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## How did the australopithecines walk? A biomechanical study of the hip and thigh of *Australopithecus afarensis*

Some biomechanical characteristics of the pelvis and lower limb of *Australopithecus afarensis* (AL 288-1) are compared with those of modern humans, in an attempt to define the pattern of australopithecine bipedal locomotion. The reconstruction of the pelvic and femoral morphology of AL 288-1 (Schmid, 1983) is used as a basic skeletal frame to infer (1) the loading constraints acting on the supporting hip; and (2) the action of some of the main muscles of the lower limb. The analysis reconstructs the placements of the australopithecine gluteal musculature, in the pattern of African pongids and of *Homo*. Only the reconstruction of the gluteal musculature on the basis of the pongid pattern is consistent with the bony structure of the fossil and would have permitted effective movements of bipedalism. Moreover, the results clearly indicate that australopithecine bipedalism differs from that of humans. (1) The extended lower limb of australopithecines would have lacked stabilization during walking; and (2) the lower limb would have shown a greater freedom for motion, which can be interpreted as the retention of a partly arboreal behavior.

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### Introduction

The earliest descriptions of the australopithecine pelvic remains have used mainly the morphological characteristics of the hip bone to document the phyletic relationships between the australopithecines and the human lineage. They incorporate the assumption that all hominids share a common bipedal pattern (Dart, 1949*a,b*; Broom & Robinson, 1950; Broom *et al.*, 1950; Le Gros Clark, 1955). For many years, study of australopithecine pelvic morphology depended on a single pelvis of *Australopithecus africanus* from Sterkfontein, which was supposed to have been erroneously reconstructed, and several more or less fragmentary hip bones from Makapan, Swartkrans, and Kromdraai, belonging to the species *A. africanus* and *A. robustus* (Robinson, 1972; Day, 1973). Thus, some morphological data on the australopithecine pelvis and lower limb remained unknown or unreliable, e.g. (1) the distance between the acetabulae, (2) the length and orientation of the pubis, and (3) the relative lengths of the femur and tibia. The discovery of AL 288-1, *Australopithecus afarensis* from Hadar, permitted reconstruction of the morphology of the entire australopithecine pelvis and of its articulation with the lower limb (Johanson *et al.*, 1982; Schmid, 1983; Stern & Susman, 1983; Berge *et al.*, 1984; Tague & Lovejoy, 1986).

Many authors interpreted the most obvious traits of the australopithecine hip bone in terms of locomotor specializations. Zihlman & Hunter (1972) were among the first researchers to point out that the lateral orientation of the australopithecine iliac blade must have implied a less efficient locomotor system than that of *Homo*, affecting medial rotation during bipedality. However, the reconstruction was based on the Makapan ilium and a human femur; this seems to have significantly altered their results. Afterwards, Lovejoy and co-workers (Lovejoy *et al.*, 1973; Lovejoy, 1975) suggest that the morphological differences between *Australopithecus* and *Homo* did not entail significant differences in their gait patterns. Stern & Susman (1983), in a more recent study using the australopithecine pelvis from Hadar, conclude that the bipedal walking of *Australopithecus afarensis* was closer to the pattern of apes, than to that of modern humans.

Consequently, the studies based on various postcranial remains have led to divergent hypotheses about gait and posture of the australopithecines. Conclusions are that (1) the australopithecines and humans share an identical bipedal pattern in terms of efficiency (Lovejoy *et al.*, 1973; Lovejoy, 1975; McHenry & Temerin, 1979); (2) the australopithecines and humans show different patterns of bipedalism (Napier, 1967; Zihlman & Hunter, 1972; Zihlman, 1978; Jungers, 1982, 1988; Berge & Ponge, 1983; Stern & Susman, 1983; Berge, 1984, 1991a,b, 1993; Berge & Kazmierczak, 1986; Sigmon, 1986; Jungers, 1991); and (3) the australopithecines show an arboreal pattern (vertical climbing or suspension in the trees) practised in alternation with terrestrial bipedalism (Prost, 1980; Senut, 1981, 1984; Schmid, 1983; Stern & Susman, 1983; Susman *et al.*, 1984; Senut & Tardieu, 1985; McHenry, 1986; Jungers, 1988).

The present study utilizes the Peter Schmid reconstruction of the Hadar pelvis and femur. It compares the femoro-pelvic morphologies of *Australopithecus afarensis* and *Homo* emphasizing their implications for bipedalism. The peculiar proportions of the australopithecine pelvis and lower limb are considered from two main aspects: first, the gravitational constraints acting on the hip; and second, the action of the gluteal, adductor, and hamstring muscles, which have been shown to be important in maintaining body balance and in controlling the movements of bipedal walking in various biomechanical studies (Steindler, 1955; Napier, 1967; Stern, 1972; Kapandji, 1975; Stern & Susman, 1981; Marzke *et al.*, 1988).

This comparison of fossil and recent specimens incorporates several simplifying assumptions. (1) It is assumed that *Australopithecus* could stand and walk with relatively extended and adducted lower limbs as there are no major morphological obstacles to such behavior. (2) Biomechanical reconstructions of the pelvis are based on projected dimensions; these obviously differ from direct dimensions measured on bones. (3) Reconstruction of the gluteal musculature of *Australopithecus afarensis* is hypothetical, there being no reliable arguments to decide *a priori* whether this musculature was closer to that of humans or apes (Zihlman & Bruner, 1979). (4) The action of muscles is assumed to be that of fibers lying close to a straight line joining the center of the origin on the hip bone to the center of the insertion on the femur; this does not take into account internal compartmentation and action via differently directed ligaments and fascias. In most cases, the construction of muscular action lines is simple. For gluteus superficialis, which has a wide origin and inserts via fascias and ligaments, I decided to consider the action line of the larger portion of the muscular mass, which directly originates and inserts on bones, i.e., the muscle ischio-femoralis for the ape-like pattern, and the muscle gluteus maximus *sensu stricto* for the human-like one. (5) The force generated by the muscle is assumed constant, independent of muscular excursion (Stern, 1974; Gans & De Vrec, 1987). Interpretations of the results must keep these simplifications in mind.

