Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion

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The large-bodied hominoid from Moroto, Uganda has until recently been known only from proconsulid like craniodental remains and some vertebrae with modern ape like features. The discovery of two partial femora and the glenoid portion of a scapula demonstrates that the functional anatomy of *Morotopithecus* differed markedly from other early and middle Miocene hominoids. Previous studies have consistently associated the vertebral remains with a short, stiff back and with orthograde postures. Although the proximal femur more closely resembles the femora of monkeys than of apes and suggests a moderate degree of hip abduction, the distal femur resembles those of extant large bodied apes and suggests a varied loading regime and an arboreal repertoire that may have included substantial vertical climbing. The femoral shaft displays uniformly thick cortical bone, beyond the range of thickness seen in extant primates, and signifies higher axial loading than is typical of most extant primates. The glenoid fossa is broad and uniformly curved as in extant suspensory primates. Overall, *Morotopithecus* is reconstructed as an arboreal species that probably relied on forelimb-dominated, deliberate and vertical climbing, suspension and quadrupedalism. *Morotopithecus* thus marks the first appearance of certain aspects of the modern hominoid body plan by at least 20 Ma. If the suspensory and orthograde adaptations linking *Morotopithecus* to extant apes are synapomorphies, *Morotopithecus* may be the only well-documented African Miocene hominoid with a close relationship to living apes and humans.

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Introduction

Hominoid[1] fossils from two early Miocene localities near the Moroto volcano in the Karamoja District, Uganda have recently been assigned to a new genus and species of Miocene hominoid (Gebo *et al.*, 1997). This new designation is based on a combination of previously known craniodental and vertebral specimens with new femoral and scapular material. The aim of this study is to present detailed descriptions and functional interpretations of the new postcrania attributed to *Morotopithecus bishopi* and to reconstruct the positional repertoire of this hominoid. *Morotopithecus* is the oldest hominoid to share several postcranial features, and presumably, locomotor characteristics, with the extant apes. This, combined with

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[1] Throughout this text, we use hominoid and ape interchangeably to refer to superfamily Hominoidea in which we include families Hominidae, Hylobatidae and, provisionally, Proconsulidae. Andrews *et al.*'s (1996) definition of Hominidae encompasses Dryopithecinae (a paraphyletic grouping of the tribes Afropithecini, Kenyapithecini and Dryopithecini), Ponginae, Oreopithecinae and Homininae, and while we do not necessarily support the phylogeny these taxonomic groupings imply, we do include its members as hominoids. We use the term stem hominoid for those primitive Miocene species (e.g., *Proconsul*) that may be members of a different clade than the one including extant hominoids, while crown hominoids refers to all hominoids within the clade that includes extant (or "modern") species.

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the fact that *Morotopithecus*, at older than 20·6 Ma, is one of the oldest known hominoids, predating similarly modern-looking hominoids by 10 million years (Moyà-Solà & Köhler, 1996), makes *Morotopithecus* a key genus in understanding early hominoid evolution. One implication of the derived appearance of the new material is that it signifies that other Miocene apes such as *Sivapithecus*, *Proconsul*, *Afropithecus* and *Equatorius* (not to mention all of the small-bodied Miocene noncercopithecoid catarrhines) which do not share many derived postcranial characteristics with the extant hominoids (but see McCrossin, 1997 and McCrossin *et al.*, 1998 with regard to *Equatorius*) may represent a different radiation than the one which gave rise to extant hominoids (Pilbeam, 1996; Gebo *et al.*, 1997; MacLatchy & Pilbeam, 1999). Even without *Morotopithecus*, however, the morphology of these other taxa suggests that they are not crown hominoids (Pilbeam, 1996).

Paleontological research at Moroto was conducted by William Bishop between 1961 and 1965. Collection at the early Miocene site Moroto II, north of the Moroto volcano, resulted in the recovery of a number of hominoid fossils then thought to be attributable to *Proconsul* (or *Dryopithecus*) *major*, including a face and maxilla [UMP (Uganda Museum of Paleontology) 62.11] mandibular specimens (UMP 62.10, UMP 66.01) and several vertebrae, including one well preserved, hominoid like, middle lumbar vertebra (UMP 67.28) (Allbrook & Bishop, 1963; Walker & Rose, 1968; Pilbeam, 1969). With the discovery of *Afropithecus*, it was later suggested that the Moroto material might best be placed in this genus (Leakey *et al.*, 1988; Andrews, 1992). Several facial and dental characters have since been identified that distinguish *Morotopithecus* from *Proconsul* and *Afropithecus* (Gebo *et al.*, 1997). Features separating *Morotopithecus* from *Afropithecus* include a greater degree of cingular development on cheek teeth, especially molars, a shorter premaxilla, a higher face, a broader nasal aperture, stylar wrinkling on the molars, a non-reduced M^3, and a much wider incisive canal (Gebo *et al.*, 1997). *Morotopithecus* differs from both *Afropithecus* and *Proconsul* in a narrower interorbital region and larger premolars relative to M^1, and from *Proconsul* in smaller M^2 and M^3 relative to M^1. In addition, the primitive nature of the postcranial remains attributed to or inferred for *Proconsul* and *Afropithecus* (Walker & Pickford, 1983; Rose, 1983, 1993; Leakey *et al.*, 1988; Leakey & Walker, 1997; Ward, 1993, 1998) contrast markedly with the known elements of *Morotopithecus*, to be discussed below.

Discovery and geochronology

The Moroto I locality (Figure 1), situated 13 km to the north of the summit of Mount Moroto, was found by J. G. Wilson in 1959 (Bishop & Whyte, 1962). Bishop and Whyte found the Moroto II site 3 km to the north of Moroto I in 1961 (Bishop & Whyte, 1962) and Bishop continued to work both sites until 1965. The hominoid postcranial specimens reported herein were collected in 1994 and consist of MUZM (Makerere University Zoology Museum) 60, the glenoid region of a large hominoid scapula from Moroto I and MUZM 80, partial right and left femora of a single hominoid from Moroto II. Pickford *et al.* (1999) also recently described a possible hominoid phalanx collected at Moroto I in 1985. Although age estimates for the two localities have varied considerably over the years (see reviews in Gebo *et al.*, 1997 and MacLatchy & Pilbeam, 1999), both localities are currently dated at older than 20·6 Ma based on $^{40}Ar/^{39}Ar$ dating of overlying basalts (Gebo *et al.*, 1997).

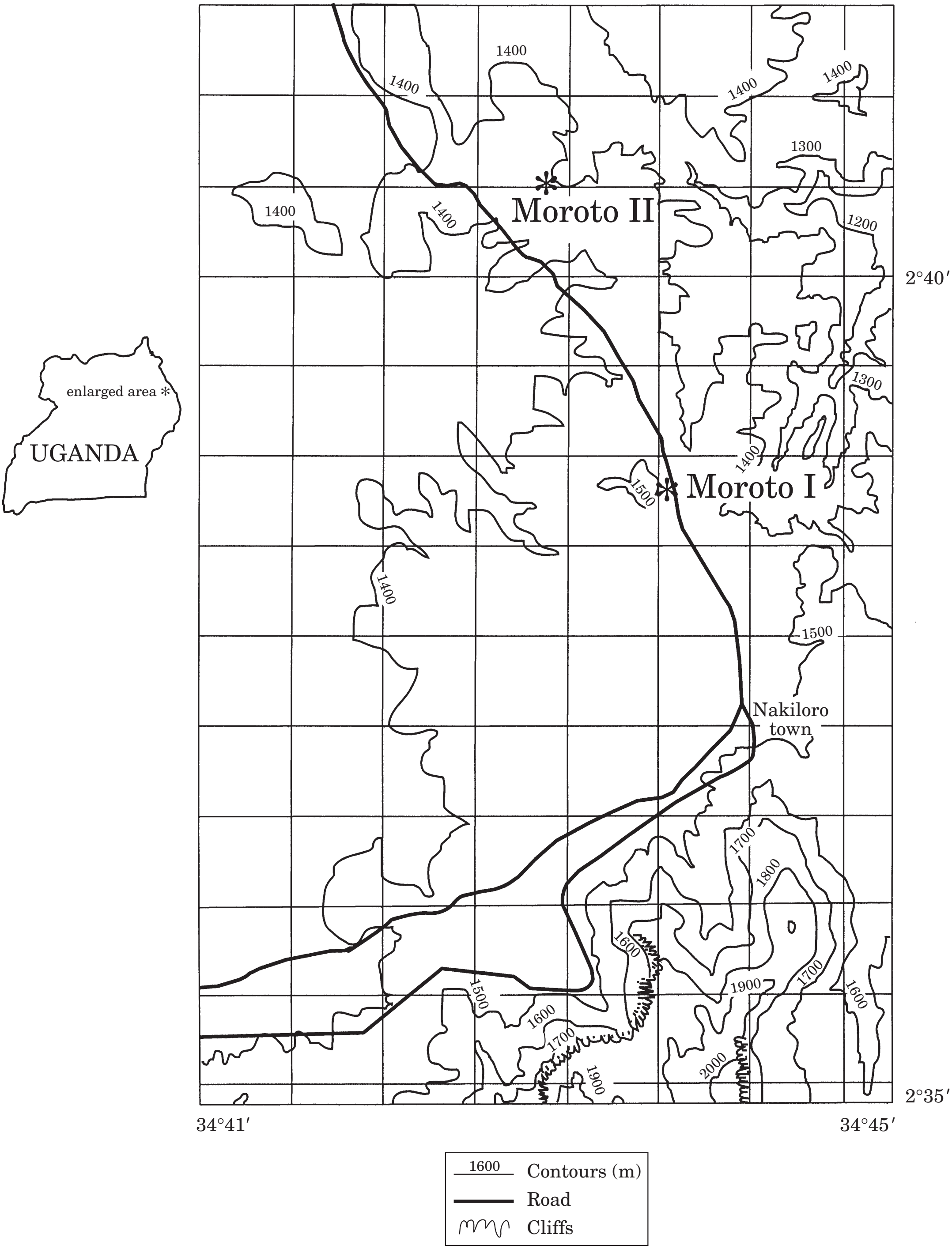

Figure 1. A map of the Moroto localities. Each grid is 1 km^2. Reproduced with permission from MacLatchy and Pilbeam (1999), Geological Society Publishing House.

Materials and methods

Comparative skeletal material was obtained from the Harvard Museum of Natural History, Cambridge, the American Museum of Natural History, New York and the Field Museum of Natural History, Chicago. Species and sample sizes are presented in relevant tables and figures.

Linear skeletal dimensions of skeletal material were obtained using digital calipers. The degree of concavity of glenoid fossae was assessed along central craniocaudal and dorsoventral axes by dividing the depth of a fossa by its length (or width) along these two axes. Measures of depth and length (or width) were made directly from tracings of the profiles of the dorsoventral and craniocaudal axes of a fossa, drawn using a carpenter's contour guide (Schmitt, 1996). Measures did not include the rim area of attachment of the labrum.

