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The Os Navicular of Humans, Great Apes, OH 8, Hadar, and *Oreopithecus*: Function, Phylogeny, and Multivariate Analyses

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ABSTRACT

To clarify fossil hominid behavior and phylogeny, and to test the accuracy of basing these studies on single bones, navicular measurements of Olduvai and Hadar hominids, *Oreopithecus*, and a representative sample of humans and great apes were compared. The measurements chosen for comparison quantify the relative orientation, articular area, and curvature of the navicular facets. The measurements demonstrate that the OH 8 navicular belongs to a rigid foot with an adducted hallux and a strong commitment to terrestriality. The Hadar naviculars belong to a foot which lacked a fixed longitudinal plantar arch and had at least a degree of hallucal opposability comparable to that of mountain gorillas. The *Oreopithecus* navicular belongs to a mobile foot with a widely divergent hallux committed to arboreal behaviors. Multiple discriminant and canonical variate analyses of navicular measurements emphasize the uniqueness of *Oreopithecus* and the similarities between OH 8 and humans, and between Hadar and African apes. The African apelike morphology of the Hadar naviculars contradicts the alleged humanlike morphology of the Hadar pelvis and knee joints. This contradiction underscores the fallacies inherent in constructing phylogenies on the basis of single bones and/or fragmentary remains, and of reconstructing locomotor behaviors on the basis of localized anatomy.

INTRODUCTION

The hands and feet are those parts of the integumentary and musculoskeletal structure which come directly into contact and interact with the physical variables of the environment. As such, their morphology closely corresponds to these variables, responding directly both ontogenetically and phylogenetically to changes in use (i.e., changes in their interactions with the physical variables of the environment) over time (Sarmiento, 1985, 1988, 1994). Because hand and foot anatomy reflect the animal's environmental interactions, they are excellent indicators of behavior. Composed of a large number of anatomical elements that combine to produce the appropriate morphology, hands and feet may also provide insights into past behaviors and are useful for reconstructing phylogenies (Schaeffer, 1947; Beigert, 1963; Lewis, 1969, 1974, 1980a, b, c; Szalay and Decker, 1974; Sarmiento, 1983, 1985, 1988, 1994; Beard et al., 1988; Gebo and Dagosto, 1988). This especially applies to the carpus and tarsus where many anatomical elements interact to provide the appropriate movements and distribute loads. The anatomical complexity of the carpus and tarsus dictates that changes in hand or foot use are achieved with relatively minimal changes in structure, i.e., the organism makes the best use of its inherited anatomy (Sarmiento, 1985, 1988). Thus, the carpus and tarsus provide an anatomical record

of those past behaviors which have been strongly selected for.

Despite their usefulness, carpal and tarsal bones have been largely ignored by most paleoanthropologists when reconstructing early hominid behaviors (Lovejoy, 1974, 1978, 1988; Robinson, 1972; Zihlman and Bunker, 1979; Stern and Susman, 1983; Latimer, 1991; McHenry, 1991; Susman and Stern, 1991; Fleagle, 1998) or phylogenies (Leakey et al., 1964; Robinson, 1965; Wolpoff, 1974; Skeleton et al., 1986; Olson, 1978, 1981, 1985; White et al., 1981; Chamberlain and Wood 1987; Edelstein, 1987; Verhaegen, 1990, 1994; Tobias, 1991a, b; McHenry, 1996; Strait et al., 1997). This is all the more surprising considering that carpal and tarsal bones are often the best preserved and most complete skeletal elements found at early hominid fossil sites, and are well represented in fossil collections. It is the object of this study, therefore, to analyze the navicular of humans, great apes, and some early "hominid" and hominoid fossils in both a functional and phylogenetic context. Because the great ape navicular articulates variably with all of the tarsal bones (Lewis, 1980b, c; Sarmiento, 1994), it should reflect functional differences throughout the tarsus. The presence of complete naviculars at many of the early hominid fossil sites (Day and Napier, 1964; Latimer et al., 1982; Clarke and Tobias, 1995) should provide a phylogenetic

perspective of changes in foot use over time. In addition, analyses and comparisons of a single bone should serve to test the accuracy of reconstructing behavior or phylogeny based on localized anatomy.

MATERIALS AND METHODS

Naviculars of Olduvai (OH 8) and Hadar (AL 333–47, 333–36) hominids, *Oreopithecus* (Basel #39), and a sample of naviculars from each of the great ape species and of humans were measured and compared for dimensions, curvature and relative orientation of facets. Differences in the frequency of terrestrial behaviors in Virunga gorillas (*Gorilla b. beringei*) relative to western gorillas (*G. g. gorilla*) justified considering the two as separate, although a specific designation for Virunga gorillas is arguable (Sarmiento, 1994; Sarmiento and Butynski, 1996; Sarmiento et al., 1996). Great ape naviculars are from the skeletal collections at the following institutions: American Museum of Natural History, New York; Museum of Comparative Zoology at Harvard University, Cambridge; Field Museum of Natural History, Chicago; National Museum of Natural History, Washington D.C.; Philadelphia Academy of Sciences, Philadelphia; Powell Cotton Museum, Birchington; Royal African Museum, Tervuren; and Swedish Museum of Natural History, Stockholm. Human naviculars are from the Dart collection in the Department of Anatomy, University of the Witwatersrand, and the Anthropology collections at the American Museum of Natural History. Fossil material is housed in the collections of the National Museum of Tanzania, Dar es Salaam (OH 8) and National Museum of Ethiopia, Addis Ababa (Hadar). *Oreopithecus* fossil material was studied at the Museum of Natural History, Basel; Istituto di Geologia Università di Firenze; and Instituto de Paleontología, Sabadell, Spain.

Lengths were measured to the nearest 0.1 mm using a digital caliper connected to a computer and collected in a Lotus spreadsheet. A carpenter's angle accurate to 0.5° was applied to the articular surfaces to measure the cuboecocuneiform angle and horizontal mesoecocuneiform angle. The remaining angles were arrived at by aligning

wires to the articular surfaces and using the carpenter angle to measure the angles made by the wires. All measurements are of the right navicular except for some (fossils) in which only the left specimen was available.

Comparisons to body size relied on naviculars of specimens with reported body weights. For those specimens without reported body weight, the sums of the midshaft cross-sectional area of the femur and tibia were used for comparisons. The length of the femur (mm) times its midshaft cross-sectional area plus the length of the tibia (mm) times its midshaft cross-sectional area were used to compare lower-limb volume to corresponding navicular measurements for each individual specimen. Measurements for lower-limb long bone lengths are after Sarmiento (1985) and Sarmiento et al. (1996). Cross-sectional areas of lower-limb long bones were arrived at by squaring the midshaft circumference and dividing it by 4π . Measurements and the indices formulated from them were chosen to reflect mechanical concerns. Figure 1 summarizes the length and angular measurements taken on the navicular and the indices formulated from these measurements. Tables 1–10 summarize comparisons of the linear and angular measurements. Figures 2–11 are bivariate plots of the proportions considered.

Functional interpretation of the navicular of fossil forms relied on nearly 20 years of studying foot use in humans and in free ranging and captive great apes (Sarmiento, 1983, 1985, 1994; Sarmiento and Butynski, in prep.). Articulation of human, great ape, and fossil foot bones in close-packed positions were used to gauge the orientation of the pedal segments imparted by the set (i.e., relative orientation) of the navicular facets. Ligamentous preparations of the foot of humans, western gorillas, common chimpanzees, and orangutans were used to further verify the relative orientations of articulated tarsals and metatarsals. Notes on OH 8, Hadar, and *Oreopithecus* foot bones were used to corroborate functional interpretations of fossil foot use based on the navicular study.

To complement results from the functional analysis and provide insights into phylogeny, a multiple discriminant and canonical variate analysis was run employing 13 linear mea-

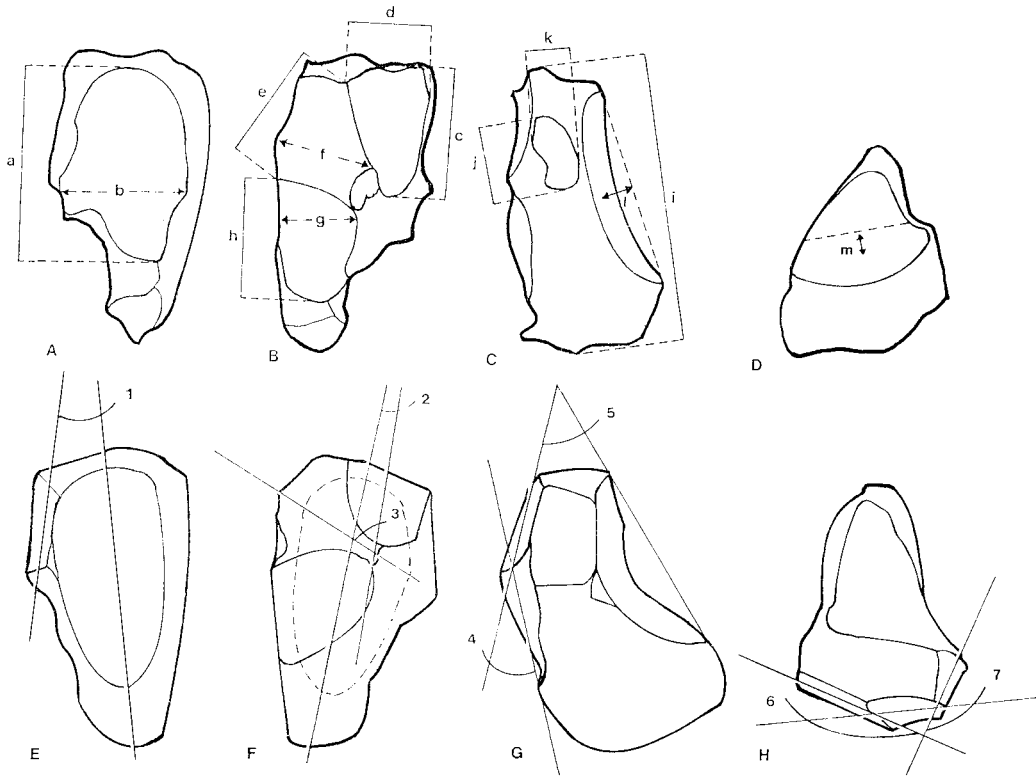


Fig. 1. Proximal (A), distal (B), lateral (C) and dorsal (D) views of the OH 8 navicular showing the measured lengths, and proximal (E), distal (F), lateral (G) and dorsal (H) views of a left gorilla navicular showing the measured angles; a = talar facet major axis (dorsoplantar) diameter, b = talar facet minor axis (mediolateral) diameter, c = ectocuneiform facet dorsoplantar diameter, d = ectocuneiform facet mediolateral diameter, e = mesocuneiform facet dorsoplantar diameter, f = mesocuneiform facet mediolateral diameter, g = entocuneiform facet dorsoplantar diameter, h = entocuneiform facet mediolateral diameter, i = navicular maximum length, j = cuboid facet dorsoplantar diameter, k = cuboid facet mediolateral diameter, l = depth of talar facet along major axis, m = depth of talar facet along minor axis; 1 = frontal talocuboid angle, $90^\circ - 2$ = navicular torsion, 3 = frontal mesoectocuneiform angle, 4 = entoectocuneiform angle 5 = sagittal taloectocuneiform angle, 6 = transverse mesoectocuneiform angle, 7 = transverse cuboectocuneiform angle. In all cases the lines chosen for angular measurements bisect facets into approximately equal halves. For comparative purposes the major bisecting axes of the talar head and cuneiform facets are referred to in the text as the dorsoplantar axes. In neither great apes nor humans do all these axes have a dorsoplantar orientation, but are held in varying inclination to a dorsoplantar axis according to talar head and navicular torsion and the frontal mesoectocuneiform angle. The cross-sectional area of the talar, ectocuneiform, mesocuneiform entocuneiform and cuboid facets are given by the products of a and b, c and d, e and f, g and h, and j and k, respectively. Relative cross-sectional area for each facet is compared as a percentage of the sum of all of the navicular facets. The subtended angle of curvature and the radius of curvature of the talar facet along the dorsoplantar (major) and mediolateral (minor) axes are given by $4 \arctan(2l/a)$ and $(l^2 + a^2/4)/2l$, and $4 \arctan(2m/b)$ and $(m^2 + b^2/4)/2m$, respectively.

measurements and 6 angles using PC SAS 6.12. Only human specimens with a distinct cuboid facet (N = 14) were included in this analysis. Due to small and irregular cuboid facets, the frontal talocuboid angle could not

be accurately measured in any human specimen and was dropped from the analysis. Results from these analyses are summarized as Mahalanobis distances in table 11 and figures 12–14.

TABLE 1
**Sagittal Taloectocuneiform, Transverse Mesoectocuneiform, and Transverse Cuboectocuneiform
 Angles (degrees) in Humans, Great Apes, and Some Hominoid Fossils**
 Mean \pm standard deviation and range; sample size in parentheses.

| | Sagittal taloectocuneiform | Transverse mesoectocuneiform | Transverse cuboectocuneiform |
|-----------------------|-----------------------------------|--------------------------------------|--------------------------------------|
| <i>P. pygmaeus</i> | 60.7 \pm 6.77 (20) 45.0–75.0 | 116.7 \pm 9.55 (20) 103.0–135.0 | 112.8 \pm 10.93 (20) 70.0–124.0 |
| <i>P. troglodytes</i> | 59.6 \pm 7.46 (22) 37.0–70.0 | 136.0 \pm 6.10 (22) 126.0–150.0 | 106.8 \pm 7.98 (22) 85.0–118.0 |
| <i>P. paniscus</i> | 65.1 \pm 5.44 (20) 52.0–74.0 | 136.8 \pm 3.56 (20) 130.0–147.0 | 96.4 \pm 7.01 (20) 76.0–112.0 |
| <i>G. g. gorilla</i> | 54.3 \pm 5.77 (19) 45.0–68.0 | 136.5 \pm 7.07 (19) 123.0–150.0 | 113.5 \pm 8.61 (19) 95.0–127.0 |
| <i>G. g. beringei</i> | 61.5 \pm 5.37 (20) 53.0–69.0 | 138.1 \pm 5.78 (20) 120.0–148.0 | 117.5 \pm 5.57 (20) 110.0–132.0 |
| <i>Homo</i> | 30.8 \pm 6.26 (24) 16.0–41.0 | 152.3 \pm 4.14 (24) 142.0–159.0 | 120.1 \pm 7.05 (16) 105.0–127.0 |
| OH 8 | 30.0 | 160.0 | 112.0 |
| Hadar | 58.5 \pm 2.12 (2) 57.0–60.0 | 141.5 \pm 2.12 (2) 140.0–143.0 | 102 \pm 2.83 (2) 100.0–104.0 |
| <i>Oreopithecus</i> | 63.0 | 136.0 | 105.0 |

TABLE 2
**Navicular Torsion, and Entoectocuneiform, Frontal Talocuboid, and Frontal Mesoectocuneiform
 Angles (degrees) in Humans, Great Apes, and Some Hominoid Fossils**
 Mean \pm standard deviation and range; sample size in parentheses.

| | Torsion | Entoectocuneiform | Frontal talocuboid | Frontal mesoectocuneiform |
|-----------------------|------------------------------------|------------------------------------|-----------------------------------|------------------------------------|
| <i>P. pygmaeus</i> | 51.4 \pm 9.87 (20) 35.0–70.0 | 46.6 \pm 9.87 (20) 26.0–70.0 | 22.4 \pm 12.77 (20) 6.0–40.0 | 46.2 \pm 16.88 (20) 15.0–83.0 |
| <i>P. troglodytes</i> | 59.4 \pm 9.49 (22) 40.0–78.0 | 32.00 \pm 9.09 (22) 15.0–48.0 | 23.9 \pm 9.47 (22) 5.0–54.0 | 31.77 \pm 7.51 (22) 17.0–43.0 |
| <i>P. paniscus</i> | 58.2 \pm 5.82 (20) 46.0–70.0 | 39.1 \pm 9.16 (20) 25.0–62.0 | 24.1 \pm 6.91 (17) 11.0–35.0 | 31.5 \pm 5.53 (20) 16.0–40.0 |
| <i>G. g. gorilla</i> | 60.0 \pm 11.14 (19) 41.0–85.0 | 35.0 \pm 11.14 (19) 15.0–59.0 | 22.4 \pm 7.37 (19) 10.0–32.0 | 28.2 \pm 8.84 (19) 15.0–42.0 |
| <i>G. g. beringei</i> | 65.9 \pm 8.63 (20) 45.0–79.0 | 34.6 \pm 8.63 (20) 26.0–50.0 | 12.15 \pm 8.51 (20) 0.0–23.0 | 22.1 \pm 9.90 (20) 12.0–38.0 |
| <i>Homo</i> | 61.0 \pm 8.40 (24) 48.0–82.0 | 20.3 \pm 8.40 (24) 3.0–34.0 | — | 37.5 \pm 12.33 (24) 10.0–60.0 |
| OH 8 | 76.0 | 6.0 | 14.0 | 38.0 |
| Hadar | 72.5 \pm 3.54 (2) 70.0–75.0 | 45.5 \pm 3.54 (2) 43.0–48.0 | 12.5 \pm 12.02 (2) 4.0–21.0 | 41.0 \pm 4.24 (2) 38.0–44.0 |
| <i>Oreopithecus</i> | 48.0 | 58.0 | 28.0 | 23.0 |

TABLE 3
**Central Angle (degrees) Subtended by the
 Dorsoplantar and Mediolateral Curvature of
 the Talar Facet in Humans, Great Apes,
 and Some Hominoid Fossils**

Mean \pm standard deviation and range;
 sample size in parentheses.

| | Dorsoplantar angle | Mediolateral angle |
|-----------------------|--------------------------------------|------------------------------------|
| <i>P. pygmaeus</i> | 108.6 \pm 18.64 (20) 69.8–141.8 | 77.7 \pm 11.02 (20) 50.9–91.0 |
| <i>P. troglodytes</i> | 112.9 \pm 8.88 (22) 96.8–128.4 | 53.7 \pm 13.28 (22) 26.2–74.9 |
| <i>P. paniscus</i> | 126.5 \pm 8.42 (28) 110.4–140.8 | 65.4 \pm 9.74 (28) 39.4–85.9 |
| <i>G. g. gorilla</i> | 113.3 \pm 12.12 (19) 81.9–140.7 | 43.8 \pm 12.08 (19) 27.4–66.4 |
| <i>G. g. beringei</i> | 113.8 \pm 7.00 (20) 100.5–125.2 | 36.5 \pm 11.81 (20) 16.3–59.0 |
| <i>Homo</i> | 86.7 \pm 4.81 (24) 69.7–94.9 | 55.5 \pm 8.93 (24) 43.1–73.7 |
| OH 8 | 87.0 | 41.5 |
| Hadar | 129.8 \pm 3.89 (2) 127.0–132.5 | 71 \pm 9.90 (2) 64.0–78.0 |
| <i>Oreopithecus</i> | 92.0 | 64.0 |

RESULTS

CANONICAL ANALYSES

Multiple discriminant analysis distinguished humans and the living great apes, with genera (i.e., *Homo*, *Gorilla*, *Pan*, and *Pongo*) showing much larger differences than species of the same genus. Mahalanobis distance summarizes the difference between any two groups as a single statistic and can be used as a test of significance between groups (table 11), and as a distance measure for clustering groups (figs. 12–14).