### Material and methods

The studied remains of *Australopithecus afarensis* from Hadar (AL 288-1, Figure 1b) consist of the left hip bone and the complete sacrum. The entire pelvis has been reconstructed by mirror molding (Schmid, 1983), and is now in Anthropologisches Institut der Universität und Museum (Zürich). Schmid (1983) also reconstructed a complete femur by joining the two components of the left diaphysis. The damaged part of the distal epiphysis has been completed on the basis of another fossil from the same site (AL 129).

The fossil of Hadar was compared to the skeleton of an adult female pygmy, *Homo sapiens*, because their sizes are more comparable. The ape-like reconstruction of the australopithecine

gluteal musculature is based on data from personal dissections, whereas the human-like reconstruction is based on anatomical literature (Testut & Latarjet, 1948; Paturet, 1951; Woodburn & Burkel, 1957; Stern, 1988). Muscular data are drawn from four dissections of the lower limbs of African apes; these are two *Pan troglodytes* (male and female) and two *Gorilla* (both males). The source of bones and muscles is now in the Laboratoire d'Anatomie Comparée and the Laboratoire d'Anthropologie of the Muséum National d'Histoire Naturelle (Paris).

The morphological comparison of the fossil of Hadar with human material is based on the following parameters: (1) An estimation of the compressive constraints on the australopithecine hip joint, using a trigonometric analysis of the human hip joint, similar to that of Pauwels (1965, p. 108) for humans, and that of Lovejoy *et al.* (1973, p. 766), for the restored fossil of Sterkfontein. The australopithecine pelvis is placed into the same condition of static equilibrium as the human one, i.e., it is cantilevered on the support extended lower limb. (2) The gluteal musculature of the Hadar fossil is reconstructed twice, once in an ape-like and once in a human-like configuration. (3) The muscular action modelled are those of gluteal muscles (gluteus maximus vs ischiofemoralis, gluteus medius and minimus), adductors (adductor magnus and pectineus), and hamstrings (biceps femoris long head). Each muscle is assumed to generate a vector along its median center line, i.e., the line joining the middle of proximal origin on the pelvis and distal insertion on the femur. The two hypothetical reconstructions of gluteal muscles generate two different sets of action lines, a human-like and an ape-like one. The action lines of adductors and hamstrings have been schematically reconstructed from a hypothetical human-like morphology. The median center line of the muscle adductor magnus joins a point which is situated on the ischial ramus to the middle of the femoral diaphysis. The median center line of the muscle pectineus joins the pecten pubis to the first quarter of the femoral diaphysis. The median center line of the muscle biceps femoris long head joins a point on the ischial tuberosity to the distal extremity of the femur. These median lines have been represented by thin sticks fixed on the pelvis, and magnitudes of forces by vectors of 5 cm. These vectors are arbitrary, as the absolute forces are unknown. The thigh is extended on the pelvis. These vectors have been projected on photographs for the three orthogonal planes of the hip joints. Consequently, the magnitudes of the force components differ according to the inclination of the vectors on each plane. This is mainly important in comparison of the abilities of the gluteal muscles to internally rotate the pelvis. The lever arms and torques may be directly estimated from the figures on which the pelvis are represented at the same scale. The torques are the products of the force components times the lengths of their lever arms.

## Results

A functional interpretation of australopithecine morphology demands consideration of the characteristic proportions of the pelvis in connection with those of the lower limb. The most important non-human traits which can be noticed on the pelvis (Figure 1), are associated with the dimensions of the lower limb. These are the extreme width of the pelvis (1) at the level of the iliac crests, and (2) at the level of the interacetabular distance (Schmid, 1983; Stern & Susman, 1983; Berge, 1984; Berge *et al.*, 1984; Berge & Kazmierczak, 1986), as well as (3) the lateral orientation of iliac crests (Zihlman & Hunter, 1972; Johanson *et al.*, 1982; Stern & Susman, 1983; Sigmon, 1986). The limb is mainly characterized by (4) a very short femur (McHenry, 1978; Jungers, 1982; Jungers & Stern, 1983), (5) a very long femoral neck, as well

