Early Hominid Postcrania and Locomotor Adaptations
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The locomotor system of modern man is a complex and unique adaptation, and the evolutionary origin and history of bipedalism are of fundamental importance in understanding the pattern of human evolution. For this reason much attention has been focused upon the postcranial skeleton of the early hominids. The fossil evidence of *Australopithecus* fortunately includes numerous postcranial remains, and these have been analyzed to determine locomotor capabilities. Bipedal, erect posture in *Australopithecus* has been demonstrated, but the full spectrum of locomotion in these hominids is not known. The use of extant models has placed undue emphasis on the striding gait and the question of its presence in *Australopithecus*. Methodological problems have hindered progress in reconstructive anatomy and biomechanical analysis. Since the locomotor system influences most activities of an organism, differences in locomotor capacities often have phylogenetic significance; if these differences are reflected in bony morphology, they should be appropriate for taxonomic criteria. Discerning the range of locomotor behaviors of the australopithecines is a challenging and important task for human evolutionary studies if we are to assimilate the anatomy, ecology, behavior, and systematics of *Australopithecus* into a synthetic, holistic view of the evolution of the Hominidae.

Analysis of Postcranial Material

There are a number of paleontological problems central to the analysis of post-cranial remains; these include incomplete and damaged specimens plus the problem of variation. Several critical parameters: body stature and weight, sex, and age, are often, by the nature of the hominid fossil record, indeterminable. This frequent lack of data on gross body proportions and paleodemography of the sample hinders any attempt at biomechanical analysis of the postcranial material. Another frequent problem is that of association; do skeletal parts found in close proximity actually belong to one individual? The discovery in recent years of several partial or relatively complete skeletons of Plio-Pleistocene Hominidae will go far in illustrating the morphological pattern of *Australopithecus* and early *Homo*, in delineating any differences within these taxa, and particularly in yielding suitable material (of one individual) for the analysis of joints. Such analysis has been infrequently attempted yet is crucial to a composite biomechanical study.

The current lack of consensus about the morphological characteristics of early hominid[1] postcrania is in considerable part a lack of agreement about appropriate techniques and relevant parameters. Much of the earlier literature was on a purely descriptive level, and later statistical treatment gave ambiguous results. This is partly because of different workers measuring the same set of fossils and getting different results; also, access to the original specimens is not readily available to all workers, who therefore must rely upon published reports and casts. Many of the original specimens are not fully prepared for study and are in need of reconstruction. A general consensus on operationalism of method is needed with respect to: (a) the basic parameters involved, (b) how to obtain the necessary data from the fossils (what to measure on the bone and how to measure it), (c) how to standardize for effects of body size, and (d) the appropriate statistical methodologies. Isolated traits must undergo extensive comparative study, and then biomechanical reconstruction, to validate preliminary inferences. Ultimately one hopes to integrate fossil postcranial data into what Zihlman (1977) calls a behavioral-evolutionary framework which (a) relates the locomotor morphology and behavior to an environmental context, (b) correlates the locomotor behavior with the morphology, using living models, and (c) attempts a synthetic limb/joint analysis. These goals may be reached via a combination of techniques, including stress analysis (Preuschoft 1971), cineradiographic analysis of related extant forms (Jenkins 1972), biomechanical reconstructions, including bone loading patterns (Zihlman and Hunter 1972; Lovejoy et al. 1973; Lovejoy 1977), and joint reconstruction analysis (Zihlman 1977).

Multivariate statistical approaches, while very promising, have yielded some contradictory results with regard to australopithecine postcranial anatomy. Using multivariate techniques (specifically canonical analysis) on a number of postcranial fossils of *Australopithecus*, Oxnard (1975) has stressed the uniqueness of these fossil remains, their clear differences with fossils placed in *Homo*, and the elimination of *Australopithecus* as a direct ancestor of *Homo*. Other workers, using the same fossils and multivariate techniques (principal coordinate and canonical analysis), have concluded that early hominid lower limb (McHenry and Corruccini 1975a) and upper limb (Ciochon and Corruccini 1976) morphology is clearly allied with Hominidae, and approaches, but is not identical with, that of *Homo*.

The problem of how to compensate for size effects in both uni- and multivariate analysis is critical. A frequent technique to eliminate size effects is to convert measurements to angles or indices, and create ratios between the structure being compared and some morphological feature used as a size standard. Ratio data often cannot be compared for lack of matching or suitably preserved body parts. Multivariate techniques have the potential to avoid latent size effects. Corruccini (1975) has criticized Oxnard and stressed the necessary distinction between size and shape. He notes that statistics computed directly from raw measurements are dominated by simple size differences. There has been a tendency to deal exclusively with isolated bones in such statistics, and to make conclusions solely from those data (e.g., Oxnard 1968a & b). The isolated bone is not the functional unit in limb morphology, and analysis should incorporate available joints (Ciochon and Corruccini 1976).

Two important issues in statistical studies are what measurements are to be employed and how to interpret the results. When isolated bones instead of articulated joint complexes are utilized the measurements used severely limit their utility, and factors such as body weight are often ignored (Zihlman 1975). Great care must be taken not to "load" the multivariate program with redundant measurements. Lovejoy (1977) has emphasized that this problem of the interrelationship of metrically assessable characters is the greatest limitation to the interpretation of multivariate results. As Day (1973) has pointed out, multivariate studies have in recent years been at best a complement to anatomical description. With additional fossil material and progress in multivariate techniques, the full impact of advanced biometrics should be realized.

An important consideration is the level of inference which is most appropriate for reconstructing postcranial anatomy and locomotor capacities in early hominids. Preliminary anatomical description should not be used as a final analysis. The observation of morphological differences is not in itself evidence of locomotor differences between two groups. The range of variation within a population must be accounted for; differences in morphology, if statistically significant, may have no obvious mechanical effect. As Lovejoy (1975) has emphasized, the important question is: does a given morphological feature have biomechanical importance? It is the biomechanical *effect* of a morphological change that is important, and this level of inference has often been lacking.

The range of variation, both metric and nonmetric, in postcranial morphology is considerable. Furthermore, the correlation between environment, locomotor behavior, and morphology may be weak in extant groups (e.g., within *Colobus* species, Zihlman 1977). Analysis should begin with accurate description of the fossil anatomy, and functional morphology discerned via extensive comparative work. Variation

should be accounted for by use of appropriate statistical techniques, and finally a total biomechanical pattern should be reconstructed. It is then possible to address the question of differences in locomotor behaviors between a fossil taxon *(Australopithecus)* and the extant relative *(Homo)*, as well as possible differences within the fossil taxon itself (i.e., between gracile and robust *Australopithecus*). Then paleoecological, phylogenetic, and taxonomic inferences may be derived, whether differences between the various groups under consideration exist or not, since either result would have significance in elucidating the pattern of evolution of early Hominidae.

Early Hominid Fossil Postcrania

Early hominid postcranial fossils are relatively rare when compared to more abundant dental, gnathic, and cranial parts. This is unfortunate since locomotor capabilities are so important in any organism's behavioral repertoire, and especially so in the evolution of the Hominidae. Recently, however, the sample of postcrania has become fairly complete and most body parts are now represented, some by relatively complete and undistorted fossils, some by the remains of several partially complete skeletons (Table 1). A review of the fossil evidence will be offered for each major anatomical region, describing basic morphologies and delineating any biomechanical differences.

Axial Skeleton

Early hominid vertebrae are relatively rare in the fossil record, and the best specimens are from just two individuals, Sts 14 (Sterkfontein) and AL 288-1 (Afar). Both Day (1977) and Robinson (1972) stress the small size of the vertebral bodies. Small size is also evident in the two articulated vertebrae (in matrix) of KNM-ER 164 (East Lake Turkana, Day 1977). A relatively well developed lumbar curvature is evidenced in Sts 14 (Robinson 1972), which concurs with lower limb evidence of bipedal erect posture.

The sacrum of Sts 14 is of typically hominid disposition and shape, but in overall size significantly smaller than that of modern man. A smaller auricular surface, smaller lumbosacral articular surface, and smaller sagittal and transverse diameters of the vertebral bodies indicate a column not as well adapted for efficient stress and weight bearing, in an individual of light body build with a fairly large pelvis for its body size (Robinson 1972; Zihlman 1970).

Body Proportions

Reconstructions of height, weight, and body proportions of australopithecines usually assume that the limb proportions are equivalent to those of modern man, an assumption which is unwarranted since the evidence indicates relatively longer upper limbs in comparison with modern human populations (Genet-Varcin 1969; McHenry 1974; Olivier 1976).

This is demonstrated by material recovered from Sterkfontein, Kromdraai, and especially Hadar. The Afar AL 288-1 humerus is 83.9% the length of the femur (Johanson and Taieb 1976). This is also apparent if the KNM-ER 739 humerus and the Omo L 40-19 ulna are articulated (they form a fair match); the result is a relatively long and quite robust upper limb. Variability within one site (e.g., at Sterkfontein, the Sts 7 humerus and Sts 14 femur) is considerable, and marked sexual dimorphism has been suggested by McHenry (1974) to account for it.

Estimates of stature and body weight for *Australopithecus africanus* (Sts 14) range from a low estimate of 107 cm height and 18-22 kg mass (Lovejoy and Heiple 1970) to a high estimate of 145 cm and 27.6 kg (McHenry 1974, 1976a). A narrower range has been discussed for robust australopithecines: 146 cm (Burns 1971) to 165 cm (Genet-Varcin 1969), and 43.2 kg (McHenry 1976a) to 68-91 kg (Robinson 1972). McHenry (1974, 1976a) has estimated the weight and stature of several East African specimens assigned to *Homo* sp. as 52.8 kg and 163 cm (mean). The low stature determination by Lovejoy and Heiple (for one *A. africanus*) is confirmed by preliminary descriptive reports on the Hadar 1974 partial skeleton; Johanson and Taieb (1976) reconstruct AL 288-1 as approximately one meter tall.

Appendicular Skeleton: Upper Limb

Fossil evidence from early hominid forelimbs is not as abundant as that from hindlimb parts, but a considerable number of specimens have now been catalogued.