The width of glenoid fossae were also measured at 1/8th increments along their lengths. Since the Moroto I glenoid is missing its most cranial portion, 3 mm, or about 10% of its measured length, was added to its length estimate. Based on comparisons with similarly sized and proportioned extant primate glenoid fossae, this total length estimate is generous and so would not accentuate any resemblance to extant hominoid glenoid fossae, which are relatively shorter craniocaudally than are those of nonhominoid primates. Interspecific statistical comparisons among means for width/length ratios were made using the Least Significant Difference (LSD) test statistic for planned comparisons (Sokal & Rohlf, 1981). Results were considered significant at P-values $<0{\cdot}05$.

Cross-sectional properties of cortical bone were calculated (1) using photographs of breaks and a CalComp Digitizing Tablet with *Generic CADD Version 6* software, and (2) from Computed Tomographic scans using the program *DIGIT* (written by Cheal, Johnson & Johnson).

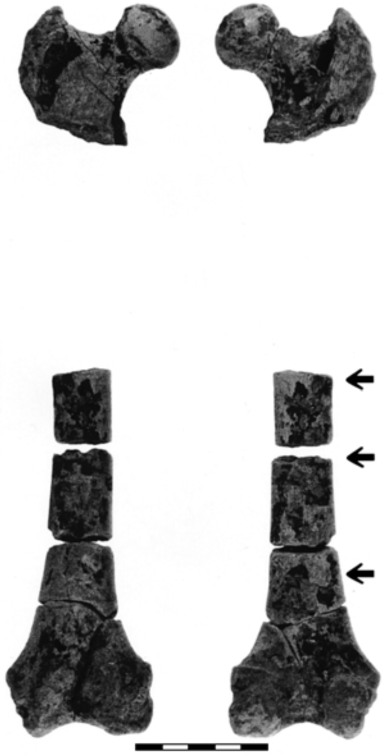

Figure 2. Anterior (left) and posterior (right) views of the right femur, MUZM 80. Locations of cross-sectional property determinations are indicated by arrows. From bottom to top they are the estimated 20%, 40% and 50% of total length. Scale bar=5 cm.

Descriptions

MUZM 80 from Moroto II consists of six fragments of the right and left femora. The right and left femoral material have similar sizes, morphology and preservation. These factors, along with the fact that all components were recovered along a single erosion gully within several meters of one another, suggest that they are best attributed to a single individual.

The right femur is represented by four pieces (Figure 2). The proximal portion is

54·0 mm long and broken obliquely at the level of the lesser trochanter medially and just proximal to the base of the greater trochanter laterally. The two shaft fragments, one of which represents an approximately midshaft portion and another which articulates with the most distal fragment, are 28·2 and 32·8 mm long respectively. The distal portion incorporates the entire articular end of the femur and measures 72·4 mm in length.

The right femoral head is abraded at the superior femoral articular margin; the missing region is 13·7 mm wide and clearly reveals the cancellous bone of the femoral head. There is also an abraded region at the inferior articular margin, with two pits, 8·5 mm and 5·3 mm in width. The anterior and posterior femoral articular margins are undamaged. The fovea capitis is oblong (9·8 mm long and 7·6 mm wide) with a maximum depth of 2·1 mm. The posterior femoral articular surface blends into the neck but the anterior margin is visible. The femoral head itself is spherical and has an anteroposterior (AP) width of 27·0 mm, a superoinferior (SI) height of 25·9 mm and a mediolateral (ML) depth of approximately 22·6 mm. The head is positioned symmetrically on the neck and the latter is not appreciably angled in the anterior or posterior direction. The neck is 22·0 mm long and has an estimated neck/shaft angle of 135°. The neck is fairly rounded in cross section, with an AP width of 17·9 mm and a SI height of 20·1 mm. There is a prominent tubercle on the posterior aspect of the neck, positioned on the superior portion of the distal one-third of the neck. The head and greater trochanter are elevated subequally above the neck. There is a small portion missing from the posterior aspect of the tip of the trochanter. The greater trochanter itself is broad and rugose with a maximum AP width of 26·8 mm wide and a SI length of 43·3 mm. There is no anterior flare. There is a flattened area on the anterior aspect of the greater trochanter for m. vastus lateralis. This flattened area is bordered anteromedially by a ridge for the insertion of m. gluteus minimus. A pit for the insertion of m. gluteus medius is superior to the proximal tip of the ridge for m. gluteus minimus. The trochanteric fossa is deep with a SI length of 27·62 mm and a maximum width above the tubercle of 10·9 mm. There is no well-developed, proximally placed posterior ridge bounding the inferior fossa. An intertrochanteric line is not evident and the intertrochanteric crest is faint. Most of the lesser trochanter is missing but the proximal portion indicates a posteromedial orientation.

The more proximal diaphyseal fragment, which is thought to correspond to the midshaft of the specimen, is only slightly flattened in the AP direction; the AP width is 18·8 mm and the ML width is 21·1 mm at the mid-point of the fragment. The distal shaft fragment articulates with the shaft of the distal femoral portion and has an AP width of 19·6 mm and an ML width of 22·6 mm at the mid-point of the fragment.

Several cortical cross sectional areas were determined, but the exact position of the section along the shaft of the femur could only be estimated as the entire shaft was not preserved. For comparative purposes, an estimated total shaft length of 279 mm was used, based on the average of four different length determinations using simple linear regression equations. Femoral head width was regressed on femoral length using a sample of 10 *Nasalis larvatus* and 10 *Mandrillus sphinx* femora (femoral length estimate=291 ± 23 mm (mean ± 95% C.I.)) and using a sample of 10 *Pan troglodytes* and 10 *Pongo pygmaeus* femora (femoral length estimate=256 ± 39 mm). Bicondylar width was regressed on femoral length using the same monkey and ape samples and yielding estimates of 315 ± 31 and 255 ± 32, respectively. The extant taxa were chosen because of size similarities with *Morotopithecus* and

Figure 3. Anterior (left) and posterior (right) views of the left femur, MUZM 80. Location of cross-sectional property determination (at estimated 80% of shaft length) is indicated by an arrow. Scale bar=5 cm.

because cercopithecoid and hominoid femoral proportions represent two extremes among catarrhines—cercopithecoids have long shafts, small femoral heads and narrow bicondylar regions, while hominoids have relatively shorter shafts, larger femoral heads and broader bicondylar regions.

Cortical area at estimated 20% of shaft length (most distal measurement) was 239·6 mm^2, at 40% it was 249 mm^2 and at 50% it was 294·5 mm^2. The cortical area at approximately 80% of shaft length, calculated from the left femur, was 292 mm^2 (see Figures 2 and 3).

The right distal femoral portion has two major fractures; one 20 mm from the proximal end, runs around the entire circumference of the shaft. The second fracture extends obliquely from the medial aspect of the circumferential fracture to the middle of the patellar groove. The most superior portion of the medial condyle is missing posteriorly. Anteriorly, an abraded region extends medially from the oblique fracture so that the medial half of the patellar groove is eroded.

The shaft of this distal fragment is AP flattened, with an AP width of 20·2 mm and a ML width of 30·9 mm. The condyles are also broad mediolaterally. The epicondylar width is 54·2 mm, the bicondylar width is 48·1 mm and the AP height from the lateral condyle to the patellar ridge is 35·8 mm. The condyles are asymmetrical in width; the medial condyle is 18·5 mm and the lateral condyle is 14·4 mm wide. The articular surfaces of both condyles are gently curved and the surfaces angle fairly steeply toward the intercondylar notch. The intercondylar notch is wide (15·6 mm) and heavily buttressed posteriorly and inferiorly. The medial epicondyle has a deep pit for the insertion of the tibial collateral ligament. The lateral epicondyle likewise is marked by a deep pit for the insertion of the fibular collateral ligament, and the popliteal groove is deep and distinct, extending from half the depth of the lateral condyle posterosuperiorly for 19·9 mm to the articular surface margin. The lateral aspect of the patellar groove reveals it to be shallow and gently curved; the groove is 30·1 mm in width and 26·0 mm in length.

The left femur is represented by two fragments: the femoral head and a proximal portion which preserves the lesser trochanter, but lacks the most proximal portion of the greater trochanter and the femoral neck (Figure 3). There is some slight abrasion on the femoral head but the articular surface margin is distinct over the entire surface. Relative to the fovea, the articular

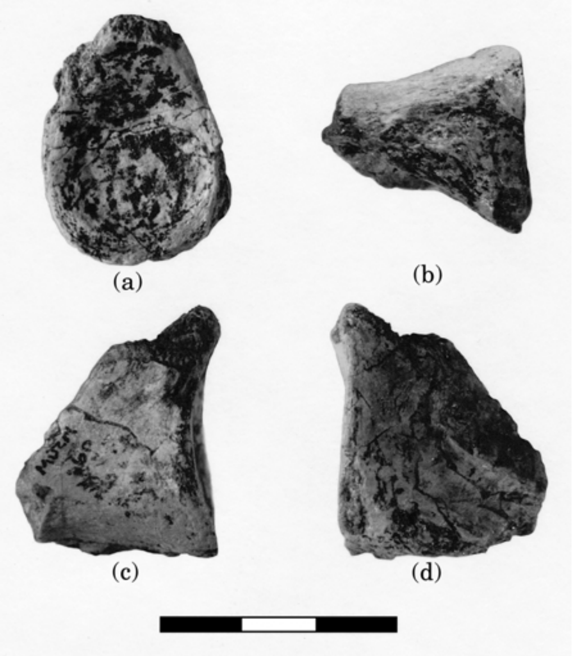

Figure 4. The scapula fragment MUZM 60 in medial (A), inferior (B), ventral (C) and dorsal (D) views. Scale bar=3 cm.

surface is distributed asymmetrically, with the preponderance of the articular surface on the anterior aspect of the head, and the head is small and relatively unexpanded. The AP width is 27·0 mm, its maximum height (SI) is 25·8 mm and its depth (ML) is 23·3 mm. The lesser trochanter has a maximum height of 16·0 mm and maximum width of 10·9 mm. There is a large pit on the lesser trochanter for the insertion of m. iliopsoas. There is a faint intertrochanteric crest extending laterally from the lesser trochanter; above it is a clear depression for the insertion of m. quadratus femoris. The external dimensions of the shaft just distal to the lesser trochanter are 19·7 mm (AP) and 25·7 mm (ML). The gluteal tuberosity is weakly developed, but visible posterodistal to the greater trochanter.

