Using the morphology of the hominoid distal fibula to interpret arboreality in *Australopithecus afarensis*

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Abstract

The fibula has rarely been considered in anthropological studies. However differences in morphology — and inferred function — of the fibula between human and non-human apes have been noted in the past and related to differences in locomotor behavior. Recent studies have pointed out the correlation between diaphyseal rigidity of the fibula and tibia and locomotor behavior in living hominids, and its possible application for inferring early hominin locomotor behavior. The problem with the application of the method proposed in these studies is the extreme rarity of associated early hominin fibula and tibia. Additionally, previous studies investigating morphological traits of fibulotalar articular facets to infer the degree of arboreality in fossil australopiths were often qualitative. In the present study, articular measurements of the distal fibula of living great apes and humans (*Pongo*, *Gorilla*, *Pan* and *Homo*) are quantified and compared to *Australopithecus afarensis* distal fibulae. Quantitative analysis is carried out for articular areas and breadths of the fibulotalar articular facets, of the angles formed by the fibulotalar articular facets and the longitudinal axis of the fibula, and of the angle between the proximal fibulotalar articular facet and the subcutaneous triangular area. Results show that the fibula of *Au. afarensis* bears some traits consistent with modern terrestrial bipedalism, like a more laterally facing lateral malleolus, in association with more ape-like traits, like the smaller distal fibulotalar articular facet area and the more inferiorly oriented fibulotalar articular facets, consistent with *Au. afarensis* being a terrestrial hominin adapted for some form of arboreality.

Key words: Early hominins; articular properties; locomotion; ankle joint

Introduction

Despite a relatively extensive hominin postcranial fossil record, there is still no consensus on the manner of bipedalism in the earliest hominins, with considerable debate specifically about the relative amount of arboreal versus terrestrial locomotion (Stern and Susman, 1983; Latimer et al., 1987; Latimer and Lovejoy, 1990a,b; Berge, 1994; Stern, 2000; Ward, 2013). Hands and feet directly contact the substrate and the study of the morphology and biomechanics of these body sections offers an invaluable clue to the locomotor adaptations of early hominins (Susman and de Ruiter, 2004; Ward et al., 2011; Zipfel et al., 2011), but are scarce in the fossil record compared to long bones. The long bones that are usually used to infer mobility patterns in early hominins and pre-hominin ancestors are the femur and the tibia, while studies on the fibula are comparatively rare. The femur and tibia have been the preferred elements of study both because they are mainly involved in the function of load bearing in humans, and they are more numerous in the fossil record. The fibula, in contrast, is generally overlooked in anthropological research (but see Marchi, 2004, 2007, 2015).

The distal fibula, together with the distal tibia and talus, form the ankle joint. The fundamental architecture of the ankle joint in the tetrapod ancestors of mammals involved a weight-bearing articulation between the fibula and the calcaneus (Schaeffer, 1941). The key event in transforming the pre-mammal foot into a mammalian one was the superimposition of the talus upon the calcaneus. This modification introduced new flexibility into the foot by permitting eversion and inversion at the subtalar joint (Lewis, 1980).

In non-human mammals, the fibula is an important supporting structure of the leg (Walmsley, 1918; Carleton, 1941; Barnett and Napier, 1953; Lambert, 1971). Early studies, focusing primarily on primates, documented the link between variation in mammalian fibular morphology and function (Carleton, 1941; Barnett and Napier, 1953). In jumping mammals a progressive approximation of the lower ends of the two bones has been observed, leading to a partial fusion (Fig. 1a). This fusion is seen in tarsiers among primates and in many insectivores. When the limb is habitually used in action against a resistant medium, such as water or earth, a powerful bony base is necessary for the insertion of the muscles acting on the paws, as in for example moles and armadillos (Fig, 1b), where the fibula is fused to the tibia at both the proximal and distal extremities. A third variant of the immobile fibula is the one observed in animals specialized for fast running, like ungulates. In these animals, the fibula is completely fused with the tibia and only a small distal portion remains free (Fig. 1c). The mobile fibula is less common within mammals and is limited to carnivores and primates (Fig. 1d). A further distinguishing feature present in mammals is the relative proportions of the tibia and fibula: the fibula being large (i.e. more robust) relative to the tibia in the burrowing and swimming mammals, small (i.e. less robust) and more flexible in saltatorial mammals, and intermediate in size in those mammals adapted for progression over uneven surfaces in the trees or on the ground such as primates and carnivores (Barnett and Napier, 1953).

Fig. 1 about here

The degree of robusticity and the general morphology of the fibula of primates and carnivores are associated with the high mobility of the bone. High fibular mobility is found in animals moving on uneven terrain like carnivores, and especially in primates living in an arboreal setting (Walmsley, 1918; Carleton, 1941; Barnett and Napier, 1953). It is the low robusticity of the human fibula (compared to the tibia) that led scholars to classify the fibula as a bone mainly involved in forming the lateral border of the ankle joint but very marginally involved in weight bearing in humans (White and Falkens, 2000). Some have even described the human fibula as vestigial (Moore and Dalley, 2006). However, studies conducted on human samples (Lambert, 1971; Takebe et al., 1984; Goh et al., 1992; Wang et al., 1996;

Funk et al., 2004) indicate that the fibula has a weight-bearing function, carrying 6.4-19.0% (depending on the study and ankle position) of the load borne by the leg.

Recent studies have explored the relationship between fibulotibial diaphyseal rigidity ratio and different locomotor behaviors in extant hominoids (Marchi, 2007; 2015). In particular, hominoids which are more arboreal (chimpanzees, orangutans and gibbons) show, relative to the tibia, more robust fibula at midshaft and distally than more terrestrial hominoids (gorillas and humans). Results have been explained as consequence of both the greater load to which the fibula is subjected in arboreal primates (Schmitt, 2003; Carlson et al., 2005), and the greater mobility of the ankle joint (DeSilva, 2009) and fibula (Barnett and Napier, 1953) in arboreal primates compared to terrestrial primates. In another study, Marchi and Shaw (2011) found that within modern humans, groups where locomotor patterns require abrupt and repeated changes in direction (i.e. field hockey players) show, relative to the tibia, higher fibular diaphyseal rigidity compared with sedentary groups and groups where locomotor travel is generally in the parasagittal plane (i.e. cross-country runners). The relationship between fibulotibial diaphyseal rigidity ratio and ankle movements have been used to explain mobility patterns of bioarchaeological populations (Marchi et al., 2011; Sparacello et al., 2014). Overall, the studies performed by Marchi and colleagues on fibulotibial diaphyseal rigidity ratio provide a valuable additional perspective that complements traditional predictions of mobility patterns based on the femur and the tibia alone (Carlson and Marchi, 2014).

