor magnus (3), the absence of an iliopubic eminence (4), and the small size of the anterior horn of the acetabular lunate surface (5). 6. On the left, cranial views of sacra illustrating the poorly developed upper lateral angles in *A. afarensis;* on the right, side views of sacra illustrating the slight development of the ventral concavity in *A. afarensis.* 7. Cranial views of iliac crests illustrating the coronal orientation of the iliac blades in *A. afarensis.* 8. Distal views of femoral condyles illustrating that the patellar groove's lateral lip (arrow) is weakly developed in *A. afarensis.* 9. On top, lateral views of distal tibiae (anterior to the left, posterior to the right) illustrating that in Lucy (leftmost specimen, reversed for ease of comparison) the distal articular surface is inclined posteriorly; on bottom, medial views of distal fibulae (anterior to the right, posterior to the left, some specimens reversed for ease of comparison) illustrating the obliquity of the talar facet's proximal margin (arrow) in *A. afarensis.* 10. Dorsal views of hallucal metatarsals illustrating the marked mediolateral curvature of the head in *A. afarensis.* 11. Distal views of metatarsal heads from rays I-V (dorsal toward the top, ventral toward the bottom) illustrating the lack of mediolateral widening of the dorsal regions in *A. afarensis.* 12. Side views of pedal proximal phalanges from ray III illustrating the marked curvature of such bones in *A. afarensis.*

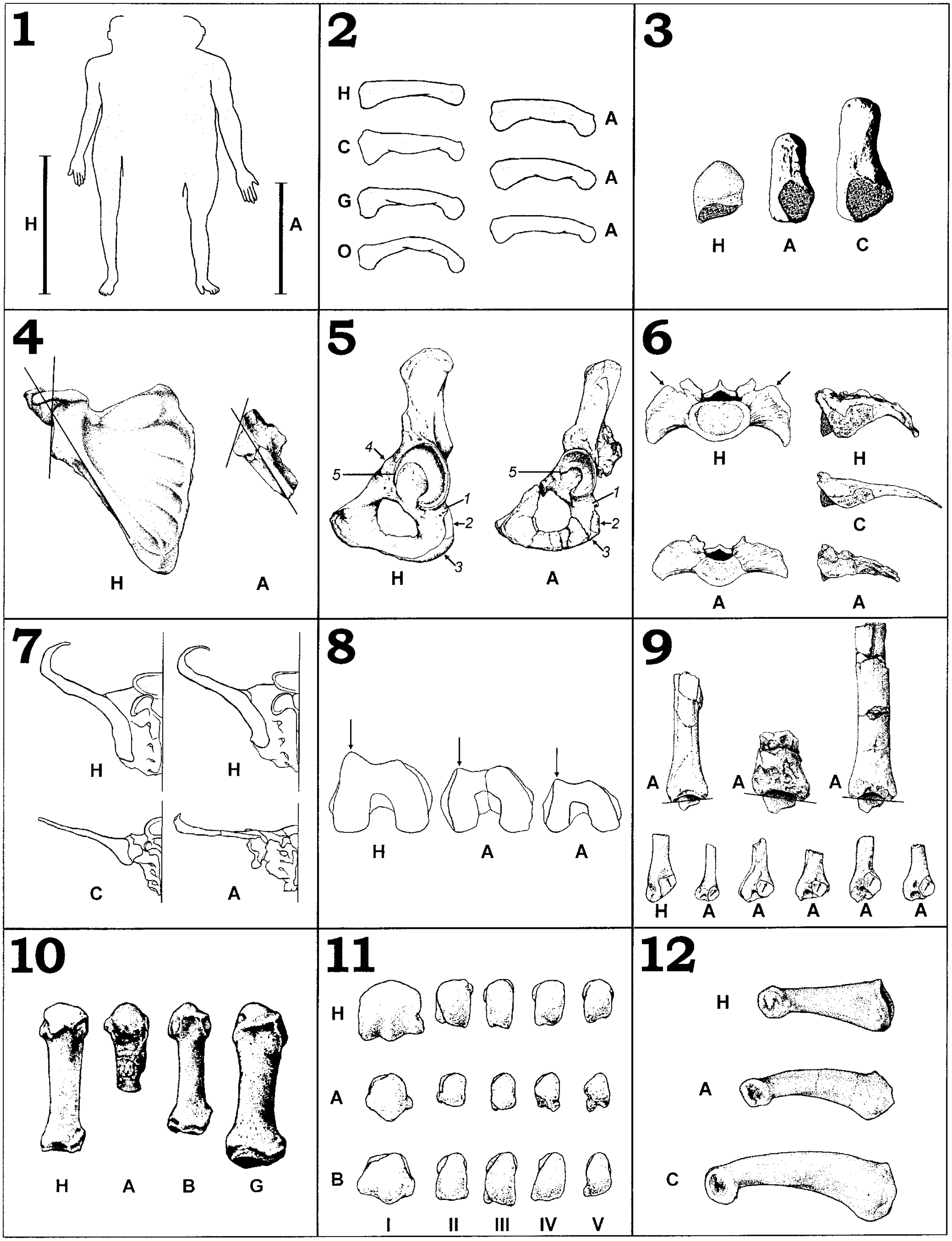
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Figure 1.

tarsus than is characteristic of the normal modern human foot.[42]

THE EMPIRE STRIKES BACK

Of course there really was no consensus that the positional behavior of *A. afarensis* was distinct from that of modern humans. The long-awaited response to such views was presented in a series of papers, largely emanating from Kent State University, between 1986 and 1990.[43–49] Table 2 lists and Figure 2 illustrates traits identified in these papers as proving the adaptive insignificance of arboreality in the life of *A. afarensis* and the human-like nature of its bipedality. Five of the seven papers were restricted to a consideration of the ankle and foot.

Many of the papers summarized in Table 2 contained suggestions to the effect that no significant adaptation to bipedalism can occur unless the commitment to this behavior is total. It was stated directly that hominoid arboreality is not to be viewed as a natural continuum and that arboreal capacity in early hominids should not be discussed in terms of "degrees" of adaptation.[44] A later contribution suggested that no selective advantage could accrue to an arboreal animal from any change that diminished its ability to climb.[50] Consequently, the presence of anatomic alterations for bipedalism that compromise climbing ability make it unlikely that arboreality remained adaptively significant. It was argued that if arboreality was adaptively significant for *A. afarensis,* its upper limb should have maintained, or even shown to a higher degree, all the features we have come to associate with pongid arboreality. In one way or another, the authors of all these papers agreed that "To suggest that *A. afarensis* still employed a significant degree of pongid-like arboreal behavior or that the stride pattern in this species included a 'primitive bent-hipped, bent-knee' gait (as has been recently suggested; see Stern and Susman, 1983; Susman et al., 1984) not only contradicts available anatomical evidence from the hip, knee, ankle, and foot but also completely contradicts the basic rudiments of neo-Darwinian theory."[47]

THE VIEW OF A CAST-OUT ANGEL

Can there be a home in neo-Darwinian heaven for those who do not believe the significance of derived traits overwhelms that of primitive traits for reconstructing the locomotor behavior of fossils? I have always had a simplistic way of looking at this issue. The whale ancestor *Ambulocetus* shows anatomic adaptations for aquatic locomotion that have clearly diminished its terrestrial expertise.[51] Still, no one has suggested that terrestrial behavior was adaptively insignificant for *Ambulocetus.* Why then conclude that arboreal behavior was adaptively insignificant for *A. afarensis* because its anatomic adaptations for bipedal locomotion diminished its arboreal expertise? Other authors have thought and written more insightfully on this problem as it relates to human evolution. Rose[30,52] envisions the adoption of terrestrial bipedalism by a human ancestor as a process in which the animal moves through a series of compromise morphologies. "For an animal with a compromise morphology each of the component activities of the [locomotor] repertoire is performed less energetically efficiently than it would be given optimal design . . . Although it is not maximally efficient, each activity within the repertoire is performed effectively, according to the purposes for which it was used."[52] Duncan and coworkers[53] stated that "Every species is composed of characteristics that reflect both its ancestry as well as its unique evolutionary pathway; understanding the overall functional pattern of the organism requires an equal consideration of all its anatomical features, regardless of whether they are apomorphies, plesiomorphies, or homoplasies. This viewpoint serves to frame the fossil as a once fully functional living organism." I am persuaded by these arguments. If you are not, then without further ado you should accept *A. afarensis* as a fully committed and human-like terrestrial biped. You may proceed directly to the Acknowledgments; do not pass GO, do not collect $200.

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JUST THE FACTS, MA'AM

Coffing[54] attributes much of the disagreement about reconstructing *A. afarensis* locomotor behavior to the previously mentioned differences in concepts of natural selection. However, it is also true that the opposing camps have doubted the accuracy, as well as the interpretation, of one another's data.