MUZM 60 is a proximal scapular fragment (Figure 4). Pickford *et al.*'s (1999) premature suggestion that the scapula is not attributable to a primate has been contradicted in detail (MacLatchy & Pilbeam, 1999). A key feature in the attribution is the ovate outline of the glenoid fossa, which is found to some degree only in hominoids, some atelines and cursorial mammals, such as the horse and deer (Roberts, 1974). Most quadrupedal mammals, both arboreal and terrestrial, have a glenoid fossa with a pear-shaped outline (Roberts, 1974). The Moroto glenoid is ovate, but cannot belong to a cursorial mammal with this morphology because the scapular spines of cursors, including bovids (e.g., *Syncerus*, *Bos*, *Ovis*), suids (e.g., *Phacochoerus*, *Potamochoerus*, *Sus*, *Hylochoerus*) tayossuids (i.e., *Tayassu*), cervids (e.g., *Cervus*, *Mazama*, *Odocoilus*, *Moschus*) tragulids (e.g., *Hyemoschus*, *Tragulus*), giraffids (e.g., *Okapia*), and perissodactyls (e.g., *Tapirus*, *Equus* and *Ceratotherium*) have a much more distal origin than do those of primates and the Moroto specimen. Some carnivores have glenoid fossae which approach an ovate shape, but carnivore glenoid fossae can be distinguished from those of hominoids on the basis of several criteria, including the presence of a notch on the craniodorsal surface of the glenoid margin, a lipped glenoid margin, and the absence of a clear attachment site for the glenoid labrum (MacLatchy & Pilbeam, 1999).

In all, the glenoid surface of the scapula is virtually complete, lacking only the most cranial part of the articular surface, including the superior glenoid tubercle, and a small part of the cranioventral attachment area of the glenoid labrum. Thus, despite the fact that there is damage to the dorsal margin of the glenoid, the labrum attachment is preserved such that the outline of all but the cranial tip of the glenoid fossa can be accurately reconstructed.

A crack extends dorsoventrally across the middle of the glenoid fossa. The fossa has a maximum dorsoventral width of 24·7 mm and a maximum height of 30·5 mm. The glenoid surface is gently concave and has a maximum depth of 2·2 mm dorsoventrally and 4·9 mm craniocaudally. The scapular neck has a minimum width of 15·4 mm and extends back from the glenoid fossa for 22·0 mm on the ventral side and for 29·0 mm on the dorsal side. The base of the scapular spine is clearly visible 13·0 mm posterior to the glenoid surface margin. The scapular neck is rugose inferiorly and the inferior glenoid tubercle is very rugose for the attachment of m. triceps brachii.

Comparative and functional anatomy

Proximal femur

The femoral head is small relative to the dimensions of the shaft. The ratio of femoral head AP width to proximal shaft AP width (at estimated 80% of shaft length) is 1·15, similar to the condition of other East African primitive catarrhines, such as *Equatorius africanus* from Maboko Island (1·17 for BMNH (British Museum of Natural History) 16331) and *Proconsul nyanzae* (1·07 for KNM (Kenya National Museums) MW 13142A), but lower than values obtained for living hominoids (1·35 for *Hylobates lar*, *n*=12; 1·30 for *Pongo pygmaeus*, *n*=4; 1·28 for *Pan troglodytes*, *n*=5 and 1·27 for *Gorilla gorilla*, *n*=7). Surface area for the right (1877 mm^2) and left (1931·5 mm^2) femoral heads and head volume determinations (9681·5 mm^3 for the right and 9626·7 mm^3 for the left; see Ruff, 1990 for formulae) further illustrate the diminutive head size. Ratios of head surface area/mid-shaft cortical area gives values of 6·5 and 6·7, below the values of great apes (8·2–12·0) and macaques (7·5–8·4) (see Figure 5 in Ruff, 1988). Ratios comparing femoral head volume to midshaft cortical area (ratio = 1·25 for left and right femoral heads) are also well below the range of values presented for great apes, macaques and *Proconsul* (Ruff *et al.*, 1989). These low linear, area and volume ratios all reflect the unusual relative dimensions of the femoral head and shaft and may imply a different pattern of loading the femur than is typical of living primates (see below).

The fact that the femoral head is also small relative to neck size may have implications for abduction. The ratio of the cube root of head volume to the square root of mid-neck periosteal area is 1·26, lower than for macaques or great apes (Ruff, 1988). Ruff (1988) has suggested that a low value for this ratio compromises the maximum range of joint excursion.

Excursion patterns may also be inferred by looking at the distribution of femoral articular surface about the fovea capitis (MacLatchy & Bossert, 1996). In *Pan*, the articular surface is distributed relatively uniformly around the circumference of the femoral head, permitting a wide range of femoral postures. In contrast, monkeys such as *Mandrillus*, *Macaca* and *Saimiri* exhibit a pronounced asymmetrical condition with significantly more articular surface on the anterior aspect of the head. This latter

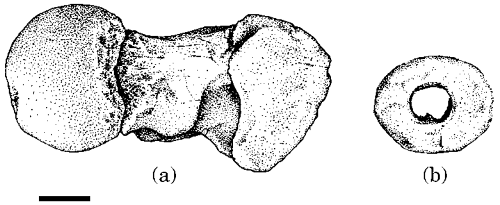

Figure 5. Superior view of MUZM 80, right side (A) and cross-section of the proximal diaphyseal fragment, believed to be located at approximately 50% of shaft length (B). Scale bar = 1 cm.

morphology, which is also found in *Morotopithecus*, is compatible with a greater emphasis on more adducted limb postures. Together, the small head and asymmetrical articular surface distribution suggest fore and aft movements of the hip with a habitually less abducted hip than occurs in *Pan*. These femoral postures are normally associated with more committed primate quadrupeds.

The femoral head also differs from those of extant apes in that it does not tilt forward over the shaft, nor does the greater trochanter overhang the shaft (Figure 5). Further, the articular surface does not mushroom over the rim toward the neck, but lies close to the surface of the femoral neck; thus, the head is not clearly distinct from the neck as in living hominoids (Harrison, 1987).

The orientation of the femoral head and neck relative to the shaft (135°) is similar to the condition of extant hominoids, some Miocene hominoids and *Ateles* and unlike the condition in cercopithecoids (Rose *et al.*, 1992; Table 1; Figure 6). Despite the angled femoral neck, the neck is not elongated and so the head is only moderately elevated (Figure 6). In the absence of a long neck, a high neck angle would not have greatly facilitated abduction.

The neck possesses a prominent crista trochanterica or mound of bone. Early catarrhines and some Miocene hominoids, such as *Proconsul*, also possess this feature. The crista is variably developed in gibbons and is absent in great apes (Rose *et al.*, 1992; Gebo & Sargis, 1994). The trochanteric fossa is large and open and extends well below the mid-point of the femoral neck as in cercopithecoids, platyrrhines and strepsirhines, and is unlike the condition in living hominoids where the fossa is deep and does not extend as far distally (Figure 6). In general, the morphology of the region of the greater and lesser trochanters is quite variable in primates. In strepsirhines, platyrrhines and some early catarrhines, the lateral ridge of the greater trochanter extends downward parallel to the shaft with a large trochanteric fossa extending for some distance distally along the neck and shaft of the femur (Gebo & Sargis, 1994). The intertrochanteric region is open and flat and a crista trochanterica is often prominent. In other early catarrhines, cercopithecoids and hominoids, the lateral ridge runs obliquely across the intertrochanteric region. In cercopithecoids, the greater trochanteric fossa still extends well distally and a crista trochanterica is also present, however, the intertrochanteric region is no longer flat and a swelling of bone or a wide ridge separates the greater trochanteric fossa from the lesser trochanteric depression. In living hominoids, this swelling has further increased in size and more clearly separates the two trochanteric fossae with the greater trochanteric fossa being short and bounded proximally. The crista is also lost in the living great apes. Harrison (1987:67) described the trochanteric fossa as being “shallow but extensive” in nonhominoid catarrhines and “deep and restricted” in extant hominoids. *Morotopithecus* most closely resembles the condition observed in cercopithecoids for the posterior fossae and intertrochanteric region, as do *Proconsul*, *Pliopithecus* and *Equatorius*.

Although weakly developed, the gluteal ridge is visible and extends to the broken part of the shaft. This is a characteristic of all great apes. The lateral aspect of the shaft is not flattened as in great apes, however,

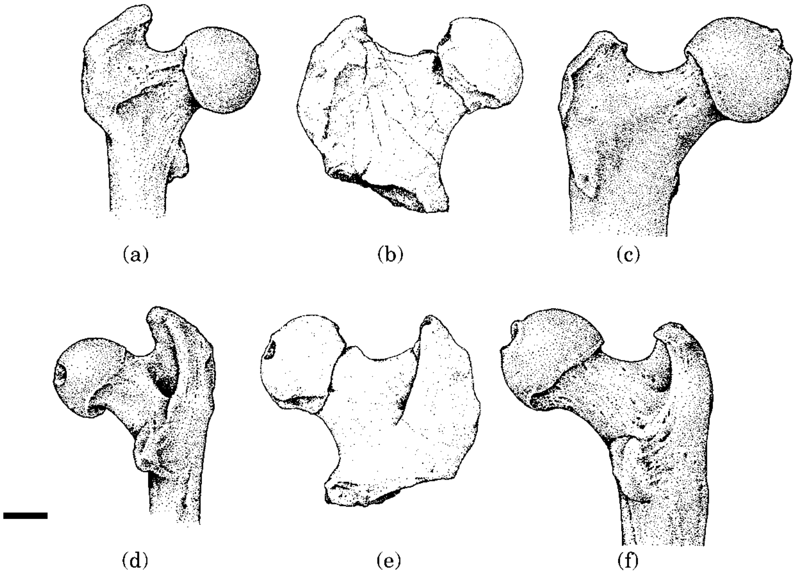

Figure 6. Anterior (top row) and posterior (bottom row) views of the proximal femora of *Papio hamadryas* (A, D), *Morotopithecus bishopi* (B, E) and *Pan paniscus* (C. F). Scale bar=1 cm.

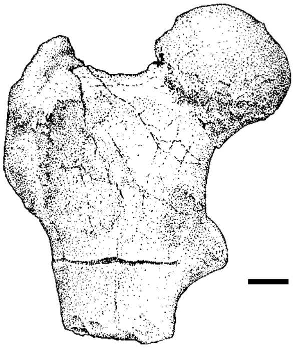

Figure 7. Composite drawing of anterior view of left and right proximal femur, showing position of the lesser trochanter. Scale bar=1 cm.

nor is there a hypotrochanteric fossa. Laterally, the greater trochanter looks similar to the same region in *Pliopithecus*, and lacks the extreme bony projections away from the trochanteric region that can be observed in taxa like *Proconsul nyanzae* (KNM-WM 13142). A linea aspera, which runs up to or above the lesser trochanter in living apes is not visible.

