Four Legs Bad, Two Legs Good

The evolutionary event that marked the beginning of the human line—the advent of bipedal walking—has puzzled anthropologists for decades; the problem is now the subject both of speculation in behavioral ecology and of anatomical analysis

FOSSIL discoveries from East Africa during recent years have dramatically transformed anthropologists' picture of human origins, particularly the early stages. So much so, according to Mary Leakey and two colleagues, that "The outstanding evolutionary question now is: what was the selection pressure that produced bipedalism?" In other words, what was it that made walking around on two legs a successful mode of locomotion for the first hominids?

The answer, suggests Leakey, in company with A. R. E. Sinclair of the University of British Columbia and Michael Norton-Griffiths of Ecosystems Ltd., Nairobi, is that "bipedalism developed for long-distance migration to scavenge from migrating ungulate populations."

The notion has the merit of being in line with recent arguments by a number of workers that for early hominids scavenging, not hunting, was an important mode of obtaining food. But the question here relates to the *beginnings* of the human line: was the role of a highly mobile scavenger sufficiently rewarding for a large-bodied, apelike creature that it could have initiated the evolutionary switch from four-footed to two-footed locomotion?

Ever since Charles Darwin first elaborated on the possible circumstances of human origins in his 1871 book *The Descent of Man*, anthropologists have been speculating on the possible cause of what is usually seen as a momentous shift in mode of getting around. A longtime popular notion was that the shift was fueled by the need by an otherwise defenseless "ape" to make and use tools and weapons for hunting and for protection against predators. This picture exemplifies the idea that the principal effect of walking on two feet was to "liberate the hands," a sentiment that still pervades serious discussion of the subject today (see box).

Recently, however, anthropologists have been focusing instead on less dramatic and more mundane explanations than weapon wielding, not least because archeological evidence indicates that the beginnings of stone tool-making postdated the origin of bipedalism by at least a million years. The suggestion of a migrating-scavenger origin of bipedalism is part of this new approach, and Leakey and her colleagues offered the idea in the hope of stimulating some discussion. They succeeded.

In a study of the ecology of the Serengeti Plains of Tanzania, Sinclair and Norton-Griffiths realized that a scavenger that could follow the huge herds of ungulates—wildebeest, zebra, and so on—that migrate through the region would have access to an abundance of food: at least one carcass a day in an area of 20 square kilometers compared with one carcass every 14 days for a territorial scavenger. Vultures, of course, fill this migratory scavenger role, but they suffer the limitation of being unable to break through the hide of a newly dead animal and must wait until one of the bigger scavengers, such as the hyena, comes along and begins the job.

> ***"The outstanding evolutionary question now is: what was the selection pressure that produced bipedalism?"***

Although hyenas can slice their way through all but the toughest of flesh, they, like other mammalian scavengers, are forced to be opportunistic in obtaining carcasses in the first place. Encumbered by relatively immobile young, the adults cannot stray very far from their home territory and must therefore wait until potential meals stray their way. "Therefore, there is in Africa an unfilled niche for a mammalian scavenger that can follow migrating ungulates," argue Leakey, Sinclair, and Norton-Griffiths, "but such a mammal would need to carry its young."

These workers suggest that hominids, equipped with a bipedal, striding gait, would be able to carry their offspring habitually and more efficiently than, say, chimpanzees and baboons do as they move on four feet through relatively open country. Hominids would therefore be able to fill the vacant niche of the migrating scavenger, or so the argument runs. By contrast, say Leakey, Sinclair, and Norton-Griffiths, if the early hominid diet consisted principally of plant foods with only a small complement of scavenged meat, as is the case with modern chimpanzees and baboons, natural selection for a powerful striding gait would have been minimal at best.

Every putative explanation of the origin of hominid bipedalism is open to criticism, not least because by their nature they are virtually impossible to test. Criteria for support therefore rest upon plausibility. With the migratory scavenger idea, there are several immediate responses to be made.

First, as biologists Henry McHenry and Peter Rodman at the University of California, Davis, pointed out several years ago, a plausible argument can be made for the origin of bipedality as a means of covering a large amount of territory in the foraging for dispersed plant foods. The idea fits into the context of hominids arising in a more open environment than apes are adapted to, perhaps feeding on the same kind of diet as apes, but from more widely dispersed sources. Walking around on two legs is therefore "an ape's way of living where an ape could not live," as McHenry and Rodman succinctly put it.