Possible Errors by Randy and Bill

1. Using an adult intraspecific regression line of scapular bar-glenoid angle (Fig. 1, part 4) versus glenoid length derived from 50 modern human scapulae, we predicted that a modern human of Lucy's size should have a bar-glenoid angle of 140 degrees, much greater than the 130 degrees observed in Lucy's scapula. Mensforth and coworkers[55] found our prediction to be in error. They reported that a similar analysis of 100 modern human scapulae yielded an expected value of ~130 degrees for the bar-glenoid angle of a Lucy-sized modern human scapula. More recently, Inouye and Shea[56] arrived at a value of 136 degrees, but pointed out that low correlations, together with the practice of extrapolating to a size below that found in one's modern sample, make any such estimate worthless. When Inouye and Shea included subadult human scapulae in their sample, the range of bar-glenoid angles encompassed Lucy's value, and the human regression line virtually ran through 130 degrees. (It appears from their graphs that Inouye and Shea used 2.25 cm, the value we reported, for Lucy's glenoid length. However, we did not include the supraglenoid tubercle in our measure-

TABLE 2. TRAITS SAID TO INDICATE HUMAN-LIKE BIPEDALITY AND ADAPTIVE INSIGNIFICANCE OF ARBOREALITY IN *A. AFARENSIS*

The head of the first rib articulates with the body of only the T1 vertebra.[43] (I)
The deltoid muscle marking on the clavicle faces anteriorly.[43] (I)
The supratalar joint space is nearly perpendicular to the long axis of the tibia.[44] (I, H)
The flexion-extension axis of the talocrural joint is oriented so that there is little conjunct axial rotation of the tibia during flexion-extension movements at the ankle.[44] (I)
The Laetoli footprints have a fundamentally human-like total morphological pattern.[45] (H)
The ilia of Lucy are bent around to provide lateral attachment for the lesser gluteal muscles.[46] (H)
The attachment points and dispositions of the gluteus maximus and quadriceps are human-like.[46] (H)
An iliopsoas groove is present on the pelvis.[46, 68] (H)
The hip abductors have a mechanical advantage surpassing that of the hip abductors in modern humans.[46] (H)
The foot has a shock-absorbing arch.[46] (H)
The upper limbs and fingers are relatively shorter than those of apes.[46] (I)
The inferolateral corner of the calcaneal corpus is expanded and a clearly defined lateral plantar process is present.[47] (H)
The posterior talar facet of the calcaneus is less convex and more vertically oriented than is that in apes.[47] (I, H)
The distal articular surface of the Hadar medial cuneiform faces more directly distally than does that in apes.[48] (I)
The proximal articular surface of the hallucal metatarsal is virtually divided into two separate facets by a slight transverse ridge.[48] (I)
The distal location of the "sub-bursal groove" for the tendon of tibialis anterior on the medial surface of the medial cuneiform is human-like.[48] (I)
The heads of metatarsals are inflated and angled dorsally.[49] (H)
The proximal articular surfaces of the pedal proximal phalanges are more superiorly oriented than are those of apes.[49] (H)
The superior cortical bone of the femoral neck is thin.[46] (I, H)

*I = interpreted as showing insignificance of arboreal behavior.
**H = interpreted as showing human-like bipedalism

ment, whereas they reported doing so for all their specimens of extant species. The measurement of Lucy's glenoid length including the supraglenoid tubercle is 2.57 cm. If Inouye and Shea had used this value, they would have predicted a bar-glenoid angle for a Lucy-sized human of 137.5 degrees using the adult human regression line and one of 132 degrees using the ontogenetic human regression line.)

If the approach used by Inouye and Shea is appropriate for assessing the significance of Lucy's cranially directed glenoid cavity, then this trait no longer belongs on the list of characters suggesting arboreality. In accepting this possibility, I am being far more generous than Bill Jungers, who has conveyed to me his conviction that it is incorrect to apply an ontogenetic allometric trend to answer a question concerning the shape of a small adult. He is now scouring museums for a few adult human scapulae as small as Lucy's.

2. We asserted that the superior border of the articular margin of Lucy's femoral head exhibited a disposition found in apes but not in humans. We said this disposition was compatible with a greater range of abduction than occurs in modern humans. Asfaw,[57] using a much larger sample than ours, found the "ape-like" condition in 9% of human individuals. MacLatchy[58] showed that if the neutral posture of the femur is assumed to occur when the fovea capitis is centered in the acetabular fossa, the neutral position of Lucy's thigh was more adducted than that of modern humans. Furthermore, despite the fact that the lunate surface of Lucy's acetabulum was restricted dorsally and cranially relative to the acetabulum of modern humans, this difference was insufficient to allow greater abduction of the thigh.

These two studies cause me to doubt greatly the significance of our observations on the articular surface of Lucy's femoral head. Nonetheless, I wish to point out that limitation of hip abduction in modern humans is probably due to passive tension in the stretched adductor muscles. Although I am almost totally sedentary, I am able to abduct my extended thigh 40 to 50 degrees and my flexed thigh 50 to 60 degrees. Observations of gymnasts lead me to conclude that people who stretch their adductor muscles can abduct the thigh at least 90 degrees. So the question about the abductibility of the *A. afarensis* hindlimb is really a question of the rest-length of its hip adductors, which we will never know.

3. Tuttle described our statements on the Laetoli footprints as an example of "haste making paleontological waste."[59] He claimed that the chimpanzee footprints described by Manter and Elftman[60] and those produced by our own "incarcerated" chimpanzees[18] were atypical by having a somewhat adducted hallux and partially curled lateral toes. He also found that traits we identified as characteristic of modern human footprints are in fact commonly absent. White and Suwa[45] agreed, adding that we had incorrectly interpreted the footprint surface at Laetoli. We did not respond, but Deloison's[61] comparison of Laetoli footprints to those of chimpanzees and modern humans found the fossil pattern to be characterized by, among other things, a narrow impression for the heel, a depression likely to be caused by a large abductor hallucis, a partly abducted big toe, and folded lateral toes. Deloison concluded that the overall form was more similar to that of a chimpanzee than that of a human. The definitive word on the subject has yet to be uttered.

4. We asserted that the relatively long toes of *A. afarensis* were compatible with use of the foot for some kind of prehension in trees, and would also have increased the length of the foot in a way that would have affected the kinematics of bipedal swing phase. White and Suwa[45] reconstructed the length of Lucy's foot, finding the

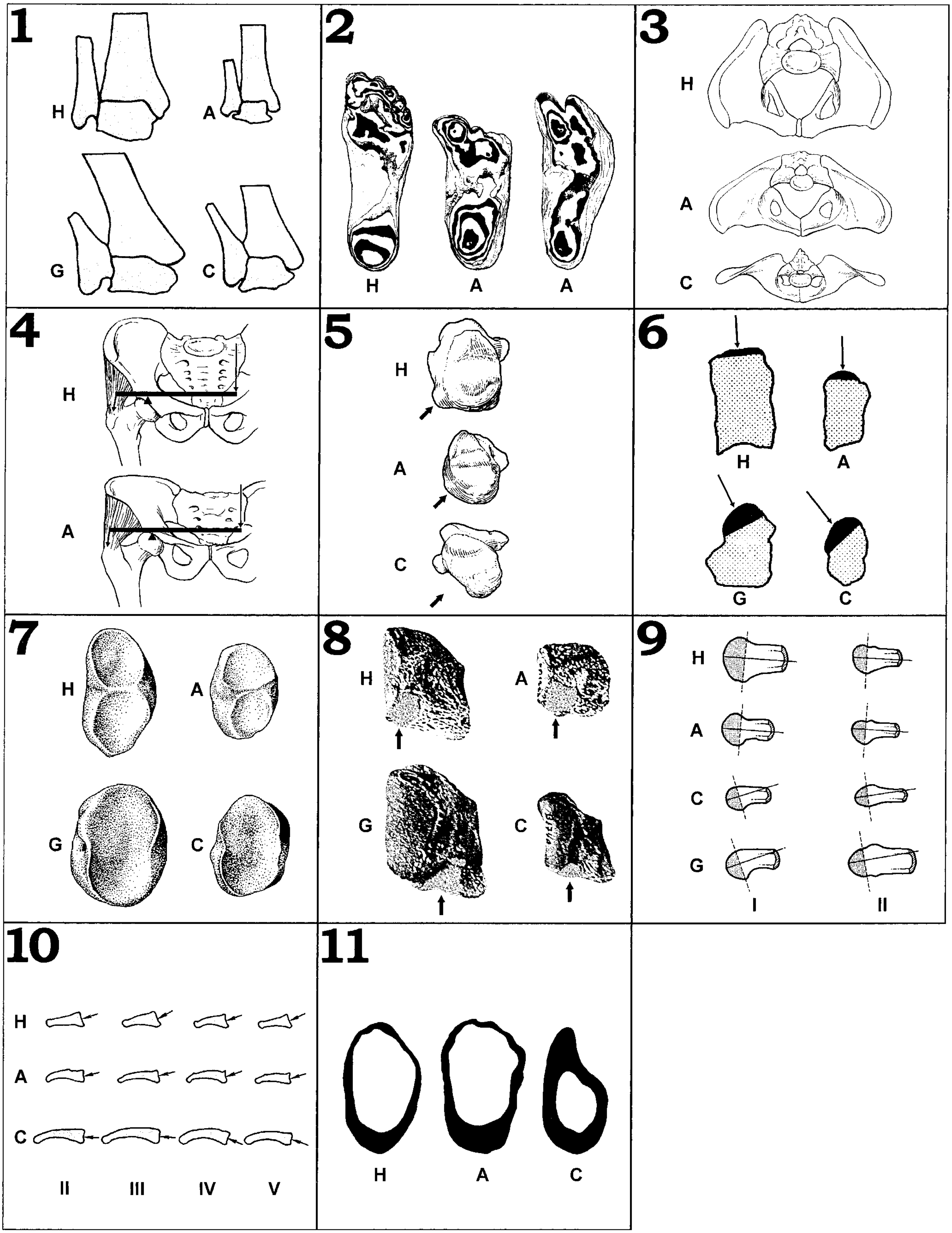
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Figure 2.

