Evolution of Human Walking

Features of her pelvis show that a three-million-year-old hominid, Lucy, was as adept at upright walking as we are. Bipedality could date from the earliest phase of human evolution

by C. Owen Lovejoy

Asked to choose the most distinctive feature of the human species, many people would cite our massive brain. Others might mention our ability to make and use sophisticated tools. A third feature also sets us apart: our upright mode of locomotion, which is found only in human beings and our immediate ancestors. All other primates are basically quadrupedal, and with good reason: walking on two limbs instead of four has many drawbacks. It deprives us of speed and agility and all but eliminates our capacity to climb trees, which yield many important primate foods, such as fruits and nuts.

For most of this century evolutionary theorists have held that human ancestors evolved this strange mode of locomotion because it freed their hands to carry the tools their larger brains enabled them to make. Over the past two decades, however, knowledge of the human fossil record has expanded. Neither a unique brain nor stone tools are in evidence among our earliest known ancestors, the australopithecines of three million years ago and more. Yet these same ancestors do clearly show many of the hallmarks of bipedal walking.

How long had human ancestors been walking upright? Was bipedality fully developed in the hominids of three million years ago, or did they sometimes revert to using all four limbs for running or climbing? The answers can help to solve the puzzle of bipedality's role in early human evolution. If upright walking was well established by the time of *Australopithecus,* its advent could date back as far as the earliest hominids, whose lineage probably diverged from other primates some eight or 10 million years ago. The development of erect walking may have been a crucial initiating event in human evolution.

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I have proposed that bipedality accompanied a set of behavioral adaptations that became the key evolutionary innovation of humanity's earliest ancestors. These adaptations included, in effect, the nuclear family: lasting monogamy together with care of the offspring by both parents. The male's contribution took the form of providing high-energy food, which expanded the mother's ability to nurture and protect each infant and also enabled her to give birth more often. Bipedality figured in this new reproductive scheme because by freeing the hands it made it possible for the male to carry food gathered far from his mate. These developments must have come long before the current hominid fossil record begins.

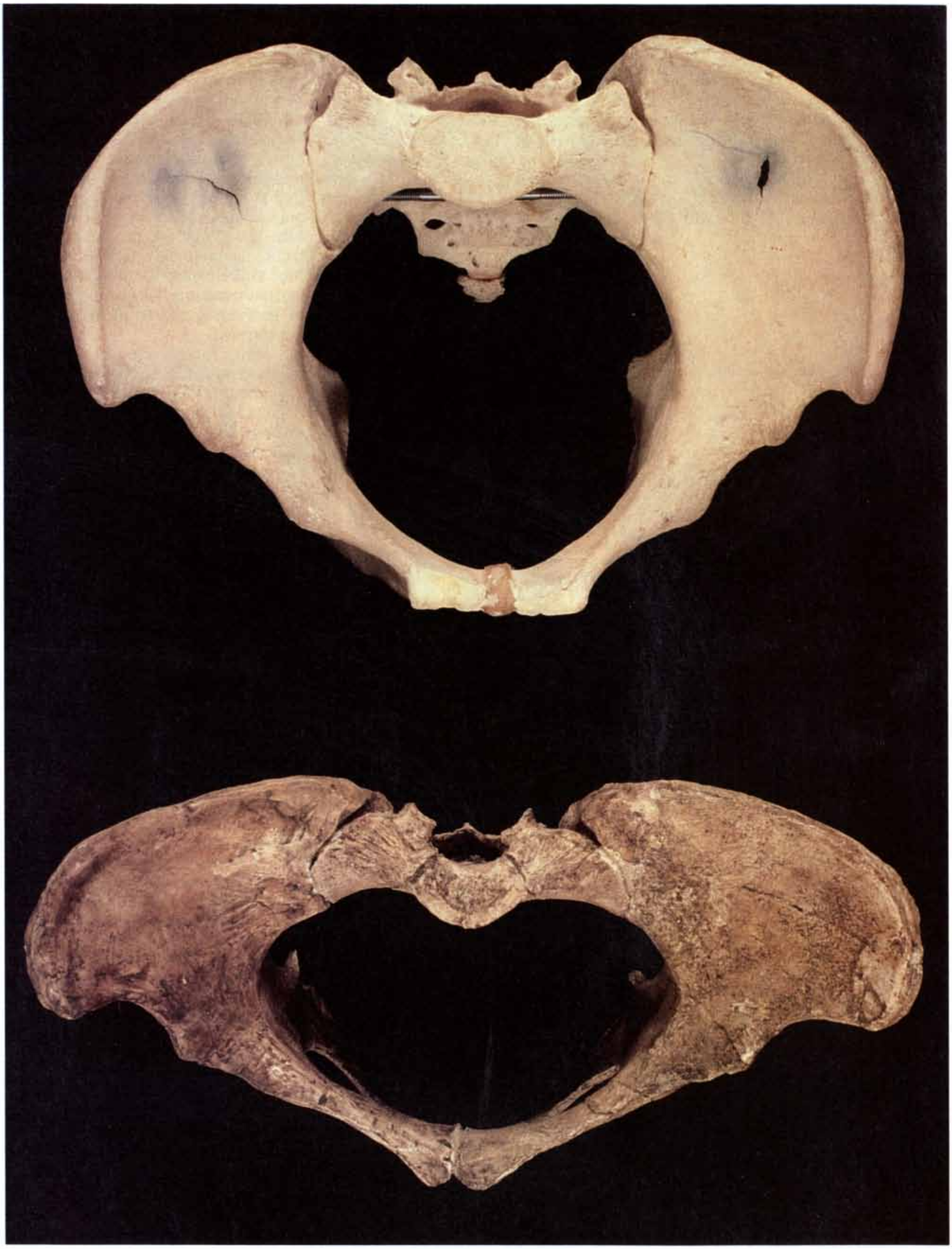
Upright walking should therefore have been perfected by the time of an australopithecine female whose fossil has become a test case for early walking. In 1974 the continuing search for human ancestors in the Afar Triangle of Ethiopia, led by Donald C. Johanson of the Institute of Human Origins in Berkeley, Calif., was splendidly rewarded by the recovery of the "Lucy" skeleton, known formally as A.L. 288-1. Although the skeleton is not quite complete, it preserves far more detail than any comparable fossil. In particular, it includes many of the lower-limb bones, one of the innominate bones that, in a mirror-image pair, make up the primate pelvis, and an intact sacrum (the fused vertebrae at the back of the pelvis). Upright walking is so dependent on this structure that an analysis of Lucy's pelvis can reveal how well she and her contemporaries walked.