The lesser trochanter is broad and triangular in shape and angles at 30° from the midline of the femoral head and greater trochanter (Figure 7). This medial placement is similar to that of *Pongo* and *Hylobates*, and unlike the more posterior placement in cercopithecoids and African apes (Table 1). Lesser trochanter position has been shown to be quite variable within species and the functional implications of its placement are not clear (Aiello & Dean, 1990).

Femoral shaft

The shaft is extremely robust in terms of cross sectional area properties compared to *Proconsul* and living hominoids where cortical area:periosteal area ratios (CA/PA) range from 0·48–0·75 (Ruff, personal communication). The CA/PA value is 0·81 for the estimated 50% cross-section, similar to the ratios found in robust bipedal hominids (Ruff *et al.*, 1993). The extreme thickness of the cortical bone in *Morotopithecus*

Table 1 Femoral neck and lesser trochanter angles

	Femoral neck angle		Lesser trochanter angle		
Taxon (N)	Mean	Range	Mean	Range	Reference
Gorilla sp. (2)		120–130	45		Piganiol & Olivier (1959)
Gorilla sp. (5)	112	110–115	52	45–60	This paper
Pan troglodytes (3)			50		Piganiol & Olivier (1959)
Pan sp. (10)	132·5	121–141			Rose *et al.*, 1992
Pan troglodytes (7)	122	115–130	52	45–60	This paper
Pongo sp. (4)	145	135–152	29	20–35	This paper
Hylobates sp. (10)	133·5	126–141			Rose *et al.*, 1992
Hylobates lar (6)	129	125–133	37	30–45	This paper
Hylobates muelleri (5)	134	130–140	39	35–45	This paper
Hylobates concolor (7)	141	135–145	36	28–45	This paper
Hylobates syndactylus (3)	145		34	30–37	This paper
Macaca sp. (4)	100		45		Piganiol & Olivier (1959)
Cercopithecus sp. (4)		110–126	50		Piganiol & Olivier (1959)
Papio sp. (2)	100		60		Piganiol & Olivier (1959)
Colobus sp. (10)	120·5	117–125			Rose *et al.*, 1992
Ateles sp. (10)	139·8	130–150			Rose *et al.*, 1992
Cebus sp. (10)	122·5	110–135			Rose *et al.*, 1992
Simiolus enjiessi	130				Rose *et al.*, 1992
Pliopithecus vindobonensis	125		30		This paper
Eppelsheim femur	135		35		This paper
Limnopithecus evansi	128				Rose *et al.*, 1992
Proconsul nyanzae (3)	130		38	30–50	This paper
Rangwapithecus gordoni	133				Rose *et al.*, 1992
Equatorius africanus	125		30		This paper
Morotopithecus bishopi	135		30		This paper

(Figure 5) has also been illustrated by comparing body weight estimates derived from bicondylar width or femoral head size with those derived from cortical area (Gebo *et al.*, 1997; MacLatchy & Pilbeam, 1999). Body weight estimates from the proximal shaft (at estimated 80% of length), midshaft (at estimated 50% of length) and distal shaft (at estimated 20% of length) of *Morotopithecus* give estimates of 52, 53 and 54 kg, respectively while femoral head diameter yields estimates of 25–30 kg and bicondylar width suggests a mass of 37–39 kg (MacLatchy & Pilbeam, 1999).

Not only are the femoral shafts of *Morotopithecus* constructed somewhat differently from those of extant hominoids, they also differ from that of *Proconsul*. Ratios of CA/PA and maximum moment of inertia in the AP and ML planes (I_x/I_y) at 50% of femoral length are known for *Proconsul africanus* (KNM-RU 2036) and are 0·67 and 0·84 respectively (Ruff, personal communication) while in *Morotopithecus* the ratios are 0·81 and 0·85. Thus the relative resistances to bending in the ML and AP planes are similar for *Morotopithecus* and *Proconsul* (and *Macaca*, all of which have a higher AP plane of development than *Pan*) but the femur of *Morotopithecus* is more heavily reinforced.

Higher cortical areas have been associated with an emphasis on axial rigidity rather than bending or torsional strength (Ruff & Runestad, 1992) although all three loading regimes could potentially cause this morphology. Given the pattern of higher CA/PA values among orang-utans (Ruff, 1989) and lorisines (Ruff & Runestad, 1992; Runestad,

1994) compared to other primates, it is possible that the high axial rigidity in *Morotopithecus* may be associated with slow and cautious climbing activities (Gebo *et al.*, 1997) that require sustained muscular recruitment. Early *Homo* and *Homo erectus/ergaster* femora also possess thick cortical bone, and in both *Morotopithecus* and hominins the extra bone seems to be the result of endosteal apposition since external dimensions are not expanded (Kennedy, 1983). A number of different explanations have been invoked to explain the thick diaphyseal cortical bone in *Homo*, including different patterns of weight transmission, retention of juvenile growth rates and dietary factors (Kennedy, 1983) and high activity levels may also be implicated. In the case of *Morotopithecus*, a biomechanical explanation is favored, although the sort of loading environment that could engender a build-up of such metabolically costly tissue remains unclear.

The distal shaft of *Morotopithecus* is elliptical in shape with an I_x/I_y ratio of 0·63 at the estimated 20% of shaft length. These distal shaft proportions are also found in great apes, but not in hylobatids and cercopithecids, whose distal shafts are more rounded. *Pongo pygmaeus* and *Pan troglodytes* have a ratio of maximum (AP) to minimum (ML) area moments of 0·5 at 20% of shaft length, while in *Mandrillus sphinx* and *Hylobates lar* the ratio is 0·78 ($n=10$ for all four taxa). The elliptical shape of the distal diaphysis in *Morotopithecus* would seem to indicate that the femur was structured to resist bending in the ML plane, such as would be incurred by abducted hindlimb postures during climbing. It is suspected a mediolaterally broad femoral shaft may also be a structural corollary of the relatively broad femoral condyles of *Morotopithecus* and other large bodied hominoids (see below).

Although distal femoral cross sectional data are not available for other Miocene hominoids, external measurements of ML and AP shaft diameters from casts indicate that the Maboko *Equatorius* femur (BMNH 16331) is more rounded (AP/ML shaft width at 20% femoral length is 0·96) while *Proconsul nyanzae* specimens (KNM-RU 3682 AP/ML=0·86 and KNM-MW 13142 AP/ML=0·83) are more elliptical, though not as elliptical as those of *Morotopithecus* (AP/ML=0·77) or *Sivapithecus* (GSP (Geologic Survey of Pakistan) 47025 AP/ML=0·75).

Distal femur

Although the medial half of the patellar facet is eroded, the lateral aspect of the trochlea reveals it to be broad, shallow and gently curved, permitting a patella to move in the ML as well as the AP plane. This region is also broad and shallow in hominoids and lorisines and is relatively narrow and deeper in cercopithecids and some ceboids, but especially in lemurids, galagids and tarsiers (Tardieu, 1983), in which a deep facet prevents dislocation of the patella during rapid and forceful knee movements.

Tardieu (1983) has quantified the distal proportions of the femur in primates and shown it to vary widely; the great apes have a ML broad femur, gibbons are intermediate and humans and cercopithecoids have distal epiphyses with more similar dimensions in AP and ML planes (Figure 8). *Morotopithecus*, like the great apes, and *Oreopithecus* (Harrison & Rook, 1997) have distal femora that are broad mediolaterally.

Associated with a distal femur that is relatively broader mediolaterally than anteroposteriorly is a relatively wide intercondylar notch (Figure 9). It is possible that rotatory capacity in the knee is enhanced if the distance between the condyles is increased without increasing the distance between the tibial spines. Tardieu (1983) postulated a correlation between the ratio of distance between tibial spines/width of intercondylar notch (lowest in gibbons, followed by monkeys, *Pan*, *Pongo*, *Gorilla*, *Homo*) and laxity

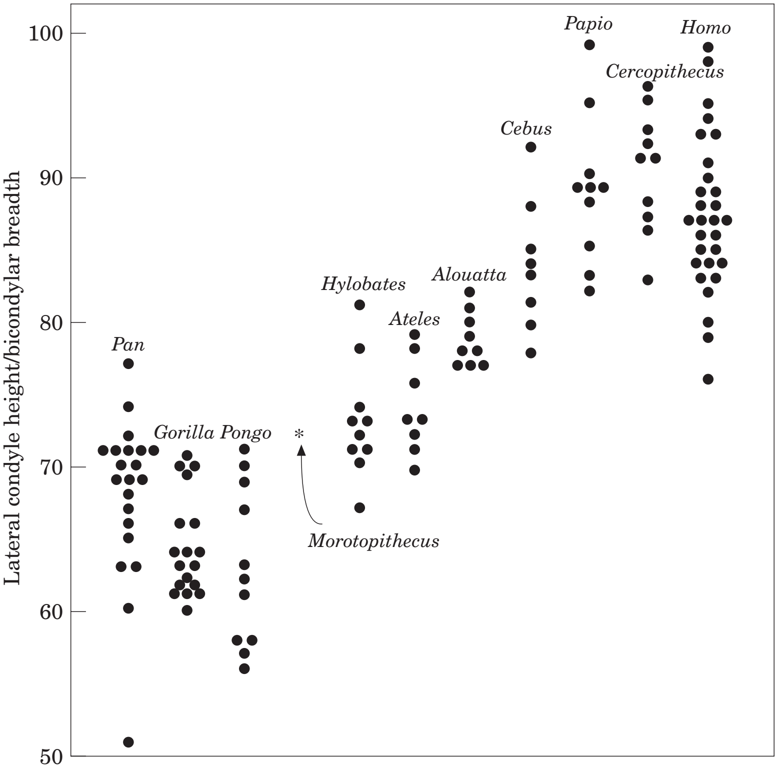

Figure 8. Ratio of the lateral condyle height to bicondylar breadth. Extant catarrhine data are from Tardieu (1983).

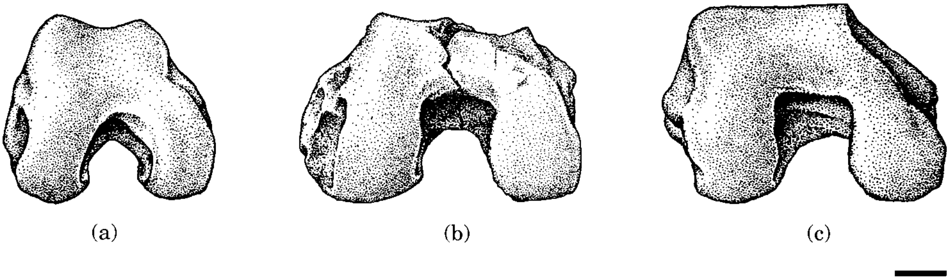

Figure 9. Inferior view of the femoral condyles of *Papio hamadryas* (A), *Morotopithecus bishopi* (B) and *Pan paniscus* (C). Scale bar=1 cm.

or "independent rotation" in the knee. Lacking a tibia, this ratio cannot be determined for *Morotopithecus*. In addition to being wide, the intercondylar notch of *Morotopithecus* is heavily buttressed posteriorly and inferiorly as it is in great apes (Figure 9).

