Were Lucy's Feet Made for Walking?

Paleoanthropologists debate the style of locomotion of the earliest known human ancestor, Australopithecus afarensis

How did human ancestors between 3 and 4 million years ago move around in their daily lives? Did they stride bipedally, in the manner of modern humans, and thus spend most of their time on the ground? Or did they retain a substantial element of their ape-like heritage and were thus anatomically adapted for climbing trees?

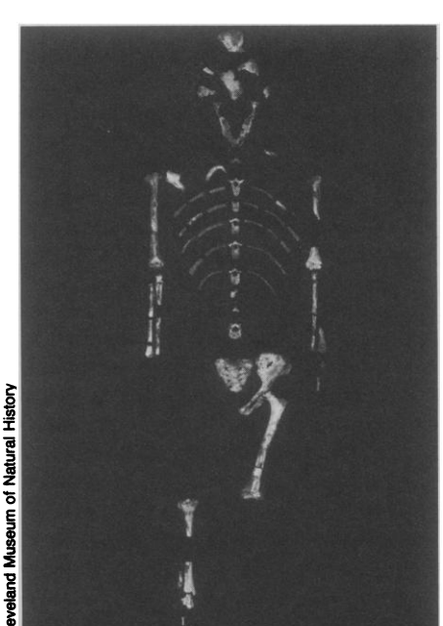
These questions formed the focus of the first scientific meeting held by the Institute of Human Origins in Berkeley.* On view were casts of the relative abundance of hominid fossils from the Hadar region of Ethiopia, which are dated at something between 3.0 and 3.6 million years, and the smaller collection of fossils and the famous footprints from Laetoli in Tanzania, which are in excess of 3.5 million years old. With a rich paleontological display of this sort, soundly argued answers could be confidently anticipated.

No one, however, expected a consensus. Rival positions had already been clearly delineated between several research groups and each was certain to mount a spirited attack on the others. This meeting was not to be a perfunctory presentation of warmed-over papers but a real opportunity to challenge and respond. The high tension atmosphere of mixed apprehension and expectation was subdued only slightly by the unfortunate absence of the French contingent, Yves Coppens, Brigitte Senut, and Christine Tardieu, from the Musée de l'Homme and the University of Paris. A potential three-cornered fight thus reduced in the event to a tussle between two teams, one based at the State University of New York at Stony Brook and the other scattered between Berkeley, Kent State University, and the Cleveland Museum of Natural History.

With the 40 percent complete famous "Lucy" skeleton to argue over, plus a host of other postcranial bones from many other individuals, it was somewhat ironic that the conference's lively discussion session should concentrate on the form and function of Lucy's fingers and toes. Why, with the pertinence of the lower back, pelvis, and lower limb to the mode of bipedality, did the discussion turn to fingers and toes? With an uncanny resemblance to the outcome of a political scrap, both sides interpret this development as a victory for their camp and a climb-down by the opposition.

"I went to the meeting expecting to eat some crow," says Randall Susman of Stony Brook, "but our fundamental thesis went unchallenged." By contrast, Tim White of Berkeley suggests that "The reason the discussion went the way it did was because they didn't want to confront Owen Lovejoy on the important parts of the skeleton. Owen's arguments were devastating to their case."

Spectators to the contest were impressed by turns with the high quality of research presented first by one side and then by the other, and there was much sagacious head-nodding at how very difficult is the business of interpretation. There was also a wide discussion of the importance of sociopolitical influences in both sides' defense of their positions. Protagonists in the Berkeley-Cleveland camp have for years promulgated the idea of an essentially modern gait in these earliest hominids and, it is said, they are reluctant to admit of anything that smacks too much of being ape-like.



Cleveland Museum of Natural History

The most complete early hominid, Lucy

Lucy's skeleton, 40 percent complete, allows comparisons between body parts.

The Stony Brook team, some of whom are primatologists, champion the expression of simian behaviors in early hominids, not least, it is said, because such a position allows them to describe Lucy and her fellows by the emotive and newsworthy sobriquet of "missing link."

Lest the friendly, and sometimes not so friendly, rivalry displayed at the Berkeley meeting should be taken by observers to indicate a state of chaos in paleoanthropological thinking about early hominid locomotion, both sides in the debate were careful to emphasize that there is complete agreement on the central point. The fossils and the footprints indicate that by 3.5 million years ago our ancestors walked on two legs rather than on four. At issue, however, are two questions. First is the style of this bipedality: was it essentially modern or did these creatures walk with a bent-hip, bent-knee stance as chimpanzees occasionally do? Second is arboreality: was the early hominids' use of trees so important a part of their lives that climbing is reflected in their anatomy?