length of her toes relative to the rest of the foot to be halfway between that of a human and a gorilla, and 45% to 50% longer than that of the average human. Nonetheless, the authors claimed that the ratio of total foot length to femur length for Lucy was at the upper end of the modern human range of variation and, therefore, of minimal consequence for her manner of bipedalism. Latimer and Lovejoy[48] compared the length of Lucy's proximal pedal phalanx to four other postcranial measures and, despite its position intermediate between gorilla and human, concluded that the fossil toe was not particularly long. We had previously published two of the same comparisons[18,22] and, with very similar numbers, came to a quite different conclusion. Lucy's toes were probably as long as the fingers of a two-year old human. The lengths of the phalanges in the A.L. 333-115 foot are comparable to those in the hands of children between the ages of nine and ten years.[62] The real question seems to be how long is "particularly" long?

5. Our use of the superior edge of the talar facet on the fibula (Fig. 1, part 9) to judge the range and set of plantarflexion at the ankle was said to be inaccurate because "talofibular joint congruence cannot be reliably assessed."[44] Latimer and colleagues[44] found no indication of a greater plantarflexion range in Lucy when they manipulated her tibia upon her talus. On the other hand, when applied to chimpanzee bones, their method did not reveal the greater range of plantarflexion that we demonstrated by radiographic images of living animals.[22] My conclusion is that there is something very different about the talar facet of Hadar fibulae, but that we have not proven its functional significance.

6. Our comments on the size of the large peroneal trochlea and its relation to the lateral plantar process were described as inexplicable, inaccurate, and implausible.[47] While I admire the alliteration, I must point out that our assessment of the sizes of these bony bumps is fully concordant with that of Deloison.[32,63]

7. Whereas Wolpoff[33,34] criticized Jungers[16] for concluding that Lucy's lower limb was relatively short, and we responded with further evidence to support this contention,[21] Kramer[64] has recently published a mathematical simulation of Lucy's bipedalism purporting to show that Lucy was not energetically compromised by her short legs: "On a mass specific basis, the configuration developed from the fossil remains of AL 288-1 uses less energy to move than, and has the same cost of transport as, the modern human configuration." The assumptions underlying Kramer's conclusion are that Lucy had the same movement profile as a modern human, that the masses of Lucy's lower limb segments were proportionally the same as in a modern human, and that it is most appropriate to compare energy use of the two species when Lucy is walking at about 80% of the speed of a modern human.

If Lucy really had the same movement profile as a modern human, this alone would cause me, but not my colleagues, to classify her as a human-like biped regardless of energetic cost. Therefore, it is of little moment to me if the calculation of energy-use based on Kramer's assumptions is correct or not. For me, the issue is the implausibility of the assumptions. Furthermore, knowing that mathematical simulations are often highly dependent on the values of input parameters, it is troublesome that Kramer uses values for Lucy's segment masses and moments of inertia that are substantially different from the estimates provided by Crompton and coworkers.[65]

Latimer and Lovejoy compared the length of Lucy's proximal pedal phalanx to four other postcranial measures and, despite its position intermediate between gorilla and human, concluded that the fossil toe was not particularly long. We had previously published two of the same comparisons and, with very similar numbers, came to a quite different conclusion.

Do Unto Others As They Have Done Unto You

Those of you familiar with the history of the dispute about the locomo-

Figure 2. Some of the traits identified in Table 2 as indicating human-like bipedality and the adaptive insignificance of arboreality in *A. afarensis.* A = *A. afarensis,* C = chimpanzee, G = gorilla, H = human. All drawings are modified from originals that appeared in the indicated references. 1. Outline tracings from midcoronally sectioned casts of ankle joints illustrating that the supratalar joint space is nearly perpendicular to the long axis of the tibia in humans and *A. afarensis.*[44] 2. Contour maps of footprints said to illustrate the fundamentally human-like pattern of the Laetoli footprints. 3. Cranial views of pelves said to illustrate that the ilia of Lucy are bent around to provide lateral attachment for the lesser gluteal muscles.[46] 4. Anterior views of hip joints and pelves said to illustrate that the hip abductors of *A. afarensis* have a mechanical advantage surpassing that of the hip abductors in modern humans.[46] 5. Posterior views of left calcanei illustrating that the calcaneal corpus' inferolateral corner (arrow) is expanded and said to possess a clearly defined lateral plantar process.[47] 6. Transverse sections of right medial cuneiforms illustrating that in *A. afarensis* the distal articular surface faces more directly distally than it does in apes.[48] 7. Proximal articular surfaces of left hallucal metatarsals said to illustrate that this surface is virtually divided into two separate facets by a slight transverse ridge in both humans and *A. afarensis.*[48] 8. Medial views of right medial cuneiforms illustrating the human-like distal location of the "sub-bursal groove" (arrow) for the tendon of tibialis anterior.[48] 9. Outline tracings of midsagittally sectioned casts of the first and second metatarsal heads said to illustrate that they are inflated and angled dorsally in both humans and *A. afarensis.*[49] 10. Outline tracings of midsagittally sectioned casts of pedal proximal phalanges said to illustrate that in *A. afarensis* the proximal articular surfaces are more superiorly oriented than in apes.[49] 11. Drawings of the femoral neck's cortical bone seen on transverse sections (superior to the top) illustrating that the superior cortical bone of the femoral neck is thin in humans and *A. afarensis.*[46]

tor behavior of *A. afarensis* know that we did not respond to criticism of our work by turning the other cheek. We, and sometimes other authors, claimed to have found the following flaws in the works of Latimer, Lovejoy, and Ohman.

1. Bill Jungers and I[66] said that Ohman's[43] claim about the uniqueness of the univertebral articulation of the human first rib was untrue. Schmid[67] pointed out that Ohman's description of Lucy's first rib as having only one facet on its head was contradicted by Johanson and coworkers,[68] who said it had a distinct double facet separated by a central ridge. Schmid also noted that the Johanson and coworkers reported Lucy's clavicle as having a rounded superior surface presenting a roughened area for the attachment of the deltoid, whereas Ohman said it had the hominid condition of a deltoid attachment at the anterior edge of the bone. In the disagreements between Ohman and Johanson and coworkers, I do not know who is correct.

2. The calculation by Latimer and coworkers[44] that conjunct rotation of the tibia during flexion or extension movements of the ankle would have been minimal in Lucy directly contradicts the results reported by Christie,[4] which were based on manipulating the specimens.

3. Lovejoy's[46] assertion that the ilia of Lucy are bent around to provide lateral attachment for the lesser gluteal muscles to act as abductors (Fig. 2, part 3) is the opposite of what we[18] and Schmid[67] claim (Fig. 1, part 7).

4. The statement that the attachment points of the gluteus maximus and quadriceps femoris in Lucy indicate that they were as big as our own and similarly disposed[46] is unsupported by evidence.

5. Statements that an iliopsoas groove is present on Lucy's pelvis[46,68] are contrary to our observations.[18]

6. Lovejoy[46] stated that the greater outward flare of Lucy's ilia, coupled with a relatively long femoral neck, gave her abductors such a big moment arm that, despite the slightly greater interacetabular distance, they had a mechanical advantage surpassing our own (Fig. 2, part 4), resulting in reduced hip joint pressure. This was disproved by Jungers[25] and Ruff.[69] Indeed, Ruff's analysis showed that if Lucy had walked as modern humans do, she would be expected to have a relatively larger acetabulocristal buttress, larger femoral head, and greater resistance of the femoral shaft to mediolateral bending than do humans. She does not.

7. We have already published[70] some of our complaints regarding the analysis of the Hadar calcanei conducted by Latimer and Lovejoy.[47] We pointed out temporal inconsistencies in their descriptions of the lateral plantar process (it grew to more human proportions from early to later papers) and their failure to include the ape-like A.L. 333-37 specimen when calculating cross-sectional areas of the calcaneal tuber.