The distinctive pelvic features of a biped reflect the very different mechanics of two- and four-legged locomotion. In order to propel itself any terrestrial mammal must apply a force against the ground in a direction opposite to the direction of travel. It does so by extending the joints of its legs, which lie between the ground and the animal's center of mass. Lengthening a leg produces a "ground reaction" that propels the torso in a direction determined by the angle between the leg and the ground.

In the quadrupedal posture of most primates the center of mass lies well forward of the hind limbs. Hence extending the hind limbs generates a ground reaction that has a large horizontal component. Because the hip and knee joints of the hind limbs are tightly flexed at the start of each cycle, their extension can be prolonged and powerful.

Our upright posture, in contrast, places our center of mass almost directly over the foot. If we stand erect and lengthen our legs by straightening the knee and rotating the ankle, the ground reaction is directed vertically and we end up on tiptoe. In order to propel our upright trunk we must reposition our center of mass ahead of one leg. The trailing limb is lengthened to produce a ground reaction while the other leg is swung forward to keep the trunk from falling. The strength of the ground reaction is limited, because much of it is still directed vertically and also because the trailing limb is already near its limit of extension owing to our upright posture: the hip joint is fully extended and the knee joint nearly so.

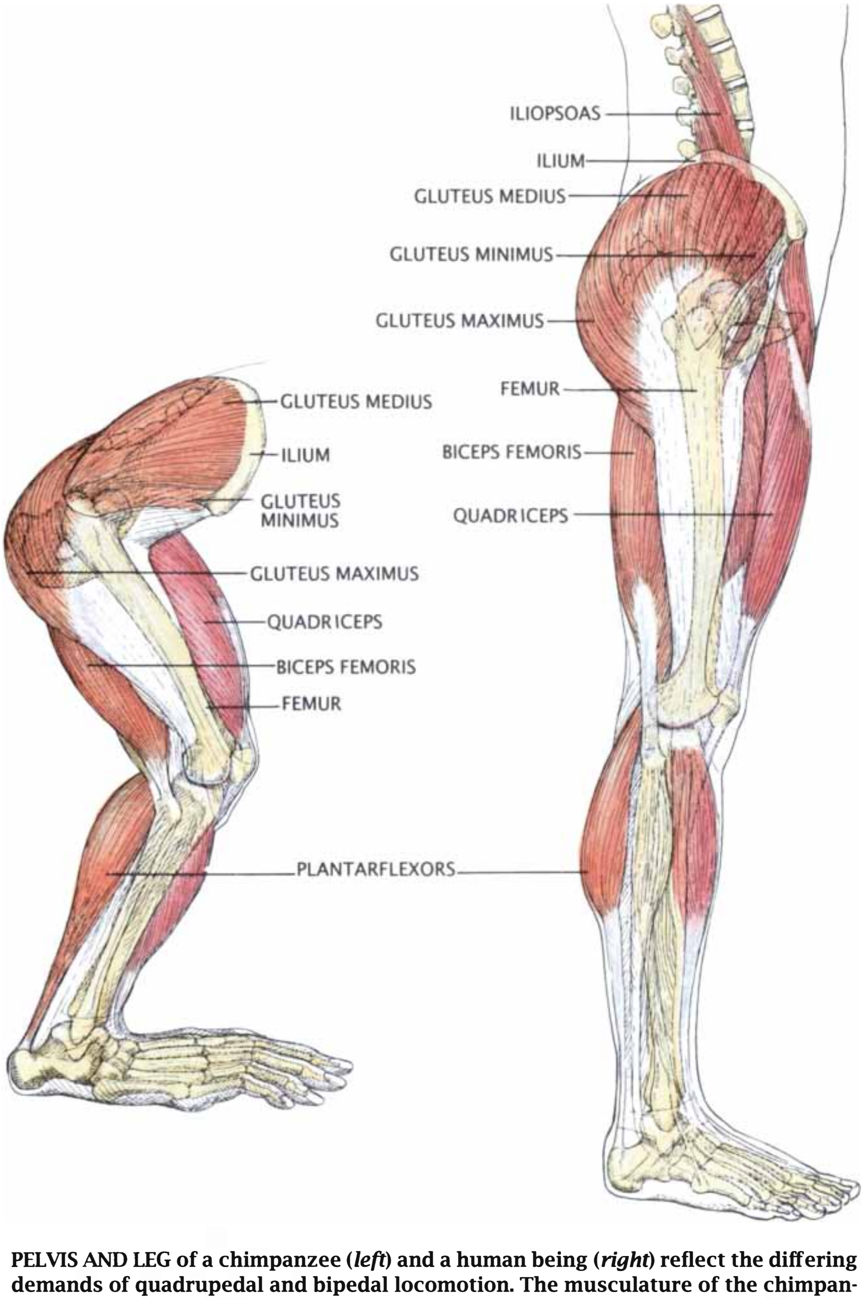
With the new bipedal strategy there came new roles for most of the muscle



PELVISES of a modern human female (*top*) and Lucy (*bottom*) are separated by three million years of evolution but bear the same hallmarks of upright walking. The major change visible in this view—the more ovoid form of the human pelvis—accompanied an expansion of the birth canal, needed because of the increase in brain size since Lucy. The author and Barbara Brown restored the Lucy pelvis from the fragmented fossil; Larry Rubens of Kent State University made the photograph.

groups in the lower limb—roles that in turn required changes in the muscles' structure or position and hence in the design of the pelvis. A comparison of the human pelvis with that of our closest living relative, the chimpanzee, highlights these changes in mechanical design.