The shift from being a tree-climbing primate to walking bipedally on the ground requires, as Lovejoy has frequently stressed, a fundamental reorganization of skeletal and muscular structures in the lower body. A chimpanzee waddles when it walks on two legs because it has a long rather than a squat pelvis, the angles at the hip and knee joints don't allow the weight to be placed directly under the center of gravity, and the muscles between the thigh bone and the pelvis function in climbing and not in balancing the pelvis during the swing phase of bipedal gait.

The lower back, pelvis, and lower limb of *Australopithecus afarensis*, which is the taxonomic name given to the Hadar and Laetoli hominids, are without question derived in the human direction. And the great toe is no longer opposable, as in apes, but is locked in line with the lateral toes, as in humans. No one describes the *A. afarensis* anatomy as completely modern, but rather as "a mosaic of human-like and ape-like features." Although the hands and feet are like those of modern humans in many ways, the digits in both are ape-like in being

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curved, a feature that betrays the frequent application of considerable stress on the bones.

The relative completeness of the Lucy skeleton has allowed William Jungers of Stony Brook to examine the limb proportions in these early hominids. Lucy, it turns out, had forelimbs of comparable length to those in modern humans but her hindlimbs were relatively short. "This arrangement means that *Australopithecus afarensis* would have had a short stride length," concludes Jungers, "which is what we see in the Laetoli footprints. It also means that *afarensis* would have been less energetically efficient than a longer-limbed hominid."

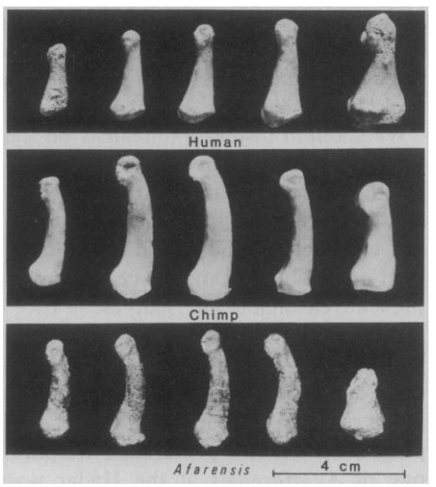
Jungers also estimates that the relative length of Lucy's foot was greater than in modern humans, being 35 percent of the hindlimb length as compared with 26 percent. At least part of the difference is due to the longer toes. "This foot/hindlimb ratio would demand a greater clearance in the swing phase, which would affect not only energetics but style of gait."

At the very least, then, Lucy's bipedal gait would have been slightly different from that of a modern human: not quite as bad as trying to walk on dry land wearing swimming flippers, but in the same direction. According to Susman and Jack Stern, colleagues of Jungers at Stony Brook, the effect of the higher foot/hindlimb ratio would be only a small component in the difference in gait between *Australopithecus afarensis* and *Homo sapiens*.

Stern and Susman have examined the anatomy of the lower back, pelvis, lower limb, and foot and have conducted electrical studies on muscle action in humans and chimpanzees. Their conclusions, published recently in a massive paper in the *American Journal of Physical Anthropology*, are several. *Australopithecus afarensis* was indeed "well down the road toward full-time bipedality," but its gait was a bent-hip, bent-knee posture reminiscent of bipedal chimpanzees. In addition, this early hominid "retained many features that enabled it to use the trees efficiently for feeding, resting, sleeping, or escape."

The Hadar fossils reveal a great range of adult body size, a feature that has been interpreted as sexual dimorphism: the big individuals were males and the smaller ones females. Stern and Susman detect morphological differences between the large and small individuals and interpret this to mean a greater penchant for arboreality in the putative females than in the putative males.

This assertion by the Stony Brook group skirts close to a sensitive issue that hangs over the Hadar hominids. Although the suggestion that the fossils represent a single species, *A. afarensis*, has met with wide approval, acceptance is by no means universal. Among the dissenters are Coppens and his colleagues, which is one reason why their absence from the Berkeley conference was regretted. The French team base their conclusions on morphological differences they see in the knee and elbow joints of the small and large specimens.



