Chimpanzee Bipedalism: Cineradiographic Analysis and Implications for the Evolution of Gait

Abstract. *Bipedal chimpanzees reorient the pelvis to achieve an upright posture but retain the same pattern of femoral flexion and extension as in quadrupedal walking. Major differences from human gait are the abducted, relatively more flexed excursion of the femur and the timing of pelvic tilt, which raises during the swing phase. The femoral head morphology in the fossil hominid* Australopithecus robustus *is evidence of an approximately vertical excursion of the femur in contrast to the adducted pattern of modern man and the abducted pattern of chimpanzees.*

Facultative bipedality in living apes and monkeys and the evolution of human bipedality are considered related phenomena (*1*). However, the precise relevance of bipedal behavior among nonhuman anthropoids to understanding the evolution of human gait remains largely undefined because detailed analyses of locomotion are so few. Published data on bipedal activity (other than in man) are most complete for the chimpanzee and are based principally on movie analysis and direct observation (*2*). I have undertaken cineradiography of bipedal and quadrupedal (knuckle-walking) locomotion in two 3-year-old chimpanzees (*Pan troglodytes*) to provide detailed documentation of joint movements and skeletal postures and excursion. Each chimpanzee, moving on a variable-speed treadmill, was radiographed with Siemens equipment, including a Sirecon duplex image intensification system; a 30-kw, grid-controlled tube with a 0.06-mm focal spot; and an Eclair GV16 16-mm camera operated at 50 frames per second. Because the image intensifier provided a maximum field size of 25.4 cm, separate sequences were taken at the level of the hip, knee, and foot in lateral projection; the construction of the x-ray apparatus and treadmill restricted anteroposterior projections principally to the level of the hip, although some footage was obtained of the knee. One thousand feet (305 m) of film was analyzed with an L and W Photo-Optical Data Analyzer 224-A.

Pelvic orientation of the bipedal chimpanzee (measured in lateral projection by a line from the posterior superior iliac spine to the ischial tuberosity) is maintained at about 10° from vertical; in contrast, pelvic orientation during knuckle-walking varies from 25° to 55° from vertical. Pelvic movements during bipedal locomotion include vertical oscillation, side-to-side movement (including tilt), and rotation about vertical axes. In vertical oscillation, the pelvis is highest at mid-stride when one limb is in the middle of the propulsive phase and the other is in the middle of the swing phase (Fig. 1, B, D, and G). Pelvic position is lowest when both limbs are in contact with the ground (Fig. 1, A, C, and H). At this time the pelvis tilts and moves laterally toward the propulsive limb (Fig. 1, B and D); simultaneously, the pelvis rotates about a vertical axis passing approximately through the hip joint of the propulsive limb, and thus the hip joint in the swing phase moves slightly ahead of the weight-bearing hip (Fig. 1, E to H). Lateral pelvic movement reverses at the end of the propulsive phase with a shift toward the limb that is about to make ground contact. Although similar vertical displacement also occurs during knuckle-walking, pelvic tilting, rotation, and lateral shift are negligible in this locomotor mode.

Femoral movements are principally flexion and extension. In knuckle-walking, the femur begins the propulsive phase with its proximodistal axis at about 50° below horizontal; the femur then extends through 35° to 50°, and frequently begins the swing phase after the knee has passed behind the hip joint. In bipedal walking the femur retains the same range of excursion relative to the pelvis; however, as the pelvis shifts approximately 30° to a more vertical orientation, the femur shifts with it and therefore has a more horizontal excursion. At the beginning of the propulsive phase, the proximodistal femoral axis is positioned at about 30° to 40° relative to horizontal and at the beginning of the swing phase is within 10° to 20° of vertical but seldom reaches the vertical position (Fig. 1, E to H). Thus during bipedalism the knee does not usually pass beneath the hip joint.