Clavicula

The fossil clavicle from Olduvai (Old. Hom. 48)[2] was described by Napier (1965) as fundamentally like that of *Homo sapiens*. Oxnard felt that the clavicle, along with the Sts 7 glenoid fragment, indicated some sort of suspensory posture (1968a and b), based on the angle of clavicular torsion. The Olduvai clavicle is damaged by an internal fracture and is missing both sternal and acromial extremities; because of this Oxnard had to reconstruct both ends and assume no significant distortion. Day (1976a), in a series of multivariate tests, was unable to discriminate Old. Hom. 48 from *Homo sapiens*.

Scapulae

The only scapular fragment to be analyzed in detail is Sts 7, described by Broom et al. (1950). These authors noted an unusual combination of features seen in *Homo* and in *Pongo*. Oxnard (1968a) saw evidence of a suspensory adaptation in the fossil; however, the scapular fragment was embedded in matrix and broken at the glenoid fossa (also the present state of the fossil), the coracoid had not been adequately exposed, and the acromion was lost.

Shoulder (Glenohumeral) Joint

The fossil evidence of the glenohumeral joint in *Australopithecus* is limited to Sts 7. In a recent paper on this glenohumeral joint[3], Ciochon and Corruccini (1976) note the rather large coracoid process and conclude, after multivariate comparative analysis, that this glenohumeral joint possibly evidences not only a suspensory posture ancestry (synplesiomorphy) but also partial suspensory locomotor posture in these early hominids. This hypothesis will receive further testing when full description and analysis of the same joint in AL 288-1 is completed; at present it is tentatively supported by some of the fossil arm, forearm, and hand bone evidence.

Humeri

Fossil humeri in a state of preservation which allows detailed study are few in number. Consequently much attention has been focused upon relatively few specimens (Sts 7, TM 1517, Kanapoi, KNM-ER 739). Unfortunately comparable body parts for the proximal humerus are only of one taxon, *Australopithecus africanus*. The Sterkfontein proximal humerus was described by Broom and Robinson (Broom et al. 1950), who noted several *Pongo*-like features. The fossil exhibits a well rounded head, a deep intertubercular groove, and prominent muscular markings (observable on Wenner-Gren cast). Day (1977) feels that the specimen evidences a powerful *m. biceps brachii* and well developed stabilizer (short scapular) muscles (also seen in KNM-ER 1473). Omo 119-73-2718 and AL 288-1 (left proximal humeri) have yet to be described. Omo 119-73-2718 is a relatively large bone with a hemispherical articular head, a prominent intertubercular groove, well developed greater and lesser tubercles, and a robust shaft; it is comparable in size to Sts 7 (observations on casts; Boaz et al. n.d.), and has been tentatively referred to *Australopithecus africanus* (Howell and Coppens 1976).

Distal humeri are better known and have been extensively described. Broom described TM 1517 as possessing a large and more irregularly spherical capitulum than modern man (Broom and Schepers 1946). Clark (1947) felt that the trochlea was not set as far anterior (to a frontal plane through the axis of the distal humerus) as in man or chimpanzee, and this might have limited flexion but allowed considerable hypertension. Straus (1948) emphasized numerous nonhominid characters and felt that the distal humerus was not useful for taxonomic discrimination (also Robinson 1972). McHenry and Corruccini (1975a) concluded that distal humeri *are* discriminatory, and placed TM 1517 as intermediate between pongids and modern humans. Day (1977) concluded that the specimen was less like *Homo sapiens* than the Kanapoi humerus. Kanapoi 1, larger in size than TM 1517 and designated *Australopithecus* cf. *africanus* (Patterson and Howells 1967), is fundamentally like that of

modern man (McHenry 1976b; McHenry and Corruccini 1975a; McHenry et al. 1976); Day has suggested placing the fossil in *Homo* (1974a).

The humerus from East Lake Turkana, KNM-ER 739, has often been the subject of speculation concerning the locomotor capabilities of robust australopithecines. The specimen is a very long[4] and robust humerus with strong muscular ridging and a well rounded capitulum. Day (1977) describes the ridging as indicative of massive deltoid, brachioradialis, as well as common hand flexor and extensor muscles. Several workers have cited the unique morphology of the fossil (McHenry 1973a; McHenry and Corruccini 1975a; McHenry et al. 1976). Kay (1973) felt that the specimen indicated "facultative rather than habitual bipedalism," and McHenry's (1976b) sorting via locomotor categories placed KNM-ER 739 within the suspensory posture category.

Forearm

Fossil evidence of the early hominid forearm is scarce and poorly preserved. There are no complete radii. Available material is confined to proximal and shaft fragments. These illustrate a rounded, recessed head and a rounded neck (SK 18b, Omo 75s-70-1317, KNM-ER 1500e, AL 288-1), a marked *m. pronator teres* insertion (SK 18b, Old. Hom. 49, KNM-ER 803d), and a well delineated interosseous border (Old. Hom. 49, KNM-ER 1500k). The total observable pattern is similar to *Homo sapiens* (Day 1977). Obviously, description of the distal radii from Hadar is anticipated. Only then, with knowledge of the morphology of the carpal articular surface and the anterior and posterior distal surfaces, can we draw firm conclusions about radial morphology.

We are fortunate to have one virtually complete and several fragmentary ulnae. The complete right ulna from the Shungura Formation, in unit E-5, has been described and assigned to *Australopithecus boisei* by Howell and Wood (1974). The Omo ulna (L 40-19) is quite long (315 mm), has a moderate dorso-ventral curvature to the shaft, and is somewhat flattened anteroposteriorly. The shaft does not project proximally beyond the olecranon process (as in *Papio*). Both the margin of the coronoid process and the ulnar tuberosity are damaged, as well as details of the radial notch. The insertions of *m. triceps brachii* and especially *m. anconeus* and *m. pronator teres* are well delineated. The supinator crest is not well marked. The ulna exhibits no noticeable interosseous margin, the articular head is less crescentic than in modern human ulnae, and a prominent styloid process is not evident (Howell and Wood 1974; personal observations).

Manus

A number of hand bones of the early hominids are available; however, there is a distinct lack of comparable body parts and several carpals are absent from the fossil record (lunate, triquetrum, pisiform). The trapezoid and hamate bones, previously absent in the fossil sample, are present in the (undescribed) material from the Hadar locality AL 333.

The TM 1526 capitate from Sterkfontein, small and well-preserved, was described by Broom and Schepers (1946) as morphologically intermediate between pongids and man. Clark (1947, 1967) concurred, specifying that the fossil differed from modern human capitates in the pronounced excavation of the lateral surface; this resulted in a "waisted" appearance which he felt to be the site of a strong interosseous (capitate-trapezoid) ligament. Robinson (1972) notes pongid features in the lack of a definite articular facet for metacarpal IV, a laterally-waisted profile, and relatively smaller articular surfaces for the scaphoid and the trapezoid. O.J. Lewis (1973) has described (from casts) the Sterkfontein and Olduvai (Old. Hom. 7r) capitates, in a major review of the comparative morphology of the wrist joint in the Hominoidea. He concludes that lateral (radial side) waisting of the capitate is not for attachment of a trapezoid-capitate interosseous ligament but is part of a unique midcarpal locking mechanism best developed in the African, knuckle-walking apes. Lewis attempts to demonstrate that the waisting on the capitate radial surface in *Pan troglodytes* is contacted by the scaphoid head in wrist extension (as the scaphoid is rotated, its head becomes locked into the constricted neck of the capitate). In *Homo sapiens*, this lateral waisting is not apparent, and an anterior trapezoid-capitate articulation (in front of the interosseous ligament, a neomorph) has replaced the primitive posterior articulation. The trapezoid is now larger in *Homo*, the metacarpal II is now articulating more distally in the carpus, and the metacarpal III develops the prominent styloid process (near the posterolateral corner of the capitate). His observations included the notation of a distinct lateral waisting in TM 1526 and Old. Hom. 7r. He describes TM 1526 as exhibiting a laterally swollen head, a posteriorly located trapezoid facet, and a pongid-like articulation for the medial side of the base of metacarpal II. He concludes that both specimens are far more *Pan*-like than previously estimated.

The right juvenile trapezium from Olduvai (Old. Hom. 7q) can be articulated with the Old. Hom. 7p scaphoid and the base of a second metacarpal (Old. Hom. 7o) to form a reasonable reconstruction of the radial side of a right hand. Further material from Olduvai includes two damaged proximal, four intermediate, and three terminal phalanges (Old. Hom. 7i-h, d-g, and a-c, respectively), perhaps all of the same hand (Day 1976a). The terminal pollical phalanx is broad and stout, and bears the impression for *m. flexor pollicis longus*. Napier's original analysis of the hand bones emphasized: (1) their differences from *Homo sapiens* in overall robustness, dorsal curvature of the

phalangeal shafts, and strength of the fibrotendinous markings, and (2) their similarity to modern man in the breadth and stoutness of the terminal phalanges, and the ellipsoidal contour of the metacarpophalangeal joint surfaces. Three metacarpals are known from Swartkrans; two specimens, SK 85 and SKW 14147, are generally comparable with *Homo sapiens* (Napier 1959; Day 1977; Day and Scheur 1973). SK 84 is a short, very robust metacarpal which is strongly curved in its longitudinal axis. It exhibits strong medial and lateral muscular markings, on the radial side for *m. opponens pollicis*, and on the ulnar side for the first palmar interosseous muscle. The saddle-shaped proximal articular surface is laterally elongated (observations on cast; Napier 1959; Day 1977; Rightmire 1972). SK 85 has been assigned to *Homo erectus* and SK 84, with some pongid features, to *Australopithecus robustus* (Napier 1959, Robinson 1972). Napier, discussing Old. Hom. 7, offers what might be an accurate description of the australopithecine manus.

"The overall picture presented by this assemblage is of a short, powerful hand with strong, curved digits, surmounted by broad, flat nails and held in marked flexion. The thumb is strong and opposable, though possibly rather short." (1962:414).