Curved toes of Australopithecus afarensis

Side view of A. Afarensis *toe bones shows them to be like those of an ape.*

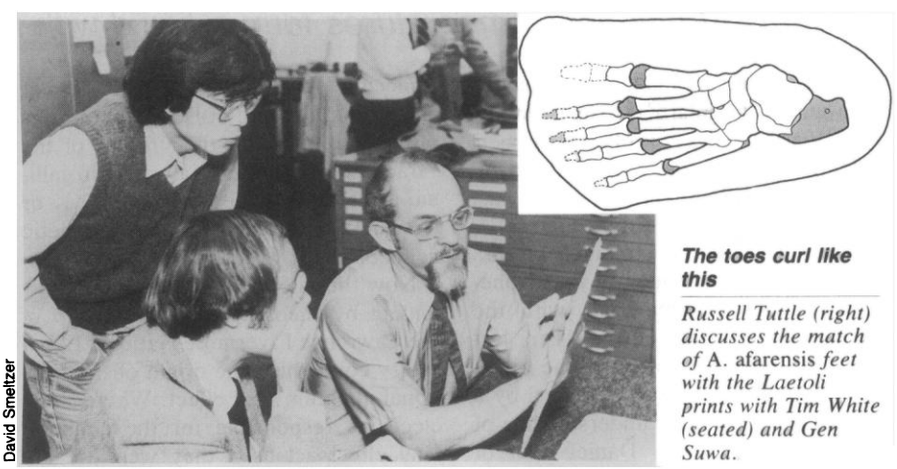
Donald Johanson, director of the Institute of Human Origins and, with White, co-namer of the species *A. afarensis*, suggested that the French arguments are weak. "We have heard what Brigitte Senut and Christine Tardieu have said . . . but they have not presented their evidence in a constructive way. They don't respond to calls." Coppens' colleagues visited Berkeley and Kent State during the past year to discuss their ideas. "We sat down with Brigitte Senut and went through every point she made, and they all fell away. Owen did the same with Christine Tardieu. There is, I'm afraid to say, still a lot of sloppy science. The science needs and respects a degree of rigor." Johanson's remarks were described privately as "totally inappropriate" and "a cheap shot at the French."

Rigor was certainly evident in Lovejoy's presentation, in which he showed that the architecture of the head of the *A. afarensis* thigh bone is built to withstand vertical forces exerted during bipedalism and not the forces encountered during climbing. He began his talk, however, by stating that he had now restored—not just reconstructed—Lucy's pelvis and that "Susman and Stern's conclusions drawn from the unrestored pelvis are not valid." Lovejoy followed this with a list of items in which, he said, the Stony Brook team had been misled or had gone astray. He also argued that the pelvis now showed that *A. afarensis* walked with an essentially modern bipedal gait.

Stern and Susman say that even if they do accept Lovejoy's restoration, which they are not inclined to, the half-human, half-ape architecture "is still compatible with a lack of full extension of the lower limb." The shape of the pelvis is in fact crucial to the Stony Brook argument about the bent-hip, bent-knee gait, as they noted in their recent *AJPA* paper. Russell Tuttle, of the University of Chicago, notes that Stern and Susman have worked only with a cast of the pelvis while Lovejoy has had access to the original. "In a case of this sort you have to go with the person who has studied the original," says Tuttle.

For Tuttle the decision on style of bipedality goes with the Berkeley-Cleveland group, but on the question of arboreality he sides with Stern and Susman, partly because he has argued a similar case for some years. The principal issue of the lengthy discussion session was, why are Lucy's fingers and toes curved? What was she grasping so powerfully?

Alan Bernstein, of the Hospital for



David Smeltzer

The toes curl like this

Russell Tuttle (right) discusses the match of A. afarensis *feet with the Laetoli prints with Tim White (seated) and Gen Suwa.*

Special Surgery, New York, said that "All you can say is that grasping is consistent with arboreal behavior, but it doesn't rule out other behaviors." By way of analogy he said that although all flying birds have feathers, not all feathered birds fly. White, Lovejoy, and their colleagues liked this argument. Tuttle, Stern, Susman, and Jungers did not. Variously they pointed out that every primate with curved fingers and toes is arboreal and those that are terrestrial have straight toe and finger bones. "If you can show us a primate with curved phalanges that is not arboreal then we will accept your argument that we must think of alternative behaviors," challenged Stern. "Ours is the parsimonious position."

Bruce Latimer, of Kent State University, rejected tree climbing as a major adaptation because of the disappearance of the opposable great toe. He also suggested that curved lateral toes might be the result of stresses involved in toe-off in a bipedal gait that uses all digits and not just the first, as in humans. Lovejoy discounted climbing because, he said, with the anatomical sacrifices made toward bipedality in the lower limbs you would expect to see an enhancement of arboreal characters in the upper limb. "You don't," he asserted. "In fact there is a reduction of such characters."