The need to stabilize an upright torso dictated the most dramatic change in musculature that has come with the adoption of bipedality: the transformation of the gluteus maximus, a relatively minor muscle in the chimpanzee, into the largest muscle in the human body. The gluteus maximus originates over much of the back of the pelvis and is attached to the back and side of the upper femur, or thighbone. As such it is defined as a hip extensor, and many classical anatomists believed it serves as the major propulsive muscle in upright walking. By straightening the hip, it was thought, the gluteus maximus contributes to the ground reaction imparted by the trailing leg.



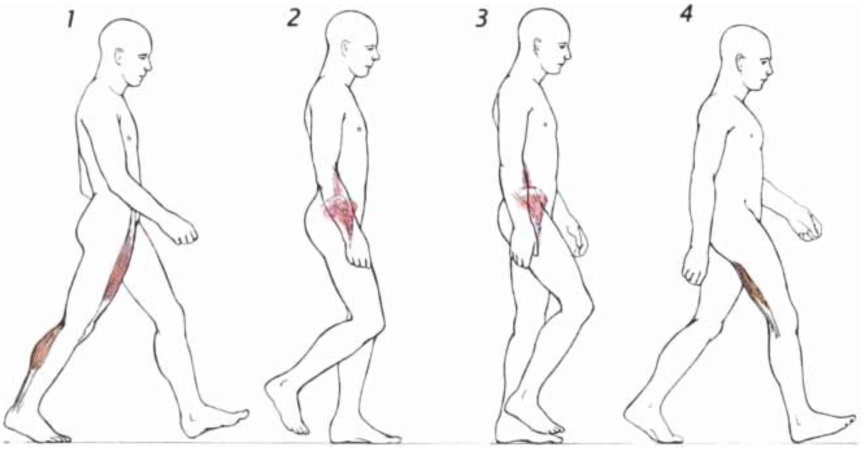
PELVIS AND LEG of a chimpanzee (*left*) and a human being (*right*) reflect the differing demands of quadrupedal and bipedal locomotion. The musculature of the chimpanzee pelvis is dominated by the gluteus medius and gluteus minimus, which help to propel the animal by extending its hip joint. They are joined in that task by the hamstrings, which include the biceps femoris. In humans the gluteus maximus dominates the pelvis; it serves the new function of stabilizing the upright trunk. (The shortening of the ilium lowers the trunk's center of mass and makes it easier to control.) Other major muscles, such as the gluteus medius and minimus, the hamstrings and the iliopsoas, also play new auxiliary roles in upright walking. Only two muscle groups—the quadriceps and plantarflexors—are left to provide propulsion.

Actually, because the hip is almost completely extended in the first place during erect walking and running, the muscle's contribution to ground reaction is limited. Its hypertrophy in human beings reflects a quite different function. When we run, our upright trunk tends to flex forward at each foot strike owing to momentum. The gluteus maximus has taken on the role of preventing the trunk from pitching forward.

A major modification of the pelvis has made the muscle's stabilizing task considerably easier. Each innominate bone in the pelvis is topped by a blade of bone called an ilium; most of the lower viscera are cradled in the space between the two ilia. In the chimpanzee and other primates the ilia are much longer than they are in humans. The long ilia have the effect of lengthening the torso; when these primates rear up, their center of mass lies well above their hip joints. In the language of engineering, their trunk has a long lever arm. A gluteus maximus working to hold such a trunk upright would tire rapidly. The dramatically shortened human ilium shortens the torso and brings the trunk's center of mass much closer to the hip joints, thereby reducing the muscle's mechanical disadvantage.

The ilium is long in the apes to accommodate a second muscle group that was transformed as our ancestors began walking upright: the anterior gluteals, composed of the gluteus medius and the gluteus minimus. In the chimpanzee these muscles contract between attachment points near the top of the ilium and on the outside of the upper femur. Their position enables them to serve as powerful hip extensors during quadrupedal locomotion, and because the ilium is long, the muscles have a large range of contraction. Human beings can forgo this almost universal skeletal feature of other primates because hip extension contributes very little to bipedal locomotion. Our anterior gluteals have been freed to assume a new role.

This new role is best understood by imagining a head-on view of a person walking. Soon after the heel of the leading foot strikes the ground, the trailing leg leaves the surface and begins to swing forward. While it does so the trunk is supported by only one hip, which lies well to the side of the



MUSCLE ACTIVITY during human striding is diagrammed. As the weight-bearing leg (here the right leg) becomes angled behind the torso (*1*), two muscle groups contract to extend it, generating a "ground reaction" that propels the body; they are the plantarflexors, which rotate the foot around the ankle, and the quadriceps, which straighten the knee. The foot then leaves the ground as weight is tranferred to the left leg. Contraction of the iliopsoas begins to tug the right leg forward (*2*) while the knee flexes passively (*3*). Near the end of the leg's swing the hamstrings contract to stop it, and the foot is planted (*4*). The left leg in turn generates ground reaction.

trunk's center of mass. On their own the pelvis and trunk would tip toward the unsupported side at each step, causing rapid fatigue; they are prevented from doing so by the action of the anterior gluteals, which are also referred to as abductors in human beings.

