Climbing to the Top: A Personal Memoir of Australopithecus afarensis

JACK T. STERN, JR.

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 hominin 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. 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. 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.” The following year came the first abstract of potential interest for reconstructing Lucy’s locomotor behavior. 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 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 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 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.

Meanwhile, other workers were making some rather different observations. While not disputing that the Hadar hominids were bipedal, Semut 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.” Tardieu's 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
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. 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 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.

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and, while Randy was sleeping, I received a phone call from an Ethiopian government official advising us to leave the country immediately.

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 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 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. 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." 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.
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 Sarmiento19, 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 papers18,21–25 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 iliosposa 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 bipedalism16,21 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 simultaneous...
neously with or even before our own. Marzke, analyzing bones and joints of the wrist, and McHenry, focusing on the capitae, 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, who made many of the same observations on the Hadar feet and hands that we did, showed no such reluctance, nor did Schmid, who focused on the ribs and pelvis. Deloison's study of modern humans. In contrast, Wolpoff, challenging Jungers's 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 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 Tar- dieu's 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 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.

During this period only one abstract was published portraying the Hadar hominid as a fully developed biped. 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.
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. Rose30,52 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 coworkers53 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.

JUST THE FACTS, MA’AM

Coffing54 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 coworkers55 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 Shea56 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, may 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

<table>
<thead>
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<th>Trait Description</th>
<th>Interpretation</th>
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* = interpreted as showing insignificance of arboreal behavior.
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The measurement of Lucy’s glenoid length including the supra-glenoid 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, using a much larger sample than ours, found the “ape-like” condition in 9% of human individuals. MacLatchy 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 abductility of the A. afairensis 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.” He claimed that the chimpanzee footprints described by Mantner and Elftman and those produced by our own “incarcerated” chimpanzees 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 agreed, adding that we had incorrectly interpreted the footprint surface at Laetoli. We did not respond, but Deloison’s 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. afairensis 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 reconstructed the length of Lucy’s foot, finding the
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 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. 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.

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.” Latimer and colleagues 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. 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. 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.

7. Whereas Wolpoff criticized Jungers for concluding that Lucy’s lower limb was relatively short, and we responded with further evidence to support this contention, Kramer 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 co-workers.

Do Unto Others As They Have Done Unto You

Those of you familiar with the history of the dispute about the locomo-
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 I66 said that Ohman’s43 claim about the uniqueness of the univertebral articulation of the human first rib was untrue. Schmidt67 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. Schmidt 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 coworkers44 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’s46 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 we18 and Schmidt67 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 disposed46 is unsupported by evidence.

5. Statements that an iliopsoas groove is present on Lucy’s pelvis46,68 are contrary to our observations.18

6. Lovejoy46 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 interacetalabular distance, they had a mechanical advantage surpassing our own (Fig. 2, part 4), resulting in reduced hip joint pressure. This was disproved by Jungers25 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 mediotratal bending than do humans. She does not.

7. We have already published70 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 planter 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 Lovejoy47 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 associates71 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 orientation48 (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 Lovejoy48 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. Deloison63 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 humans48 (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 colleagues53 pointed out inaccuracies in the statement that the metatarsal heads of *A. afarensis* are angled dorsally as in humans, but not pongids48 (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 I23 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 primates46 (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
have always been impressed by Pauwels' 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 seemed to have demonstrated precisely this point in their thorough quantitative comparison of humans and African apes. Rak, 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,\textsuperscript{78} for any speed there is an optimal stride length that minimizes energy cost.\textsuperscript{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.\textsuperscript{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\textsuperscript{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. \textit{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\textsuperscript{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. 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,\textsuperscript{64,85} but the majority of such patients exhibit a descent, not an elevation, of the pelvis on the nonsupport side.\textsuperscript{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\textsuperscript{87} 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.\textsuperscript{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\textsuperscript{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\textsuperscript{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\textsuperscript{68} 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.\textsuperscript{30,52,89,90} My reading of the relevant physiological literature has convinced me that

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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.
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 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 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 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, Paciulli and Richmond demonstrated a correlation between ontogenetic changes in phalangeal curvature and those in locomotor behavior for macaques, gibbons, chimpanzees, and gorillas.

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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 quite similar 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 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. The very preliminary description of these bones mainly served to convince me that the ulna lacked 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.”

*Australopithecus anamensis*

In 1994, Leakey and coworkers\(^\text{104}\) 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, and the lateral facet of the distal articular surface faces inferi orthy. 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\(^\text{11}\) found it to be further removed from that of *Homo* than are the humeri of living apes, or that Hill and Ward\(^\text{105}\) had found its morphology to be consonant with the general pattern in *Australopithecus*. A recent multivariate study by Lague and Jungers\(^\text{106}\) 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 chimpanzee-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. Henrich and colleagues\(^\text{107}\) 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 radius of Asian apes and, according to Henrich and coworkers,\(^\text{107}\) 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.\(^\text{108}\) They also come from individuals comparable in size to, or larger than, the biggest Hadar individual.

The evidence 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.

White and colleagues inferred that *A. afarensis* has a capitate, hamate, lunate, the proximal end of a proximal pedal phalanx from the Maka site in Ethiopia. They described a ~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 more 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 halluc. 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 Tobias115 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 Berger116 analyzed new finds from Sterkfontein Member 4 using an approach similar to that used by Oxnard117 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 should be viewed with the scepticism shown by Oxnard.

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Spoor and colleagues124–126 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
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\textsuperscript{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\textsuperscript{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 $\approx 95$ as compared to values of 85 for Lucy, 74 for human pygmies, and 98 for bonobos.\textsuperscript{21} Ko-rey\textsuperscript{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\textsuperscript{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,\textsuperscript{130} using a variety

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.
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. 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 Col- lard’s decision to transfer *Homo habilis* to *Australopithecus* habilis. One is then tempted to view *H. habilis* as a more craniodentally advanced descendant 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. rami- dis* 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*. 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?

**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.

**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*. 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*, 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?

**CONCLUSION**

In 1986, after the first wave of papers on *A. afarensis* locomotion had appeared, Henry McHenry 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 had not changed his mind: ‘The host of ‘ape-like traits seen in these early hominids probably implies that their bipedalism was kine-
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 adap-
tively 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 hominin 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. 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 sidelong. Only later did some unknown creature 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.

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 rami
dus 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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REFERENCES


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