Differences between the species of *Australopithecus* cannot be determined with any accuracy. A sufficient sample with suitably preserved corresponding body parts is not available. Description of the hand bones from the Hadar hominid AL 288-1 and new, unpublished material from the AL 333 locality should complement our knowledge of gracile australopithecine hand morphology. The new Afar specimens are remarkable not only in their abundance but also for their superb state of preservation. If they prove to be consistent with the morphological pattern discussed above, then one may draw firm conclusions about the form of the early hominid hand (in at least one lineage). The problem will then be to delineate behavioral potentialities from that pattern.

Lower Limb, and Bipedal Efficiency in *Australopithecus*

A great deal of the earlier literature focused upon: a) whether the australopithecines were bipedal, and b) if they were bipedal, was the bipedal adaptation the same as seen in modern man. Naturally, attention was centered upon the lower limb, particularly pelvic and femoral, anatomy of the early hominids.

The essentially hominid nature of the australopithecine pelvis is well known. The focus here will be on the delineation of differences in pelvic (and lower limb) morphology between *Australopithecus* and *Homo* (and between species of *Australopithecus*), and the elucidation of their biomechanical significance. It is suggested that much of the work claiming significant gait differences between *Australopithecus* and *Homo*, and between gracile and robust australopithecines, has been based upon inadequate reconstruction, and these conclusions are at least partially in error.

Os Coxae

The controversy in the study of early hominid innominates has been in the interpretation of those features in *Australopithecus* which are not identical with *Homo*. The recovery of a complete coxal bone from Sterkfontein, the basis for most of our knowledge of the pelvic anatomy of *A. africanus*, has been complemented by the discovery of a juvenile ilium and ischium from the Makapan Limeworks (MLD 7 and 8, Dart 1949) and, more recently, of a relatively complete left innominate from Hadar, AL 288-1 (Johanson and Taieb 1976). Fortunately this sample includes most of the major morphological landmarks of all three pelvic bones. The ilium of *Australopithecus robustus* (and *A. boisei*) is represented by SK 50 and SK 3155b; the ischium is represented only by SK 50, a poorly preserved specimen.

The ilium of *Australopithecus*, the best known element of its pelvis, is typically hominid in its low, wide, and laterally disposed shape. It shows both the convex anterior and concave posterior gluteal surfaces of the ala. The iliac crest is less arched in its mid-length (is more horizontal anteroposteriorly) than in modern man but does form a sigmoid curve. The auricular surface is relatively small, although the relationship of this to body size is problematic (Broom et al. 1950; Clark 1955; Day 1973; Lovejoy 1975; McHenry 1975c; Robinson 1972; Zihlman 1967). Distinctions from *Homo* are in the structure and disposition of the anterior margin of the ilium: in more projecting anterior superior and inferior iliac spines, with a more recurved margin between them ipsilaterally, in a longer acetabulospinous distance, and in a greater interspinous distance (between contralateral anterior superior spines, forming greater lateral iliac flare). This distinct morphology is witnessed in all specimens, and has been the subject of considerable speculation. The original descriptions of Sts 14 and SK 50 emphasized the more anterior position of the anterior superior spines, giving the pelvis a "beaked" appearance (Broom et al. 1950; Broom and Robinson 1952). The anterior inferior iliac spine is well developed, particularly in SK 50. The anterior margin in SK 50 forms a distinct notch between superior and inferior spines, and projects forward in a pronounced fashion to reach the ventrally protuberant anterior superior iliac spine (the same pattern is visible, although less accentuated, on Sts 14). The anterior inferior spine bears the impressions of *m. rectus femoris* and the iliofemoral ligament, and the impression of the reflected head of *m. rectus femoris* is visible on the body of the ilium (just posterior to the anterior inferior spine and just superior to the rim of the acetabulum) on the original specimens (Day 1973; Robinson 1972).

There has been considerable disagreement concerning the distribution and relative thickness of cortical bone in the anterior aspect of the ala. In modern man this area illustrates two thickenings of bone, radiating out from the acetabulum to the anterior iliac crest in a "V"-shaped fashion: the acetabulocristal and acetabulospinous pillars. The former (the iliac pillar) is a pronounced bony buttress which runs from the center of the body of the ilium to the iliac or cristal tubercle. The latter is a bony ridge from the acetabulum to the anterior superior iliac spine. Since in *Homo* the anterior superior spine is curved medially, the iliac pillar divides the gluteal surface of the ilium into anterior and posterior planes. The question arose as to whether *Australopithecus* possessed an iliac pillar and cristal tubercle.

Although Mednick (1955) and Napier (1964) asserted that no cristal tubercle was present, other workers have noted its presence, albeit in less pronounced form (Dart 1949; Howell 1955; Robinson 1972). The disagreement probably arose from focusing upon the cast of the Sts 14 right innominate, which is lacking the anterior iliac crest. The tubercle is visible on the left innominate from Sterkfontein (illustrated by Robinson 1972:299). The iliac pillar can be seen in *Australopithecus*, though clearly less pronounced (Dart 1949; Day 1973; Genet-Varcin 1969; McHenry 1975c; Zihlman 1970). The pillar is also of a somewhat different form, being more anterior in position. This is probably an effect of lack of modern medial rotation of the anterior superior spines, thus placing both acetabulocristal and acetabulospinous pillars closer to one plane (Lovejoy 1975; Lovejoy et al. 1973). This results in effectively merging the two buttresses into one more subtle thickening directed to the area of the anterior iliac crest (Robinson 1972).

The pronounced beaking in SK 50 is not seen in the SK 3155b innominate (Brain et al. 1974; McHenry 1975c), but it is clearly from a juvenile individual. The relatively minor iliac differences between gracile and robust australopithecines are not demonstrably reflective of any functional difference but may simply be correlative of body size differences (Robinson 1972).

The pubic bones are not well known for *Australopithecus*. The pubic bone in Sts 14 has been discussed as relatively long (Broom et al. 1950; Robinson 1972). Sts 14 is not accurately reconstructed at the *symphysis pubica* since the left pubic bone crosses the midline into the right side. Both Lovejoy (1975) and Day (1973) have expressed the opinion that a corrective reconstruction would reduce the apparent "pongid" length and place the length of the pubis within the modern human range. The pubic symphysis is relatively small (Zihlman 1967). All specimens with the relevant area preserved (just lateral to the iliopubic eminence) show a well developed iliopsoas groove (Day 1973; Zihlman 1967; clearly visible on Wenner-Gren casts of Sts 14, SK 50, and SK 3155b). A distinct pectineal line can be seen on Sts 65 and is apparent on Sts 14 (although here the superior pubic ramus is damaged, Day 1973). This damage is quite evident on the superior ramus where *pecten pubis* and the obturator crest would approximate each other in the vicinity of the pubic tubercle. The distorted inferior pubic ramus might account for the unique shape of the obturator foramen (noted by Broom et al. 1950 as distinctly larger in superior-inferior diameter than in medio-lateral).

The morphology and dimensions of the ischium in *Australopithecus* have been a source of controversy; this disagreement has focused upon the length of the ischium and the nature of the ischial tuberosity. Broom and Robinson described the Sts 14 and SK 50 ischia as more anthropoid-like than the ischia of modern man. They emphasized the greater distance between the inferior margin of the acetabulum and the superior tip of the ischial tuberosity (Broom et al. 1950; Broom and Robinson 1952). It was then suggested by several authors that the "long" ischium in *Australopithecus* represented an incomplete bipedal adaptation, by retaining a more pongid-like, power oriented hip extensor mechanism (Clark 1955; Napier 1964; Straus 1962; Zihlman 1967, 1970). Cursory examination of casts of Sts 14 and SK 50 plus numerous modern human ischia appears to confirm the above observation, but the apparently "long" ischium of Sts 14 is in fact a visual artifact, resulting from an ischial tuberosity of somewhat different morphology and surface area, a relatively wide *sulcus tuberoglenoidalis*, and a relatively small acetabulum. The distance between the acetabular margin and the ischial tuberosity (superior margin) reflects the combination of the above characters and has no biomechanical significance. What *is* significant is the distance from the center of the acetabulum to the impression on the ischial tuberosity of the common head of origin of the hamstring muscles (the mechanical lever arm of the hamstrings); this metric dimension must then be corrected for gross body size differences, usually via a ratio involving acetabular diameter. When the biomechanical ischial length is thus determined, the Sts 14 ischium is very *short*, in the upper ranges of modern human populations (Howell 1955; Lovejoy 1973, 1975; Lovejoy et al. 1973; McHenry 1975b; Robinson 1972; Schultz 1969).

Robinson (1972, 1977) maintains, however, that the ischium is long in SK 50. The length of the SK 50 ischium (biomechanical length, as defined above) is considerably longer than that of Sts 14 (60 and 43 mm, respectively, Lovejoy et al. 1973). The problem is how to correct this length for body size in SK 50. As noted, most workers have used maximum acetabular diameter as the correcting factor. In SK 50, this dimension is 50 mm (Lovejoy 1975). Thus the relative length of the Swartkrans ischium is expressed as:

$$\frac{\text{Maximum Acetabular Diameter}}{\text{Biomechanical Length of Ischium}} \times 100 = 50/60 \times 100 = 83\%$$

This computation is equal to Robinson's (1972) value

for Sts 14 (83%). (Robinson,1977, cites an ischial length of 69 mm for SK 50, but states that the SK 50 ratio is 62%). Despite the striking visual impression of a long ischial shank in this fossil, SK 50 may well possess a functional ischial length equivalent to that in Sts 14 and well into the range of modern man. Given the condition of the acetabulum in SK 50 (it is clearly distorted), it is impossible to accurately determine ischial length. As Lovejoy (1975) has illustrated, regardless of the measurements and indices Robinson utilized, his data on modern humans ($\bar{x}$ = 68, range 56-81, n = 40) do not merit excluding his 62% figure for the "*Paranthropus*" innominate. If a small acetabulum is a populational character of *Australopithecus*, compared to modern *Homo sapiens*, then acetabular diameter may be an unsuitable parameter for size correction, especially given the state of preservation of SK 50. Lovejoy, Heiple, and Burstein (1973) suggest the use of maximum iliac height but this is not determinable on SK 50. Standardizing via the auricular surface area of the ilium may also be inappropriate, since this is smaller in *Australopithecus* than in modern populations, and the auricular surface is absent in SK 50.[5] Obviously, suitable parameters for size correction applicable to *Australopithecus* are needed. The importance of ischial length is that wide ranging inferences about locomotor differences between *A. africanus* and *A. robustus* have been based upon this one morphological observation (i.e., Robinson 1972), an observation clearly not substantiated by the available sample.