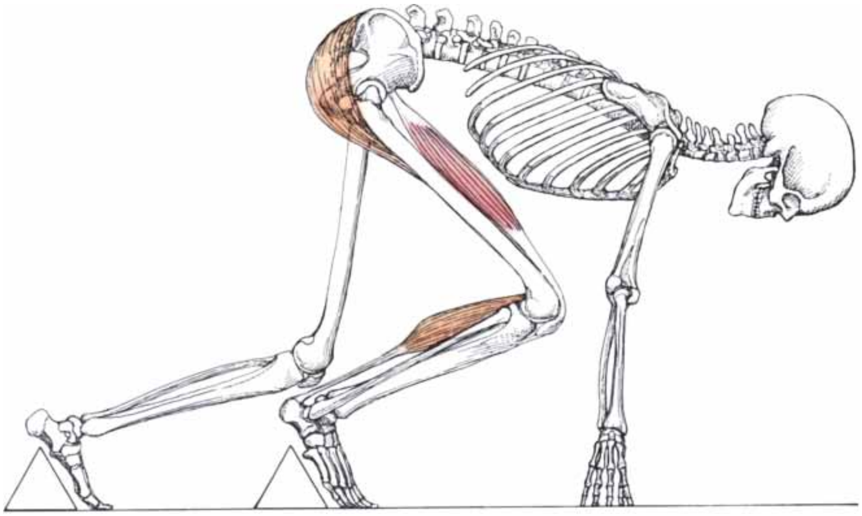
The transformation of the anterior gluteals from propulsive muscles to stabilizing ones required major changes in their position. A top view of the human and chimpanzee pelvises reveals a radical reorientation of the iliac blades in the human pelvis. In the chimpanzee the blades are flat and lie more or less in a single plane across the back of the torso. In humans each ilium has been rotated forward, carrying with it the upper attachment point of the gluteals. Their lower attachment point falls on the outside of the upper femur, where the bone forms a neck that angles in to meet the pelvis at the hip joint. The abductors are thus disposed laterally in humans, away from the hip joints, which puts them in position to balance the pelvis against the weight of the trunk.

The reorientation of the ilia required two other changes in pelvic design not dictated directly by the mechanics of bipedality. If the ilia had simply been rotated forward, the space between them would have been sharply narrowed, leaving no room for the lower viscera. In compensation the sacrum, which separates the ilia at the back of the pelvis, has grown wider and the ilia have changed in shape: they are dished, so that the bending that has reoriented the abductors takes place well to the side, leaving ample room within the pelvis.

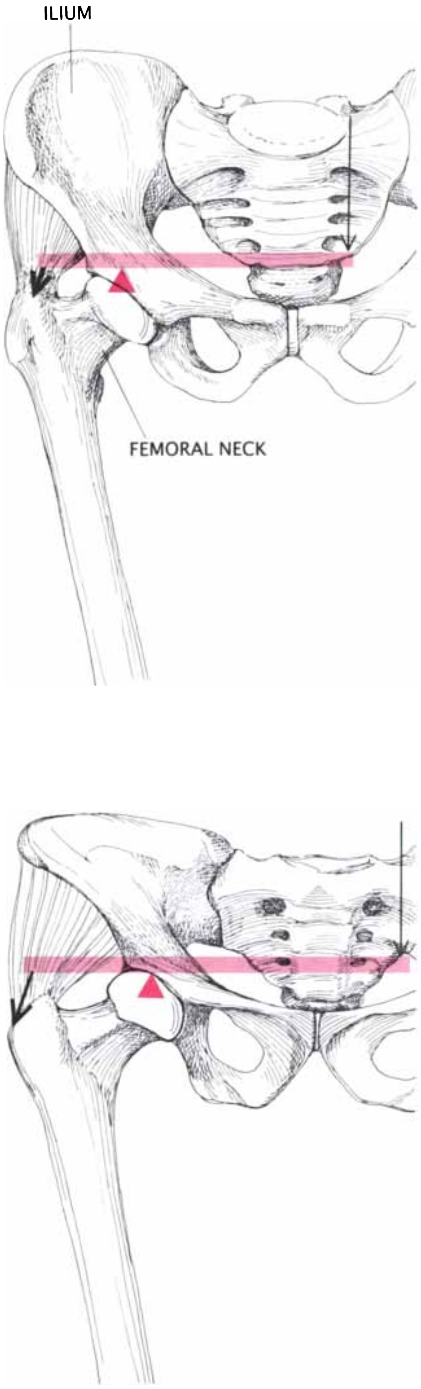
By increasing the distance between the hip joints, however, this widening of the central pelvis placed the abductors in a position of considerable mechanical disadvantage. The force the abductors must exert to offset the weight of the trunk depends in part on how far to the side of the trunk's center of mass each hip joint lies. The greater the separation of the hip joints is, the longer the trunk's lever arm will be and the harder these muscles will have to contract to offset its weight. They will be more likely to tire during walking, and the safety of the hip joint itself may be threatened, since the joint is subjected to both the weight of the torso and the abductors' force of contraction.

A front view of the human pelvis reveals the evolutionary solution. The abductors' own lever arm can be increased, and their work made easier, if their upper and lower attachment points are moved farther out from the hip joint. Two features of the human pelvis serve that purpose. The complex curvature of the human ilium includes an outward flare, which displaces the upper attachment point of the abductors to the side of the hip. In addition the human femoral neck is longer than that of the chimpanzee. The longer femoral neck serves to move the abductors' lower attachment point outward as well, adding to their leverage.

One set of muscles—the anterior gluteals—that help to propel chimpanzees has thus become co-opted to stabilize the human pelvis. A new role is also evident for another set of propulsive muscles in the chimpanzee: the hamstrings. They connect the lower pelvis to the back of the femur; in quadrupedal locomotion



SPRINTER on the starting block briefly recovers the advantages of being quadrupedal: the hip and knee joints are tightly flexed, preparing the limbs for prolonged and powerful extension, and the center of mass is positioned well forward of the legs, which gives the ground reaction a strong horizontal component. Ordinary walking or running sacrifices these advantages. An upright posture requires the hip and knee joints to be almost fully extended and places the body's center of mass almost directly over the legs. Both factors tend to limit the strength of the ground reaction.