There may also be a problem regarding their assessments of posterior talar facet curvatures in the fossil calcanei. The authors calculated the included angle of this facet to be 82 degrees for the A.L. 333-8 specimen (the lower the value of included angle, the flatter is the surface). Such a value is close to the mean of 78.5 degrees they report for humans and far from means they found in African apes (gorilla = 100 degrees, chimpanzee = 110 degrees). On the other hand, Deloison,[32] who calculated an undefined "index of curvature" of the same facet, found that the value in the fossil fell within the normal range of chimpanzees and outside that of modern humans.

Latimer and Lovejoy[47] stated that damage to the A.L. 333-55 calcaneus precluded reliable measurement of the included angle of its posterior talar facet, but they did offer an estimate of its radius of curvature equal to the value of 24.5 mm for A.L. 333-8 (the higher the value of radius of curvature, the flatter is the surface). Indeed, in A.L. 333-55, the facet is crossed by a longitudinal crack, but Latimer and associates[71] previously assured us that "owing to good apposition it is of no metric consequence." Using a cast of the specimen, I calculated the A.L. 333-55 posterior talar facet radius of curvature to be 16 mm and its included angle to be 96 degrees. Such values are concordant with Deloison's assessment of the better preserved A.L. 333-8 specimen.

8. The identification of the tibialis anterior "facet" on the Hadar medial cuneiform as being human-like in position and orientation[48] (Fig. 2, part 8) has been challenged by Deloison,[72] who found this structure to be so variable in both humans and chimpanzees as to preclude any conclusion about affinities of the fossil.

9. Latimer and Lovejoy[48] described the proximal articular facet of the A.L. 333-54 hallucal metatarsal as having indentations in both its medial and lateral edges (Fig. 2, part 7). They say this conformation was not found in their sample of African apes but is common in humans. Deloison[63] described the facet in chimpanzees as being bilaterally constricted, but that in humans as reniform. She concluded that the similarity is between the fossil and apes. Furthermore, she found both regions of the fossil's proximal articular surface to be concave, with radii of curvatures that match those in chimpanzees.[61]

10. The statement that in *A. afarensis* the proximal articular surfaces of the pedal proximal phalanges have the degree of superior orientation found in modern humans[48] (Fig. 2, part 10) has been shown to be incorrect by Duncan and coworkers,[53] whose quantitative analysis proved that the orientation in the fossils is intermediate between that in humans and African apes.

11. Duncan and colleagues[53] pointed out inaccuracies in the statement that the metatarsal heads of *A. afarensis* are angled dorsally as in humans, but not pongids[48] (Fig. 2, part 9). The same authors could not duplicate Latimer's and Lovejoy's results on metatarso-phalangeal joint excursion and suggested that the method used was unreliable.

12. Susman and I[23] disputed the statement that the thin superior cortical bone of the femoral neck in Hadar femora is a trait aligning them with humans and distinguishing them from arboreal primates[46] (Fig. 2, part 11). I have to admit that of all the traits said to align the fossil with humans and push it away from apes, this was the one that gave me the most concern that we might be wrong. I

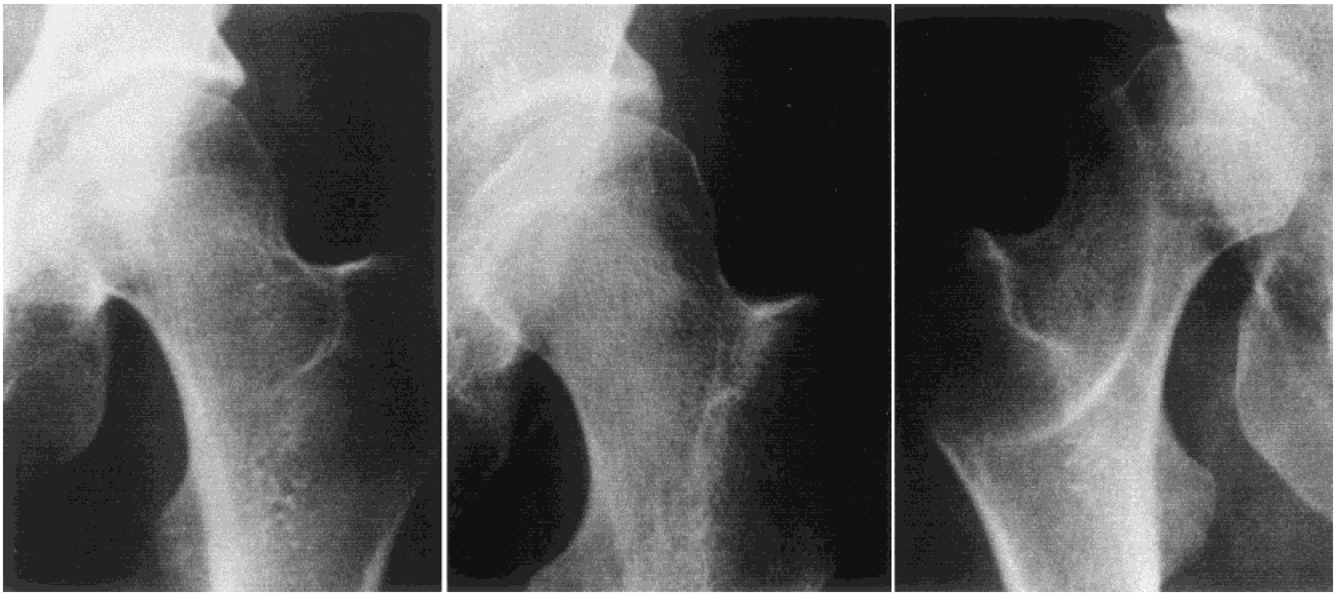

Figure 3. Radiographs of the hips of three ambulatory cerebral palsy patients.[76] Despite the fact that such patients walk with abnormal flexion at the hips and knees, two of the radiograghs (leftmost and rightmost) show a pattern of thin bone in the superior cortex of the femoral neck and thick bone in the inferior cortex. The resemblance of this pattern to that in people with normal gait suggests that the determinants of cortical bone distribution in the femoral neck have yet to be determined with sufficient precision to enable its use in the reconstruction of bipedal kinematics. (Reproduced with permission of C. B. Howard and W. B. Saunders Co. Ltd.)

have always been impressed by Pauwels'[73] explanation of why humans have this trait. Nonetheless, not knowing the condition in apes, Randy and I determined to see what comparable sections through human and nonhuman primate femoral necks would show. We did an extremely cursory job, looking only at one specimen each of *Homo, P. troglodytes, P. paniscus, Gorilla, Symphalangus,* and *Ateles*. All we could say was that most of the nonhuman primates in our sample also had thinner cortical bone on the superior aspect of the femoral neck than on its inferior aspect. We didn't quantify our results, and I expected that had we done so humans would have been at the extreme of the primate range, joined there by the A.L. 128-1 proximal femur and probably some other fossil specimens of the same period. Indeed, my fears were justified, for a few years later Ohman and coworkers[74] seemed to have demonstrated precisely this point in their thorough quantitative comparison of humans and African apes. My only solace was the authors' concession that the trait no longer precluded arboreal behavior, but simply demonstrated that such behavior could only have been an insignificant component of the *A. afarensis* locomotor repertoire. Then along came a paper by Rafferty,[75] who extended the analysis of femoral neck structure to cercopithecoids and strepsirhines. She found the distribution of cortical bone in the femoral necks of these two groups, most species of which are predominantly arboreal, to be similar to that in humans. It seems that apes and atelines are unusual in having a more even distribution of cortical bone around the femoral neck. Rafferty surmised that this more even distribution was linked to the less stereotyped locomotor behavior of a climber-clamberer. So one conclusion would have to be that *A. afarensis* was not a pongid-like or ateline-like climber-clamberer. I feel comfortable with that view. I also believe that much is yet to be learned about what determines the distribution of cortical bone in the femoral neck. After all, radiographs of cerebral palsy patients, who walk with limited extension of the hip, appear to illustrate the same general pattern of femoral neck bone distribution as that found in people who walk normally[76] (Fig. 3).

IS THERE HOPE FOR RESOLUTION?

I imagine that the scenario of argument and counterargument has become tiresome to many noncombatants. What hope is there for resolving the debate on *A. afarensis* locomotion? Maybe the answer lies in some truly novel ideas and data that have emerged in the last several years.

New Ideas About Old *Afarensis* Material

Rak,[77] accepting the notion that the sagittal plane excursions of Lucy's limbs were the same as those in modern humans, proposed a difference between Lucy's and modern humans' manners of walking with regard to rotation of the pelvis around a vertical axis. He suggested that Lucy's wide pelvis and long femoral neck enabled her to have a human-like stride length without suffering an increase in vertical excursion of the center of mass that would otherwise occur because of her short lower limbs. According to Rak, an increase in vertical excursion of the center of mass would have brought about both an increased cost of locomotion and increased joint reaction forces.

