



Spring 2013

Functional Perspectives On The Evolution Of The Hominin Pedal Arch And Obligate Bipedality: The Al 333-160 Fourth Metatarsal From Hadar, Ethiopia

Paul Mitchell
University of Pennsylvania

Follow this and additional works at: http://repository.upenn.edu/anthro_seniortheses

 Part of the [Anthropology Commons](#)

Recommended Citation

Mitchell, Paul, "Functional Perspectives On The Evolution Of The Hominin Pedal Arch And Obligate Bipedality: The Al 333-160 Fourth Metatarsal From Hadar, Ethiopia" (2013). *Anthropology Senior Theses*. Paper 140.

This paper is posted at ScholarlyCommons. http://repository.upenn.edu/anthro_seniortheses/140
For more information, please contact repository@pobox.upenn.edu.

Functional Perspectives On The Evolution Of The Hominin Pedal Arch And Obligate Bipedality: The AL 333-160 Fourth Metatarsal From Hadar, Ethiopia

Abstract

Based on comparisons to non-statistically representative samples of humans and two great ape species (common chimpanzees *Pan troglodytes* and lowland gorillas *Gorilla gorilla*), Ward et al. (2011a) concluded that a complete hominin fourth metatarsal (4th MT) from Hadar, AL 333-160, belonged to a committed terrestrial biped with fixed transverse and longitudinal pedal arches, which was no longer under selection favoring substantial arboreal behaviors. According to Ward et al., the Hadar 4th MT had (1) a torsion value indicating a transverse arch, (2) sagittal plane angles between the diaphyseal long axis and the planes of the articular surfaces indicating a longitudinal arch, and (3) a narrow mediolateral to dorsoplantar base ratio, an ectocuneiform facet, and tarsal articular surface contours all indicating a rigid foot without an ape-like midtarsal break. Comparisons of the Hadar 4th MT characters to those of statistically representative samples of humans, all five great ape species, baboons and proboscis monkeys show that none of the correlations Ward et al. make to localized foot function were supported by this analysis. The Hadar 4th MT characters are common to catarrhines that have a midtarsal break and lack fixed transverse or longitudinal arches. Further comparison of the AL 333-160 4th MT length, and base, midshaft and head circumferences to those of catarrhines with field collected body weights show that this bone is uniquely short with a large base. Its length suggests the AL 333-160 individual was a poor leaper with limited arboreal behaviors and lacked a longitudinal arch. Its large base implies cuboid-4th MT joint mobility. A relatively short 4th MT head circumference ii indicates AL 333-160 had small proximal phalanges with a restricted range of mobility. Overall, AL 333-160 is most similar to the 4th MT of eastern gorillas, a slow moving quadruped that sacrifices arboreal behaviors for terrestrial ones. This study highlights evolutionary misconceptions underlying the practice of using localized anatomy and/or a single bony element to reconstruct overall locomotor behaviors and of summarizing great ape structure and behavior based on non-statistically representative samples of only a few living great ape species.

Disciplines

Anthropology

FUNCTIONAL PERSPECTIVES ON THE
EVOLUTION OF THE HOMININ PEDAL ARCH AND
OBLIGATE BIPEDALITY: THE AL 333-160 FOURTH
METATARSAL FROM HADAR, ETHIOPIA

By
Paul Mitchell
In
Anthropology

Submitted to the
Department of Anthropology
University of Pennsylvania

Thesis Advisor: Dr. Janet Monge

2013

Table of Contents

Abstract.....	i
Introduction.....	1
Materials and Methods.....	3
Results.....	8
Discussion.....	17
Conclusions	33
Appendix A.....	36
Appendix B.....	39
Figures.....	43
Tables.....	53
Acknowledgements.....	68
References Cited.....	69

Abstract

Based on comparisons to non-statistically representative samples of humans and two great ape species (common chimpanzees *Pan troglodytes* and lowland gorillas *Gorilla gorilla*), Ward et al. (2011a) concluded that a complete hominin fourth metatarsal (4th MT) from Hadar, AL 333-160, belonged to a committed terrestrial biped with fixed transverse and longitudinal pedal arches, which was no longer under selection favoring substantial arboreal behaviors. According to Ward et al., the Hadar 4th MT had (1) a torsion value indicating a transverse arch, (2) sagittal plane angles between the diaphyseal long axis and the planes of the articular surfaces indicating a longitudinal arch, and (3) a narrow mediolateral to dorsoplantar base ratio, an ectocuneiform facet, and tarsal articular surface contours all indicating a rigid foot without an ape-like mid-tarsal break. Comparisons of the Hadar 4th MT characters to those of statistically representative samples of humans, all five great ape species, baboons and proboscis monkeys show that none of the correlations Ward et al. make to localized foot function were supported by this analysis. The Hadar 4th MT characters are common to catarrhines that have a midtarsal break and lack fixed transverse or longitudinal arches. Further comparison of the AL 333-160 4th MT length, and base, midshaft and head circumferences to those of catarrhines with field collected body weights show that this bone is uniquely short with a large base. Its length suggests the AL 333-160 individual was a poor leaper with limited arboreal behaviors and lacked a longitudinal arch. Its large base implies cuboid-4th MT joint mobility. A relatively short 4th MT head circumference

indicates AL 333-160 had small proximal phalanges with a restricted range of mobility. Overall, AL 333-160 is most similar to the 4th MT of eastern gorillas, a slow moving quadruped that sacrifices arboreal behaviors for terrestrial ones. This study highlights evolutionary misconceptions underlying the practice of using localized anatomy and/or a single bony element to reconstruct overall locomotor behaviors and of summarizing great ape structure and behavior based on non-statistically representative samples of only a few living great ape species.

Introduction

After Piltown man was shown to be a fraud (Spencer, 1990), many paleoanthropologists embraced *Australopithecus* as an exclusive member of the human lineage, ancestral to the genus *Homo* (Keith, 1947, Le Gros Clark, 1946, Le Gros Clark, 1947, Le Gros Clark, 1950, Le Gros Clark, 1955a, Le Gros Clark, 1955b and Mayr, 1950). Initially, studies on *Australopithecus* locomotor anatomy were equivocal as to the range of behaviors it practiced (Kimbel and Delezene, 2009). At the time, nearly all agreed that *Australopithecus* was not a human-like exclusive, obligate biped (Day, 1969, Napier, 1964, Robinson, 1962, Robinson, 1965 and Robinson, 1967). The possibility that some of its member species were terrestrial quadrupeds was seriously entertained (Kern and Straus, 1949 and Straus, 1948). In the 1970s, with the discovery of the Lake Turkana hominin fossils and misidentification of *Homo* for *Australopithecus* femora (Kennedy, 1985, Lovejoy, 1975, Lovejoy, 1978 and Walker, 1973), a new generation of paleoanthropologists advanced the belief that *Australopithecus* was a habitual terrestrial biped, and possibly a more efficient one than modern humans (Lovejoy, 1975, Lovejoy, 1978, Robinson, 1972a and Robinson, 1972b). While original descriptions of Hadar *Australopithecus* continued to advance this view, principally in attempts to justify a *Homo* ancestry (Johanson and Taieb, 1976, Johanson et al., 1976 and Taieb et al., 1974), some workers noted a number of African ape-like characters in the Hadar *Australopithecus* lower limb associating them to arboreal behaviors (McHenry, 1986, Senut and Tardieu, 1985, Stern and Susman, 1983, Susman et al., 1984, Tardieu, 1979 and Tardieu, 1983). Thus, the two opposing views of *Australopithecus* behavior that still prevail to this day crystallized: (1) *Australopithecus* was a habitual terrestrial

biped unlikely to practice arboreal behaviors (Latimer, 1991, Latimer and Lovejoy, 1989, Latimer and Lovejoy, 1990, Lovejoy, 2005a, Lovejoy, 2005b and Ward et al., 2011a), and (2) *Australopithecus* was a part-time, facultative terrestrial biped that commonly engaged in arboreal behaviors (McHenry, 1991, Stern, 2000 and Susman et al., 1984). Proponents of these two opposing views, however, sometimes failed to test their hypotheses through studies of comparative and functional anatomy. Instead, they associated localized anatomy exclusively to bipedality when the anatomy occurred in humans but not in common chimpanzees, and exclusively to arboreality when the anatomy occurred in common chimpanzees, but not humans (Lauder, 1995, Sarmiento, 1998 and Sarmiento et al., 2002).

A recent comparative study of a complete fourth metatarsal (4th MT) from Hadar (AL 333-160) by Ward et al. (2011a) follows this tradition. Based on its (1) ectocuneiform facet, (2) torsion, (3) cuboid facet curvature and proportions, and (4) sagittal plane angles made by its diaphyseal long axis with its proximal and distal articular planes, Ward et al. claimed the AL 333-160 4th MT showed Hadar *Australopithecus* had fixed transverse and longitudinal pedal arches, and was a habitual terrestrial biped unlikely to be under selection for “substantial arboreal behaviors (Ward et al., 2011a:753)”. The study, however, only compares Hadar 4th MT characters to those of ten common chimpanzees (*P. troglodytes*), ten lowland gorillas (*G. gorilla*) and ten modern humans. It does not include three out of five great ape species, and fails to test for alternate behaviors which may be associated to or result in these putatively bipedal characters. Moreover, the study also fails to demonstrate a causal relationship between the cited characters and the functions ascribed to them, and ignores much of

the literature which quantifies African ape-like characters in the Hadar foot (Berillon, 2003, Berillon, 2004, Deloison, 2004, Sarmiento and Marcus, 2000, Stern and Susman, 1983 and Susman et al., 1984). Considering that evolution proceeds as behavioral shifts through structural continuity, and necessitates localized anatomical structure to have at least a duality of function (Darwin, 1859), Ward et al. (2011a) claims of bipedal exclusivity for so many 4th MT characters require testing. In this regard, it is the object of this study to analyze the Hadar 4th MT with a more complete data set of great apes and primates that allows testing of the claimed bipedal exclusivity of its characters. It is hoped that through such a comparison, better statistically and taxonomically supported conclusions concerning Hadar *Australopithecus* locomotor behaviors can be achieved.

Materials and methods

Australopithecus afarensis 4th MT (AL 333-160) measurements as reported by Ward et al. (2011a) were compared to those of adult male and female humans, eastern gorillas, western gorillas, bonobos, chimpanzees, orangutans, baboons, and proboscis monkeys housed in the following museums: National Museum of Natural History, Washington, DC (USA), American Museum of Natural History, New York (USA), Academy of Natural Sciences, Philadelphia (USA), Penn Museum, Philadelphia (USA), Museum of Comparative Zoology, Harvard University, Cambridge (USA), Cleveland Museum of Natural History, Cleveland (USA), Cotton-Powell Museum, Kensington (UK), British Museum of Natural History, London (UK), Royal Institute of Natural Sciences, Brussels (Belgium), Royal Museum of Central Africa, Tervuren (Belgium), Humboldt Zoology Museum, Berlin (Germany), Zoology Museum, University of Amsterdam

(Netherlands), Swedish Museum of Natural History, Stockholm (Sweden), National Museum of Kenya, Nairobi (Kenya), Raymond Dart Collection, Department of Anatomy, Witwatersrand University (RSA).

Right 4th MTs from comparative samples were measured for length, and for mediolateral and anteroposterior dimensions of the base, midshaft, and head, according to methods described and figured by Sarmiento (1994) and Sarmiento and Oates (2000). Summary statistics for these measures are found in Table 1. Metatarsal length was taken as a maximum length. Midpoint of this length was taken as the level for measuring midshaft dimensions. All length measures were taken with a digital caliper accurate to the 0.01 mm and collected directly into a Lotus or Excel spreadsheet where they were recorded to an accuracy of 0.1 mm. For purpose of comparison, base (b), midshaft (ms) and head (h) dorsoplantar (dp) and mediolateral (ml) diameters were used to calculate base, midshaft and head circumferences where base circumference = $2dpb + 2mlb$, midshaft circumference = $\text{Pi}(msml + msdp)/2$, where $\text{Pi} = 3.142$, and head circumference = $2hdp + 2hml$. Measured individuals, with the exception of gorillas and humans, were grouped according to species with equal or subequal numbers of adult males and females comprising each group. Chacma (*Papio c. ursinus*), anubis, (*P. c. anubis*) and yellow baboons (*P. c. cynocephalus*) were compared at the generic level (*Papio* used hereafter). Bornean and Sumatran orangutans were considered monospecific (*Pongo* used hereafter). Given marked size-differences between male and female gorillas, and differences in tree use among the two eastern gorilla subspecies (*G. b. beringei*, the mountain gorilla, and *G. b. graueri*, Grauer's gorilla; see Sarmiento et al., 1996 and Sarmiento, 2003), males and females of

each eastern gorilla subspecies were considered as separate groups. Human males and females were considered separately given the closer similarity in body size between human females and AL 333-160. Due to loss or breakage of comparative material, not every individual yielded a complete set of measurements for the 4th right metatarsal. In these cases the left bone was measured. When both bones did not yield a complete set of measures, whichever measures were available on the most complete metatarsal were recorded.

Fourth metatarsal length was plotted against its base, midshaft and head circumferences with bivariate plots for each group compared by means of density ellipses set at a 95% confidence interval (Fig. 1, Fig. 2 and Fig. 3). Except for fossils, the datum points of each group are removed for clarity. Table 9 and Table 10 present data for the linear regressions of the density ellipses. For bivariate plots, 4th MT measurements of the following fossils as reported in the literature were also included: Skhul 4 (*H. sapiens*; Trinkaus, 1975), La Ferrassie 1 (*H. neanderthalensis*; Trinkaus, 1975), LB 1/24 (*H. floresiensis*; Jungers et al., 2009). StW 485 (*Australopithecus africanus*) measurement was taken on the original fossil and provided by Esteban Sarmiento (personal communication). OH 8 (*H. habilis*) measurement was taken on a cast of the original fossil. An estimate of OH8 4th MT length was arrived at from the length of the damaged OH8 4th MT (OH8D), and the average ratio in human 4th MTs of the proximodistal length of the distal epiphysis (PDE) divided by the length from base to distal end of the diaphysis (BEL), and also by the corresponding ratio in StW485 where OH8 estimated length = OH8D(1 + PDE/BEL). All statistical analyses were undertaken with the statistical program JMP 9.0.

Fourth metatarsals were also measured for base-diaphysis angles and torsion after Sarmiento (1994) and Ward et al. (2011a) (see Appendix A). Angles were recorded using a carpenter's angle accurate to a degree. Summary statistics for base-diaphysis angle and torsion measures are provided in Table 12 and presented in box plot form in Fig. 4 and Fig. 5, respectively. Fourth metatarsals were also examined for the presence or absence of the ectocuneiform facet (Fig. 6). The latter entailed rearticulating the cuboid, ectocuneiform and the 4th MT to verify if there was a true facet. This facet was observed only in *H. sapiens*, *G. gorilla*, and *Papio*. Human and lowland gorilla sexes were grouped together for ectocuneiform facet presence (Table 13), since no significant sexual dimorphism for this feature was detected in the sample. Frequencies of the ectocuneiform facet for these groups are summarized in Table 13, where the number of indeterminate facets is also noted. Although larger samples of humans and gorillas were examined, representative sample sizes were pared to $n = 19$ in humans and gorillas to facilitate comparisons using a two-tailed Fisher's exact test. Differences in ectocuneiform facet occurrence among the compared groups were taken to be statistically significant when P values were less than or equal to 0.05 ($P \leq 0.05$; Table 14). For comparison to Ward et al. (2011a), summary statistics of the individual measures and ratios of dorsoplantar vs. mediolateral diameter of the 4th MT base in AL 333-160, humans, great apes, baboons and proboscis monkeys are also reported (Table 15). Fig. 7 presents a box plot representation of the DP/ML ratio data. Only individuals with full epiphyseal fusion of long bones, and eruption of canine and third molars were considered for average, standard deviation, and range of variation

comparisons, and included in summary statistics, bivariate plots, linear regression statistics, and box plots.

To further determine differences and similarities between AL 333-160 and great ape, human and Old World monkey 4th MTs, a narrow allometric approach was used (Gilbert and Rossie, 2007, Jungers, 1987, Sarmiento and Meldrum, 2011 and Smith, 1980). Spreadsheets containing the primate data were computer searched using the find function to detect overlap with the reported AL 333-160 values. All corresponding measurements for those primate individuals which have any one measured value overlapping with AL 333-160 or the AL 333 foot bone measures, including body weight, and phalangeal length are listed in Table 2, Table 3, Table 4, Table 5, Table 6, Table 7 and Table 8. To increase size-range, allometric comparisons may include sub-adult (sa; non-fully erupted canine and M3) and juvenile individuals (juv; M3 fully enclosed in crypt with M1 and M2 crowns developed) for all groups, and are noted accordingly (see Table 2). Phalangeal lengths and 5th MT measures of AL 333 fossils foot bones (Table 8) are included in the narrow allometry comparisons to further test AL 333 foot function and considered in the discussion.

Human body weights reported were taken at death and are from the Dart Collection records, Department of Anatomy, University of the Witwatersrand and Hamann-Todd Collection records, Cleveland Museum of Natural History. Because human weights at death may reflect weight loss due to infirmity, calculated weights based on femoral head dimensions after methods described by McHenry (1992) are also reported (see Table 2). Unless otherwise specified, body weights for non-human primates compared are from notes collected by Esteban Sarmiento and/or from

museum tags, all of field collected specimens. As noted for some non-human primates, weight was calculated based on sex and species specific regressions of lumbar vertebral volumes vs. known body weights after methods described in Sarmiento et al. (1996).

Narrow allometry tables list only those individuals with a 4th MT measure similar to AL 333-160 where similar is taken to be values which are (1) ± 1 mm of the AL 333-160 value for 4th MT length, and head and base circumferences; (2) ± 0.5 mm for midshaft circumference and (3) ± 0.1 mm for linear mediolateral and dorsoplantar 4th MT measures. Values of comparative measures similar to those of the AL 333-160 are listed in bold type. Specimens, which display two or more 4th MT measures similar to AL 333-160 are presented in Table 6. Table 7 also compares 4th MT measures in specimens which have a body weight within the range of McHenry's (1992) estimated *A. afarensis* body weight of 44.6–60.1 kg, as based on the male human and male hominoid regressions, respectively. Considering that the majority of AL 333 fossils which yield weight estimates in McHenry's study are supposed males and are the larger of the two sizes found among the AL 333 hominoid remains, it is likely that AL 333-160 found in these deposits also corresponds to the larger (male) individual.

Results

4th MT length: summary statistics and narrow allometry

The AL 333-160 4th MT length is similar to the mean 4th MT length of female *G. b. graueri* (Table 1). Of those groups with 4th MT lengths that overlap the AL 333-160 value, the AL 333-160 length is one to two standard deviations below the mean 4th MT length of human females, *G. b. beringei* females, *G. b. graueri* males, and male and

female *P. troglodytes*, *N. larvatus* and *Papio*. The AL 333-160 length is more than two standard deviations below the mean of human males. *G. b. beringei* males, and male and female *G. gorilla*, *P. paniscus*, *Pongo* and *N. larvatus* show no overlap with the AL 333-160 length value.

