

BIPEDAL ADAPTATIONS IN THE HOMINID PELVIS

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INTRODUCTION

Two major features are unique to humans among all the living primates: A very large brain, and moving about upright on two legs exclusively. One of these, bipedalism, appeared long before the other. Many anatomical features of *Australopithecus afarensis* anatomy demonstrate habitual bipedal locomotion, and the 3.6 million-year-old footprints discovered by Paul Abell at Laetoli in 1978 confirm it unequivocally (White, 1980). Not until the appearance of *Homo erectus*, some 1.7 million years later, could hominids be considered on their way to being large-brained (Stanford, et al., 2006).

While certain adaptations seen in the knee (e.g. the valgus angle), in the foot (such as a fully adducted hallux), and to a lesser extent in the cranium (a fully inferior foramen magnum) are all strong indicators for bipedalism (Lewin and Foley, 2004), the most interesting evolutionary changes necessary for upright posture occurred in the hominid pelvis. All of these adaptations are present not only in the pelvises of modern humans, but also in all members of the Genus *Homo*, and in the earliest known hominids, the *Australopithecines*.

PELVIC ADAPTATIONS FOR BIPEDALISM

The hominid pelvis displays many unique features (when compared to that of quadrupedal primates) that support bipedalism. The major adaptations are seen in the sacrum and the ilia, as well as in the overall configuration and orientation of the pelvic bones.

Several important changes occur in the sacrum. The broadening of the sacrum (and overall broadening of the pelvis) is critical for erect posture since it provides a basin for the support of the viscera, a function performed by the rib cage in quadrupeds (Snell and Donhuysen, 1968; Wolpoff, 1999).

The hominid sacrum is also positioned differently, tilting forward relative to the ilium. This change in orientation supports the convex curvature of the lumbar spine (in the sagittal plane and oriented anteriorly), known as "lordosis." This curvature, combined with the

concave curvature of the thoracic spine, keeps the center of gravity of the torso directly over the pelvis (Wolpoff, 1999). The forward tilt provides another important benefit: It places the sacroiliac joints in vertical alignment with the acetabula, significantly reducing the muscle action required to stabilize/balance the torso while standing (ibid.).

These changes in the sacrum facilitate standing on two legs, but more pelvic changes are required to walk on two legs. To walk, we push off with one foot and swing the other leg forward. Once the other leg begins this swing, it necessarily loses contact with the ground, requiring the first leg to bear all of the weight of the body. This is where some big changes were required in the shape of the pelvis and the function of some muscles.

The ilia in quadrupedal primates (such as Chimpanzees and Gorillas) are tall, slender, and lie in the coronal plane (Lovejoy, 2005). The anterior gluteal muscles (gluteus medius m. and gluteus minimus m.) attached to the dorsal surface of the ilium in apes act as powerful extensors for quadrupedal locomotion (Lovejoy, 1988). In hominids, the ilia are rotated and curved medially, bringing the lateral edge of the blade forward and projecting the top of the ilia outward laterally. The result is that the attachment points of the anterior gluteal muscles are now in a position superior rather than posterior to the acetabulum, turning these muscles into abductors for the oxofemoral joint (ibid.).

In their new role, the gluteal abductors are not so much used to abduct the leg, but rather to stabilize the pelvis mediolaterally when all of the body's weight is on that leg. Without this capability, the hominid pelvis (and thorax) would topple over toward whichever leg was lifted off the ground (Snell and Donhuysen, 1968). Gorillas and chimpanzees lack such abductors, and are forced to execute gross movements to shift their weight from side to side whenever they walk bipedally. The lateral extension of the top of the hominid ilium improves the efficiency of the stabilizing mechanism by moving the abductor attachment points to a location lateral of the hip joint, giving the muscles more leverage (Wolpoff, 1999).

The rotation of the ilium also projects the medial edge of the blade dorsally, allowing the gluteus maximus to become the major hip extensor in hominids. Its primary job relating to bipedalism is to stabilize the pelvis and thorax, keeping them from pitching forward when the hip flexors are used to swing a leg forward while walking (Lovejoy, 2005).

The hominid pelvis distinguishes itself from quadrupedal primates in another fashion, through the development of robust anterior iliac spines as excellent anchors for some of the muscles used in walking (Wolpoff, 1999). The anterior superior iliac spine is the origin of the sartorius muscle, a knee extensor that helps to put the foot forward. The anterior inferior iliac spine is the origin of the rectus femoris (the only muscle in the quadriceps group which functions as a hip flexor) that helps swing the leg forward while walking.