I am concerned that the relationships among energy cost, vertical excursion of the center of mass, and pelvic rotation are not as simple as Rak suggests. While it is true that for modern humans faster walking speeds are associated with longer strides and greater vertical oscillations of the center of mass,[78] for any speed there is an optimal stride length that minimizes energy cost.[79,80] At shorter stride lengths there will be less vertical oscillation but greater energy expenditure. When walking normally at any speed, we could always force ourselves to rotate the pelvis more in order to decrease the extent of center-of-mass fall, but we do not do so.[78] I presume there is an energy cost associated with pelvic rotation and that adopting more than is customary would offset any savings afforded by a reduced vertical oscillation of the center of mass. Nevertheless, if Rak's idea is correct, it would certainly mean that Lucy's gait would look different from that of a modern human even to a casual observer, though in a way far different than we suggested.

Berge[81–83] attempted to reconstruct the lines of action of muscles about the hip joint in A.L. 288-1, in one case assuming a human-like morphology and in another an ape-like disposition. She concluded that the ape-like disposition would actually have enabled Lucy to be a better biped. However, she stated that because extensors of the thigh in A.L. 288-1 had relatively longer moment arms than do those of humans, these muscles would have been more powerful in their ability to move the hip than to stabilize it. Berge further concluded that stability at the hip and knee in the coronal plane required a sort of waddling gait with large axial rotatory movements of the pelvis and counter-rotations of the shoulders, entailing a greater energy cost. Finally, her estimates of muscle torques led Berge to conclude that *A. afarensis* had a greater ability than humans do to move their lower limbs in different spatial positions, thereby promoting arboreal capability.

I have already mentioned Ruff's[69] demonstration that Lucy lacked certain osteologic traits expected to be present had she walked as do modern humans. Ruff concluded that Lucy may have walked bipedally in a way that allowed her trunk center of gravity to lie closer to a vertical line through the support-side hip joint. He suggested this could be accomplished if she laterally flexed her trunk toward the support side and elevated her pelvis on the nonsupport side. He likened this to the gait of a human with bilaterally painful hip joints because such individuals and Lucy would both have the goal of reducing hip joint reaction force.

I presume there is an energy cost associated with pelvic rotation and that adopting more than is customary would offset any savings afforded by a reduced vertical oscillation of the center of mass. Nevertheless, if Rak's idea is correct, it would certainly mean that Lucy's gait would look different from that of a modern human even to a casual observer, though in a way far different than we suggested.

Actually, the citation Ruff offered in support of this analogy provides a somewhat erroneous analysis of the gait of patients with a painful hip. It is true that during stance phase on the painful side, lateral lurch of the trunk toward that side is apparent,[84,85] but the majority of such patients exhibit a descent, not an elevation, of the pelvis on the nonsupport side.[84] Contralateral pelvic elevation could only be effective in reducing support-side hip joint force if it were brought about using muscles of the trunk. Use of support-side lesser gluteal muscles to accomplish this elevation would actually cause an increase in the hip joint reaction force. In this regard it is interesting to note that Schmid's[67] interpretation of Lucy's iliac blade orientation emphasizes increase in leverage of lateral flexors of the trunk.

Ruff also says that lateral trunk flexion and contralateral pelvic elevation probably characterize chimpanzee bipedalism, an assertion confirmed by the work of Tardieu.[86] Ruff's conclusion that Lucy's bipedal walking was less energetically efficient than that of modern humans is consistent with the view that although Lucy was a facultative biped, she probably was not a long-distance traveler.

Recently Ruff and colleagues[87] have drawn attention to the fact that Lucy and several other australopithecines have very robust femoral shafts relative to femoral head size. They concluded that overall mechanical loading of the skeleton was increased in these ancient hominids to about the same level as in modern African apes. As I read such statements, I wonder how this analysis of cortical stress would have been affected had Ruff not assumed full extension of the thigh during the support phase. Maybe walking with a less than fully extended hip and knee would necessitate relatively robust femoral shafts, but I am not smart enough to solve this problem.

Speaking of walking with a less than completely extended hip and knee, Crompton and coworkers[65] claim that their mathematical simulations of Lucy's bipedalism, bolstered by preliminary experimental data on humans, show that bent-hip, bent-knee gait is mechanically ineffective and likely to produce a rapid, large rise in core body temperature. My own response[88] to these arguments is that although bent-hip, bent-knee gait is more energetically costly than normal human bipedal walking, the cost is not as large as might be imagined and would not be prohibitive in an animal that used its bipedalism primarily as a feeding adaptation.[30,52,89,90] My reading of the relevant physiological literature has convinced me that such a mode of locomotion would be no more likely to result in an increased body temperature than would any other activity of comparable energetic cost. It is also worth mentioning that Schmitt and colleagues[91,92] have gathered force-plate and accelerometer data showing that the energetic disadvantage of bent-hip, bent-knee walking might be compensated for by an advantage in terms of joint-force reduction.

Some interesting functional analyses relating to vertebral morphology have been published in the last few years. Abitbol[93] argued that if Lucy had walked in the completely upright manner of a modern human, the superior surface of her sacrum would have been inclined only 20° from vertical as compared to an average of 60° in modern humans. Such a near-vertical superior sacral surface would require a truly extraordinary amount of lumbar lordosis to bring the trunk upright, and would place Lucy at great risk of spondylolisthesis. Abitbol suggested that Lucy would have walked either with her pelvis tilted backward or her trunk tilted forward, or a combination of both. Sanders[94] has recently published a functional analysis of two *A. afarensis* lumbar vertebrae (both probably L3) and the superior articular facets of Lucy's sacrum. One of the *A. afarensis* lumbar vertebrae is dorsally wedged, indicating lumbar lordosis; the other is not. The superior articular facets of the sacrum are relatively widely spaced, as in humans, and are relatively large, even larger than those of humans. Maybe such traits reflect a need to resist a relatively greater tendency toward spondylolisthesis.

Some fascinating new data on bony development in primates are quite relevant to an interpretation of *A. afarensis* locomotion. Responding to the notion that the curved fingers of *A. afarensis* might be primitive retentions that tell us little about actual use of the hand,[95] Paciulli[96] and Richmond[97,98] demonstrated a correlation between ontogenetic changes in phalangeal curvature and those in locomotor behavior for macaques, gibbons, chimpanzees, and gorillas. Richmond[98] concluded that "The sensitivity of phalangeal curvature to functional use in extant primates suggests that it faithfully reflects arboreal use in early hominids."

A second developmental study, this one on the distal femoral epiphysis of humans and apes, was undertaken by Christine Tardieu, no stranger to the debate on *A. afarensis* locomotion. Some of what she discovered runs counter to her own stated views. Tardieu observed that in juvenile humans the opposing surfaces of the distal femoral metaphysis and epiphysis are nearly flat, whereas in young apes these surfaces are characterized by interdigitating grooves and ridges. With respect to both characteristics, the immature Hadar femora match the human condition. Tardieu and Preuschoft[99] have interpreted the pongid state as being necessary for stabilization of the epiphysis during arboreal activities. If this is true, it is potent evidence against the practice of such activities by juvenile *A. afarensis*.

Some fascinating new data on bony development in primates are quite relevant to an interpretation of A. afarensis locomotion. Responding to the notion that the curved fingers of *A. afarensis* might be primitive retentions that tell us little about actual use of the hand, Paciulli and Richmond demonstrated a correlation between ontogenetic changes in phalangeal curvature and those in locomotor behavior for macaques, gibbons, chimpanzees, and gorillas.

Tardieu[100] has also shown that the bony distal femoral epiphyses of human children between the ages of 10 and 12 years bear remarkable resemblances to the adult distal femora from Hadar in that they are mediolaterally wide, lack a pronounced lateral lip of the patellar groove, and have an almost circular lateral condyle. While Tardieu found no contradiction between these results and her longstanding view that *A. afarensis* was only a facultative biped, I consider the similarity in shape between the distal femur of a juvenile human and that of *A. afarensis* to be profoundly significant. If the shape of a juvenile distal femur is accurately reflected by its bony epiphysis, Tardieu has demonstrated that traits both she and I thought were essential for human-like bipedality are not so; they are absent in young humans, who are quite expert bipeds. This may indeed turn out to be the case, but in a more recent study Tardieu[101] has found that the cartilaginous distal femur of human fetuses is, in some cases, more similar in shape to that of an adult than are the juvenile bony epiphyses on which she previously reported. She recognizes the necessity of acquiring a growth series of cartilaginous epiphyses in order to resolve this issue.

New Fossils

Since our initial publications on *A. afarensis* locomotion, not only has additional postcranial material of this species been described, but there have been discoveries of other species, older, contemporaneous, and younger, that bear on the probability that *A. afarensis* was a partly arboreal, funny-walking biped.