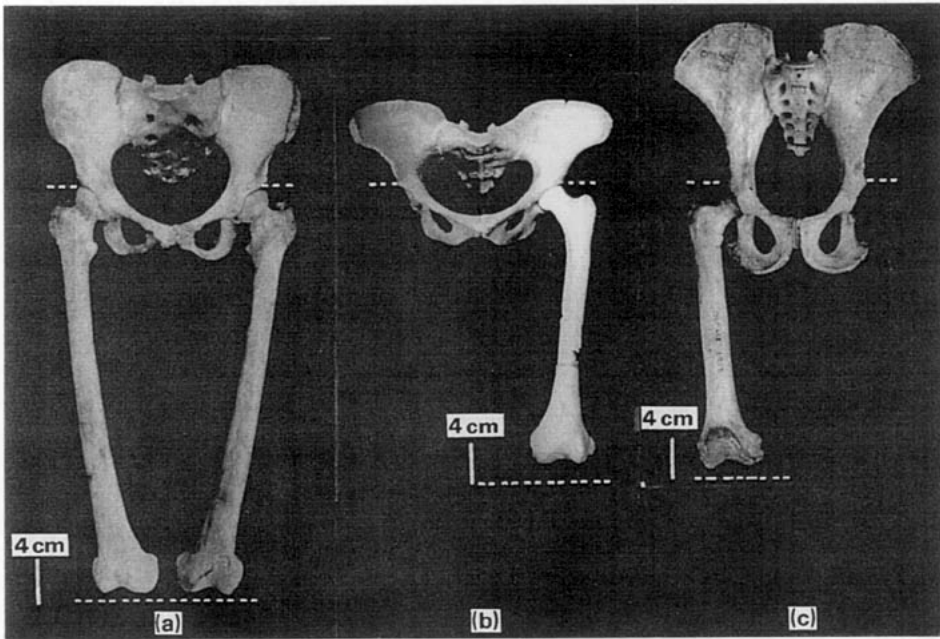


Figure 1. Pelves and femurs of adult hominoids (frontal view). (a) *Homo sapiens* (female pygmy); (b) *Australopithecus afarensis* (AL 288-1, P. Schmid's reconstruction); (c) *Pan troglodytes* (female).

as (6) a flat greater trochanter (Napier, 1964; Zihlman, 1971; Lovejoy, 1975; Corruccini & McHenry, 1980).

#### *The loading constraints on the hip joint*

The study of the compressive constraints on the hominid hip uses a biomechanical diagram deriving from Pauwels' studies of the human pelvis. Figure 2 shows the pelves of *Australopithecus* and *Homo* (anterior view), horizontally balanced and supported on the left femur. The australopithecine lower limb is assumed to be fully extended in an upright stance as in humans. The projection of the lever arm of the weight of the trunk (OM) in the frontal plane has been estimated by Pauwels (1965) using calculations of the coordinates of the center of gravity during the support phase. This lever arm (OM) is here considered to be the same on the two pelves, i.e., 60% of the interacetabular distance according to the calculation of Pauwels. The action of the body weight ( $W$ ) then tends to rotate the pelvis out of equilibrium to the side opposite to the supporting limb. Contraction of the abductor muscles lateral to the supporting limb would then balance the body weight (Steindler, 1955; Pauwels, 1965; Stern, 1988).

Naturally, the torque produced by the body weight ( $W$ ) must be counterbalanced by the torque produced by the muscular force ( $F$ ), according to:

$$F \times OH = W \times OM \text{ or } OM/OH = F/W \quad (1)$$

The projection on Figure 2 (a and b) indicates that the ratio of the lever arms  $OM/OH$  is approximately the same for *Australopithecus* and *Homo*. Consequently, the same weight ( $W$ ) will require the same muscular force ( $F$ ) in *Australopithecus* and *Homo*.



1975). Non-human hominoids mainly have the caudal portion of the superficial gluteus (muscle femorococcygeus, Jouffroy, 1962, 1971), and the cranial portion only develops in humans (muscle gluteus maximus proprius). In African apes, the muscle femorococcygeus is particularly thick: it mainly originates from the sacrotuberous ligament and from the ischial tuberosity (muscle ischiofemoralis). If it is assumed that the gluteal musculature of the first hominids retained some primitive traits, a caudally well-developed superficial gluteus also could have originated on the ischial tuberosity.

Actually, the uniqueness of the australopithecine pelvic and femoral morphology does not allow a clear attribution to the fossil of a human-like or an ape-like gluteal pattern. Moreover, the impressions of muscular attachments are not clearly visible on the fossil, or may be variously interpreted (Stern, 1972; Marzke *et al.*, 1988). This raises the question whether the superficial muscle of *Australopithecus* was attached to the ischial tuberosity. Zihlman & Brunner (1979) note that "It is possible that an ischiofemoral attachment for the inferior portion of gluteus maximus remained on the australopithecine ischium" (p. 155). In contrast, Lovejoy *et al.* (1973) and Lovejoy (1975), suggest that the morphology of the australopithecine ischial tuberosity did not significantly differ from that of humans; this implies that its muscular attachments may have been similar to those of humans. Therefore, as it is impossible *a priori* to estimate a combination of human-like and ape-like muscular characteristics, I propose two conflicting reconstructions of the gluteal musculature for the same fossil. These are based respectively on a human-like and an African ape-like muscular organization.

*First hypothesis: an ape-like gluteal pattern*

(1) Ape gluteal pattern

In African apes, the superficial gluteal musculature originates from the lower part of the hip bone (Figure 3a). This superficial muscle may be described as a muscular complex including the tensor fasciae latae (Jouffroy, 1962, 1971; Sigmon, 1974, 1975). The complex originates from the gluteal fascia, the sacrotuberous ligaments and the ischial tuberosity; it reaches the femur with an extensive insertion on the diaphysis and on the aponeurosis of the vastus lateralis. This complex is made of a thin cranial portion and a thick caudal portion. The cranial portion of the superficial complex (tensor fasciae latae and gluteus maximus proprius) has only a very small direct origin from the posterior inferior iliac spine; distally it inserts on the iliotibial tract (Sigmon, 1972). In these specimens, the cranial portion did not show any direct insertion on the femur as observed by Stern (1972). The caudal portion of the superficial complex is clearly thicker than the cranial portion. This fasciculated muscle originates directly from the lateral region of the ischial tuberosity (muscle ischiofemoralis) and reaches the femoral diaphysis with a direct insertion lying on approximately the first third of the thigh (Figure 4a).

The deeper gluteal musculature is formed by (1) the thick gluteus medius, the fibers of which converge from the gluteal face of the ilium to the upper edge of the greater trochanter; and (2) by the gluteus minimus, which originates from the lower part of the gluteal face of the ilium, and converges to the ventral edge of the greater trochanter.