The medial and lateral condyles are asymmetrical in size, with the medial condyle being 1·3 times broader than the lateral. This is the condition seen in living great apes. Gibbons and cercopithecoids both have lateral and medial condyles more

Figure 10. Lateral view of the distal femora of *Pongo pygmaeus* (A), *Pan troglodytes* (B) and *Morotopithecus bishopi* (C). Arrows indicate the well-developed popliteal grooves. Scale bar=1 cm.

nearly similar in size (Tardieu, 1983; Ruff, 1988). The functional significance of condylar asymmetry is debated. It has been interpreted as facilitating rotation at the knee via a screw-like mechanism in lorisids and great apes (Tardieu, 1981, 1983), and a correlation between asymmetry and degree of varus of the knee joint has also been proposed, with a more varus femoral orientation causing the medial condyle to bear more weight than the lateral condyle, resulting in its relative enlargement (Preuschoft, 1970; Jungers & Susman, 1984). Ruff (1988) has suggested that both of these explanations are to some degree unsatisfactory, since gorillas, which he proposes have a knee morphology that emphasizes weight support over mobility compared to other great apes, have great condylar asymmetry, and since orang-utans have an apparently valgus knee joint despite condylar asymmetry. A third hypothesis by Fleagle (1977; Fleagle & Meldrum, 1988) is that asymmetry is a reflection of the differential weight bearing that results from rotating the femur on the tibia during abducted femoral excursion. None of these hypotheses associate condylar asymmetry with a joint that is adapted primarily for efficient quadrupedal progression. Tardieu and Fleagle explicitly associate asymmetry with knee rotation, while the third hypothesis associates it with a habitually bowlegged, abducted stance.

The lateral epicondyle is marked by a deep and distinct groove for the popliteus muscle (Figure 10). In most primates, including humans, the popliteal groove or fossa is not as distinct; among living apes, *Pan* and *Pongo* have as deep a groove, and the groove is also well-developed in *Sivapithecus* and in Pliocene hominids. In humans, the popliteus acts to laterally rotate the femur on the fixed tibia (or medially rotate the tibia on the femur). Its function during bipedal locomotion is as yet unclear, but it seems to be important in rotation and in turning and it has been implicated in “unlocking the knee” during the first few degrees of flexion. It is also thought to have a postural role in aiding the posterior cruciate ligament to prevent the femur from sliding forward during crouching (Barnett & Richardson, 1953). The role that the popliteus plays in locomotion in apes and monkeys is currently being investigated using electromyography. Preliminary results

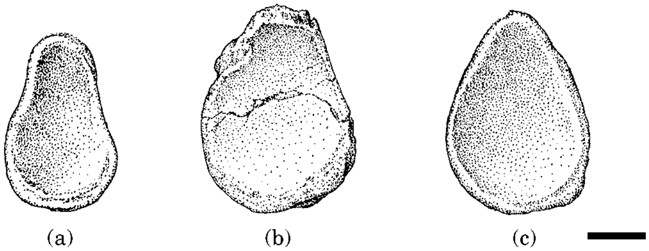

Figure 11. Medial view of the glenoid fossae of *Papio hamadryas* (A), *Morotopithecus bishopi* (B) and *Pan paniscus* (C). Scale bar = 1 cm. Reprinted with permission from MacLatchy & Pilbeam, 1999, Geological Society Publishing House.

for *Pongo*, *Pan* and *Erythrocebus* indicate that while popliteus is rarely active in the monkey, and then only when changing direction during turning behaviors, there is frequent and high level activity in *Pan* and *Pongo*, especially during vertical climbing (MacLatchy *et al.*, 1998). Popliteus is thus postulated to be important in rotating and stabilizing the knee during transmission of force through the hindlimb during vertical climbing.

Scapula

A highly mobile shoulder joint is considered a key morphological adaptation in hominoids, enabling characteristic positional behaviors such as brachiation and forelimb suspension. However, the comparative morphology of the shoulder socket remains understudied, perhaps due in part to the paucity of glenoid cavities in the fossil record.

The partial scapula of *Morotopithecus* retains only the region proximal to the neck, with the glenoid fossa largely preserved. Roberts' 1974 study of the structure and function of the primate scapula remains one of the few comparative studies of the glenoid region (see also Anapol, 1983). As discussed above, Roberts divided glenoid fossae into two groups based on their outline: pear-shaped, as typified by a baboon, and ovate, as typified by a chimpanzee (Figure 11). Roberts (1974) speculated that the ovate shape permits freedom of movement in primates and is an adaptation for rapid limb motion with a high acceleration increment in cursors.

One of the key features of the ovate morphology is that, relative to craniocaudal length, the dorsoventral width of the middle region of the cavity is broader than in the pear-shaped glenoids. This morphology is compatible with loading of the glenoid cavity over a dorsoventrally wide range of movement. Comparisons of the relative width of the glenoid reveals a distinct difference among primates (Figure 12). *Pan* and *Hylobates* have particularly broad glenoids. In fact all living hominoids have significantly broader glenoids than nonhominoid anthropoids at the mid-fossa. Notably, the glenoid cavity of the highly suspensory *Ateles* is convergent on hominoids. The Moroto glenoid is broad dorsoventrally, like that of living hominoids. In contrast, *Pliopithecus*, one of the few other Miocene catarrhines for which a glenoid has been recovered, does not have a dorsoventrally broad articular surface.

Roberts (1974) described the craniocaudal curvature of pear-shaped glenoids as an arc with a decreasing radius, and proposed that the cranial lip prevented dislocation of the humerus when retracted through a large angle. He described ovate glenoids as having a smooth circular arc, permitting concentric rotation of the humeral head in the glenoid socket.

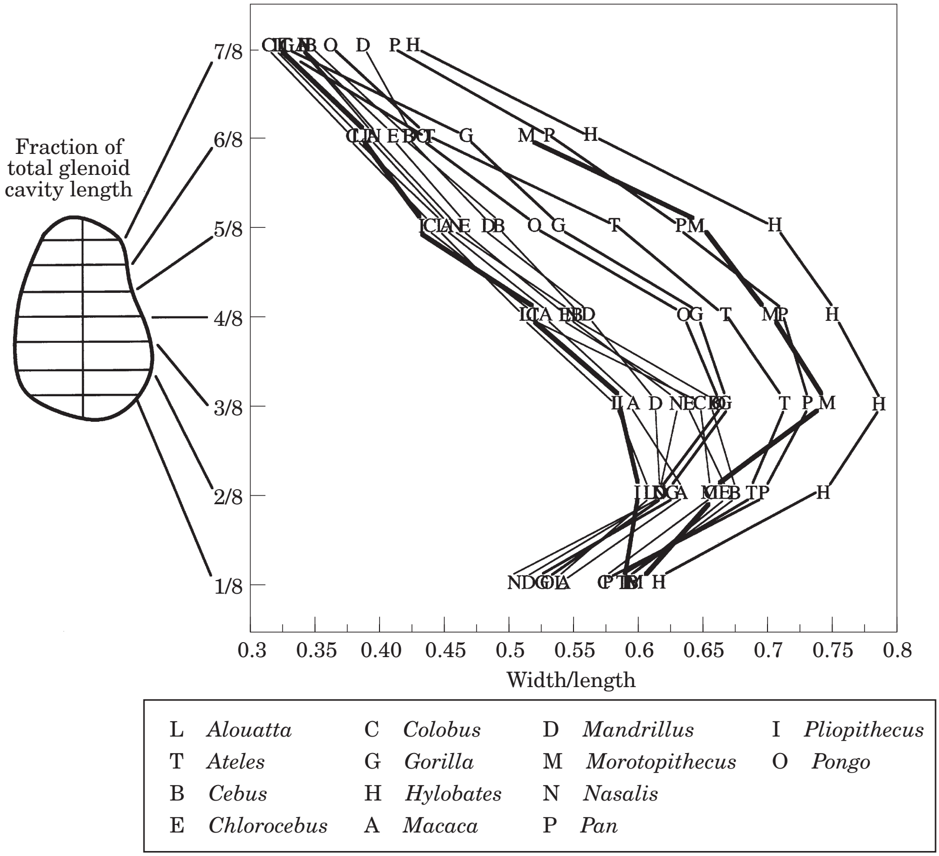

Figure 12. The ratio of the dorsoventral width of the glenoid fossa to the maximum craniocaudal length was determined at 1/8th increments along the length of the fossa. At the width measurement of one half (4/8) the total length, all of the hominoids (including *Morotopithecus*) and *Ateles* are significantly broader for their length than are all other anthropoids (including *Pliopithecus*) as determined by Fisher's Least Significant Difference Test Statistic at $P<0{\cdot}05$. Sample sizes for extant species are as follows: *Alouatta seniculis*: 7 males, 9 females; *Ateles* sp.: 1 male, 4 females, 3 unknown sex; *Cebus apella*: 5 males, 4 females, 3 unknown sex; *Chloropithecus aethiops*: 7 males, 5 females; *Colobus polykomos*: 8 males, 4 females; *Gorilla gorilla gorilla*: 9 males, 8 females; *Hylobates lar lar*: 6 males, 6 females; *Macaca fascicularis*: 6 males, 6 females; *Mandrillus sphinx*: 6 males, 5 females; *Nasalis larvatus*: 7 males, 8 females; *Pan troglodytes troglodytes*: 11 males, 10 females; *Pongo pygmaeus pygmaeus*: 5 males, 7 females.

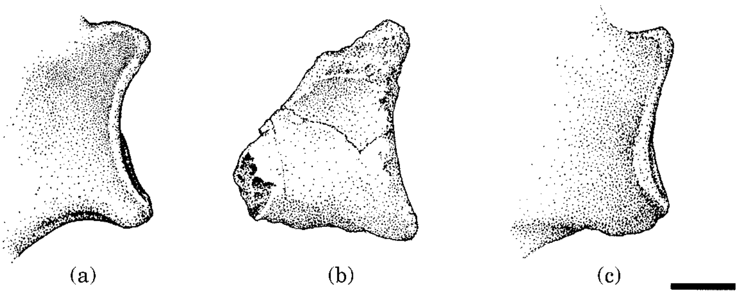

Figure 13. Ventral view of the glenoid fossae *Papio hamadryas* (A), *Morotopithecus bishopi* (B) and *Pan paniscus* (C). Scale bar=1 cm.