Ardipithecus ramidus

The oldest of the australopithecines is *Ardipithecus ramidus,* dated to ~4.4 Myr. The first description of this species referred to portions of the humerus, radius, and ulna of a single individual.[102] The very preliminary description of these bones mainly served to convince me that the ulna lacked any features associated with knuckle-walking. Many people who are interested in the origins of bipedalism are keenly awaiting a more detailed presentation of the *A. ramidus* material. Meanwhile, we must content ourselves with a statement attributed to Tim White: "Let's just say *ramidus* had a type of locomotion unlike anything living today. If you want to find something that walked like it did, you might try the bar in Star Wars."[103]

Australopithecus anamensis

In 1994, Leakey and coworkers[104] combined ~4.1-Myr-old specimens from Kanapoi and Allia Bay, Kenya, to create the new australopithecine species, *A. anamensis*. The evidence that *A. anamensis* was bipedal is provided by certain features of proximal and distal ends of a tibia that is larger than any found at Hadar: the articular surface of the lateral condyle is concave, the lateral condyle is nearly as large as the medial condyle, and the lateral facet of the distal articular surface faces inferiorly. Leakey and colleagues pointed out that the Kanapoi humerus, known for many years, has often been seen as human-like. They did not mention that Feldesman's multivariate analysis[17] found it to be further removed from that of *Homo* than are the humeri of living apes, or that Hill and Ward[105] had found its morphology to be consonant with the general pattern in *Australopithecus*. A recent multivariate study by Lague and Jungers[106] also concluded that the Kanapoi humerus "is not much more 'human-like' than any of the other australopithecine fossils, despite prior conclusions to the contrary." Indeed, it clustered with the Hadar specimens in a group that was unique among hominoids but was somewhat more chimp-like than human-like.

Another postcranial specimen from Allia Bay is a large radius that was described prior to the naming of *A. anamensis* but now is attributed to it. Heinrich and colleagues[107] portrayed this specimen as a larger version of Lucy's radius. Its ape-like traits, including an eccentrically placed proximal articular fovea associated with a beveled margin of the radial head, a long radial neck, and a well-developed crest for insertion of the brachioradialis, were interpreted as being well-suited to arboreal activity. The specimen also shared some human-like traits with A.L. 288-1: a robust radial neck, a relatively straight shaft, and a dorsally convex and ventrally concave distal shaft. The large lunate facet on the distal articular surface, and curvatures of this surface, are similar to features of the radii of Asian apes and, according to Henrich and coworkers,[107] are also similar to the A.L. 288-1 radius. These characteristics were said to enhance flexibility in climbing.

More recent postcranial finds attributed to *A. anamensis* are a capitate and proximal manual phalanx from Allia Bay.[108] They also come from individuals comparable in size to, or larger than, the biggest Hadar individuals. The capitate is even more ape-like than that of *A. afarensis* in that it has a facet for the second metacarpal that faces directly laterally, as opposed to distolaterally. The proximal phalanx from the hand is said to have the same degree of curvature and strong markings for the fibrous digital flexor sheath as do the manual proximal phalanges from Hadar.

White and colleagues inferred that *A. afarensis* "retained a powerful upper limb, but an upper limb that lacked the key arboreal adaptation of great length." Jungers replied with evidence that humans cannot be distinguished from African apes with regard to humerus length relative to body mass.

More of *A. afarensis*

In 1993, White and coworkers[109] described a ~3.4-Myr-old humerus from the Maka site in Ethiopia. They ascribed it to an adult *A. afarensis* male. It is very robust, has a large deltoid tuberosity, an extremely well-developed supracondylar ridge, and human-like retroflexion. White and colleagues inferred that *A. afarensis* "retained a powerful upper limb, but an upper limb that lacked the key arboreal adaptation of great length." Jungers[110] replied with evidence that humans cannot be distinguished from African apes with regard to humerus length relative to body mass. White[111] then said that Jungers should have included orangutans and gibbons in his comparison, and that every other aspect of *A. afarensis* anatomy shows that it was not at home in the trees, so who cares about its humeral length.

Kimbel and coworkers[112] reported on further discoveries at Hadar: a partial upper limb skeleton including a complete left ulna, dated at ~3.0 Myr, and a humeral shaft dated at ~3.4 Myr. Both specimens were considered to be from males. The ulna lacks any trait that could be construed as adaptive for knuckle-walking, and in this regard resembles human ulnae. The humerus is similar in all regards to that from Maka. The authors used these specimens to estimate the ulna-length/humerus-length index for an *A. afarensis* male (~91%) and compared to this index that of Lucy (~92.5%). They noted that the resulting values are distinctly closer to those of chimpanzees ($\bar{x} = 95\%$) than to those of modern humans ($\bar{x} = 80\%$). This seems to provide convincing evidence that the upper limbs of *A. afarensis* were relatively much longer than those of humans.

Ward and coworkers[113] recently described a capitate, hamate, lunate, the distal end of a metacarpal, and the proximal end of a proximal pedal phalanx from a single individual (KNM-WT 22944) found at the ~3.5 Myr old South Turkwel site in Kenya. On the whole, the morphologies of these specimens were said to be very similar, but not identical, to those of *A. afarensis* from Hadar. The authors found no reason to assign them to a different species. Some aspects of the carpal bones are ape-like, others are human-like. The distal metacarpal is said to be most similar to a human third metacarpal. The hamate has a massive hamulus, even larger than that of the Hadar hamate. This feature was said to indicate a large transverse carpal ligament, a deep carpal tunnel, and/or a strong flexor carpi ulnaris. However, because Neandertals also have large hamate hamuli, readers are warned against concluding that powerful forearm musculature is indicative of a climbing adaptation. The distal projection of the hamulus was said to suggest that its flexor carpi ulnaris was functionally more like that of extant apes than that of humans. Ward and associates conclude that there are no obvious indicators in the South Turkwel hand of specialized adaptations for climbing or suspension. They described the proximal part of the South Turkwel pedal phalanx as having an articular surface for the metatarsal that faces somewhat dorsally, making it resemble that of humans more closely than that of great apes. According to Leakey and coworkers,[108] "The dorsally-oriented metacarpal facet on the pedal phalanx of KNM-WT 22944 suggests that this individual was adapted for habitual bipedal locomotion."

South African Australopithecus sp.

From Sterkfontein Member 2 (~3.5 Myr) come the four bones that comprise "Little Foot."[114] Clarke and Tobias described the talus and the tuberosity of the navicular as quite human-like. On the other hand, the navicular facets for the cuneiforms were said to be oriented as in apes, suggesting an abducted forefoot, and the medial cuneiform was said, in most respects, to be like that of an ape, forming a joint with the first metatarsal. That suggests a wide range of movement and a naturally abducted position of the hallux. The authors conclude that "It is becoming clear that *Australopithecus* was likely not an obligate terrestrial biped, but rather a facultative biped and climber." My joy at this discovery and its interpretation has been considerably lessened by, of all people, Randy Susman. He recently saw the original specimen and found the hallucal tarsometatarsal joint to be less ape-like than he had anticipated.

Australopithecus africanus

Berger and Tobias[115] have reported on proximal and distal tibial fragments from Sterkfontein Member 4 (~2.7 Myr). They describe the articular surface of the lateral tibial condyle as being extremely convex, and thus ape-like. A further resemblance to apes, and also to the Hadar proximal tibia, is the indication that the lateral meniscus had a single site of attachment anterior to the external tibial spine. Berger and Tobias also described ape-like attachment areas of the semimembranosus and tibialis posterior. While little of functional significance could be gleaned from the distal tibial fragment, its articular surface appears to have a posterior tilt and thereby is allied to those of living apes and Lucy. In summary, the authors found these specimens to be the most ape-like of any Plio-Pleistocene hominid tibia and, indeed, even more ape-like than the tibia of *A. afarensis*.

McHenry and Berger also noted that the two associated skeletons attributed to *H. habilis* seem to have the same more ape-like interlimb proportions that characterize *A. africanus.* These authors conclude that because *A. afarensis* is craniodentally primitive as compared to both *A. africanus* and *H. habilis,* whereas its limb proportions are more human-like, the place of all these species in the human lineage is confused by extensive homoplasy. To me, their results also show that previous portrayals of *A. africanus* as having a fully human-like locomotor repertoire should be viewed with the scepticism shown by Oxnard.