(2) Australopithecine ape-like gluteal pattern.

Had the gluteal musculature of *Australopithecus afarensis* retained some ape-like traits (Figure 4b), the superficial muscle would have had a well-developed caudal portion (muscle ischiofemoralis), and a very small (or absent) cranial portion inserted on the ilium. The median center line of the caudal portion (muscle ischiofemoralis) joins the latero-caudal region of the

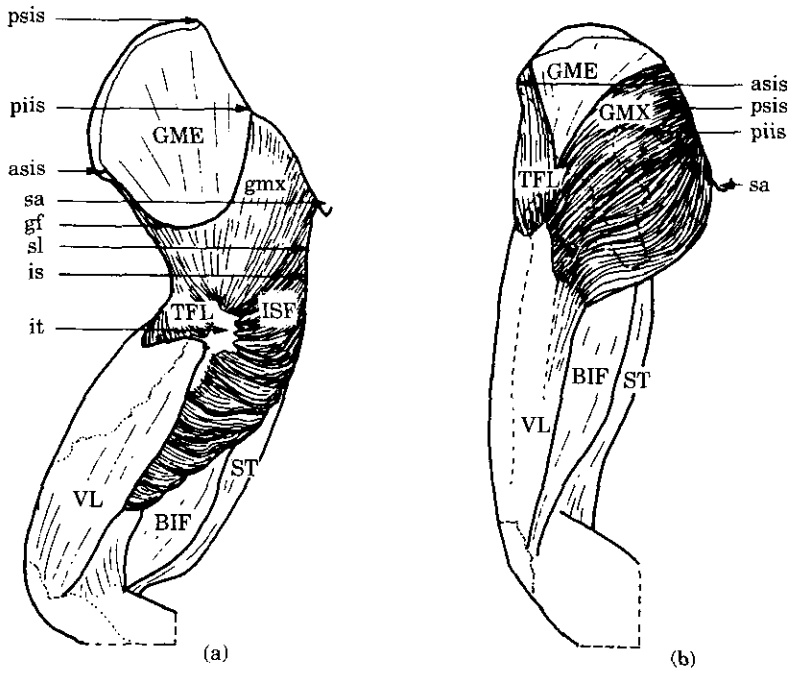


Figure 3. The superficial gluteal muscle in African apes and humans (lateral view of the left hip and hindlimb). (a) *Pan troglodytes* (female), (b) *Homo sapiens* (from Woodburne & Burkel, 1957). asis: anterior superior iliac spine; it: iliotibial tract; BIF: biceps femoris long head; gf: gluteal fascia; GME: gluteus medius; gmx: gluteus maximus proprius; GMX: gluteus maximus; is: ischial tuberosity; ISF: ischiofemoralis; piis: posterior inferior iliac spine; psis: posterior superior iliac spine; sa: sacrum extremity; st: sacrotuberous ligaments; ST: semitendinosus; TFL: tensor fasciae latae; VL: vastus lateralis.

ischial tuberosity to the first third of the femoral diaphysis. In contrast, the gluteus medius will have a very extensive origin from the whole external face of the ilium. The gluteus minimus will originate along the ventral edge of the ilium. The median center lines of the gluteus medius and minimus have been reconstructed from the centers of the origins and distal insertions (Figure 4b).

*Second hypothesis: a human-like gluteal pattern*

(1) Human gluteal pattern

In humans, the superficial gluteal complex comprises two parts. The ventrally situated tensor fasciae latae is not very different from that of apes (Figure 3b). The dorsal portion, the gluteus maximus, is thick, and has a relatively broad origin both on the dorsal part of the ilium and on the lateral edge of the sacrum, but not on the ischial tuberosity. Distally, the muscle inserts on the proximal part of the femoral diaphysis, approximately on its first quarter.

The deeper gluteal musculature is comprised of (1) the gluteus medius, the origin of which is much narrower and more arched on the ilium than is the ape-like one. It is limited dorsally by the insertion of the gluteus maximus, and caudally by the insertion of the gluteus minimus. (2) The gluteus minimus has a more laterally and cranially extended origin in the human-like than in the ape-like reconstruction; it converges on the greater trochanter (Figure 5a).