A perhaps more substantive objection concerns the teeth of our earliest ancestors. "The scheme makes a lot of sense in itself," observes McHenry, "but early hominid teeth don't seem to be particularly suited to a diet high in meat." In fact, he says, the trend is in the opposite direction: over time the cheek teeth get bigger and flatter and the incisors and canines get smaller. "This is not what you'd expect in a committed scavenger." Walter Leutenegger of the University of Wisconsin agrees with McHenry, saying that evidence from the fossil teeth, face, and cranium "suggests a high degree of vegetarianism for these early hominids."

If the overall size and shape of the teeth give scant support to the migratory scavenger notion, so too does microscopic analysis of the tooth surfaces. For instance, Alan Walker of The Johns Hopkins University finds that patterns of wear on early hominid tooth enamel are more like those of a fruit eater, such as a chimpanzee, than those of a meat eater.

Last, one could argue that without stone tools, the earliest hominids would have faced the same limitation suffered by vultures, namely the inability to break through tough hide. It may be that, like vultures, these first hominids took their turn at the carcass after better equipped scavengers, such as hyenas, had sliced through the hide. But this strategy would have put the relatively defenseless and decidedly slow bipedal hominids in direct competition with some very dangerous and swift creatures indeed. Leakey, Sinclair, and Norton-Griffiths suggest that this danger would have provided selection pressure for the skill to fashion stone tools, which would allow rapid and independent access to fresh carcasses. This proposed sequence of events is offered to explain the delay between the first documented bipedalism—at least 3.75 million years ago, and probably much earlier—and the first evidence of stone tools—about 2.5 million years ago.

If the adaptation to a migratory scavenger niche had driven the evolution of bipedality, say Leakey and her colleagues, the need for the rapid and simultaneous evolution of striding gait anatomy in the hip and the foot would have been great. This might contrast, they propose, with the evolution of bipedality for the purportedly less demanding foraging of fruit, so that evolutionary changes in the hip and foot might not be so tightly coupled. Differences of this sort might be visible in the fossil record, suggest Leakey, Sinclair, and Norton-Griffiths, and this would help to "distinguish between the two hypotheses."

Such a distinction would be a tough call at best, observes McHenry, who has recently been examining the best fossil evidence for early bipedality. Specifically, McHenry has been studying certain parts of the postcranial skeleton of the earliest known hominid, *Australopithecus afarensis*, with that of one of its putative descendants, *Australopithecus africanus*. Fossil remains of *afarensis* have been discovered in deposits dated at about 3.75 million years ago in Tanzania and from a little later in time from Ethiopia. *Australopithecus africanus* fossils come from deposits dated at 2.5 million years ago from the Sterkfontein cave in South Africa.

Comparison of the anatomical adaptations to locomotion in these two species should be interesting, says McHenry, because of the significant evolutionary changes in the teeth, face, and cranium. As might be expected, the head of *A. afarensis* is altogether more apelike than that of *africanus*: the face sticks out more, the base of the cranium is relatively flat rather than flexed, as it is in humans, and the teeth, though not those of an ape, are distinctly apelike, having big canines, big incisors, and relatively small cheek teeth.

Clearly, something significant had been going on in the origin of *africanus* from *afarensis*, presumably something to do with a change in feeding patterns. "One might expect the changes in anterior dentition between *A. afarensis* and *A. africanus* to be related to changes in behavior that would affect the locomotor skeleton as well," McHenry therefore comments. But, as he was

Freed Hands or Enslaved Feet?

"It is now a virtual cliché in expositions of human evolution to refer to the 'freeing of the hand' which accompanied the transition from an arboreal life-style to a ground-dwelling, bipedal, one," observes Graham Richards, a psychologist at the North East London Polytechnic, England. In fact, he argues, in the evolutionary shift from moving around on four feet to two feet that marked the origin of the human line, the "enslavement of the foot" was a more significant event. Richards also favors an emphasis on continuity rather than abrupt change in considering the consequences for human hands and dexterity of the novel upright stance, an approach that Purdue University anthropologist Dean Falk terms "an exciting new direction of thinking."