Among specimens with similar 4th MT lengths, the estimated AL 333-160 body weight range is greater than that of all monkeys, pygmy chimpanzees, and a juvenile orangutan, within the body weight range of common chimpanzees and humans, and below the range of all eastern gorillas (Table 2). AL 333-160 has an absolutely larger base circumference than all compared individuals. The midshaft circumference of the Hadar fossil falls within the range of humans and eastern gorillas and greater than that of all other groups. AL 333-160 head circumference is within the human values, smaller than all eastern gorillas and common chimpanzees, and larger than all other comparative specimens.

4th MT base circumference: summary statistics and narrow allometry

The base circumference of AL 333-160 is similar to the corresponding mean value of male *H. sapiens* (Table 1). It is below the range of male *G. b. beringei* and above that of female *G. b. graueri*, *P. paniscus*, *N. larvatus*, and *Papio*. Among those groups with 4th MT base circumferences overlapping the AL 333-160 value, the AL 333-160 value is one or two standard deviations above the corresponding mean values of female *H. sapiens*, female *G. b. beringei*, female *G. gorilla*, and *Pongo*, but below the corresponding mean value of male *G. b. graueri*. The AL 333-160 value is more than two standard deviations above that of *P. troglodytes* and below that of male *G. gorilla*.

Among specimens with similar base circumferences, the body weights of all humans, one female western gorilla, and one female orangutan fall within the AL 333-160 range, but all other specimens have greater body weights (Table 3). AL 333-160 has the shortest 4th MT length. Its midshaft circumference falls within the range of all comparative specimens except the single male eastern gorilla. The head circumference is smaller than all great apes and within the human range.

4th MT midshaft circumference: summary statistics and narrow allometry

The midshaft circumference of AL 333-160 4th MT is similar to the corresponding mean value in *Pongo* (Table 1). It is well below the range of the midshaft circumference values in male *H. sapiens* and male *G. b. beringei* and above the range for this value in *P. paniscus*, *N. larvatus*, and *Papio*. Among those groups that overlap the AL 333-160 midshaft circumference value, the AL 333-160 value is from one to two standard deviations below the mean value of female *H. sapiens*, female *G. b. beringei*, male *G. b. graueri*, and female *G. gorilla*, and above the mean value of female *G. b. graueri* and *P. troglodytes*. The AL 333-160 midshaft circumference value is significantly smaller than the mean value in male *G. gorilla*.

Among the specimens that share a similar midshaft circumference with the Hadar fossil, AL 333-160's body weight falls in the human and common chimpanzee ranges. It is greater than that of the single female orangutan and less than that of all gorillas except a single female western gorilla that has a lighter body weight (Table 4). The 4th MT length of AL 333-160 is shorter than all specimens with similar midshaft circumferences except for a single female human that has a similar length, and two female eastern gorillas, one who shares a similar length and one who has a shorter

length. The AL 333-160 base circumference is larger than in all specimens except a single large female western gorilla. The AL 333-160 head circumference is larger than in all humans but smaller than in all other specimens.

4th MT head circumference: summary statistics and narrow allometry

Among those groups with values that overlap the AL 333-160 head circumference, the AL 333-160 value is close to the mean of female *H. sapiens* and *P. paniscus*, two standard deviations below the mean of male *H. sapiens*, female *G. b. graueri* and *P. troglodytes* and is more than two standard deviations above the mean for *Papio* (Table 1). The head circumference of AL 333-160 is below the range of variation of the corresponding measure in male and female *G. b. beringei*, male *G. b. graueri*, male and female *G. gorilla*, and *Pongo* and above the range of values for *N. larvatus*.

Among specimens with similar head circumferences, humans and a female eastern gorilla share similar body weights, a male common chimpanzee has a larger body weight, and all others have smaller body weights (Table 5). AL 333-160 has a shorter 4th MT length than all specimens except for a single eastern gorilla and common chimpanzee. The Hadar fossil has a larger base circumference than all comparative specimens except of a single male human with a similar value. The midshaft circumference of AL 333-160 is larger than in all great apes and monkeys and smaller than all humans except a single female human with which it shares a similar value.

4th MT multiple shared values: narrow allometry

Those specimens which share similar 4th MT length and midshaft circumference with the Hadar fossil, all have smaller base circumferences (Table 6). Eastern gorillas exceed the AL 333-160 body weight range and head circumferences, while the human has a body weight within this range but a smaller head circumference. One male human has a similar base and head circumference and body weight, but has a markedly longer 4th MT length and larger midshaft. The orangutan and western gorilla which share base and midshaft circumferences with AL 333-160 have greater body weights, longer 4th MT lengths, and larger head circumferences. AL 333-160 also shares similar dorsoplantar and mediolateral head measures with a *P. paniscus* and *P. troglodytes* specimen.

Body weight: narrow allometry

AL 333-160 has a shorter 4th MT length than all specimens with a body weight in its estimated range except a single female eastern lowland gorilla with a shorter 4th MT. AL 333-160 shares a similar base circumference with a female gorilla and has a base circumference larger than all other specimens except a larger juvenile male western gorilla and male human (Table 7). The midshaft circumference of AL 333-160 falls within the ranges of common chimpanzees and orangutans, is larger than the female eastern gorilla and pygmy chimpanzees, and is smaller than humans and western gorillas. AL 333-160 has a smaller head circumference than western gorillas, common chimpanzees, orangutans, and male humans and is either in the range of or similar to the head circumference of pygmy chimpanzees, a female eastern gorilla, and a female human.

4th MT base circumference vs. length

AL 333-160 is above the regression line calculated for base circumference vs. length for all groups except *G. b. beringei* males (Table 9 and Fig. 1). Although OH8 and StW 485 have lengths which are similar to the AL 333-160 value, they have noticeably shorter base circumferences, with StW 485 having the shortest base circumference among the fossils. The Skhul 4 base circumference is slightly longer, but its 4th MT is considerably longer than AL 333-160. La Ferrassie has both a longer base circumference and a length.

AL 333-160 is within the 95% density ellipse for *G. b. graueri* males and on the border of the density ellipse for *G. b. graueri* females, *G. b. beringei* females, and *H. sapiens* females (Fig. 1). It shares the *G. b. graueri* male density ellipse with OH8, La Ferrassie, and Skhul 4. It shares with OH8 and StW 485 the *G. b. graueri* female, *G. b. beringei* female, and *H. sapiens* female density ellipses.

4th MT midshaft circumference vs. length

AL 333-160 is above the regression line calculated for midshaft circumference vs. length for all groups except for *G. b. graueri* males, *G. b. beringei* males and females, and *H. sapiens* males and females (Table 10 and Fig. 2). AL 333-160 and StW 485 closely overlap showing similar values, while OH8 has a slightly longer circumference and LB 1/24 has a slightly shorter length. Skhul 4 and La Ferrassie 1 both have longer lengths and longer midshaft circumferences than the other four fossils.

AL 333-160 is within the 95% density ellipse for *G. b. beringei* females, *G. b. graueri* females, *G. b. graueri* males, and *H. sapiens* females (Fig. 2). It shares (1) the *G. b. beringei* female density ellipse with StW 485, OH8, and LB 1/24; (2) the *G. b. graueri* female density ellipse with StW 485 and LB 1/24; and (3) the *G. b. graueri* male and *H. sapiens* female density ellipse with StW 485, OH8, LB 1/24, La Ferrassie 1, and Skhul 4.

4th MT head circumference vs. length

AL 333-160 is below the regression line calculated for head circumference vs. length for all groups except for female *H. sapiens*, *P. paniscus*, *Pongo*, *N. larvatus*, and *Papio* (Table 11 and Fig. 3). Both Skhul 4 and La Ferrassie 1 have noticeably longer lengths and longer head circumferences, with La Ferrassie 1 having the longest head circumference among the fossils.

AL 333-160 is within the 95% density ellipse for *G. b. berginei* females, *G. b. graueri* females, *H. sapiens* females, *P. paniscus*, and *P. troglodytes* (Fig. 3). It shares the *P. troglodytes* density ellipse with Skhul 4. It does not share a density ellipse with La Ferrassie 1, which has both longer length and head circumference.

4th MT base-diaphysis angle

The AL 333-160 base-diaphysis angle is within the range of variation of the corresponding measure in male and female *H. sapiens*, male *G. b. beringei*, and *P. troglodytes*, but is below the range of variation of this measure in male and female *G. gorilla*, *P. paniscus*, *Pongo*, and *Papio* (Table 12 and Fig. 4). Among those groups,

which overlap the AL 333-160 base-diaphysis angle value, this value is two standard deviations greater than the mean value for male *H. sapiens*, and one standard deviation greater than the mean value for female *H. sapiens*. The AL 333-160 value is one standard deviation smaller than the mean value for male *G. b. beringei*, and three standard deviations smaller than the mean *P. troglodytes* value (Table 12).

4th MT torsion

The AL 333-160 4th MT torsion is within the range of variation of male and female *H. sapiens*, male *G. b. beringei*, *P. troglodytes*, *P. paniscus*, *Pongo*, and *Papio*, but is greater than the maximum value for male and female *G. gorilla*, and *P. troglodytes* (Table 12 and Fig. 5). Among those groups overlapping the AL 333-160 torsion value, the latter is (1) two standard deviations smaller than the mean value of female *H. sapiens*; (2) one standard deviation smaller than the mean values of male *H. sapiens* and *Papio*; (3) two standard deviations greater than the mean values of male *G. b. beringei* and *P. paniscus*, and (4) three standard deviations greater than the mean *Pongo* and *P. troglodytes* values (Table 12).

4th MT ectocuneiform facet occurrence

The 4th MT ectocuneiform facet has a relatively high incidence of occurrence in humans (57.89%) and baboons (47.37%) but is less frequently present in gorillas (5.26%) (Table 13). There are significant differences in facet occurrence among (1) humans, gorillas, and baboons; (2) humans and gorillas; (3) baboons and gorillas, but not among baboons and humans (Fig. 6 and Table 14).

4th MT base dorsoplantar and mediolateral measures and ratios

The AL 333-160 dorsoplantar diameter is within the range of all groups sampled with exception of female *G. b. graueri*, *P. paniscus*, *P. troglodytes*, *N. larvatus*, and *Papio*, all of which have values less than that of AL 333-160 (Table 15). Males of *H. sapiens*, *G. b. beringei*, *G. b. graueri*, and *G. gorilla* have ranges for dorsoplantar diameter which overlap the AL 333-160 value, but the mean value of each of these groups is one or two standard deviations above the AL 333-160 value. Females of *G. b. beringei*, and *G. gorilla*, and all *Pongo* also have overlapping values with AL 333-160, but their means are one to two standard deviations below the AL 333-160 value. *H. sapiens*, females have mean values one standard deviation below the AL 333-160 value.

The AL 333-160 mediolateral base diameter is within the range of all sampled groups except for male *G. b. beringei*, which has values greater than that of AL 333-160, and of *P. paniscus*, *N. larvatus*, and *Papio*, all of which have values less than that of AL 333-160 (Table 15). Among those groups with ranges that overlap the AL 333-160 value, (1) female *G. b. beringei*, female *G. gorilla*, and *Pongo* have mean mediolateral diameters within ± 0.5 mm of AL 333-160 value, (2) males of *G. b. graueri* and *G. gorilla* have mean values two standard deviations above the AL 333-160 value, and (3) male and female *H. sapiens*, female *G. b. graueri*, and *P. troglodytes* have mean values between one and two standard deviations above the AL 333-160 value.

The AL 333-160 4th MT DP/ML base ratio overlaps the corresponding ratio of every group sampled (Table 15 and Fig. 7) with the exception of female *G. b. beringei*. In the latter group the individual with the highest ratio shows a value that

is less than one percent smaller than the AL 333-160 ratio. The AL 333-160 value is (1) two standard deviations greater than the mean ratio for male and female *G. b. beringei*, male *G. b. graueri*, *P. paniscus*, *P. troglodytes*, and *Pongo*; (2) one standard deviation greater than the mean for female *G. b. graueri* and male and female *G. gorilla*; (3) one standard deviation smaller than the mean for *N. larvatus* and *Papio*; and (4) two standard deviations smaller than the mean ratio for male and female *H. sapiens*.

Discussion

Critical evaluation of the Ward et al. study

Given the small sample sizes in Ward et al. (2011a) ($n = 10$ each for humans, common chimpanzees and lowland gorillas) and limited number of great ape species sampled (two of the five extant species), none of the 4th MT characters claimed to be diagnostic of fixed longitudinal and transverse pedal arches and of bipedality were exclusive to fixed pedal arches or exclusive to habitual bipeds when larger sample sizes and all great ape species were considered. Base-diaphysis angle was more variable than reported by Ward et al. (2011a), with adult humans overlapping mean values for *P. paniscus*, *G. b. beringei*, and *Papio* species (Fig. 4). Fourth metatarsal torsion, showed considerable overlap between the human range and the means of all measured groups (Fig. 5). The ectocuneiform facet, putatively associated in AL 333-160 with lateral planto-dorsal foot rigidity and bipedality (Ward et al., 2011a), was as common in baboons as in humans (Table 13 and Table 14) with half the humans lacking the facet. Notably, humans do not show a uniformly high and distinct dorsoplantar to mediolateral

base ratio (Table 15). Although this ratio is on average higher in humans than in great apes, there is a large range of overlap (Fig. 7). Moreover, all the measured groups except for female *G. b. beringei* have a range of variation for this ratio that overlaps that of AL 333-160 (Table 15 and Fig. 7). On the basis of this ratio, AL 333-160 does not align any closer to humans than it does to *Nasalis* or male and female gorillas, the latter of which have mean ratio values more closely approximated by AL 333-160.

As such, Ward et al.'s (2011a) arguments linking the above characters exclusively to habitual bipedality or to fixed pedal arches are not supported. Great apes are neither habitual bipeds nor have fixed pedal arches, but may exhibit these characters. Irrespective of the results of the present study, Figs. 3 and 4 in Ward et al. (2011a) show overlap between great apes and humans based on the above characters, rendering the attribution of full-time terrestrial bipedality based on these characters unwarranted. Moreover, some humans lack the characters Ward et al. (2011a) claim are exclusive to fixed arches and habitual bipedality. The presence of the AL 333-160 characters in quadrupedal cursors and in climbers, which are non-habitual bipeds, can be used to argue that these characters must also satisfy the mechanical requisites of quadrupedality and arboreality. Nevertheless, the AL 333-160 4th MT does give some indication as to the behavioral capabilities of this taxon. Any single bone or anatomical element cannot accurately diagnose an animal's locomotor repertoire, but may falsify some hypothetical behaviors and support others (see below).

AL 333-160 arboreality

Similarities between AL 333-160 and female eastern gorillas in body weight and metatarsal length indicate arboreal behaviors in AL 333-160 were limited to relatively large diameter supports and probably comprised but a small minority of the animal's daily activity. Metatarsal length contributes to the span of the grasp in pedal hook postures of the foot, and thus limits the maximum support diameter that can be grasped between the sole and the lateral toes. The relationship between support diameter and the weight the support can sustain, associates metatarsal length with the likelihood of an animal finding within reach a support suitable for a weight-sustaining grasp (Sarmiento, 1985 and Sarmiento and Meldrum, 2011). A short 4th MT relative to body weight suggests AL 333-160 was only able to apply a load-sustaining pedal hook grasp (with the lateral toes in opposition to the sole) on relatively small diameter supports and was thus less likely to find a stable support using this grasp. Moreover, in arboreal behaviors the weight-sustaining normal force generated by the pedal grasps must have been secondary to the normal force produced by body weight distribution and limb adduction in producing the frictional force at the foothold necessary to remain on the support.

Hallux opposability in the AL 333 fossils also seems to be limited and similar in degree to that seen in female eastern gorillas (Sarmiento and Marcus, 2000). Without a deep cleft between the great toe and the lateral metatarsals, metatarsal length does not have a direct bearing on the span of the opposable grasp. As such, a big toe opposable grasp could only be applied on the smallest supports. Notably, the toes of AL 333 hominoids are even shorter (albeit slightly) than those of eastern gorillas of comparable weight (Table 8), suggesting an even greater emphasis on terrestriality at the expense

of arboreality than observed in eastern gorillas. Because we did not identify any ontogenetic characters in the 4th MT that develop solely in response to either terrestrial or arboreal behaviors, we cannot be sure whether AL 333-160 practiced arboreal behaviors in its locomotor repertoire or had totally forsaken these behaviors for terrestrial ones. Although the AL 333-160 individual, as well as the lineage it belonged to, must have been under selection for terrestrial behaviors, we have no evidence to test Ward et al.'s (2011a:753) claim that AL 333-160 belonged to a lineage unlikely to have been “under selection [that] continued to favor substantial arboreal behaviors.”

AL 333-160 terrestriality

Metatarsal length is also related to stride length. In order to increase stride length, digitigrade or semidigitigrade cursors may lengthen their metatarsals. Because relative magnitude of bending moments acting on the metatarsals decreases with increasing approximation of the metatarsal long axes to the vertical cursors orienting their metatarsals vertically (parallel to the weight vector) can lengthen their metatarsals without generating high bending moments. High bending moments can result in bone and joint failure and are thus important to avoid. With horizontally oriented metatarsals (perpendicular to the weight vector) high bending moments may be avoided by shortening the metatarsals. The short AL 333-160 4th MT length relative to body weight, therefore, reflects not only an animal that was a relatively slow-moving non-cursor, but also possessed metatarsal long axes oriented perpendicular to the weight vector. The latter is supported by the indicated absence of a longitudinal arch in the AL 333 tarsals (Sarmiento and Marcus, 2000; see below). In humans, owing to the longitudinal arch and a foot that unloads at the ball with its heel off the ground in varying degrees of

plantarflexion, the metatarsals are held in more vertical postures than they would have been held in AL 333-160. Human metatarsals, therefore, can afford to be longer and the tarso-metatarsal joint smaller than in AL 333-160 even given the relatively greater loads human metatarsals may endure as a result of habitually bipedal postures. Short metatarsals relative to body weight, also suggest AL 333-160 was a less effective leaper than humans, orangutans, and chimpanzees either when on the ground or in trees.

AL 333-160 joint size

Joint size is a factor of both the magnitude of forces transferred across the joint and joint mobility (Sarmiento, 1988). More than likely, the relatively large metatarsal base size of AL 333-160, reflects both of these concerns and also that the 4th MT diaphysis is short relative to body weight and held horizontal to the substrate. The dorsoplantar to mediolateral width ratio in AL 333-160 could reflect dorsoplantar sliding movements at the cuboid-4th MT joint, or joint stability against dorsoplantar bending moments. Unfortunately, without a matching conarticular it is impossible to be certain if either one or both of these functions are linked to the AL 333-160 dorsoplantar to mediolateral base-width ratio. The relatively small metatarsal head of AL 333-160 reflects both relatively small phalanges and limited mobility at the metatarsophalangeal joint (Duncan et al., 1994). The associated foot bones (AL 333-115) from the same deposits as AL 333-160 verify the implied small phalangeal size (Table 8). Relative to orangutans, the AL 333-160 phalangeal articulation also suggests a restricted range of flexion-extension, and in these respects approximates the human and eastern gorillas

condition. As in humans and eastern gorillas the AL 333-160 small metatarsal head probably also reflects relatively weak long and short flexors tendons and poorly developed or aponeurotic intrinsic foot musculature. In contrast, the relatively large orangutan metatarsal head size reflects large proximal phalanges with wide range of flexion-extension movement and powerful short and long flexors. The large dorsoplantar to mediolateral width ratio of the orangutan metatarsal head suggests a limited range of adduction–abduction at the joint compared to a wide range of flexion-extension (Sarmiento, 1985). With a similarly large ratio, AL 333-160 also appears to have a more limited adduction–abduction range compared to flexion-extension at the metatarsophalangeal joint as do all great apes and humans. In fact, irrespective of other measures, the AL 333-160 4th MT head dimensions are most closely approximated by two chimpanzees (Table 5).