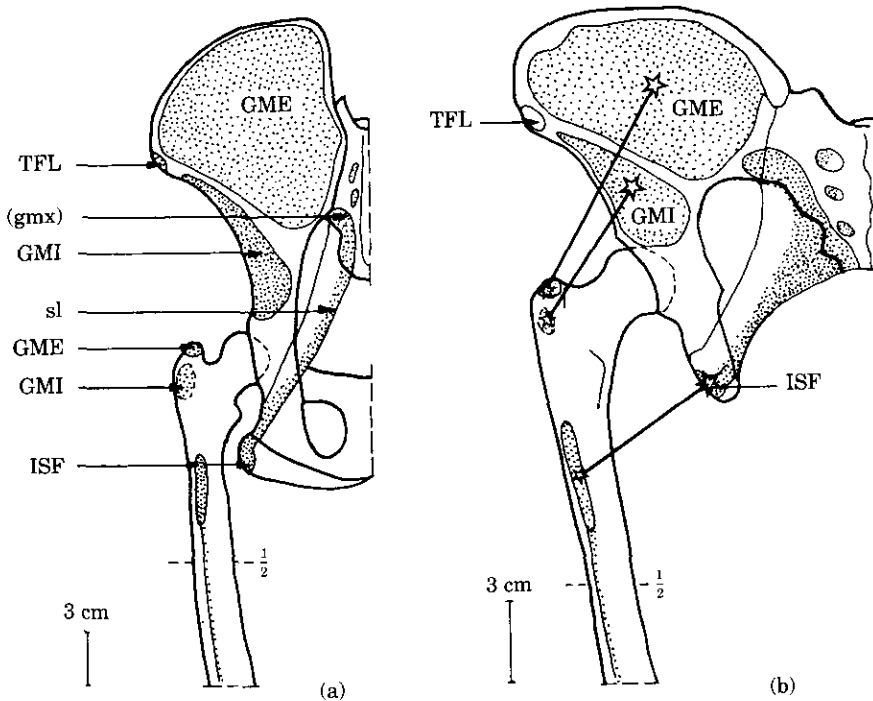


Figure 4. Reconstruction of an ape-like pattern for gluteal insertions on the australopithecine pelvis and femur (dorsal view of the left hip and femur). (a) *Pan troglodytes*; (b) AL 288-1. GME: gluteus medius; GMI: gluteus minimus; gmx: gluteus maximus proprius; ISF: ischiofemoralis; sl: sacrotuberous ligaments; TFL: tensor fasciae latae; \*—\*: median center lines of the ape-like gluteal muscles of AL 288-1. For explanation, see text.

## (2) Australopithecine human-like gluteal pattern.

Had the gluteal musculature of *Australopithecus afarensis* developed a fully human-like organization (Figure 5b), the superficial musculature would have had a well-developed cranial portion (gluteus maximus proprius), with no caudal portion corresponding to the muscle ischiofemoralis. In the case of a human-like structure, the insertion of the muscle gluteus minimus will have a more cranially extended origin on the australopithecine ilium than its homolog in the case of an ape-like structure (Figure 4b). Thus, the appropriate median center line of the gluteus maximus is lying in a straight line from the center of the postgluteal plane on the ilium to the first quarter of the femoral diaphysis. The median center lines of gluteus medius and minimus have been respectively defined as the lines which join the centers of the muscular surfaces on the ilium to the centers of femoral insertions (Figure 5b).

Comparison of the abilities of the muscles to generate the movements for bipedalism requires a decision about the gluteal reconstruction most consistent with the bony structure of the fossil.

### *Reconstruction of muscular functions in the australopithecine pelvis: comparison with Homo*

(1) Principles. The two hypothetical gluteal reconstructions of *Australopithecus* have been schematically compared with that of *Homo* (female pygmy) by considering the projected median center lines of muscles in the three planes of pelvis. The median center lines



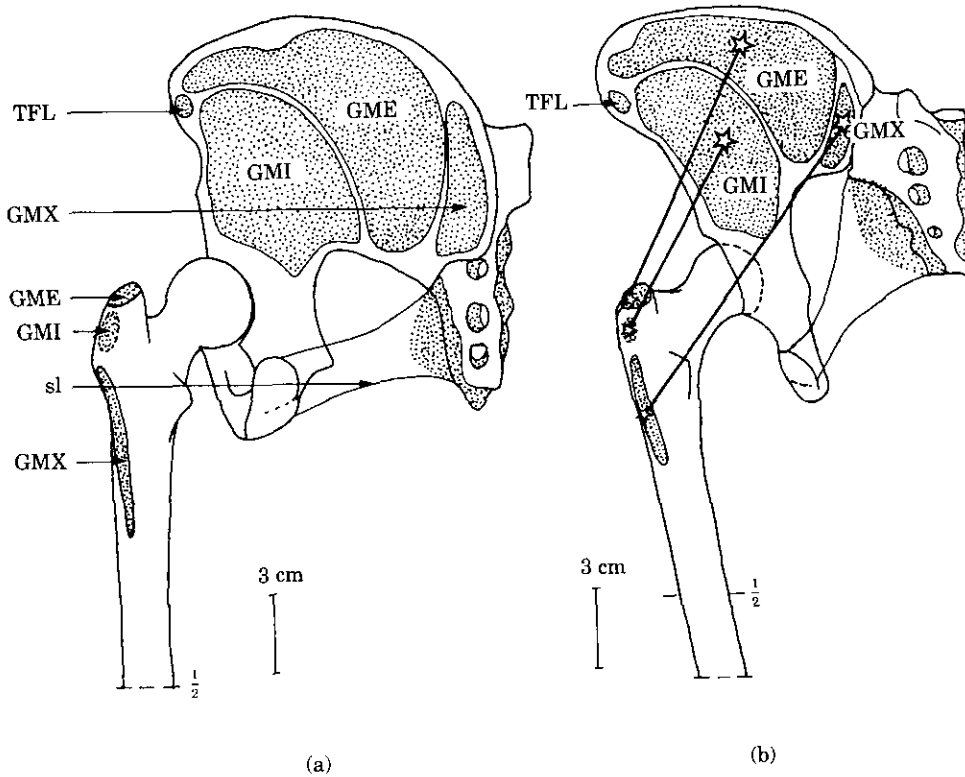


Figure 5. Reconstruction of a human-like pattern for gluteal insertions on the australopithecine pelvis and femur (dorsal view of the left hip and femur). (a) *Homo sapiens* (female pygmy); (b) AL 288-1. GME: gluteus medius; GMI: gluteus minimus; GMX: gluteus maximus; sl: sacrotuberous ligaments; TFL: tensor fasciae latae; \*—\*: median center lines of the human-like gluteal muscles of AL 288-1. For explanation, see text.

corresponding to adductors and hamstrings, respectively, have been also projected on the frontal and on the sagittal planes of pelvis.