Asked to describe how he thought *A. afarensis* moved, Lovejoy said it had "a unique mode of locomotion," a phrase that delighted the Stony Brook contingent. "This was a major concession," says Jungers. "He's always said it was completely modern before." Beyond saying the locomotion was unique, however, Lovejoy declined to be specific, a reluctance that Stern and his colleagues took to indicate an absence of ideas. "We shouldn't impose our ideas on the fossils," retorted Lovejoy. "We should let the fossils speak for themselves." Tuttle considered this statement to be not very helpful and said it was incumbent upon Lovejoy and his colleagues to present reasonable alternatives.

And so it went on, sometimes rather boisterously. Meanwhile, in his usual quiet demeanor, Henry McHenry, of the University of California at Davis, had pointed out that the postcranial morphology of *A. afarensis* at the Hadar was very similar to that of *Australopithecus africanus*, a presumed descendant. One so-far-undescribed finger bone of *A. africanus* from South Africa is said to be curved in the manner of Lucy's, but not to the degree. By contrast with the similarities in the postcranial skeleton, the head and teeth of these two species differ considerably. Whatever locomotor behavior is implied by the skeletal architecture of *A. afarensis* and *A. africanus* is, says McHenry, "a relatively stable adaptation." This stability might be taken to imply that the arboreal features retained are there not simply as evolutionary baggage but as important functional structures.

White contends that, as humans we are overimpressed by the features in the postcranial skeleton that are ape-like, which, he suggests, are relatively few. A chimpanzee would recognize how very human-like Lucy's skeleton is, he says.

Although the presentations revealed strong polarities among the main protagonists, it emerged that many observers would feel comfortable with a compromise position, an argument promulgated by Tuttle. He sees *A. afarensis* as having had an essentially modern bipedal gait while retaining significant anatomical adaptations to arboreality.

Tuttle was, however, pretty much alone on another issue, that of whether the feet of *A. afarensis* as seen in the Hadar foot bones could have made the footprints at Laetoli. White, who was involved in excavating the prints, thinks they could, because, he says, the feet and the prints are essentially modern in form. Stern and Susman also think they could, but in this case it is because they see the feet and the prints as those of a climbing animal. Tuttle, who has studied the prints in detail, says the feet and the prints don't match, principally because he would expect the curved toes to have left a distinct impression. There is no such impression.

White and a graduate student Gen Suwa have reconstructed a Lucy-sized foot, based on inferences from bones at Hadar and Olduvai Gorge, and demonstrated that the diminutive foot would indeed fit within the diminutive prints at Laetoli. Nevertheless, the absence of deep impressions from the lateral toes still left Tuttle unimpressed. "The Laetoli prints are much more human-like than can be inferred from the Hadar foot bones," he says. "If someone were to find curved toes at Laetoli I would change my mind, but not until then."

Lucy's fingers and toes really did cause some problems.—**ROGER LEWIN**

Fractional Quantum Numbers in Solids

A new theory explains how electrons in solids in strong magnetic fields at cryogenic temperatures form a liquid with fractional quantum numbers

The semiconductor silicon, the material on which the microelectronics industry is largely built, is probably the best understood of all solids. Another semiconductor, gallium arsenide, is fast catching up. So, it is fitting that solid-state physicists were astounded 3 years ago by reports of a new physical phenomenon in these materials with the name quantum Hall effect. Then last year, as the excitement over the quantum Hall effect was being replaced by a satisfactory theoretical understanding of the unusual behavior, Daniel Tsui of Princeton University and Horst Stormer and Arthur Gossard of Bell Laboratories raised the ante with their report of the "fractional" quantum Hall effect in gallium arsenide that they cooled to 2 K or less and subjected to intense magnetic fields of about 15 tesla.

Now the interest has shifted to a new finding by theorist Robert Laughlin of the Lawrence Livermore National Laboratory concerning the origin of the fractional quantum Hall effect. Whereas the electrons responsible for the quantum Hall effect act as if they were weakly interacting particles in a gas, those giving rise to the fractional quantum Hall effect act as if they were very strongly interacting particles in a liquid. Theorist Bertrand Halperin of Harvard University says that, if Laughlin's explanation turns out to be right, it would mark a fundamentally new way to think about the way electrons can cooperate in a solid. Although there are no obvious technological applications for the fractional quantum Hall effect right now, the intellectual novelty is comparable to that of the quantum theory of superconductivity