Although the method outlined above could be applied to the hominin fossil record to provide further clues on early hominin locomotory patterns, the rarity of associated australopith tibia and fibula prevents any exhaustive investigation at present. The only early australopith associated tibiae and fibulae are those from A.L. 288-1 (Johanson and Taieb, 1976), but the partial distal fibula is too fragmentary to apply the method developed by

Marchi (2004, 2007). Though four additional distal fibula fragments of *Australopithecus afaresis* (i.e. A.L. 333-9a, A.L. 333-9b, A.L. 333-85, A.L. 333w-37) are present in the fossil record from the Hadar region of Ethiopia (Johanson and Taieb, 1976; Lovejoy et al., 1982), none is associated with a tibia.

A functional study of these five Hadar distal fibulae was performed by Stern and Susman (1983). The authors found that *Au. afarensis* fibulae deviate from the modern human fibula with regard to shape and orientation of the fibulotalar articular facet. In *Au. afarensis*, the proximal border of the articular surface runs a course that is oblique to the long axis of the fibula as is observed in apes, as opposed to the modern human condition where the proximal border runs perpendicular to the long axis of the fibula. When the fibular shaft is oriented vertically, the proximal portion of the fibulotalar articulation of the Hadar fibulae faces more inferiorly than in modern humans, and is closer to the modern great ape condition. Stern and Susman (1983) observed that the lateral malleolus of *Au. afarensis* faces less anteriorly than in modern apes, though the pronounced lateral orientation of the subcutaneous triangular surface (STS) of the fibula which characterizes most humans is not seen in the Hadar hominins. Finally, the Hadar specimens have very broad peroneal grooves interpreted as indicating to the authors more powerful peroneal muscles than in modern humans. Stern and Susman (1983) also noted that, compared to the other Hadar fibulae, the A.L. 288-1at (possibly female) distal fibula is far more similar to that of an ape than to that of a modern human, suggesting the possibility of sexual dimorphism in frequency of arboreality in *Au. afarensis*.

The morphology of *Au. afarensis* fibula also suggested to Stern and Susman (1983) elevated plantarflexion of the foot which was interpreted as evidence for arboreality. However, this interpretation has been challenged by Latimer et al. (1987) who concluded that the congruence of the talofibular joint cannot be reliably assessed from the fibula alone. More recently, DeSilva, (2009) proposed that the anatomy of the distal tibia of *A. afarensis* did not show evidence of an inverted set to the ankle nor of loading of the ankle in dorsiflexion, therefore compromising the ability of *Au. afarensis* to climb in an ape-like manner. Interestingly, a more recent study conducted on modern hunter-gatherers who regularly climb trees (Vekataraman et al., 2013b) found extraordinary ankle dorsiflexion (similar to wild chimpanzees) during climbing which was not associated with any skeletal signature of hyper-dorsiflexion. The findings of Vekataraman et al. (2013b) therefore points toward a more complex than expected relationship between hominin arboreal competence and ankle skeletal features. Many other studies have been conducted on the postcranial material of *Au. afarensis,* but still an unequivocal interpretation of the amount of arboreality in this species has not been reached (see references in Stern, 2000; Ward, 2002 and Ward et al., 2012). However, few studies have examined the functional morphology of the distal fibula of *Au. afarensis*.

Building upon recent studies which suggest the importance of relative fibular strength in determining the amount of arboreality in extant hominoids (Marchi, 2007) the aim of this paper is to quantify distal fibular articular morphology in living large-bodied hominids (orangutans, gorillas, chimpanzees and humans) to test form:function hypotheses in this region of the ankle. Many of the distal fibular characteristics investigated by Stern and Susman (1983) will be considered in this study: the main difference from their study is that a quantitative statistical treatment of each trait will be provided. The method will then be applied to the Hadar specimens (A.L. 288-1at, A.L. 333-9a, A.L. 333-9b, A.L. 333-85, A.L. 333w-37) to test the hypothesis that the fibulae of *Au. afarensis* show an overall configuration more similar to modern apes than to modern humans.

Materials and Methods

Sample

Distal fibular articulation properties were collected on a sample constituted of adult modern humans (*n* = 29), chimpanzees (*n* = 27), gorillas (*n* = 27) and orangutans (*n* = 24) (Table 1). The modern human population comes from the Dart Collection, University of the Witwatersrand, South Africa and includes Zulu, Mixe, Soto and Xhosa individuals. The great ape sample includes a wide individual size range, from 30 kg for the smallest orangutan females to more than 200 kg for the largest male gorillas (body size estimated from superoinferior femoral head diameters following Ruff, 2003; results not shown here), thus encompassing the *Au. afarensis* estimated average size range (44 kg for males, 29 kg for females, McHenry, 1992). The great ape sample includes some captive individuals (11 chimpanzees, 1 gorilla, 2 orangutans, Table 1).

Table 1 about here

Concerning the gorilla sample, the original aim was to investigate mountain gorillas (*Gorilla beringei*) and lowland gorillas (*Gorilla gorilla*) as separate categories. Previous studies conducted on the articular regions of both the medial cuneiform (Schultz, 1934; Tocheri et al., 2011) and the talus (Dunn et al., 2014) found that they differ substantially between mountain and lowland gorillas. Zipfel et al. (2011) found a difference between the two species of gorillas for the medial malleolus of the ankle. It was therefore deemed probable that fibular articular properties also differed between mountain and lowland gorillas. After collecting data for 21 *G. gorilla,* data on six *G. beringei* were collected and the analyses on the articular properties considered in the present study was performed (see below). Results (Supplementary Online Material [SOM] Figs. 1, 2) show that all the variables overlap in the two groups. The distribution of *G. beringei* is almost always within the interquartile range of *G. gorilla* for each variable. Statistical evaluations of differences among species were also carried out using Kruskal-Wallis analysis of ranks, followed by post-hoc multiple comparisons of mean ranks for all group tests. Results (not shown here) indicate that *G. beringei* and *G. gorilla* are not significantly different from each other for the variables considered in this study (see below). Keeping in mind the low sample size of mountain gorillas compared to lowland gorillas, the generally low variability of the former led to a pooling of the data. The results presented in this study are based on the pooled sample, which I will refer to from now on as gorillas.