The form of the ischial tuberosity in *Australopithecus* is somewhat different than that of modern man, including differences in shape, disposition, and extent up the ischial shank. The narrow, flattened tuberosity in Sts 14, with a rather sharp lateral edge, was noted by Broom et al. (1950). The tuberosity does not extend as far towards the acetabulum (because it is interrupted by a large tuberoglenoidal sulcus). The distinct impressions made by the common origin of *m. semitendinosus* and *m. biceps femoris* (long head) on the lower part of the tuberosity, and by *m. semimembranosus* on the more superior part, are not visibly differentiated. Chopra (1962) reported that all primates with a flattened tuberosity and sharp lateral ischial border possess a *m. gluteus maximus* which passes laterally, not over, the tuberosity. Since Sts 14 possessed this type of tuberosity, he concluded that in *Australopithecus africanus m. gluteus maximus* was an abductor as in pongids, not an extensor (as in hominids). To the contrary, the australopithecine ilium indicates an origin of *m. gluteus maximus* posterior to the hip joint and thus an action as a powerful extensor. Robinson (1972) also has reported that in the Sts 14 original specimen the tuberosity surface is absent and areas of cancellous bone are exposed. The SK 50 ischial tuberosity exhibits an unusual flange-like eversion (Howell 1955; visible on cast); the tuberosity surface is damaged also (Robinson 1972).

The known acetabula of australopithecines are absolutely and relatively smaller in diameter than *Homo* (Day 1973; Lovejoy 1976b; Napier 1964; Robinson 1972; Zihlman 1967), which correlates with smaller femoral head diameters and smaller body size. The SK 50 acetabulum is relatively small and would be smaller if corrected for distortion. The SK 3155b acetabulum is almost exactly equal in diameter to Sts 14 (McHenry 1975c). Napier (1964) states that the acetabulum of SK 50 is more laterally disposed (more pongid-like) than in Sts 14 but given the condition of the former fossil this is not justified. The only other robust australopithecine fossil with an intact acetabulum is SK 3155b; here, however, the essential landmarks necessary to accurately orient the pelvis (minimally, the anterior superior iliac spine and the pubic symphysis) are absent. All known early hominid acetabula are relatively deep.

Femora

The hominid femur is a stout bone which clearly reflects a bipedal adaptation, and thus fossil hominid femora are very important in gait reconstruction. Fortunately australopithecine femora are fairly numerous, but complete and undistorted femora are rare (KNM-ER 999, 1472, 1481a; AL 288-1). Most fossil femora are proximal, distal, or diaphyseal fragments.

The proximal femoral anatomy of *Australopithecus* is well known and a fairly distinct morphological pattern is obvious. All observers have noted the presence of a small femoral head (even when standardized via femoral shaft diameter, measured just inferior to the lesser trochanter, Day 1977; McHenry and Corruccini 1976; Napier 1964; Wood 1976). Our knowledge of head diameters for *A. africanus* is based upon the reconstructed head in Sts 14, which is severely damaged. We may note, however, the lack of significant differences in acetabular diameter between gracile and robust early hominids and logically correlate the small acetabula with small femoral heads (Zihlman 1970). The small femoral head was not proportionately small for the length of the femur (Lovejoy 1975; Walker 1973). Two hominid femora from East Lake Turkana, KNM-ER 1472 and 1481a, have femoral heads considerably larger than *Australopithecus* and comparable to *Homo* (Leakey 1973a; McHenry and Corruccini 1976).

Jenkins (1972) has stated that the femoral head coverage is different in *A. robustus*, and intermediate in form between the posterior elongation of the articular surface characteristic of *Pan*, and the anterior prolongation seen in *Homo* (correlating with the more shallow, laterally disposed acetabulum of chimpanzee, and the deeper, more ventrally disposed acetabulum of man). In man, a small articular facet encroaching onto the anterior aspect of the neck is present, in the absence of an anterior sub-capital sulcus, but with a frequency of only 10 per cent (Harty 1973). As Lovejoy (1975) has noted, the Jenkins (1972) reconstruction is

based upon the damaged and distorted SK 50 acetabulum and the SK 82 proximal femur, which on the basis of gross size differences are clearly *not* a suitable match.

Australopithecus possessed long femoral necks (Day 1969; Lovejoy and Heiple 1972; McHenry and Corruccini 1976; Napier 1964; Walker 1973; Zihlman 1970), relatively flattened anteroposteriorly (Day et al. 1976; Johanson and Coppens 1976).[6] The neck is set upon the femur at a lower collo-diaphyseal angle (*coxa vara*) than in modern human populations (*coxa valga*) (Day 1977; Lovejoy 1976b; Walker 1973; Zihlman 1970). The values listed in Lovejoy (1977) and Lovejoy and Heiple (1970) range from 115° (SK 83, Old. Hom. 20, KNM-ER 738 & 815) to 120° for SK 82; the mean in one Amerindian sample was 128° (*1 S.D.* = 3.6±).

The morphology of the greater trochanter is noticeably different in *Australopithecus*. This traction apophysis appears smaller, and exhibits less lateral flare and vertical (proximal) extension than in modern humans (Day 1969; McHenry and Corruccini 1976; Zihlman 1970). Impressions for the insertion of *mm. gluteus minimus et medius, obturator internus* and *gemellus superior et inferior* are visible (Day 1969; Day et al. 1976; Johanson and Coppens 1976). The morphology of this region in KNM-ER 1472 and 1481a is again more like that of *Homo* (greater lateral flare, Lovejoy 1977; also KNM-ER 999, Day and Leakey 1974). The quadrate tubercle (on the intertrochanteric crest, at the distal end of the greater trochanter) is apparent in KNM-ER 1503 (Day et al. 1976), in the proximal femora from Hadar (Johanson and Coppens 1976), and can be seen on a cast of SK 82 (this area is damaged in SK 97).

Although some australopithecine femora illustrate a posteriorly positioned lesser trochanter (Day 1969; Napier 1964), there is considerable variation in both australopithecine (Walker 1973) and modern populations with regard to this trait. The position of the lesser trochanter does not lie significantly outside the range of *Homo sapiens* (Lovejoy 1975). Day (1973) states that the vertical groove for the iliopsoas conjoint tendon is visible as it approaches the lesser trochanter, in SK 82 and 97.

Although Napier (1964) suggested intrageneric differences in the depth of the trochanteric fossa, all *Australopithecus* femora possess deep fossae (Day 1969; Day et al. 1976; Johanson and Taieb 1976; Lovejoy 1975a), with a clearly delineated groove for the tendon of *m. obturator externus* (Day 1973; Lovejoy 1975; Walker 1973).

Controversy has arisen over the presence and significance of the intertrochanteric line and the femoral tubercle in *Australopithecus*. Day (1969) and Napier (1964) had stated that these were absent. Many specimens, however, do exhibit a weak intertrochanteric line and femoral tubercle (Day 1977; Day et al. 1976; Johanson and Coppens 1976; Robinson 1972; Walker 1973). The weak line resembles more a synovial reflec-

tion than a ligamentous attachment, and is known to be an age-related feature with considerable variability (Lovejoy 1975). The line and tubercle are not apparent on casts of SK 82 and 97, but Robinson (1972) states that they are visible on the originals, with the femoral tubercle being more incorporated into the greater trochanter than in modern man.

Cresting on the proximal posterior aspect of the shaft conforms to a modern pattern, with a well developed *crista hypotrochanterica* and pectineal line (Day 1969). More distally, the spiral line and the lateral lip of *linea aspera* are seen on femoral shaft fragments from Hadar (Johanson and Coppens 1976). The femoral shaft can be quite stout in certain specimens.

The distal femoral anatomy of *Australopithecus* is extremely modern. This includes the relatively deep (non-pongid-like) patellar fossa with an elevated lateral lip, a narrow but deep intercondyloid fossa, and the relatively elongated and flattened lateral condyles (Broom and Schepers 1946; Clark 1947; Lovejoy et al. 1973). The proportions of the condylar articular surfaces are modern (Walker 1973), contrary to Kern and Straus (1949) and Preuschoft (1971). The posterior 1/2 of the groove for the *m. popliteus* tendon is visible in TM 1513 near the lateral margin of the lateral condyle (Clark 1947). The attachment of the posterior cruciate ligament is observable on the medial condyle in the Hadar specimen (Johanson and Coppens 1976), as well as a deep popliteal groove postero-inferior to the lateral epicondyle. Day (1973) found grooving for *m. popliteus* and asymetrical grooves for the menisci (on the condylar surfaces) in Sts 34 and TM 1513, evidence for the presence of a knee un-locking and locking mechanism (respectively) similar to that of *Homo*.

The bicondylar (femoro-condylar) angle of TM 1513 was determined by Clark (1947) as ca. 7°, simulating the midline of the shaft via the highest point of the intercondyloid fossa. Kern and Straus (1949) felt that an angle of 7° was neither unique nor discriminatory. Heiple and Lovejoy reconstructed the bicondylar angle in TM 1513 and Sts 34 (as the angle of the central axis of the femur with the vertical to the bicondylar plane) and found the previous estimates too low, since the centroid axis of the femur did not necessarily include the highest point in the intercondyloid fossa. Their estimates were 14° for TM 1513 and 15° for Sts 34, figures higher than those for modern man ($\bar{x} = 11°$) and substantially beyond those for *Pan* (6°; Heiple and Lovejoy 1971; Lovejoy and Heiple 1970). The very high femoro-condylar angles have been confirmed by additional material and by other workers (Day 1973; Johanson and Taieb 1976; Walker 1973).