(2) Movements in the frontal plane: abduction and adduction of the thigh. On Figure 6, the pelvis are viewed in the frontal plane (posterior aspect). The torques are those of the gluteal and adductor muscles (pectineus, and adductor magnus). The distances of the force components relative to the center of the hip joint (lever arms) suggest that the possibility for abduction of the thigh by the torques produced by the gluteal muscles (GME, GMI) is at least equivalent for the two reconstructions of *Australopithecus* (Figure 6b,c), and for the human pelvis (Figure 6a). However, adduction of the thigh depends on the reconstruction of the superficial gluteus. A human-like gluteus maximus (GMX on Figure 6b) does not facilitate the adduction of the hip because the torque corresponding to the median center line of GMX will equal zero, whereas the torque corresponding to the median center line of the ape-like ischiofemorals (ISF on Figure 6c), is by far more effective for adduction. However, it appears that the australopithecine adductor musculature (PEC, ADM on Figure 6b,c) must have been much more powerful than that of humans (the lever arms of PEC and ADM are clearly longer on the australopithecine pelvis than on the human one).

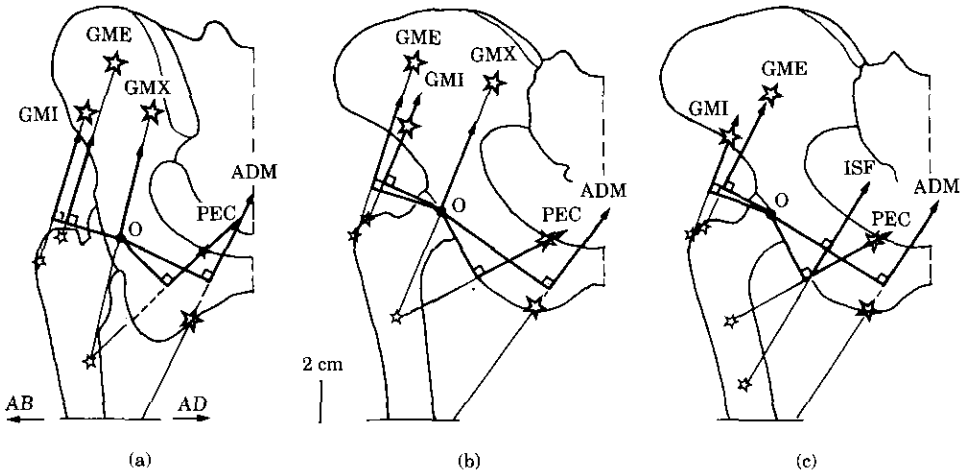


Figure 6. Abduction-adduction of the australopithecine thigh by action of the gluteal and adductor muscles. The pelvis are oriented in the frontal plane (dorsal view of the left hip) with the lower limb extended (same scale for the three pelvis). \*—\*: median center lines of muscles. The torques are represented as thick lines. AB: abduction of the thigh; AD: adduction. (a) *Homo sapiens* (female pygmy); (b) human-like reconstruction of the gluteal muscles on AL 288-1; (c) ape-like reconstruction of the gluteal muscles on AL 288-1. ADM: adductor magnus; GME: gluteus medius; GMI: gluteus minimus; GMX: gluteus maximus; ISF: ischiofemoralis; O: rotation center of the hip joint; PEC: pectineus.

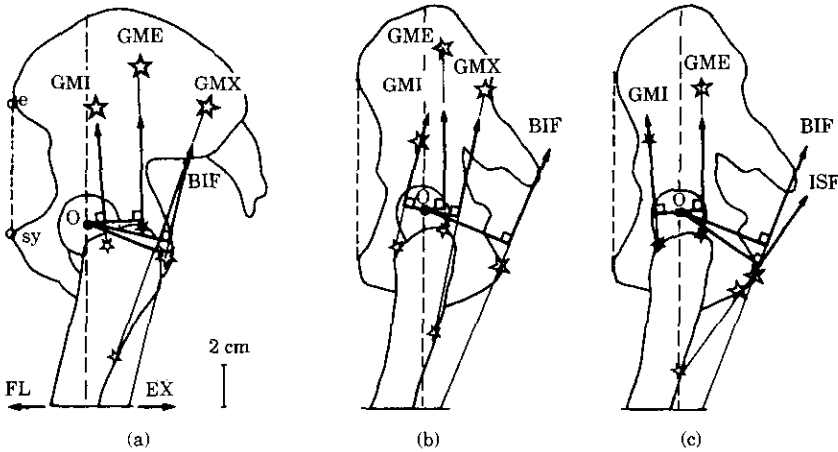


Figure 7. Extension-flexion of the australopithecine thigh by action of the gluteal and hamstring muscles. The pelvis are oriented in the sagittal plane (external view of the left hip) with the segment e-sy vertical, and the lower limb extended (same scale for the three pelvis). \*—\*: median center lines of muscles. The torques are represented as thick lines. EX: extension of the thigh; FL: flexion. (a) *Homo sapiens* (female pygmy); (b) human-like reconstruction of the gluteal muscles on AL 288-1; (c) ape-like reconstruction of the gluteal muscles on AL 288-1. BIF: biceps femoris long head; GME: gluteus medius; GMI: gluteus minimus; GMX: gluteus maximus; ISF: ischiofemoralis; O: rotation center of the hip joint.