Repeated attempts to reduce the number of measured variables in the discriminant analysis, including stepwise discrimination always led to a less distinctive pattern than the one arrived at when all the variables were considered. When grouped separately, neither the angles nor the length measurements gave patterns comparable to the combined data. Although the number of measured variables is relatively high compared to the sample size for each group, this is the strongest case one of us (LM) has seen where all of the chosen variables have considerable importance in discriminating among groups.

TABLE 4
**Length of the Radii (mm) of the Dorsoplantar (major) and Mediolateral (minor) Curvatures
 of the Talar Facet and of Differences between these Two Lengths, in Humans,
 Great Apes, and Some Hominoid Fossils**

Mean \pm standard deviation and range; sample size in parentheses.

| | Dorsoplantar | Mediolateral | Difference |
|-----------------------|--------------------------------------|---------------------------------------|-------------------------------------|
| <i>P. pygmaeus</i> | 13.53 \pm 2.58 (20) 10.17–19.59 | 11.72 \pm 1.91 (20) 8.46–15.53 | 1.81 \pm 2.6 –2.82 to 8.61 |
| <i>P. troglodytes</i> | 14.68 \pm 1.37 (22) 12.22–17.55 | 20.30 \pm 6.46 (22) 13.16–38.35 | 5.62 \pm 6.23 –1.96 to 24.36 |
| <i>P. paniscus</i> | 13.06 \pm 1.09 (28) 10.99–15.16 | 14.29 \pm 2.00 (28) 10.78–20.81 | 1.23 \pm 2.22 –1.95 to 8.63 |
| <i>G. g. gorilla</i> | 19.84 \pm 2.56 (19) 14.50–25.64 | 30.98 \pm 8.83 (19) 17.89–49.98 | 11.14 \pm 7.62 –0.26 to 24.33 |
| <i>G. g. beringei</i> | 19.88 \pm 1.92 (20) 15.88–24.49 | 35.31 \pm 15.98 (20) 15.44–73.59 | 15.43 \pm 15.31 –1.51 to 52.74 |
| <i>Homo</i> | 20.47 \pm 1.81 (24) 17.14–23.97 | 23.23 \pm 3.16 (24) 17.31–28.94 | 2.76 \pm 3.39 –2.59 to 9.61 |
| OH 8 | 17.04 | 23.16 | –6.12 |
| Hadar | 13.68 \pm 0.078 (2) 13.62–13.73 | 13.56 \pm 2.19 (2) 12.01–15.11 | 0.116 \pm 2.27 –1.49 to 1.72 |
| <i>Oreopithecus</i> | 12.15 | 10.41 | 1.74 |

TABLE 5
Cross-Sectional Areas of the Ectocuneiform, Mesocuneiform, and Entocuneiform Facets as Percentages of the Total Cross-Sectional Facet Area of the Navicular Bone in Humans, Great Apes, and Some Hominoid Fossils
 Mean \pm standard deviation and range; sample size in parentheses.

| | Ectocuneiform | Mesocuneiform | Entocuneiform |
|-----------------------|---------------------------------------|--------------------------------------|--------------------------------------|
| <i>P. pygmaeus</i> | 16.64 \pm 1.37 (20) 13.83–18.66 | 13.50 \pm 1.93 (20) 9.72–16.79 | 16.41 \pm 2.20 (20) 12.84–20.86 |
| <i>P. troglodytes</i> | 12.93 \pm 1.48 (22) 10.98–15.78 | 14.55 \pm 1.98 (22) 11.51–19.07 | 21.28 \pm 3.13 (22) 15.07–26.07 |
| <i>P. paniscus</i> | 14.20 \pm 1.19 (28) 12.70–16.69 | 15.16 \pm 1.93 (28) 9.63–19.81 | 16.80 \pm 1.98 (28) 11.75–20.09 |
| <i>G. g. gorilla</i> | 11.77 \pm 0.898 (19) 10.12–13.90 | 14.68 \pm 2.10 (19) 11.60–18.01 | 21.63 \pm 2.45 (19) 18.01–26.57 |
| <i>G. g. beringei</i> | 12.41 \pm 1.48 (20) 10.19–15.13 | 16.01 \pm 1.18 (20) 14.32–17.98 | 20.49 \pm 3.22 (20) 14.75–26.75 |
| <i>Homo</i> | 14.63 \pm 2.41 (24) 11.29–20.31 | 19.37 \pm 2.24 (24) 15.1–23.95 | 21.07 \pm 2.19 (24) 17.00–25.57 |
| OH 8 | 17.50 | 17.43 | 13.33 |
| Hadar | 14.36 \pm 2.04 (2) 12.91–15.80 | 18.45 \pm 3.40 (2) 16.04–20.85 | 17.72 \pm 0.09 (2) 17.65–17.78 |
| <i>Oreopithecus</i> | 14.37 | 14.48 | 17.14 |

TABLE 6
Cross-Sectional Areas of Talar and Cuboid Facets as Percentages of Total Cross-Sectional Articular Area of Navicular in Humans, Great Apes, and Some Hominoid Fossils
 Mean \pm standard deviation and range;
 sample size in parentheses.

| | Cuboid | Talar |
|-----------------------|-------------------------------------|--------------------------------------|
| <i>P. pygmaeus</i> | 13.68 \pm 1.98 (20) 9.13–16.73 | 39.78 \pm 2.72 (20) 34.80–44.53 |
| <i>P. troglodytes</i> | 7.97 \pm 1.70 (22) 5.07–11.54 | 43.26 \pm 3.00 (22) 37.12–49.30 |
| <i>P. paniscus</i> | 10.71 \pm 1.45 (28) 8.26–13.58 | 43.13 \pm 3.15 (28) 37.40–52.30 |
| <i>G. g. gorilla</i> | 8.51 \pm 1.62 (19) 4.21–10.97 | 43.43 \pm 2.41 (19) 38.01–47.55 |
| <i>G. g. beringei</i> | 7.10 \pm 1.32 (19) 3.73–9.67 | 44.35 \pm 3.61 (20) 39.11–52.41 |
| <i>Homo</i> | 4.30 \pm 1.79 (14) 1.54–7.61 | 42.42 \pm 2.92 (24) 37.06–51.01 |
| OH 7 | 6.18 | 45.55 |
| Hadar | 13.17 \pm 1.65 (2) 12.00–14.34 | 36.32 \pm 3.75 (2) 36.05–36.58 |
| <i>Oreopithecus</i> | 8.40 | 45.62 |

It is very difficult to interpret the contribution of the variables a posteriori (Marcus, 1990). Six of the nine canonical variates lead to significant differences. Not summarized in the figures, the third through sixth canonical variates separate the two gorillas subspecies, the two chimpanzees species, and the orangutan even more distinctly than shown in figure 12. All of the fossils are also more distinctively separated along some of these canonical axes. This is consistent with the large distances between the fossils and the living taxa (figs. 13, 14). The two Hadar naviculars whether considered separately or together, are not significantly different from either chimpanzee species (table 11). OH 8 is most similar to, but differs significantly from humans ($p = 0.014$).

DISCUSSION

RELATIVE ORIENTATION OF NAVICULAR FACETS

The angles formed by the articular planes of the navicular facets reflect the set of the

TABLE 7
Articular Cross-Sectional Areas (mm²) of the Ectocuneiform, Mesocuneiform, and Entocuneiform Facets of the Navicular in Humans, Great Apes, and Some Hominoid Fossils
 Mean \pm standard deviation and range; sample size in parentheses.

| | Ectocuneiform | Mesocuneiform | Entocuneiform |
|-----------------------|--------------------------------------|--------------------------------------|---------------------------------------|
| <i>P. pygmaeus</i> | 130.7 \pm 30.9 (20) 78.0–178.1 | 106.0 \pm 27.8 (20) 56.0–158.8 | 127.7 \pm 28.6 (20) 78.0–182.2 |
| <i>P. troglodytes</i> | 124.6 \pm 24.5 (22) 92.1–175.5 | 140.0 \pm 27.3 (22) 98.7–188.2 | 204.9 \pm 43.0 (22) 134.5–286.7 |
| <i>P. paniscus</i> | 118.0 \pm 18.1 (28) 93.2–164.7 | 126.4 \pm 25.1 (28) 76.2–179.1 | 139.5 \pm 23.4 (28) 93.0–203.3 |
| <i>G. g. gorilla</i> | 191.8 \pm 38.3 (19) 142.6–260.0 | 236.2 \pm 37.7 (19) 157.7–302.9 | 354.5 \pm 89.9 (19) 243.6–570.9 |
| <i>G. g. beringei</i> | 178.8 \pm 44.3 (20) 109.6–268.7 | 230.4 \pm 52.5 (20) 161.7–326.1 | 298.7 \pm 101.9 (20) 173.8–553.3 |
| <i>Homo</i> | 205.5 \pm 41.4 (24) 137.9–328.7 | 271.7 \pm 41.6 (24) 190.0–374.4 | 294.7 \pm 34.6 (24) 229.5–353.2 |
| OH 8 | 148.1 | 147.5 | 112 |
| Hadar | 152.8 \pm 26.2 (2) 134.4–171.3 | 195.4 \pm 30.5 (2) 173.9–217.0 | 188.2 \pm 6.47 (2) 183.6–192.8 |
| <i>Oreopithecus</i> | 61.0 | 61.5 | 72.8 |

TABLE 8
Articular Cross-Sectional Areas (mm²) of the Talar and Cuboid Facets of the Navicular in Humans, Great Apes, and Some Hominoid Fossils
 Mean \pm standard deviation and range;
 sample size in parentheses.

| | Talar | Cuboid |
|-----------------------|---------------------------------------|-------------------------------------|
| <i>P. pygmaeus</i> | 310.3 \pm 66.7 (20) 218.0–437.3 | 106.6 \pm 26.9 (20) 64.5–159.5 |
| <i>P. troglodytes</i> | 415.2 \pm 61.8 (22) 307.1–607.8 | 77.8 \pm 23.6 (22) 34.7–133.4 |
| <i>P. paniscus</i> | 358.3 \pm 51.6 (28) 268.0–517.7 | 89.3 \pm 18.5 (28) 61.8–147.1 |
| <i>G. g. gorilla</i> | 704.7 \pm 115.9 (19) 537.7–901.5 | 140.4 \pm 44.4 (19) 60.8–235.6 |
| <i>G. g. beringei</i> | 642.4 \pm 162.6 (20) 411.4–885.7 | 103.8 \pm 30.2 (20) 55.3–149.0 |
| <i>Homo</i> | 597.2 \pm 89.8 (24) 455.7–822.3 | 61.4 \pm 27.7 (14) 18.8–108.64 |
| OH 8 | 385.4 | 52.3 |
| Hadar | 385.7 \pm 7.24 (2) 380.6–390.8 | 140.2 \pm 21.6 (2) 124.9–155.5 |
| <i>Oreopithecus</i> | 193.8 | 35.7 |

tarsal and metatarsal bones (figs. 15–18). In turn, the set of these bones bears on the mobility, rigidity, and weight-bearing capabilities of the foot (Elftman and Manter, 1935; Manter, 1941; Elftman, 1960; Day and Wood, 1968; Lewis 1980a, b, c; Sarmiento, 1994). The large sagittal taloectocuneiform angle (fig. 1G #5) in great apes and Hadar australopithecines (table 1) emphasizes the transfer of talar head loads to the substrate through the navicular's plantar tubercle (or secondarily through the entocuneiform), but sacrifices the percentage of load transferred to the ectocuneiform. The great ape angle is associated with a mobile midtarsal joint and dorsiflexed set of the talonavicular joint (fig. 15). The small sagittal taloectocuneiform angle in humans, on the other hand, emphasizes talar head load transfer to the cuneiforms at the expense of its transfer to the substrate. The human orientation is associated with a longitudinal arch and a rigid midtarsal and tarsometatarsal joint, and preferential loading of the ball of the foot (as opposed to the dis-

TABLE 9
Maximum Navicular Length, Combined Cuneiform Facet Area, Total Navicular Facet Area (TFA), and TFA as a Percentage of the Sum of the Midshaft Cross-Sectional Areas of the Femur and Tibia in Humans, Great Apes, and Some Hominoid Fossils
 Mean \pm standard deviation and range; sample size in parentheses.

| | Maximum length, mm | Cuneiform facet area, mm ² | Total navicular facet area | |
|-----------------------|-----------------------------------|--|--|--|
| | | | mm ² | % femur + tibia x-sectional areas |
| <i>P. pygmaeus</i> | 27.4 \pm 2.69 (20) 23.4–33.4 | 364.4 \pm 80.6 (20) 229.5–501.2 | 781.4 \pm 160.3 (20) 531.1–1093.2 | 171.42 \pm 47.79 (20) 90.79–250.55 |
| <i>P. troglodytes</i> | 36.1 \pm 2.92 (22) 31.7–42.6 | 469.5 \pm 73.3 (22) 343.5–631.0 | 962.4 \pm 142.8 (22) 685.3–1356.1 | 131.05 \pm 18.10 (22) 96.42–169.81 |
| <i>P. paniscus</i> | 33.3 \pm 2.44 (28) 30.0–41.3 | 384.0 \pm 56.1 (28) 299.4–518.0 | 831.6 \pm 110.0 (28) 676.6–1153.6 | 142.05 \pm 22.10 (28) 109.87–201.1 |
| <i>G. g. gorilla</i> | 46.8 \pm 5.25 (19) 38.6–56.0 | 782.5 \pm 144.0 (19) 611.2–1080.0 | 1627.6 \pm 286.6 (19) 1266.5–2148.3 | 126.2 \pm 23.9 (18) 98.11–198.0 |
| <i>G. g. beringei</i> | 45.3 \pm 5.17 (20) 37.5–54.1 | 707.9 \pm 178.4 (20) 464.7–1065.6 | 1448.8 \pm 354.8 (20) 954.8–2068.5 | 103.96 \pm 20.91 (18) 79.46–161.15 |
| <i>Homo</i> | 39.6 \pm 3.63 (24) 34.2–47.1 | 771.9 \pm 83.0 (24) 654.8–969.9 | 1404.9 \pm 159.6 (24) 1150.6–1703.4 | 126.85 \pm 17.39 (22) 101.20–177.94 |
| OH 8 | 33.2 | 408.4 | 846.0 | — |
| Hadar | 37.2 \pm 0.50 (2) 36.9–37.6 | 536.4 \pm 2.17 (2) 534.9–537.9 | 1062.3 \pm 31.0 (2) 1040.3–1084.2 | — |
| <i>Oreopithecus</i> | 25.3 | 195.3 | 424.8 | — |

tal tarsal row and metatarsal bases) during weight support (Sarmiento, 1994).

The sagittal entoectocuneiform angle (fig 1G #4, table 2) imparts a plantar divergence of the entocuneiform relative to the ectocuneiform facet³ (fig. 15). The larger the angle, the higher the degree of divergence. With a plantar orientation of the entocuneiform facet, talar head load can be transferred to the substrate through the navicular and plantar tubercles of the entocuneiform. In taxa with an opposable hallux, the angle may reflect enhanced opposition depending on the set of its conarticular and the final set imparted to the hallucal long axis. In humans and OH 8,

³ Contributions of the measured navicular angles to the set of the foot bones consider talar torsion values approximating 90° and a talar facet held with its major axis in the vertical. With increasing deviation of the major axis of the talar facet toward the horizontal and lower navicular torsion values, the sagittal entoectocuneiform angle would increasingly contribute to medial divergence of the hallux relative to the third metatarsal. Likewise with horizontal postures of the major axis of the talar facet a high sagittal taloectocuneiform angle results in a more laterally divergent third metatarsal relative to the hallux and the talar head.

the small angle value (table 2) is in accord with an abducted hallux, a fixed longitudinal plantar arch, and an entocuneiform which does not transfer any appreciable weight to the substrate. The larger angle in the Hadar fossils probably reflects weight transfer from the entocuneiform to the substrate, and some degree of hallucal opposability. The very large angle of *Oreopithecus* is in accord with its markedly abducted hallucal postures (Kohler and Moya-Sola, 1997).

The transverse mesoectocuneiform angle (fig. 1H #6, table 1) reflects the degree of divergence of the 2nd and 3rd pedal rays (fig. 16). A large angle approximating 180° as seen in humans and OH 8 imparts a nearly parallel orientation to the long axes of the second and third pedal rays. Conversely, the smaller angle values seen in great apes, Hadar, and *Oreopithecus* impart a divergent orientation to the long axes of the pedal rays.