Differences in locomotion between captive and wild-shot animals are expected due to the artificiality of captive environments. Several studies compared long bone properties within species between wild-shot and captive individuals. Sarmiento (1985), in a comparison of wild-shot and captive orangutans, found that only the differences in long-bone torsion were considered reflective of the differences in locomotor behaviors between the two groups. In another study (Burr et al., 1989), captive *Macaca nemestrina* showed greater second moments of area in humerus and femur relative to body mass than wild-shot individuals in absolute value, but profiles of relative magnitude of second moments of area along femoral/humeral diaphyses did not differ between the two groups. In a comparative analysis of wild-shot and captive *Lemur catta*, Demes and Jungers (1993) did not find significant differences between groups in length, cross-sectional area and section modulus of the humerus and femur. More recently, a study on the morphometric mapping of the chimpanzee femur (Morimoto et al., 2011) found significant differences between groups in the distal diaphyses diaphyseal shape, and a study on the articular surface of the distal tibia (Ventakaraman et al., 2013a) found significant difference between great apes from wild and captive settings. Finally, other studies did not find a significant difference between wild and captive animals in the cross-sectional areas and polar moments of area in the metacarpals and metatarsals within living great apes (Marchi, 2005).

Although a previous study found no differences on fibular cross-sectional properties in hominoid among wild-shot and captive individuals (Marchi, 2007), data on the distal articular properties of the fibula were not evaluated in that study. Here, captive and wild-shot chimpanzees were tested for significant differences in order to determine if wild-shot and captive chimpanzees could be pooled for analysis in the present study. Due to the small sample size and possible non-normal distributions, Mann-Whitney U-tests between wild-shot and captive variables of fibula (ln transformed ratios, see below) were carried out for chimpanzees. Results are reported in SOM Table 1. Differences between wild-shot and captive animals are not significant for any parameter. Wild-shot and captive chimpanzees were therefore pooled for analysis of the variables included in this study. Only one captive animal was present in the gorilla sample, and two in the orangutan sample and their values were comparable to those of wild-shot individuals, resulting in a pooling of those data as well.

The fossil sample includes five *Au. afarensis* distal fibulae from Hadar, Ethiopia (A.L. 288-1at, A.L. 333-9a, A.L. 333-9b, A.L. 333-85 and A.L. 333w-37). Measurements were taken from high quality casts at the University of the Witwatersrand and checked against comparable measurements (when present) in the literature (Lovejoy et al., 1982; Stern and Susman, 1983). Because only the distal-most fibular section of the fossil hominins is available, only linear breadth and angles of the distal fibular articulation of the extant samples were included in the study.

Variables used in the study

All the variables chosen for this study represent features that are of biomechanical importance in relation to fibula function in different locomotor behaviors (Table 2). The distal fibulotibial articular facet deserves a separate discussion. Table 3 provides a description of the presence of this trait in the modern human sample analyzed. In great apes (*n* = 78: 27 chimpanzees, 27 gorillas, 24 orangutans) a proper articulation between the tibia and fibula is always present distally. The articulation is made up by a synovial joint facet on the fibula, just proximal to the proximal fibulotalar articulation, and one on the tibia, just proximal to the medial border of the tibiotalar articular surface. In addition to the human individuals for which measurements have been collected (*n* = 29, included in this study) another 40 modern human skeletons have been visually examined (from the Dart Collections, University of the Witwatersrand, South Africa), for a total of 69 individuals. In humans, the presence of the distal articular facet on the fibula is almost always associated with its tibial counterpart (only once the articular facet was present on the distal fibula but not on the distal tibia, Table 3). However, the presence of the distal articular facet on the tibia is often not associated with the articular facet on the fibula. Of the 69 modern humans examined, 48 presented the articulation on the distal tibia but only 26 had the corresponding articulation on the fibula. As noted above, all the 78 modern great apes examined (results not shown here) present an articular facet distally on both the tibia and fibula. Therefore, the absence of a distal articular facet on the fibula is a human-like trait. However, modern humans often present an articular facet on the fibula (which may be associated with its counterpart on the tibia or not, Table 3) and therefore its presence on a fossil fibula cannot be used as evidence of ape-like distal fibular morphology.

Tables 2 and 3 about here

Linear measurements obtained from the distal fibula (Fig. 2b; Table 2), used to calculate the area of the distal fibular articular facets, were defined in the following manner:

1. FiTal1SI: the supero-inferior breadth of the proximal portion of the fibulotalar articular facet (FiTal1Ar) (Fig. 2b).
2. FiTal1AP: the antero-posterior breadth of the FiTal1Ar (Fig. 2b).

3. FiTal2ML: the mediolateral breadth of the distal portion of the fibulotalar articular facet (FiTal2Ar) taken parallel to the articular surface (Fig. 2b,c).

4. FiTal2AP: the antero-posterior breadth of the FiTal2Ar (Fig. 2b).

5. FiLipSI: the supero-inferior breadth of the distal fibulotibial articular surface (FiLipAr) (Fig. 2b).

6. FiLipAP: the antero-posterior breadth of the FiLipAr (Fig. 2b).

Fig. 2 about here

Linear breadths were chosen to represent major dimensions of each articular surface and entered into geometric formulae for calculating total surface areas on the distal fibula (Fig. 2a). FiLipAr and FiTal2Ar are shaped like a triangle in all species (fossils included, personal observation) therefore the triangle area formulas [FiLipAr area = (FiLipSI × FiLipAP) / 2] and [FiTal2Ar area = (FiTal2ML × FiTal2AP) / 2] were used to estimate these areas. FiTal1Ar is variable in shape in great apes and humans and may be either rectangular or elliptical. FiTal1AP and FiTal1SI were therefore used both in the rectangle (FiTal1AP × FiTal1SI) and ellipse [π × (FiTal1AP / 2) × (FiTal1SI / 2)] area formula and averaged for each individual. Other studies have reported on the accuracy of modeling articular surfaces as ovals, rectangles, partial cylinders or partial spheres (Godfrey et al., 1995, Rafferty, 1996; Ruff, 2002). Although some error is present, those studies have shown that the estimates are reasonably accurate when compared to measurements taken from latex molds of the same articular surfaces. Specific studies on the modeling of the distal fibular articulation have not been performed; however, the distal fibular articular facets are almost flat and the use of geometric formulae for ellipses, triangles and rectangles is at present the best approximation possible of the real articular areas. Further studies by means of imaging processing programs (i.e. ImageJ) are necessary to validate this assumption.