AL 333-160 torsion

As seen in the comparative sample, metatarsal torsion is a highly variable character. As first noted by Elftman and Manter (1935), it is strongly prone to environmental input and modified by foot use. The high variation in metatarsal torsion in orangutans probably corresponds to variability in toe postures (Sarmiento, 1985 and Tuttle, 1969). High metatarsal torsion may be expected in orangutans, which use the foot in strongly supinated postures and may flex the interphalangeal joints and hold the toes laterally rotated so that the distal phalanx is held lateral to its corresponding metatarsophalangeal joint. Such variable toe postures may also explain the high metatarsal torsion in some African apes. On the other hand, low metatarsal

torsion among some humans corresponds not only to a low transverse arch but may also be associated to toes that are held medially rotated so that the distal phalanx is held medial to its corresponding metatarsophalangeal joint (Fig. 8). Although humans are bipeds and baboons quadrupeds, both are cursors using the foot mainly as a propulsive lever and benefiting from the added foot rigidity provided by a transverse pedal arch. As such the high metatarsal torsion value of baboons in part reflects a transverse arch but not one that is necessarily fixed or as pronounced as in humans. No doubt, however, as in some great apes and humans, baboon 4th MT torsion also reflects the rotated set of their phalanges. In either case, torsion values are not exclusively linked to presence or absence of a human-like fixed transverse arch, or even have distinctive values that allow for such exclusive association. With all the characters that suggest a mobile transverse arch in the Hadar AL 333 fossils (see below) the relatively high torsion of the AL 333-160 metatarsal cannot be convincingly linked to a fixed human-like arch and bipedality any more than can the baboon or orangutan torsion values.

AL 333-160 diaphyseal angles

Likewise, the plantar inclination of the 4th MT cuboid facet (i.e. a $<90^\circ$ diaphyseal base angle) is also highly variable and not exclusively related to a longitudinal arch. Theoretically, a longitudinal arch would benefit from dorsal inclination of this facet ($>90^\circ$ base-diaphyseal angle). Such an inclination acts to reduce shear across the joint, resulting from both bipedal weight support and lower limb propulsion as the cuboid functions as the wedge-shaped keystone of the lateral longitudinal arch (Fig. 9).

Perhaps in humans plantar orientation of the cuboid facet is associated with the fact that rotational forces from weight support and propulsion cause tension along the plantar edge of the joint, but compression along its dorsal edge (Sarmiento, 1985 and Tuttle, 1969). In this regard, plantar inclination is associated with a reduced distance from the fulcrum (the ball of the foot) to the plantar edge of the joint, reducing the magnitude of rotational forces on the plantar side of the joint that need to be balanced by ligaments. Plantar inclination, however, lengthens the distance from the plantar to the dorsal edge of the joint, reducing the magnitude of compressive forces that need to be applied at the dorsal edge of the bone to balance rotational forces. If the latter explanation applies, all vertebrates, which use the foot as a propulsive lever would be expected to have an acute base diaphyseal angle. The variation within all species in the comparative sample, however, suggests that the beneficial effects provided by cuboid facet orientation are probably not critical to any one behavior, and thus angle values are not exclusively linked to bipedality or cursoriality, i.e. some cursors have values typical of arboreal climbers and vice versa.

While Ward et al. (2011a) did not provide a definition for the plantar surface-diaphyseal angle that allowed for confident replication of this measurement (see Appendix A), it appears that the angle is made by the long axis of the diaphysis with an axis tangential to the plantar border of the phalangeal articulation. In this regard, it may be expected that dorsiflexed postures combined with limited plantarflexion at the metatarsophalangeal joint result in the high angle values in AL 333-160 Ward et al. report. Such hyper-dorsiflexed postures of the metatarsophalangeal joint are as much a

feature of terrestrial quadrupeds as they are of bipeds and not exclusively related to a longitudinal arch or to bipedality (Sarmiento, 1994).

AL 333-160 ectocuneiform facet

As with all the above features presented by Ward et al. (2011a), the presence of an ectocuneiform facet on the 4th MT is not exclusively related to a longitudinal arch or to bipedality. In fact, nearly half of the humans sampled lacked a clear ectocuneiform facet. Ward et al. (2011a) suggest this facet increases dorsoplantar foot rigidity, but it is unclear why this would be the case. Theoretically, this joint should reduce shear at the tarsometatarsal joints resulting from medially directed loads on the 4th and 5th metatarsals, enabling a portion of these loads to transfer from the 4th MT to the ectocuneiform. Such loads would be expected in supinated forefoot postures where the 4th and 5th MTs are the only bony elements transferring weight to the substrate; a load transfer that is also suggested by the lateral concavity of the 5th metatarsal diaphysis of AL 333-78 (Latimer et al., 1982). Just as likely, the 4th MT-ectocuneiform articulation may be an incidental result of a more anterior position of the talus relative to the cuboid and calcaneus. Such an anterior talar position causes anterior (distal) displacement of the navicular carrying the ectocuneiform past the cuboid and resulting in the ectocuneiform-4th MT facet. Anterior talar displacement occurs with pronation of the subtalar joint (plantarflexion, eversion and lateral rotation; Sarmiento and Marcus, 2000). The presence of this character in humans and baboons (Table 13 and Table 14), therefore, may be simply related to the pronated foot postures associated with terrestriality.

Pedal arches and the AL 333 foot bones

Ward et al. (2011a:750) note, “Skeletal evidence for the presence of pedal arches in *A. afarensis* has been ambiguous, because key bones from the midfoot have been lacking.” Except for the cuboid and mesocuneiform, however, all tarsal and metatarsal bones (albeit MT II and MT III are represented only by heads) are known for the AL 333 fossils. These, together with the presented 4th MT, 5th MT and proximal phalangeal lengths (Table 8), provide a clear picture of an eastern gorilla-like foot which had sacrificed arboreality for terrestriality, but lacked the pedal specializations of bipedal or quadrupedal cursors. The proximodistally narrow navicular (AL 333-36, AL 333-47), and proximodistally short ectocuneiform (AL 333-79), attest to a short distal tarsus concurring with the short 4th and 5th metatarsals (AL 333-160, AL 333-78, Table 8) in indicating a relatively short outlever of the foot (Sarmiento and Marcus, 2000 and Schultz, 1963). The weight bearing plantar tubercles on the anterior calcaneus (AL 333-8), the navicular (AL 333-36, AL 333-47), and the ento- and ectocuneiforms (AL 333-28, AL 333-79) and the dorsiflexed calcaneal neck (AL 333-8), all indicate the tarsometatarsal joints were held against the substrate and the distal tarsal row transferred weight to the substrate (Sarmiento and Marcus, 2000). A groove for the adductor digiti minimi on the plantar aspect of the 5th MT base suggests dorsiflexion at the cuboid-5th metatarsal joint (Sarmiento, 1998). A large fibular trochlea and absence of a human-like lateral plantar tubercle (AL 333-8 and AL 333-55) indicates the *ossi-metatarsi quinti* muscle, the homologue of the lateral plantar ligament, lacked the plantar and distal position beneficial for maintaining a human-like longitudinal

arch (Lu et al., 2011). In view of the above, there is no evidence of an appreciable longitudinal arch in the AL 333 pedal remains (see Appendix B).

The notched ectocuneiform hamulus, the laterally oriented and recessed ball-like naviculo-ectocuneiform joint, the large central angle subtended by the talar facet of the navicular, the large naviculo-cuboid facet and adjoining pseudojoint between the sustentaculum tali and navicular (AL 333-36, AL 333-47), and on the entocuneiform (AL 333-28), the relative orientation of the navicular and mesocuneiform facets, and medial deflection of the first metatarsal facet relative to that of the navicular, suggest a relatively broad foot without a fixed transverse tarsal arch (Sarmiento, 1994 and Sarmiento and Marcus, 2000). Moreover, the sustentacular pseudojoint indicates the space below the talar head was pinched off and together with a small triangular medial facet on the talar head (AL 333-75) suggests the absence of a human-like spring ligament (plantar calcaneo-navicular ligament; Latimer et al., 1982;) associated with fixed pedal arches (Sarmiento, 1994 and Sarmiento and Marcus, 2000).

In the AL 333-8 and AL 333-55 calcanei the divergent lines of pull provided by the lateral ape-like position of the fibular trochlea and the retrotrochlear ridge when contrasted to those provided by the medial plantar process also indicate a mobile transverse tarsal joint and tarsus. Given the differences in their line of pull, the muscles and connective tissue finding attachments on these processes could apply a force to impede pedal dorsiflexion through a wide range of tarsal rotation (Lu et al., 2011). In spite of an implied flexible transverse tarsal joint the medial deflection of the distal half of the ectocuneiform facet (AL 333-79) and the lateral concavity of the shaft of the 5th

MT (AL 333-78) indicate rays were directed parallel to the pedal long axis and thus the foot had compromised some of its grasping abductory ability for propulsion.

Every AL 333 tarsal and metatarsal bone, individually but more so in association, suggests considerable mobility at the tarsal joints, arguing against a fixed transverse arch or a human-like longitudinal arch (see also Berillon, 2003 and Harcourt-Smith, 2002). All elements indicate the tarsometatarsal joints were held against the substrate and the distal tarsal row transferred weight to the substrate (Sarmiento and Marcus, 2000). The relatively short/small hallucal proximal phalanx, as compared to the lateral phalanges (Table 8), indicates the hallux did not have a human-like propulsive and weight-bearing function associated with a longitudinal plantar arch, providing further evidence of the absence of this arch in AL 333 individuals.

The Laetoli footprints and the Hadar AL 333 foot

The Laetoli tracks have been cited as evidence that Hadar fossils represent human-like bipeds (Campbell and Loy, 2000, Tuttle et al., 1991a and Tuttle et al., 1991b) and may be argued to bolster Ward et al.'s arguments as to AL 333-160 foot structure and function. Given that as much as 500,000 years and 11° latitude separate the AL 333 fossils from the Laetoli tracks (Ditchfield and Harrison, 2011 and Kimbel et al., 1994), there is no direct evidence which indicates that the makers of the tracks and the Hadar AL 333 pedal remains belong to the same taxon. Significantly, the prints do not provide evidence as to the frequency with which bipedal behaviors were practiced, which is a key difference distinguishing humans from great apes (Sarmiento, 1998). More importantly, the Laetoli tracks do not have the resolution to provide conclusive

evidence of a modern human foot with fixed longitudinal and transverse pedal arches and have supported a wide range of interpretations (Leakey and Harris, 1987, White and Suwa, 1987, Raicheln et al. 2010, Meldrum et al., 2011), so that, even if the AL 333 taxon was conclusively shown to have made them, it would not serve to strongly support Ward et al.'s (2011a) contention.

Reconstructing behaviors from fossil remains

Human-like bipedality is not a dichotomous character diagnosed by any single feature; rather it involves a large and complex set of anatomical traits (Haile-Selassie, 2001). Unfortunately, the practice of summarizing the character states of all great apes based on unrepresentative sample sizes of lowland gorillas and common chimpanzees, and of assuming characters absent in this unrepresentative sample are exclusive to bipedality and thus humans, without causal models accounting for exclusive bipedal associations has been *de rigueur* in paleoanthropology. Despite three decades of research showing an anterior position and inferior orientation of the foramen magnum (Cramer, 1977, Fenart and Deblock, 1973 and Pickford, 2005), a bowl-shaped pelvis (Sarmiento, 1987 and Sarmiento, 1998); a femoral neck with human-like cortical bone distribution (Rafferty, 1998), a high femoral carrying angle (Tardieu and Preuschoft, 1996), a high femoral neck angle (Sarmiento, 1985), a femoral neck obturator groove (Stern and Larson, 1990), a tibio-talar articular plane perpendicular to the tibial long axis (Sarmiento, 2007), metatarsals with dorsally domed heads, proximal phalanges with dorsally canted metatarsal articular surfaces (Meldrum, 1991 and Sarmiento, 1994), etc., are not exclusive to humans or habitual bipeds, and that some of these characters may

even be primitive for hominoids, paleoanthropologists continue to propound these characters as diagnostic of humans and of habitual bipedality, and use their presence in fossils to justify a hominin classification (Brunet et al., 2002, Brunet et al., 2005, Johanson and Taieb, 1976, Kimbel and Delezene, 2009, Leakey et al., 1995, Lovejoy, 2005a, Lovejoy, 2005b, Pickford and Senut, 2001, Senut et al., 2001, White et al., 1994 and White et al., 2009). The opportunistic nature of evolution and one of the chief mechanisms by which adaptation is postulated to occur in higher organisms, namely adaptive shifts through structural continuity (Darwin, 1859), makes it highly unlikely that any localized anatomy can be exclusively associated to any one single locomotor behavior. In members of an evolving lineage, or in species practicing multiple behaviors, localized anatomy satisfies the mechanical requirements of multiple behaviors. Although in modern humans a localized anatomy may be exclusively associated to bipedality, in living primates and ancestral hominins this same anatomy may also be associated to other behaviors. As such, it is logically flawed to use any one localized anatomy alone without corroborating evidence to infer human-like bipedality in fossil taxa. Doing so in effect denies evolutionary change and ignores the extensive record of mosaic evolution in primates (McHenry, 1994 and Hamrick, 2011).

If localized anatomy is compatible with multiple behaviors, some of which may have never been practiced by an animal in possession of this anatomy, how can the behaviors of extinct animals ever be reconstructed from fragmentary and/or incomplete fossils? As is often the case that fragmentary fossils are inconclusive for classification (Sarmiento et al., 2002), it is also the case that fragments of localized anatomy, although divulging localized mechanical properties, are in themselves inconclusive for

reconstructing an animal's locomotor behaviors. In these cases, the localized anatomy may have physical properties that satisfy the mechanical requisites of multiple locomotor behaviors. One or all of these behaviors may have been practiced either by the animal in question or by its ancestors and/or will be practiced by its descendants. For instance, a metatarsophalangeal articulation with a dorsiflexed set satisfies both the mechanical requisites of bipedality and quadrupedality (Meldrum, 1991 and Sarmiento, 1994). On the basis of this joint alone, one behavior cannot be ruled out over the other. In members of an evolving lineage this anatomy may be associated in some to quadrupedality, in others to bipedality, and possibly in the remainder to both quadrupedality and bipedality. In this regard, showing conclusively that some specific locomotor behaviors were practiced and others were not, requires localized anatomy from disparate areas of the body that all show compatibility (as opposed to incompatibility) with a hypothesized behavior. For example, finding an animal with short toes, straight metatarsal shafts and a dorsiflexed set of the metatarsophalangeal joints would not resolve whether it was quadruped or biped. Finding its hand had long fingers and a mobile wrist joint with no modifications for weight support and was thus incompatible with quadrupedal behaviors implies that the short toes, straight metatarsal shafts and a dorsiflexed set of the metatarsophalangeal joints were most likely used in bipedal behaviors.

Given the wide range of behaviors practiced by hominoids, finding that localized anatomy from disparate areas is compatible with a behavior does not necessarily indicate that the animal in possession of this anatomy definitely practiced the compatible behavior. Characters dependent on environmental input (i.e. behaviors

practiced) for their development, such as torsions, joint sets, bone trabecular patterns and diaphyseal cortical thicknesses, and cross-sectional diameters, are the most useful for predicting from fossil or skeletal material the behaviors an animal practiced during its lifetime and may also divulge frequency of practiced behaviors (Sarmiento, 1985). Presence of characters dependent on behavioral input for their expression suggests that the particular behavior resultant in their expression was commonly practiced (Sarmiento, 1985). Because characters dependent on behavioral input for their expression may also develop in response to more than one behavior, to rule out one or another behavior it is also necessary to examine localized anatomy in disparate areas of the organism to test for compatibility. Discovering that disparate localized anatomical areas in an organism possess characters that could only have developed as a response to the localized demands of a specific behavior suggests that the animal practiced this behavior.

Fully sampling living hominoid diversity and understanding the behavioral correlates of localized anatomy through observations of living animals and modeling of localized anatomical function is instrumental for diagnosing behaviors in fossil forms. Evolutionary models reconstructing common ancestral behaviors based on shared anatomy of living taxa present a range of possible behaviors that members of descendant lineages may have practiced, providing a guide to the most likely behaviors and thus the most relevant to test for in fossil members of descendant lineages. Therefore, the foremost activity that will illuminate our understanding of the behaviors of extinct taxa is filling gaps in our understanding of the behaviors and ecology of living animals to refine evolutionary models that correlate form to function and to habitat over

time. Because our study of the 4th MT considers only one area of localized anatomy, and the AL 333 hominins from the Sidi Hakoma member may be as much as 300,000 years older than the associated AL 288-1 skeleton (Kimbel et al., 1994 and Walter, 1994) and do not necessarily represent the same taxon, it would be presumptive to assume based on only what is known of the AL 333 skeleton and foot, to claim it is exclusive to either bipedal or quadrupedal behaviors. The foot is compatible with both terrestrial bipedality and quadrupedality. Given the body weight, toe length and finger length of the AL 333 fossils (Bush et al., 1982, Latimer et al., 1982 and McHenry, 1992; Table 8) arboreality is unlikely, but cannot be discounted entirely. AL 333-160 must surely have used trees on occasion, as do modern humans and mountain gorillas. If the foot belongs to a biped, it suggests that the animal's bipedality was different from that of modern humans.

Conclusions

A study of the AL 333-160 4th MT characters using greater sample sizes and taxonomic diversity than reported by Ward et al. (2011a) does not support the claim that the AL 333-160 individual had fixed transverse and longitudinal pedal arches exclusive to human bipedality. Although metatarsal torsion and joint sets are known to be highly influenced by foot use and environmental input (Elftman and Manter, 1935, Sarmiento, 1985), a large range of overlap in the values shown by humans, great apes, and monkeys in both torsion and base-diaphysis angle precludes these measures from being exclusive indicators of pedal arches or any one behavior including bipedality. The same applies to the 4th MT dorsoplantar/mediolateral base ratio, which in our sample

also exhibits a similarly large range of overlap. Present in baboons, humans and rarely in gorillas a 4th MT ectocuneiform facet appears to be a terrestrial character and possibly the incidental result of pronated foot postures. Baboons also approximate the human values for torsion, base diaphyseal angle and the base dorsoplantar/mediolateral ratio indicating these characters also reflect terrestrially but are not exclusively related to bipedal behaviors.

