NEW PERSPECTIVES ON THE EVOLUTION OF BIPEDALISM

by Alison S. Brooks

❖ ❖ ❖

Early scholars of natural history recognized that bipedalism, tool use, and language were among the most important defining characteristics of our species. In 1780, Blumenbach actually classified humans in a separate order, the "Bimana" or two-handed animals, implying only two limbs used for locomotion. Even as late as the 1950s, many thought that large brains and bipedalism had evolved together, an impression supported by the large brain of the "Piltdown Man" forgery. But as recent fossil evidence makes clear, bipedalism actually developed long before there was any sign of enlarged brains, tool-making, or any kind of symbolic behavior that would suggest language abilities.

Why did our lineage adopt such an unusual way of getting around, a way that is exceedingly rare among mammals? There are other bipeds, but kangaroos move by hopping on their hind legs, balanced by a long heavy tail, and many birds such as ostriches run on the ground with bent knees, also balanced by a tail. Humans are the only striding, tailless bipeds. Because we started out as tailless apes, our bodies had to change in many ways to balance the body over that one leg during walking and running. Our head is balanced atop the spine rather than out in front of it, and our spine itself is S-curved, to balance the mass of the upper body over the legs. This alone causes us a great deal of grief by putting strain on the lower back and neck. Our pelvis changed from a long linear shape with flat blades (ilia) extending up the back to a basin shape that cradled the abdominal organs but created problems later on in evolution for birthing a large-brained baby. The new shape of the pelvis changed the position of the muscles attached to those blades, which were used to pull the leg back but now extend to the side over the hip joint to keep you from falling over when you pick up one leg and stand on the other. Otherwise (or if those muscles aren't functioning well) you would have to walk the way chimpanzees and some other four-footed animals do—leaning sideways over the leg you stand on to keep your balance and prevent falling towards the leg you are lifting. The hip joints are bigger than in apes of comparable body weight since they carry our full weight whenever we are moving or standing. To make it easier to balance on one leg, our knees are positioned directly under the body, which makes the thigh bone (femur) slant inwards from hip to knee. Finally our foot changed from a grasping appendage to a propulsive one, with a bigger, straighter and stronger big toe in line with the shorter lateral toes for pushing off, and with both a longitudinal and transverse arch to stiffen the foot for toe-off. This literally puts a spring in our steps when we run.

Fossil Evidence for Bipedalism

Even the very fragmentary fossil remains from early in human evolution suggest that adaptation for bipedalism was an early and essential step, so to speak, on the road to becoming human. At 6-7 million years ago (mya), two early ancestors represented by the fossils *Sahelanthropus tchadensis* from Chad and *Orrorin tugenensis* from Kenya appear to have already changed their way of getting around. The hole in the base of *Sahelanthropus*'s skull for its spinal cord had become reoriented so it points downward rather than backward, and it is positioned a little further forward suggesting that the head was becoming more balanced on top of a vertical upper spine. The cross-section and width of the femur of *Orrorin* suggests that it was already bearing more weight, although the hip joint would have been smaller than in modern humans. In addition, the long narrow neck of the femur, which joins it to the hip socket, indicates that the pelvis (which is missing) was already much broader than in apes. The curved toe and finger bones and the muscle markings and shape of the upper arm bone suggest that *Orrorin* also spent a lot of time climbing around in trees, to sleep, eat, or escape from predators.

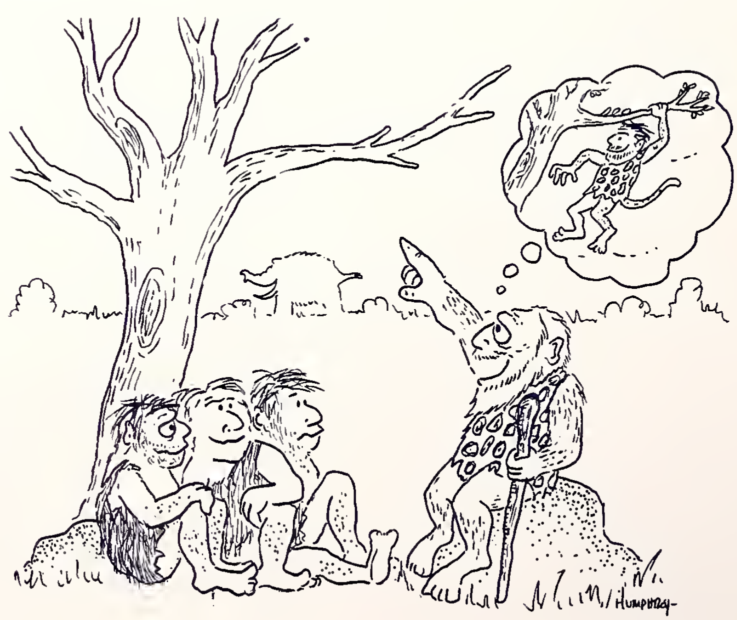
An almost complete skeleton of *Ardipithecus ramidus* from Ethiopia, dating to 4.4 mya and published in October 2009, has an even more curious combination of traits. The upper blades of the pelvis (ilia) are shorter and broader than in apes, and the pelvis as a whole apparently has a basin shape, suggesting a degree of adaptation for upright walking. But the foot retains a fully opposable big toe for grasping and climbing in trees, and it does not have either a longitudinal or a transverse arch.