Joint surfaces transmit compressive loads and determine the range of motion and joint stability during locomotion (Godfrey et al, 1991; Rose, 1993; Rafferty and Ruff, 1994; Hamrick et al., 2000; Ruff, 2002; Drapeau, 2008). Animals that load the fibula, like more arboreal apes (Barnett and Napier, 1953; Schmitt, 2003; Carlson et al., 2005), are expected to have relatively larger fibulotalar articulations (Preuschoft, 1970) than animals that load their fibula less. The ratio (FiTal2Ar area / FiTal1Ar area) was therefore used as an index that emphasizes an important biomechanical feature of the osseous morphology correlated with fibula load bearing. The other articular surface of biomechanical importance used in this study is FiLipAr. When dealing with measurements that are not ratios, the gross effects of body size must be removed. To identify behaviorally significant differences in FiLipAr it was therefore necessary to control for the effects of body size (Ruff, 1987). For the fossil specimens included in this study, body mass estimation is available only for A.L. 288-1at (McHenry, 1992). A proxy for body mass must be therefore found to standardize FiLipAr area for all five fossil specimens. The fibula bears a lower part of the body mass compared to the tibia, but still has some weight-bearing function (Lambert, 1971; Takebe et al., 1984; Goh et al., 1992; Wang et al., 1996; Funk et al., 2004). The role of load bearing in non-human primates is even more important due to the greater mobility of the ankle necessary in arboreal environment (see Marchi, 2007 and references therein) and the downward inclination of the fibulotalar articulations (Preuschoft, 1970). It is therefore reasonable to hypothesize that the distal fibulotalar articular facet area (FiTal1Ar area + FiTal2Ar area) is correlated to body mass in primates. A bivariate regression was performed between the ln transformed sum of FiTal1Ar and FiTal2Ar areas and ln transformed estimated body mass (at the power of 2/3) on the extant sample. Body mass was estimated from the superoinferior diameter of the femoral head following Ruff (2003). Results displayed a good correlation between the total fibulotalar articular facet area and estimated body mass (r = 0.90, %SEE = 3.1, *n* = 104).

FiLipAr area was therefore divided by (FiTal1Ar area + FiTal2Ar area) to take into account differences in body mass between extant and fossil species.

Angles measured in the study (Fig. 3; Table 2) were defined as follows:

1. FiTalTH1: the angle of FiTal1Ar with the longitudinal axis of the fibula in antero-posterior view (Figs. 3a,b). The smaller the angle the more parallel to the longitudinal axis of the bone (and perpendicular to the ground) the articulation is. The bone is positioned with the posterior surface resting on the substrate and with the longitudinal axis passing from the center of the proximal fibular articulation and the junction of FiTal1Ar and FiTal2Ar (Fig. 4).
2. FiTalTH2: the angle of FiTal2Ar with the longitudinal axis in antero-posterior view (Fig. 3a,b). The bone is positioned as for FiTalTH1.
3. FiTalTH3: the angle between FiTal1Ar and STS (following Stern and Susman, 1983). For this measurement, the fibula is positioned with FiTal1Ar resting on the substrate (Fig. 3c). The greater the angle the more anteriorly oriented is STS.

Figs. 3 and 4 about here

Linear measurements (Fig. 2b,c) were taken with digital calipers while angles (Fig. 3) were taken in ImageJ from pictures of the bones. For the angles of the proximal (FiTal1Ar) and distal (FiTal2Ar) fibulotalar articular facets to the longitudinal axis of the fibula, the camera was positioned on a copy stand for maximum stability at a distance of 50 cm from the bone. The fibula was positioned with the posterior surface resting on the substrate and with the FiTal1Ar perpendicular to the substrate (Fig. 3a,b). For the angle between the FiTal1Ar and the triangular subcutaneous surface (STS, Stern and Susman, 1983) the fibula was positioned with FiTal1Ar in contact with the substrate and with the camera objective at the same level as the lateral malleolus and at a distance of 50 cm from the bone. Foam was used to keep the bone in position (Fig. 3c). A right side fibula from each individual in the extant sample was selected for study. The left side was taken when the right side was absent or damaged.

The fossil specimens are fragmentary and as already observed by Stern and Susman (1983) it is difficult to position them to take angles. After positioning the complete fibulae of extant comparative sample species according to their longitudinal axis and resting with the posterior surface of the bone on the substrate, the longitudinal axis (passing through the center of the proximal fibular articulation and the junction of FiTal1Ar and FiTal2Ar) lies tangent to the most proximal point of the roughened surface for the syndesmotic distal tibiofibular joint (Fig. 4): all fossil specimens included this area (see Fig. 10 in Johanson et al., 1982 and Fig. 9 in Lovejoy et al., 1982). The fossil specimens were positioned with the longitudinal axis defined as described above.

Analytical methods

To assess differences among extant species, ln transformed areas and angles of the distal articulations of the fibula were compared. First, the variables (Table 2) were subjected to a principal component analysis (PCA) to evaluate how well these variables as a whole segregate living hominids. The fossil sample was grouped a priori and entered as separate OTUs (i.e. *Au. afarensis*) into the discriminant analysis (Richmond and Jungers, 2008). Second, comparisons of area proportions and angles among the complete samples of the extant species analyzed in this study were carried out using Tukey multiple comparison tests. Box plots were used to represent group data distributions graphically. Initially, the evaluation of differences among *Au. afarensis* fossil specimens and extant samples was carried out using Kruskal-Wallis analysis of ranks between species, followed by post-hoc multiple comparisons of mean ranks for all group tests. Although patterns in the distribution of the variables were clearly discernible in the analyses, *Au. afarensis* was always not significantly different from any extant group (results not shown here), probably because of its very small sample size (*n* = 5). Therefore, each *Au. afarensis* specimen was compared to the group mean of each extant species for each variable. The distance between each fossil and each extant group was expressed as the number of SDs from the mean of that group. *Au. afarensis* fossil specimens were also evaluated relative to the comparative extant samples through visual comparison with group distributions in the box plots. All statistical analyses were done using STATISTICA 7 (StatSoft).

Results

Table 4 provides descriptive statistics for raw areas and angles of the distal fibula for each species.