There was no sudden liberation of the hands with the advent of bipedality, Richards proposes, but instead "a transfer into the new life-style of many of the same motor-coordination habits which had characterized the preceding arboreal phase." As a psychologist, Richards likes to view the transition in Piagetian terms, and therefore says that what was novel about life for the first hominids was not so much the elaboration of new forms of behavior but rather the application of existing behaviors to a new environment.

In terms of anatomy, the advent of bipedality was achieved in the feet by the loss of the splayed great toe, which moved alongside the other toes and so formed a platform for stability and propulsion, and was accompanied in the hands by the development of the opposable thumb, which allowed a precision grip. The interesting question for Richards is, by how much did the manual behaviors of the tree-climbing protohominid differ from the precision-grip manipulation that was available to the first hominids? "Not much," is his answer. The reason is that "the gripping, grasping, and pulling operations involved in locomotion [by an arboreal ape] are also central to object manipulation," he says. "Using the Piagetian concepts of 'accommodation' and 'assimilation,' the emergence of tool use can be plausibly pictured as resulting from relatively minor accommodations of existing behavioral schema following the move from the trees."

Hominids were anatomically equipped for a striding bipedal gait and a precision grip at least 3.75 million years ago, and yet another 1.5 million years were to pass before significant brain expansion and tool-making to any kind of standard design were to appear. This sequence of events in the prehistoric record leads Richards to observe that " 'freeing of the hand' can thus hardly be claimed to have led in any immediate sense to stone tool-making."

The "enslavement of the foot" may, however, have had significant consequences, specifically in releasing neurological resources. An arboreal ape uses all four limbs in climbing trees, and this demands an amount of neurological control and coordination that exceeds that required in bipedal locomotion. When the feet became enslaved by the constraints of bipedality, part of the motor region of the brain that controlled them would become redundant and, speculates Richards, would be available for co-option by the nearby hand centers, an idea that Falk regards as plausible. "The net neurological effect of enslavement of the foot then would be to bring about a reorganization, rather than an enlargement, at the cerebral level," says Richards. He doubts that this would be discernible in fossil brains.

The evolutionary picture Richards envisages here, therefore, involves relatively small behavioral shifts accommodated by relatively small neurological shifts, in the first instance at least. "Talking about 'freed hands' when there is little indication as to whether they were either enslaved in the first place or in any genuine sense 'liberated' subsequently, helps nobody understand what really happened." ■ **R. L.**

ADDITIONAL READING

G. Richards, "Freed hands or enslaved feet?" *J. Hum. Evol.* **15**, 143 (1986).

soon to discover, "such appears *not* to be the case."

In examining aspects of the wrist, shoulder, pelvis, and thigh bone in these two species, McHenry came to the following conclusion: "Except in relatively minor details, the postcranium in the first bipeds, *A. afarensis* and *A. africanus*, are very similar to one another and unlike any living hominoid [apes and humans]." McHenry had expected to see differences between the two species, some degree of change in a human direction between *afarensis* and *africanus*, for example. Instead he saw stability, stability of an identifiable *Australopithecus* locomotor adaptation, which was distinct from the modern human adaptation.

For many years McHenry had interpreted the presence of certain primitive aspects of the locomotor skeleton of *africanus* as the result of an absent or weak selection pressure on them, a view he called the "baggage hypothesis." But having done the comparison with *afarensis* and seen the continuity of so many such characters, McHenry believes that this explanation is "much less likely." In other words, these primitive characters might well be an integral part of a specific australopithecine bipedal adaptation.

For instance, the most striking feature of the early *Australopithecus* skeleton is the curved hand and foot bones, which, says McHenry, must imply significant tree-climbing in the daily lives of these creatures. This is not to say that these early hominids shuffled along in a stooping, simian gait when they walked on the ground. Rather, suggests McHenry, *Australopithecus* bipedality involved "different firing patterns of the muscles, different movement of the hip joint, and so on. They were nuances on the striding gait, that's all."

For McHenry, the most significant aspect of these studies is that they add emphasis to the notion of mosaic evolution, a dissociation between evolutionary change in different parts of the body. Upright walking preceded dental changes, which in turn preceded significant enlargement of the brain. The evolution of hominids did not, apparently, involve a large feedback loop that tied these three human characters together as one. "Our reconstruction of the lifeways of these early hominids must take this fact into account," McHenry urges. ■

ROGER LEWIN

ADDITIONAL READING

C. O. Lovejoy, "The origin of man," *Science* **211**, 341 (1981).
A. R. E. Sinclair, M. D. Leakey, M. Norton-Griffiths, "Migration and hominid bipedalism," *Nature (London)* **324**, 307 (1986).
W. Leutenegger, "Origin of hominid bipedalism," *ibid.* **325**, 305 (1987).
H. M. McHenry, "The first bipeds," *J. Hum. Evol.* **15**, 177 (1986).