THE EMERGENCE OF BIPEDAL PELVIC TRAITS

A great deal of time and ink has been spent analyzing and debating whether Australopithecines walked just as humans do, but most agree that Lucy and her relatives provide the earliest conclusive proof of habitual bipedalism among primates. All of the above-mentioned characters of a bipedal pelvis can be observed in the fossil remains of hominids dating back to the Pliocene (McHenry, 1994), yet the pelvis of *A. afarensis* is clearly different from that of modern humans (figure 1).

McHenry (1994) summarizes the pelvic adaptations supporting bipedalism that are shared between *A. afarensis* and *H. sapiens* as follows:

- Fossil specimens attributed to *A. afarensis* clearly indicate the presence of a lumbar lordosis, which, when combined with the thoracic kyphosis, facilitates habitual erect posture;
- the sacral ala are expanded laterally, broadening the pelvis (creating a larger space to support the viscera);
- the iliac blades are mediolaterally expanded (also creating more room to support the viscera), superoinferiorly shortened (making room for the lumbar lordosis), and anteriorly rotated. The rotation placed the origin of the anterior gluteals such that they became hip abductors, where they are critical to mediolateral pelvic stabilization during striding (Lovejoy, 2005). This rotation also moved the origin of the gluteus maximus muscles to positions from which they can control trunk extension sagittally at the time of heel strike;
- the appearance of robust anterior iliac spines to support some hip and knee flexors;

- and the appearance of a distinct iliopsoas groove, which carries another hip flexor used during bipedal gait.

There are also significant differences between the pelvises of early hominids and *H. sapiens*. Many paleoanthropologists agree that the Australopithecine pelvis displays an evolutionary mosaic of both derived and primitive traits (Tuttle, 1981; Lovejoy, 2005; Marchal, 2000; Ashton, 1981; and McHenry, 1982). There are disagreements, however, on the implications of this mixture of traits.

Ashton (1981) performed in-depth analysis of over two dozen pelvic variables for many specimens representing extant apes, *H. sapiens*, and Australopithecines. Of one set of ten features of innominate bones studied, including the length of the ischium, the orientation of the iliac blade, and the position of the anterior superior iliac spine, all of them showed a resemblance to great apes and a uniform lack of similarity with modern humans.

Ashton's analysis of osteometric features relating to the transmittal of weight from the vertebral column to the femora (e.g. the position of the acetabulum, the position of the auricular surface, the separation between the acetabulum and the sacroiliac joint) showed, without exception, a resemblance to the human pelvis and they differed from extant apes. He concludes that Australopithecines are "quite different in their overall morphology from any hypothetical creature intermediate in form between men and apes," and suggests that even though they display certain features conducive to upright posture and gait, he does not believe these features represent an earlier form on the path of human bipedal evolution.

McHenry (1982) believes that Ashton's interpretations go a bit too far, and proposes that the primitive traits in the Australopithecine pelvis which should be shared with the Last Common Ancestor are overshadowed by the many derived traits shared with humans. He ends this point by saying that "taxonomic and phylogenetic affinities should be based solely on shared derived traits."

C. Owen Lovejoy (1988) is firmly in the camp with those who believe *Australopithecus* represents an early human ancestor. He points out that wider ilia provided *A. afarensis* with a greater mechanical advantage for the hip abductors than humans, possibly making them more efficient at walking (since the greater leverage afforded by the more laterally-placed abductors reduces the effort required to stabilize

the pelvis). Lovejoy (2005) makes the case that the later changes seen in the lower portions of human pelvis and the reduced flaring of the human ilia are unrelated to bipedalism, and instead result from the need for a larger birth canal for a "massively brained" fetus. It is possible that the development of a large brain forced a compromise in the morphology of the pelvis, making late hominids less efficient bipeds.

Another piece of evidence pointing to Australopithecines as human ancestors comes from Christine Berge's research (1998) comparing juvenile and adult pelvises from Australopithecines, as well as human pelvises ranging from neonates to adults. Berge found a striking similarity between the morphology of the adult Australopithecus pelvis and that of a neonatal *H. sapiens*.