There are two smaller components of

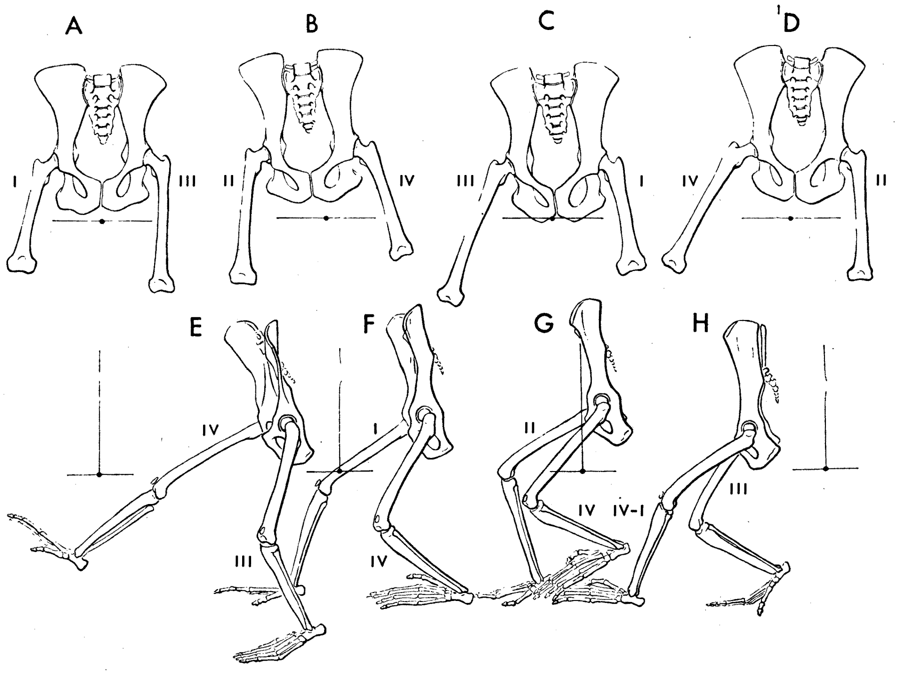

Fig. 1. Skeletal postures of a bipedal chimpanzee interpreted from cineradiography in anteroposterior (above) and lateral (below) projections. Comparable phases of each stride may be identified by Roman numerals: *I* is the beginning of the propulsive (stance) phase when the limb initially makes ground contact; *II*, the middle of the propulsive phase when the limb bears all the body weight (the opposite limb is normally in the nonpropulsive or swing phase *IV*); *III*, the end of the propulsive phase when the limb is completing its forward thrust and is about to be lifted from the ground; and *IV*, the nonpropulsive (swing) phase when the limb is not in contact with the ground and is being moved forward to phase *I*. The horizontal lines give fixed reference planes from which relative vertical movements of the pelvis may be estimated. Lateral displacements of the pelivs may be determined with reference to the fixed points in A to D, and forward progression of. the pelvis may be determined with reference to the fixed vertical lines in E to H.

femoral excursion. The first is abduction at the end of the propulsive phase (Fig. 1C, right side) and the beginning of the swing phase (Fig. 1D, right side). Adduction occurs during the initial propulsive phase when the pelvis shifts laterad over the propulsive limb. The second component is several degrees of femoral flexion, which immediately follows foot contact at the beginning; this movement is then followed by femoral extension as described above.

During bipedal walking, excursion at the knee joint is about 90°. At the end of the swing phase, the lower leg is almost maximally extended and frequently the tibia and fibula are rotated slightly laterad [indicated radiographically by the separation of the fibular shaft from the posterior aspect of the tibial shaft (Fig. 1E, right side)]. Flexion occurs principally during the first half of the propulsive phase (Fig. 1, F and G). During the second half, propulsion is effected primarily through femoral extension, the lower leg remaining at approximately a right angle to the femur. In some of the bipedal sequences the knee everted at the end of the propulsive phase (as evidenced radiographically by the change in condylar and patellar positions; compare Fig. 1, E and H, left side).

Dorsiflexion and plantarflexion at the ankle ranges from about 25° to 35° during bipedal movement. During the initial part of the swing phase, the metatarsals are dorsiflexed to within 75° to 80° of the tibia, and during the terminal part of the swing phase the tibio-metatarsal angle is 100° to 110° (Fig. 1E). The "ball" of the foot (that is, the sole underlying the metatarsophalangeal joints) is used to push off during the terminal part of the propulsive phase (Fig. 1H, right side); the divergent hallux is often non–weight-bearing at this point. The foot inverts to a variable extent during the swing phase.

The similarity between bipedalism in chimpanzees and humans may be expressed in terms of the components of human gait: pelvic rotation, pelvic tilt, hip and knee flexion, knee and ankle interaction, and lateral displacement of the pelvis (*3*). Bipedal chimpanzees use the same movement patterns except for a reversed sequence of pelvic tilt; the pelvis on the side of the swing phase is elevated, whereas in humans it is depressed. The major dissimilarity is the abducted, flexed femoral excursion of the chimpanzee. Femoral flexion and extension *relative to the pelvis* remain approximately the same during bipedal and quadrupedal activity; thus, bipedal walking represents a quadrupedal limb movement employed when the pelvis has been reoriented to permit bipedal posture. The principal propulsive force of the foot is applied on the ground ahead of the hip joint, in contrast to behind the hip as in humans. Furthermore, since the abducted limb position removes the feet farther from the center of gravity than in humans, relatively larger vertical and lateral displacements of the center of gravity are necessary to maintain balance during the single stance phase of walking.