Table 4 about here

Principal component analysis

A principal component analysis (PCA; correlation matrix, varimax rotation) was conducted on two area ratios (FiTal2Ar area / FiTal1Ar area and FiLipAr area / TotFibTalAr area) and three angles (FiTalTH1, FiTalTH2 and FiTalTH3) of the distal articulation of the fibula (Fig. 5). The two extracted components explain 64.9% of the total variance where PC1 and PC2 account for 44.0% and 20.9%, respectively. The eigenvalue for PC1 is 2.201 and 1.044 for PC2. Principal components 1 and 2 are presented in Table 5. All of the variables significantly contribute to the variation. However, FiTal2Ar area (relative to FiTal1Ar area) and the three angle variables (FiTalTH1-3) appear to account for most of the variation. Principal component 1 discriminates humans from African great apes with orangutans in between; all the *Au. afarensis* specimens fall outside the human cloud. However, A.L. 333-9b and A.L. 333-85 are quite close to the human distribution while A.L. 288-1at, A.L. 333w-37a and A.L. 333-9a fall in the African great ape distribution. Principal component 2 discriminates African great apes and humans from orangutans although some overlap is present. On PC2, all *Au. afarensis* specimens fall outside the human cloud with four (A.L. 333-9a, A.L. 333-9b, A.L. 333-85 and A.L. 333w-37) falling into the lower portion of the African great apes cloud. A.L. 288-1at falls far away from the African great apes cloud and also outside the orangutan cloud.

Fig. 5 and Table 5 about here

Bivariate analysis

Results of the Tukey multiple-comparison tests between extant species for distal fibular articular surface areas and angles are given in Table 6. Humans display the relative (to FiTal1Ar area) highest FiTal2Ar area and orangutans the relative lowest (significant result) FiTal2Ar area within hominids (Fig. 6a). Although differences among species are not always significant, a clear trend of increase in FiTal2Ar area from more arboreal (orangutan) to more terrestrial (humans) hominids is present. However, humans show the lowest FiLipAr area and are significantly lower than gorillas and orangutans though not significantly different from chimpanzees for this measure (Fig. 6b). In general, high overlap among great apes is present for this variable. Humans are also characterized by distal fibular articular surfaces less downward oriented (lower FiTalTH1 and FiTalTH2, Fig. 7, Table 6) than great apes. Orangutans, however, also show lower FiTalTH2 than African great apes and are statistically no different to humans (Fig. 7 b; Table 6). Humans display significantly lower FiTalTH3 than great apes (Fig. 7c; Table 6) which results in a more laterally oriented STS than great apes.

Australopithecus afarensis values for each variable taken into consideration here are provided in Table 7. In the boxplot of FiTal2Ar area / FiTal1Ar area ratio, four out of five australopith specimens fall close to the middle of the distribution of orangutans and in the lower quartile range of chimpanzees (Fig. 6a). The only exception is A.L. 288-1at which falls below the lower quartile of orangutans. Results in Table 8 corroborate these findings: A.L.

288-1at is 2.2 SD below the orangutan mean while the other australopith specimens are within 1 SD of the orangutan mean. For FiLipAr area / TotFibTalAr area ratio, because of the overlap among extant species it is difficult to determine if the fossil specimens are closer to one extant species or the other (Fig. 6b). However, only A.L. 288-1at and A.L. 333-9b fall in the human upper quartile range, while the other three australopiths fall outside the human range (Fig. 6b). Group means comparisons (Table 8), show that A.L. 288-1at and A.L. 333-9b are within 1 SD of humans, chimpanzees and orangutans, A.L. 333-9a within 1 SD of orangutans, chimpanzees and gorillas, and A.L. 333-85 and A.L. 333w-37 are within 1 SD from orangutans and gorillas.

Four *Au. afarensis* specimens (A.L. 288-1at, A.L. 333-9a, A.L. 333-9b and A.L. 333w-37) fall in the interquartile range of great apes (within 1 SDs from chimpanzee, gorilla and orangutan mean) and outside the human interquartile range for FiTalTH1, while A.L. 333-85 falls in the human interquartile range (Fig. 7a). Group means comparisons corroborate these findings (Table 8). For FiTalTH2, A.L. 288-1at, A.L. 333-85 and A.L. 333w-37 fall within the African great ape interquartile range, A.L. 333-9a falls in the chimpanzee interquartile range and A.L. 333-9b falls close to both human and orangutan medians (0.3 SD above and 0.4 SD below respectively, Table 8). For the angle between FiTal1Ar and the STS (i.e. FiTalTH3), *Au. afarensis* is quite close to the human distribution: A.L. 333-9a, A.L. 333-9b and A.L 333-85 are close to the median of the range of humans and within 1 SD from the mean (Fig. 7c; Table 8). A.L. 333w-37 and A.L. 288-1at are in the upper quartile of human distribution (and in the lower quartile of chimpanzee distribution) (Fig. 7c). Results in Table 8 corroborate these findings.

Overall, modern humans are characterized by relative (to the proximal, FiTal1Ar) high distal fibulotalar articular facet (FiTal2Ar) area, FiTal1Ar more medially projecting than in extant apes, and a subcutaneous triangular surface facing more laterally than in apes. Modern humans also show low distal tibiofibular surface (FiLipAr) area and FiTal2Ar more medially projecting than extant apes although differences are non-significant with chimpanzees and orangutans for the two variables, respectively. African great apes highly overlap for distal fibular articular properties and are more similar to modern humans than to orangutans for relative FiTal2Ar area but are segregated from both modern humans and orangutans in possessing downward inclination of the proximal and distal fibulotalar articular facets. Orangutans are similar to African great apes in possessing downward projecting FiTal1Ar and anteriorly projecting STS, but more similar to modern humans in possessing more medially projecting FiTal2Ar. *Australopithecus afarensis* is closer to great apes for the relative FiTal2Ar area, in between modern humans and great apes for FiTalTH1, and closer to modern humans for the orientation of the STS, which results in this region being more laterally oriented than in great apes. Because of the poor performance in distinguishing extant hominids on the basis of their locomotion, FiLipAr and FiTalTH2 cannot be used to characterize *Au. afarensis* locomotor behavior.

Discussion

The distal fibula of extant hominids

The first aim of this paper was to quantify distal fibular articular morphology in extant orangutans, gorillas, chimpanzees and humans to understand which traits are more relevant for characterizing their locomotor behavior, with particular attention to the degree of arboreality. Five metrics were used to test the hypothesis that the distal fibula could distinguish extant hominids on the basis of their degree of arboreality: (FiTal2Ar area / FiTal1Ar), [FiLipAr area / (FiTal1Ar area + FiTal2Ar area)], FiTalTH1, FiTalTH2 and FiTalTH3. Results show that relative FiLipAr area and FiTalTH2 are not effective at differentiating humans from non-human hominids, while the other three variables bear signals correlated to the different locomotor behaviors of extant hominids.