The transverse cuboectocuneiform angle (fig. 1H #7, table 1) reflects the degree of divergence of the two most lateral rays relative to the third ray and ectocuneiform (fig. 16). The smaller the value of this angle, the

TABLE 10
Talar Facet Cross-Sectional Area in Relation to Lower Limb Volume and Weight,^a and as a Percentage of the Sum of the Midshaft Cross-Sectional Areas of the Femur and Tibia in Males and Females of Humans and Great Apes
 Mean \pm standard deviation and range; sample size in parentheses.

| | Talar facet area ^{1/2} / lower limb volume ^{1/3} (%) | Talar facet area ^{1/2} / weight ^{1/3} (%) | Talar facet area (% femur + tibia x-sectional areas) |
|-----------------------|--|--|--|
| <i>P. pygmaeus</i> | | | |
| Males | 0.555 \pm 0.0768 (10) 0.418–0.670 | $7.61 \times 10^{-5} \pm 1.42 \times 10^{-5}$ (8) 5.52×10^{-5} to 9.41×10^{-5} | 62.34 \pm 17.32 (10) 37.26–88.89 |
| Females | 0.577 \pm 0.0631 (10) 0.497–0.701 | $8.36 \times 10^{-5} \pm 8.80 \times 10^{-6}$ (7) 7.31×10^{-5} to 9.84×10^{-5} | 73.79 \pm 19.22 (10) 45.55–104.44 |
| <i>P. troglodytes</i> | | | |
| Males | 0.525 \pm 0.0366 (15) 0.474–0.602 | $8.69 \times 10^{-5} \pm 6.39 \times 10^{-6}$ (4) 8.06×10^{-5} to 9.72×10^{-5} | 56.01 \pm 10.03 (15) 40.18–80.00 |
| Females | 0.529 \pm 0.0077 (7) 0.513–0.537 | $8.87 \times 10^{-5} \pm 6.24 \times 10^{-6}$ (3) 8.30×10^{-5} to 9.74×10^{-5} | 58.04 \pm 4.07 (7) 53.02–64.32 |
| <i>P. paniscus</i> | | | |
| Males | 0.704 \pm 0.0296 (15) 0.638–0.754 | $8.71 \times 10^{-5} \pm 5.64 \times 10^{-6}$ (12) 7.51×10^{-5} to 9.34×10^{-5} | 61.34 \pm 5.79 (17) 52.40–71.71 |
| Females | 0.693 \pm 0.0667 (10) 0.611–0.811 | $9.02 \times 10^{-5} \pm 5.30 \times 10^{-6}$ (5) 8.21×10^{-5} to 9.77×10^{-5} | 60.71 \pm 13.17 (11) 43.52–90.65 |
| <i>G. g. gorilla</i> | | | |
| Males | 0.520 \pm 0.0235 (10) 0.480–0.564 | $7.91 \times 10^{-5} \pm 6.57 \times 10^{-6}$ (4) 7.25×10^{-5} to 8.93×10^{-5} | 54.63 \pm 13.14 (10) 40.89–93.17 |
| Females | 0.562 \pm 0.0459 (8) 0.499–0.653 | $9.44 \times 10^{-5} \pm 7.03 \times 10^{-6}$ (4) 8.78×10^{-5} to 10.55×10^{-5} | 55.41 \pm 8.26 (8) 46.00–64.52 |
| <i>G. g. beringei</i> | | | |
| Males | 0.486 \pm 0.0312 (10) 0.439–0.557 | $7.33 \times 10^{-5} \pm 5.77 \times 10^{-6}$ (5) 6.59×10^{-5} to 8.32×10^{-5} | 44.60 \pm 7.24 (10) 32.77–57.10 |
| Females | 0.492 \pm 0.0558 (9) 0.402–0.622 | $7.67 \times 10^{-5} \pm 7.30 \times 10^{-6}$ (2) 6.94×10^{-5} to 8.40×10^{-5} | 45.42 \pm 9.13 (9) 34.34–66.92 |
| <i>H. sapiens</i> | | | |
| Males | 0.487 \pm 0.0217 (16) 0.443–0.532 | — — | 53.52 \pm 6.86 (14) 41.83–74.69 |
| Females | 0.503 \pm 0.0346 (8) 0.465–0.566 | — — | 55.17 \pm 10.83 (8) 38.23–63.59 |

^a The square root of the talar facet cross-sectional area (cm) is expressed as a percentage of the cube root of lower limb volume (cm) and of the cube root of weight (g^{1/3}).

greater the degree of lateral ray divergence. In this regard, pygmy chimpanzees have the most divergent set and humans the least divergent set of the two most lateral rays.

Torsion of the navicular (fig. 1F #2) affects the orientation of the talar head relative to the dorsoplantar axis of the ectocuneiform. Torsion values approximating 90° indicate that the major bisecting axis of the talar facet

approximates the dorsoplantar (major) axis of the ectocuneiform facet (fig. 17). With vertical postures of the dorsoplantar axis of the ectocuneiform, high torsion imparts a plantarly rotated set to the talar facet and results in a high transverse plantar arch. In gorillas at least, the high torsion values are associated with a higher transverse arch than that seen in either chimpanzees or orangutans

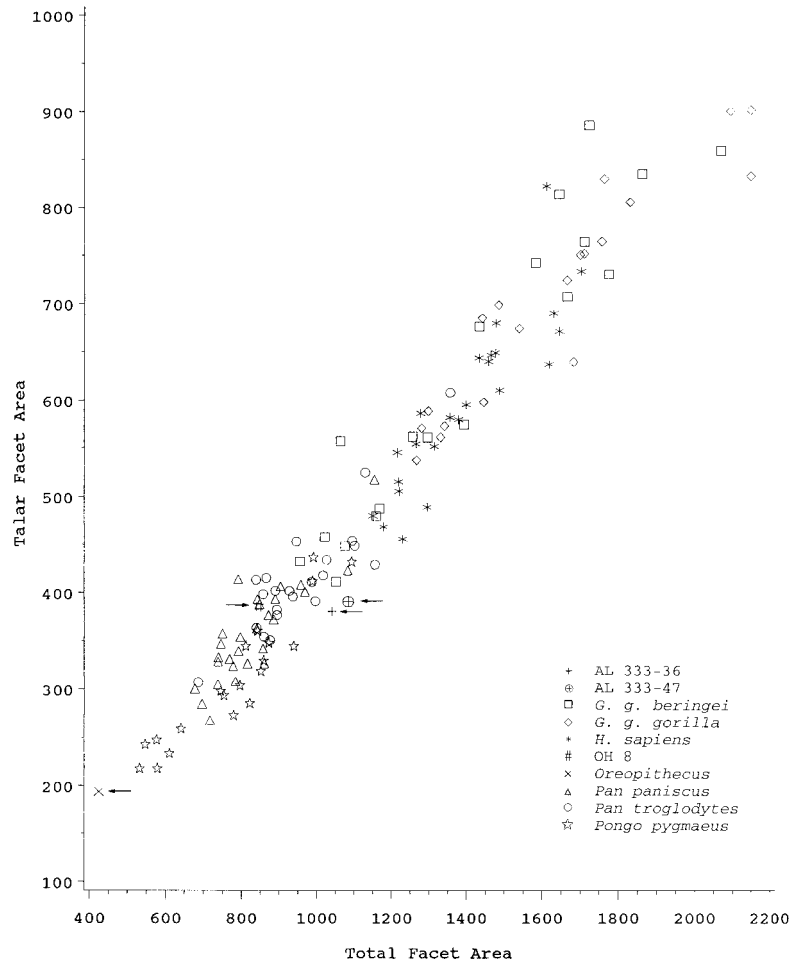


Fig. 2. Talar facet cross-sectional area (mm²) vs. total navicular facet cross-sectional area (mm²) in humans, great apes, and fossil hominoids. Arrows point to fossils.

(Sarmiento, 1994). Because the rotated set of the navicular is also affected by talar head torsion, and the dorsoplantar axis of the ectocuneiform may be set oblique to the vertical (fig. 17; Sarmiento 1994), humans do not necessarily have navicular torsion values as great as gorillas, despite a high transverse plantar arch (table 2). Without evidence from other joint sets, torsion of the OH 8 and Hadar naviculars indicates a transverse plantar arch height which is at least comparable to that of gorillas.

The frontal talocuboid angle (fig. 1E #1) influences the set of the navicular relative to the cuboid, and also reflects the height of the transverse plantar arch (fig. 18). Small angles

indicate that the major bisecting axis of the talar head is plantarly rotated relative to the cuboid in close-packed positions of the talocuboid joint. A low talocuboid angle, therefore, attests to the relatively high transverse arch of mountain gorillas (table 2; Sarmiento, 1994). Because in humans and great apes the cubonavicular facet does not necessarily lie in a sagittal or parasagittal plane, talocuboid angles do not directly reflect plantar arch height. Nevertheless, the low angle values in both OH 8 and the Hadar fossils when taken together with high navicular torsion (table 2) indicate that these fossils had a rather high transverse plantar arch when the tarsals were in the close-packed position.

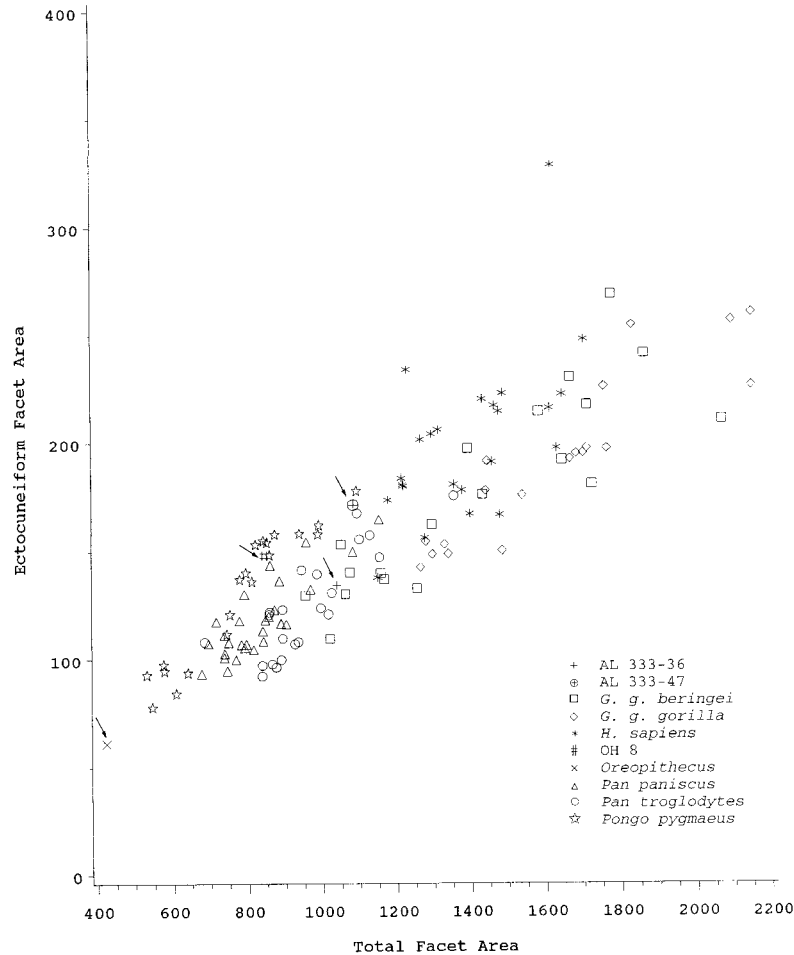


Fig. 3. Ectocuneiform facet cross-sectional area (mm^2) vs. total navicular facet cross-sectional area (mm^2) in humans, great apes, and fossil hominoids. Arrows point to fossils.

The frontal mesoectocuneiform angle (fig. 1F #3) imparts a relative rotational set to the mesocuneiform and ectocuneiform (fig. 17). Although a large angle may imply greater opposition between the second and the third digit, metatarsal and cuneiform torsion also affects the final opposition set relative to the hallux. Considering a nonopposable hallux, the large angle in humans (table 2) is best associated with a tight curvature of the transverse plantar arch. In orangutans, on the other hand, the large angle may be best associated with some degree of second to third digit opposition and a high but mobile transverse arch. The transverse arch enhances the foot's ability to withstand bending moments

in the sagittal plane and is important in both arboreal and terrestrial behaviors (Sarmiento, 1994).

CURVATURE AND RELATIVE SIZE OF NAVICULAR FACETS

Differences in the relative cross-sectional area of the navicular's talar, cuboid, and cuneiform facets reflect differences in mobility and load-bearing capabilities at each joint. Because planar articulations commonly imply relatively restricted joint motion (Sarmiento, 1988), the relative area of the cuneiform facets (largely planar articulations in great apes and humans) is in large part an

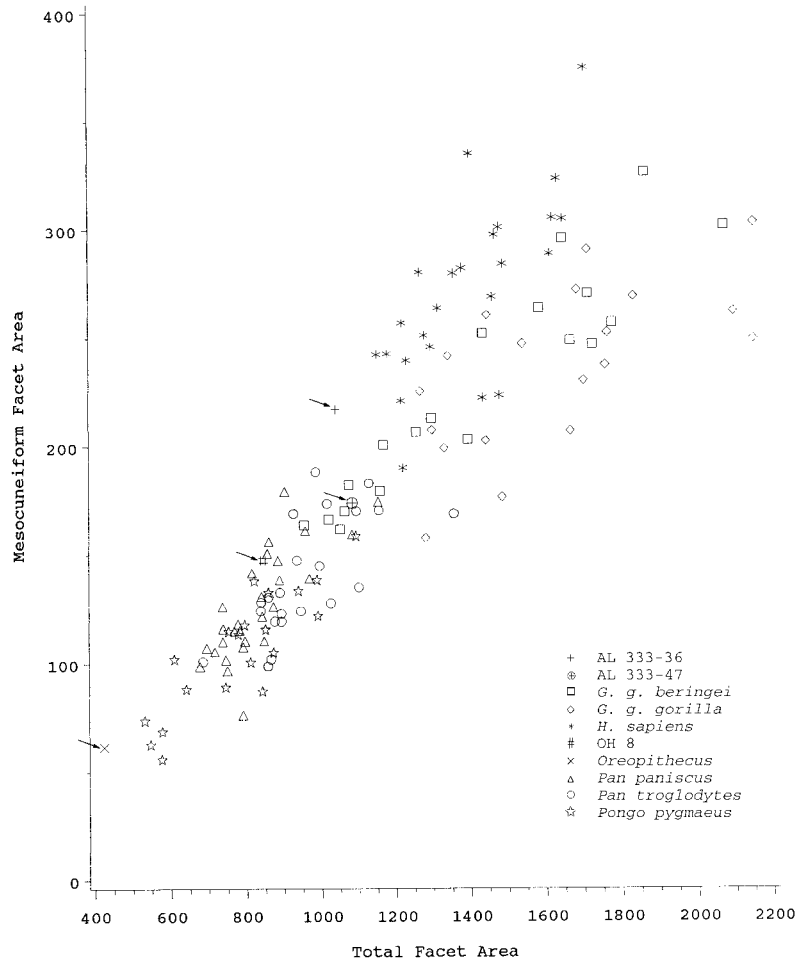


Fig. 4. Mesocuneiform facet cross-sectional area (mm^2) vs. total navicular facet cross-sectional area (mm^2) in humans, great apes, and fossil hominoids. Arrows point to fossils.

indication of the relative load transmitted across each joint. The relatively large ectocuneiform and small entocuneiform facet areas in OH 8, and the large entocuneiform and small ectocuneiform facet areas in common chimpanzees, and gorillas (table 5), reflect contrastingly different navicular loading patterns. In OH 8 loading of the third digital ray was achieved at the expense of the entocuneiform and hallux. In gorillas and common chimpanzees, loading of the entocuneiform and hallux is achieved at the expense of loading the third digital ray. In humans, the relatively large combined cuneiform facet area (fig. 8, table 9) reflects a small or nearly ab-

sent cuboid facet and transmission of the talar head load largely to the cuneiforms.

Absence or presence of a relatively small cuboid facet in humans, (fig. 6; tables 6 and 8) reflects a foot loaded parallel to its long axis and rarely subjected to a large magnitude of mediolateral forces. Conversely, the large cuboid facet in pygmy chimpanzees, and orangutans can be associated with loading of the foot in supinated postures with the foot's mediolateral axis held approximately vertical and parallel to the weight vector. In African apes, loads across the cubonavicular joint may also result from the force of the peroneus longus tendon balancing a hallucal

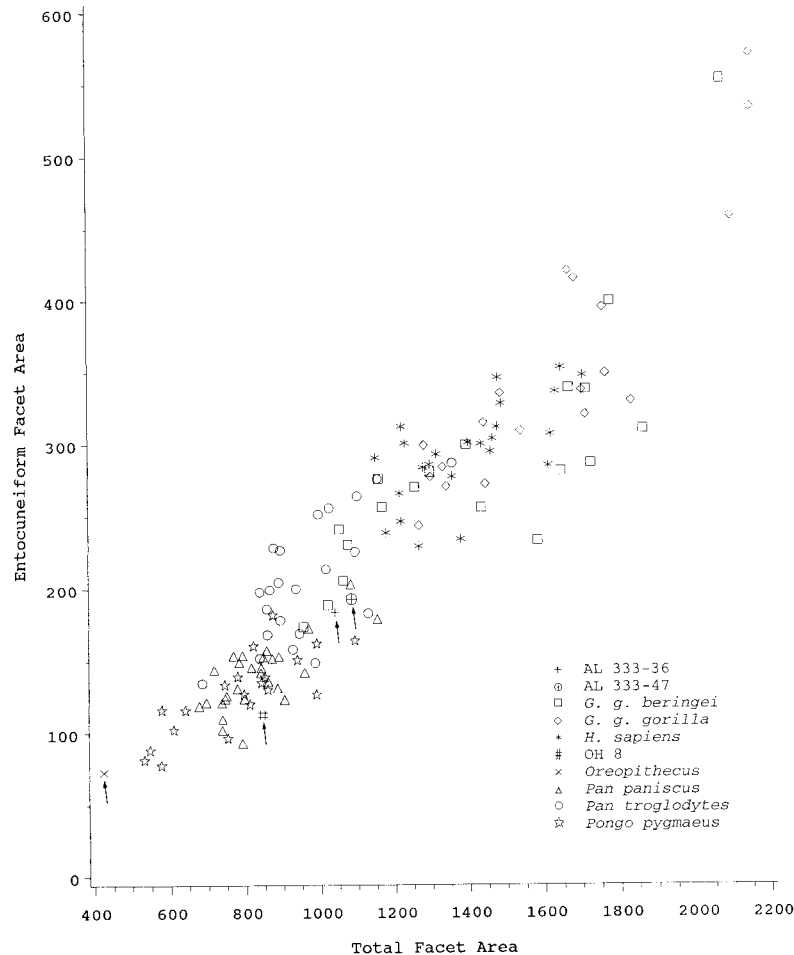


Fig. 5. Entocuneiform facet cross-sectional area (mm^2) vs. total navicular facet cross-sectional area (mm^2) in humans, great apes, and fossil hominoids. Arrows point to fossils.

grasp. Similar foot postures and/or hallucal opposability are implied by the relatively large cuboid facets of the Hadar naviculars.

The biconvex talar facet implies different loading capabilities from those of the more planar cuboid or cuneiform facets. In contrast to planar articulations, curved articulations present a perpendicular surface to force vectors of varying orientation (Sarmiento 1988). They, therefore, have an advantage over planar articulations in that they enable loading of a segment in varying orientation relative to the body weight and/or support, and are less susceptible to shear forces (Sarmiento, 1988). The large degree of dorsoplantar curvature of the great ape and Hadar naviculars

(table 3) implies that loads born by the talar head can be transmitted through the navicular to either of the cuneiforms, to the cuboid, to the substrate, or to any combination of these three.