ABDUCTOR MUSCLES (the gluteus medius and minimus) contract to counterbalance the torso when the human pelvis is supported on only one leg. The hip joint acts as a fulcrum, with the weight of the torso and unsupported leg bearing down on one side and the abductors acting on the other (*top*). The abductors are at a mechanical disadvantage: the hip joint lies well to the side of the torso's center of mass, giving the body weight a long lever arm. In the Lucy pelvis (*bottom*) the body-weight lever arm was even longer, but greater lateral flare of the ilium and a longer femoral neck placed the abductors farther from the hip joint, increasing their mechanical advantage.

they serve as powerful hip extensors, which contribute even more to ground reaction than the anterior gluteals do. In bipedal walking, in contrast, they serve not to extend the limb but to control it.

A biped must swing each leg forward rapidly when it is not bearing weight. Because the limb is carried almost fully extended in a biped rather than tightly flexed, as it is in a quadruped, its center of mass lies well away from the pelvis. Like a long pendulum, an extended leg has a large moment of inertia, and it takes powerful muscle impulses to start and stop its swing. The iliopsoas, a muscle that originates within the pelvis and extends forward to an attachment point on the femur just below the hip joint, contracts to tug the limb forward. Once the leg has completed its arc, its swing must be checked. The position of the hamstrings, which is largely unchanged from the position in other primates, enables them to contract and decelerate the limb.

In human beings, then, the demands of stabilizing the pelvis and controlling the limb occupy several muscle groups that serve for propulsion in the chimpanzee. Only two muscle groups, the quadriceps and the plantarflexors, are left in positions that enable them to produce a ground reaction. The quadriceps are a mass of four muscles that make up most of the front of the human thigh. They end in a stout tendon, which crosses the patella, or kneecap, and is anchored to the top of the tibia, the main bone of the lower leg.

As the weight-bearing leg becomes angled behind the torso during walking or running, this powerful muscle mass contracts and straightens the knee. The plantarflexors, which originate at the back of the lower leg and are attached to the heel by the Achilles tendon, contract in synchrony with the quadriceps and cause the foot to rotate about the ankle. The extension of the knee and the rotation of the foot together lengthen the trailing leg, producing a strong ground reaction.

How well developed was this set of muscular adaptations by the time of Lucy and her kin, according to the fossil evidence? The discovery included a largely intact sacrum, but the innominate bone that accompanied it had been broken and partially crushed; it consisted of about 40 separate pieces fused into a single mass by the matrix of stone in which it was preserved. Often a fossil in this condition can be reduced to its separate pieces and then reassembled like a jigsaw puzzle. The pieces of Lucy's innominate, however, could not safely be separated. Instead I took a cast of each piece and assembled the casts in proper anatomical juxtaposition; the restored innominate was then mirror-imaged to create its opposite number. The result was a complete pelvis of an almost three-million-year-old human ancestor.

The pelvis bears all the hallmarks of bipedality seen in our own. Its ilia are much shorter than those in the pelvis of an ape. The shortening would have lowered the trunk's center of mass and made it easier to keep upright. The ilia have also become bent around to provide lateral attachment for the abductor muscles that stabilize the bipedal pelvis when it is supported on one leg. The attachment points for the gluteus maximus, abductors and quadriceps can be seen, and they indicate that in Lucy these muscles had attained a size and disposition remarkably similar to our own arrangement. The same is true for the iliopsoas, the hip flexor that initiates the swing of the leg: a groove on the brim of the pelvis, ahead of the hip joint, matches the groove that indicates the muscle's course in the human pelvis.

In one respect Lucy seems to have been even better designed for bipedality than we are. Her ilia flare outward more sharply than those of a modern pelvis and her femoral necks are longer. Her abductor muscles thus enjoyed a greater mechanical advantage than these muscles do in modern females. Some of the abductors' advantage merely compensated for the slightly wider separation of her hip joints (which gave her trunk a longer lever arm). Yet accurate measurements of both the abductor and the trunk lever arms—possible because the Lucy pelvis is so complete—show that her abductor advantage is still greater than our own. Her abductors had to exert less force to stabilize the pelvis, which also reduced the pressure on the hip-joint surfaces.

Why should a three-million-year-old hominid have had this mechanical advantage over her descendants? The answer lies in the accelerated growth of the human brain during the past three million years. Lucy's pelvis was almost singularly designed for bipedality. The flaring ilia and long femoral necks increased her abductors' lever arm, but they yielded a pelvis that in top view was markedly elliptical, resulting in a birth canal that was wide but short from front to back. The constriction was tolerable because Lucy predated the dramatic expansion of the brain; her infant's cranium would have been no larger than a baby chimpanzee's. The process of birth in Lucy and her contemporaries would have been slightly more complex than in an ape, but much easier than the modern human birth process [*see illustration on page 125*].