The lengths of australopithecine femora apparently varied considerably (as did their robusticity). Broom et al. (1950) reconstructed the Sts 34 femur as 310 mm long. Lovejoy and Heiple (1970), utilizing the new bicondylar angle determination, reconstructed a length of 276 mm for Sts 14, and, using a composite Sts

14/SK 82, 310 mm for *A. robustus.* Walker (1973) reconstructs a length of 250 mm for Sts 14, and 360 mm for a composite (Old. Hom. 20/KNM-ER 993) femur of *A. boisei.* The crushed femur of AL 288-1 is ca. 280 mm long (Johanson and Taieb 1976).

Leg: Tibiae and Fibulae

The tibia (shaft and distal end) from Olduvai, Old. Hom. 35, was described by Davis (1964). He concluded that the horizontal, slightly anteriorly disposed distal articular surface indicated an ankle region of modern morphology. The proximal shaft morphology, according to Davis, indicated significant differences from *Homo.* He described the area of origin for *m. tibialis posterior* as more extensive than that of *m. flexor digitorum longus* (on the tibia), a pongid condition. He suggested that *m. popliteus* pulled in a vertical direction and *m. soleus* had a less extensive tibial attachment. Day (1977) and Lovejoy (1975) independently concluded that Davis had misidentified the soleal line. Apparently the "strong marked crest" discussed by Davis (1964) *is* the soleal line, the upper, more anteriorly located portion. The soleal line is more vertically disposed than in some modern tibiae, but this trait is variable (e.g., Lovejoy 1977). There is thus no need to suggest anything but an oblique line of action of *m. popliteus* (Lovejoy 1975). The area for *m. popliteus* is damaged and surface bone is missing (visible on the Wenner-Gren cast). A prominent soleal line is evident in the AL 129-1b proximal tibia from the Afar triangle (Johanson and Coppens 1976). A well preserved tibial fragment from East Lake Turkana, KNM-ER 741, illustrates a basically modern morphology. The Old. Hom. 35 tibia was originally part of Old. Hom. 6, a *"Homo habilis"* Bed I paratype (Leakey, Tobias, and Napier 1964); KNM-ER 741 was assigned to *Australopithecus,* although Day (1977) has suggested that it has more affinity with *Homo* (along with KNM-ER 1471, 1476b, and 1481a). Unfortunately, matching tibial parts are not available for comparison in taxonomic assignment, and all such attempts are strictly suggestive.

The Old. Hom. 35 figula is essentially modern in morphology (Davis 1964). The right distal fibula and tibia of AL 288-1, undescribed, should hopefully confirm our interpretations of this area for *Australopithecus.*

Pes

Several relatively complete early hominid tali are known. The first recovered, TM 1517 from Kromdraai, is a small specimen with considerable damage to the inferior surface. It exhibits a relatively narrow articular surface for the malleoli, and a broader, more horizontal (less angulated), more medially extensive neck with a relatively large articular surface for the navicular. The horizontal neck angle (angle between the axis of the neck and that of the trochlea) is wide (estimated as 32°by Day and Wood 1968; Wood 1974c).

The medial lip of the trochlea is elevated as in *Homo* (observation on cast; Clark 1947; Gregory 1949; Preuschoft 1971; Wood 1974c). The Olduvai talus (Old. Hom. 8) also exhibits a relatively high horizontal neck angle (28°, incorrectly cited as 32.5° by Robinson 1972), as does KNM-ER 1476a (Day 1976a; Day et al. 1976; Day and Wood 1968; Wood 1974c), although the Old. Hom. 8 talus has a higher torsion angle of the neck (40°) than TM 1517 (34°) (Day and Wood 1968). Multivariate analysis has consistently segregated Old. Hom. 8 and TM 1517 from the more modern talus from East Lake Turkana, KNM-ER 813a (Day and Wood 1968; Wood 1974a and b). The KNM-ER 813a talus, and probably KNM-ER 1464 (per Day 1976a and b, and contra Leakey 1973b), would be placed in *Homo* on the basis of their strikingly modern morphology: a narrow neck/body angle, a high torsion angle of the head, and a less extensive navicular articular facet (Leakey 1972; Wood 1974c).[7] There is evidence of two morphological patterns, one which is assigned to *Homo* (KNM-ER 813) and another to *Australopithecus* (TM 1517, and Old. Hom. 8, originally a paratype of *"Homo habilis"* Leakey, Tobias, and Napier 1964, and suggested as more appropriately placed in *Australopithecus,* Day 1976a and b; Wood 1974c).

The only published calcaneum is that of Old. Hom. 8, fragmentary but with a horizontal, very modern *sustentaculum tali* (Day and Napier 1964). The Old. Hom. 8 medial cuneiform, according to Lewis (1972a), has a primitive *(Pan gorilla*-like) distal articular surface, being markedly convex superiorly and concave inferiorly. The Olduvai metatarsals show the thick proximal cross-section, with large proximal joint surfaces, characteristic of a hominid pedal loading pattern (Preuschoft 1971). The index of robusticity is hominid (Archibald et al. 1972, contra Day and Napier 1964). The general proportions of the pes, with a relatively long tarsus, average-length metatarsus, and short phalanges (compared to non-human primates), is characteristic of hominid entaxonic weight-bearing (Lessertisseur and Jouffroy 1975).

The terminal hallucial phalanx from Olduvai, Old. Hom.10, is typically hominid in being extremely broad and stout with axial torsion and valgus deviation, and has been discussed as the toe bone of a "fully modern bipedal strider" of the genus *Homo* (Day and Napier 1966; Day 1967, 1974b) although Wood (1974c) has discussed placing it into *Australopithecus.*

Biomechanics of Early Hominid Locomotion
Forelimb

The forelimb remains of *Australopithecus* illustrate a distinct morphological pattern. The lack of comparable body parts between gracile and robust forms is critical and any conclusions must be qualified (as to whether a given part is available for study in both taxa). We can conclude that all australopithecines possessed relatively longer arms than modern man, and

that the upper limb morphology has some distinctly pongid-like features. These two observations are obviously related and the crux of the issue is whether the second reflects (1) retention of adaptive complexes to suspensory/supportive posture and locomotor behaviors in the common African ape ancestor (synplesiomorphy), or (2) the actual use of such morphological adaptations in habitual forelimb suspensory/supportive behavior. The evidence for the latter suggestion with regard to the pectoral girdle is the glenoid fragment from Sterkfontein (Oxnard 1968a), particularly dealt with in the morphometric analysis of this glenohumeral joint by Ciochon and Corruccini (1976).

The morphology of known (at least gracile) *Australopithecus* humeri is consistent with that of an animal with fully developed rotatory capabilities at the glenoid fossa, with the head of the humerus secured via strong rotator-cuff muscles and, presumably, a strong superior glenohumeral ligament (since the entire weight of the upper limb at rest is countered by the superior glenohumeral ligaments, Basmajian 1972). There is evidence of a powerful *m. biceps brachii*, long head. The humeral shaft (robust forms) indicates development of powerful abduction (also seen in short scapular muscles). The humeri for all australopithecines indicate strong common forearm and hand flexors. If the distal humerus can be used to discriminate knucklewalkers (possessing a steep lateral wall of the olecranon fossa, McHenry 1976b; Day 1976b), then there is no evidence of knuckle-walking in the australopithecine elbow join.

Conclusions about the forearm are virtually limited to the Omo L40-19 ulna, which exhibits traits resembling pongids, hominids, and numerous features which are totally unique. The ulna (known only for robust forms) suggests some sort of supportive, postural, and/or active locomotor use of the forelimb (Howell and Wood 1974; Day 1977). When the morphology of the ulna is considered in conjunction with that of the humerus, there is evidence in at least the robust lineage of the use of the upper limb in a non-*Homo sapiens* fashion.

The australopithecine manus is also illustrative of a myriad of features, some of which are hominid-like, some pongid-(particularly, *Pan*-)like, and some totally unique. Again the lack of comparable body parts between the early hominid lineages obstructs full analysis, yet one can conclude that at least some carpal bones, in all forms, were quite primitive (i.e.,*Pan*-like). The robustness of the digits and particularly the well developed lateral ridging on the palmar phalangeal surfaces combines with evidence in the shoulder and in the distal humerus to indicate an animal capable of very strong flexion, pronation, and supination in the superior member.

McHenry (1937b) has emphasized that body size is critical in interpreting the morphology of the

KNM-ER 739 humerus, and in a sense this applies to the entire forelimb anatomy. Certainly the interpretation of the robustness of the KNM-ER 739 humerus depends upon whether *Australopithecus boisei* is reconstructed at 100 or 200 pounds. The total morphological pattern of the upper limb, albeit known from an insufficient sample, is reasonably consistent and is suggestive of use of the forelimb in behaviors not ordinarily adopted by modern man. The evidence is found in the morphology, size, robusticity, and proportions of the various skeletal elements, and is apparent in all forms of *Australopithecus*.

The lack of suitable parameters for discussing locomotor behaviors in early hominids is a serious problem. The use of broad categories such as "brachiation" in this context is inadequate, since the forelimb anatomy of the extant pongids varies considerably (particularly in the manus, Lewis 1973; Tuttle 1975), as does the manner in which these apes utilize the forelimb in locomotor, postural, and feeding behavior. The unique forelimb anatomy of *Australopithecus* may be the result of a different complex of postural-locomotor adaptations and behaviors, with several underlying broad similarities to extant pongids but *in toto* different from them all. Our sample of extant hominoids is very limited when compared to the total range of adaptive complexes which must have occurred in hominoid evolution. The Neogene faunas give us an indication of this diversity, but unfortunately the hominoid sample is more often dental and gnathic remains rather than postcranial. The postcrania preserved do not show strong affinities to modern ape morphology. The anatomy and morphometric affinities of the Miocene ape postcrania are in many ways strikingly primitive (i.e., cercopithecoid-like; Corruccini et al. 1976; Napier and Davis 1959; Morbeck 1972; O'Connor 1974) and should not be equated with those of modern apes (e.g., Lewis 1973; Conroy and Fleagle 1972; Zwell and Conroy 1973). Tuttle (1967) has shown that the human hand does not reflect the same kind of adaptations to knuckle-walking seen in the extant African apes, but this does not preclude the possibility of some form of supportive role of the forelimb (terrestrial or arboreal), especially if the adaptation were more pronounced in the soft tissues and would not be fossilized. Lovejoy (1977) has suggested that if one can delineate a complete bipedal adaptation (striding gait) in *Australopithecus*, then the use of other locomotor behaviors is *a priori* excluded. This viewpoint is based upon the modern human gait, seen as a very restrictive locomotor adaptation; the existence of a different type of bipedal adaptation, in an animal of different body proportions, means that bipedal behavior in *Australopithecus* did *not* necessarily preclude the resumption of other postures and locomotor behaviors.