The 4th MT measures reported by Ward et al. (2011a), however, do provide insight into AL 333-160 foot use and function. Relative to estimated body weight of the AL 333 remains the short AL 333-160 4th MT length and large base circumference reflect a somewhat slow-moving non-cursor, which was a poor arboreal or terrestrial leaper, and positioned its metatarsals fully horizontal to the substrate and perpendicular to gravity. As such, it lacked the inclined or vertical metatarsal postures of digitigrade or semi-digitigrade cursors including those seen in the longitudinal pedal arch of habitual bipeds. A relatively small metatarsophalangeal joint and a small proximal phalanx with restricted flexion-extension and abduction–adduction movements are characters that approximate both the eastern gorilla and human condition, and also reflect relatively limited forces across the joint and limited pedal grasping abilities. The similarities in body weight and metatarsal length between AL 333-160 and female eastern gorillas suggest that arboreal behaviors in AL 333-160 were not frequent and were limited to large diameter supports. The other AL 333 tarsals, metatarsals, and phalanges corroborate the above inferences further indicating a gorilla-like foot committed to terrestriality but with no fixed longitudinal or transverse arches.

Associating selective features of a single 4th MT to pedal arches and habitual bipedality using statistically non-representative samples of humans and two African ape species underestimates intraspecies variation and species diversity, and overestimates the exclusive association any one selected 4th MT character or characters may have to a behavior or localized structure, e.g. pedal arches. Because evolution proceeds as adaptive shifts through structural continuity and localized anatomy in living primates satisfies the mechanical requirements of multiple behaviors, it is logically flawed to exclusively associate localized anatomy to single behaviors. Establishing causal relations between structure and function through mechanical models of localized anatomy, understanding how the mechanical requisites of living primate behaviors are satisfied by localized anatomy and how they ontogenetically modify this anatomy, and constructing evolutionary models of ancestors based on ecology and shared anatomy of living primates are all ingredients essential for accurately reconstructing behavior from skeletal or fossil remains. The long-standing debate concerning the locomotor behaviors of *Australopithecus afarensis* (Harcourt-Smith and Aiello, 2004 and Kimbel and Deleuzene, 2009) evidences the complexity of reconstructing behavior from fossil taxa and casts doubt upon suggestions that any single, atomized anatomical element or character can alone provide conclusive proof for any particular behavior. As such, claims, which attempt to directly associate localized anatomy with particular locomotor behaviors deserve careful scrutiny and rigorous attempts at falsification. The results of this study show that such generalizations drawn from isolated localized anatomies aimed at finding exclusive associations to behaviors are likely to be misleading when reconstructing the behaviors of extinct taxa.

Appendix A

Ward et al. (2011a) do not provide a full account of their methods for many of the measures they report on, precluding our replication of some of them. Ward et al. Fig. 3 graph shows *A. afarensis* has a base-diaphysis angle of approximately 96° but does not show which of the two angles made by the intersecting lines overlaying the photograph of the fossil is reported. Given the values Ward et al. (2011a) report for humans and African apes we assumed that they reported the dorsal angle, which is the supplement of the plantar angle we measured and reported in our study. The 103° base diaphyseal angle depicted by the lines overlaying a photograph of a human metatarsal in Ward et al.'s Fig. 3, however, is outside the range they report for humans in the supporting online material and in their Fig. 3 graph. Ward et al. do not report what anatomical landmarks define the plantar surface axis so that we were unable to replicate with confidence their plantar surface/diaphyseal and plantar surface/base angle. Moreover, there are reasons to doubt the accuracy of all three angles reported by Ward et al. in Fig. 3, i.e. diaphyseal/base, plantar surface/diaphyseal and plantar surface/base. These three angles represent two angles of the same triangle and the complement of the third angle of this triangle. As such, the base diaphyseal angle of AL 333-160 should equal the plantar surface/diaphysis angle plus the plantar surface/base angle. However, the values Ward et al. report do not equal each other and suggest a considerable degree of error, which incidentally is equal to the range of variation shown for these values in the reported African apes.

Ward et al. Fig. 4a, refers the reader to reference 11, Berillon (2003), as the source of the measurements and method for measuring 4th MT cuboid facet curvature. Berillon (2003), however, does not report on 4th MT cuboid facet curvature. We suspect that Ward et al. intended to reference DeSilva (2010), which in their study appears as reference 10, DeSilva (2009). DeSilva (2010) reports means and standard deviations of the anteroposterior height/depth of the 4th MT cuboid facet as a ratio of its dorsoplantar length in 33 chimpanzees (sampling both species), 29 lowland gorillas, 10 white-handed gibbons, eight macaques, six baboons (representing more than one species), and five mandrills. He reports neither degrees of arc subtended, nor radius of curvature as is traditionally used to define curvature (Sarmiento and Marcus, 2000 and Susman and Brain, 1988). Moreover, DeSilva is not clear as to where along the cuboid facet (i.e. what parasagittal plane) his measurements are taken from. (Ward et al. Fig. 4a suggests it is along the medial border of the facet). Because the 4th MT cuboid facet is often saddle-shaped in humans and African apes and may present both a concavity and convexity which changes according to where the facet is parasagittally sectioned it is unclear what exactly DeSilva is measuring. It is unknown if the anteroposterior height he uses to arrive at his ratio combines the depth of the concavity and the height of the convexity? Given that we were unable to replicate this measure, and that we cannot reconcile the DeSilva ratio to degree of arc subtended and radius of curvature (absolute lengths are needed to arrive at the latter), we excluded the measure from our comparison. Nevertheless, although DeSilva (2010) does not report range of variation for his ratio, his standard deviations show that AL 333-160 has values which overlap

with gorillas and humans; thus, the AL 333-160 curvature is not exclusive to pedal arches or bipedality and concords well with all the evidence we were able to quantify.

In an erratum posted April 15, 2011, Ward et al. (2011b), noted their Fig. 4b graph had the Y axis mislabeled and should read ML/DP instead of DP/ML (the Y axis is labeled ML+DP but the caption for the graph reads DP/ML). After tabulating our measurements we suspected it was an error, but remained somewhat circumspect so we calculated the inverse ratio DP/ML prior to the appearance of the erratum and left it as such in our study.

Appendix B

A number of studies that make the claim that *A. afarensis* has longitudinal and transverse pedal arches, are commonly referenced by workers arguing that the AL 333 fossils represent a biped and an exclusive member of the human lineage. To prevent readers from forming the unwarranted impression that our study ignores facts that would otherwise falsify our conclusions, it seems appropriate to review the anatomy these studies use to arrive at claims of pedal arches for the AL 333 fossils.

DeSilva and Throckmorton (2011), measuring the inclination of the inferior articular surface of the tibia from (1) medio-lateral X-rays of living human feet, (2) photographs of the tibiae of humans and all great ape species except pygmy chimpanzees and (3) a dozen fossil hominids, concluded that two AL 333 tibiae (AL 333-6, AL 333-7) have a “rear foot arch” but AL 288-1ar lacks one. The term “rear foot arch” was conceived by DeSilva and Throckmorton to describe the anterior set (i.e. inclination) of the inferior articular surface of the tibia relative to the tibial shaft long axis as measured in degrees. While it is true that most humans have an anterior set of the inferior articular surface of the tibia relative to the tibial shaft long axis (Davis, 1964) and most humans have a longitudinal arch, DeSilva and Throckmorton do not elucidate on the causal relationship between the two and only attempt to show that in humans there is a statistical correlation (albeit a very tenuous one). Given that their data on the set of the inferior articular surface show half the human range of values fully overlaps with those of great apes, none of which have fixed pedal arches, there is no reason to conclude that an anterior or posterior set can prove or disprove whether a fossil has or

does not have a longitudinal pedal arch. Moreover, DeSilva and Throckmorton fail to explain how this angle can be accurately measured to tenths of a degree from tibiae that are damaged and preserve only a very small fraction of the shaft (i.e. AL 333-7, StW 358, StW 389, StW 567, KNM-ER 1481, KNM-ER 1500, KNM-ER 2596, KNM-WT 15,000) or even those preserving less than half the shaft (i.e. A.L. 333-6, A.L. 288-1ar; see Kern and Straus, 1949). Incidentally, AL 333-7, the one Hadar fossil they report as having an anterior set $\sim 1.5^\circ$ greater than seen in great apes, is a heavily eroded fragment preserving approximately 30 mm of the tibial shaft (Lovejoy et al., 1982). As such, DeSilva and Throckmorton provide no conclusive evidence as to the set of the inferior tibial articular surface in the AL 333 fossils, not to mention whether or not they have a longitudinal pedal arch.

Lamy (1986) notes the AL 333-75 and AL 288-1 tali have a head with a bare area inferomedially corresponding to the plantar calcaneonavicular ligament in the interval between the sustentaculum tali and the navicular facets. As described by Latimer et al. (1982:701) in AL 333-75 "A small triangular facet is present on the inferomedial corner of the navicular surface for articulation with the plantar calcaneocuboid ligament." From this morphology, Lamy concludes that AL 288-1 and AL 333-75 have a human-like spring ligament and thus a longitudinal plantar arch. Chimpanzees, however, show a facet on the talar head for the plantar calcaneonavicular ligament but lack the human-like spring ligament and a longitudinal arch (see Fig. 26 in Sarmiento, 1994). The relatively small size of the calcaneonavicular facet in Hadar, smaller than in chimpanzees, strongly contrasts with the large and well-demarcated (by both set and curvature) human one, and indicates that the support for the Hadar talar head came

mainly from the closely set sustentaculum tali and navicular. Unlike in humans, the tendon of the tibialis posterior muscle in Hadar would not have played as great a role in arch support, and more than likely lacked the human characteristics, i.e. fibrocartilage investing its superior aspect as it passes below the talar head and an extensive attachment on the navicular, cuneiforms, cuboid and bases of the 2nd–4th MT (Sarmiento, 1994). The presence of a small facet for the calcaneonavicular ligament in Hadar, therefore, argues against, not for the presence of a longitudinal plantar arch, at least not an arch that was supported as in humans.

In a biomechanical analysis of the AL 333 calcanei, Latimer and Lovejoy (1989) note the presence of a lateral plantar process and argue that this process, together with the large inflated medial process of the tuber calcanei indicates human-like bipedal heel strike and the presence of a plantar arch. Their claim of a lateral plantar process contradicts their earlier descriptions (Latimer et al., 1982); for AL 333-8, “the lateral process is indistinct, in its place a bony ridge runs obliquely across the calcaneal body ending in the massive peroneal trochlea” (Latimer et al., 1982:701); in AL 333-37, “The lateral tuberosity is relatively indistinct” (Latimer et al., 1982:702); and in AL 333-55, “...an inflated ridge of bone courses back from the peroneal trochlea to the small lateral process of the calcaneal tuberosity” (Latimer et al., 1982:702). Their observation that the lateral process is indistinct or small, together with a much more lateral and decidedly less plantar disposition than in modern humans, indicates that the muscles and ligament attaching on the process had a reduced lever arm for preventing dorsiflexion at the tarsal and tarsometatarsal joints. The ligaments and plantar fascia were also probably less developed than in modern humans or attached elsewhere (see text). Moreover, the

Hadar lateral process is probably not the homologue of the fibular (peroneal) trochlea as is the human lateral plantar process (Weidenreich, 1940), given that the Hadar lateral process is not plantar in its disposition and occurs together with a fibular (peroneal) trochlea described as 'massive' (Latimer et al., 1982). As such, the Hadar structure could be more accurately referred to as a well-developed retrotrochlear ridge. Contrary to Kimbel and Delezene (2009), the well-formed retrotrochlear ridge in Hadar does not imply the presence of a human-like longitudinal arch. Likewise, Latimer and Lovejoy's (1990) contention that limited abduction-adduction mobility at the hallucal metatarsal joint in Hadar as surmised from the damaged entocuneiform (AL 333-28) and the 1st MT base (AL 333-54) indicates a longitudinal arch, finds little support. The abducted position of the hallux depends in large part on the set of the navicular and its articulations. The AL 333 naviculars indicate a degree of hallucal abduction similar to that seen in eastern gorillas and these animals lack fixed pedal arches (Sarmiento and Marcus, 2000).

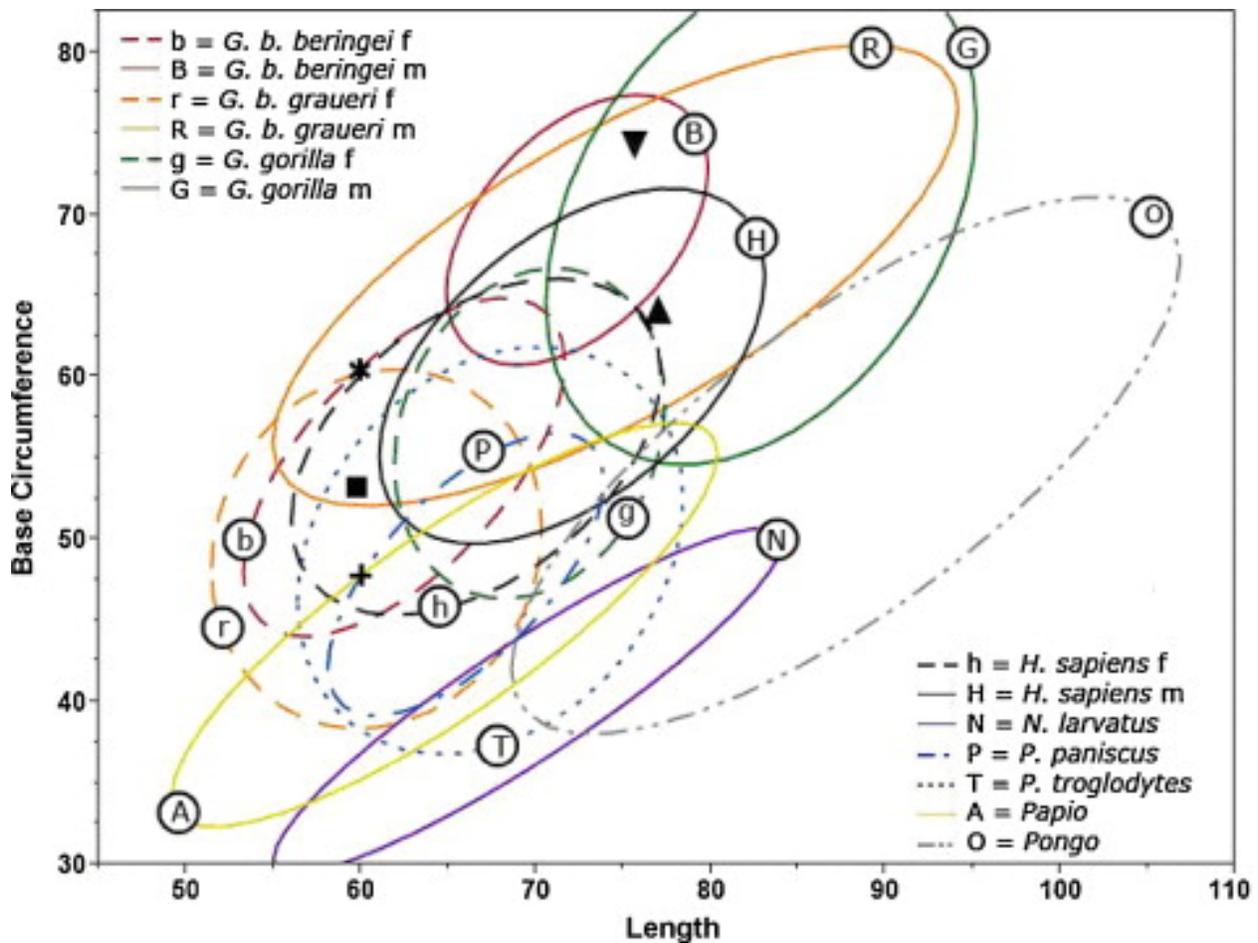


Fig. 1. Bivariate plot of base circumference vs. length of fourth metatarsal (see Table 9 for regression statistics). 95% confidence interval ellipses are as follows: red dashed line: *G. b. beringei* f; red line: *G. b. beringei* m; orange dashed line: *G. b. graueri* f; orange line: *G. b. graueri* m; green dashed line: *G. gorilla* f; green line: *G. gorilla* m; black dashed line: *H. sapiens* f; black line: *H. sapiens* m; purple line: *N. larvatus*; blue dash/dot line: *P. paniscus*; blue dotted line: *P. troglodytes*; yellow line: *Papio*; grey dash/double dot line: *Pongo*. *: AL333-160, ▲: Skhul 4, ▼: La Ferrassie 1, ○: LB 1/24, ■: OH8, and +: STW 485. Due to incomplete preservation of fossils, note that LB 1/24 appears only in Fig. 2, OH8 appears only in Fig. 1 and Fig. 2, and STW 485 appears only in Fig. 1 page 5.

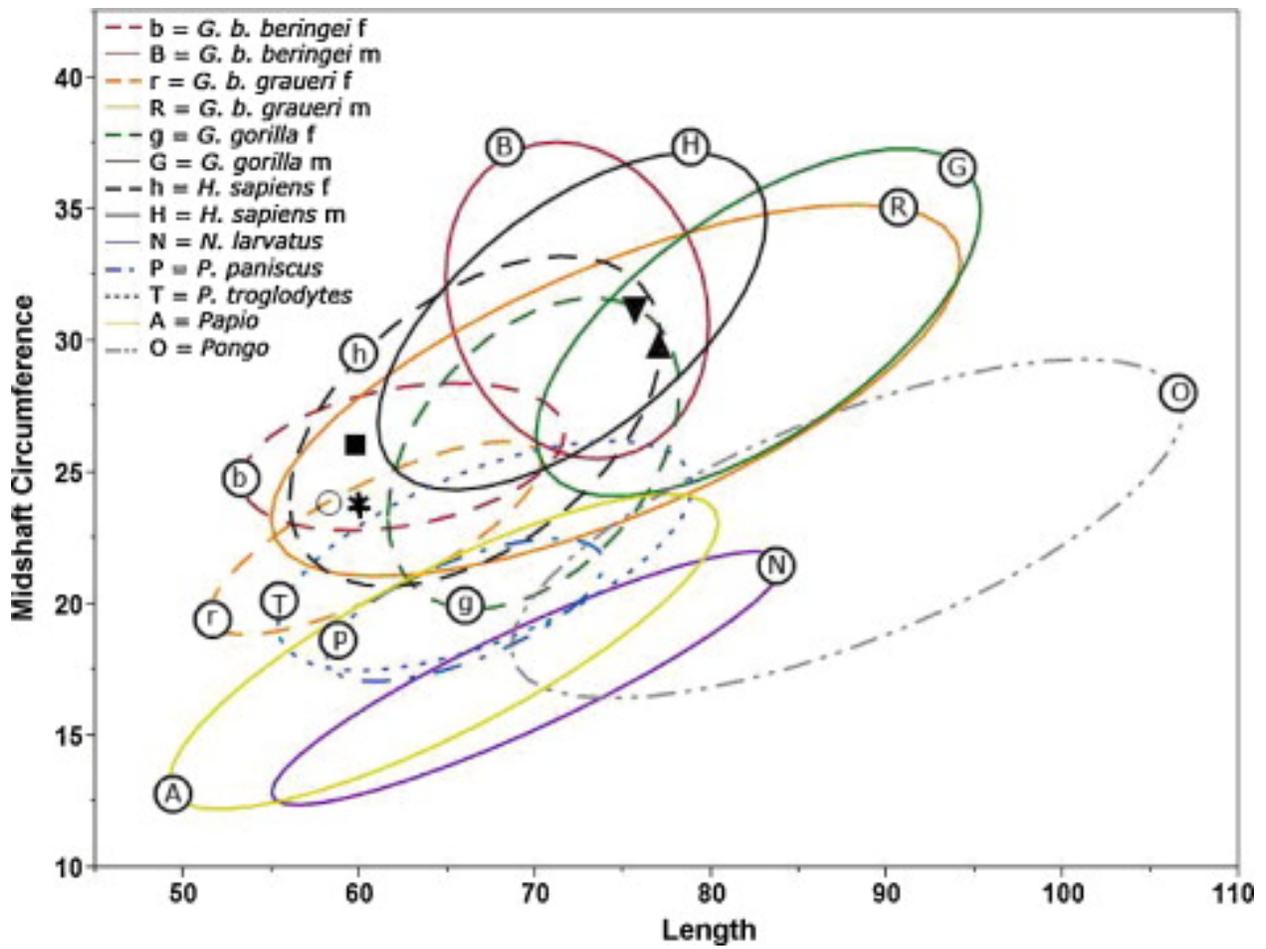


Fig. 2. Bivariate plot of midshaft circumference vs. length of fourth metatarsal (see Table 9 for regression statistics. See Fig. 1 for ellipse and data point key).