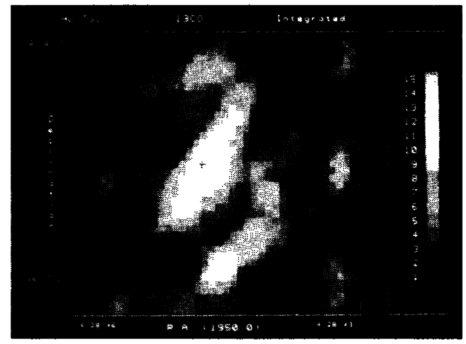
Glimpses of Solar Systems in the Making

New observations at both visible and radio wavelengths are allowing theorists to test their ideas of how planetary systems come to be

BEFORE the flight of the Infrared Astronomy Satellite (IRAS) in 1983, astronomers' understanding of planetary formation could have been described, with only slight exaggeration, as a huge edifice of theory balanced on a single data point of fact: our own solar system. Since then, however, researchers have been able to expand their empirical base considerably. The all-sky infrared survey conducted by IRAS turned up some two dozen nearby stars that showed "infrared excesses," interpreted as heat from extended disks of gas and dust surrounding each star. Since these were exactly the kind of disks that observers had expected to find around stars that were forming planets, the IRAS discoveries have been followed up by a flurry of ground-based observations. Among the fruits of that effort are three new results presented in Pasadena, California, at the January meeting of the American Astronomical Society.

■ β *Pictoris.* Although β Pictoris is an inconspicuous object to the naked eye—at a distance of 53 light-years it is only the second brightest star in the dim southern constellation of Pictor, the painter's easel—it is actually an A5 star, several times brighter and more massive than the sun. It appears to be less than 1 billion years old, allowing for considerable uncertainty, and is thus quite young by stellar standards.

In April 1984, after IRAS had identified β Pictoris as having an infrared excess, Bradford A. Smith of the University of Arizona and Richard J. Terrile of the Jet Propulsion Laboratory managed to obtain an image of the source. They verified that β Pictoris is indeed surrounded by a disk: the structure appears edge-on from our vantage point and extends at least 400 astronomical units to either side of the central star. (One astronomical unit is about 150 million kilometers, the distance from the earth to the sun. For comparison, Pluto is 40 astronomical units from the sun.) On the other hand, Smith and Terrile's image covered only one wavelength band, centered around 0.89 micrometer at the far red end of the visible spectrum. They were therefore unable to say much about the size and composition of the particles in the disk. Now, however, two



The disk around HL Tauri. *As shown in this map of carbon monoxide around the star, the disk extends roughly 1000 astronomical units outward from HL Tauri and is nearly edge-on to Earth. Steven Beckwith and Anneila Sargent have found that the disk rotates according to Kepler's laws of planetary motion.*

independent groups have rectified that problem. Benjamin Zuckerman of the University of California, Los Angeles, and his colleagues* have imaged the disk in three wavelength bands, centered at 0.45, 0.55, and 0.9 micrometer. Francesco Parsce and Christopher Burrows of the European Space Agency, currently on assignment to the Space Telescope Science Institute in Baltimore, have imaged the disk in four wavelength bands covering the same range.

On the most important fact the two groups are in agreement: within the admittedly large errors (about 20%), the reflectivity of the disk material is independent of wavelength. If anything, it is slightly tilted toward the red. This immediately suggests that the light from β Pictoris is being reflected from particles that are considerably larger than 1 micrometer. If the particles were much smaller than that, their size would be less than the wavelength of visible light and they would scatter much more strongly at the shorter wavelengths. (This size effect, which was first analyzed by Lord Rayleigh in the 19th century, arises from the wave nature of light and has nothing to do with what the particles are made of; in Earth's

* Jonathan Gradie and Joan Hayashi, University of Hawaii; Harland Epps, University of California, Los Angeles; Robert Howell, University of Wyoming.