The type of biomechanical analysis seen in studies on the human hindlimb are not yet available for the

hominoid forelimb, although considerable progress has been made in recent years. A full analysis of the australopithecine forelimb must be done in the context of a comparative study of pongid forelimb anatomy, with emphasis on how locomotor behaviors and soft tissue adaptations are reflected in the bony skeleton. An emphasis on the varied and complex use of the limbs in postural, locomotor, and feeding behaviors in the Hominoidea is essential in reconstructing such possible behaviors in early hominids. I suspect such analysis would find the role of the forelimb in australopithecine behavior to be unique among hominoids.

Hindlimb

The functional morphology and biomechanics of modern human bipedalism are well known, as are the major evolutionary changes involved. The focus with *Australopithecus* is to what degree are these changes in anatomical adaptive complexes developed. A major, perhaps pivotal, adaptation to bipedalism, of a broad, short, laterally displaced iliac blade, and re-orientation of the gluteal muscles, is witnessed in *Australopithecus*. Thus australopithecines had achieved the placement of *m. gluteus maximus* to a position behind the hip joint, enabling the muscle to be a powerful thigh extensor (Clark 1955; Washburn 1950). Although Robinson et al. (1972) suggest that there has been no major change in the function of *m. gluteus maximus* from hominoid to hominid, the hypertrophy of the muscle, particularly in its cross-sectional area, directly relates to its powerful role in hip extension (Ishida 1968; Lovejoy 1975, 1977; Reynolds 1931). *M. Gluteus maximus* in apes actually consists of two divisions: (a) a more superior portion, the sacroiliac part (in *Pongo, m. gluteus maximus proprius*), innervated by the inferior gluteal nerve and acting as a powerful abductor and lateral rotator, and (b) a more inferior portion, the ischiofemoral part innervated by the flexores femoris nerve and possessing some extensor capability. The evolution to the hominid condition entailed the loss of the ischiofemoral portion (Sigmon 1975; Tuttle et al. 1975). *M. gluteus maximus* became most important in full extension of the thigh, especially in situations demanding considerable power, as well as aiding in the maintenance of stability at the knee joint (via its partial insertion into the iliotibial tract) and in checking the forward momentum of the limb in swing phase (Robinson et al. 1972; Basmajian 1972; Washburn 1950).

One of the most significant aspects of the modern human bipedal adaptation is the system of lateral pelvic balance control (Reynolds 1931). The reorientation of the iliac blades, positioning the anterior gluteal surface and margin in a lateral-ventral position, aligns *mm. gluteus medius et minimus* for abduction of the hip joint (losing their extensor function in pongids). This abduction acts to limit the displacement of the center of gravity in a horizontal plane. When one leg is in stance phase the abductors cantilever the pelvis from the femur and limit contralateral pelvic lowering of the limb in (unsupported) swing phase. Action on vertical displacement is accompanied by limitation of displacement in a sagittal plane, via internally (medially) rotating the thigh beginning at heel-strike, and externally (laterally) rotating from toe-off. Absence of this abductor-rotator control of limb progression results in a clinical manifestation (Trindelenberg gait) which involves a smaller cadence, the feet placed further apart, and considerably more side-to-side "rolling."

The greater lateral iliac flare and greater distance between anterior superior iliac spines have been considered indicative of less efficient lateral balancing in *Australopithecus* (Zihlman 1967), via positioning the internal rotators more laterally (therefore in a less efficient position). Furthermore, the supposed lack of an iliac tubercle and pillar (Napier 1964; Mednick 1955) would indicate less developed gluteus medius and minimus musculature. Zihlman and Hunter (1972) have attempted a biomechanical reconstruction of the hip joint, focusing upon internal rotation and abduction in MLD 7 (adolescent left ilium). They conclude that *Australopithecus* developed considerably more torque in internal rotation than modern man, but had to exert more force to rotate the trunk for less distance at a lower speed. The medial movement of the anterior superior spine from *Australopithecus* to *Homo* allowed more direct pull and shortened the power arm of the internal rotators, facilitating more efficient internal rotation. The authors concluded that the relatively more massive upper limbs aided in internal rotation (also Genet-Varcin 1969).

Lovejoy and his associates have studied the abductor complex in *Australopithecus* and have reached very different conclusions. They feel that the beaked anterior superior spine is the result of compensation for greater iliac flare. The beaking is simply the adjustment necessary to place the anterior superior spine into the correct ventral plane for alignment of the inguinal ligament and *m. sartorius* (Lovejoy 1976, 1977; Lovejoy et al. 1973). The combined effect of a more lateral anterior iliac region, a longer acetabulospinous distance, a longer femoral neck, a smaller collodiaphyseal angle, and a very high femoro-condylar angle is to give the abductors a long lever arm (right angle distance between abductor line of action and the center of the acetabulum) for control of pelvic tilt, reducing the muscle force necessary for equilibrium and the total force on the hip joint (Lovejoy 1973, 1975, 1977). Thus the long femoral neck, greater iliac flare, and more protuberant anterior superior spine form an adaptive complex for minimizing pelvic sagging, hip joint pressure, and energy expenditure in bipedal striding (Lovejoy 1976; Lovejoy et al. 1973). Lovejoy concludes that the longer femoral neck and more protuberant anterior superior iliac spine would

allow effective internal rotation like that of modern man (1973). He further correlates this complex in australopithecines with the distinctly less flared greater trochanter. Efficient abductor lever arm length is accomplished by long femoral neck, lateral iliac flare, and protuberant spine, and therefore a flared greater trochanter is not necessary. The small acetabulum and femoral neck diameter would simply reflect small body size and relatively low femoral head pressure (Lovejoy et al. 1973).

This entire pattern of pelvic and femoral morphology may be related to one important dimension: interacetabular diameter. The australopithecine pelvis is characterized by a relatively large false-pelvis diameter and relatively small true-pelvis diameter. The major change from *Australopithecus* to *Homo*, according to this paradigm, would entail maximizing interacetabular (pelvis minor) dimensions for the passage of full-term fetuses with relatively enlarged cranial capacities (Lovejoy 1973; Lovejoy et al. 1973). In this regard, Leutenegger (1972, 1974) has shown that *Australopithecus* had relatively small fetal cranial diameters compared to pelvic outlet breadth. Changes in *Homo*, accompanying rapid encephalization in the lower and middle Pleistocene (McHenry 1975a), would include increasing anteroposterior pelvic outlet diameter via lengthening the superior pubic ramus and increasing retroflexion of the inferior end of the sacrum; increased coronal interacetabular distance would be accomplished via an increase in sacral breadth, which would place the alae of the ilium in a more sagittal orientation (reducing lateral iliac flare and beaking). The shortening of the abductor lever arm (less iliac flare, shorter femoral necks, and a greater collodiaphyseal angle) would result in less efficient abduction and greater femoral head pressure. Greater femoral head pressure would also result from increased body weight, thus selecting for maximum diameter of the femoral articular head and the acetabulum. Given some absolute limit on maximum body width at the hip joint, relative femoral neck length would be decreased as birth canal diameter increased. The medial approximation of the anterior superior spines would maintain efficient internal rotation (by maintaining the length of the internal rotator level arm), and develop the characteristic acetabulocristal and acetabulospinous pillars of *Homo sapiens*.

The distinct characteristics of *Australopithecus* in the ilium (confirmed in multivariate sorting by McHenry and Corruccini 1975b) and the femur can be related to a bipedal adaptation in a form of small body size, small interacetabular diameters, and full-term fetuses with small cranial diameters. Lovejoy, and Wood (1973), emphasize that a different pattern need not imply less efficient bipedalism. I feel that the tendency to equate anything morphologically not identical with *Homo sapiens* to some sort of less efficient bipedalism is the result of (a) looking at the striding gait as an adaptive

pinnacle, and as the sole activity selected for in lower limb evolution, and (b) the lack of animals with which to compare. Certainly striding gait is not the only bipedal locomotor activity of modern man, and such a gait was the result of the interaction of selective pressures and adaptive compromises for bipedal locomotion and the obstetrics of large-brained newborn. The human gait is unique, so we have little knowledge of the possible adaptive pathways involved in reaching that pattern. Presumably the postcrania of *Australopithecus* evidence one such adaptive complex different from that of modern man. The existence of two such morphologies need not preclude their involvement in an ancestral-descendent lineage. The two morphologies can be used to sort *Australopithecus* from *Homo*, at least for the ilium and proximal femur; this has been confirmed by the discovery of two well preserved innominate fragments from eastern Africa. Both Old. Hom. 28 (Olduvai Gorge) and KNM-ER 3228 (East Lake Turkana) exhibit a large acetabulum, a distinct acetabulocristal pillar of modern form and position, and an essentially modern ischial tuberosity. The Olduvai specimen was recovered from deposits of Bed IV and has been assigned to *Homo erectus* (Day 1971). KNM-ER 3228 was recovered from the Lower Member, Koobi Fora Formation, and has been assigned to *Homo* sp. (Leakey 1976).

The available australopithecine ischia do not imply any significant difference from modern humans in the biomechanics of hip extension (i.e., longer ischia and more power-oriented hamstrings; Robinson 1972; Sigmon 1975). *Australopithecus* (all forms) had already evolved a shortened ischium which developed the hamstrings into purely propulsive muscles, extending the thigh with greater speed and less power, through a longer arc, than in pongids (Robinson et al. 1972). The femur lengthened as a propulsive strut, and the insertion of *m. gluteus maximus* moved superiorly on the femoral shaft, specializing for power extension. Presumably this indicates (along with the protuberant anterior superior spine for *m. sartorius* insertion and anterior inferior spine for *m. rectus femoris*, straight head insertion) greater development of the quadriceps than the hamstring muscle group and the requirements of the principal stresses of the hindlimb met by one-joint muscles (both characterize modern man, Haxton 1947).