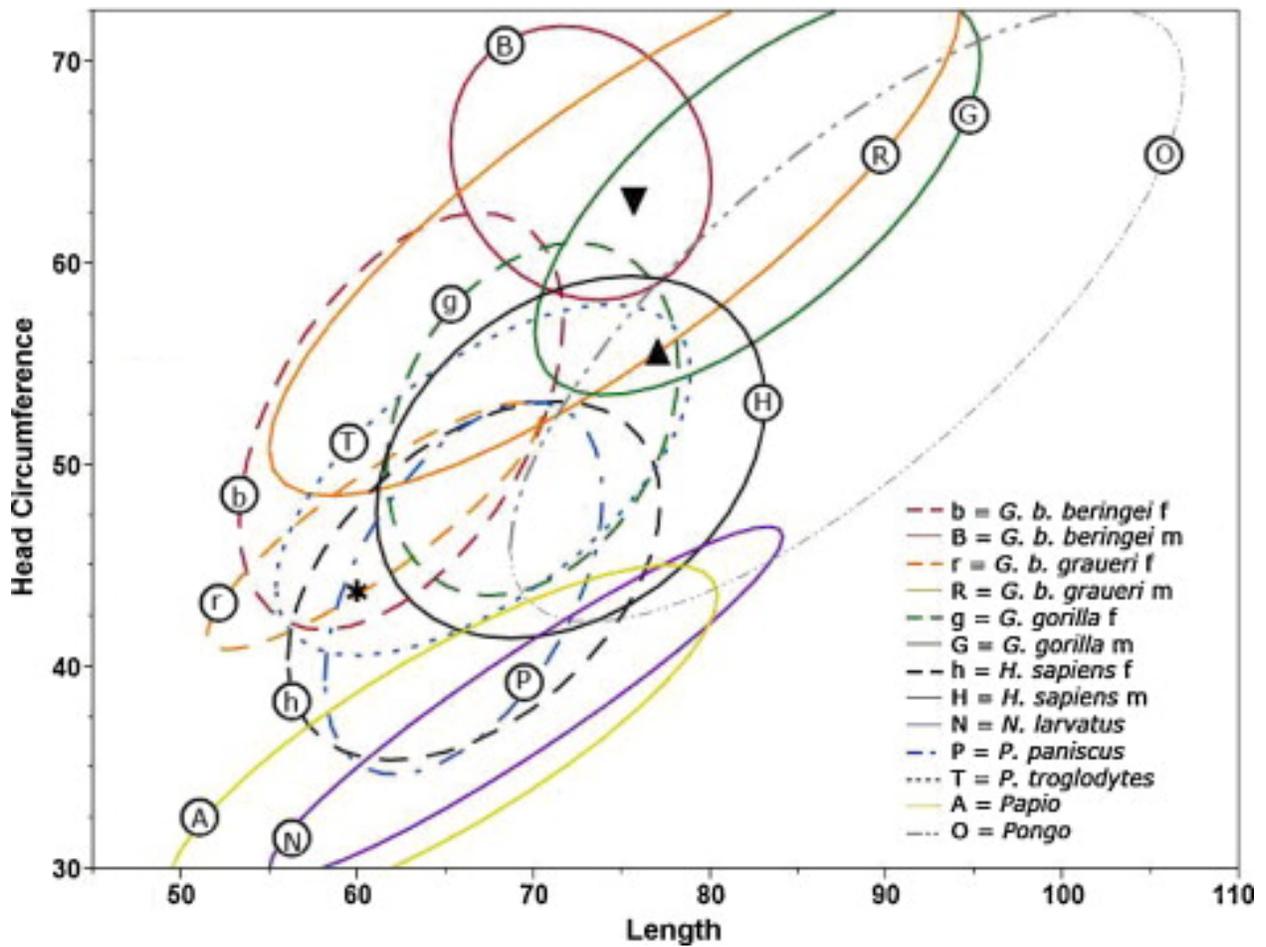


Fig. 3. Bivariate plot of head circumference vs. length of fourth metatarsal (see Table 9 for regression statistics. See Fig. 1 for ellipse and data point key).

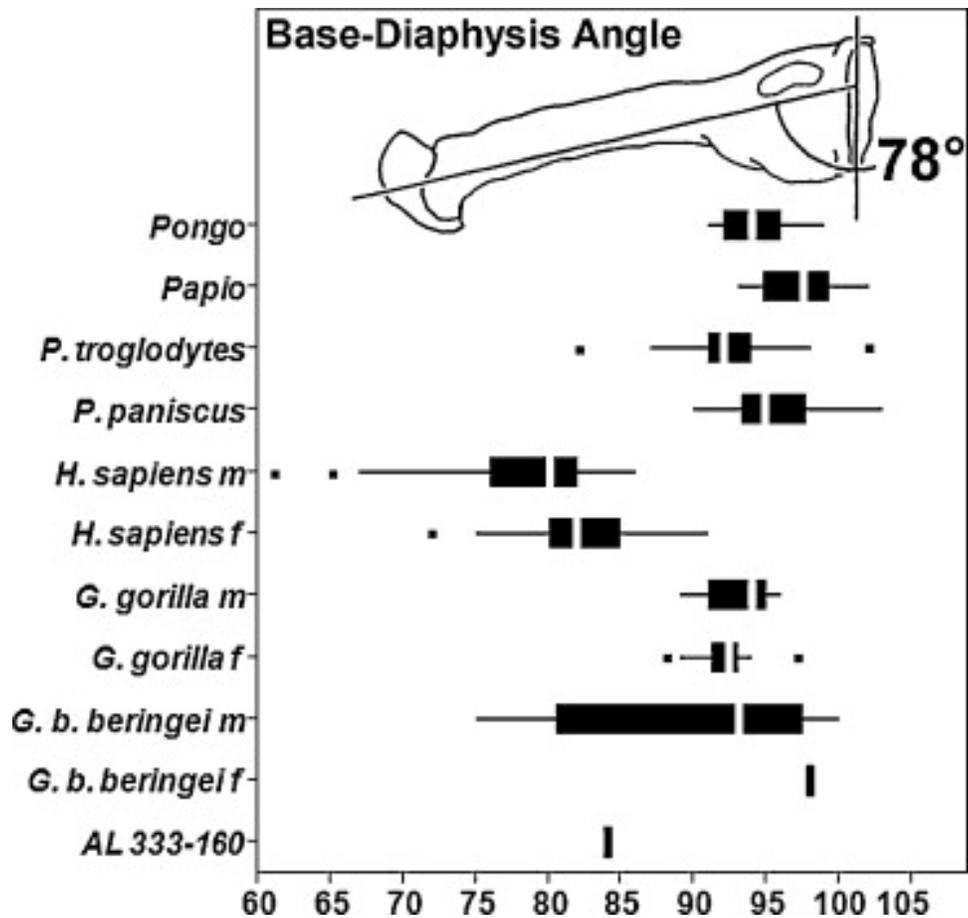


Fig. 4. Box plots of fourth metatarsal base-diaphysis angle with inset of human right 4th MT illustrating measured angle. Black rectangles: the inter-quartile range (IQR), white horizontal bar bisecting black rectangles: median, black lines extending to the left and right of box: lowest and the highest data within 1.5 IQR of the lower and upper quartile, respectively. Outliers above or below 1.5 IQR are figured as points. See Appendix A for discussion concerning Ward et al.'s (2011a) measures.

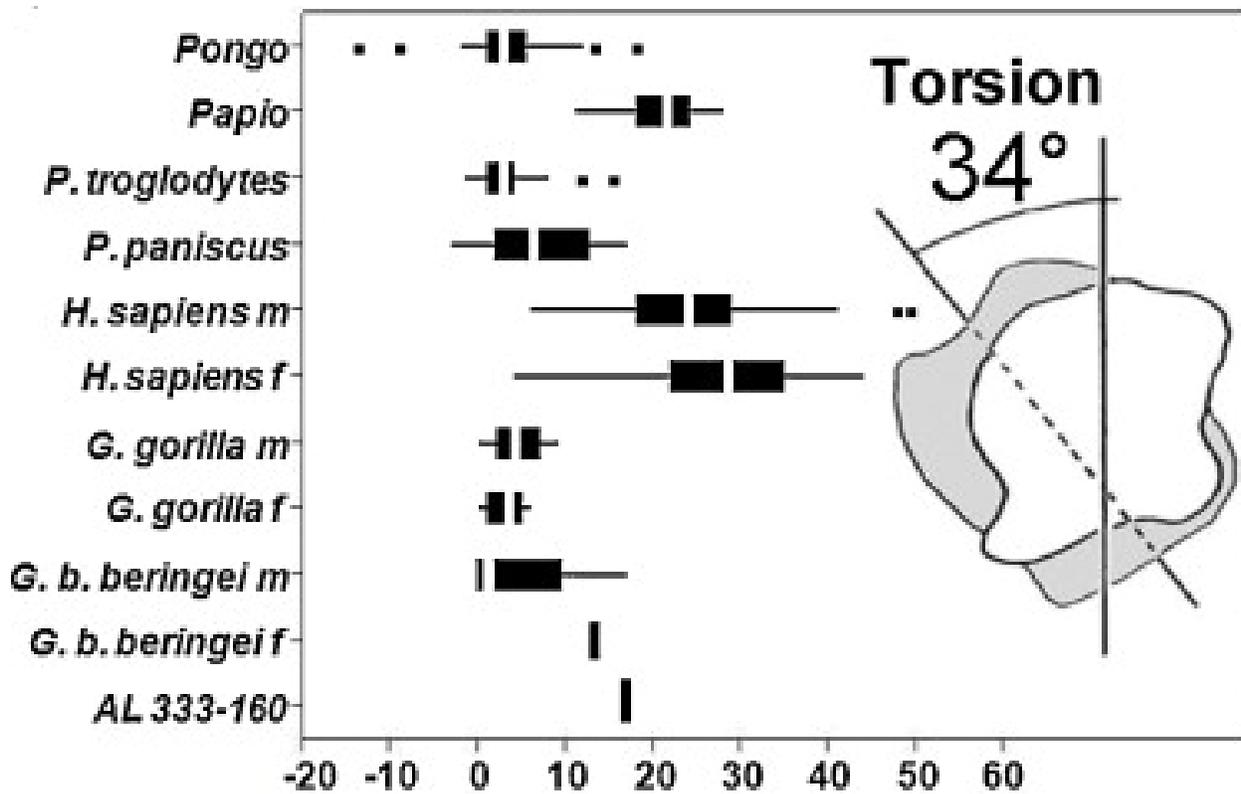


Fig. 5. Box plots of fourth metatarsal torsion with inset illustrating torsion of a human right 4th MT as viewed distally. Medial rotation of the head (i.e. axis in the plane of movement of the proximal phalangeal joint) relative to the base (long axis of the base) is expressed as a negative value. See Fig. 4 for explanation of plots.

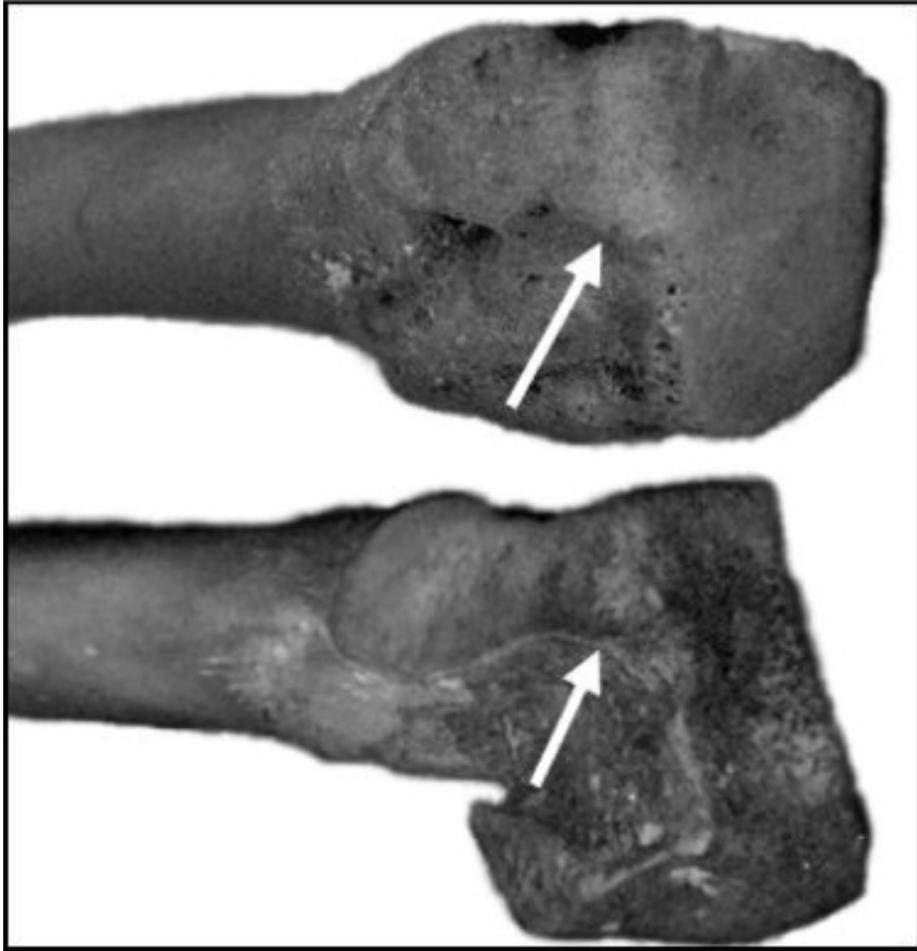


Fig. 6. Ectocuneiform facet (indicated by white arrow) on right fourth metatarsal of human (above) and baboon (below).

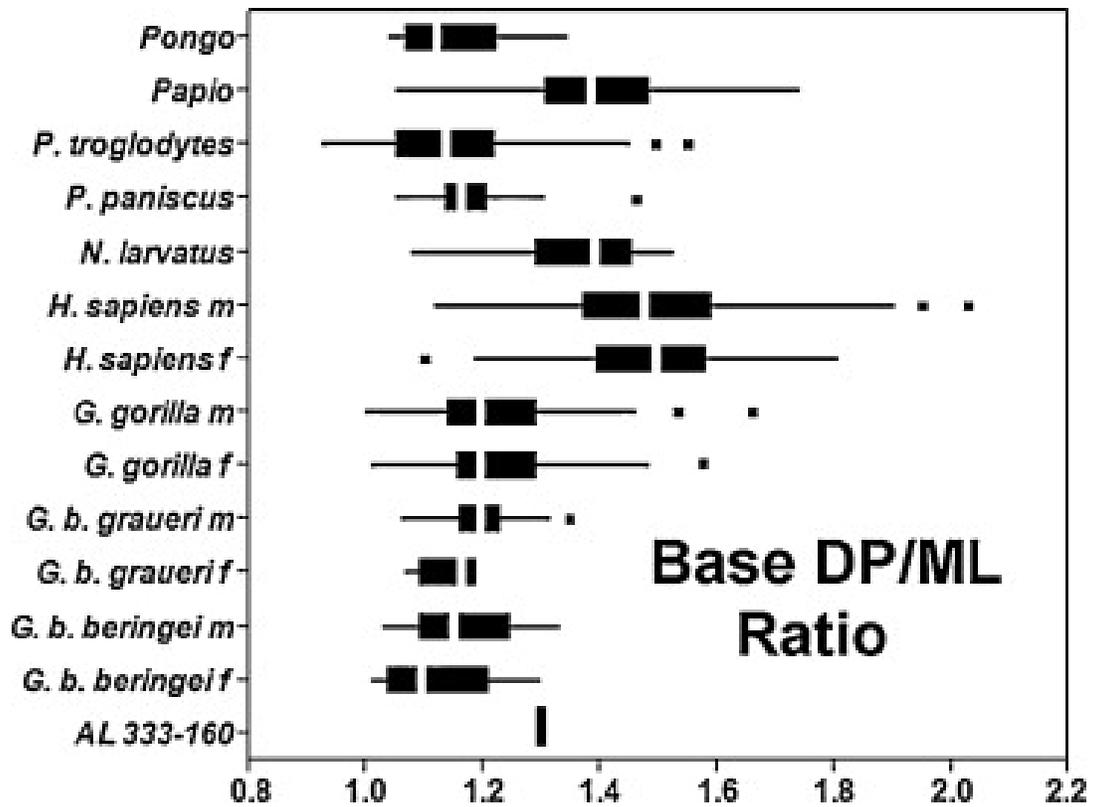


Fig. 7. Box plots of fourth metatarsal base DP/ML ratio. See Fig. 4 for explanation of plots. See Appendix A for discussion concerning Ward et al., 2011a and Ward et al., 2011b measures.



Fig. 8. Variation in rotational set of the toes in four eleven year-old human males. The rotational set reflects metatarsal and phalangeal torsion (Sarmiento and Marcus, 2000). Notice the strong medially rotated set of the 5th toe in all individuals, and the strong medially rotated set of the 4th toe and laterally rotated set of the 1st toe in the individual on the upper right. Such variation in toe rotational set is also seen in African apes and orangutans (author's unpublished data and Esteban Sarmiento, personal communication) and explains why (1) great apes lacking a transverse arch may have 4th and 5th metatarsal torsion values overlapping those of humans, (2) humans lacking great toe opposability may have 1st MT torsion values overlapping those of great apes and (3) metatarsal torsion values cannot be exclusively related to presence of a transverse arch or great toe opposability.