The data presented above are critical to evaluating features which are shared by apes and man, both fossil and living, and which have been considered in terms of the evolution of human bipedalism. One such feature, the bicondylar angle (or obliquity of the femoral shaft), purportedly relates to femoral posture; the angle represents the deviation of the femoral shaft from a parasagittal plane, if one assumes that a tangent to the femoral condyles is horizontal (*4, 5*) (Fig. 2H). In man the angle is about 10° and in the gorilla and chimpanzee about 1° to 2°; on the basis of femoral fragments, the apparent bicondylar angle in both *Australopithecus robustus* and *A. africanus* is 14° to 15° (*6*). On these grounds Lovejoy and Heiple (*6*) concluded that both species possessed an adducted (valgus) stance as in modern man with the knee joints medial to the hips. However, to include pongids such as chimpanzees in this comparative analysis may be misleading, for bipedal chimpanzees only use an extended femorotibial position (which is the posture measured by bicondylar angle) briefly during each stride and vary the degree of adduction-abduction both during the stride (Fig. 1, E to H) and in various

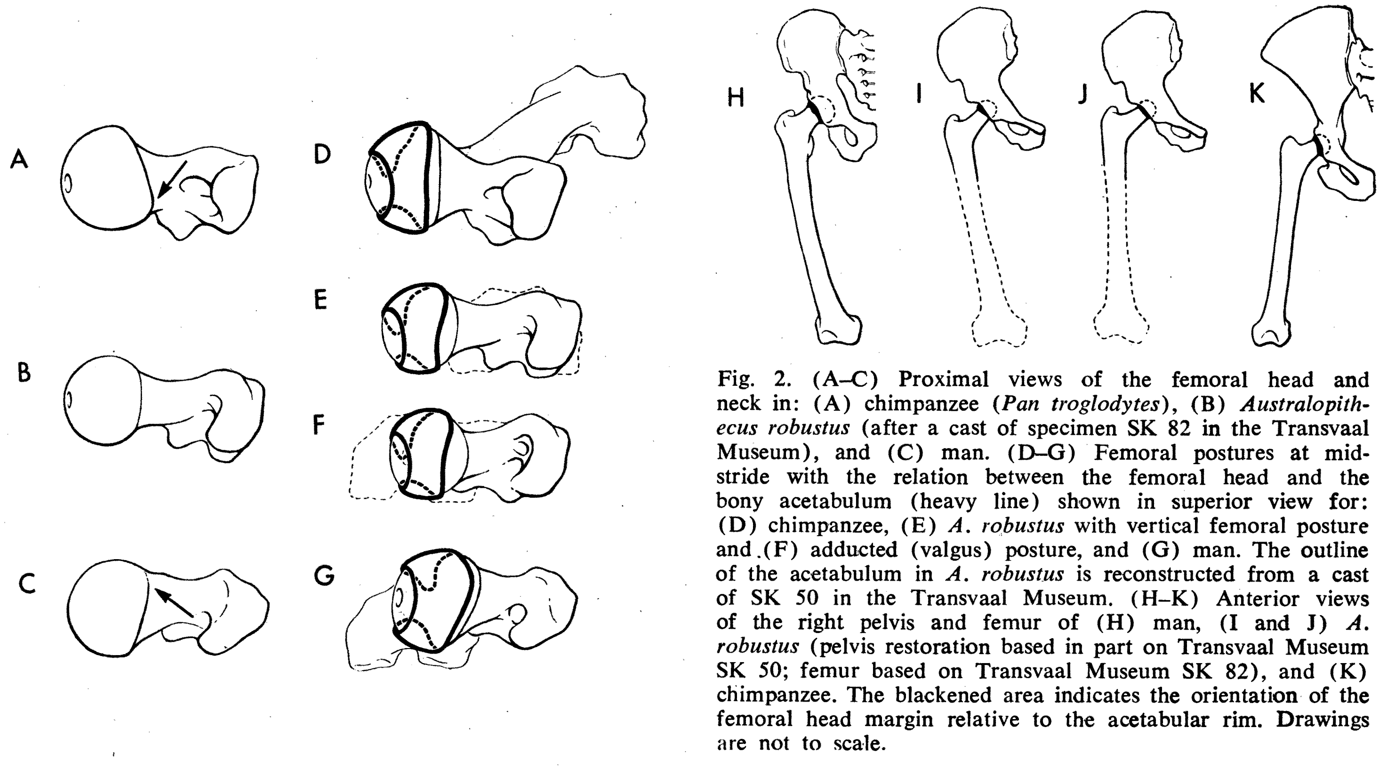

Fig. 2. (A–C) Proximal views of the femoral head and neck in: (A) chimpanzee (*Pan troglodytes*), (B) *Australopithecus robustus* (after a cast of specimen SK 82 in the Transvaal Museum), and (C) man. (D–G) Femoral postures at midstride with the relation between the femoral head and the bony acetabulum (heavy line) shown in superior view for: (D) chimpanzee, (E) *A. robustus* with vertical femoral posture and (F) adducted (valgus) posture, and (G) man. The outline of the acetabulum in *A. robustus* is reconstructed from a cast of SK 50 in the Transvaal Museum. (H–K) Anterior views of the right pelvis and femur of (H) man, (I and J) *A. robustus* (pelvis restoration based in part on Transvaal Museum SK 50; femur based on Transvaal Museum SK 82), and (K) chimpanzee. The blackened area indicates the orientation of the femoral head margin relative to the acetabular rim. Drawings are not to scale.