The evidence for the morphology of the hip and knee joints in *Australopithecus* indicates modern form. There is a relatively broad superior aspect of the lunate facies of the acetabulum and modern femoral head coverage. The visible markings for the Y-shaped ligament of Bigelow (iliofemoral) indicate the presence of this mechanism for prevention of hyperextension at the hip joint, via ligamentous, not muscular, action (Joseph 1960). Habitual full extension of the lower limb reduced the stress upon the long bones (Kummer 1968), eliminating much tonic muscular ac-

tivity required for idealized erect posture and approximating the "best fit" position of the femoral head in the acetabulum (Hall 1965). Such habitual extension of the lower limb is evidenced in the well defined iliopsoas groove and its vertical fiber markings near the lesser trochanter.

The size of the distal femoral condyles, the high valgus angle to the femur, and details of the intercondyloid fossa indicate a knee joint fundamentally modern in design. The relatively narrow *spatium interosseum*, the lack of fibular robusticity, and the lack of developed tibial curvature indicate decreased bending stresses at the knee compared to pongids. The fundamentally modern femoral condyles, with elliptical prolongation of femoral-tibial articulation, maximize the surface area of vertical weight transmission. Maximum cross-sectional area of weight transmission (perpendicular to the line of gravity) over the supporting strut, with dorsal/caudal migration of the center of gravity, optimizes stability of the lower limb. The stability of the knee joint, dependent upon its supportive soft tissues (Hall 1965), is apparent in *Australopithecus* from impressions of the intra-articular cruciate ligaments (Day et al. 1976; Johanson and Coppens 1976).

The morphology of the ankle joint is not well understood, but based upon the horizontal articular surface of the distal tibia and the talar trochlea, one may presume that the stability of the talo-crural joint was maintained (as in man) by tonic contraction of *m. triceps surae* (particularly *m. soleus*, Joseph 1960; Tuttle 1975). The australopithecine foot appears to illustrate the type of bow-string loading adaptation (longitudinal and transverse arching) seen in modern humans (Kummer 1975).

There are definite limitations to our reconstructions of lower limb and joint biomechanics in early hominids. The analyses of Lovejoy are quite sound methodologically, but are based upon work on casts of Sts 14 (the proximal femur of which is entirely reconstructed, Day 1973) and the distal femora from Sterkfontein, which are considerably larger than Sts 14 (Walker 1973). I doubt that these reconstructions are fundamentally in error, but until confirmation is made via the analysis of the AL 288-1 lower limb (complete body parts of one associated individual), they must remain suggestive. The implications of Lovejoy's work is that the anterior iliac region and the proximal femur of modern man should show considerable sexual dimorphism (demonstrated for the pelvis by Coleman 1969). Males, without the necessity of maximizing the birth canal diameter, should retain more australopithecine-like features (more lateral iliac flare, more pronounced anterior superior spine, narrower sacrum, shorter pubis, and longer femoral neck and/or smaller neck-shaft angle). He sees evidence of this dimorphism in a sample of Amerindian pelves (Lovejoy 1975), but a thorough review of the literature on modern human sexual dimorphism in these areas

of the pelvis and femur ought to be attempted to substantiate this. In this regard, Walker (1973) has noted sexual dimorphism in the collo-diaphyseal angle, with females having angles up to 3° greater than males.

There is substantial evidence for two separate morphologies in the early hominid talus; these can be used to discriminate *Australopithecus* and *Homo*, yet interpretation of such differences in a functional paradigm is difficult. There is considerable complexity in the correlation of talar neck angles to locomotor habits (Barnett 1955), and we know that a high horizontal neck angle does not necessarily imply a habitually abducted hallux (i.e., Old. Hom. 8). Lovejoy (1977) has emphasized talar variability in modern man, and the role of the three joints which lie between the talus and hallux in modifying the influence of the talar horizontal neck angle upon hallucial position. The Old. Hom. 8/TM 1517 talar morphology does not necessarily imply lack of a striding gait (i.e., Day and Napier 1964; Day and Wood 1968). A logical assumption is that the australopithecine foot was used in a wider variety of locomotor contexts, on a more varied set of substrates, than modern man. It is difficult, however, to demonstrate this directly, with the bony morphology, or indirectly, with inferences about the long tendons and ligaments of the foot. The foot is used in modern man to adjust to different terrain and loading patterns; this compensates for the simple and relatively rigid design of the knee joint (Elftman 1945). If the australopithecine foot is indicative of greater flexibility, then this function of the ankle joint would be critical since a modern knee morphology had already been accomplished. Data correlating the morphology (and variation) of the talus and other tarsals with locomotor behaviors in a wide variety of primates could aid in this matter. More foot fossils have been recovered, yet to be described, from Hadar. These include the talus from AL 288-1, and several fragmentary calcanea, navicula, and tali, a cuneiform, metatarsals, and phalanges from locality AL 333.

Limitations and Applications: Postcranial Data

The methodological problems discussed above impose limitations on the analysis of early hominid postcranial fossils. One of the most difficult problems is in the unique nature of the fossil morphology, and the lack of living analogies. Thus, it is difficult to conceptualize the locomotor behaviors of these early hominids and correlate it with morphology.

We can conclude that, as yet, there is no consistent and demonstrable difference in the postcranial skeleton of gracile and robust australopithecines other than size. This is a conclusion reached by a number of workers familiar with the original material (Day 1977; Walker 1973; Wood 1974c). The central thesis of Robinson (1972), that there are sufficient morphological (and inferred locomotor) differences between the

two lineages to warrant generic distinction (correlated with his interpretation of the dental and cranial evidence), is not supported by the presently available material. Far too much of this thesis depends upon the interpretation of the SK 50 ischium, discussed above, which cannot be substantiated. The non-modern morphology of the "*Paranthropus*" talus and carpals is also reflected in gracile australopithecine foot and hand morphology and thus do not support his generic distinctions.

What is needed to determine possible intra-generic differences is a partial or relatively complete associated skeleton (of one individual) in direct association with cranial and dental parts clearly assignable to a robust early hominid. Then the morphology of robust forms could be determined with a high level of confidence and possible specific differences delineated. Without such evidence there is the danger of circularity of reasoning, assigning postcranial fossils to a given species on the basis of assumed differences in morphology and behavior. It is interesting to note that all relatively complete associated skeletons recovered belong to the gracile australopithecine/early *Homo* lineage. If this situation persists in areas of good to excellent (complete) preservation (i.e., Koobi Fora, Hadar), then perhaps some taphonomic process was operating which has some paleoecological significance.

The postcranial morphology of *Australopithecus* can be used as taxonomic criteria at the generic level. There is a distinct set of characters, well seen in most of the forelimb, ilium, femur, and foot, which is not modern and is clearly sortable from that of *Homo*, even in the lowermost Pleistocene. The diagnosis of the genus *Australopithecus* can thus be extended to include elements of the postcranial morphology. The consistency and distinctiveness of this morphology supports the generic separation from *Homo* and confirms the notion of an australopithecine adaptive grade.

Locomotion in *Australopithecus*

Locomotor adaptations in *Australopithecus* were a mosaic of pongid, modern *Homo,* and totally unique morphologies and behaviors. These early hominids had rather primitive limb proportions and apparently used both forelimbs and hindlimbs in a greater variety of behaviors than modern man. The upper limb evidence suggests use in postural and supportive activities. Whether this can be correlated with paleoecological data (e.g., Vrba's 1975 reconstruction of the environment at the Transvaal sites, as suggested in Ciochon and Corruccini 1976) remains to be seen and should prove quite illuminating.

The lower limb evidence indicates that *Australopithecus* was an erect biped with a fully developed striding gait and stabilization adaptations at the pelvis. If Zihlman and Hunter (1972) are correct, in that the capacity for internal rotation at the hip joint was

achieved in a different fashion in *Australopithecus*, then the longer arms of these hominids might have been very useful in assisting internal rotation. Striding bipedalism was achieved via a different pattern; it is entirely possible that the outward manifestation of the striding gait in *Australopithecus* was unlike that of *Homo sapiens*. This pattern may have involved a difference in cadence as well as different use of the forelimb in walking. Arm swinging is important in man's gait and its nature and vigor varies considerably between individuals, and also varies with the nature and inclination of the terrain, cadence, and speed and type of movement. Given the difference in body proportions and size in *Australopithecus,* a unique type of locomotor behavior is expected for these hominids.

What emerges from the study of australopithecine postcranial morphology is a distinctive pattern: a unique combination of body size, limb proportions, and limb morphology. The earlier emphasis in the literature, on fitting this postcranial morphology into either modern human or extant pongid models, has limited progress in understanding the data. Given the nature of the evolutionary process and the sampling problems of paleontological research, the discovery of major adaptive grades in any lineage is not surprising. There is every reason to expect the early hominids to have undergone some sort of adaptive radiation and to have evolved different adaptive complexes. The australopithecine data evidence just such evolutionary diversity in adaptation. Delineating and understanding these adaptations, and the total way of life of the early hominids, constitutes a major goal of paleoanthropology and demands an understanding of their locomotor capabilities. The postcranial skeleton of *Australopithecus* has been instrumental in reconstructing early hominid locomotion, and continuing study should fully delineate the pattern of evolution which led to the modern human gait.