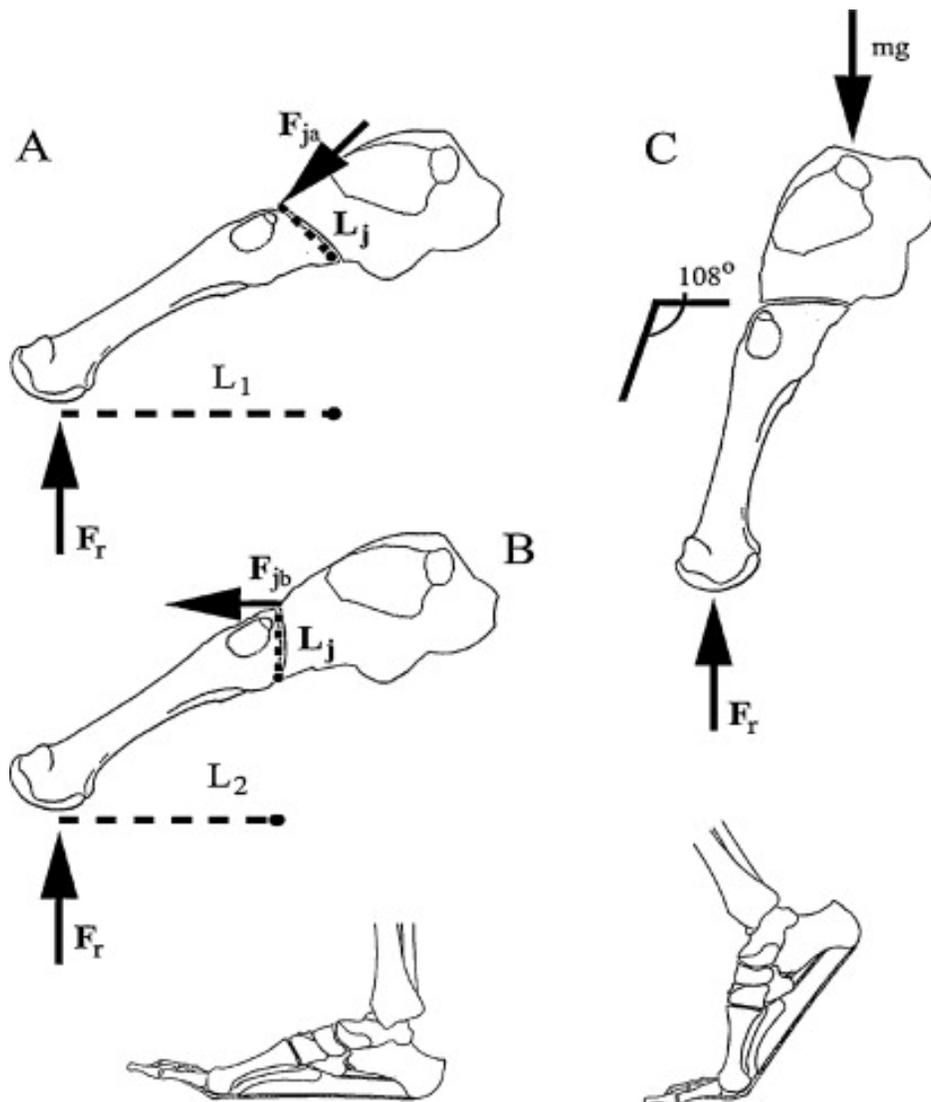


Fig. 9. Line drawings of the medial surface of the human cuboid and 4th MT with static analysis of the rotational forces applied at the 4th MT cuboid articulation by the resultant of that portion of the body weight (p) borne by the ball of an arched foot (where $F_r = p \times mg$) in a joint with a high base-diaphyseal angle of 108° (A) compared to one with a low angle of 72° (B). For purpose of comparisons examples A and B have the same F_r magnitude, dorsal 4th MT length, and dorsoplantar joint length (L_j). The plantar edge of the 4th MT cuboid articulation is taken as the point of rotation. The horizontal

distance (L_1) from F_r (the point of contact of the ball of the foot with the substrate) to the plantar edge of the 4th MT in A is longer than the corresponding distance in B (L_2), resulting in a relatively greater force across the joint (F_j) necessary to achieve equilibrium in A relative to B, where $F_r \times L = F_j \times L_j$, and $F_{ja} = F_{jb}L_1/L_2$. Although a static analysis of ligament forces across the joint is not provided, the plantar flexion of the 4th MT base associated with a low diaphyseal angle further stabilizes the joint by increasing the lever arm of the ligaments balancing rotational forces across the joint. At toe-off (C) when the heel is lifted fully off the ground and all the body weight is borne by the ball of the foot a high diaphyseal angle orients the cuboid 4th metatarsal joint perpendicular to gravity, minimizing rotational forces across the joint. While such a cuboid 4th MT joint orientation and a large base diaphyseal angle may be expected in a biped given a proportionately greater lower limb joint load, in humans body weight at toe off is borne largely by the great toe. African apes, on the other hand, may place a greater load on the lateral side of the foot at the end of the stance phase. This may provide an explanation as to why humans on average have a lower base-diaphyseal angle than African apes.

Table 1

Mean, number sampled (N), standard deviation (S.D.), and range of 4th MT length, and base, mid-shaft and head circumferences, in mm., in AL 333-160 and the comparative sample.

	4th MT Length			Base Circ.			Midshaft Circ.			Head Circ.		
	Mean (N)	S.D.	Range	Mean (N)	S.D.	Range	Mean (N)	S.D.	Range	Mean (N)	S.D.	Range
AL 333-160	59.9			60.4			23.86			43.8		
Skhul 4	77			64			29.83			55.6		
La Ferrassie 1	75.6			74.4			31.24			63.2		
LB 1/24	58.3			n/a			23.86			n/a		
STW 485	60			47.8			23.64			n/a		
OH8	59.75			53.28			26.05			n/a		
<i>H. sapiens</i> (m)	72.03 (107)	4.51	59.65 – 83.01	60.71 (107)	4.47	48.92 – 71.76	30.77 (107)	2.61	24.54 – 40.08	50.44 (107)	3.67	40.84 - 64.88
<i>H. sapiens</i> (f)	66.53 (79)	4.32	58.22 – 79.58	55.66 (80)	4.25	44.26 – 63.82	26.97 (79)	2.56	21.46 – 34.19	44.31 (79)	3.63	35.21 – 55.06
<i>G. b. beringei</i> (m)	72.28 (15)	3.21	67.13 – 78.28	69.09 (13)	3.4	65.69 – 77.24	31.56 (13)	2.46	27.87 – 36.33	65.01 (12)	2.77	60.68 – 70.01
<i>G. b. beringei</i> (f)	62.26 (13)	3.63	55.76 – 68.15	54.48 (12)	4.26	48.92 – 65.62	25.63 (12)	1.14	23.8 – 27.37	52.22 (12)	4.22	47.06 – 62.4
<i>G. b. graueri</i> (m)	74.51 (20)	8.01	55.26 – 88.77	66.28 (20)	5.8	53.89 – 73.1	28.15 (20)	2.88	22.08 – 33.32	61.75 (20)	5.41	51.07 – 69.48
<i>G. b. graueri</i> (f)	60.85 (7)	3.86	56.61 – 65.83	49.44 (7)	4.52	42.21 – 55.54	22.54 (7)	1.5	19.92 – 24.57	47.03 (7)	2.5	43.85 – 50.19
<i>G. gorilla</i> (m)	82.85 (47)	5.03	69.65 – 92.33	70.27 (47)	6.39	56.79 – 80.6	30.72 (36)	2.7	21.93 – 36.6	63.42 (36)	4.04	52.34 – 72.08
<i>G. gorilla</i> (f)	69.61 (29)	3.16	65.18 – 75.55	56.56 (29)	4.16	50 – 63.78	25.75 (17)	2.41	21.81 – 31.29	52.32 (17)	3.57	46.87 – 58.92
<i>P. paniscus</i>	65.95 (17)	3.22	61.73 – 73.77	47.89 (17)	3.56	41 – 56.12	19.81 (17)	1.11	18.46 – 22.4	43.95 (17)	3.77	36 – 52.22
<i>P. troglodytes</i>	67.35 (87)	4.51	55.44 – 75.87	49.35 (87)	5.13	36.9 – 65	21.87 (57)	1.78	18.81 – 26.3	49.31 (57)	3.55	41.34 – 57.76
<i>Pongo</i>	87.68 (38)	7.81	75.54 – 109.3	54.61 (38)	6.76	43.5 – 69.21	22.9 (38)	2.63	18.89 – 31.17	57.5 (38)	6.22	48.42 – 68.1
<i>N. larvatus</i>	69.5 (11)	5.94	56.81 – 75.65	40.09 (11)	4.34	32.42 – 47.9	17.22 (11)	1.97	13.56 – 19.58	38.33 (11)	3.54	31.82 – 43.16
<i>Papio</i>	64.74 (47)	6.38	48.72 – 75.71	44.68 (49)	5	33.78 – 56.14	18.23 (47)	2.44	12.5 – 23.08	36.31 (47)	3.59	30.12 – 44.16

Table 2

AL 333-160 4th MT measurements in mm. compared to those of human, great ape, proboscis monkey and baboon individuals with approximately (+/-1mm) the same 4th metatarsal length.^{a, b}

	Sex	Wt. Kg.	Length	BDP	BML	MSDP	MSML	HDP	HML	Base Circ.	Midshaft Circ.	Head Circ.
AL 333-160		44.6-60.1	59.9	17.1	13.1	9.1	6.1	13.4	8.5	60.4	23.9	43.8
<i>H. sapiens</i>	M	40.2(49.8)	59.6	17.2	12.1	9.3	7.5	12.1	8.8	58.7	26.3	41.8
<i>H. sapiens</i>	F	45.5	60.5	16.6	11.3	7.5	8.6	12.3	7.9	55.7	25.3	40.5
<i>H. sapiens</i>	F	63.6	60.6	15.6	11.7	7.9	8.5	15	8.1	54.5	25.7	46.2
<i>H. sapiens</i>	F	52.3	60.1	15.6	9.6	9.4	5.9	10.4	7.2	50.5	24.1	35.2
<i>G. b. beringei (sa)</i>	M	87	59	15.1	12.9	8.3	7.3	16	10.3	55.9	24.4	52.6
<i>G. b. beringei</i>	F	71.5	59.9	13.7	13.1	9.8	7.4	16.1	9.6	53.4	26.9	51.4
<i>G. b. beringei</i>	F	68	58.9	14	11.5	8.7	6.4	15.3	8.7	50.8	23.8	47.8
<i>G. b. beringei</i>	F	67	59.8	14	13.8	9.7	7.5	16.7	10.1	55.4	27	53.6
<i>G. b. graueri</i>	F	78	59.2	13.6	11.5	8.6	6.2	15.1	8.5	50.1	23.3	47.1
<i>G. b. graueri</i>	M	110	59.2	14.6	13.2	8.5	5.6	17.3	8.8	55.6	22.1	52.4
<i>P. paniscus</i>	F	21.5	60.9	13.2	10.4	6.8	5.3	12.7	7.7	47.3	19	40.9
<i>P. troglodytes</i>	F	31.4	58.9	12.3	11.7	6.8	5.7	13.3	9.1	48	19.7	44.9
<i>P. troglodytes</i>	M	42.5	60.7	15.6	12.8	7.3	6.1	15	10.2	56.7	21.1	50.4
<i>P. troglodytes (sa)</i>	F	31.5	60.2	12	12.5	7	5.7	14.4	9.1	49	19.9	46.9
<i>P. troglodytes</i>	F	50	59.7	12.4	11	7.1	6	14.7	8.6	46.8	20.6	46.6
<i>Pongo (juv)</i>	M	12.7	60.3	8.8	7.7	5	4.3	12.7	7.9	33	14.6	41
<i>N. larvatus</i>	F	11.3	59.8	10.1	7	4.4	4.7	7.9	8.8	34.1	14.3	33.5
<i>Papio (sa)</i>	F	?	60.4	13.8	8.8	5.1	6.1	8.8	8.8	45.3	17.5	35.2
<i>Papio</i>	F	16	60.8	11.7	8.2	5.1	6.1	9.3	8.2	39.8	17.6	35.1
<i>Papio</i>	F	10.5	60.4	11.7	8	4.5	5.1	8.2	7.8	39.5	15.2	32.2
<i>Papio</i>	F	12.3	59.6	11.7	7.4	4.9	4.9	8.5	7.7	38.3	15.5	32.5
<i>Papio</i>	F	13.5	59.2	11.2	8.6	4.3	5.6	8.3	7.3	39.6	15.5	31.2
<i>Papio</i>	F	14.5	60.8	11.9	9.2	5.2	5.4	9.1	7.2	42	16.5	32.7
<i>Papio</i>	F	10.2	59	10.8	7.4	4.4	5.3	8.5	7.1	36.4	15.3	31.2

^a Body weight in kilograms. BDP= base dorsoplantar width, BML= base mediolateral width, MSDP= midshaft dorsoplantar width, MSML= midshaft mediolateral width, HDP= head dorsoplantar width, HML= head mediolateral width, (sa)= subadult (juv)= juvenile. Human body mass estimates in parentheses calculated with the following formula: body mass= 2.239 x femoral head diameter - 39.9 (McHenry, 1992). Primate body mass estimates in parentheses calculated with methods described in Sarmiento et al. (1996).

^b AL 333-160 measures and those in comparative sample closely approximating the AL 333-160 value in bold.

Table 3

AL 333-160 4th MT measurements in mm. compared to those of human and great ape individuals with approximately (+/- 1mm) the same fourth metatarsal base circumference^a

	Sex	Wt. Kg.	Length	BDP	BML	MSDP	MSML	HDP	HML	Midshaft Circ.	Base Circ.
AL 333-160	?	44.6-60.1	59.9	17.1	13.1	9.1	6.1	13.4	8.5	23.9	43.8
<i>H. sapiens</i>	M	50.2 (54.2)	74.8	17.5	12.7	11.3	7.3	13	9.2	29.2	44.4
<i>H. sapiens</i>	F	52.1(58.1)	68.1	17	12.8	12.7	7.8	12.8	8.5	32.1	42.6
<i>H. sapiens</i>	F	40.0 (44.8)	64.3	17.7	12	8.7	6.1	12.9	8.1	23.2	42
<i>G. b. graueri</i>	M	160	65.6	16.7	13.4	10.4	6.3	19.5	10	26.2	59.1
<i>G. gorilla</i>	F	?	75.4	17.2	13.1	9.7	6.5	17.4	10.7	25.5	56.1
<i>G. gorilla</i>	F	62	67.9	16.3	13.8	9.8	8.5	18	9.7	28.7	55.6
<i>G. gorilla</i>	F	55.5	72.5	16.7	13.6	8.6	8	16	11	26.1	54.1
<i>G. gorilla</i>	F	76	68	16.2	14.5	7.6	7.5	17.1	10.7	23.6	55.6
<i>G. gorilla</i>	M	71	72	16	14	9.6	6.9	16.7	10	26	53.4
<i>Pongoe</i>	M	72.7	102	15.4	14.7	8.3	7.7	19.8	13.7	25.1	67
<i>Pongo</i>	M	86.6	95.5	15.5	14.8	8.4	7.3	19.4	12.4	24.4	63.6
<i>Pongo</i>	F	40	86	16.4	14.1	7.9	6.7	16.9	11.6	23	57

^a See Table 2 for abbreviations and explanation.

Table 4

AL 333-160 4th MT measurements in mm. compared to those of human and great ape individuals of with approximately (+/- 0.5mm) the same fourth metatarsal midshaft circumference^a

	Sex	Wt. Kg.	Length	BDP	BML	MSDP	MSML	HDP	HML	Head Circ.	Base Circ.
AL 333-160	?	44.6-60.1	59.9	17.1	13.1	9.1	6.1	13.4	8.5	60.4	43.8
<i>H. sapiens</i>	F	52.3 (33.3)	60.1	15.6	9.6	9.4	5.9	10.4	7.2	50.5	35.2
<i>H. sapiens</i>	F	46.0 (44.7)	71.8	14.2	13	9.3	6.2	12.7	8.4	54.3	42.1
<i>H. sapiens</i>	F	31.2 (50.0)	65.2	15	12.6	8.9	6.6	12.5	8	55.2	41
<i>H. sapiens</i>	F	38.1 (43.9)	62.7	15.8	11	8.9	6.5	11.8	7.9	53.7	39.5
<i>G. b. beringei</i>	F	68	58.9	14	11.5	8.7	6.4	15.3	8.7	50.8	47.8
<i>G. b. beringei</i>	F	83	55.8	13.2	11.3	8.5	6.8	14.7	9.5	48.9	48.4
<i>G. gorilla</i>	F	72.5	69.9	15.4	12.9	7.9	7.5	15.4	9	56.6	48.7
<i>G. gorilla</i>	F	59	69.7	14	12.1	8.5	6.4	14.5	9.4	52.3	47.9
<i>G. gorilla</i>	F	65	69.2	15.1	14.2	7.6	7.5	15.5	8.7	58.6	48.5
<i>G. gorilla</i>	F	73	65.7	14.6	12.7	8.7	6.5	15	8.6	54.6	47.1
<i>G. gorilla</i>	F	76	68	16.2	14.5	7.6	7.5	17.1	10.7	61.3	55.6
<i>P. troglodytes</i>	M	50	61.8	14.7	14.1	7.5	7.5	16.1	9.9	57.7	51.8
<i>P. troglodytes</i>	M	52.2	68.6	14.3	13.2	7.7	7.4	16	9.9	55	51.8
<i>P. troglodytes</i>	M	54	69	13.7	12.5	8.5	6.6	17	10.4	52.4	54.8
<i>P. troglodytes</i>	F	45.4	68.9	14.5	12.9	8.5	6.7	16.2	10	54.8	52.3
<i>P. troglodytes</i>	F	41	74.4	14.2	12.7	8.1	7	16.2	9.5	53.8	51.4
<i>P. troglodytes</i>	M	49.9	69.9	13.2	11.2	8	7.4	15.8	9.7	48.8	50.9
<i>P. troglodytes</i>	M	70	71.4	14.8	13	8.2	6.8	17.7	11.2	55.5	57.8
<i>P. troglodytes</i>	M	46.7	73.1	14.2	12	7.9	7	16.7	11	52.5	55.3
<i>Pongo</i>	F	31.8	81	14.7	11.9	8.2	7	16.2	9.8	53.1	52

^a See Table 2 for abbreviations and explanation.