McHenry and Berger[116] analyzed new finds from Sterkfontein Member 4 using an approach similar to that used by Oxnard[117] to study previously known material from South Africa. After assigning all the postcranial specimens to size categories, the authors found that 95% of those representing the upper limb were classified as medium or large, while 90% of those from the lower limb were classified as small. This strong indication that *A. africanus* was characterized by distinctly ape-like interlimb proportions was supported by an analysis of the Stw 431 associated material, which showed that the size of its elbow joint surfaces relative to the S1 body or acetabulum were comparable to those of apes and much larger than those of humans. Similar analyses on *A. afarensis* showed its intermediate position between apes and humans. McHenry and Berger also noted that the two associated skeletons attributed to *H. habilis* seem to have the same more ape-like interlimb proportions that characterize *A. africanus*. These authors conclude that because *A. afarensis* is craniodentally primitive as compared to both *A. africanus* and *H. habilis,* whereas its limb proportions are more human-like, the place of all these species in the human lineage is confused by extensive homoplasy. To me, their results also show that previous portrayals of *A. africanus* as having a fully human-like locomotor repertoire[118–120] should be viewed with the scepticism shown by Oxnard.[113,121–123]

Spoor and colleagues[124–126] offered a very different approach to understanding *A. africanus* locomotor behavior. They demonstrated that the posterior and anterior semicircular canals of humans are relatively larger

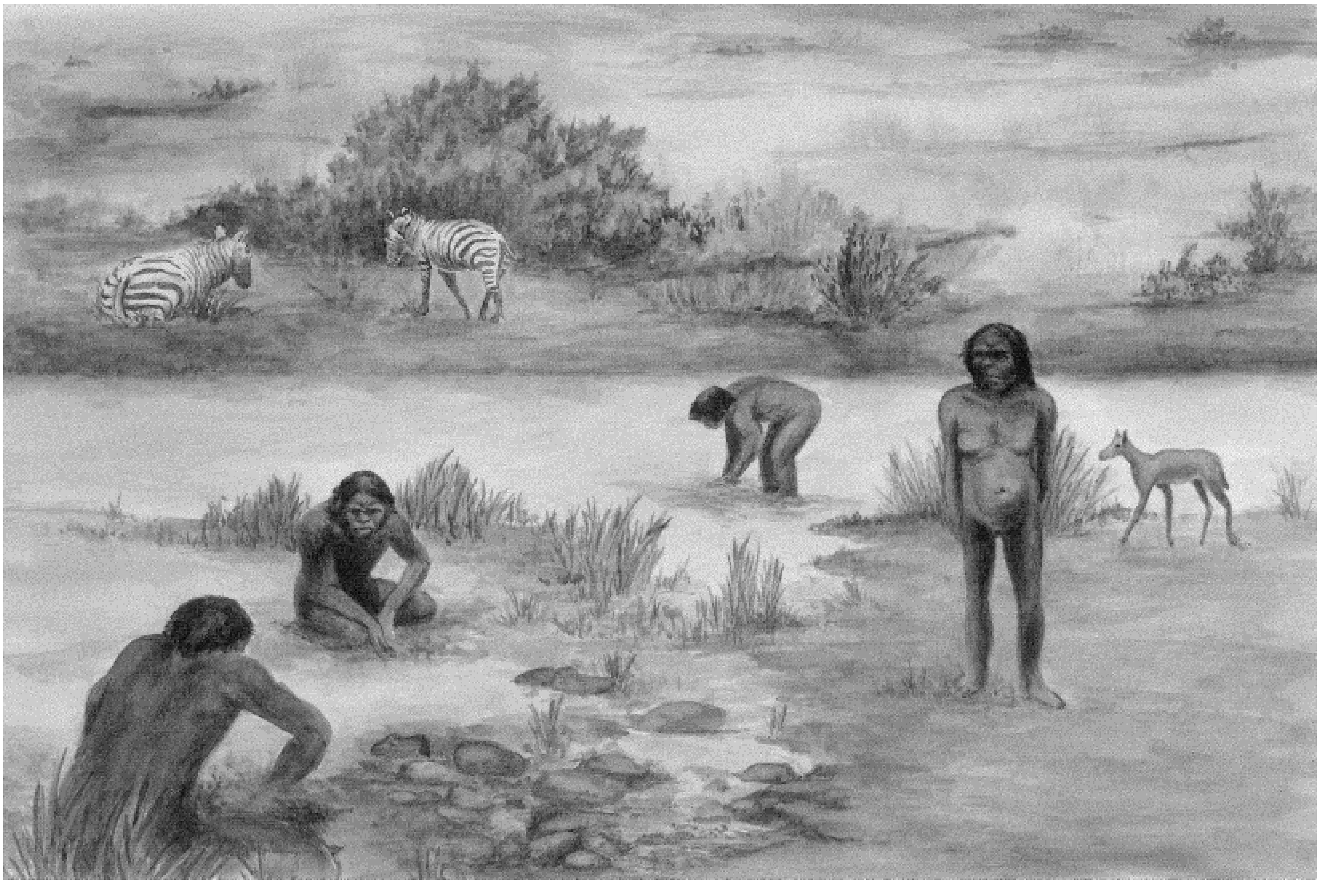

Figure 4. A depiction of *Australopithecus* making a life for itself on the African savanna. This was the commonly accepted view in the early 1970s. Illustration adapted from *Emergence of Man: The Missing Link* (c) 1972 Time-Life Books, Inc. All Rights Reserved.

than those of apes, whereas the lateral semicircular canal of humans is relatively smaller. Arguing that large vertical canals are probably an adaptation to human-like obligatory bipedalism, and finding that the three canals of *A. africanus* are of the same relative dimensions as those of apes, they concluded that this early hominid was probably a facultative biped, combining arboreal activities with a form of terrestrial bipedalism that lacked such complex movements as running and jumping.

Bouri Hata hominids

Craniodental specimens assigned to the new taxon *A. garhi*[127] have been recovered from several different areas of the ~2.5 Myr old Hata beds, Bouri Formation, in the Ethiopian Middle Awash. In the same beds were found shafts of various long bones and a proximal pedal phalanx. Although the postcranial elements could not be conclusively assigned to *A. garhi,* they still are valuable indicators of hominid locomotor anatomy during this period. A number of the limb bone shafts are thought to come from a single individual and to enable calculation of reasonably accurate limb length proportions. Such calculations indicate that Bouri Hata hominids were distinguished from *A. afarensis* by relative femoral elongation resulting in a human-like humerofemoral index. On the other hand, they are said to share with *A. afarensis* a high brachial index. The Bouri Hata proximal pedal phalanx is said to be similar to that of *A. afarensis* in curvature.

Homo (Australopithecus?) habilis

As the debate about the locomotor anatomy of *A. afarensis* was unfolding, Johanson and coworkers[128] published their discovery of the ~1.8-Myr-old O.H. 62 partial skeleton from Olduvai Gorge, attributing it to *Homo habilis* based on craniodental evidence. The associated bits and pieces of its humerus, radius, ulna, femur, and tibia were said to be very similar to Lucy's, with one notable exception: the humerofemoral index of O.H. 62 was estimated at ≥95 as compared to values of 85 for Lucy, 74 for human pygmies, and 98 for bonobos.[21] Korey[129] pointed out that the error associated with calculating a humerofemoral index from the reconstructed lengths of the O.H. 62 limb bones is so great that one cannot justifiably assert either that it was significantly greater than in Lucy or significantly less than in a common chimpanzee ($\bar{x} = 102$). Asfaw and colleagues[127] claim that any statement that the humerofemoral index is more primitive in O.H. 62 than in Lucy is erroneous because the length of the O.H. 62 femur cannot be accurately estimated. However, Hartwig-Scherer and Martin,[130] using a variety of other measurements on limb bones, confirmed that interlimb proportions of O.H. 62 are far more pongid-like than are those of *A. afarensis*.

Emanating from East Lake Turkana and dated at ~1.9 Myr is the KNM-ER 3735 specimen comprising parts of the skull and of both the upper and lower limbs.[131] The postcranial material is in poor condition, but those measurements that could be taken indicate an upper limb that was much bigger than the lower limb, nearly to the degree found in a chimpanzee. Features of the distal humerus and proximal radius indicate climbing abilities as marked as in *Pan*. Phalangeal fragments were said to belong to a hand capable of extremely powerful flexion. Leakey and colleagues did not definitively assign the specimen to a known species, but considered the possibility that it might be a male *H. habilis*. Clearly, they were uncomfortable with the idea that a creature of this anatomy could evolve into *H. erectus* during the 200 Kyr time span available.

If the O.H. 62 and KNM-ER 3735 partial skeletons are indeed attributable to *Homo,* they present a picture of locomotor anatomy that differs markedly from that of all others members of our genus. This was a major consideration in Wood and Collard's[132] decision to transfer *Homo habilis* to *Australopithecus habilis*. One is then tempted to view *A. habilis* as a more craniodentally advanced descendent of something like *A. africanus*.

Were the Hominids Predating *A. afarensis* Less Well Adapted to Terrestrial Bipedalism Than Were Lucy and Her Hadar Relatives?

The postcranial material of *A. ramidus* has not been described in sufficient detail for any conclusion to be reached about its locomotion. The tibia of *A. anamensis* seems very much like that of *A. afarensis,* suggesting a no more primitive kind of bipedalism. The upper limb material, while pointing to an arboreal adaptation, also seems to be little different from that of *A. afarensis*.

Do New Finds of *A. afarensis* or The Contemporaneous Sterkfontein Member 2 *Australopithecus Sp.* Reveal Anything New About the Locomotion of 3.0–3.5 Myr Old Hominids?

New finds of *A. afarensis,* largely because they show great humeral robusticity and long forearms, add support to any suggestion that it possessed an adaptively significant component of arboreality. The analysis of "Little Foot" by its discoverers led them to claim it came from a creature with a grasping hallux. My colleague Randy Susman doubts it is more apelike than the hallux of *A. afarensis,* which we and others have stated possessed a modicum of mobility.