From 4.4 to ca. 1.9 mya, members of the genus *Australopithecus*, whose most complete skeletons so far are Lucy and the recently reported skeletons of *Australopithecus sediba* (*Science* 4/9/2010), were more committed to habitual bipedal walking, with an S-curved spine, a very wide basin-shaped pelvis, an inward-slanting femur, a large big toe close to the other shorter toes, an expanded heel, and some degree of arch in the foot. That *Australopithecus* walked upright is also demonstrated by the footprint trail at Laetoli, (near Olduvai Gorge in northern Tanzania), where a larger and a smaller *Australopithecus* walked together through wet muddy ash 3.6 mya. Their stride may have been different from ours, however, as their toes were still long and curved for climbing in the trees, and their legs were short compared to their arms.

Only with *Homo erectus* at ca. 1.8 mya do we see a full-commitment to life on the ground and reduction or elimination of many of the features that made it easier to get around in the trees: longer arms, an upwardly oriented shoulder joint for hanging, and grasping toes with a limited arch. The "Turkana boy" skeleton of an adolescent dated to 1.5 mya has the long legs and basin-shaped pelvis of a fully bipedal human, while a slightly earlier foot skeleton from Olduvai Gorge has short toes and a human-like arch. A recently published set of footprint tracks in Kenya from 1.5 mya suggests real "toe-off" striding and a fully-human arch. Variations in the pelvis after *Homo erectus* apparently have more to do with providing space for a larger-brained infant than with perfection of bipedal locomotion.

Why Walk on Two Legs?

Why did our lineage adopt this peculiar mode of getting around? It would not have made it any easier to escape from predators—most chimpanzees and all monkeys can outrun us over short distances. An early argument held that bipedalism developed to free the hands to make tools. But as there is no sign of elaborate tool-making for a least the first 3-4 million years after the first bipedal members of our lineage such as *Sahelanthropus* and *Orrorin*, it seems more likely that later tool-makers took advantage of hands that were already partly freed. Another argument suggests that bipedalism developed to facilitate moving between widely-spaced feeding trees, but *Ardipithecus* seems to have inhabited fairly dense woodland. Did we become bipedal to see over the tall grass? (My own experience in the western Rift Valley suggests that the grass in many places is more than six feet high, and Lucy was about 3.5 feet tall.) Two other theories that are plausible but difficult to demonstrate are 1) that bipedalism makes a primate appear larger and more threatening to potential challengers and predators (male gorillas run short distances on their hind legs to threaten intruders) or 2) that bipedalism makes it easier to carry



food and infants to a safe place to feed (but see the comment on Ardi's likely closed woodland habitat, above). And even if we initially became capable of bipedal walking for one of the above reasons, why abandon the safety of the trees altogether after 1.8 million years ago, since by then our ancestors had lost their climbing toes, short legs, long arms and upwardly mobile shoulders for hanging from branches?

Born to Run?

A new theory, proposed by Bramble, Lieberman and colleagues in a series of papers from 2004 on, is that it is not about bipedal walking at all. Rather we were "born to run," and it is running that constitutes one of several major adaptations that helped shape our bipedal morphology after *Australopithecus*. How can this be, as human runners are relatively slow. Human legs and feet are well-adapted, however to endurance running. In jogging or "marathon-mode," the long spring-like tendons in our legs (such as the Achilles tendon) and the arches in our feet store and then release energy like a spring during one part of the running step for later release. Our shorter toes are well-adapted for pushing off, while long legs make it possible to cover a given distance in fewer steps. Finally our long waist and other structures allowed the upper body to counteract the twisting forces generated by running and stabilize the body. This is why runners feel compelled to pump their arms back and forth in opposite directions to the corresponding legs when they run. Also, a new (in *H. erectus)* ligament to the back of the head stabilizes the head on the spine. Running also makes maximum use of our large gluteal muscles, which first become enlarged in the genus *Homo*, while walking uses them only minimally.

In addition to these adaptations in our lower limbs, specializations for heat loss allow us to run for exceptionally long distances even in the middle of the day. These adaptations include our elongated bodies compared to apes, hair loss, increased number of sweat glands, mouth-breathing while running, and possibly adaptations of the circulatory system to better cool the brain.

Bramble and Lieberman compare our endurance running to trotting, which several running mammals are able to maintain for considerable periods of time. Well-conditioned humans, however, "trot" faster than dogs and can even out trot horses in hot conditions. Mammals can move faster when galloping than trotting, but they cannot pant and gallop at the same time. Since non-human mammals cool mostly by panting, they can die of heat exhaustion (hyperthermia) when forced to gallop for extended periods of time in the heat. The authors argue that our human ability to run with long strides, sweating, and other heat-loss adaptations account for why so many humans, even into their 70's and 80's, are able to run marathons.