Table 5

AL 333-160 4th MT measurements in mm. compared to those of humans, great apes, proboscis monkey, and baboon individuals with approximately (+/-1mm) the same fourth metatarsal head circumference^a

	Sex	Wt. Kg.	Length	BDP	BML	MSDP	MSML	HDP	HML	Base Circ.	Midshaft Circ.	Head Circ.
AL 333-160	?	44.6-60.1	59.9	17.1	13.1	9.1	6.1	13.4	8.5	60.4	23.9	43.8
<i>H. sapiens</i>	M	41.0(55.1)	74.4	17.5	11.2	11.8	7.6	13.5	8.3	57.3	30.5	43.5
<i>H. sapiens</i>	M	50.2(54.2)	74.8	17.5	12.7	11.3	7.3	13	9.2	60.3	29.2	44.4
<i>H. sapiens</i>	F	43.0(52.9)	71.1	17.2	12	10.8	7.2	13.1	8.9	58.4	28.3	43.9
<i>H. sapiens</i>	F	37.0(52.0)	67	16.7	12.3	9.2	6.9	12.8	8.7	58.1	25.2	42.9
<i>H. sapiens</i>	F	45.4(44.9)	68.8	17.6	10.1	9.6	6.1	12.8	9.2	55.5	24.6	44
<i>G. b. graueri</i>	F	59	56.6	12.3	10.4	7.1	6.6	14.2	7.8	45.3	21.4	43.9
<i>P. paniscus</i>	F	(34)	64.2	13	10.8	7.3	4.9	13.6	7.8	47.6	19	42.8
<i>P. paniscus</i>	F	33	63.8	12.4	11.1	7	5.5	13.1	8.9	46.9	19.7	44.1
<i>P. paniscus</i>	F	27	66.7	15	10.3	6.9	5.4	13.7	7.9	50.6	19.3	43.2
<i>P. paniscus</i>	F	40	65.5	12.7	10.6	7.3	5.1	13.5	8.5	46.6	19.4	44.1
<i>P. paniscus</i>	F	(22)	61.7	13.2	11.5	7.1	5.9	13.1	9.2	49.3	20.4	44.6
<i>P. troglodytes</i>	M	63	66.7	11.5	11.5	6.6	6.1	13.6	8.7	46	19.9	44.5
<i>P. troglodytes</i>	M	(42)	55.4	11.8	8.7	6.6	5.5	13.5	8.6	41	19	44.3
<i>N. larvatus</i>	M	23.6	75.6	14.1	9.8	6	6	11.6	10	47.9	18.9	43.2
<i>Papio</i>	M	(23)	72.4	15.1	11.6	6.6	7.3	11.1	11	53.3	21.8	44.2
<i>Papio</i>	M	(25.5)	72.6	15.4	9.6	5.9	7.4	11.6	10.1	50.2	20.8	43.4

^a See Table 2 for abbreviations and explanation.

Table 6

AL 333-160 4th MT measurements in mm. compared to those of humans and great apes with more than one 4th MT measure similar to that of AL 333-160^a

	Sex	Wt. Kg.	Length	BDP	BML	MSDP	MSML	HDP	HML	Base Circ.	Midshaft Circ.	Head Circ.
AL 333-160	?	44.6-60.1	59.9	17.1	13.1	9.1	6.1	13.4	8.5	60.4	23.9	43.8
<i>H. sapiens</i>	F	52.3(33.3)	60.1	15.6	9.6	9.4	5.9	10.4	7.2	50.5	24.1	35.2
<i>H. sapiens</i>	M	50.2(54.2)	74.8	17.5	12.7	11.3	7.3	13	9.2	60.3	29.2	44.4
<i>H. sapiens</i>	F	45.4(48.9)	68.8	17.6	10.1	9.6	6.1	12.8	9.2	55.5	24.6	44
<i>H. sapiens</i>	F	40.0(44.8)	64.3	17.7	12	8.7	6.1	12.9	8.1	59.4	23.2	42
<i>G. b. beringei</i>	F	68	58.9	14	11.5	8.7	6.4	15.3	8.7	50.8	23.8	47.8
<i>G. b. graueri</i>	F	78	59.2	13.6	11.5	8.6	6.2	15.1	8.5	50.1	23.4	47.1
<i>G. gorilla</i>	F	76	68	16.2	14.5	7.6	7.5	17.1	10.7	61.3	23.6	55.6
<i>P. paniscus</i>	F	27	65.5	12.7	10.6	7.3	5.1	13.5	8.5	46.6	19.4	44.1
<i>P. troglodytes</i>	M	(42)	55.4	11.8	8.7	6.6	5.5	13.5	8.6	41	19	44.3
<i>Pongo</i>	M	86.6	95.5	15.5	14.8	8.4	7.3	19.4	12.4	60.7	24.4	63.6

^aSee Table 2 for abbreviations and explanation.

Table 7

AL 333-160 4th MT measures in mm. compared to those of humans and great apes within the AL 333-160 body weight range.

	Sex	Wt. Kg.	Length	BDP	BML	MSDP	MSML	HDP	HML	Base Circ.	Midshaft Circ.	Head Circ.
AL 333-160	?	44-60	59.9	17.1	13.1	9.1	6.1	13.4	8.5	60.4	23.9	43.8
<i>H. sapiens</i>	F	45.4(48.9)	68.8	17.6	10.1	9.6	6.1	12.8	9.2	55.5	24.7	44
<i>H. sapiens</i>	M	53.4(60.7)	69.6	17.7	14.2	10.5	7.5	14.5	10.3	63.7	28.3	49.5
<i>H. sapiens</i>	M	62.5(62.3)	76.4	15.9	12.2	11.6	7.2	15	9.9	56.1	29.5	49.8
<i>G. b. graueri</i>	F	59	56.6	12.3	10.4	7.1	6.6	14.2	7.8	45.3	21.4	43.9
<i>G. gorilla (juv)</i>	M	44	73.9	17.5	14	9.3	7.3	16.5	11.4	62.9	25.9	55.8
<i>G. gorilla</i>	F	55.5	72.5	16.7	13.6	8.6	8	16	11	60.6	26.1	54
<i>P. paniscus</i>	M	48	65	9.2	11.4	6.6	5.2	12.9	7.3	41	18.5	40.5
<i>P. paniscus</i>	F	44	73.8	12.9	15.2	7.7	6.3	15.8	10.3	56.1	22	52.2
<i>P. paniscus</i>	M	48	70.8	13	12	7	5.5	13.6	6.6	50	19.7	40.4
<i>P. troglodytes</i>	M	45	63.7	12.9	12.4	6.5	5.5	9.2	14.5	50.5	18.8	47.3
<i>P. troglodytes</i>	M	49.9	69.9	13.2	11.2	8	7.4	15.8	9.7	48.8	24.1	50.9
<i>P. troglodytes</i>	M	55	69	13.5	11.6	7.6	7	16.8	10.1	50.2	22.9	53.7
<i>Pongo</i>	F	45.4	88.4	14.4	11.5	7.8	6.5	15.9	10.7	51.8	22.5	53.2
<i>Pongo (sa)</i>	M	54.4	92.7	13.7	12.1	8.9	6	17.9	10.6	51.6	23.4	57
<i>Pongo</i>	F	44.5	82.5	11.5	10.7	7.1	5.9	16.3	9.7	44.2	20.4	52

^aSee Table 2 for abbreviations and explanation.

Table 8

Fourth and Fifth MT and proximal phalangeal lengths in mm of AL 333 feet compared to those of *G. b. beringei* and a human with approximately the same 4th MT length, and to two humans with approximately the same 2nd proximal phalangeal length.^{a, b, c}

	Sex	Wt. Kg.	4th MT length	5th MT length	PP1 length	PP2 length	PP3 length	PP4 length	PP5 length
AL 333a	?	44-60	59.9	67.2	27.5b	32.2	34.5	32.8	28.6
<i>G. b. beringei</i>	F	67	59.8	67.6	27.7	37.3	38.1	33.1	31.1
<i>G. b. beringei</i>	F	68	58.9	62.8	24.5	32.5	35.3	35.5	29.7
<i>G. b. beringei</i>	F	81	58.6	62.7	27.6	34.6	37.2	38	30.4
<i>G. b. beringei</i>	F	71.5	59.9	64.1	26.8	33.3	37.8	37.1	31
<i>H.sapiens</i>	M	40.2	59.6	59.7	31.4	27.1	24	22.4	21.3
<i>H.sapiens</i>	M	68.5	74.8	73.6	38.1	31.8	28	27.3	24.2
<i>H.sapiens</i>	M	51.8	70.2	71.8	37.5	32.2	31.8	28.8	26.4

^a Phalangeal lengths AL 333-115, 4th MT length AL 333-160, 5th Mt length estimated from AL 333-78 and AL 333-115 (Latimer et al., 1982). PP= proximal phalanx.

^b Hadar 1st proximal phalanx length is based on proportion of bone length to base radius in *G. beringei*(N=37) and humans(N=30) and has a +/- 1.5 mm error.

^c Hadar measures and those in comparative sample closely approximating the Hadar value in bold.

Table 9

Linear regression statistics of base circumference plotted against fourth metatarsal length in mm. See Figure 1.

	Intercept	Slope	R ²	R ² Adj.	Sample number
<i>H. sapiens (m)</i>	24.39	0.504	0.259	0.252	107
<i>H. sapiens (f)</i>	27.14	0.43	0.192	0.182	79
<i>G. b. beringei (m)</i>	40.396	-0.122	0.023	-0.066	13
<i>G. b. beringei (f)</i>	19.409	0.01	0.107	0.017	12
<i>G. b. graueri (m)</i>	27.087	0.526	0.528	0.502	20
<i>G. b. graueri (f)</i>	41.462	0.131	0.013	-0.185	7
<i>G. gorilla (m)</i>	32.276	0.459	0.13	0.111	47
<i>G. gorilla (f)</i>	39.541	0.244	0.035	-0.001	29
<i>P. paniscus</i>	-0.023	0.726	0.422	0.4	17
<i>P. troglodytes</i>	30.21	0.284	0.062	0.051	87
<i>Pongo</i>	-3.078	0.658	0.577	0.566	38
<i>N. larvatus</i>	-6.481	0.67	0.841	0.824	11
<i>Papio</i>	1.029	0.676	0.718	0.711	47

Table 10

Linear regression statistics of midshaft circumference plotted against fourth metatarsal length. See Figure 2.

	Intercept	Slope	R²	R² Adj.	Sample number
<i>H. sapiens (m)</i>	5.415	0.352	0.368	0.362	107
<i>H. sapiens (f)</i>	8.09	0.284	0.229	0.219	79
<i>G. b. beringei (m)</i>	40.4	-0.122	0.023	-0.066	13
<i>G. b. beringei (f)</i>	19.409	0.01	0.107	0.018	12
<i>G. b. graueri (m)</i>	9.546	0.25	0.481	0.453	20
<i>G. b. graueri (f)</i>	4.077	0.303	0.612	0.534	7
<i>G. gorilla (m)</i>	2.744	0.339	0.421	0.404	36
<i>G. gorilla (f)</i>	5.505	0.29	0.165	0.11	17
<i>P. paniscus</i>	4.931	0.226	0.431	0.394	17
<i>P. troglodytes</i>	6.756	0.225	0.37	0.359	57
<i>Pongo</i>	2.218	0.236	0.492	0.478	38
<i>N. larvatus</i>	-3.507	0.298	0.812	0.791	11
<i>Papio</i>	-2.112	0.314	0.672	0.664	47

Table 11

Linear regression statistics of head circumference in mm. plotted against fourth metatarsal length. See Figure 3.

	Intercept	Slope	R ²	R ² Adj.	Sample number
<i>H. sapiens (m)</i>	32.383	0.251	0.095	0.086	107
<i>H. sapiens (f)</i>	19.552	0.372	0.196	0.185	79
<i>G. b. beringei (m)</i>	74.087	-0.125	0.019	-0.08	12
<i>G. b. beringei (f)</i>	18.231	0.545	0.235	0.158	12
<i>G. b. graueri (m)</i>	20.404	0.555	0.676	0.658	20
<i>G. b. graueri (f)</i>	12.396	0.569	0.773	0.728	7
<i>G. gorilla (m)</i>	18.943	0.538	0.473	0.457	36
<i>G. gorilla (f)</i>	30.645	0.31	0.087	0.026	17
<i>P. paniscus</i>	5.455	0.584	0.248	0.198	17
<i>P. troglodytes</i>	18.942	0.453	0.376	0.364	57
<i>Pongo</i>	4.219	0.608	0.583	0.571	38
<i>N. larvatus</i>	0.771	0.563	0.891	0.879	11
<i>Papio</i>	6.232	0.465	0.681	0.674	47

Table 12

Mean(X), number sampled (N), standard deviation (S.D.), and range of base-diaphysis angle and torsion in degrees °. See Figures 4-5.

	Base-Diaphysis Angle			Torsion		
	Mean (N)	S.D.	Range	Mean (N)	S.D.	Range
AL 333-160	84			17		
<i>H. sapiens (m)</i>	78.86 (91)	4.61	61 - 86	23.99 (91)	8.16	6 - 49
<i>H. sapiens (f)</i>	82.5 (64)	4.26	72 - 91	28 (64)	8.39	4 - 44
<i>G. b. beringei (m)</i>	89.8 (5)	9.68	75 - 100	3.80 (5)	7.43	0 - 17
<i>G. b. beringei (f)</i>	98 (1)	n/a	n/a	13 (1)	n/a	n/a
<i>G. gorilla (m)</i>	93.4 (15)	2.2	89 - 96	4.6 (15)	2.56	0 - 9
<i>G. gorilla (f)</i>	92.31 (16)	2.06	88 - 97	3.25 (16)	2.11	0 - 6
<i>P. paniscus</i>	95.75 (12)	3.44	90 - 103	6.79 (12)	6.06	-3 - 17
<i>P. troglodytes</i>	92.38 (37)	3.3	82 - 102	3.26 (37)	3.24	-1.5 - 16
<i>Pongo</i>	93.96 (25)	2.42	91 - 99	3.16 (25)	6.32	-14 - 18
<i>Papio</i>	97.17 (18)	2.71	93 - 102	21.39 (18)	4.39	11 - 28

Table 13

Number of individual humans, gorillas and baboons sampled with a present, absent or indeterminate right 4th MT ectocuneiform facet. Percentage of total number of individuals with condition in parentheses.

	Total	Present	Indeterminate	Absent
<i>H. sapiens</i> Number	19	11 (57.9)	2 (10.5)	6(31.6)
<i>G. gorilla</i> Number	19	1(5.26)	1(5.26)	17(89.5)
<i>Papio</i> Number	19	9(47.4)	2(10.5)	8(42.1)

Table 14

Statistical significance of differences in ectocuneiform facet occurrence in humans, gorillas and baboons.

	P Value	Significant Difference
<i>H. sapiens vs. G. gorilla vs. Papio</i>	0.002	Yes
<i>H. sapiens vs. G. gorilla</i>	0.003	Yes
<i>H. sapiens vs. Papio</i>	0.8924	No
<i>G. gorilla vs. Papio</i>	0.0025	Yes

Table 15

Mean (X), sample number (N) and standard deviation (s.d.) of the 4th MT base dorsoplantar (DP) and mediolateral (ML) diameters in mm and DP/ML diameter ratios in AL 333-160 humans, great apes, baboons and proboscis monkeys.

	BDP			BML			BDP/BML		
	Mean (N)	S.D.	Range	Mean (N)	S.D.	Range	Mean (N)	S.D.	Range
AL333-160	17.1			13.1			1.31		
<i>H. sapiens (m)</i>	18.12 (107)	1.53	13.62 - 22.04	12.23 (107)	1.24	9.13 - 15.51	1.49 (107)	0.17	1.12 - 2.02
<i>H. sapiens (f)</i>	16.58 (80)	1.37	13.38 - 19.97	11.24 (80)	1.14	8.64 - 14.11	1.48 (80)	0.14	1.1 - 1.81
<i>G. b. beringei (m)</i>	18.57 (13)	1.11	16.65 - 20.6	15.98 (13)	1.02	14.16 - 18.02	1.17 (13)	0.09	1.03 - 1.33
<i>G. b. beringei (f)</i>	14.41 (12)	1.47	12.98 - 18.45	12.83 (12)	0.97	11.29 - 14.36	1.13 (12)	0.1	1.01 - 1.3
<i>G. b. graueri (m)</i>	18.01 (20)	1.72	14.5 - 20.5	15.13 (20)	1.35	12.45 - 16.95	1.19 (20)	0.07	1.06 - 1.34
<i>G. b. graueri (f)</i>	13.52 (7)	0.7	12.31 - 14.49	11.2 (7)	2.02	7.18 - 13.28	1.25 (7)	0.31	1.07 - 1.94
<i>G. gorilla (m)</i>	19.29 (47)	1.69	14.96 - 21.95	15.84 (47)	1.88	10.92 - 18.96	1.23 (47)	0.13	1 - 1.66
<i>G. gorilla (f)</i>	15.54 (29)	1.3	13.51 - 18.37	12.74 (29)	1.23	10.29 - 14.75	1.23 (29)	0.13	1.01 - 1.57
<i>P. paniscus</i>	12.96 (17)	1.01	11.35 - 15.15	10.98 (17)	0.98	9.15 - 12.91	1.18 (17)	0.09	1.05 - 1.46
<i>P. troglodytes</i>	13.14 (87)	1.26	10.38 - 16.1	11.54 (87)	1.59	8.07 - 16.5	1.15 (87)	0.13	0.92 - 1.55
<i>Pongo</i>	14.57 (38)	1.84	11.47 - 18.75	12.74 (38)	1.68	10.27 - 15.98	1.15 (38)	0.09	1.04 - 1.35
<i>N. larvatus</i>	11.53 (11)	1.26	9.6 - 14.11	8.52 (11)	1.13	6.61 - 9.95	1.36 (11)	0.13	1.08 - 1.53
<i>Papio</i>	13 (49)	1.36	10.4 - 15.51	9.33 (49)	1.33	6.49 - 13.04	1.41 (49)	0.13	1.05 - 1.74

Acknowledgements

The author thanks Esteban Sarmiento and Jeff Meldrum for an invaluable contribution of data, discussion, and methodological advice on this research, Peter Dodson, Elizabeth Strasser, Maciej Henneberg, Jeff Laitman, Scott Williams, Dave Frayer, William Harcourt-Smith, and Alan Mann for helpful comments, the University of Pennsylvania University Scholars Program, McNair Scholars Program, Department of Anthropology, Department of Earth and Environmental Sciences Paleobiology Stipend, and the Penn Museum for funding and support. Special thanks are due to Lyman Jellema at the Cleveland Museum of Natural History for his help and advice. Finally, and most importantly, the author thanks Janet Monge for her mentorship, generosity, and inspiration.