(3) Movements in the sagittal plane: flexion and extension of the thigh. On Figure 7, the pelvis are viewed in the sagittal plane (left side). The gluteal muscles, and the long head of the biceps femoris produce torques acting on the hip joint. The two reconstructions of the australopithecine musculature differ markedly from the human pelvis in the ability to flex and to

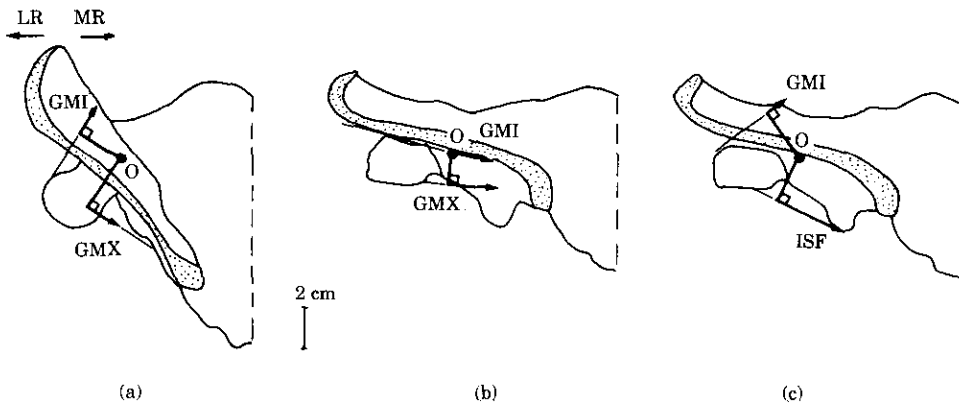


Figure 8. Medial-lateral rotations of the australopithecine thigh by action of the gluteal muscles. The left pelvis are oriented in the transverse plane (cranial view of the left hip) with the lower limb extended (same scale for the three pelvis). \*—\*: median center lines of muscles. The torques are represented as thick lines. LR: lateral rotation of the thigh, MR: medial rotation. (a) *Homo sapiens* (female pygmy); (b) human-like reconstruction of the gluteal muscles on AL 288-1; (c) ape-like reconstruction of the gluteal muscles on AL 288-1. GMI: gluteus minimus; GMX: gluteus maximus; ISF: ischiofemoratis; O: rotation center of the hip joint. The muscle gluteus medius is not represented.

extend the thigh. The ventral situation of the lower arm of GMI relative to the center of the hip joint (Figure 7b,c), offers more potential for ventroflexing of the thigh than does the human arrangement (Figure 7a), whatever the hypothetical reconstruction of the muscle. Figure 7 shows that the different length of the GMI lever arm in hominids mainly results from the varying orientation of the femoral head in the acetabulum. In contrast, the ability to extend the thigh differs for the several reconstructions of the australopithecine gluteal musculature. On the australopithecine pelvis, gluteal musculature (GMX on Figure 7b) would be less effective for extending the thigh than would be the human gluteus maximus: whereas the ischiofemoratis (ISF on Figure 7c), offers more abilities for extending the thigh than even the human gluteus maximus. The australopithecine hamstring musculature is here represented by the muscle biceps femoris (BIF on Figure 7b,c). It is probable that the australopithecine hamstring which is associated with a longer lever arm than in humans (Figure 7a), would have been much better at extending the hip.

(4) Movements in the transverse plane: lateral and medial rotations of the thigh. On Figure 8, two torques produced by the gluteal musculature have been represented in the transverse plane of pelvis (GMX vs ISF, and GMI). The distance of the projected vectors for the gluteal reconstructions on the fossil, relative to the center O, suggests important differences in their ability to rotate the thigh medially and laterally. In comparison to human muscle (Figure 8a), the human-like australopithecine median center line of the gluteus minimus (Figure 8b) appears to be particularly ineffective for medial rotation of the thigh due to the shortness of its lever arm (the torque produced by GMI is equal to zero). In contrast, an ape-like australopithecine median center line of the gluteus minimus (Figure 8c) seems to be as effective as a human one (because the torque produced by GMI equals that of the same muscle on the human hip). An equivalent difference between both the reconstructions of the fossil exists for the median center line of the superficial gluteus. An ape-like median center line on the fossil (ISF on Figure 8c) appears to be better for lateral rotation of the thigh

(longer lever arm), than is a human-like reconstruction of the gluteus maximus on the same fossil (GMX on Figure 8b).

### Discussion

Numerous studies have pointed out that the morphology of the pelvic and lower limb bones of *Australopithecus* (see Figure 1) presented a mosaic pattern. These elements have retained some ape-like traits, in spite of the fact that the structure already contains human-like characteristics (Zihlman & Brunner, 1979; Prost, 1980; Jungers, 1982, 1988; Jungers & Stern, 1983; Stern & Susman, 1983; Berge & Kazmierczak, 1986; Berge, 1993). The combination of ape-like and human-like structural features is generally interpreted as reflecting a transitional form in the evolution of hominids (Stern & Susman, 1983). However, discussions about the muscular functions of *Australopithecus*, and more specifically about the role of its gluteal musculature, assume *a priori* that the muscles were in a close to human pattern (Zihlman & Hunter, 1972; Lovejoy *et al.*, 1973; Lovejoy, 1978; McHenry, 1986). Actually, the human gluteal pattern is particularly original, and even unique, in comparison to those of other living hominoids (Waterman, 1929; Stern, 1972; Sigmon, 1974, 1975). Consequently, it stands to reason that the action of the gluteal muscles will depend on decisions about muscular reconstruction.