CONVERGENT BIPEDAL ADAPTATION

Is hominid bipedalism such an unlikely adaptation that it is unique, or could it develop independently under other conditions? A significant amount of fossil remains have been found for *Oreopithecus bambolii*, a Miocene hominoid from the Tuscany region. Its pelvis differs from its contemporaries such as *Dryopithecus*, and multiple features may be linked with bipedality (Kohler and Moya-Sola, 1997).

Specifically, the *Oreopithecus* pelvis shows a hominid-like anterior inferior iliac spine; a pubis closely resembling *A. afarensis*, and its ischial spine is almost identical to that of *Homo*. *Oreopithecus* specimens also show a lordosis, a trait heretofore considered unique to hominids (ibid.).

Kohler and Moya-Sola (1997) propose that *Oreopithecus* may represent convergent evolution of bipedal traits. This is certainly a possibility since *Oreopithecus* was isolated on the island of Tuscany-Sardinia during the Miocene, an environment void of predators. They suggest that while not a habitual biped, *Oreopithecus* may have adapted to standing erect for the purpose of feeding, returning to a quadrupedal mode for locomotion.

CONCLUSIONS

Significant adaptations to the feet and knees were required for efficient bipedal locomotion, but without the many evolutionary

changes seen in the hominid pelvis, upright posture and a human-like gait would be impossible.

While the pelvis of early hominids differs from that of modern humans, they possess all of the traits necessary for habitual bipedalism. The differences seen in *H. sapiens* are the result of later adaptations necessary for the passage of a larger-brained fetus through the pelvis during birth, and do not represent refinements for bipedalism (it is even possible these changes adversely affected the mechanical efficiency of bipedal posture and locomotion).

Lastly, some evidence suggests that bipedal posture in primates may have evolved independently in the hominid lineage and in *Oreopithecus*.

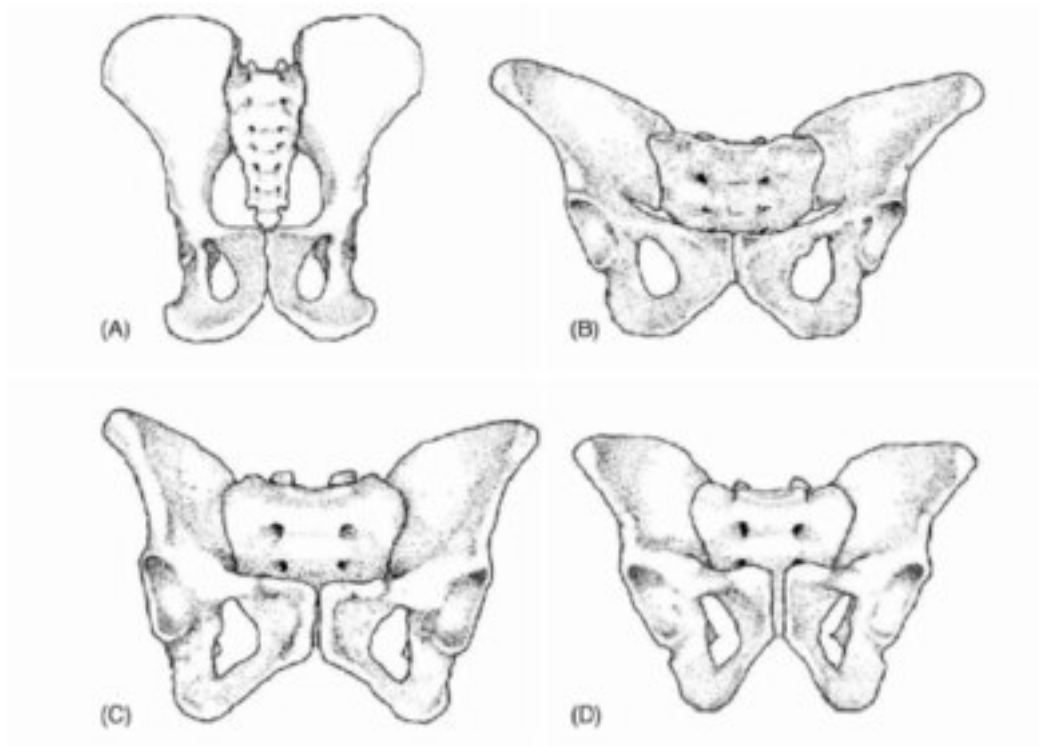


Figure 1: Comparison of pelvises from (A) Pan, (B) Australopithecus, (C) Human female, and (D) Human male (from Lovejoy, 2005, figure 5).

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