References Cited

- Berillon, G., 2003. Assessing the longitudinal structure of the early hominid foot: a two-dimensional architecture analysis. *Hum. Evol.* 18(3-4), 113-122.
- Berillon, G., 2004. In what manner did they walk on two legs? An architectural perspective for the functional diagnostics of the early hominid foot. In: Meldrum, D.J, Hilton, C.E. (Eds.), *From Biped to Strider: The Emergence of Modern Human Walking, Running, and Resource Transport*. Kluwer Academic and Plenum, New York, pp. 85-100.
- Brunet, M., Guy, F., Pilbeam, D., Lieberman, D.E., Likius, A., Mackaye, H.T., De Leon, M.P., Zollikofer, C.P.E., Vignaud, P., 2005. New material of the earliest hominid from the upper Miocene of Chad. *Nature* 434, 752-755.
- Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Djimdoumalbaye, A., Beauvillain, A., Blondel, C., Bocherens, H., Boisserie, J.R., DeBonis, L., Coppens, Y., Dejax, J., Denys, C., Düringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Campomanes, P.P., De Leon, M.P., Rage, J.C., Sapanetkk, M., Schusterq, M., Sudrek, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A., Zollikofer, C., 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418, 145-151.
- Bush, M.E., Lovejoy, C.O., Johanson, D.C., Coppens, Y., 1982. Hominid carpal, metacarpal, and phalangeal bones recovered from the Hadar formation: 1974-1977 collections. *Amer. J. Phys. Anthropol.* 57, 651-677.
- Campbell, B.G., Loy, J. 2000. *Humankind Emerging*. Allyn and Bacon, Boston.
- Cramer, D.L., 1977. *Craniofacial Morphology of Pan paniscus*. Contrib. to Primatol. 10. S. Karger, Basel.
- Darwin, C., 1859. *The Origin of Species by Means of Natural Selection or the Preservation of Favored Races in the Struggle for Life*. The Modern Library, Murray, New York.
- Davis, P.R., 1964. Hominid fossils from Bed I Olduvai Gorge, Tanganyika, a tibia and a fibula. *Nature* 201, 967-970.
- Day, M.H., 1969. Femoral fragment of a robust australopithecine from Olduvai Gorge, Tanzania. *Nature* 221, 230-233
- Deloison, Y., 2004. A New Hypothesis on the Origin of Hominid Locomotion. In: Meldrum, D.J, Hilton, C.E. (Eds.), *From Biped to Strider: The Emergence*

- of Modern Human Walking, Running, and Resource Transport. Kluwer Academic and Plenum, New York, pp. 35-47.
- DeSilva, J.M., 2010. Revisiting the midtarsal break. *Amer. J. Phys. Anthropol.* 141, 245–258.
- Ditchfield, P., Harrison, T., 2011. Sedimentology, Lithostratigraphy and Depositional History of the Laetoli area.. In: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context: Geology, Geochronology, Paleoecology, and Paleoenvironment, Vertebrate Paleobiology and Paleoanthropology*. Springer, Dodrecht, Netherlands, pp. 47-76.
- Duncan, A.S., Kappelman, J., Shapiro, L.J., 1994. Metatarsophalangeal joint function an positional behavior in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 93, 67 81.
- Eftman, H., Manter, J., 1935. The evolution of the human foot, with special reference to the joints. *J. Anat. London* 70, 56-67.
- Fenart, R., DeBlock, R., 1973. *P. paniscus* and *P. troglodytes* craniometrie. Tome 1. *Ann. Mus. Afrique Centrale. Ser. en 8^o. Sci. Zool.* no. 204.
- Gilbert, C.G. Rossie J.B., 2007. Congruence of molecules and morphology using a narrow allometric approach. *Proc. Natl. Acad. Sci. U. S. A.* 104,11910–11914
- Haile-Selassie, Y., 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* 412,178-181.
- Hamrick, M. 2011. The developmental origin of mosaic evolution in the primate limb skeleton. *Evol. Biol.* 1–9.
- Harcourt-Smith, W.E.H.,2002. Form and function in the hominoid tarsal skeleton. Ph.D. Thesis, University College London, London.
- Harcourt-Smith, W.E.H., Aiello, L., 2004. Fossils, feet, and the evolution of human bipedal locomotion. *J. Anat.* 204, 403–416.
- Johanson, D.C., Taieb, M., 1976. Plio-pliestocene hominid discoveries in Hadar Ethiopia. *Nature* 45, 217-234.
- Johanson, D.C., Lovejoy, C.O., Burstein, A.H., Heiple, K.G., 1976. Functional implications of the Afar knee joint (abstract). *Amer. J. Phys. Anthropol* 44, 188.

- Jungers, W.L., 1987, Body size and morphometric affinities of the appendicular skeleton in *Oreopithecus bambolii* (IGF 11778). *J. Hum. Evol.* 16, 445–456.
- Jungers, W.L., Harcourt-Smith, W.E.H., Wunderlich, R.E., Tocheri, M.W., Larson, S.G., Sutikna, T., Rhokus Awe Due, Morwood, M.J., 2009. The foot of *Homo floresiensis*. *Nature* 459, 81-84.
- Keith, A., 1947. Australopithecinae or Dartians. *Nature* 159, 377.
- Kern, H.M., Straus, W.L. Jr., 1949. The femur of *Plesianthropus transvaalensis*. *Amer. J. Phys. Anthropol.* 7, 53-77.
- Kennedy, G.E. 1985. Bone thickness in *Homo erectus*. *J. Hum. Evol.* 14, 699-708.
- Kimbel, W.H., Deleuzene, L.K., 2009. Lucy Redux: a review of research on *Australopithecus afarensis*. *Yrbk. Phys. Anthropol.* 52, 2–48.
- Kimbel, W.H., Johanson, D.C., Rak, Y., 1994. The first skull of *Australopithecus afarensis* and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* 368, 449-451.
- Lamy, P., 1986. The settlement of the longitudinal plantar arch of some African Plio-Pleistocene hominins: a morphological study. *J. Hum. Evol.* 15, 31–46.
- Latimer, B.M., 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. *Origine(s) de la bipédie chez les hominides*. CNRS, Paris, pp. 369-386.
- Latimer B.M., Lovejoy, C.O., 1989. The calcaneus of *Australopithecus afarensis* and its implication for the evolution of bipedality. *Amer. J. Phys. Anthropol.* 78, 369-386.
- Latimer, B.M., Lovejoy, C.O., 1990a. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. *Amer. J. Phys. Anthropol.* 82, 125-133.
- Latimer, B.M., Lovejoy, C.O., 1990b. Metatarsophalangeal joints of *Australopithecus afarensis*. *Amer. J. Phys. Anthropol.* 83, 13-23.
- Latimer, B.M., Lovejoy, C.O., Johanson, D.C., Coppens, Y., 1982. Hominid tarsal, metatarsal, and phalangeal bones recovered from the Hadar formation: 1974-1977 collections. *Amer. J. Phys. Anthropol.* 57, 701-719.

- Lauder, G.V., 1995. On the inference of function from structure. In: Thomason, J.J. (Ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge, pp. 1–18.
- Leakey M.G., Feibel, C.S., McDougall, I., Walker A., 1995. New four-million-year-old hominid species from Kanapoi and Allia bay, Kenya. *Nature* 376, 565-571.
- Leakey, M.D., Harris, J.M., 1987. *Laetoli: A Pliocene Site in Northern Tanzania*. Oxford University Press, Oxford.
- Le Gros Clark, W. E., 1946. Significance of the Australopithecinae. *Nature* 157, 863-865.
- Le Gros Clark, W. E., 1947. The importance of the fossil Australopithecinae in the study of human evolution. *Sci. Prog.* 139, 377-395.
- Le Gros Clark, W. E., 1950. Hominid characters of the Australopithecine dentition. *J. Roy. Anthropol. Inst.* 80, 37-54.
- Le Gros Clark, W. E., 1955a. The os inominatum of the recent Pongidae with special reference to that of the Australopithecinae. *Amer. J. Phys. Anthropol.* 13, 19-27.
- Le Gros Clark, W. E., 1955b. *The fossil evidence for human evolution*. University Press, Chicago.
- Lovejoy, C.O., 1975. Biomechanical perspectives on the lower limb of early hominids. In: Tuttle, R.H. (Ed.), *Primate Functional Morphology and Evolution*. Mouton, The Hague, pp. 291-326.
- Lovejoy, C. O., 1978. A biomechanical review of the locomotor diversity of early hominids. In: Jolly, C.J. (Ed.), *Early Hominids of Africa*. St. Martins Press, New York, pp. 403-429.
- Lovejoy, C.O., 2005a. The natural history of human gait and posture. Part 1. Spine and pelvis. *Gait and Posture* 21, 95-112.
- Lovejoy, C.O., 2005b. The natural history of human gait and posture. Part 1. Hip and thigh. *Gait and Posture* 21, 113-124.
- Lovejoy, C.O., Johanson, D.C., Coppens, Y., 1982. Hominid lower limb bones recovered from the Hadar Formation: 1974–1977 collections. *Am. J. Phys. Anthropol.* 57, 679–700.

- Lu, Z., D.J. Meldrum, D.J., Huang, Y., He, J., Sarmiento, E.E., 2011. The Jinniushan hominin pedal skeleton from the late Middle Pleistocene of China. *Homo: J. Comp. Hum. Biol.* 62, 389–401.
- Mayr, E., 1950. Taxonomic categories in fossil hominids. *Cold Spring Harbor Symposium on Quantitative Biology* 13, 109-118.
- Martin, R., Salle, K., 1964. *Lehrbuch der Anthropologie IV*. Gustav Fischer, Stuttgart.
- McHenry, H.M., 1986. Size variation in the postcranium of *Australopithecus afarensis* and extant species of Hominoidea. *Hum. Evol.* 1, 149-156.
- McHenry, H.M., 1991. First steps? Analyses of the postcranium of early hominids. In: Coppens, Y., Senut, B. (Eds.), *Origine(s) de la bipédie chez les hominides*. CNRS, Paris, pp. 133-141.
- McHenry, H.M., 1992. Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 87, 407-431
- McHenry, H.M., 1994. Tempo and mode in human evolution. *Proc. Nat. Acad. Sci.* 91, 6780-6786.
- Meldrum, D.J., 1991. The kinematics of the cercopithecine foot on arboreal and terrestrial substrates with implications for the interpretation of hominid terrestrial adaptations. *Am. J. Phys. Anthropol.* 84:273-289
- Meldrum, D.J., 2004. Fossilized Hawaiian footprints compared to Laetoli hominid footprints. In: Meldrum, D.J., Hilton, C.E. (Eds.), *From Biped to Strider: The Emergence of Modern Human Walking, Running, and Resource Transport*. Kluwer Academic and Plenum, New York, pp. 63-84.
- Meldrum, D.J., 2007. New Perspectives on the Laetoli trackways: The earliest hominid footprints. In: Lucas S.G., Spielman J.A., Lockley, M.G. (Eds.), *Cenozoic Vertebrate Tracks and Traces*. New Mexico Museum of Natural History and Science Bulletin 42, 233-239
- Meldrum D.J, Lockley, M.G., Lucas S.G., Musiba, C.M., 2011. Ichnotaxonomy of the Laetoli trackways: The earliest hominin footprints. *J Afr Earth Sci* 60, 1-12.
- Napier, J. R., 1964. The evolution of bipedal walking in the hominoids. *Archives for Biology* 75, 673-708.
- Pickford, M., 2005. Orientation of the foramen magnum in late Miocene to extant

- African apes and hominids. *Anthropologie* 43(23), 191-198.
- Pickford, M., Senut, B., 2001. Millenium ancestor, a 6 million year old bipedal hominid from Kenya. *S. Afr. J. Sci.* 97, 1-2, 22.
- Rafferty, K.L., 1998. Structural design of the femoral neck in primates. *J. Hum. Evol.* 34, 361-383.
- Raichlen, D.A., Gordon, A.D., Harcourt-Smith, W.E.H., Foster, A.D., Haas, R. Jr., 2010 Laetoli Footprints Preserve Earliest Direct Evidence of Human-Like Bipedal Biomechanics. *PLoS One* 5(3), e9769
- Robinson, J.T., 1962a. The origin and adaptive radiation of the Australopithecinae. In: Kurth, G. (ed.), *Evolution and Hominisation*. Gustav Fischer Verlag, Stuttgart.
- Robinson, J.T., 1962b. Australopithecines and artefacts at Sterkfontein. Part I. Sterkfontein stratigraphy and the significance of the extension site. *S. Afr. Archaeol. Bull.* 17(66), 87-107.
- Robinson, J.T., 1965. *Homo habilis* and the Australopithecines. *Nature* 205, 121-124.
- Robinson, J.T., 1967. Variation and the taxonomy of the early hominids. In: Dobzhansky, T., Hecht, M.K. Steere, W.C. (Eds.), *Evolutionary Biology*. Apple-Century-Crofts, New York, pp. 69-100.
- Robinson, J.T., 1972a. *Early Hominid Posture and Locomotion*. University Press, Chicago.
- Robinson, J.T., 1972b. The bearing of East Rudolf fossils on early hominid systematics. *Nature* 240, 239-240.
- Sarmiento, E.E., 1983. The significance of the heel process among Anthropoids. *International J. Primatology* 4(2), 127-152.
- Sarmiento E.E., 1985. *Functional Differences in the Skeleton of Wild and Captive Orangutans and their Adaptive Significance*. Doctoral dissertation, New York Univeristy. University Microfilms International, Ann Arbor, Michigan.
- Sarmiento, E.E., 1987. The phylogenetic position of *Oreopithecus* and its significance in the origin of the Hominoidea. *Amer. Mus. Nat. Hist. Novitates* 2881.
- Sarmiento, E.E., 1988. Anatomy of the Hominoid Wrist Joint: Its evolutionary and functional implications. *International J. Primatology* 9(4), 281-345.

- Sarmiento, E.E., 1994. Terrestrial traits in the hands and feet of gorillas. *Amer. Mus. Nat. Hist. Novitates* 3091.
- Sarmiento EE., 1995. Cautious climbing and folivory: a model of hominoid differentiation. *Hum. Evol.* 10, 289–321.
- Sarmiento, E.E., 1998. Generalized quadrupeds, committed bipeds and the shift to open habitats: an evolutionary model of hominid divergence. *Amer. Mus. Nat. Hist. Novitates* 3250.
- Sarmiento, E.E., 2002. Forearm rotation and the 'origin of the hominoid lifestyle': a reply to Stern and Larson. *Amer. J. Phys. Anthropol.* 119, 92-94.
- Sarmiento, E.E. 2003. Distribution, taxonomy, genetics, ecology and causal links of gorilla survival: The need to develop practical knowledge for gorilla conservation. In: Taylor, A., Goldsmith, M. (Eds.), *Gorilla Biology*. Academic Press, New York, pp. 432-471.
- Sarmiento, E.E. 2007. Explaining the "exclusively bipedal" characters in australopithecines and their significance in classification. *Amer. Assoc. of Paleoanthropology*, <http://www.paleoanthro.org/pdfs/Paleo%20Abstracts%202007_meetings%20version.pdf>.
- Sarmiento, E.E., Butynski, T., Kalina, J., 1996. Gorillas of Bwindi-Impenetrable Forest and the Virunga Volcanoes. *Amer. J. Primatology* 40, 1-21.
- Sarmiento, E.E, Marcus, L., 2000. The os navicular of humans, great apes, OH8, Hadar and *Oreopithecus*: phylogenetic, functional and multivariate analyses. *Amer. Mus. Nat. Hist. Novitates* 3288.
- Sarmiento, E.E., Meldrum, D.J., 2011. Behavioral and phylogenetic implications of a narrow allometric study of *Ardipithecus ramidus*. *J. Comp. Hum. Biol.* 62, 75- 108.
- Sarmiento E.E., Oates, J.F., 2000. The Cross River Gorillas: A distinct subspecies. *Amer. Mus. Nat. Hist. Novitates* 3304.
- Sarmiento, E.E., Stiner, E., Mowbray, K., 2002. Morphology based systematics and problems with hominoid and hominid systematics. *New Anat.* 269, 55-69.
- Sarmiento, E.E., Wrangham, R., 2012. Letter to the Editor: the role of shallow water habitats in human evolution: a response to Herries et al., 2010 critique of Wrangham et al., 2009. *Am. J. Phys. Anthropol.* 148, 56–158.

- Schultz, A.H., 1963. Relations between the lengths of the main parts of the foot skeleton in primates. *Folia Primatol.* 1, 150-171.
- Senut, B., Pickford, M., Gommery, D., Mein, P., Chepoi K., Coppens, Y., 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *C. R. Acad. Sci. Paris Ser. II A* 332, 137-144.
- Senut, B., Tardieu, C., 1985. Functional aspects of Plio-Pleistocene limb bones: implications for taxonomy and phylogeny. In: Delson, E. (Ed.), *Ancestors: the hard evidence*. Alan R. Liss, New York, pp. 193-201.
- Smith, R.J., 1980. Rethinking allometry. *J. Theoretical Biol.* 87, 97–111.
- Spencer, F. 1990. *Pittdown: A Scientific Forgery*. Oxford University Press, New York.
- Stern, J.T., 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. *Evol. Anthropol.* 9(3), 113-133.
- Stern, J.T., Larson, S.G., 1990. Electromyographic studies of the obturator muscle in non-human primates: implications for interpreting the obturator externus groove. *Am. J. Phys. Anthropol.* 24, 403–427.
- Stern, J. T., Susman R.L., 1983. The locomotor anatomy of *Australopithecus africanus*. *Am. J. Phys. Anthropol.* 60, 279-316.
- Straus, W.L. Jr., 1948. The humerus of *Paranthropus robustus*. *Amer. J. Phys. Anthropol.* 6, 285-309.
- Susman, R.L., Brain, T.M., 1988. New first metatarsal (SKX 5017) from Swartkrans and the gait of *Paranthropus robustus*. *Am. J. Phys. Anthropol.* 77, 7-15.
- Susman, R.L., Stern J.T., Jungers, W.L. 1984. Arboreality and bipedality in the Hadar Hominids. *Folia Primatol.* 43, 113-156.
- Taieb, M. Johanson, D.C., Coppens, Y., Bonnefille, R., Kalb, R., 1974. Decouverte d'hominides dans les series plio-pleistocenes d'Hadar (Bassin de l'Awash; Afar, Ethiopie) *C.R. Acad. Sci. [D] Paris* 279, 735-738.
- Tardieu, C., 1979. Aspects Biomechaniques de l'articulation du genou chez les primates. *Bull. Soc. Anat. Paris* 4, 66-86.

- Tardieu, C., 1983. Analyse morphofonctionnelle de l'articulation du genou chez les Primates et les Hominides fossiles. Cah. Paleoanthrop. CNRS, Paris, pp. 1-108.
- Tardieu, C., Preuschoft, H., 1996. Ontogeny of the knee joint in humans, great apes, and fossil hominids: Pelvi-femoral relationships during postnatal growth in humans. Folia Primatol. 66, 68-81.
- Trinkaus, E., 1975. A functional analysis of the Neanderthal foot. Doctoral Dissertation. University of Pennsylvania, Philadelphia.
- Tuttle, R.H., 1967. Knuckle-walking and the evolution of the hominoid hand. Amer. J. Phys. Anthropol. 26, 171-206.
- Tuttle, R.H., 1969. Quantitative and functional studies on the hands of the Anthroidea. I. The Hominoidea. J. Morph. 128, 309-363.
- Tuttle, R.H., Webb, D., Tuttle, N. 1991a. Laetoli footprint trails and the evolution of hominid bipedalism. In: Coppens, Y., Senut, B. (Eds.), Origine(s) de la bipédie chez les hominides. Cahiers de Paleoanthropologie Editions du CNRS, Paris
- Tuttle, R.H., Webb, D.M., Bakash, M., 1991b. Laetoli toes and *Australopithecus afarensis*. Hum. Evol. 6(3),193-200
- Walker, A.C., 1973. New Australopithecine femora from East Rudolf Kenya. J. Hum. Evol. 2, 545-555.
- Walter, R.C., 1994. Age of Lucy and the first family: single crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Denen Dora and lower Kada Hadar members of the Hadar Formation, Ethiopia. Geology 22, 6–10.
- Ward C.V., Kimbel, W.H., Johanson, D.C., 2011a. Complete fourth metatarsal and arches in the foot of *Australopithecus afarensis*. Science 331, 750-753.
- Ward, C.V., Kimbel, W.H., Johanson, D.C. 2011b. Erratum posted April 15, 2011. Science 331, 750.
- Weidenreich, F. 1940. The external tubercle of the human tuber calcanei. Am. J. Phys. Anthropol. 23, 473–486.
- White, T.D., 1980. Evolutionary implications of *Pliocene hominin* footprints. Science 208, 175–176.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., WoldeGabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326, 75–86.

White, T.D., Suwa, G., Asfaw, B., 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371, 306-312.