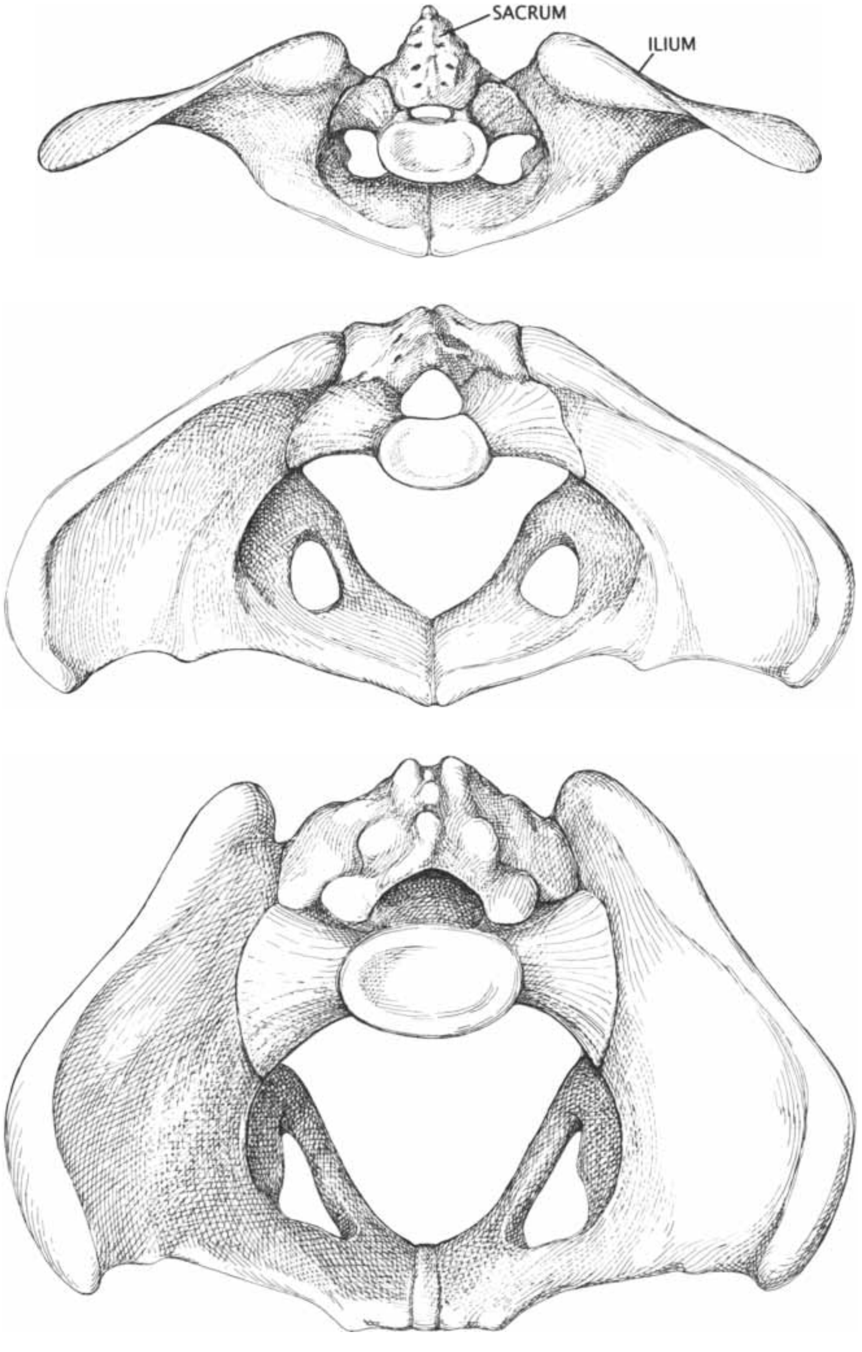
As human ancestors evolved a larger brain, the pelvic opening had to become rounder. The pelvis had to expand from front to back, but at the same time it contracted slightly from side to side. In the process the flare of the ilia was reduced, leaving us with a somewhat shorter abductor lever arm than Lucy's. (These changes are less pronounced in the modern male pelvis, where the abductors retain some of their former mechanical advantage.) Meanwhile the head of the modern femur has become enlarged to withstand increased pressure from the harder-working abductors. The difficulty of accommodating in the same pelvis an effective bipedal hip joint and an adequate passage for a large infant brain remains acute, however, and the human birth process is one of the most difficult in the animal kingdom.

The close resemblance of Lucy's pelvis to that of a modern human and its dramatic contrast to the pelvis of a chimpanzee make it clear that she walked fully upright. But was her bipedal progression truly habitual? Had she forsaken all other kinds of locomotion? The muscular rearrangements that enabled her to walk upright would not have allowed efficient quadrupedal movement on the ground. Perhaps, however, she often took to the trees and climbed, as most primates do, using all four limbs.

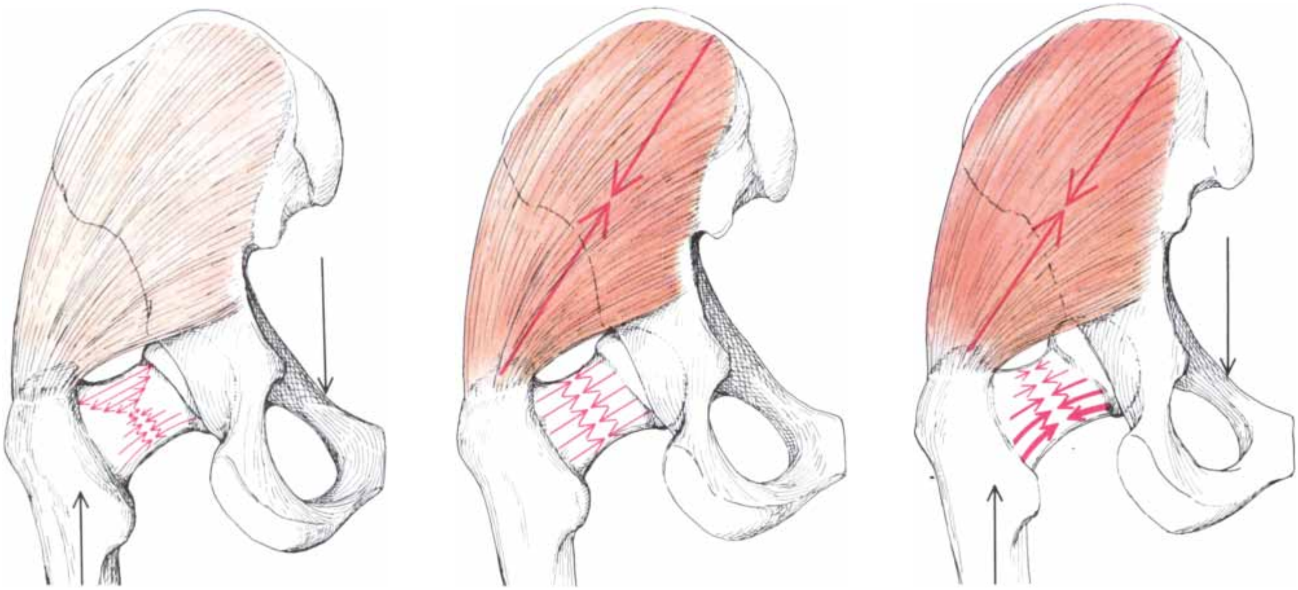
Basic evolutionary principles provide one kind of verdict on the possibility. A species cannot develop detailed anatomical modifications for a particular behavior, such as bipedality, unless it consistently employs that behavior. For natural selection to have so thoroughly modified for bipedality the skeleton Lucy inherited, her ancestors must already have spent most of their time on the ground, walking upright. Analysis of the Lucy fossil, however, can yield more direct evidence.