All non-human apes are characterized by a downward inclination of the proximal fibulotalar articular facets (FiTal1Ar) as opposed to humans which display more medially projecting FiTal1Ar. The downward orientation of the fibulotalar articulation in great apes was hypothesized by Preuschoft (1970) as a sign that a greater component of the vertical force transmitted through the talus is borne by the fibula than in modern humans. Empirical studies conducted on the diaphyseal rigidity of tibia and fibula (Marchi, 2004, 2007, 2015) have shown that non-human hominids have a relative (to the tibia) more robust fibular diaphysis compared to modern humans, interpreted as a consequence of the greater lateral component of the substrate reaction force (Schmitt, 2003; Carlson et al., 2005), and greater dorsiflexion and eversion of the ankle joint (Barnett and Napier, 1953; DeSilva, 2009) in arboreal environments.

Non-human hominids also have relatively larger FiTal1Ar (i.e. smaller FiTal2Ar area/ FiTal1Ar area) than modern humans. Analyses of FiTal1Ar and FiTal2Ar areas separately (results not shown here) show a trend of decrease in FiTal1Ar area from orangutans, to chimpanzees, to gorillas, to humans and an inverse trend for FiTal2Ar area. Given that humans show the smallest FiTal1Ar area and the largest FiTal2Ar area a body size effect should not be responsible for these results at the hominid level. However, within great apes a relationship between body size and fibulotalar areas is present, with larger species having smaller FiTal1Ar area and larger FiTal2Ar area than smaller species. On the other hand, these results also correlate with the degree of arboreality. The most arboreal hominids (orangutans) have the largest FiTal1Ar area while the less arboreal hominids (humans) have the smallest. It may be hypothesized that the highly mobile ankle of non-human hominids requires larger FiTal1Ar (compared to humans) to increase the congruence between the distal fibula and the talus during extreme inversion/eversion movements in arboreal environments, and that for larger non-human hominid species (i.e. gorillas) the more loaded fibula leads to an increase in FiTal2Ar area, which being the more inferiorly facing facet is subjected to higher compressive forces during load-bearing. The change in overall function of the fibula in humans, i.e. less of a load-bearing function and increase of its role in providing a lateral buttress for the ankle joint, may have led to a change in the relative size of FiTal1Ar and FiTal2Ar. Although the relative size of the fibulotalar articulation is a useful trait in segregating non-human from human hominids, a satisfactory biomechanical explanation for this result cannot be provided yet. Kinetic and kinematic studies of the ankle joint movements in hominids walking on both arboreal and terrestrial substrates are needed to test the above proposed hypotheses.

The more anteriorly oriented subcutaneous triangular surface (STS) of non-human apes compared to humans has been interpreted as a consequence of the more developed peroneal groove and larger peroneal muscles in non-human apes than in humans (Stern and Susman, 1983; McLean and Marzke, 1994; Aiello and Dean, 2002). Electromyographic studies performed on non-human and human primates found that peroneal muscles are active during the support phase of locomotion on either horizontal or vertical trunks in chimpanzees, probably for eversion of the foot, but also in the second half of the stance phase in humans (Stern and Susman, 1983). Quantitative studies performed to determine the relative mass of the peroneal muscles in non-human great apes and modern humans seem to indicate heavier peroneal muscles in great apes (Tuttle, 1970; Thorpe et al., 1999; Payne et al, 2006). It might be hypothesized, therefore, that large peroneal muscles are more advantageous in arboreal great apes than in terrestrial humans. However, all of these studies have taken only a few individuals into consideration, and thus a statistical treatment of the results is not possible. More studies are needed in order to understand the possible role of the peroneal muscles in affecting fibular bending loads and therefore their role in producing the more anterior orientation of STS in non-human apes compared to modern humans.

It is also worth considering the variables that proved unsuccessful in segregating human from non-human hominids. FiLipAr surface area is generally smaller in humans compared to non-human hominids and there is no difference among non-human hominids. A larger sample size may, therefore, be necessary to obtain a significant difference between chimpanzees and humans. As for the lack of difference between orangutans and humans for FiTalTH2, the discrepancy between Preuschoft's (1970) prediction and our results cannot yet be reconciled. Experimental studies quantifying the relationship between compressive forces on the fibulotalar articular facets and joint extension are needed to test this hypothesis.

Implications for Australopithecus afarensis

The comparison between extant human and non-human apes and *Au. afarensis* from Hadar shows a distal fibular morphology of the Hadar hominins that is overall different from any extant hominid and more similar to humans (derived) for some aspects (FiTalTH3) and to great apes (presumed primitive) for others (FiTal2Ar area/FiTal1Ar area, FiTalTH1). The analysis of the morphology of the distal fibula of the Hadar hominins provides further evidence of the unique locomotor adaptations of *Au. afarensis*.

Since the time of first discovery and description of *A. afarensis,* a lively discussion has been going on regarding its arboreality. Although a consensus is far from being reached at present, a relatively long and abductable upper limb and curved hand phalanges seem to indicate a certain importance of arboreal behavior in the *Au. afarensis* locomotor repertoire (Stern, 2000; Richmond, 2003; Alemseged et al., 2006). Although studies indicated some traits linked to arboreal locomotion for the lower limb and foot of *Au. afarensis* (Stern and Susman, 1983; Duncan et al., 1994; Stern, 2000), there are also studies providing evidence for terrestrial bipedal locomotion adaptation in the species (White, 1980; Latimer et al., 1987; Latimer and Lovejoy, 1990a,b; Alemseged et al., 2006; DeSilva, 2009; Kimbel and Delezene, 2009; Haile-Selassie et al., 2010; Ward et al., 2012). In particular, studies of the functional morphology of the ankle inferred from the geometry of the distal tibia found that early hominins did not have an inverted set to the ankle joint and they did not load their ankles in dorsiflexion (DeSilva, 2009). Because of this morphology DeSilva suggested that early hominins did not have the necessary morphological adaptation for vertical climbing as we observe today in extant apes.