The impressions of gluteal insertions on the australopithecine hip bones are hardly obvious (Stern, 1972; Zihlman & Brunner, 1979; Jungers, pers. comm.). The present study proposes two distinct reconstructions of the gluteal musculature for the fossil from Hadar (AL 288-1), respectively one based on the morphology of African pongids and that of humans. Both reconstructions offer important morphological differences, respectively with the functional patterns of the pongids and humans, because the proportions of the australopithecine pelvis and lower limbs are unique. An ape-like reconstruction of the australopithecine gluteal musculature would be characterized (Figure 4b) by (1) a well developed superficial gluteus in its caudal portion (ischiofemoralis) compared with a very reduced cranial portion (gluteus maximus proprius); and (2) an extensive gluteus medius on the dorsal face of the ilium. As compared with this australopithecine ape-like pattern, a human-like reconstruction of the same muscles on the fossil (Figure 5b) would be characterized mainly by (1) the disappearance of the caudal portion of the superficial gluteus and, in contrast, the expansion of the cranial portion (*gluteus maximus*); and (2) a more cranially developed *gluteus minimus*.

The comparison of muscular functions (which are estimated from median center lines of muscles), indicates that an ape-like gluteal organization would offer better ability than a human-like one. It would not only move the lower limb in all directions, but also effect the movements of the bipedal gait, i.e. realize extension, adduction and medial rotation of the thigh. First, an ape-like superficial gluteus (prevalence of the caudal portion of the muscle) would be far more effective mainly for extending and adducting the australopithecine thigh than would a human-like *gluteus maximus*. Moreover, the morphology of the australopithecine ilium does not permit reconstruction of a fully human-like superficial gluteus. The postgluteal plane of the ilium (which corresponds to the cranial origin of the muscle on the ilium) is far narrower on the australopithecine ilium than on the human one. This should indicate at least an intermediate gluteal pattern, i.e. one in which the caudal portion of the muscle predominates. This portion then originates from the sacrum and from the sacrotuberous ligament rather than from the ischial tuberosity. Second, medial rotation of the thigh on the hip is one of the most fundamental movements in bipedalism, in so far as the hip rotates horizontally on the supporting thigh during the walk (Plas & Viel, 1975).

Medial rotation of the pelvis around the vertical axis, and of the femur and tibia is maximal at about 15% on the stance (Inman *et al.*, 1981). In case of an ape-like origin of gluteus minimus on the australopithecine ilium, the possibilities for medial rotation seem to be equivalent to the humans. However, a human-like insertion of gluteus minimus on the australopithecine ilium (i.e., with a more cranial extension of the origin on the gluteal plane) does not give more possibilities for medial rotation because the main portion of the muscle should lie too far dorsally for it to act as an effective medial rotator. This is due mainly to the lateral orientation of the australopithecine iliac blade, which is connected with a laterally orientated femoral diaphysis. Thus, a fully human-like pattern of gluteus minimus seems to be relatively inconsistent with the bony structure of the australopithecine pelvis and lower limb. It is more probable that the gluteal muscles of AL 288-1 retained some ape-like traits.

The australopithecine pelvic morphology also differs in the ability to maintain hip and knee extension during the walk. Similar bipedal conditions must be stated explicitly for the comparison among hominids. As there is no major obstacle for extension of the australopithecine lower limb, it has been supposed on the figures that the fossil of Hadar could stand (and walk) with extended and adducted lower limbs as do humans. However, by comparison with humans, the australopithecine extensors of the hip and thigh (gluteal muscles, hamstring muscles), seem to have been relatively more powerful in their capacity to move the pelvis, than to stabilize it, because the muscles lie much further from the hip joint than do their human homologs.

Also, the capacity for responding to gravitational stresses is not equivalent for the hip joints of *Australopithecus* and *Homo*. At first sight, the ratio of load arm to muscular lever arm (OM/OH on Figure 2) seems to indicate that the australopithecine pelvic and femoral morphology was biometrically equivalent to the human morphology (Berge & Kazmierczak, 1986). However, Jungers (1991), who measured the same ratio of lever arms, but on another reconstruction of AL 288-1, found a mechanical disadvantage for the fossil. The present study suggests that the bony structure of the australopithecine hip joint is less adapted for weight bearing than is the human one, because the compressive force on the hip joint does not pass through the femoral neck as it does on the human femur but in a more overhanging position. Thus, *Australopithecus* and *Homo* mainly differ in the capacity to stabilize the lower limb during the walk. This is in spite of the fact that they could walk with relatively more extended and adducted lower limb than do apes which are unable to simultaneously extend the knee and the hip. The lack of stability of the australopithecine hip joint reflects characteristics that have been discussed for the morphology of the knee (Tardieu, 1983, 1986; Senut & Tardieu, 1985).

The present results lead to the conclusion that the bipedalism of *Australopithecus* must have differed from that of *Homo*. Not only did *Australopithecus* have less ability to maintain hip and knee extension during the walk, but also probably moved the pelvis and lower limb differently. It seems that the australopithecine walk differed significantly from that of humans, involving a sort of waddling gait, with large rotatory movements of the pelvis and shoulders around the vertebral column (Berge, 1991*a,b*). Such a walk, likely required a greater energetic cost than does human bipedalism. The stride length and frequency of australopithecines, and consequently their speed, should have differed from that of *Homo* in contrast to some recent hypotheses of dynamic similarity among hominids (Charteris *et al.*, 1982; Reynolds, 1983, 1987; Alexander, 1984).

A previous paper has suggested that the pelvic proportions of *Australopithecus* could provide some arguments for an arboreal locomotion (Berge, 1990). The results of the present study

suggest amplification of this opinion. The present comparison of torques on the hominid pelvis suggests that the australopithecines had a greater possibility for movement with their lower limbs in different spatial positions, than do humans. They could effect abduction-adduction, flexion, and lateral rotation of the thigh. The change in the pelvic and lower limb structure, from *Australopithecus* to *Homo*, could be interpreted as an important change in the locomotor pattern of hominids, which became increasingly terrestrial and specialized for walking and running over longer distances.

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