The analysis focuses on the neck of the femur, where much of the stress of locomotion is concentrated. When the leg is bearing weight, the hip joint transmits the weight of the torso to the femoral neck. The neck acts as a cantilevered beam: a beam that is anchored at one end to a supporting structure (the shaft of the femur) and carries a load at the other end. Cantilevering results in high bending stresses at the beam's anchorage—compression along the bottom of the beam and tension along the top—and the stresses increase with the length of the beam. A long femoral neck such as Lucy's reduces pressure on the hip joint by improving the leverage of the abductors, but the neck itself is subject to higher bending stresses.

The femoral neck of the chimpanzee is much shorter than the modern human one; nonetheless, it is robustly engineered to withstand the loads im-



ROTATION OF THE ILIA took place as human ancestors began walking upright. In a quadrupedal ape such as a chimpanzee (*top*) the ilia (seen here from above) lie almost flat against the back of the torso. In Lucy (*middle*) they have become bent around, providing lateral attachment points for the abductor muscles, which stabilize the pelvis during walking. The bending takes place well away from the center of the pelvis, leaving room for the viscera; in addition the sacrum, which separates the ilia, has widened. These changes are retained in the modern human pelvis (*bottom*), which has also become longer from front to back to create a more ovoid birth canal.

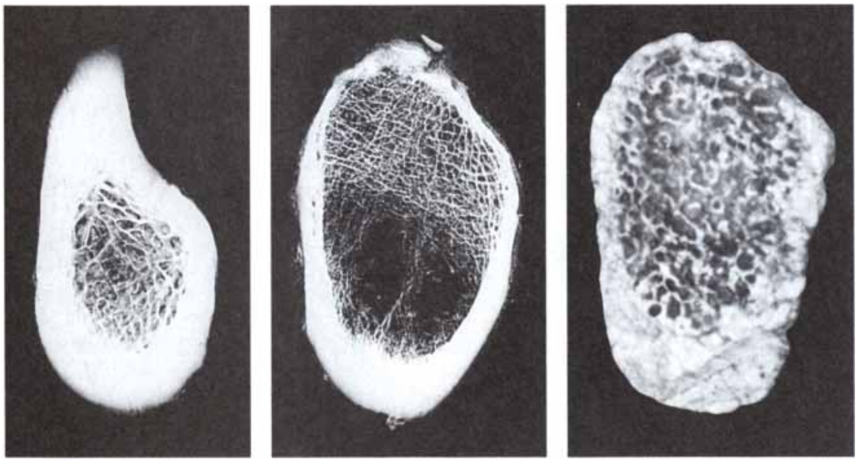


NECK OF THE FEMUR (shown from the back) is subjected to stress from two sources during human walking. Body weight imposes bending stress: tension on the top of the neck and compression on the bottom (*left*). At the same time the abductors, acting almost parallel to the femoral neck, subject its entire diameter to compression (*middle*). The sum of the two stress patterns is a gradient of stress running from low stress at the top to high compressive stress at the bottom (*right*).

posed by the animal's terrestrial and arboreal acrobatics. A cross section of the bone reveals a central marrow-filled channel surrounded by a thick layer of dense bone. Dense bone is weaker under tension than it is under compression, and so the upper surface of the structure, which will be subjected to tension when the neck is bent, carries a markedly thicker layer of bone. With this ridge of thick bone (a bone "spike" in cross section), the chimpanzee femoral neck imitates the principle of an I beam: material is placed where it can best resist bending stresses.

Because the human femoral neck is longer than the chimpanzee's and must resist the combined force of body weight and abductor contraction, one would expect it to be even more robustly constructed. A cross section of the human bone reveals a surprise: the outer ring of solid bone is thick only at the bottom, and the rest of the neck is bounded by a thin shell of bone and filled in by a lattice of fine bone plates called trabeculae. Such porous bone, as one might expect, is weaker than solid material. The upper part of the femoral neck, where tensile stresses are presumably the highest, actually contains less bone than any other part of the structure. How can our femoral neck survive the greater stresses imposed by its length and function when it seems so much less sturdy than the femoral neck of the chimpanzee?

The answer lies in the action of muscles that operate only in bipedal locomotion: the abductors. These muscles have lines of action that are not vertical but are sharply inclined, which makes them roughly parallel to the femoral neck. When they contract, they push the femoral neck into the hip socket, compressing the neck along its length. This compressive stress combines with the stresses that result from bending (tension on the top of the femoral neck and compression on the bottom). The effect is to eliminate tension at the top of the femoral neck and create a gradient of increasing stress running from the top of the femoral neck, where stress is now minimal, to the bottom, where stress is very high but purely compressive. The bottom of the human femoral neck has a robust layer of solid bone, and even the porous bone that fills in the rest of the section