TABLE I
Early Hominid Postcranial Fossils[8]
Catalog code:

TM Transvaal Museum	Old. Hom. Olduvai
Sts Sterkfontein	Omo. L and F Omo
SE Sterkfontein Member 5	KNM-ER East Lake Turkana
SK and SKW Swartkrans	AL Hadar (Afar)
MLD Makapansgat	

AXIAL SKELETON
Vertebrae
 cervical:
  SK 854 (C2=axis)
  KNM-ER 164 (C7)
 thoracic:
  Sts 14 & 73
  SK 3981a (T12)
  KNM-ER 164 (T1)
  AL 288-1 (6 thoracics)
 lumbar:
  Sts 14 (6 lumbars)
  SK 853, 3981b (L5)
  L 105-7

AL 288-1 (one)
sacral:
Sts 14
AL 288-1
fragments:
Sts 65 (centrum)
SE 2398
AL 288-1

Costae
Old. Hom. 50 (shaft)
KNM-ER 164b-c
AL 288-1 (numerous fragments)

Joints
Sts 14 (intervertebral and sacroiliac)
AL 288-1 (intervertebral and sacroiliac)

APPENDICULAR SKELETON
Superior Member —
Clavicula
Old. Hom. 48 (formerly Old. Hom. 8) missing both ends
MLD 20 "acromial extremity" NOT HOMINID (equid phalanx? per Day)

Scapulae
Sts 7 glenoid fragment
KNM-ER 1500o left (L) glenoid fragment
AL 288-1 frag. right (R)

Humeri
TM 1517 distal R end (Kromdraai)
Sts 7 proximal R
SK 50 distal half
SK 860 crushed distal end
MLD 14 frag. R distal NOT HOMINID? (per Day)
MLD 39 frag. R distal
Kanapoi Hominid 1 (KP 271) distal L
Old. Hom. 13 distal half of shaft
L 338Y-9 juvenile shaft
Omo 119-73-2718 prox. L
KNM-ER: 739 R, missing just proximal end
740 distal L
1473 prox. R
15001 distal supracondylar portion
1504 distal R
1591 prox. R
3735 distal R
AL 225-4 distal
AL 288-1 prox. R and distal L

Radii
Sts 68 prox. NOT HOMINID (baboon? per Day)
SK 18b prox. fragment
MLD: 15 frag. R
16 prox. R
32 L prox. frag.
Old. Hom. 49 R shaft (previously known as FLK NN 134)
Omo 75s-70-1317 prox.
KNM-ER: 803d L shaft frag.
803p frag.
1500e R. prox.
1500k R frag.
AL 288-1 prox. and distal R, and distal L

Ulnae
TM 1517 prox. R (Kromdraai)
Old. Hom. 36
L 40-19 complete R
Omo 141-72-23 prox. L

KNM-ER: 803c L shaft
1500f R prox.
1500i prox. R shaft
AL 288-1 prox. and distal R and L

Manus
TM 1517h L metacarpal II, prox. hand phalanx (Kromdraai)
— metacarpal is probably a R metatarsal and not necessarily hominid (Day and Scheuer 1973; Robinson 1972)
TM 1526 R capitate (Sterkfontein)
SK 84 L metacarpal I (the canine tooth which has been listed as SK 84 is correctly catalogued as SK 845)
SK 85 L metacarpal IV
SKW 14147 metacarpal V
Old. Hom. 7: a terminal R pollical phalanx, juvenile
b terminal phalanx, juvenile
c terminal phalanx, juvenile
d intermediate R juvenile phalanx, II
e intermediate R juvenile phalanx, IV
f intermediate R juvenile phalanx, III
g intermediate R juvenile phalanx, V
h prox. phalanx, juvenile?
i prox. phalanx, juvenile?
o base, metacarpal II, R, juvenile?
p R juvenile scaphoid
q R juvenile trapezium
r L juvenile capitate
(all other formerly included in Old. Hom. 7 now removed as NOT HOMINID, per Day 1976a)
Old. Hom. 8
Old. Hom. 18 phalanx
Omo 18-70-1848 L intermediate phalanx, III
Omo 28-73-4570 intermediate phalanx, III
KNM-ER 164b-c two phalanges
KNM-ER 803t base of metacarpal IV
AL 288-1 L capitate, two phalanges

Joints
a. Glenohumeral:
Sts 7
KNM-ER 1500
AL 288-1
b. Elbow:
TM 1517 (Kromdraai)
AL 288-1
c. Hand:
partial — AL 288-1 and new material from AL 333

Inferior Member —
(Os) Coxae
TM 1605 small iliac frag., juvenile? (Kromdraai)
Sts 14
Sts 65 R ilio-pubic frag.
SK: 50 damaged R ilium/ischium
1590d
3155b R iliac fragment, adolescent
MLD: 7 L ilium
8 R ischium (MLD 7/8 one individual, adolescent?)
21 frag. ilium
25 adolescent L ilium
35 infant ilium frag.?
AL 288-1 L
(Old. Hom. 28 L, minus pubis *Homo erectus*)
(KNM-ER 3228 R cf. *Homo erectus*)

Femora
TM 1513 distal L (Sterkfontein)
TM 3601 distal R (locality?)
Sts: 14 damaged L

34 distal R
65 prox.
SK: 82 prox. R   rag.
83 prox. frag.
97 prox. R
1590d
MLD 17 head only
Old. Hom. 20 prox. shaft and neck, L
Old. Hom. 28 L shaft (*Homo erectus*)
L 754-8
KNM-ER: 736 L shaft
737 L shaft
738 prox. L
803a
?813b (see under tibiae)
815 prox. L
993 distal R
999 L
1463 R shaft
1465 prox. L
1472 R
1475a prox. R
1475b frag. shaft
1481a L
1500b distal L
1500d L neck
1503 prox. R
1505 prox. L
1592 distal R
1807 R shaft
1809 R shaft
1822 frag.
3728 L prox. end and shaft
3730 distal frag.

AL: 128-1 L prox. frag.
129-1a (or 129-1) R distal
129-1c (or 129-3) R prox. frag.
211-1 R prox. frag.
211-1 R shaft
288-1 L

Tibiae

Old. Hom. 34 part of shaft
Old. Hom. 35 L shaft and distal end (formerly OH 6)
KNM-ER: 741 prox. L
803b L shaft
803g frag. prox. end
813b frag.?
1471 prox. R
1476b & c prox. L
1481b prox. L
1481c distal L
1500a prox. L
1500c distal L
1500h R distal
1500j R shaft frag.
1500r crushed frag.
1810 prox. L
2594a prox. L
2594b shaft frag.
2596 distal frag.
AL 129-1b (or 129-2) R prox.
AL 288-1 prox. and distal R

Fibulae

Old. Hom. 35 L shaft and distal end (formerly Old. Hom. 6)
KNM-ER: 803n L frag.
803o R shaft frag.
1481 distal L

1500g R distal
AL 288-1 R distal

Pes

TM 1517 R talus and distal phalanx (Kromdraai)
Old. Hom. 8 7 tarsals, 5 metatarsals, 2 phalanges
Old. Hom. 10 distal hallucial phalanx
Old. Hom. 43 metatarsal
L 576-18 distal R hallucial phalanx
F 511-6 hominid metatarsal III
KNM-ER: 803e L talus
803f base, L metatarsal V
803j L metatarsal III
803k intermediate phalanx, III
803l intermediate phalanx, II
803m terminal phalanax, III or IV
803q frag. prox. phalanx of hallux
813a R talus
997 L metatarsal III
1464 R talus
1476a L talus
1500m base, R metatarsal III
1815 R talus
AL 288-1 R talus

Joints
a. Hip joint:
Sts 14
AL 288-1
b. Knee joint:
KNM-ER 1481a/b
KNM-ER 1500a/b
AL 129-1a/1b
AL 288-1

PARTIAL TO SOMEWHAT COMPLETE
ASSOCIATED SKELETONS

(*one* individual in *direct* association)
TM 1517 (Kromdraai)
Sts 14
KNM-ER: 803 (cf. *Homo erectus?*)
1481a-d (lower leg partial skeleton)
1500 (*Australopithecus* aff. *africanus*)
1808
AL 288-1
AL 333: at least several individuals represented by numerous cranial and postcranial fragments (undescribed and unpublished)

Notes

[1]"Early hominid" here includes all species of *Australopithecus*, and early members of the genus *Homo* (*Homo* sp. indet., *Homo habilis*). "Australopithecine" here refers to just the species of *Australopithecus* (*A. africanus, A. robustus, A. boisei*).

[2]There is only one clavicle from Olduvai, formerly catalogued as Old. Hom. 8, a paratype of *Homo habilis* (Leakey, Tobias, and Napier 1964); it is now catalogued as Old. Hom. 48.

[3]The Sts 7 scapula was recently prepared by E. Vrba, aiding Ciochon and Corruccini in assessing some key anatomical landmarks (especially the coracoid process).

[4]Estimated total length - 328 mm (McHenry et al. 1976), compared to 290-310 mm for Sts 7 (Broom et al. 1950), and 235 mm for AL 288-1 (Johnson and Taieb 1976).

[5]I have made a measurement (on casts) of minimum width of the ilium (anteroposterior), from the anterior-most point of the greater sciatic notch to the most posterior point in the interspinous notch of the anterior iliac margin. I then formed a ratio of minimum iliac width over ischial length, and determined for:

Sts 14- $\dfrac{45}{43}$ mm X 100= 105%

SK 50- $\dfrac{61}{60}$ mm X 100= 102%

Correlating for size differences in this manner places both Sts 14 and SK 50 in approximately the same range.

[6]The australopithecine femoral neck is relatively long, whether one measures length via (a) the distance from the intertrochanteric crest to the subcapital sulcus, standardized via femoral shaft diameter just distal to the greater trochanter (Wood 1976), or (b) the length of a line, perpendicular to the centroidal axis of the shaft, from the most lateral point of the greater trochanter to its tangential intersection with the most cephalward part of the femoral head (biomechanical femoral neck length, per Lovejoy 1975).

[7]Using Lovejoy's (1975) sample of 128 modern *Homo sapiens* tali (x=19°, 1 S.D. =3.4°), the horizontal neck angle of Old. Hom. 8 lies just within and TM 1517 just beyond three standard deviations from the modern mean.

[8]For cataloguing by site, a selected bibliography includes Day (1976a & b), Howell and Coppens (1974), Johanson and Taieb (1976), Leakey and Isaac (1976), M. Leakey (1971), Oakley and Campbell (1967), and Robinson (1972).

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