Because curvature compromises the total available articular surface area perpendicular to weight-bearing loads (Sarmiento, 1988), curved articular surfaces must have more area than planar articular surfaces to withstand comparable loads (Sarmiento, 1988). Increasing surface area without increasing the degree of dorsoplantar curvature, the relatively wide mediolateral talar facet diameter in humans (fig. 7) reflects a need to increase total perpendicular area available to weight-

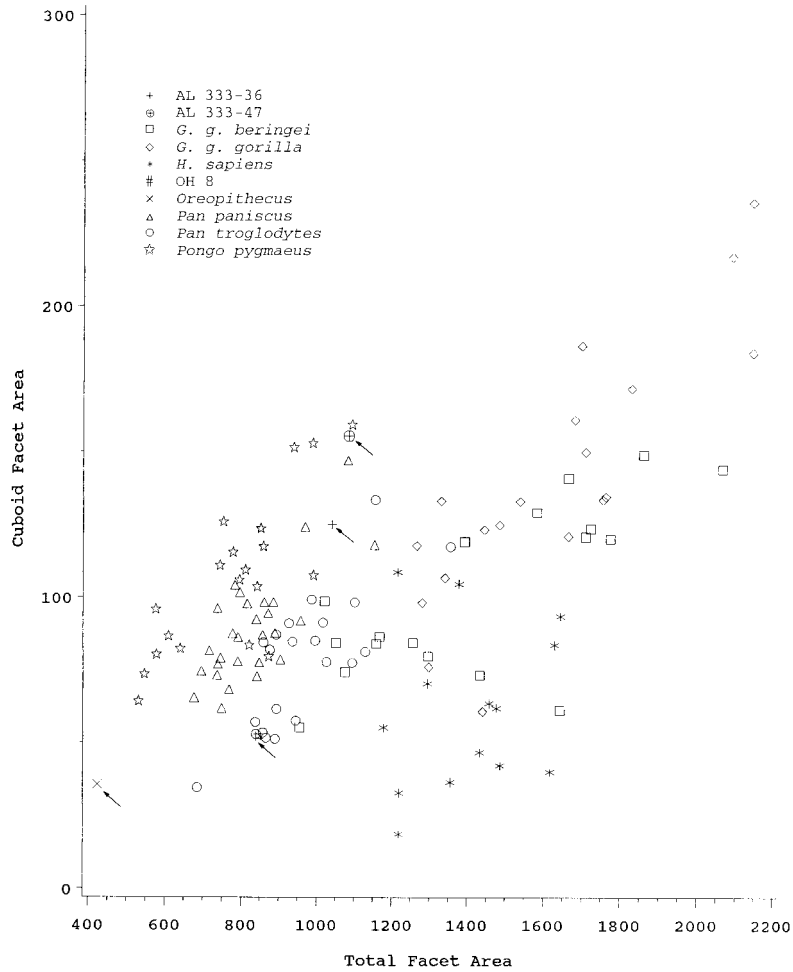


Fig. 6. Cuboid facet cross-sectional area (mm^2) vs. total navicular facet cross-sectional area (mm^2) in humans, great apes, and fossil hominoids. Arrows point to fossils.

bearing loads. With a limited degree of dorsoplantar curvature and a relative surface area comparable to that of gorillas and common chimpanzees⁴ (tables 3 and 9, fig. 10), the human talar facet sacrifices its capacity to transmit loads of varying orientation, but

⁴ Cross-sectional surface area is a more accurate estimate of the maximum surface area available perpendicular to load than of true articular area. Articular cross-sectional area tends to increasingly underestimate true articular area with an increase in articular curvature, where arc length (curvature $^{\circ}$) $\text{cord}^2 + 2 \text{ arc height}$) $\pi/720^{\circ}$ and cross-sectional diameter is equal to cord length. Because great apes have a more pronounced dorsoplantar curvature of the talar facet than do humans, cross-sectional area underestimates their true talar facet area more than in humans.

maximizes the total load it can transmit per available articular area in comparison to African apes. A similar trade-off is seen in the navicular of *Oreopithecus* and OH 8. The nearly parallel set of the OH 8 and human cuneiform and talar articular surfaces (tables 1 and 2), moreover, imply load transmission from the talus through the navicular is largely to the cuneiforms. In humans, this implied weight transmission is also indicated by the relatively large combined surface area of the cuneiform facets (fig. 8).

Curved articular surfaces, when associated with differences in the dimensions and curvatures of conarticulars, also imply joint mobility. To maintain a comparable surface area

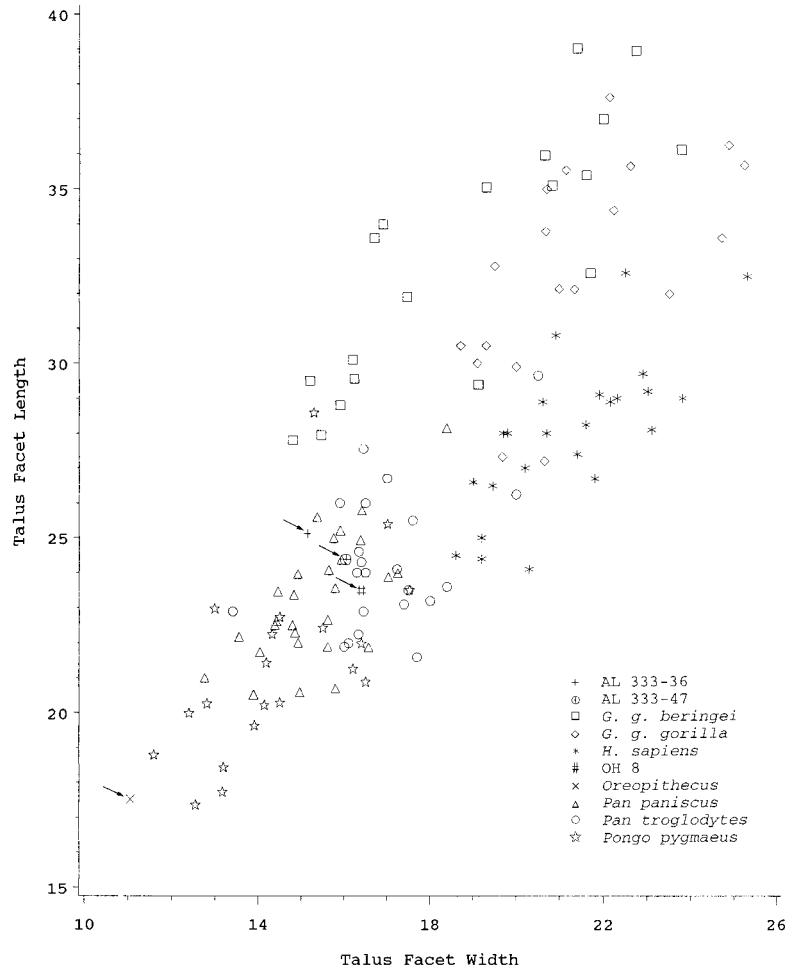


Fig. 7. Dorsoplantar (major axis) diameter (mm) vs. mediolateral (minor axis) diameter (mm) of the talar facet (i.e., talar facet length vs. talar facet width) in humans, great apes, and fossil hominoids. Arrows point to fossils.

in contact throughout a range of joint motion, joints providing movement must have a larger articular area (at least of one of their con-articulars) than those serving only to bear loads (Sarmiento, 1988). In orangutans, the large ectocuneiform facet with marked biconcave curvatures (fig. 3, tables 5 and 7) reflects considerable mobility at the naviculo-ectocuneiform joint (Rose, 1988). Marked mobility probably also explains the relatively large mediolateral degree of curvature of the orangutan talonavicular joint (table 3), which out of all the great apes most closely approximates a ball and socket analog (Rose, 1988).

In light of its marked dorsoplantar and mediolateral curvatures (table 3), the relatively small cross-sectional area of the orangutan talar facet (table 6) reflects the large size of the navicular's other facets (fig. 2). This size is most likely a correlate of a mobile foot which is loaded in a variety of postures (i.e., the talar head load is variably transferred among the three cuneiforms and cuboid). In contrast, a small degree of mediolateral curvature of the talar facet (table 3) with marked differences in its dorsoplantar vs. its mediolateral radius of curvature in gorillas and common chimpanzees (table 4) indicates limited rotatory (circumductory) motion at the

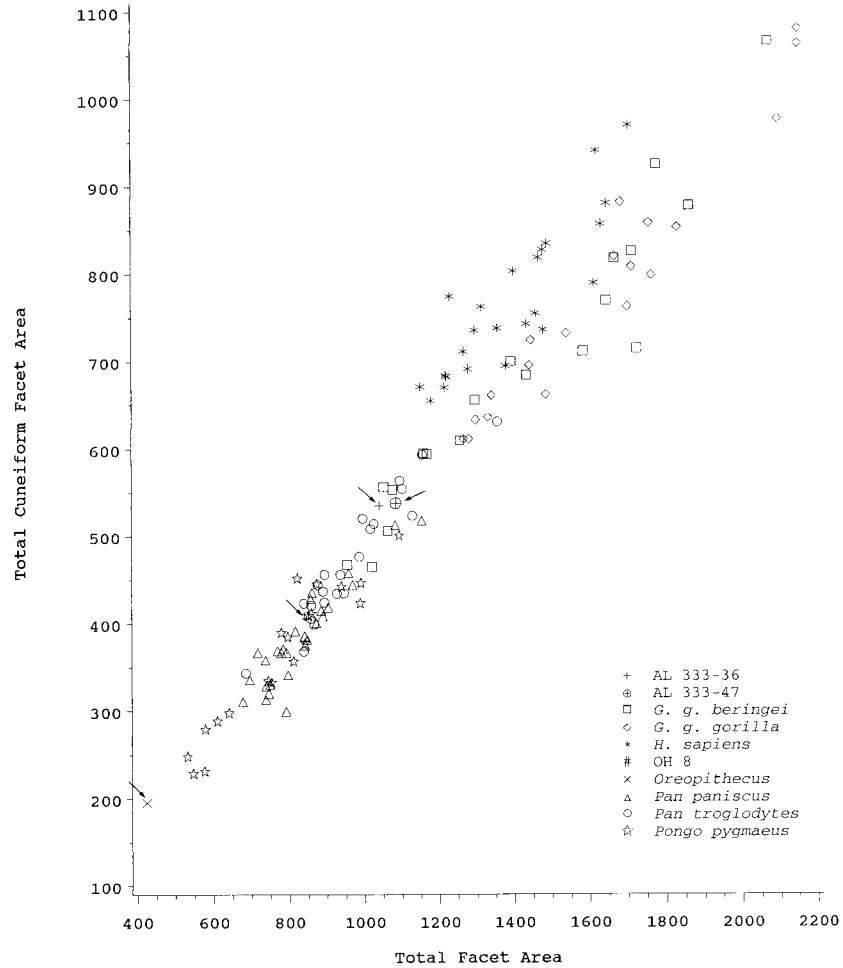


Fig. 8. Total cuneiform facet cross-sectional area (mm^2) vs. total navicular facet cross-sectional (mm^2) area in humans, great apes, and fossil hominoids. Arrows point to fossils.

talonavicular joint, at least during loading. The same is probably true of OH 8 which in spite of an absolutely small talar facet has a very large mediolateral radius curvature that is much greater than its dorsoplantar radius of curvature. With large degrees of dorso-plantar and mediolateral curvature, and no appreciable difference in the two radii of curvature (both of which are small), the relatively small talar facet of Hadar finds a closer mechanical analog to that of pygmy chimpanzees and orangutans, and suggests considerable rotatory mobility during loading. However, without matching conarticulars to gauge mobility at the joint it is not possible to know whether the Hadar talonavicular

joint compromised load bearing for mobility to the same degree seen in orangutans.

VARIATION IN RELATIVE SIZE AND SET OF NAVICULAR FACETS

Large variation and overlap in navicular angles and relative size of navicular facets within and among human and great ape samples correspond, in part, to variation in overall foot structure, i.e., corresponding variation in the abducted-adducted set of the hallux, the divergent set of the rays, and the height of the plantar longitudinal and transverse arches (figs. 15–18). Large within-sample variation in the set of the navicular facets,

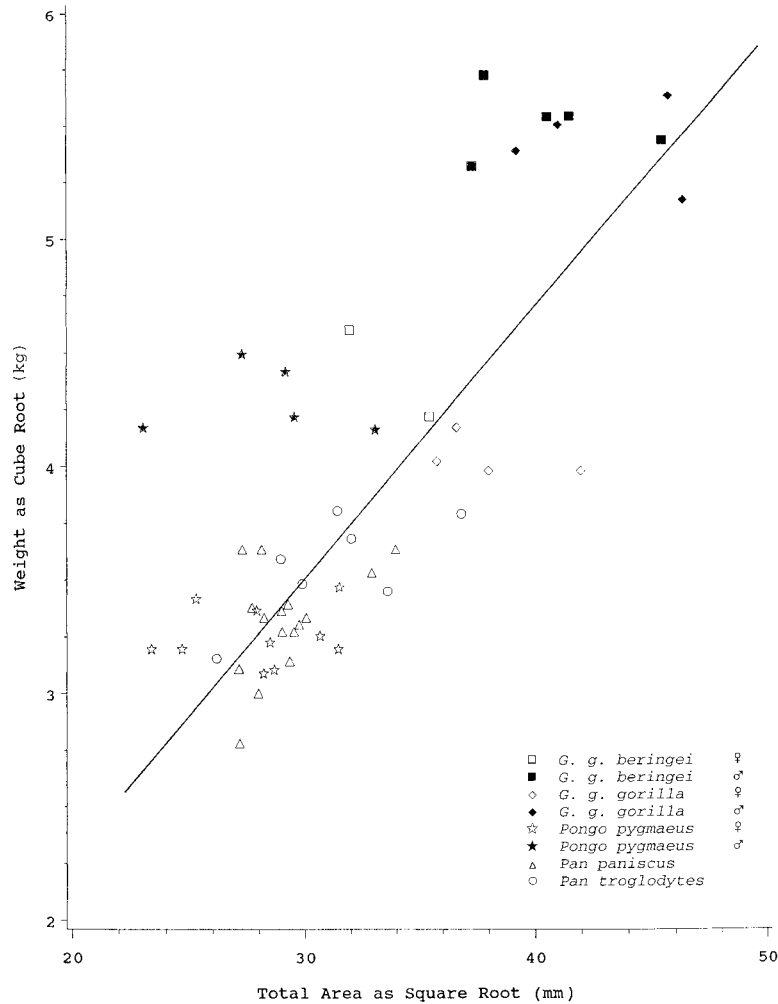


Fig. 9. Bivariate plot of cube root of body weight ($\text{kg}^{1/3}$) vs. square root of total navicular facet cross-sectional area (mm) in great apes. $N = 62$, Slope = 6.58, y intercept = -143.77. At 95% confidence limits OH 8, the two Hadar naviculars, and *Oreopithecus* were calculated to have body weights of 12.0–100.3 kg, 17.6–143.6 kg (AL 333-47), 18.6–155.1 kg (AL 333-36), and 4.4–39.5 kg respectively.

however, need not all be reflected in corresponding variation in overall foot structure. Because the foot is composed of a number of linked bony segments, the set of each facet on any one segment is not necessarily translated to all the linked segments, but may be corrected for by the joint sets of other segments in the link. Day and Wood (1968) noted such a correction of set in the talonavicular articulation of OH 8 which provides for an adducted hallux despite a divergent talar neck. The same probably applies to the within-sample variation in the dimension and

contours of the navicular's articular facets. Other segments in the link may redirect load and/or correct for variation in navicular joint mobility. For any one taxon, the overall foot structure need not demonstrate as much within-sample variation, as is reflected in the dimensions and contours of any one navicular facet. Despite overlap in the range of values for the set, dimensions, or contours of individual facets, humans and great apes each have a characteristic and distinct foot structure (Tuttle, 1970; Sarmiento, 1983, 1985, 1994; Rose, 1988).

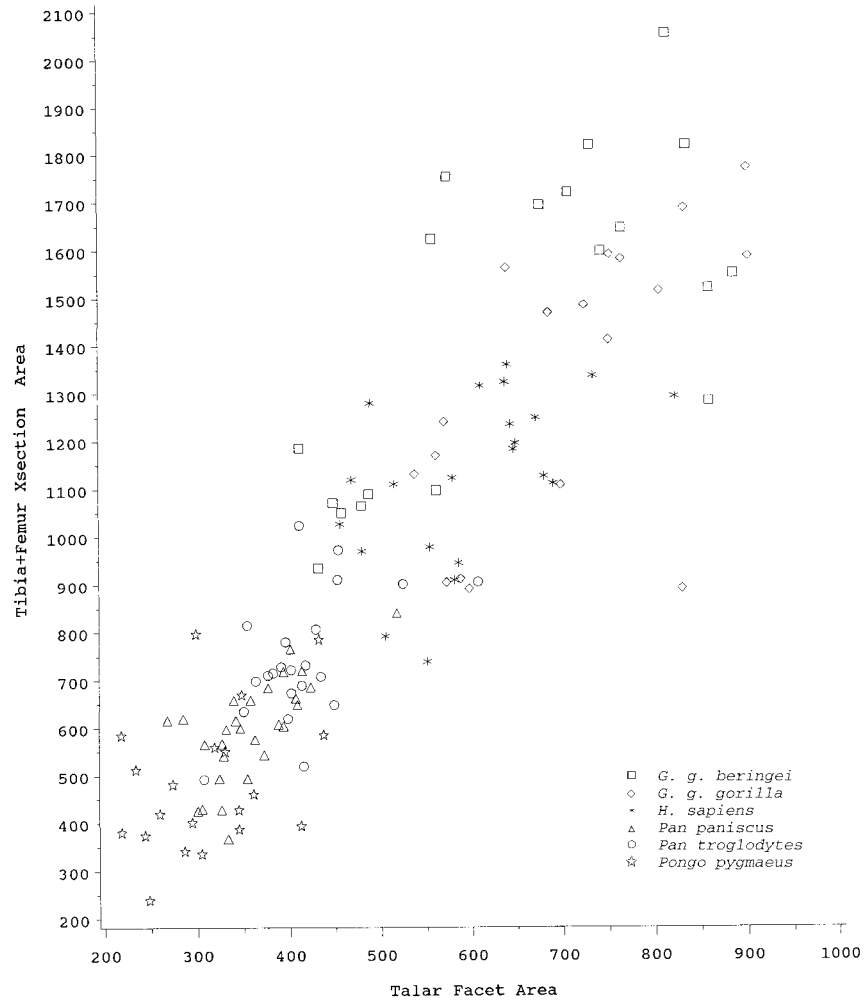


Fig. 10. The sum of the femoral and tibial cross-sectional areas (mm^2) vs. talar facet cross-sectional area (mm^2) in humans, great apes, and fossil hominoids.

Because each characteristic great ape and human foot structure places constraints on the range of variation in the relative size and set of each navicular facet, and the navicular has at least four facets, it is highly unlikely (unless the sets, curvatures, and dimensions for different facets on the same navicular are all positively correlated) that all four facets on anyone navicular when compared individually will each have sets, dimensions, and/or contours that deviate markedly (more than 1 standard deviation) from their respective means. Despite a large overlap in the range of variation between human and great ape samples for each of the individual navicular

facet measurements (tables 1–10), there is little or no overlap when all navicular measurements are taken together, even the two most similar samples are separated by at least 3.8 Mahalanobis distance units (table 11). When taken together, therefore, the navicular measurements do reflect the characteristic foot structure of each sample.