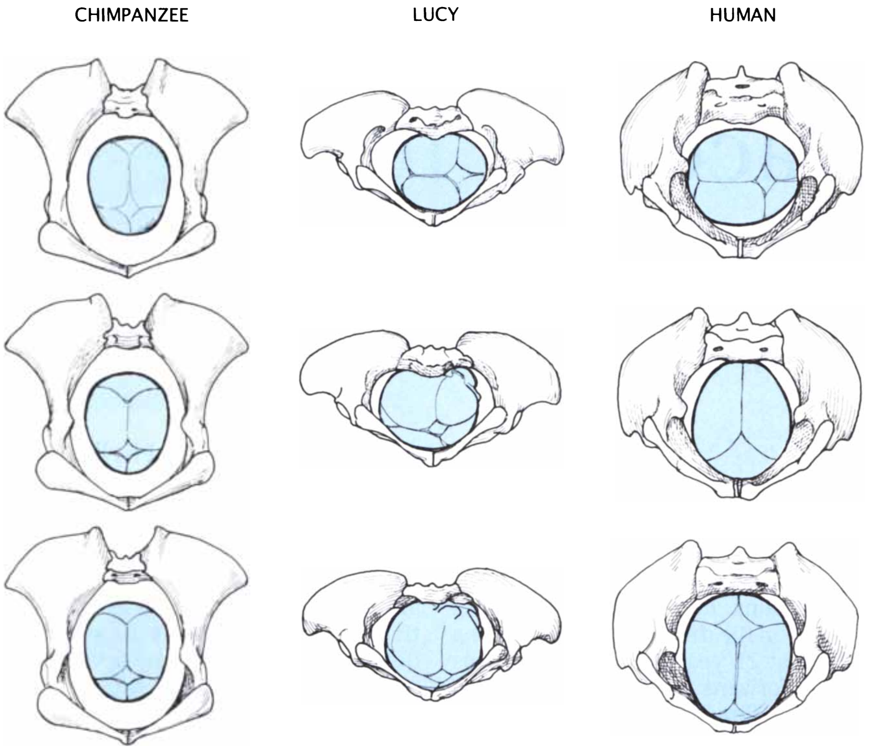
INTERNAL STRUCTURE of the femoral neck distinguishes habitual bipeds. Seen in cross section, the femoral neck of the chimpanzee (*left*) has a robust thickness of bone together with a reinforcing ridge (visible in this section as a spike) at the top. These features enable the chimpanzee femoral neck to withstand the high bending stresses imposed by climbing and leaping. The human femoral neck (*middle*) has only a thin layer of bone at the top. It is suited only to the stresses of upright walking and running, when the abductor muscles counteract tension on the top of the neck. A fossil femoral neck from a contemporary of Lucy (*right*) has the same structure as the human one; it was designed exclusively for bipedal walking.

is reasonably strong as long as it remains under compression.

Other muscles work with the abductors to keep the femoral neck under compression when it is loaded. The most important of them is the piriformis, which originates on the front of the sacrum and extends to the outer end of the femoral neck. That orientation enables the muscle to increase the femoral neck's level of compression. The synchronized action of all these muscles when body weight is supported on one leg makes it possible for this seemingly fragile bone to cope with its load.

Because of its distribution of bone, however, the femoral neck is indeed vulnerable if the abductors and other muscles do not act in the proper synchrony. The femoral neck is a primary site of fracture in old age, and not just because bone quality is reduced in old people. These "broken hips" are also a product of reduced muscular coordination. Thus the design of the human femoral neck requires the muscular action of bipedal walking. The bone is poorly engineered for climbing and arboreal acrobatics, where it would be frequently subjected to bending stresses without being compressed at the same time by the abductors.

The femoral neck in *Australopithecus,* because it was even longer than that of modern humans, was subject to even greater bending stresses. If these human ancestors had often taken to the trees, stressing their femoral neck without coordinated compression by the abductors, the bone would have had to have been even more robust than it is in the apes. Was it? The same site where Lucy was found also yielded several femurs that had broken during their long burial, affording a view of the neck's internal structure. Each specimen clearly shows the human feature of thin bone on the upper part of the femoral neck. Lucy's femoral neck, then, was suited exclusively for bipedality. She was not just capable of walking upright; it had become her only choice.



BIRTH PROCESS has competed with bipedality in shaping the modern human pelvis. In the chimpanzee pelvis (shown from the back) the head of the fetus descends without difficulty through the inlet (*top*), midplane (*middle*) and outlet (*bottom*) of the birth canal. In Lucy the birth process was somewhat more difficult: her short, flaring ilia were well suited to bipedality but resulted in a birth canal that was broad but constricted from front to back. Her infant's cranium could pass through only if it was first turned sideways and then tilted. The much larger brain in the human infant demands a rounder birth canal. The necessary lengthening of the pelvis reduced the flare of the ilia and hence the mechanical advantage of the abductor muscles; even so, the human birth process is complex and traumatic, requiring a second rotation of the fetal cranium within the birth canal. The illustration is based on one by Robert G. Tague of Louisiana State University and Linda Budinoff of Kent State.

I have concentrated on the pelvic anatomy of Lucy because the hallmarks of bipedality are so vivid there. A review of the rest of her skeleton and of other *Australopithecus* skeletons would reveal equally dramatic modifications that favor bipedality and rule out other modes of locomotion. The knee, for example, is adapted for withstanding greater stress during complete extension than the knee of other primates, and its design brings the femur and the tibia together at a slight angle, so that the foot can easily be planted directly under the body's center of mass when body weight is supported on one leg. The ankle is also modified for supporting the entire body weight, and a shock-absorbing arch helps the foot to cope with the added load. The great toe is no longer opposable, as it is in quadrupedal apes, but runs parallel to the other digits. The foot is now a propulsive lever for upright walking rather than a grasping device for arboreal travel. The arms have also become less suited to climbing: both the limb as a whole and the fingers have grown shorter than they are in the apes.

Lucy's ancestors must have left the trees and risen from four limbs onto two well before her time, probably at the very beginning of human evolution. I have suggested an explanation of why bipedality, with its many disadvantages, appeared long before our ancestors could have put their freed hands to use in carrying tools or weapons: it was part of a novel reproductive strategy that included provisioning by the male, a strategy that enabled the first hominids to flourish and diversify. The explanation will continue to be debated, but the evidence is conclusive that this curious form of locomotion was among the first anatomical characteristics to mark the ascent to cognitive life.

FURTHER READING

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