Implied in the reclassification of *H. habilis* to *Australopithecus,* and in the suggestion that *A. garhi* might be the ancestor of true early *Homo*, is the possibility that among the descendants of *A. afarensis* is one species (*garhi*) that was evolving toward a more human-like locomotor adaptation and another (*africanus→habilis*) that was evolving away from one. But what is the likelihood of this scenario if *A. afarensis* itself was a fully terrestrial human-like biped?

What Do Younger Australopithecines Tell Us About *A. afarensis* Locomotion?

Perhaps the most interesting new insights into early hominid locomotion come from discoveries of material that postdate *A. afarensis*. By virtue of having an elongated lower limb, the ~2.5-Myr-old Bouri Hata hominid appears further advanced toward the evolution of human-like bipedalism than was *A. afarensis*. It remains to be determined whether its relatively long forearm is a functionally irrelevant retention of a primitive trait or signifies that adaptively significant arboreal behavior coexisted with relatively advanced bipedalism, as we proposed for *H. habilis.*[133] On the other hand, despite possessing rather obvious osteologic signs of terrestrial bipedalism, *A. africanus* and *A. habilis* seem more arboreally adapted than *A. afarensis*. Implied in the reclassification of *H. habilis* to *Australopithecus,*[127] and in the suggestion that *A. garhi* might be the ancestor of true early *Homo,*[110] is the possibility that among the descendants of *A. afarensis* is one species (*garhi*) that was evolving toward a more human-like locomotor adaptation and another (*africanus→habilis*) that was evolving away from one. But what is the likelihood of this scenario if *A. afarensis* itself was a fully terrestrial human-like biped?

CONCLUSION

In 1986, after the first wave of papers on *A. afarensis* locomotion had appeared, Henry McHenry[134] acknowledged that he could no longer hold to his decade-long belief that all the primitive characters of australopithecine postcranial anatomy were simply evolutionary baggage that had little to do with locomotion: "The Hadar postcranial material sample of *A. afarensis* make this hypothesis much less likely." In 1991, after the second wave of analyses appeared, McHenry[135] had not changed his mind: "The host of 'ape-like' traits seen in these early hominids probably implies that their bipedalism was kinematically and energetically differ-

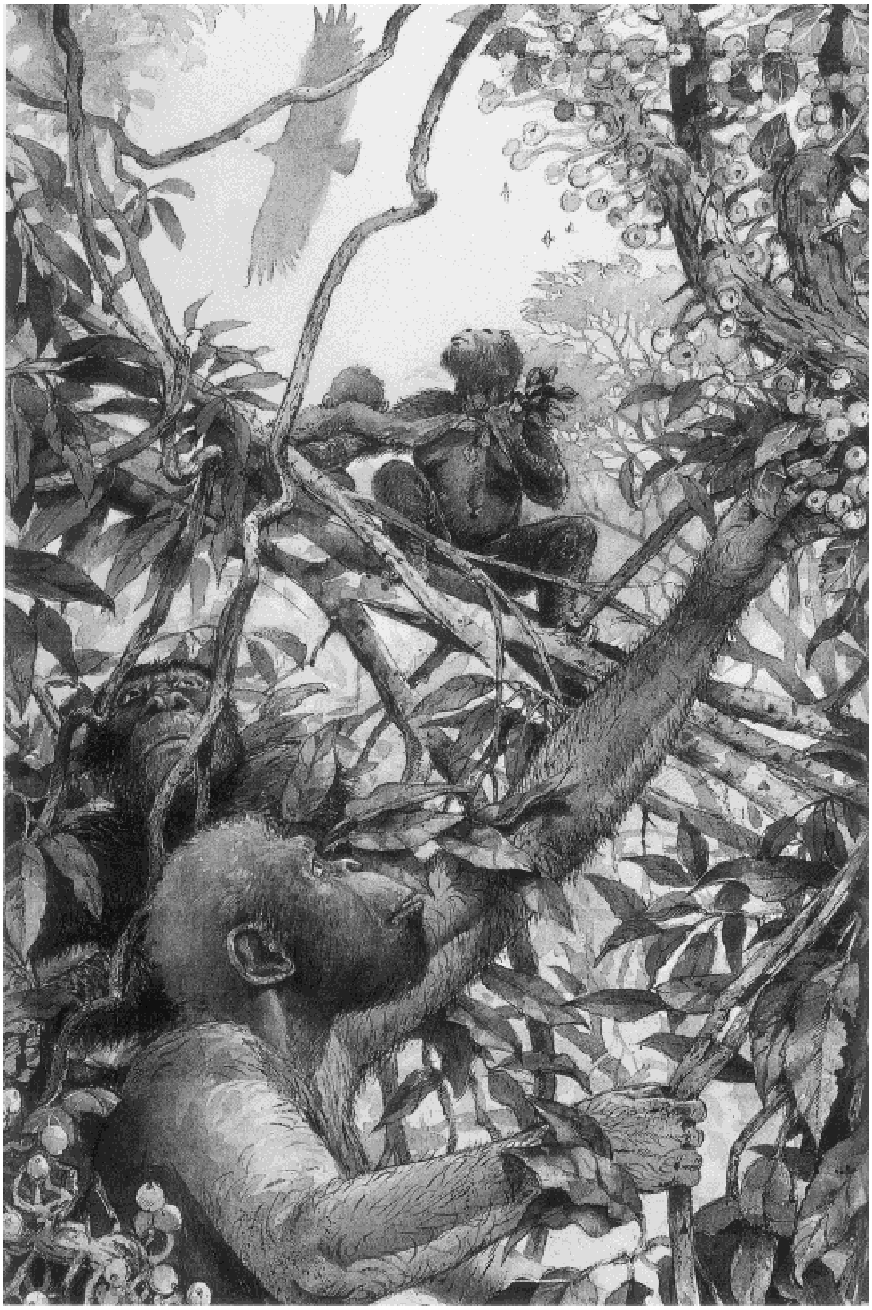

Figure 5. A depiction of *Australopithecus* making a life for itself in trees of the dense forest. This drawing, by Richard Schlecht, was published in the February 1997 issue of National Geographic Magazine as part of an article entitled The Dawn of Humans, The First Steps (Gore, R). Clearly, at least in popular depictions, the pendulum has swung regarding the importance of arboreality in the behavior of *Australopithecus*.

ent than modern humans and may imply that they were more efficient tree-climbers than are modern humans. This arborealism was different from ape-like tree climbing, however, because the hindlimb was specialized for bipedality . . .." Now, 25 years after Lucy's discovery, it remains my opinion that nothing has been discovered, no criticism offered, nor any analysis published that should cause rejection of McHenry's conclusions. Indeed, the majority of new information that has come to light points even more firmly to them.

In 1972, Time-Life Books portrayed *Australopithecus* as a human-like biped making a life for itself on the savanna of Africa (Fig. 4). Three years ago, National Geographic portrayed the very same creature feeding high in the trees of the dense forest (Fig. 5). While pictures in the popular press do not constitute evidence, they do reflect the fact that ever-increasing numbers of anthropologists are accepting arboreal behavior as an adaptively significant component of early australopithecine behavior.

I was never as certain about the nature of *A. afarensis* bipedalism as I was about its retained adaptations for movement in the trees. I am no more or less certain now. Whereas we suggested a form of bipedalism with less extension at the hip and knee than is characteristic of modern humans, others have proposed differences concerning axial rotation of the pelvis or lateral flexion of the trunk. Moreover, a significant number of people still hold to the view that early australopithecine bipedalism was fully human-like. I have often felt there is a bias in favor of viewing early hominid bipedalism as characterized by completely extended lower limbs because it is difficult for modern humans to walk with bent knees and hips. It seems inconceivable that such a manner of progression could last for more than the briefest of geologic times before evolving into our superior way of doing things. Returning to my simplistic analogy to cetacean evolution, I think if we were whales we would have great difficulty understanding how an ancestor could survive a million years while being such a poor swimmer. I have tried to overcome this bias. Along with others, I believe the bipedal adaptation first arose to improve access to food sources close to the ground, movement between such sources, or both.[30,52,89,90] Bipedalism probably persisted in this nascent but effective state for a million years, with no indication that it would be anything other than an evolutionary sidelight. Only later did some unknown event impel one of the creatures with this adaptation to abandon the trees more completely than any of its predecessors had done and become a tool-making hunter or tuber-gatherer.

I was never as certain about the nature of *A. afarensis* bipedalism as I was about its retained adaptations for movement in the trees. I am no more or less certain now.

This memoir is at its end. The siren calls of electrodes, strain gauges, and force plates beckon. For out of obscurity was I taken, and unto obscurity shall I return, at least until the *ramidus* material is made generally available and Randy walks into my office to proclaim that we are as well qualified as anyone to perform its comprehensive functional analysis.

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