FOOT USE AND INHERITED VS. EPIGENETIC CHARACTERS

Foot use (i.e., the series of external forces applied to the foot through a range of foot joint movements), through ontogenetic plas-

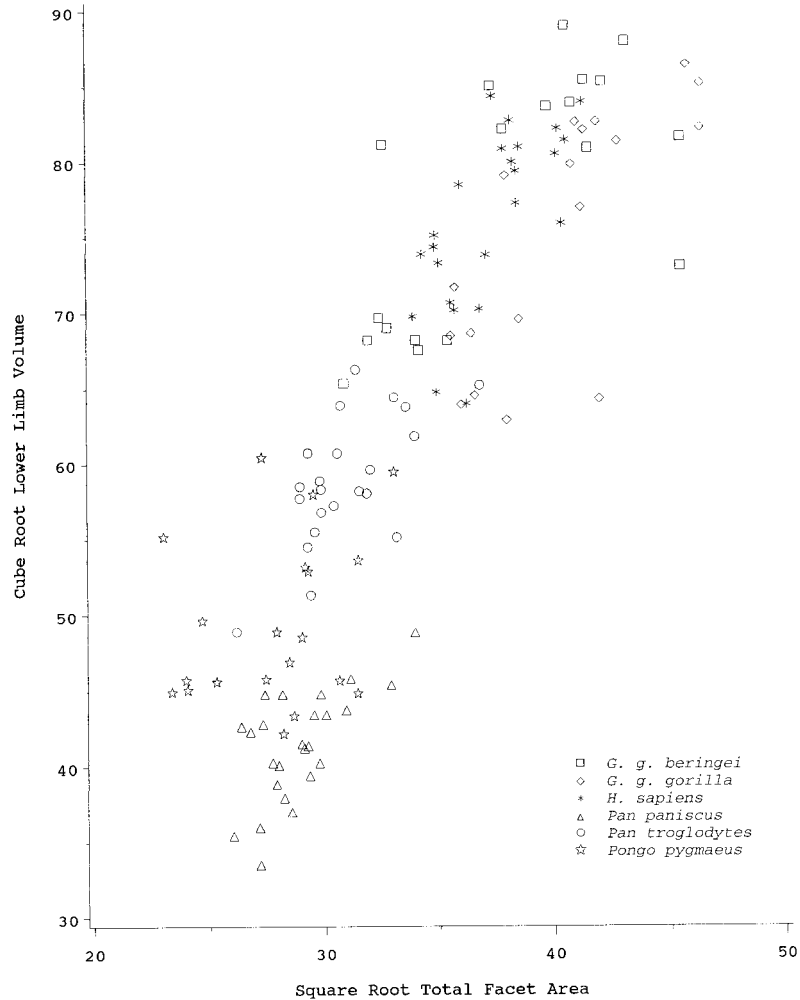


Fig. 11. Cube root of lower limb-volume (mm) vs. square root of total navicular cross-sectional area (mm) in humans, great apes, and fossil hominoids.

ticity in the dimension and relative orientation of facets, modifies the inherited morphology of the various segments to achieve the adult foot structure (Sarmiento, 1985). With shifts in behavior, ontogenetic plasticity allows the foot to adapt to a new use permitting selection for the inherited morphology which best suits this new use in descendant populations. Although both OH 8 and humans have an adducted hallux (Day and Napier, 1964; Day and Wood, 1968), differences in the set of the talonavicular joint between the two may in part represent differences in the number of generations hallucal adduction has been selected for.

Localization of forces and differences in the duration of growth among the segments comprising a structure are probably important factors in determining which segments are most strongly modified. The latest segments to complete epiphyseal fusion and fully develop have a longer time to respond to use, and thus may be more likely to be altered ontogenetically in response to use. Late developing segments may very well be a focus of ontogenetic plasticity, since their epiphyses fuse at a time when the animal is closest to its adult weight. Because at this time the forces on the foot may be expected to most closely approximate those of the adult, late devel-

TABLE 11
Mahalanobis Distance^a
 Mahalanobis D above diagonal zeros; unbiased D below diagonal.

| | AL333-36 | AL333-47 | G.g.b. | G.g.g. | <i>Homo</i> | OH8 | Ore. | Pan p. | Pan t. | <i>Pongo</i> |
|--------------|----------|----------|---------|--------|-------------|----------|-------|--------|--------|--------------|
| AL333-36 | 0 | ns6.84 | ***8.10 | *6.73 | 9.73 | **10.77 | 15.17 | ns6.03 | **7.03 | ***9.66 |
| AL333-47 | 1.61 | 0 | **7.48 | **7.13 | 11.25 | ***11.63 | 13.26 | ns6.17 | ns6.26 | 7.97 |
| G.g.b. | 5.92 | 5.21 | 0 | 4.07 | 10.02 | 10.96 | 13.49 | 7.53 | 5.65 | 10.99 |
| G.g.g. | 4.28 | 4.79 | 3.43 | 0 | 8.33 | 10.33 | 14.45 | 6.34 | 4.34 | 9.47 |
| <i>Homo</i> | 7.67 | 9.22 | 8.98 | 7.41 | 0 | *7.04 | 18.04 | 10.84 | 8.84 | 12.38 |
| OH8 | 7.72 | 8.68 | 8.94 | 8.31 | 4.64 | 0 | 18.34 | 10.86 | 9.75 | 13.05 |
| Ore. | 12.39 | 10.44 | 11.45 | 12.38 | 15.77 | 15.53 | 0 | 11.19 | 11.43 | 13.02 |
| Pan p. | 3.32 | 3.53 | 6.70 | 5.59 | 9.73 | 8.85 | 9.18 | 0 | 3.78 | 6.28 |
| Pan t. | 4.68 | 3.67 | 4.95 | 3.71 | 7.89 | 7.72 | 9.43 | 3.17 | 0 | 7.24 |
| <i>Pongo</i> | 7.62 | 5.78 | 9.89 | 8.49 | 11.14 | 11.02 | 10.99 | 5.54 | 6.44 | 0 |

^a Mahalanobis distances are based on 6 angles and all 13 length measurements. All of the human and great ape naviculars were correctly assigned to their taxon. When the "leave one out" or "cross-validation" option was invoked, seven *G. g. gorilla* were assigned to other taxa (three to *P. troglodytes*, three to *G. g. beringei*, and one allied to AL 333-36), two *G. g. beringei* were placed in *G. g. gorilla*, and both Hadar specimens and *Oreopithecus* were placed in *P. paniscus*. Unbiased distance D_u after Marcus (1993); each D^2 can be tested using an F test. D_u is calculated from the following:

$$D_u^2 = D^2[(N - g - p - 1)/(N - g)] - [(n_1 + n_2)p/(n_1n_2)]$$

N = total sample size (118); p = number of variables (19); n_1 and n_2 = sample sizes of the taxa being compared; g = number of groups (10).

Significance: ns, not significant; *, significant at 0.05; **, significant at 0.01; ***, significant at 0.001. All other distances are significant at 0.0001.

Abbreviations: G.g.b., *G. g. beringei*; G.g.g., *G. g. gorilla*; *Homo*, *H. sapiens*; Ore., *Oreopithecus*; Pan p., *Pan paniscus*; Pan t., *Pan troglodytes*; *Pongo*, *Pongo pygmaeus*.

oping segments are able to fine tune an adult foot to its newly acquired use.

Segments in direct interaction with environmental forces (i.e., those of the hands and feet) are more likely to encounter greater variation in forces both in direction and magnitude, and may be expected to exhibit more plasticity and be less conservative than more proximal segments (i.e., those closer to the animal's center of gravity). In the case of proximal segments, intervening segments redirect and buffer environmental forces, so that changes in foot and hand use may cause only negligible changes in the resultant forces proximal segments are subjected to. In this regard, the morphology of proximal segments is shaped by forces channeled through inherited structures (i.e., muscles, connective tissue, and adjacent segments), and thus more likely to be conservative.

BODY WEIGHT, LOWER LIMB SIZE, AND NAVICULAR FACET AREA

Relationships of body weight, lower-limb cross-sectional area, or lower-limb volume to

total navicular or talar facet cross-sectional area (figs. 9–11; tables 9–10) reveal trade-offs between body size, lower-limb loading, and joint mobility. Although large facet surface areas relative to joint load are characteristic of mobile joints (Sarmiento, 1988), differences in joint mobility are not necessarily reflected by differences in ratios of facet cross-sectional area to body weight. In this regard, comparatively large navicular facet areas relative to body weight in female gorillas and common chimpanzees (fig. 9, table 10) are more a factor of the lower limb bearing a proportionately greater percentage of the weight than an indicator of navicular joint mobility. Because midshaft cross-sectional area of the lower-limb long bones is a factor of the load borne by the lower limbs, ratios of talar or total navicular facet area to midshaft cross-sectional area more accurately reflect facet size relative to facet load, and hence are better indicators of navicular joint mobility. In pygmy chimpanzees and orangutans, therefore, the comparatively higher values for these ratios (fig. 10, tables 9 and

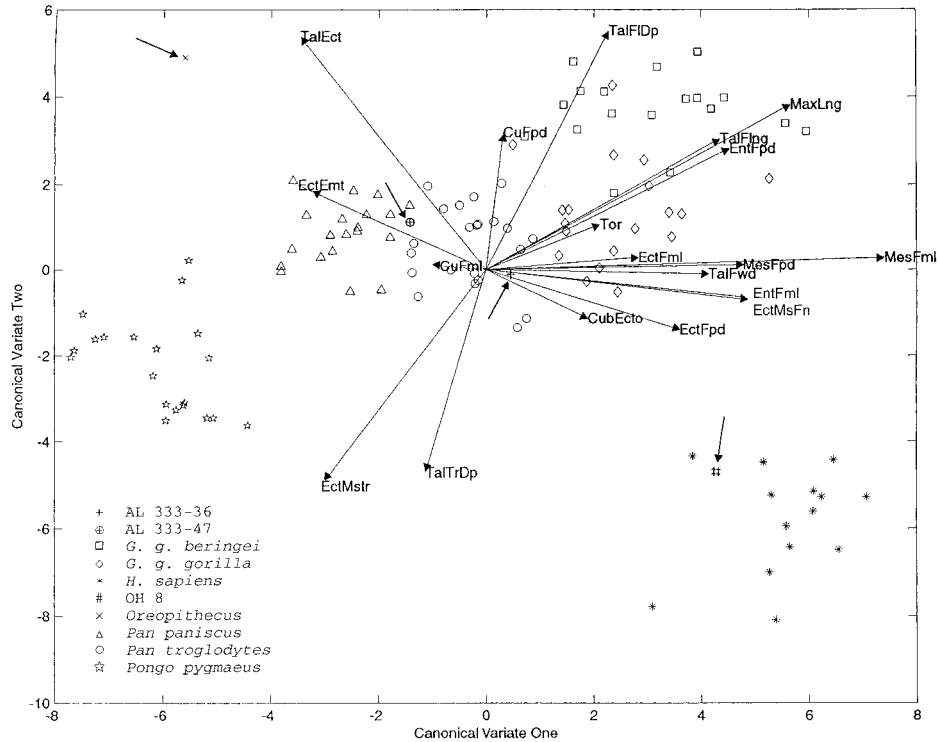


Fig. 12. A plot of the first two canonical variates with vectors representing the contribution of each of the measured variables to the scatter within and among measured taxa. Arrows point to fossils. Note the distinctiveness of *H. sapiens*, the uniqueness of *Oreopithecus* and the similarities of Hadar and African apes, of OH 8 and *Homo*, and of great ape species or subspecies within genera. The vectors representing the frontal mesoectocuneiform angle (EctMsFn) and the mediolateral diameter of the entocuneiform facet (EntFml) are nearly overlapping. Vector lengths are exaggerated by a factor of ten, and owing to a two-dimensional projection, are not proportional to their actual length. Eighty percent of the variance among means relative to the within-group variance is summarized by the first two canonical variates (see figure 14 for plotted means of the first two canonical variates). Program written in Matlab version 5.1. This "biplot" is after Rohlf (1997); see Marcus (1993) for a discussion. The program and navigular data are available from one of us (LM). TalFng = talar facet dorsoplantar (major axis) diameter, TalFwd = talar facet mediolateral (minor axis) diameter, EctFpd = ectocuneiform facet dorsoplantar diameter, EctFml = ectocuneiform facet mediolateral diameter, MesFdp = mesocuneiform facet dorsoplantar diameter, MesFml = mesocuneiform facet mediolateral diameter, EntFml = entocuneiform facet mediolateral diameter, EntFdp = entocuneiform facet dorsoplantar diameter, MaxLng = navicular maximum length, CuFdp = cuboid facet dorsoplantar diameter, CuFml = cuboid facet mediolateral diameter, TalFIDp = depth of talar facet along major axis, TalTrDp = depth of talar facet along minor axis; CubEcto = transverse cuboectocuneiform angle, EctMstr = transverse mesoectocuneiform angle, Tor = navicular torsion, EctMsFn = frontal mesoectocuneiform angle, TalEct = sagittal taloectocuneiform angle, EctEmt = entoectocuneiform angle.

10) more than likely reflect comparatively greater joint mobility. The relatively larger total navicular facet cross-sectional areas of western gorillas when compared to those of mountain gorillas (fig. 9, table 9) likewise reflect more mobile navicular joints in western gorillas, and correlate well with arboreal

behaviors, which are considerably limited among mountain gorillas (Sarmiento, 1994; Sarmiento et al., 1996).

Relative reduction in navicular facet area with an increase in body size among humans and great apes (figs. 9 and 10; tables 9 and 10) is in part a factor of relative decrease in

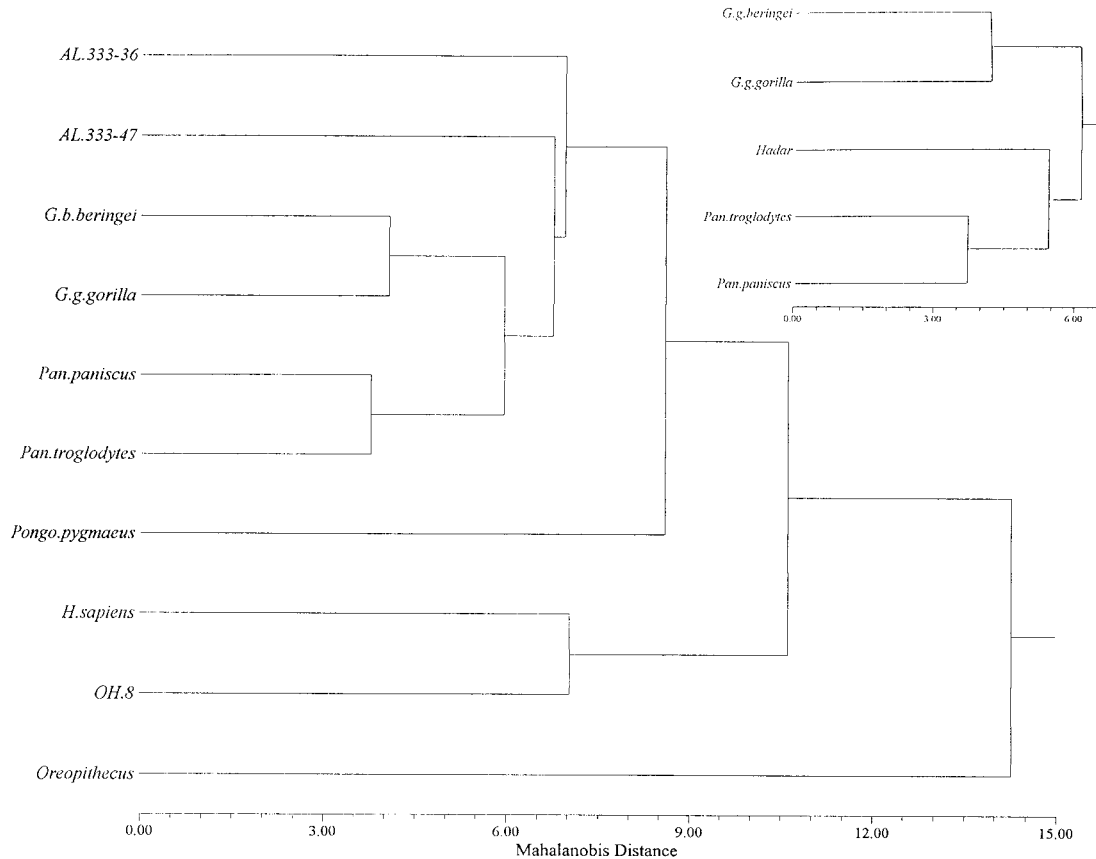


Fig. 13. Dendrograms of the studied taxa constructed using unweighted pair group method (Rohlf, 1997). Inset shows portion of dendrogram which differs when both Hadar naviculars are considered as a single sample.

strength (proportional to muscle cross-sectional area) with increase in body size (a corollary of volume), as predicted by the square cube law. With proportionately weaker muscles, large-sized animals are unable to stabilize rotational forces of the same relative magnitude as small-sized animals, and must limit their range of joint motion (around a point of load equilibrium) to limit the magnitude of rotational forces. The relatively larger facet areas of orangutan and gorilla females when compared to their male counterparts reflect such a trade-off between body size and joint mobility (fig. 9, table 9). In terms of behavior, these differences are revealed in a greater commitment to arboreal behaviors (Sarmiento, 1985, 1994; Sarmiento et al., 1996) and probably more variable foot

use among females. Additionally, orangutan and gorilla females may be expected to show quicker foot segment and body movements, given proportionately larger joint surface areas to dissipate kinetic energy than their corresponding adult males. The relatively small navicular joint surface areas of humans despite a considerably smaller body size than gorillas (tables 9 and 10) is the result of a marked commitment to bipedality and the additional loading on the feet associated with bipedal behaviors.