stances. Thus, the assumption on which the bicondylar angle measurement is based—that a tangent to the condyles is always horizontal—is invalid for the chimpanzee. Even in modern man the condylar tangent in a normal stance may deviate from horizontal (*7*). Whereas the apparently high bicondylar angle in *A. africanus* (Transvaal Museum 1513 and Sts 34) appears to be best interpreted in terms of an adducted femoral posture, the possibility remains that the functional significance of this feature is not the same as for modern man. In evaluating the locomotor ability of fossil forms, evidence of skeletal excursion is more meaningful than single measurements which may not be of comparable functional significance among differently adapted species.

The configuration of the margin of the femoral head in chimpanzee and man reflects some basic differences in femoral excursion. On the human femur, the articular surface is prolonged onto the femoral neck along the superior margin (arrow, Fig. 2C). In the chimpanzee, similar prolongation occurs along the posterior margin (arrow, Fig. 2A). Inasmuch as the femoral head and acetabulum are approximately congruent, the configuration of the margin of the femoral head relates to the depth and orientation of the acetabulum and the excursion of the femur. The superior margin in man is related to a relatively deep and ventrally facing acetabulum, and also to the fact that the femur normally moves in an adducted (valgus) position (Fig. 2, G and H). In the chimpanzee, the prolonged posterior margin is related to an excursion pattern of an abducted (varus) and flexed femur (Fig. 2, D and K) and an acetabulum that is relatively shallower and faces laterad. The intermediate configuration of the femoral head margin in *A. robustus* (for example, Transvaal Museum SK 82; Fig. 2B), together with the relatively shallow acetabulum (Transvaal Museum SK 50), is evidence that femoral excursion was of an intermediate pattern (Fig. 2, E and J). If the *A. robustus* femur were adducted as much as in man, a disproportionate area of articular surface would lie outside the bony acetabulum (Fig. 2, F and I). Although a very broad glenoid labrum may have made this possible, such an arrangement appears unlikely in view of the usual congruency of articular surfaces at the hip.

Major structural similarities of the australopithecine pelvis to that in modern man are convincing evidence of advanced adaptation to bipedality (*8*). However, certain obvious dissimilarities, such as the greater flaring of the iliac blades, may be explicable in terms of a more abducted femoral excursion. Furthermore, the present interpretation of a lack of valgus posture in some early Pleistocene hominids is in agreement with the biomechanical analyses of Napier and Preuschoft (*9*).

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Phosphorylase: A New Isozyme in Rat Hepatic Tumors and Fetal Liver

Abstract. *A third set of phosphorylase a and b isozymes, distinguishable kinetically and immunologically from liver and muscle forms, is present in various rat hepatomas, and is also present, together with the adult liver form, in fetal rat liver. This is one of several striking examples of suppression of isozymes of adult liver coupled with the appearance of fetal isozymes in hepatomas.*

Malignant neoplasms are characterized by anomalies of genetic expression, manifested by ectopic production of polypeptide hormones (*1*), and by the synthesis of tumor-specific antigens (*2*), while organ-specific antigens are suppressed (*3*). This phenomenon has a counterpart in enzyme alterations of experimental rat hepatomas; also involving the suppression of isozymes which play a functional role in the adult, differentiated liver cell, and their replacement by other isozymes which are low or absent in adult liver (*4*, *5*). It is of further significance that in some instances both antigens and isozymes associated with tumors are found in normal fetal tissue, suggesting that genes coding for proteins synthesized in the fetal state and which are repressed during normal embryonic development are reexpressed in tumors (*5–7*).

We report recent results from our laboratory, which provide a striking new illustration of this pattern of isozyme alteration in demonstrating the presence in certain rat hepatomas of a third form of glycogen phosphorylase, which differs kinetically from the rat liver type and is distinguishable immunologically from the rat muscle type. It exists in both a and b forms, which are interconvertible by a phosphatase and kinase, also present in these tumors. Its presence in other normal tissues remains to be investigated, but it is undetectable in adult rat liver and skeletal muscle. However, it is present at relatively low activity in fetal rat liver.

Evidence for the existence of this set of phosphorylase isozymes is presented in Fig. 1, A–E. By isoelectric focusing of partially purified supernatant fractions of homogenized and centrifuged tissue, both the muscle and liver phosphorylases appear as single peaks with respective isoelectric points of 6.2 and 5.9 (Fig. 1, A and B). The