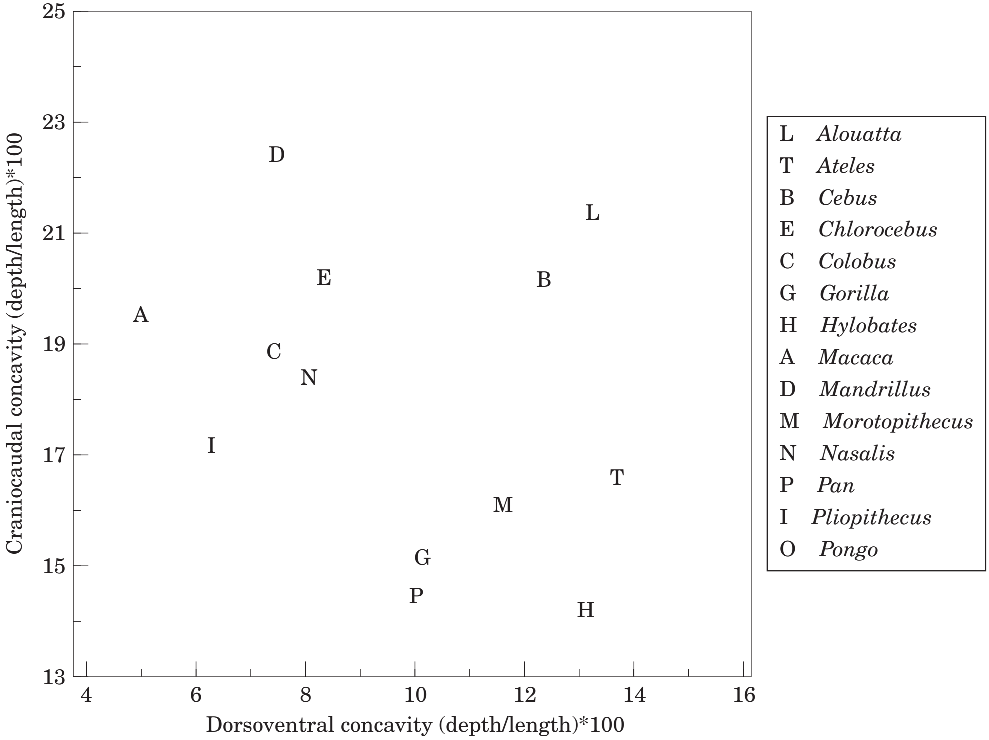

Figure 14. The depth of the glenoid fossa relative to its length along the craniocaudal and dorsoventral axes is plotted. Hominoids (including *Morotopithecus*) and *Ateles* are moderately curved along both axes while other catarrhines tend to have much greater curvature along the craniocaudal axis compared to the dorsoventral axis. *Cebus* and *Alouatta* have fossae that are highly curved along both axes. Sample sizes are as in Figure 12.

Figure 13 shows that while *Papio* does have a more craniocaudally curved glenoid than *Pan*, the curvature is smooth and does not increase cranially. Rather than assess just craniocaudal curvature, a more functionally informative approach is to compare the degree of curvature of the glenoid fossa along craniocaudal and dorsoventral axes. In all primates surveyed, the craniocaudal axis of the glenoid fossa is more curved than the dorsoventral axis of the fossa.[2] A comparison of the relative concavity of the glenoid fossa along the two axes reveals distinct patterns among anthropoids (Figure 14). Hominoid glenoid cavities are characterized by moderate curvature in both the craniocaudal and dorsoventral directions, permitting a wide range of rotational shoulder movements. Cercopithecoids tend to have glenoid cavities that are moderately to very curved in the craniocaudal direction but less curved dorsoventrally. This asymmetrical

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[2] For most primates, curvature asymmetry in the dimensions of the humeral head parallel asymmetry in the glenoid fossa. Of the primates included in this study, all of the hominoids except *Pongo*, and all of the cercopithecoids have humeral heads that are wider dorsoventrally than craniocaudally. The three ceboids and *Pongo* have humeral heads that are more symmetrical, i.e., the width and height of the humeral heads do not differ. Thus, assuming that the curvature of the humeral head is uniform, the radius of curvature is generally greater in the dorsoventral than in the craniocaudal direction, just as in the glenoid cavity. Constancy of curvature may not be a valid assumption, however, since the humeral heads of quadrupeds are usually characterized as being flattened proximally, presumably because this makes the glenohumeral articulation more stable in the protracted, weight bearing position (Larson, 1993).

curvature would favor flexion/extension over rotatory movements. The three platyrrhine genera measured for this study present an interesting contrast. *Ateles*, like hominoids, is moderately curved in both dorsoventral and craniocaudal directions. It is slightly more curved than *Hylobates*, but like the latter has relatively uniform curvature. *Cebus* and *Alouatta*, however, are highly curved along both the craniocaudal and dorsoventral axes. This may represent an attempt to maintain stability *sensu* Roberts yet also reflect a capacity for a wide range of movements generated by climbing and occasional suspension.

The Moroto glenoid closely resembles those of extant hominoids, and is thus postulated to have been loaded over a wide range of movements, such as would occur during forelimb suspensory and forelimb dominated climbing behaviors including vertical ascension. This behavioral repertoire contrasts with those of other early and middle Miocene hominoids who have been reconstructed as having generalized pronograde quadrupedal repertoires. This glenoid thus marks the earliest record of forelimb suspensory behavior in hominoids.

Vertebra

Recent reappraisals of the middle lumbar vertebra UMP 67.28 recovered by William Bishop at Moroto II have confirmed Walker & Rose's (1968) initial report that the Moroto vertebra resembles the extant hominoid condition (Ward, 1993; Sanders & Bodenbender, 1994). Although craniocaudal vertebral length most closely resembles that of male baboons (Sanders & Bodenbender, 1994), the vertebra shares many features with hominoids to the exclusion of cercopithecoids, including robust pedicles, lack of anapophyses, reduced ventral keeling and a caudally inclined spinous process (which is correlated with reduced dorsoventral mobility) (Ward, 1993; Sanders & Bodenbender, 1994) (Figure 15). The location of origin and orientation of the transverse processes also resemble the condition found in extant hominoids: the processes arise from the pedicle and are oriented dorsally (Sanders & Bodenbender, 1994), increasing the moment arm of iliocostalis and longissimus dorsi to resist flexion (Shapiro, 1993). This has been interpreted to mean that the Moroto hominoid had a stiff back, and that an upright posture and quadrumanous climbing were part of its positional repertoire. Such a behavioral pattern is in marked contrast with other early Miocene hominoids, such as *Proconsul nyanzae* and *P. heseloni*, whose vertebrae are more like those of cercopithecoids and who have been reconstructed as generalized quadrupeds (Ward, 1993; Rose, 1993, 1994).

The extant hominoid-like features of the Moroto lumbar vertebrae are rare among Miocene hominoids. The lumbar morphology of other early and middle Miocene African hominoids, including *Afropithecus*, is unknown; however, no other postcranial features argue for anything but pronograde quadrupedalism in these taxa (see reviews by Pilbeam, 1996; Leakey & Walker, 1997; Ward, 1998). While recent reports for *Equatorius* from Maboko Island, Kenya suggest hominoid-like features in the radius and cuboid (McCrossin, 1997; McCrossin *et al.*, 1998), lumbar vertebrae attributed to *Equatorius* [or *Nacholapithecus* (Ishida *et al.*, 1999)] from the Nachola region of northern Kenya are primitive and suggest a long, flexible vertebral column (Rose *et al.*, 1996; Nakatsukasa *et al.*, 1998) as do *Equatorius* vertebrae from Tugen Hills, Kenya (Ward *et al.*, 1999).

Thus, the absence of evidence for well-developed orthograde and suspensory behavior among other Miocene genera may indicate that this positional behavior was an attribute of only one hominoid lineage (the one that gave rise to all extant apes) and is not simply the result of an inadequate fossil

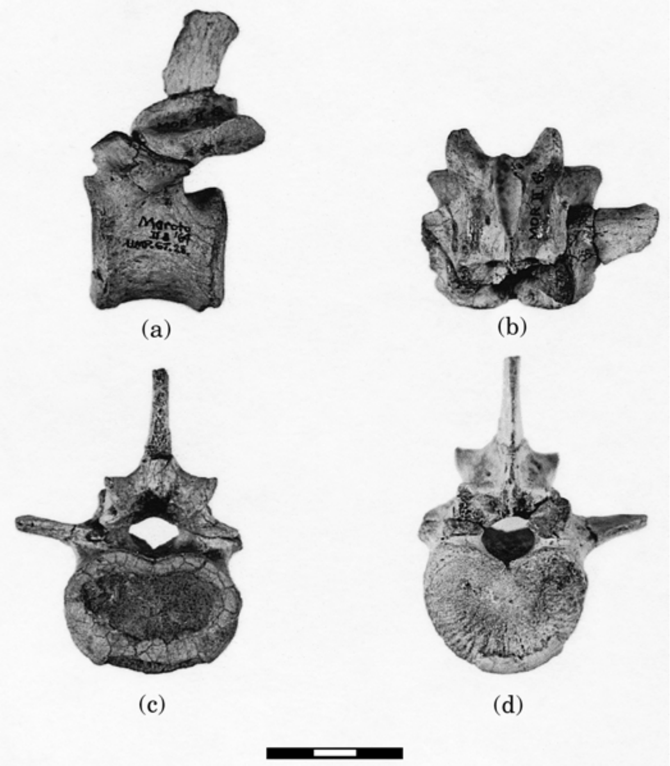

Figure 15. Lateral (A), dorsal (B), caudal (C) and cranial (D) views of lumbar vertebra UMP 67.28. Scale bar=3 cm.

record (Harrison, 1982). It is not until the late Miocene of Europe that a lumbar morphology resembling that of extant hominoids is again documented, in *Oreopithecus* and possibly *Dryopithecus*. Although detailed descriptions of a new 9·5 million-year-old *Dryopithecus laietanus* skeleton from Can Llobateres, Spain have not been published, Moyà-Solà & Kohler (1996) have reported that the fragmentary lumbar vertebrae of *Dryopithecus* while "somewhat elongated" (p. 158) are "proportionally shorter than those of cercopithecoids and proconsulids" (p. 157). As recently reviewed by Shapiro (1993), shortening of the lumbar region, achieved by reducing the number of vertebrae and/or shortening the craniocaudal length of vertebral bodies, is thought to be related to locomotor modes involving orthogrady and behaviors such as brachiation (Keith, 1923), bridging behavior (Cartmill & Milton, 1977) and vertical climbing at large body size (Jungers, 1984) have all been implicated. The detailed metric comparisons by Sanders & Bodenbender (1994) have shown that *Morotopithecus* did not have short lumbar vertebrae. According to Moyà-Solà & Köhler (1996), however, *Dryopithecus* shares with *Morotopithecus* and extant hominoids transverse processes which arise from the pedicles and caudally directed spinous processes, both correlated with "stiff-backed" behavior in primates. *Oreopithecus bambolii* (dated at 8·4 Ma) lumbar vertebrae are reduced in length and number and also have transverse processes that arise from the base of the pedicles (Straus, 1963; Harrison & Rook, 1997).