Despite marked sexual dimorphism in body weight, orangutans and gorillas of corresponding sexes have similar-sized navicular facet areas (fig. 9). This phenomenon is a correlate of sexual dimorphism and a pubescent growth spurt which doubles body

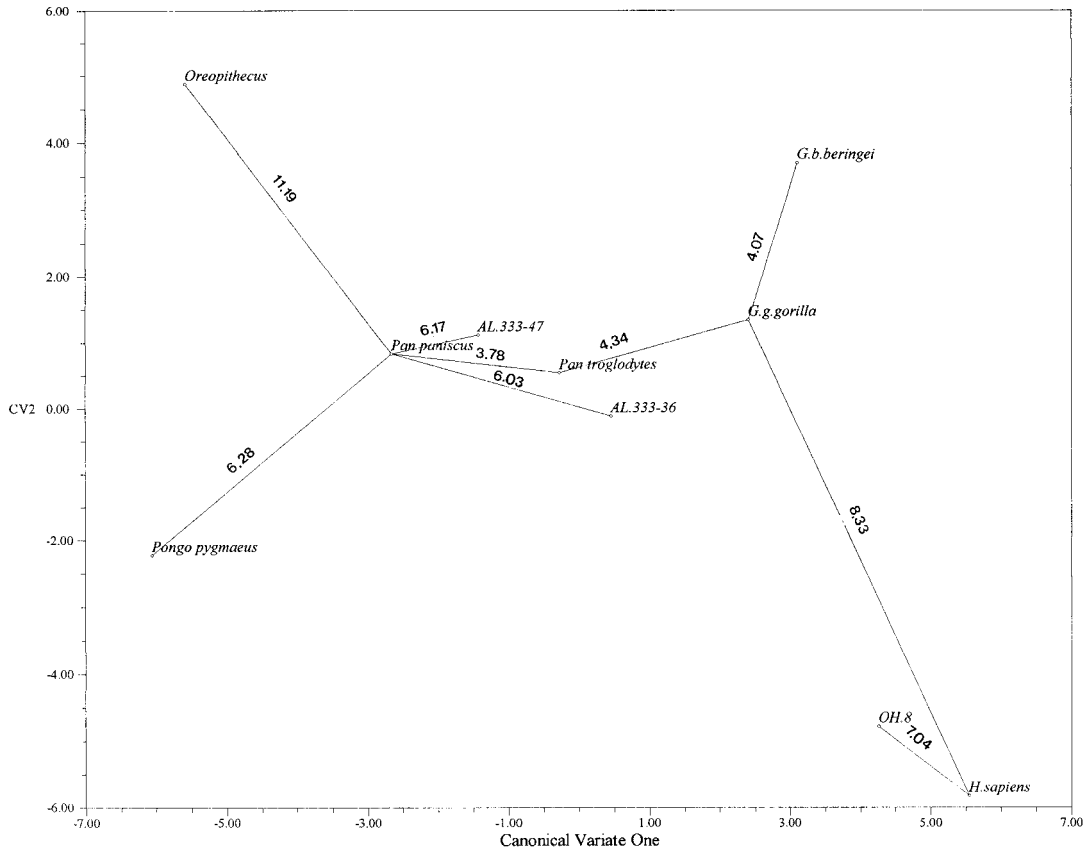


Fig. 14. Plot of mean canonical variate scores for studied taxa. All fossils are based on single samples. The actual Mahalanobis D for all of the canonical variates separating taxa is given as the value above each connecting line (table 11). Connecting lines represent a Minimum Spanning Tree (after Rohlf, 1997). Owing to a two-dimensional projection, the actual lengths of the connecting lines on the plot represent only a fraction of the D values.

size without a corresponding increase in foot size. With nearly adult foot size and navicular facet area to body weight ratios closer to their female counterparts, subadult male orangutans and gorillas are also more arboreal, and show more variable foot use than when fully adult (Sarmiento, 1985, 1994; personal obs.).

Considering that (1) facet cross-sectional area is largely a factor of joint load and mobility, and (2) neither of these variables in humans and great apes have a constant relationship with body weight, predictions of body weight in fossils from interspecies regressions of navicular facet area have a large degree of error (fig. 9).

Likewise navicular facet size does not seem to have a constant relationship to lower-limb volume (fig. 11, table 10). With varied foot use and navicular mobility and loading, including direct transfer of weight by the navicular to the substrate, African apes have the relatively largest navicular facet areas (table 10). A much larger size ratio in African apes than in humans is expected given our hypertrophied lower limbs, limited navicular joint mobility, and a longitudinal arch that prevents navicular to substrate contact. However, a comparable or larger ratio in African apes than in orangutans despite the orangutan's small lower limbs underscores the effect of terrestrial loading and generalized

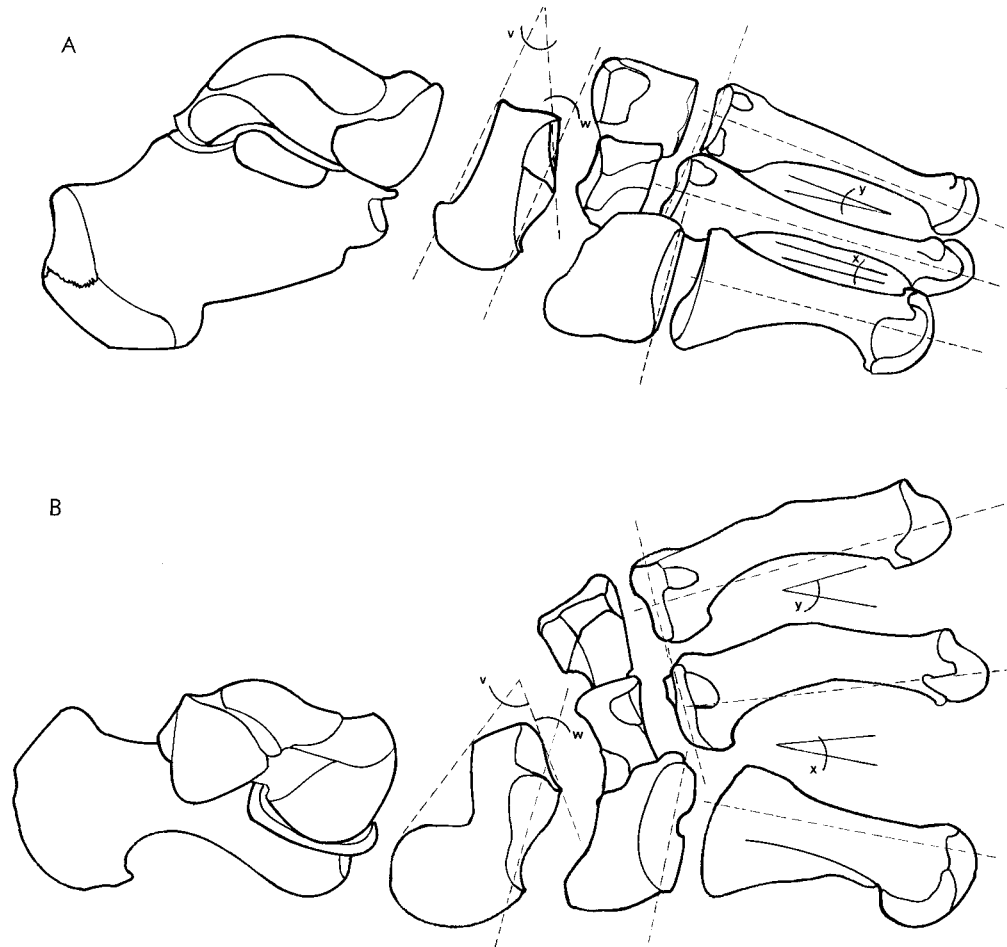


Fig. 15. Contributions of the entoectocuneiform and sagittal taloectocuneiform angles (w and v respectively) to the relative set of the first through third metatarsal in close-packed position as seen in line drawings of the exploded left foot of a human (A) and of a gorilla (B) in medial view. The large sagittal taloectocuneiform angle in gorillas imparts a dorsiflexed set to the third metatarsal and is associated with a dorsiflexed talar head, i.e. small angle of talar neck inclination (Day and Wood 1968). The gorilla entoectocuneiform angle imparts a plantar set to the entocuneiform relative to the ectocuneiform and is associated with an abducted hallux, i.e. plantar divergence of the hallux relative to second (x) and third metatarsals (y). The human taloectocuneiform and entoectocuneiform angles are associated with a plantar flexed talar head (i.e., large angle of talar neck inclination), nearly aligned first to third metatarsals, and a longitudinal plantar arch. Due to a fixed transverse arch in humans, however, the long axis of the second and third metatarsals must have a more plantar inclination than the hallux, and the value of x and y are negative. Because the major axis of the navicular's talar facet is not necessarily held vertically, the sagittal taloectocuneiform and entoectocuneiform angles may also impart some degree of medial divergence to the hallux.

foot use on African ape total navicular facet area. Although knowledge as to behavior and lower-limb use could possibly be used to improve predictions of body weight based on facet size, such information is not always present in isolated fossil naviculars.

NAVICULAR FUNCTION AND IMPLIED LOCOMOTOR BEHAVIORS

The relatively small Mahalanobis distances between Hadar and African ape naviculars (table 11) attest largely to a similar mor-

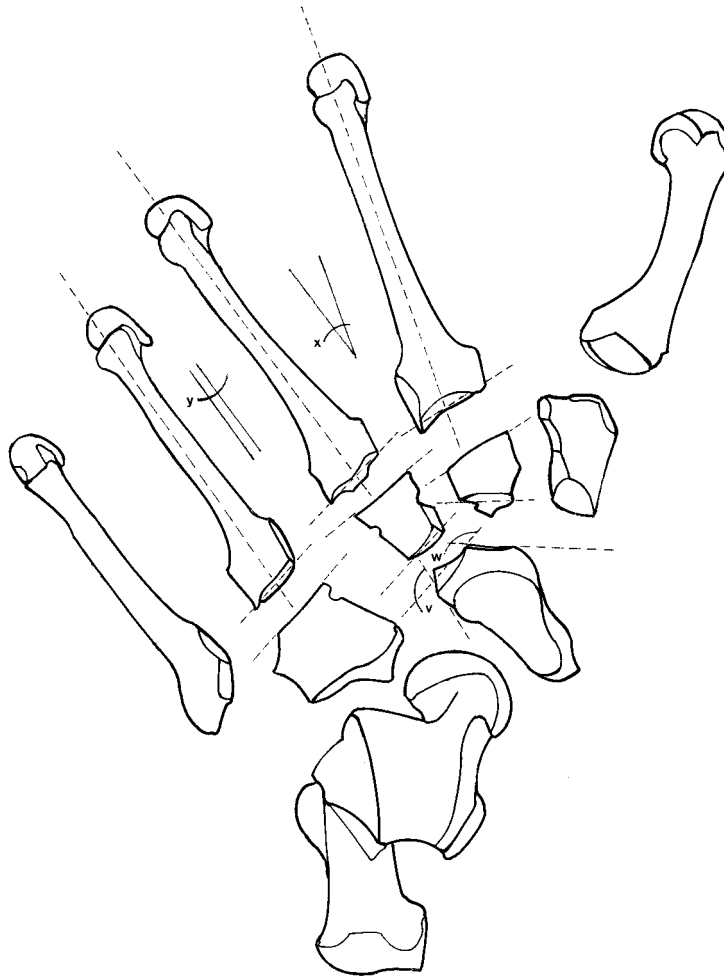


Fig. 16. Dorsal view of the exploded left tarsus and metatarsus of a pygmy chimpanzee in the close-packed position showing the contribution of the transverse mesoectocuneiform angle (w) and the transverse cuboectocuneiform angle (v) to the divergence of the second through fourth metatarsals. Correction of the talocuboid angle by the facet sets on the cuboid and ectocuneiform results in third and fourth metatarsals that are nearly aligned (y). A relatively low transverse mesoectocuneiform angle results in a second metatarsal that is divergent from the most lateral three (x) despite a partial correction of this set by the mesocuneiform.

phology and imply similarities in function. The exclusive association of a localized morphology and its implied function to a specific locomotor behavior, as is routine practice among paleoanthropologists (Napier, 1962; Day and Napier, 1964; Robinson, 1972; Conroy and Fleagle, 1972; Stern and Susman, 1983; Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990a, b; Lovejoy, 1978, 1988; McHenry, 1991; Leakey et al., 1995; Ohman et al., 1997; Ward et al., 1999), may

be used by some to argue that the Hadar fossils represent knuckle-walkers. This interpretation is at odds with evidence from the pelvis and knee joint, which although poorly quantified and never adequately tested, is almost unanimously taken as indicative of bipedality (Lovejoy, 1974; 1978; Stern and Susman, 1983; Susman et al., 1984; McHenry, 1991; Susman and Stern, 1991; Ohman et al., 1977; Fleagle, 1998). The Hadar naviculars, however, come from a different ho-

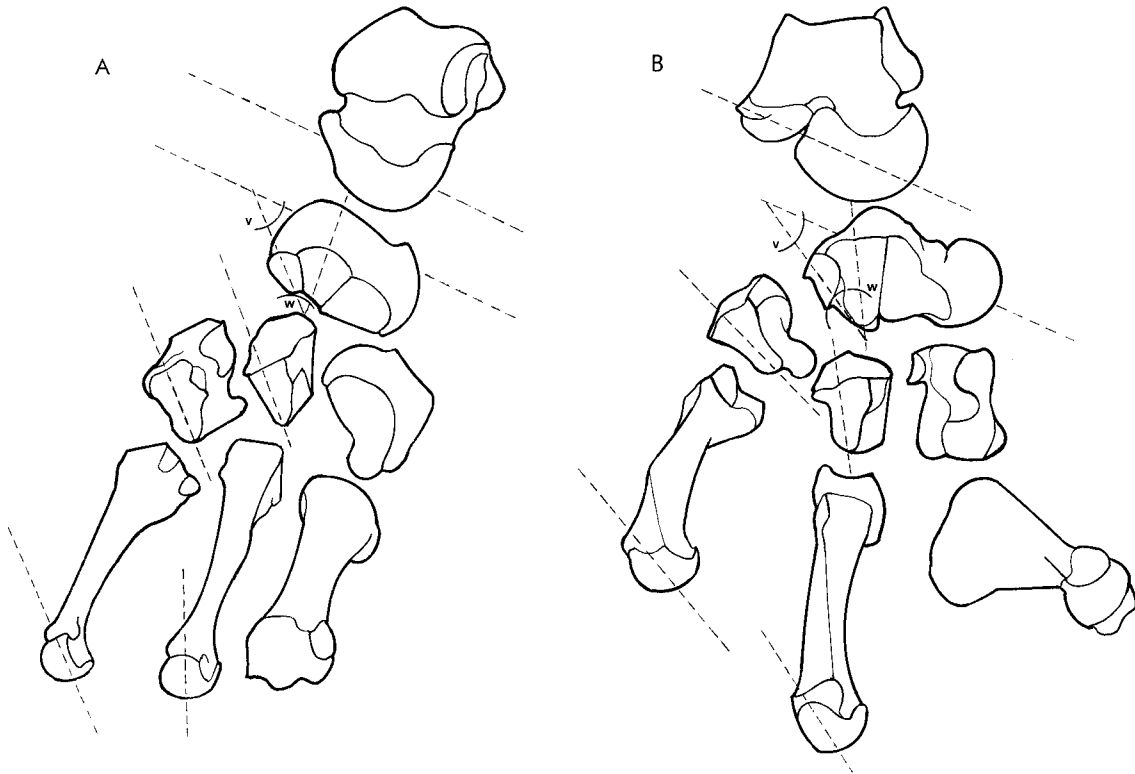


Fig. 17. Contribution of navicular torsion (v) and the frontal mesoectocuneiform angle (w) to the relative set of the ectocuneiform, mesocuneiform, and the talar facet in the close-packed position as seen in line drawings of an exploded right foot of a human (A) and a gorilla (B) from a dorsodistal view. High values of the frontal mesoectocuneiform angle in humans (w) do not result in marked opposition of the second and third metatarsals given metatarsal, ectocuneiform, and mesocuneiform torsion values which correct for the imparted set. Despite similar torsion values in humans and gorillas, the metatarsal, ectocuneiform, and mesocuneiform torsion all contribute to causing more marked opposition of the second and third metatarsals in gorillas. Marked talar torsion or large frontal mesoectocuneiform angles, are also associated to a high transverse arch (see text).

rizon (AL 333w/333) and an earlier time period than the Hadar pelvis (AL 288-1an,-ao) (Johanson et al., 1982), and the two remains may represent different taxa with different locomotor behaviors (Ferguson, 1984, 1986; Senut and Tardieu, 1985; Olson, 1981, 1985; Gommery, 1997).

At Hadar a contradiction in implied behavior, however, also arises when comparing remains from the same horizon and may not necessarily be the result of sampling different taxa. The alleged bipedal knee joint morphology is also seen in fossils from the same horizon as the naviculars (AL 333w-56, 333-4, 333-111, 333x-26, 333-42), and the dimensions, curvature, set, and configuration

of the navicular articulation on the AL 288-1 talus suggest an African apelike navicular similar to those from the AL 333/333w horizon. The contradictions in behavior implicit in the navicular, pelvic, and knee joint morphology actually arise from the practice of associating localized anatomy exclusively to any one locomotor behavior and underscores the fallacy inherent in such a practice. Because behavioral changes during evolution (i.e., adaptive shifts) require localized structures to satisfy the mechanical requisites of two or more behaviors (Darwin, 1859), exclusive association of localized morphology to any one locomotor behavior denies evolutionary change. Arguments for bipedality

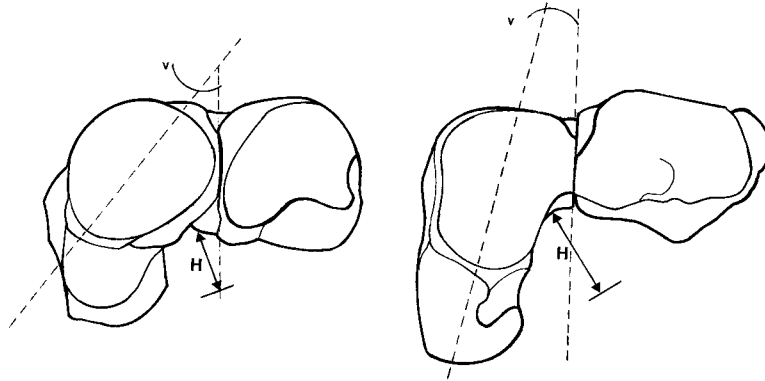


Fig. 18. Proximal views of the right cuboid and navicular of a human (A) and a common chimpanzee (B) in a close-packed position showing the contribution of the talocuboid angle (v) to the height of the transverse arch (h). In the close-packed position the small angle shown by chimpanzees results in a higher transverse arch than normally seen in humans. The human arch, however, unlike that of chimpanzees, exhibits a fixed height. Owing to a small, irregular, and often absent cuboid facet, the human talocuboid angle could not be accurately measured.

based on localized morphology do not exclude the likelihood that these morphologies and their implied localized functions also served other behaviors (table 12). The presence of many of the alleged bipedal characters in cursorial quadrupeds and the mechanical advantages these characters impart to quadrupeds, support the theory that many of the allegedly bipedal human characters arose as a result of selection pressures for cursorial quadrupedality (Sarmiento, 1998). The absence of a humanlike lumbar lordosis, the orientation of the acetabulum's lunate surface, and the relative size of the humeral and femoral midshaft circumferences and first sacral body cross-sectional area, all characters which are altered ontogenetically as a result of use, show that AL 288-1 had a body-to-limb weight distribution and pelvic joint postures similar to those of quadrupeds (Sarmiento, 1998).