The distal fibulotalar articular facet (FiTal2Ar) of the Hadar hominins is relatively smaller than in modern humans and African great apes and within the range of orangutans. Orangutans are the most arboreal of the great apes, and even though a consensus on the degree of arboreality of *Au. afarensis* has not yet been reached, the overall postcranial skeletal morphology of the Hadar hominins does not lend any support for committed arboreal behavior as observed in modern-day orangutans. A difference in locomotor behavior that has been recently documented between orangutans and African great apes concerns the hand-assisted bipedal locomotion on small branches performed with extended lower limb joints of the former (Thorpe and Crompton, 2006; Thorpe et al., 2007). Although we do not know if this behavior is frequent enough to leave functional signals on the bone, if it was, it could have produced a load pattern on the fibula that is different from both humans and African great apes and therefore a unique combination of traits in the distal fibula. Before attempting a functional explanation of this result in *Au. afarensis*, kinematic and kinetic studies of orangutans walking with extended lower limb joints need to be carried out to understand the frequency of this behavior and if it leaves any functional signal on the fibula. Following the results of the theoretical analysis of Preuschoft (1970), the downward orientation of the proximal and distal fibulotalar articular facets found in the Hadar hominins would indicate that their distal fibula was subjected to higher vertical load than in modern humans and similar to non-human apes; such results would suggest some degree of arboreality in their locomotor repertoire.

From the analysis of the distal fibular morphology of the Hadar hominins, it appears that *Au. afarensis* already possessed a more laterally oriented lateral malleolus compared to non-human apes, although in general not as laterally oriented as in modern humans. This trait is associated with a relatively broad and deep peroneal groove in the fibula compared to the average of modern human (Johanson et al., 1982; Latimer and Lovejoy, 1990a). The above traits together could suggest that the peroneal muscles of Hadar hominins were smaller than in non-human apes but larger than in modern humans. Stern and Susman (1983), on the basis of electromyography studies associated this anatomy to either the need of large peroneals in the arboreal use of the foot, or on a different mechanism to transfer weight onto the ball of the hallux at the end of the stance phase. Latimer and Lovejoy (1990a) proposed that the larger peroneal groove (and therefore peroneal muscles) in *Au. afarensis* could mean that the transition to a shorter belly of the gastrocnemius and soleus muscles and to an elongated Achilles tendon observed in modern humans was not yet complete and that the peroneal muscles produced a greater proportion of plantarflexion torque in these hominins. The results of the present analysis are not conclusive in clarifying the reason for larger peroneal muscles in *Au. afarensis* compared to modern humans. More studies on the relationship among peroneal muscles, peroneal groove and locomotor behavior in extant hominids are necessary to better understand the results of the present study.

What we can infer from the study of the distal articular properties of the fibula is that the Hadar hominins were loading their distal leg in a unique way, different from what we observe in any of the extant hominids. In fact, although some characteristics observed here are in agreement with bipedal terrestrial locomotion (i.e. more laterally oriented lateral malleolus), they also show a unique set of traits that may imply higher mobility at the level of the ankle joint as shown by the ape-like downward orientation of the fibulotalar articular facets and relative larger distal fibulotalar articular facet. These results are not in disagreement with the hypothesized lack of inverted set to the ankle joint and of load of the ankles in dorsiflexion (Latimer et al., 1987; DeSilva, 2009), but neither do they contradict active arboreal behavior in *Au. afarensis* (Duncan et al., 1994; Stern, 2000).

There are various possible reasons for the ambiguity of the results obtained from the study of the morphology of the distal fibular articulation. One reason may be that the anatomy of Hadar hominins reflects the not yet complete human-like bipedal adaptations of *Au. afarensis*, reflecting some primitive, ape-like retentions in the fibula which are less functionally restrictive for bipedal locomotion than, for example, the distal tibia morphology (DeSilva, 2009). More *Au. afarensis* fossil fibulae and distal fibulae from earlier hominins are necessary to test this hypothesis. A second reason may be that because of the unique combination of traits in the lower limb of *Au. afarensis* (Kimbel and Delezene, 2009) the way in which the fibula was loaded is different from that observed in extant hominids (Marchi, 2007 and references therein). In order to test this hypothesis, associated tibiae and fibulae of *Au. afarensis* should be investigated with the method developed by Marchi (2007) to understand the way the bones were loaded in living individuals. Finally, we need to entertain the possibility that the kind of arboreal behavior employed by *Au. afarensis* was so different from that of extant non-human hominids that it did not leave recognizable functional signals on the fibula, or elsewhere. A recent study (Ventakaraman et al., 2013b) found that frequent arboreal behavior employed by contemporary hunter-gatherer populations does not leave any detectable signal in the ankle joint. The authors found that the high dorsiflexion angle of the ankle was associated with longer fibers in the gastrocnemius muscle compared to populations which did not climb trees. An anatomical study of the distal fibula of these arboreal hunter-gatherer populations could be used to test if the unique set of traits found in the distal fibula of *A. afarensis* tells us about a climbing biped.

The extremely low distal fibulotalar articular facet area of A.L. 288-1at deserves a separate discussion. Given that A.L. 288-1at is a very small individual (McHenry, 1992), the smallest within the fossil sample included in the present analysis, a body size effect is the first explanation that comes to mind when trying to interpret this result. However, A.L. 288-1at falls within the distribution of the other Hadar hominins for all the other variables included in the present study (Figs. 6 and 7). Moreover, the three larger Hadar fibulae (A.L. 333-9B, A.L. 333-85 and A.L. 333w-37) do not follow any particular size pattern (Figs. 6 and 7), making any body size effect in the results unlikely. As previously noted (Lovejoy et al., 1982), the overall morphology of A.L. 288-1at is not different from the other Hadar fibulae and the analyses provided in the present study agree with such a conclusion. However, the very small distal fibulotalar articular facet of A.L. 288-1at falls outside the distribution of any living hominids included in this analysis. A foot belonging to a taxa contemporary and different from *Au. afarensis* in Ethiopia has been recently described (Haile-Selassie et al., 2012) indicating the presence of multiple hominin lineages in the 3-4 Myr ago time interval. Although the morphology of the distal fibula alone cannot be used to test the presence of multiple species at Hadar, the extreme difference of A.L. 288-1at compared to the other Hadar fossils highlighted in the PCA (Fig. 5) does not preclude such a possibility. Finally, estimated body size for A.L. 288-1at is usually taken to be 27.3 kg (McHenry, 1992). While extant orangutans and chimpanzees included in the present study cover the body size of A.L. 288-1at, the smallest human included weighed 51 kg (data not shown here). In order to understand if the extremely low distal fibulotalar articular facet of A.L. 288-1at is unusual for hominins future analyses should include small-bodied humans.