Oreopithecus and *Dryopithecus* are the only other nonhominine fossil taxa with an inferred orthograde component to their positional behavior.

Summary of inferred positional repertoire, and implications for hominoid emergence

The vertebral and scapular remains of *Morotopithecus* closely resemble those of modern apes and suggest that *Morotopithecus* possessed two of the hallmarks of extant ape locomotion: orthogrady and substantial forelimb mobility. The femur possesses a mosaic of features. The distal portion suggests ape-like joint mobility, while the proximal femur does not. One striking feature of the distal femur is the well developed popliteal groove, possibly indicative of vertical climbing. The disjunction between inferred knee and hip mobility, and the uniquely thick diaphyseal cortical bone suggest that *Morotopithecus* may have loaded its femora in a way that is not analogous to the weight-bearing pattern of any living primate. For instance, in the absence of a highly mobile hip, *Morotopithecus* may not have relied on hindlimb postures requiring marked abduction and so regularly subjected its hindlimbs to axial loading. Some combination of behaviors requiring a stiff back and high forelimb mobility but not high hip mobility (e.g., vertical climbing, forelimb suspension, cautious climbing) may thus have been employed.

The adaptive significance of the acquisition of forelimb dominated locomotion and suspensory behavior in hominoids has been linked to foraging (e.g., Tuttle, 1975), with advantages including an enhanced ability to access high quality items like fruit in areas such as terminal branches (Avis, 1962) or open canopy (Napier, 1967) where small supports abound. Suspension may also increase speed and decrease the path length of arboreal travel in these habitats (Temerin & Cant, 1983), as well as allow an increase in body size (Cachel, 1979; Cant, 1987). While suspensory abilities have been emphasized in most scenarios of hominoid evolution, quadrumanous climbing has also been highlighted (Fleagle, 1976). With few exceptions, locomotor innovation and its associated foraging changes is seen as critical, although it has also been suggested that selection for large body size *per se*, and the dietary niches this makes available, may also have driven hominoid divergence (Wheatley, 1987).

Since *Morotopithecus* possesses both large size and suspensory adaptations, it is currently not possible to evaluate whether they may have played a separate or linked role in hominoid divergence. In addition, the very nature of parallelism makes it difficult to determine how many times selection for either (or both) may have operated during hominoid evolution. If the postcrania of *Morotopithecus* reflect the early stage of the radiation that gave rise to extant hominoids as we suspect (see below), then it appears that the distinctive forelimb and axial adaptations of hominoids may have been acquired before the hip increased markedly in mobility. An early hominoid locomotor niche may thus have been similar to Stern's (1975) description for the last common ancestor of apes and humans:[3] ". . . an animal that employed its forelimb much as does the living orang-utan and its hindlimb in a somewhat more quadrupedal manner. Such might be the behavior of a smaller bodied version of the orang-utan that had begun to employ its forelimbs in climbing, suspension and other tensile activities [and evolved a stiff lumbar region] but had not yet reached the size which was to cause it to abandon so completely pronograde quadrupedality" (p. 67).

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[3] At the time, humans were considered by most workers to be most closely related to either all great apes or to chimpanzees and gorillas and Stern's last common ancestor referred not to the crown hominoid morphotype but to what we would now see as the late Miocene human-chimpanzee ancestor.

Table 2 Summary of postcranial features of *Morotopithecus bishopi*

Group	Femur	Scapula	Lumbar vertebra†
Primitive Catarrhine features	Fovea capitis* Crista trochanterica Femoral neck not elongated* Moderate femoral neck angle (≤135°)* Lesser trochanter angle 30°* Long greater trochanteric fossa Articular surface of head lies close to the femoral neck Small femoral head Few nutrient foramina around the head or epicondyles No hypotrochanteric fossa No linea aspera ridge up to or above the lesser trochanter	Scapular spine has a proximal origin* No craniodorsal notch on glenoid fossa margin*	Body is craniocaudally long
Derived features shared with all extant hominoids	Wide patellar facet	Glenoid fossa relatively broad dorsoventrally Glenoid fossa is moderately curved both craniocaudally and dorsoventrally	Robust pedicles Lumbar centrum has reduced ventral keeling‡ Lumbar centrum has reduced spooling Lumbar centrum not laterally hollowed Caudally inclined spinous process Transverse processes have a dorsal point of origin Dorsally and caudally inclined transverse processes
Derived features shared with *Pongo*, *Pan* and *Gorilla*	Wide intercondylar notch Well buttressed intercondylar notch Deep popliteal groove Asymmetrical femoral condyles ML broad and AP narrow condylar proportions AP flattened distal shaft Gluteal ridge present		No anapophyses

*These features are also found in some or all extant hominoids.
†Vertebral features are taken from Sanders & Bodenbender (1994).
‡This feature is intermediate between the condition in cercopithecoids (distinct keeling) and hominoids (slight or absent).

Phylogeny

An in-depth phylogenetic analysis will be the subject of subsequent studies and at this time only preliminary observations as they relate to the postcrania are noted. Table 2 lists postcranial features of *Morotopithecus* which may be phylogenetically relevant. While the distal femur has some possible synapomorphies with hominoids, the proximal femur is primitive. The form of the scapula appears derived relative to the primitive catarrhine condition and resembles that of extant hominoids, although the glenoid morphology of *Ateles* clearly converges on that of living apes and *Morotopithecus*.

Sanders & Bodenbender (1994) identified a number of features that allied the Moroto vertebrae with those of extant hominoids, with only the lack of anapophyses linking it specifically with the great apes. Whether the entire suite of hominoid lumbar features could have evolved independently in different hominoid lineages is open to speculation. Given the rarity of these features among extant primates and in the fossil record, it seems plausible that they are synapomorphies (MacLatchy & Pilbeam, 1999). If so, later Miocene hominoids that lack such features as those listed in Table 2 either "re-evolved" quadrupedalism, or are more distantly related to extant hominoids than is *Morotopithecus*. This scenario of hominoid evolution contradicts the pattern of mosaic acquisition of features throughout the Miocene proposed by some (Begun *et al.*, 1997; Ward, 1998), but is consistent with Harrison's (1987) view that hominoids are united by synapomorphic postcranial functional complexes.

Morotopithecus suggests that the basic back and forelimb adaptations necessary for a locomotor lifestyle with significant similarities to those of extant hominoids had evolved by 20·6 Ma. We place *Morotopithecus* in a pre-hylobatian position as the sister taxon of the crown hominoid clade, and suggest that *Oreopithecus* and possibly *Dryopithecus* are the only Miocene species that are similar enough or sufficiently well documented to be confidently placed within this clade.

Conclusion

New postcranial material of a large-bodied hominoid from Moroto, along with a previously described vertebra, document a postcranium with significant similarities to living apes and humans. The modern vertebral features of the *Morotopithecus* (e.g., Sanders & Bodenbender, 1994) and the round glenoid fossa are in sharp contrast with other early Miocene hominoids, which have dentitions similar to that of *Morotopithecus*, but archaic postcrania, indicating a generalized quadrupedal positional repertoire (Ward, 1993; Ward *et al.*, 1993; Rose, 1994; Nakatsukasa *et al.*, 1998; Walker, 1998). Overall, *Morotopithecus* is reconstructed as a highly arboreal species that probably relied on forelimb-dominated climbing, vertical and cautious climbing and suspension in addition to quadrupedalism. At more than 20 Ma in age, it represents the oldest hominoid with these adaptations and thus the oldest hominoid species for which direct relationships to living apes and humans can be inferred. Hence, *Morotopithecus* is a key taxon in understanding the evolution of modern hominoid postcranial adaptations and positional behavior.

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References

Aiello, L. & Dean, C. (1990). *An Introduction to Human Evolutionary Anatomy*. San Diego: Academic Press.

Allbrook, D. & Bishop, W. W. (1963). New fossil hominoid material from Uganda. *Nature* **97,** 1187–1190.

Anapol, F. (1983). Scapula of *Apidium phiomense*: a small anthropoid from the Oligocene of Egypt. *Folia primatol.* **40,** 11–31.

Andrews, P. (1992). Evolution and environment in the Hominoidea. *Nature* **360,** 641–646.

Andrews, P., Harrison, T., Delson, E., Bernor, R. L. & Martin, L. (1996). Distribution and biochronology of European and southwest Asian Miocene Hominoids. In (R. L. Bernor, V. Fahlbusch & H. Mittman, Eds) *The Evolution of Western Eurasian Neogene Mammal Faunas*, pp. 168–207. New York: Columbia University Press.

Avis, V. (1962). Brachiation: The crucial issue for man's ancestry. *Southwestern J. Anthropol.* **18,** 119–148.

Barnett, C. & Richardson, A. (1953). The postural function of the popliteus muscle. *Ann. Phys. Med.* **1,** 177–179.

Begun, D. R., Ward, C. V. & Rose, M. D. (1997). Events in hominoid evolution. In (D. R. Begun, C. V. Ward, M. D. Rose, Eds) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 389–416. New York: Plenum Press.

Bishop, W. W. & Whyte, F. (1962). Tertiary mammalian faunas and sediments in Karamoja and Kavirondo, East Africa. *Nature* **196,** 1283–1287.

Cachel, S. (1979). A paleoecological model for the origin of higher primates. *J. hum. Evol.* **8,** 351–359.

Cant, J. G. (1987). Positional behaviour of female Bornean orangutans. *Am. J. Primatol.* **12,** 71–90.

Cartmill, M. & Milton, K. (1977). The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. *Am. J. phys. Anthrop.* **47,** 249–272.

Fleagle, J. G. (1976). Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia primatol.* **26,** 245–269.

Fleagle, J. G. (1977). Locomotor behaviour and skeletal anatomy of sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yearb. phys. Anthrop.* **20,** 441–453.

Fleagle, J. G. & Meldrum, D. J. (1988). Locomotor behaviour and skeletal morphology of two sympatric pithecine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. *Am. J. Primatol.* **16,** 227–249.

Gebo, D. L., MacLatchy, L., Kityo, R., Deino, A., Kingston, J. & Pilbeam, D. (1997). A hominoid genus from the early Miocene of Uganda. *Science* **276,** 401–404.

Gebo, D. L. & Sargis, E. J. (1994). Terrestrial adaptations in the postcranial skeletons of guenons. *Am. J. phys. Anthrop.* **93,** 341–371.

Harrison, T. (1982). Small-bodied apes from the Miocene of East Africa. Ph.D. Dissertation, University College London.