Although it may be argued that the pelvis is phylogenetically more conservative than the navicular (see above) and thus the latter is more likely to reflect use, while the former is more likely to reflect heritage, the Hadar pelvic, femoral, and navicular morphology if associated must have satisfied the mechanical requisites of many of the same behaviors. In this regard, it is not possible to fully interpret what the range of these behaviors may have been without analyzing all of the animal's

morphology. No matter how bipedal, quadrupedal or climbing-like a localized morphology may be, it is usually not possible to predict on the basis of that morphology alone the overall morphology of an unknown fossil taxon and the range of behaviors the unknown morphology enabled. In this regard, functional analysis of the navicular alone is limited to the functional role the navicular may have had in the foot, and in a range of hypothesized behaviors usually based on those seen in living taxa.

FOSSIL FOOT USE

OH 8

In OH 8 the comparatively shallow talar facet, small sagittal taloectocuneiform and entoectocuneiform angles and the large transverse mesoectocuneiform angle suggest the presence of a fixed longitudinal arch. The laterally expanded tubercle midway on the lateral border of the navicular which serves as the attachment site for the calcaneonavicular (spring) ligament, and the large articular area for this ligament on the talar head indicate a longitudinal plantar arch with energy-storing properties comparable to or approximating those of humans (Alexander, 1989). A dorsiflexed talar head and plantar processes on the navicular and entocuneiform, however, suggest the longitudinal arch height was low-

er than is characteristic of humans, and the distal tarsal row contacted the substrate (Day and Wood, 1968). Given a fixed longitudinal arch, however, only a small percentage of the weight borne by the foot could have been transferred to the substrate by the navicular and entocuneiform, hence the relatively small plantar tubercles.

Although the small frontal talocuboid angle (table 2) indicates a high transverse pedal arch, the development of a hamulus and groove for the peroneus longus tendon on the plantar surface of the ectocuneiform indicates this arch was not fixed. Considering very little rotatory mobility at the talonavicular (as implied by the shallow talar facet with different mediolateral and dorsoplantar radii of curvature) and calcaneocuboid joints (Lewis 1980c), transverse arch mobility must have resulted mainly from movement at the subtalar joint.

The sagittal entoectocuneiform angle and the set of the talonavicular, naviculoentocuneiform, and the first tarsometatarsal joints all indicate an adducted hallux which was achieved through a different combination of joint sets than that seen in humans (Day and Wood, 1968; Oxnard and Lisowski, 1980; Oxnard, 1984). Although some degree of opposability may have been possible, depending on the unknown metatarsophalangeal joint set, this would have been very limited.

The adducted hallux and large transverse mesoectocuneiform angle reflect a compact foot that was strongly committed to terrestriality. The relatively small cuboid facet suggests the foot was usually loaded in pronated postures (with the foot's mediolateral axis approximating the horizontal and its long axis in the plane of forward movement). The relatively large ectocuneiform facet (fig. 3, tables 5 and 7) and small mesocuneiform and entocuneiform facets (figs. 4 and 5, tables 5 and 7) indicate a preference for loading the lateral side of the foot at the expense of the hallux. Differences relative to humans in the orientation of the subtalar and talocrural joints (Lewis, 1980c) probably reflect differences in terrestrial foot use in both quadrupedal and bipedal behaviors, and may have also been important for proper foot orientation in vertical climbing or walking along horizontal branches. Given the rela-

tionship between body size and tree use (Cartmill and Milton, 1977; Sarmiento, 1983, 1985, 1988, 1994, 1998; Cartmill, 1985), an animal corresponding in size to the OH 8 foot, regardless of its terrestrial specializations, was no doubt better suited to move arboreally than humans and or male gorillas (Sarmiento, 1985, 1994, 1998).

Hadar

When considered in light of the other AL 333/333x pedal remains, the Hadar naviculars do provide considerable insight into foot use and function. The large sagittal taloectocuneiform angle, the large degree of dorsoplantar talar facet curvature (table 1) and the large inflated navicular tuberosity indicate that the Hadar foot lacked the longitudinal plantar arch characteristic of modern humans. The navicular's large plantar tuberosity and the overlying horizontal portion of the talar facet enabled talar head loads to be transmitted directly to the substrate through the navicular. The well-developed plantar process on the entocuneiform (AL 333-28) and the plantar set of the naviculoectocuneiform facet suggest the entocuneiform also participated in transferring weight to the substrate. Although the high values of the frontal mesoectocuneiform angle and low values of the frontal talocuboid angles (table 2) reflect some degree of a transverse pedal arch, the presence of a plantar process flanked distally by the peroneus longus groove on the AL 333-79 ectocuneiform suggests the transverse arch was either lower than that of humans or was mobile. Given a high and fixed transverse arch, the peroneus longus tendon bowstrings and does not groove the plantar surface of the ectocuneiform (Sarmiento, 1994). The implied mobility at the talonavicular joint also indicates the Hadar foot did not have a fixed transverse pedal arch.

The large cuboid facet (fig. 6 and tables 6 and 8) and mobility at the talonavicular joint suggest the Hadar foot was loaded in supinated postures as is customary among great apes when climbing vertical supports of relatively large diameter (Sarmiento, 1985, 1994). Considering the large, inflated tuber calcaneus (Latimer and Lovejoy, 1989), prominent plantar processes on the anterior

TABLE 12
Mechanical Function and Associated Behaviors of Human Postcranial Characters Used to Support Australopithecine Bipedality, and the Living Nonhuman Primates Exhibiting These Characters

| Character | Mechanical function | Associated behaviors | Nonhuman primate showing character |
|---|---|--|--|
| 1. Lateral orientation of iliac's gluteal surfaces | Maintenance of lower limb movement in the plane of forward motion | Cursorial bipedality and quadrupedality | Patas monkeys, baboons, and geladas |
| 2. Relatively short ilia | Gluteal musculature with short contractile length and large outlever to inlever ratio | Cursorial bipedality and quadrupedality | Cercopithecoids, <i>Alouatta</i> , and <i>Lemur</i> |
| 3. Reduction of vertical distance from hip joint to sacrum | Reduction of hip joint moment arms resulting from body weight | Bipedality and vertical climbing | <i>Oreopithecus</i> and sloths approximate humans more than any living primate |
| 4. Wide sacrum and wide iliac alae | Large lower limb span and x-sectional area of hip musculature. Mediolateral stability in erect body postures | Bipedality and vertical climbing | Gorillas (wide ilia), lorisines (wide sacra) |
| 5. Enlarged postauricular area of ilium | Provides surface area for enlarged erector spinae m. | Cursorial bipedality and quadrupedality | Patas monkeys, baboons, and geladas |
| 6. Strong anterior inferior iliac spine | Provides surface area for attachment of iliofemoral ligament and rectus femoris m. Ligament checks extension of extended hip joint, muscle flexes hip. | Bipedality and vertical climbing | Orangutans |
| 7. Ischial spine | Provides surface area for strongly developed sacrotuberous ligament and pelvic diaphragm. Ligament stabilizes rotational forces at sacroiliac joint | Bipedality and arboreal climbing | Orangutans, but best developed in <i>Oreopithecus</i> |
| 8. Iliac pillar and iliac tubercle | Buttress of iliac alae resists bending moments. Powerful iliac and gluteal musculature and abdominal musculature. Powerful trunk and hip movements | Bipedality and quadrupedality | Baboons |
| 9. Thickened cortical bone on inferior femoral neck | Hip joint loaded in a relatively narrow range of joint postures | Quadrupedality, leaping, terrestrial bipedality | Cercopithecoids, nonateline ceboids, indriids, <i>Varecia</i> , and <i>Lemur</i> |
| 10. Femoral bicondylar angle | Orients long axis of leg parallel to body weight vector | Striding bipedality, arboreal climbing | Lorisines, atelines, and orangutans |
| 11. Mediolateral axis of trochlea perpendicular to leg and to weight vector | Orients leg parallel to body weight vector on horizontal substrate | Cursorial quadrupedality and bipedality | Cercopithecines |
| 12. Plantar process of tuber calcanei | Attachment site for short digital flexors and plantar aponeurosis. Enables grasps irrespective of ankle joint postures. Redistributes digital tendon force, doubling force of friction per applied muscular force in pedal grasps. Transmits load to the substrate in plantigrade foot postures | Arboreal climbers, plantigrade quadrupeds and bipeds | Lorisines, atelines, and hominoids |

TABLE 12
(Continued)

| Character | Mechanical function | Associated behaviors | Nonhuman primate showing character |
|--|---|---|---|
| 13. Planar first tarso-metatarsal joint | Restricted mobility at first tarso-metatarsal joint | Cursorial terrestriality, and/or arboreality along relatively large-diameter supports | Callithricids and gelada baboons |
| 14. Dorsiflexed set of metatarsophalangeal joints and dorsally expanded metatarsal heads | Hyperextension of metatarsophalangeal joints | Semidigitigrade or digitigrade behaviors, terrestriality | Patas monkeys, baboons, and some macaques |

Notes:

1. Waterman, 1927; Straus, 1929; Schultz, 1930; Reynolds, 1931; Robinson, 1972; Lovejoy, 1979; Sarmiento, 1985, 1998.
- 2, 3. Waterman, 1927; Straus, 1929; Reynolds, 1931; Broom and Robinson, 1950; Le Gros Clark, 1955; Biegert and Mauer, 1972; Lovejoy, 1974, 1978; Stern and Susman, 1983; Sarmiento, 1987.
4. Waterman, 1927; Schultz, 1930, 1936; Reynolds, 1931; Le Gros Clark, 1955; Zihlman, 1969, 1978; Robinson, 1972; Stern and Sussman, 1983; Sarmiento, 1985, 1998; McHenry, 1991.
5. Straus, 1929; Schultz, 1936; Le Gros Clark, 1955; Sarmiento, 1998.
6. Weidenreich, 1913; Straus, 1929; Schultz, 1936; Robinson, 1972; Lovejoy et al., 1973; Stern and Susman, 1983; Sarmiento, 1998.
7. Waterman, 1927; Le Gros Clark, 1955; Abitbol, 1988; Kohler and Moya-Sola, 1997; Sarmiento, 1998.
8. Mednick, 1955; Zihlman, 1969; Robinson, 1972; Lovejoy et al., 1973; Lovejoy, 1974, 1978; Stern and Susman, 1983; MacLatchy, 1996.
9. Lovejoy, 1988; Lovejoy et al., 1996; Ohman et al., 1997; Rafferty, 1998.
10. Zihlman, 1969, 1978; Heiple and Lovejoy, 1971; Robinson, 1972; Walker, 1973; Sarmiento, 1985, 1995, 1998; Stern and Susman, 1983; McHenry, 1991; Tardieu and Preuschoft, 1996.
11. Lewis 1980b, c; Latimer et al., 1987; Sarmiento, 1994, 1998; Carrano, 1997.
12. Sarmiento, 1983, 1985, 1994; Gebo, 1986; Latimer and Lovejoy, 1989; Meldrum et al., 1997.
13. Morton, 1924; Schultz, 1936; Hill, 1960; Jolly, 1965, 1970; Latimer and Lovejoy, 1990a.
14. Jolly, 1965; Latimer and Lovejoy, 1990b; Sarmiento, 1998; Ward et al., 1999.

calcaneus, navicular, and entocuneiform (this study), the dorsiflexed set at the metacarpophalangeal joints, and the short phalanges (Stern and Susman 1983; Latimer and Lovejoy, 1990a,b), the Hadar foot was much better suited for terrestrial plantigrade postures than for arboreal grasps. Substrate contact by the distal tarsus indicates a human bipedal stride involving heel-to-ball weight transfer **could not** have been commonly employed. The more divergent set of the second and third rays as implied from the transverse mesoentocuneiform angle and the mobile transverse arch suggests a less compact foot than in modern humans, one which was not as strongly committed to terrestrial behaviors.

Mobility at the talonavicular joint and the relative plantar orientation of the entocuneiform facet indicates more abducted postures

of the hallux in Hadar than is characteristic of humans. Because the degree of hallucal abduction is defined by the set of the talonavicular, naviculoentocuneiform, first tarsometatarsal and metatarsophalangeal joints (Day and Wood, 1968; Lewis, 1980b, c; Sarmiento, 1994), and these are not all present among the Hadar AL 333/333w remains, estimates as to degree of hallucal abduction are equivocal. Regardless, a degree of hallucal abductability comparable to or greater than that seen in mountain gorillas is a reasonable estimate.

The Hadar navicular is best interpreted as belonging to the foot of a generalized quadrupedal which probably employed plantigrade bipedal postures and limited its arboreal behaviors to supports of relatively large diameter (Sarmiento, 1989, 1991, 1998).

Oreopithecus

The large sagittal taloectocuneiform and entoectocuneiform angles and the relatively small transverse mesoectocuneiform angle (table 1 and 2) indicate the *Oreopithecus* foot had markedly divergent rays. The low navicular torsion with the strong medial inclination of the talar neck specifically indicate a markedly divergent hallux. Among the hominoids such a marked divergence is unique to *Oreopithecus* and is corroborated when the associated tarsal and metatarsal bones are articulated (Kohler and Moya-Sola, 1997). A shallow talar facet with small and approximately equal radii of curvature (table 4) corresponds to a loose talonavicular joint with rotatory ability. Such joint laxity is also reflected in the calcaneo-cuboid joint (Sarmiento, 1987; Szalay and Langdon, 1987) and in the single continuous navicular facet on the talar head. A talar facet which is large relative to the cuneiform facets (fig. 8) suggests an emphasis on mobility at the talonavicular relative to the naviculocuneiform joints. The absence of weight-bearing tubercles on the navicular and entocuneiform (Sarmiento, 1987) suggest that the foot lacked a commitment to terrestrial behaviors and/or was not often used for walking along large diameter horizontal supports. The large cuboid facet (fig. 6 and table 6) is in accord with powerful hallucal opposability and a foot loaded in supinated postures.

The *Oreopithecus* navicular best corresponds to the foot of an arboreal vertical climber. A relatively mobile foot with a wide opposable grasp, this foot could be apposed against vertical trunks when climbing, or used along horizontal supports of diameters permitting hallucal grasps.

PHYLOGENY IMPLICIT IN NAVICULAR MEASUREMENTS

It is striking how close the phenetic tree based on the Mahalanobis distances between samples of human and great ape navicular measurements (fig. 13) coincide with hominoid phylogenies as hypothesized by early anatomists (Keith, 1916, 1934, 1940; Morton 1927; Schultz, 1936; Le Gros Clark, 1971). Because navicular measurements were chosen to reflect largely functional concerns, co-

inciding phylogenies and phenetics may be unexpected, especially when epigenetic and inherited characters are given equal weight. Early anatomists and systematists, however, did not usually test the inferred homologies used to construct phylogenies for the likelihood of parallelisms (Sarmiento, 1998). Thus, these phylogenies are in essence phenetic trees, i.e., they equate degree of overall morphological similarity with the degree of relationship. Without the morphological complexity necessary to test for homologies, quantification of overall similarities in fragmentary fossils may be the only analysis possible. Results from such an analysis, however, do not accurately reflect phylogenetic affinities, since they conflate shared derived characters (synapomorphies) and parallelisms (plesiomorphies) and do not distinguish inherited characters from those originating ontogenetically with use.

Through cladistic analysis and knowledge as to what navicular characters are primitive vs. derived, testing for homologies may be possible. For instance, a weight-bearing plantar tubercle with a variable sustentacular articulation is a shared derived character of the African ape navicular absent in other catarrhines and the earliest known fossil hominoids (i.e. *Oreopithecus* and *Sivapithecus*; Sarmiento, 1994, this study). The presence of a large weight-bearing plantar tubercle and a sustentacular facet on the navicular of Hadar forms may be used to argue that many of the angles and metric characters shared by Hadar and African apes are also homologous. As such, the Hadar naviculars would seem to share a special relationship with African apes exclusive of humans and orangutans. As with all cladistic analyses this argument assumes orthoselection with minimal reversals. In this case, the assumptions are that the large plantar tubercle and sustentacular facet was not (1) independently acquired by chimpanzees, gorillas and/or Hadar fossils, (2) a shared trait of humans and African apes which was later lost in humans, or (3) a shared hominoid trait that was independently lost in humans, orangutans, and *Oreopithecus*. With relatively few comparative taxa as outgroups and a limited number of shared derived characters for comparison, such an analysis may prove equivocal. In most cases more than a bit of

localized morphology is necessary for phylogenetic resolution (Sarmiento, 1987).

Regardless of its inaccuracy, navicular phenetics and the cladistic analysis that can be done on the limited number of navicular characters *does* reflect phylogeny to some degree. In this regard, there must be a limit as to how much the naviculars of closely related forms may differ from each other and/or how similar the navicular of more distally related forms may be. Similarities in inherited anatomy predispose the types of problems an organism encounters in its environment and the behaviors used to solve these problems. Differences in inherited anatomy, on the other hand, reduce the likelihood of encountering similar problems in the environment or arriving at similar solutions. Even if the same problems are encountered and similar solutions arrived at, inherited differences are more apt to result in greater differences in navicular morphology in more distally related taxa than in closely related ones.

Notably navicular phenetics also approximates the currently accepted hominoid phylogeny (Sarmiento, 1998). The only disagreement exists at the point of human divergence, and humans have a decidedly specialized foot committed to terrestrial bipedality (Weidenreich, 1922; Morton, 1924; Schultz 1963; Sarmiento, 1994, 1998). The close similarities in the navicular of OH 8 and humans, and of Hadar australopithecines and African apes, and the unique navicular of *Oreopithecus* must reflect to some degree phylogenetic affinities. This applies whether or not the measured characters also reflect functional concerns. As regards the navicular, the AL 333/333w remains are more likely to represent ancestral African apes than ancestral humans. The measured differences between OH 8, Hadar, and *Oreopithecus* naviculars are consistent with generic differences among humans and living great apes.

CONCLUSIONS

The *Oreopithecus*, Hadar, and OH 8 naviculars, in order of decreasing geologic age, show decreasing hallucal abduction, increasing commitment to terrestrial behaviors, and

a decreasing Mahalanobis distance to human naviculars. Such a sequence of evolutionary changes in the foot are in accord with those predicted in human phylogeny by current models of hominoid and hominid divergence (Sarmiento, 1995, 1998).

Results from this study inspire caution as to how much of an animal's phylogeny or overall behavior can be interpreted from a single bone. Phylogenies are unlikely to be accurate without the morphologic complexity necessary to test for homologies, and without at least a limited understanding of character polarity. When interpreting either phylogeny and/or function from fossil remains, incomplete remains are likely to lead to spurious conclusions. Interpretations of australopithecine systematics and behavior, therefore, can only be credible when all of the morphological evidence is accounted for. In retrospect, the notion that the australopithecine gait could have been predicted based on a single os coxa (Sts 14) and some nonassociated fragmentary femora (Lovejoy, 1974; see also Johanson et al., 1976) is supercilious.