An ability to run long distances in the heat of the day would have conferred considerable advantages on early humans, who incorporated increasing amounts of meat into their diets but seem to have lacked sophisticated weaponry for hunting or for challenging other carnivores at kill sites. In 2006, Liebenberg published a study of so-called persistence hunting by modern San peoples in the Kalahari Desert in Botswana. (One of these hunts can be viewed at (http://www.youtube.com/watch?v=fUpo_mA5RP8.) Hunts in the heat of the day last from two to eight hours of running after the animal through sand and brush over distances of 25-35 km. at average speeds of 6-10 km/hour, which is not especially fast even by marathon standards. At this point, the animal collapses from heat exhaustion, sometimes not even requiring the hunter to finish it off.

Since persistence hunting requires considerable tracking abilities, has a risk of dehydration, and is rare among modern hunters, Pickering and Bunn challenged Bramble and Lieberman's scenarios. Did early humans who lived in savanna woodlands rather than in desert bushlands have the ability to track animals as the San do? Lieberman and others replied that even non-human carnivores have the ability to follow prey, that following a wounded animal also would have required tracking skills, and that persistence hunting even today is often more successful than hunting with a bow and arrow. Further, hunters can carry water in an ostrich eggshell or a skin bag. Did they actually run down animals? We can only ask how they might have acquired large prey otherwise, without sophisticated weaponry. Running may have developed out of an earlier adaptation to bipedal walking as a way to cope with increasing aridity and use of open environments by our ancestors after 1.8 mya.

Further work on running, much of it by Lieberman, his colleagues and students, has demonstrated that shorter toes lower the energetic cost of running but not of walking, and that habitual barefoot runners (studied in America and Kenya) land on the balls of their feet (or sometimes on the mid-foot) rather than on the heel. Even with a highly cushioned modern running shoe, landing on the heel generates more "shock" or force that travels up the leg, while landing on the forefoot almost entirely eliminates any collisional force on impact, making barefoot running comfortable and easy to do on even the hardest surfaces. Studies on the developmental history of these adaptations in childhood and on physiological effects of hormones on bone growth have also added to our understanding of this fundamental and unique human adaptation.

References

Bennett, M.R., *et al.* 2009. Early Hominin Foot Morphology Based on 1.5 Million-Year-Old Footprints from Ileret, Kenya. *Science* 323: 1197-1201.

Berger, L.R., *et al.* 2010. *Australopithecus sediba*: A New Species of *Homo*-Like Australopith from South Africa. *Science* 328: 195-204.

Bramble, D.M., and Lieberman, D.E. 2004. Endurance Running and the Evolution of *Homo*. *Nature* 432: 345-352.

Devlin, M. J., and D.E. Lieberman. 2007. Variation in Estradiol Level Affects Cortical Bone Growth in Response to Mechanical Loading in Sheep. *Journal of Experimental Biology* 210: 602-613.

Liebenberg, L. 2006. Persistence Hunting by Modern Hunter-Gatherers. *Current Anthropology* 47(6): 1017-1025.

Lieberman, D.E., and D.M. Bramble. 2007. The Evolution of Marathon Running Capabilities in Humans. *Sports Medicine* 37(4-5): 288-290.

Lieberman D.E., *et al.* 2007. The Evolution of Endurance Running and the Tyranny of Ethnography: A Reply to Pickering and Bunn. *Journal of Human Evolution* 53: 439-442.

Lieberman D.E., *et al.* 2006. The Human Gluteus Maximus and Its Role in Running. *Journal of Experimental Biology* 209: 2143-2155.

Lieberman, D.E. *et al.* 2010. Foot Strike Patterns and Collision Forces in Habitually Barefoot Versus Shod Runners. *Nature* 463: 531-535.

Pickering, T.R., and H.T. Bunn. 2007. The Endurance Running Hypothesis and Hunting and Scavenging in Savanna-Woodlands. *Journal of Human Evolution* 53: 434-438.

Richmond, B.G., and W.L. Jungers. 2008. *Orrorin tugenensis* Femoral Morphology and the Evolution of Hominin Bipedalism. *Science* 318: 1662-1665,

Rolian, C., *et al.* 2009. Walking, Running and the Evolution of Short Toes in Humans. *Journal of Experimental Biology* 212: 713-721.

White, T.D., *et al.* 2009. *Ardipithecus ramidus* and the Paleobiology of Early Hominids. *Science* 326: 75-86. (See also articles in the same issue by Lovejoy, O. *et al.*)

Zollikofer C.P.E., *et al.* 2005. Virtual Cranial Reconstruction of *Sahelanthropus tchadensis*. *Nature* 434: 755-759.

Alison S. Brooks is professor of anthropology at George Washington University and editor of "AnthroNotes."