Harrison, T. (1987). The phylogenetic relationships of the early catarrhine primates: a review of the current evidence. *J. hum. Evol.* **16,** 41–80.

Harrison, T. & Rook, L. (1997). Enigmatic anthropoid or misunderstood ape? The phylogenetic status of *Oreopithecus bambolii* reconsidered. In (D. R. Begun, C. V. Ward, M. D. Rose, Eds) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 327–362. New York: Plenum Press.

Ishida, H., Kunimatsu, Y., Nakatsukasa, M. & Nakano, Y. (1999). New hominoid genus from the middle Miocene of Nachola, Kenya. *Anthropological Science* **107 (2), 189–191.**

Jungers, W. L. (1984). Scaling of the hominoid locomotor skeleton with special reference to lesser apes. In (H. Preuschoft, D. Chivers, W. Brockelman & N. Creel, Eds) *The Lesser Apes*, pp. 146–169. Edinburgh: Edinburgh University Press.

Jungers, W. L. & Susman, R. L. (1984). Body size and structural allometry in African apes. In (R. L. Susman, Ed.) *The Pygmy Chimpanzee: Evolutionary Morphology and Behaviour*, pp. 131–311. New York: Gustav-Fisher.

Keith, A. (1923). Man's posture: its evolution and disorders. *The British Medical Journal* **1,** 451–454.

Kennedy, G. (1983). Some aspects of femoral morphology in *Homo erectus*. *J. hum. Evol.* **12,** 587–616.

Larson, S. (1993). Functional morphology of the shoulder in primates. In (D. L. Gebo, Ed.) *Postcranial Adaptations in Nonhuman Primates*, pp. 45–69. DeKalb: Northern Illinois University Press.

Leakey, M. & Walker, A. (1997). *Afropithecus* function and phylogeny. In (D. R. Begun, C. V. Ward, M. D. Rose, Eds) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 225–239. New York: Plenum Press.

Leakey, R., Leakey, M. G. & Walker, A. C. (1988). Morphology of *Afropithecus turkanensis* from Kenya. *Am. J. phys. Anthrop.* **76,** 289–307.

MacLatchy, L. & Bossert, W. (1996). An analysis of the articular surface distribution of the femoral head and acetabulum in anthropoids with implications for hip function in Miocene hominoids. *J. hum. Evol.* **31,** 425–453.

MacLatchy, L. M. & Pilbeam, D. P. (1999). Renewed research in the Ugandan early Miocene. In (P. Andrews & P. Banham, Eds) *Late Cenozoic Environments and Hominid Evolution: a tribute to Bill Bishop*, pp. 15–25. London: The Royal Geological Society.

MacLatchy, L. M., Wunderlich, R. & Stern, J. (1998). Distal femora of *Morotopithecus* and *Sivapithecus*. *J. Vert. Paleontol.* **18(3), 60A.**

McCrossin, M. (1997). New postcranial remains of *Kenyapithecus* and their implications for understanding the origins of hominoid terrestriality. *Am. J. phys. Anthrop. Supplement* **24,** 164.

McCrossin, M. L., Benefit, B. R. & Gitau, S. N. (1998). Functional and phylogenetic analysis of the distal radius of *Kenyapithecus* with comments on the origin of the African great ape and human clade. *Am. J. phys. Anthrop. Supplement* **26,** 158.

Moyà-Solà, S. & Köhler, M. (1996). A *Dryopithecus* skeleton and the origins of great ape locomotion. *Nature* **379,** 156–159.

Napier, J. R. (1967). Evolutionary aspects of primate locomotion. *Am. J. phys. Anthrop.* **27,** 333–342.

Nakatsukasa, M., Yamanaka, A., Kunimatsu, Y., Shimizu, D. & Ishida, H. (1998). A newly discovered *Kenyapithecus* skeleton and its implications for the evolution of positional behavior in Miocene East African hominoids. *J. hum. Evol.* **34,** 657–664.

Pickford, M., Senut, B. & Gommery, D. (1999). Sexual Dimorphism in *Morotopithecus bishopi*, an early Middle Miocene hominoid from Uganda and a reassessment of its geological and biological contexts. In (P. Andrews & P. Banham, Eds) *Late Cenozoic Environments and Hominid Evolution: a tribute to Bill Bishop*, pp. 27–38. London: The Royal Geological Society.

Piganiol, G. & Olivier, G. (1959). L'architecture du femur des primates. *C.R. Assoc. Anat.* **45,** 660–677.

Pilbeam, D. (1969). Tertiary Pongidae of East Africa: evolutionary relationships and taxonomy. *Peabody Mus. Nat. Hist. Bull.* **31,** 1–185.

Pilbeam, D. (1996). Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. *Mol. Phylogen. Evol.* **5,** 155–168.

Preuschoft, H. (1970). Functional anatomy of the lower extremity. In (G. H. Bourne, Ed.) *The Chimpanzee*, pp. 221–294. Basel: Karger.

Roberts, D. (1974). Structure and function of the primate scapula. In (F. A. Jenkins, Ed.) *Primate Locomotion*, pp. 171–200. New York: Academic Press.

Rose, M. D. (1983). Miocene hominoid postcranial morphology: Monkey-like, ape-like, neither or both? In (R. L. Ciochon & R. S. Corruccini, Eds) *New Interpretations of Ape and Human Ancestry*, pp. 405–417. New York: Plenum Press.

Rose, M. D. (1993). Locomotor anatomy of Miocene Hominoids. In (D. L. Gebo, Ed.) *Postcranial Adaptations in Nonhuman Primates*, pp. 252–272. DeKalb: Northern Illinois University Press.

Rose, M. D. (1994). Quadrupedalism in some Miocene catarrhines. *J. hum. Evol.* **26,** 387–411.

Rose, M. D., Leakey, M. G., Leakey, R. F. & Walker, A. C. (1992). Postcranial specimens of *Simiolus enjiessi* and other primitive catarrhines from the early Miocene of Lake Turkana, Kenya. *J. hum. Evol.* **22,** 171–237.

Rose, M. D., Nakano, Y. & Ishida, H. (1996). *Kenyapithecus* postcranial specimens from Nachola, Kenya. *African Study Monographs, Supplement* **24,** 3–56.

Ruff, C. B. (1988). Hindlimb articular surface allometry in Hominoidea and *Macaca*, with comparisons to diaphyseal scaling. *J. hum. Evol.* **17,** 687–714.

Ruff, C. B. (1989). New approaches to the structural evolution of limb bones in primates. *Folia primatol.* **53,** 142–159.

Ruff, C. B. (1990). Body mass and hindlimb bone cross sectional and articular dimensions in anthropoid primates. In (J. Damuth & B. J. MacPhadden, Eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp. 119–369. Cambridge: Cambridge University Press.

Ruff, C. B. & Runestad, J. A. (1992). Primate limb bone structural adaptations. *A. Rev. Anthropol.* **21,** 407–433.

Ruff, C. B., Walker, A. & Teaford, M. K. (1989). Body mass, sexual dimorphism and femoral proportions of *Proconsul* from Rusinga and Mfangano Islands, Kenya. *J. hum. Evol.* **18,** 515–536.

Ruff, C. B., Trinkaus, E. & Larsen, C. S. (1993). Postcranial robusticity in *Homo* 1: temporal trends and mechanical interpretation. *Am. J. phys. Anthrop.* **91,** 21–53.

Runestad, J. A. (1994). Humeral and femoral diaphyseal cross sectional geometry and articular dimensions in Prosimii and Platyrrhini (Primates) with application for reconstruction of body mass and locomotor behavior in Adapidae (Primates-Eocene). Ph.D. Dissertation, Johns Hopkins University.

Sanders, W. J. & Bodenbender, B. E. (1994). Morphometric analysis of lumbar vertebra UMP 67-28: implications for spinal function and phylogeny of the Miocene Moroto hominoid. *J. hum. Evol.* **26,** 203–237.

Schmitt, D. (1996). Humeral head shape as an indicator of locomotor behavior in extant strepsirhines and Eocene adapids. *Folia primatol.* **67,** 137–151.

Shapiro, L. (1993). Functional Morphology of the vertebral column in primates. In (D. L. Gebo, Ed.) *Postcranial Adaptations in Nonhuman Primates*, pp. 121–149. DeKalb: Northern Illinois University Press.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. San Francisco: W. H. Freeman.

Stern, J. T. (1975). Before bipedality. *Yearb. Phys. Anthropol.* **19,** 59–68.

Straus, W. L. (1963). The classification of *Oreopithecus*. In (S. L. Washburn, Ed.) *Classification and Human Evolution*, pp. 146–177. Chicago: Aldine.

Tardieu, C. (1981). Morpho-functional analysis of the articular surfaces of the knee joint in primates. In (A. B. Chiarelli & R. S. Corruccini, Eds) *Primate Evolutionary Biology*, pp. 68–80. Berlin: Springer-Verlag.

Tardieu, C. (1983). *L'Articulation du Genou*. Paris: CNRS.

Temerin, T. L. & Cant, J. G. H. (1983). The evolutionary divergence of Old World monkeys and apes. *Am. Nat.* **122,** 335–351.

Tuttle, R. (1975). Parallelism, brachiation and hominoid phylogeny. In (W. P. Luckett & F. S. Szalay, Eds) *Phylogeny of the Primates*, pp. 447–480. New York: Plenum Press.

Walker, A. (1998). *Proconsul* function and phylogeny. In (D. R. Begun, C. V. Ward, M. D. Rose, Eds) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 209–224. New York: Plenum Press.

Walker, A. & Rose, M. (1968). Fossil hominoid vertebra from the Miocene of Uganda. *Nature* **217,** 980–981.

Walker, A. & Pickford, M. (1983). In (R. L. Ciochon & R. S. Corruccini, Eds) *New Interpretations of Ape and Human Ancestry*, pp. 325–351. New York: Plenum Press.

Ward, C. V. (1993). Torso morphology and locomotion in *Proconsul nyanzae*. *Am. J. phys. Anthrop.* **92,** 291–328.

Ward, C. V. (1998). *Afropithecus*, *Proconsul* and the primitive hominoid skeleton. In (E. Strasser, J. Fleagle, H. McHenry & A. Rosenberger, Eds) *Primate Locomotion*, pp. 337–352. New York: Plenum Press.

Ward, C. V., Walker, A., Teaford, M. F. & Odhiambo, I. (1993). Partial skeleton of *Proconsul nyanzae* from Mfangano Island. *Am. J. phys. Anthrop.* **90,** 77–111.

Ward, S., Brown, B., Hill, A., Kelley, J. & Downs, W. (1999). *Equatorius*: a new hominoid genus from the middle Miocene of Kenya. *Science* **285,** 1382–1386.

Wheatley, B. P. (1987). The evolution of large body size in orang-utans: a model for hominoid divergence. *Am. J. Primatol.* **13,** 313–324.