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REFERENCES

- Abitbol, M. M.
1988. Evolution of the ischial spine and of the pelvic floor in the Hominoidea. *Am. J. Phys. Antropol.* 75: 53–67.
- Alexander, R. McN.
1989. Elastic mechanisms in animal movement. New York: Cambridge Univ. Press.
- Beard, K. A., M. Dagosto, D. Gebo and M. Godinot
1988. Interrelationship among primate higher taxa. *Nature* 331: 712–714.
- Biegert, J.
1963. The evaluation of characteristics of the skull, hands and feet for primate taxonomy. In S. L. Washburn (ed.), *Classification and human evolution*: 116–145. Chicago: Aldine.
- Biegert, J., and R. Mauer
1972. Rumpskettlänge, Allometrien und Körperproportionen bei catarrhinen Primaten. *Folia Primatol.* 17: 142–156.
- Broom, R., and J. T. Robinson
1950. Notes on the pelvis of the fossil ape-man, *Pleisianthropus*. *Am. J. Phys. Anthropol.* 8: 489–494.
- Carrano, M. T.
1997. Morphological indicators of foot posture in mammals, a statistical and biomechanical study. *Zool. J. Linn. Soc.* 12: 77–104.
- Cartmill, M.
1985. Climbing. In M. Hildebrand, D. M. Bramble, K. F. Leim and D. B. Wake (eds.), *Functional vertebrate morphology*: 73–88. Cambridge: Belknap Press.
- Cartmill, M., and K. Milton
1977. The lorisform wrist joint and the evolution of brachiating adaptations in the Hominoidea. *Am. J. Phys. Anthropol.* 47: 249–272.
- Chamberlain, A. T. and B. A. Wood
1987. Early Hominid phylogeny. *J. Hum. Evol.* 16: 119–133.
- Clarke, R. J., and P. V. Tobias
1995. Sterkfontein member 2 foot bones of the oldest South African hominid. *Science* 269: 521–524.
- Conroy, G. C. and J. G. Fleagle
1972. Locomotor behaviors in living and fossil pongids. *Nature* 237: 103–104.
- Darwin, C.
1859. *The origin of species by means of natural selection or the preservation of favored races in the struggle of life*. New York: Modern Library.
- Day, M. H., and J. R. Napier
1964. Fossil foot bones. *Nature* 201: 969–970.
- Day, M. H., and B. A. Wood
1968. Functional affinities of the Olduvai hominid 8 talus. *Man* 3: 440–455.
- Edelstein, S. J.
1987. An alternative paradigm for hominid evolution. *Hum. Evol.* 2: 169–174.
- Eftman, H.
1960. The transverse tarsal joint and its control. *Clin. Orthop.* 16: 41–46.
- Eftman, H. and J. Manter
1935. The evolution of the human foot, with special reference to the joints. *J. Anat.* 70: 56–67.
- Ferguson, W. W.
1984. Revision of fossil hominid jaws from the Plio/pleistocene of Hadar, in Ethiopia, including a new species of the genus *Homo* (Hominoidea; Homininae). *Primates* 25: 519–529.
1986. The taxonomic status of *Praeanthropus africanus* (Primates: Pongidae) from the late Pliocene of eastern Africa. *Ibid.* 27: 485–492.
- Fleagle, J. G.
1998. *Primate adaptation and evolution*. 2nd ed. New York: Academic Press.
- Gebo, D. L.
1986. The anatomy of the prosimian foot and its application to the primate fossil record. Ph.D. Diss. Duke Univ., Durham.
- Gebo, D. L., and M. Dagosto
1988. Foot anatomy, climbing and the origin of the Indriidae. *J. Human Evol.* 17: 135–154.
- Gommery, D.
1997. Le atlas et les axes des Hominides du Plio-pleistocène: morphologie et systématique. *C.R. Acad. Sci. Paris* 325: 639–642.
- Heiple, K. G., and C. O. Lovejoy
1971. The distal femoral anatomy of Australopithecus. *Am. J. Phys. Anthropol.* 35: 75–84.
- Hill, W.C.O.
1960. *Primates: comparative anatomy and taxonomy*. IV. Cebidae, Pt. A. Edinburgh: Edinburgh Univ. Press.
- Johanson, D. C., C. O. Lovejoy, K. G. Heiple, and A. H. Burstein
1976. Biomechanical implications of the Afar knee joint. *Am. J. Phys. Anthropol.* 44: 188.

- Johanson, D. C., M. Taieb, and Y. Coppens
1982. Pliocene hominids from the Hadar formation, Ethiopia (1973–1977): stratigraphic, chronologic and paleo-environmental contexts, with notes on hominid morphology and systematics. *Am. J. Phys. Anthropol.* 57: 373–402.
- Jolly, C. J.
1965. The origins and specializations of the long-faced Cercopithecoidea. Ph.D. diss., Univ. of London.
1970. The seed eaters: a new model of hominid differentiation based on baboon analogy. *Man* 5: 5–26.
- Keith, A.
1916. Lo schema dell'origine umana. *Revista di Antropologia* 20: 3–20.
1934. The construction of man's family tree. London: Watts.
1940. Fifty years ago. *Am. J. Phys. Anthropol.* 26: 251–267.
- Kohler, M., and S. J. Moya-Sola
1997. Ape-like or hominid-like? The positional behavior of *Oreopithecus bambolii* reconsidered. *Proc. Natl. Acad. Sci.* 94: 11747–11750.
- Latimer, B.
1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In Y. Coppens and B. Senut (eds.), *Origine(s) de la bipédie chez les hominides*: 169–176. Paris: CNRS.
- Latimer, B., and C. O. Lovejoy
1989. The calcaneus of *Australopithecus afarensis* and its implication for the evolution of bipedality. *Am. J. Phys. Anthropol.* 78: 369–386.
1990a. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. *Ibid.* 82: 125–133.
1990b. Metatarsophalangeal joints of *Australopithecus afarensis*. *Ibid.* 83: 13–23.
- Latimer, B., C. O. Lovejoy, D. C. Johanson, and Y. Coppens
1982. Hominid tarsal, metatarsal and phalangeal bones recovered from the Hadar formation: 1974–1977 collections. *Am. J. Phys. Anthropol.* 57: 701–719.
- Latimer, B., J. C. Ohman, and C. O. Lovejoy
1987. Talocrural joint in African hominoids: implications for *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 74: 155–175.
- Leakey, L., P. V. Tobias, and J. Napier
1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202: 7–10.
- Leakey M. G., C. S. Feibel, I. McDougall, and A. Walker
1995. New four-million-year-old hominid species from Kanapoi and Allia bay, Kenya. *Nature* 376: 565–571.
- Le Gros Clark, W. E.
1955. The os inominatum of the recent Pongidae with special reference to that of the Australopithecinae. *Am. J. Phys. Anthropol.* 13: 19–27.
1971. *The antecedents of man*. New York: Quadrangle Press.
- Lewis, O. J.
1969. The hominoid wrist joint. *Am. J. Phys. Anthropol.* 30: 251–267.
1974. The wrist articulations of the Anthropoidea. In F. A. Jenkins (ed.), *Primate locomotion*: 143–169. New York: Academic Press.
1980a. The joints of the evolving foot. Pt. I. The ankle joint. *J. Anat.* 130: 527–543.
1980b. The joints of the evolving foot. Pt II. The intrinsic joints. *Ibid.*: 833–857.
1980c. The joints of the evolving foot. Pt. III. The fossil evidence. *Ibid.* 131: 275–298.
- Lovejoy, C. O.
1974. The gait of australopithecines. *Yearb. Phys. Anthropol.* 17: 147–161.
1978. A biomechanical review of the locomotor diversity of early hominids. In C. J. Jolly (ed.), *Early Hominids of Africa*, 403–429. New York: St. Martins Press.
1979. A reconstruction of the pelvis of AL-288 (Hadar Formation, Ethiopia). *Am. J. Phys. Anthropol.* 50: 460.
1988. Evolution of human walking. *Sci. Am.* 259: 118–125.
- Lovejoy, C.O., K.G. Heiple, and A.H. Burstein
1973. The gait of *Australopithecus*. *Am. J. Phys. Anthropol.* 32: 33–40.
- Lovejoy, C.O., T. D. White, M. J. Cohn, and J. C. Ohman
1996. The Maka femur: A case study in the application of analytical paradigms dictated by new developments in morphological ontogeny. *Am. J. Phys. Anthropol., Suppl.* 22: 152.
- MacLachy, L. M.
1996. Another look at the Australopithecine hip. *J. Hum. Evol.* 31: 455–476.
- Manter, J. T.
1941. Movements of the subtalar and transverse tarsal joints. *Anat. Rec.* 80: 397–410.
- Marcus, L. F.
1990. Traditional morphometrics. In F. J. Rohlf and F. L. Bookstein (eds.). *Pro-*

- ceedings of the Michigan morphometrics workshop: 77–112. Univ. Michigan Mus. Zool. Spec. Publ.
1993. Some aspects of multivariate statistics for morphometrics. *In* L. F. Marcus, E. Bello, and A. G. Valdecasas, (eds.), *Contributions to morphometrics*: 99–130. Madrid: Monografias Museo Nacional Ciencias Naturales.
- McHenry, H. M.
1991. First steps? Analyses of the postcranium of early hominids. *In* Y. Coppens and B. Senut (eds.), *Origine(s) de la bipédie chez les hominides*: 133–141. Paris: CNRS.
1996. Homoplasy, clades and hominid phylogeny. *In* W. E. Meikle, F. C. Howell, and N. G. Jablonksi (eds.), *Contemporary issues in human evolution*: 77–91. San Francisco: California Acad. Sci.
- McHenry, H. M., R. S. Corruccinni, and F. C. Howell
1975. Analysis of an early hominid ulna from the Omo basin, Ethiopia. *Am. J. Phys. Anthropol.* 44: 295–304.
- Mednick, L. W.
1955. The evolution of the human ilium. *Am. J. Phys. Anthropol.* 13: 203–216.
- Meldrum, D. J., M. Dagosto, and J. White
1997. Hindlimb suspension and hind foot reversal in *Varecia variegata* and other arboreal mammals. *Am. J. Phys. Anthropol.* 103: 85–102.
- Morton, D. J.
1924. Evolution of the human foot. II. *Am. J. Phys. Anthropol.* 7: 1–52.
1927. Human origin. *Am. J. Phys. Anthropol.* 10: 173–203.
- Napier, J. H.
1962. Fossil hand bones from Olduvai Gorge. *Nature* 196: 409.
- Ohman, J. C., T. J. Krochta, C. O. Lovejoy, R. P. Mensforth, and B. Latimer
1997. Cortical bone distribution in the femoral neck of hominoids: implications for the locomotion of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 104: 117–131.
- Olson, T. R.
1978. Hominid phylogenetics and the existence of *Homo* in Member I of the Swartkrans formation, South Africa. *J. Hum. Evol.* 7: 159–178.
1981. Basicranial morphology of the extant hominoids and Pliocene hominids: the new material from the Hadar formation, Ethiopia, and its significance in early human evolution and taxonomy. *In* C. B. Stringer (ed.), *Aspects of human evolution*: 99–128. London: Taylor and Francis.
1985. Cranial morphology and systematics of the Hadar fossil hominids and *A. africanus*. *In* E. Delson and I. Tattersall (eds.), *Ancestors: the hard evidence*: 102–119. New York: Alan R. Liss.
- Oxnard, C. E.
1984. *The Order of Man*. New Haven, CT: Yale Univ. Press.
- Oxnard, C. E., and F. P. Lisowski
1980. Functional articulation of some hominoid foot bones: implications for the Olduvai (Hominid 8) foot. *Am. J. Phys. Anthropol.* 52: 107–117.
- Rafferty, K. A.
1998. Structural design of the femoral neck in primates. *J. Hum. Evol.* 34: 361–383.
- Reynolds, E.
1931. The evolution of the human pelvis in relation to the mechanics of erect posture. *Pap. Peabody Mus. Archaeol. Ethnol. Harvard Univ.* 11: 249–334.
- Robinson, J. T.
1965. *Homo habilis* and the australopithecines. *Nature* 205: 121–124.
1972. *Early hominid posture and locomotion*. Chicago: Univ. Chicago Press.
- Rohlf, F. J.
1997. NTSYSpc version 2.02h. Setauket, NY: Exeter Software.
- Rose, M. D.
1988. Functional anatomy of the cheiridia. *In* J. H. Schwartz (ed.), *Orangutan biology*: 509–524. London: Plenum Press.
- Sarmiento, E. E.
1983. The significance of the heel process in anthropoids. *Int. J. Primatol.* 4(2): 127–152.
1985. Functional differences in the skeleton of wild and captive orang-utans and their adaptive significance. Ph.D. diss., New York Univ., New York.
1987. The phylogenetic position of *Oreopithecus* and its significance in the origin of the Hominoidea. *Am. Mus. Novitates* 2881: 44 pp.
1988. Anatomy of the hominoid wrist joints, its evolutionary and functional implications. *Int. J. Primatol.* 9: 281–345.
1991. Functional and phylogenetic implications of the differences in the pedal skeleton of Australopithecines. *Am. J. Phys. Anthropol., Suppl.* 12: 232.
1994. Terrestrial traits in the hands and feet of gorillas. *Am. Mus. Novitates* 3091: 56 pp.

1995. Cautious climbing and folivory: a model of hominoid differentiation. *Hum. Evol.* 10(4): 289–321.
1998. Generalized quadrupeds, committed bipeds and the shift to open habitats: an evolutionary model of hominid divergence. *Am. Mus. Novitates* 3250: 78 pp.
- Sarmiento, E. E., and T. M. Butynski
1996. Present problems in gorilla taxonomy. *Gorilla J.* 12: 5–7.
- In prep. The foot musculature of Bwindi gorillas: its functional and phylogenetic significance.
- Sarmiento, E. E., T. M. Butynski, and J. Kalina
1996. Gorillas of Bwindi-Impenetrable Forest and the Virunga Volcanoes: taxonomic implications of morphological and ecological differences. *Am. J. Primatol.* 40: 1–21.
- Schaeffer, B.
1947. Notes on the origins and function of the artiodactyl tarsus. *Am. Mus. Novitates* 1356: 24 pp.
- Schultz, A. H.
1930. The skeleton of the trunks and limbs of higher primates. *Hum. Biol.* 2: 303–438.
1936. Characters common to higher primates and characters specific to man. *Q. Rev. Biol.* 11: 259–283; 425–455.
1963. Relations between the lengths of the main part of the foot skeleton in primates. *Folia Primatol.* 1: 150–171.
- Senut, B., and C. Tardieu
1985. Functional aspects of hominid limb bones: implication for taxonomy and phylogeny. *In* E. Delson and I. Tattersall (eds.), *Ancestors: the Hard Evidence*: 175–203. New York: Alan R. Liss.
- Skelton, R. R., H. M. McHenry, and G. M. Drawhorn
1986. Phylogenetic analysis of early hominids. *Curr. Anthropol.* 27: 21–43.
- Stern, J. T., and R. L. Susman
1983. The locomotor anatomy of *Australopithecus africanus*. *Am. J. Phys. Anthropol.* 60: 279–316.
- Strait, D.S., F. E. Grine, and M. A. Moniz
1997. A reappraisal of early hominid phylogeny. *J. Hum. Evol.* 37: 17–82.
- Straus, W. L., Jr.
1929. Studies on the primate ilia. *Am. J. Anat.* 43: 403–460.
- Susman, R. L., and J. T. Stern
1991. Locomotor behavior of early hominids: epistemology and fossil evidence. *In* Y. Coppens and B. Senut (eds.), *Origine(s) de la bipédie chez les hominides*: 121–131. Paris: CNRS.
- Susman, R. L., J. T. Stern, Jr., and W. L. Jungers
1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* 43: 113–156.
- Szalay, F. S., and R. L. Decker
1974. Origin, evolution and function of the tarsus in late Cretaceous eutherians and Paleocene primates. *In* F. Jenkins (ed.), *Primate locomotion*: 223–259. New York: Academic Press.
- Szalay, F. S., and J. H. Langdon
1987. The foot of *Oreopithecus*: an evolutionary assessment. *J. Hum. Evol.* 15: 585–621.
- Tardieu, C., and H. Preuschoft
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.
- Tobias, P. V.
1991a. Olduvai Gorge, Vol. 4: the skulls endocasts and teeth of *Homo habilis*. Cambridge: Cambridge Univ. Press.
- 1991b. Relationships between apes and humans. *In* A. Sahni and R. Gaur (eds.), *Perspectives in human evolution*: 1–19. Delhi: Renaissance Publishing House.
- Tuttle, R. H.
1970. Postural propulsive and prehensile capabilities in the cheiridia of chimpanzees and other great apes. *In* G. H. Bourne (ed.), *The chimpanzee*. 2: 167–253. Basel: Karger.
- Verhaegen, M.
1990. African ape ancestry. *Hum. Evol.* 5: 295–297.
1994. Australopithecines: ancestors of the African apes? *Ibid.* 7: 63–64.
- Walker, A.C.
1973. New Australopithecus femora from East Rudolf Kenya. *J. Hum. Evol.* 2: 545–555.
- Ward, C.V., M.G. Leakey, B. Brown, F. Brown, J. Harris and A. Walker
1999. South Turkwel: A new Pliocene hominid site in Kenya. *J. Hum. Evol.* 36: 69–95.
- Waterman, H. C.
1927. Studies on the evolution of the pelvis of man and other primates. *Bull. Am. Mus. Nat. Hist.* 11: 585–641.
- Weidenreich, F.
1922. Der Menschenfuss. *Z. Morphol. Anthropol.* 22: 51–282.

- White, T. D., D. C. Johanson, and W. H. Kimbel
1981. *Australopithecus africanus*: its phylogenetic position reconsidered. *S. Afr. J. Sci.* 77: 445–470.
- Wolpoff, M. H.
1974. The evidence of two australopithecine lineages in South Africa. *Yearb. Phys. Anthropol.* 17: 113–139.
1999. *Paleoanthropology*. New York: McGraw Hill.
- Wood, B. A.
1974. Olduvai Bed I postcranial fossils; a re-assessment. *J. Hum. Evol.* 3: 373–378.
- Zihlman, A. L.
1969. Human locomotion: a reappraisal of the functional and anatomical evidence. Ph.D. diss., Univ. California at Berkeley.
1978. Interpretations of early hominid locomotion. *In* C. J. Jolly (ed.), *Early Hominids of Africa*: 361–377. New York: St Martins Press.
- Zihlman, A. L., and L. Bunker
1979. Hominid bipedalism: then and now. *Yearb. Phys. Anthropol.* 22: 132–162.

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