Conclusion

The results of the study of the distal fibulotalar articular properties show that permanently terrestrial hominins are characterized by high (relative to the proximal) distal fibulotalar articular facet area, medially facing fibulotalar articular facets, and laterally facing lateral malleolus. Non-human apes are characterized by lower (relative to the proximal) distal fibulotalar articular facet area, downward facing fibulotalar articular facets, and anteriorly facing lateral malleolus. The more arboreal orangutans differ from African great apes in possessing a more medially facing distal fibulotalar articular facet associated with relatively smaller distal fibulotalar articular facet area. The fibula of the Hadar hominins show some traits in agreement with modern terrestrial bipedalism, like the more laterally facing lateral malleolus, in association with more ape-like traits like the smaller distal fibulotalar articular facet area and the more downward oriented fibulotalar articular facets. Further biomechanical investigation on the fibular morphology of extant hominids and, in particular, of extant populations habitually involved in tree climbing activities, including studies on the association between loading patterns and diaphyseal strength on the tibia and fibula bone pair, are needed to provide a better understanding of the degree of arboreality of early hominins.

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Figure legend

Fig. 1 - Different fibula morphologies in mammals

Figure 2 – Distal fibula linear measurements taken in this study. Medial (a and b) and anterior (c) views of distal articulation of the right fibula of a chimpanzee showing: a. the area surfaces of the proximal (FiTal1Ar) and distal (FiTal2Ar) part of the fibulotalar articulation, and of the fibula-tibial distal articulation (FiLipAr); b. the linear breadths taken to calculate the area (linear breadths are explained in the text); c. mediolateral breadth of the FiTal2Ar.

Figure 3 –Distal fibula angles taken in this study. Frontal view of the distal articulation of the right fibula of a chimpanzee (a) and of a human (b). Note the different angles formed with the longitudinal axis by the horizontal (FiTalTH1) and vertical (FiTalTH2) portion of the fibulotalar articulation in the two species. In non-human hominids the fibulotalar articulations are facing more downward than in humans; (c) distal view of the fibula of a chimpanzee positioned to take the angle (FiTalTH3) between the vertical portion of the fibulotalar articulation (1) and the subcutaneous triangular surface (2).

Figure 4 – Example of positioning of a chimpanzee fibula. Frontal view. A: most proximal point of the roughened surface for the syndesmotic distal tibiofibular joint.

Figure 5 – Principal component analysis of distal fibular variables in extant hominids and *A. afarensis*. The two extracted components (PC1 and PC2) explain 64.9% of the total variance: PC1 accounts for 44.0% and PC2 for 20.9%.,

Figure 6 – Calculated area of the distal fibular articular facets in extant hominids and *A. afarensis*. (a) distal fibulotalar articular facet area (FiTal2Ar) relative to proximal fibulotalar articular facet area (FiTal1Ar) and (b) distal fibulotibial articular facet area (FiLipAr) relative to the distal fibulotalar articular facet area (TotFibTalAr).

Figure 7 – Angles between the different structures of the distal fibula in extant hominids and *A. afarensis*. (a) Angle of the proximal fibulotalar articular facet with the longitudinal axis of the fibula (FiTalTH1); (b) the angle of the distal fibulotalar articular facet with the longitudinal axis of the fibula (FiTalTH2); (c) angle of the distal fibulotalar articular facet with the subcutaneous triangular surface (FiTalTH3).

Table 1 – Sample composition.

Species	Males	Females	Males		Females		NI[1]	Total
			Captive	Wild caught	Captive	Wild caught		
Homo sapiens[2]	16	13	-	-	-	-	-	29
Pan troglodytes[3, 4, 5, 6]			5	9	6	5	2	27
Gorilla gorilla[3, 4, 5, 6]			-	14	1	5	1	21
Gorilla beringei[3]			-	3	-	3	-	6
Pongo pygmaeus[3, 4, 5]			-	9	2	13	-	24

[1] Sex and provenience not identified.

[2] From the Dart Collection, University of the Witwatersrand, South Africa.

[3] From the National Museum of Natural History, Smithsonian Institution, USA.

[4] From the Primatological Collection, University of Zurich-Irchel, Switzerland.

[5] From the Zoologische Staatssammlung, Munich, Germany.

[6] From the Zoological Collection, University of the Witwatersrand, South Africa.

Table 2 – Variables used in analysis.

Variable	Anatomical description	Suggested mechanical implication
FiTal2Ar area / FibTal1Ar area	Ratio of the distal and proximal fibulotalar articular surface areas	Possible indicator of fibula load bearing (Preuschoft, 1970)
FiLipAr area / TotFibTalAr area	Ratio of the distal fibulotibial articular and total distal fibulotalar articular surface areas	Possible indicator of fibula mobility (Aiello and Dean, 2002)
FiTalTH1	Angle of the proximal portion of the fibulotalar articular facet with the longitudinal axis of the fibula	Possible indicator of fibula mobility (Preuschoft, 1970; Stern and Susman, 1983)
FiTalTH2	Angle of the distal portion of the fibulotalar articular facet with the longitudinal axis of the fibula	Possible indicator of fibula mobility (Preuschoft, 1970; Stern and Susman, 1983)
FiTalTH3	Angle of the proximal portion of the fibulotalar articular facet with the subcutaneous triangular surface	Possible indicator of development of peroneal muscles (Stern and Susman, 1983; Latimer and Lovejoy, 1990a)

Table 3 – Presence of distal fibulotalar articular surfaces on the fibula and tibia of modern humans.

Trait	Emergence (%)	Absolute number
Fibulotalar articular surface on the tibia	70%	48/69
Fibulotalar articular surface on the fibula	41%	28/69
Fibulotalar articular surface present on the fibula when also present on the tibia	54%	26/48
Fibulotalar articular surface present on the tibia and not on the fibula	46%	22/48
Fibulotalar articular surface present on the fibula and not on the tibia	3.5%	1/28

Table 4 – Mean and standard error of the distal fibular area and angle parameters used in the study: raw values.

Variables[1]	*Pongo* (SE) (min-max) *n* = 24	*Pan* (SE) (min-max) *n* = 27	*Gorilla* (SE) (min-max) *n* = 27	*Homo* (SE) (min-max) *n* = 29	*Au. afarensis* (SE) (min-max) *n* = 5
FiTal2Ar area / FiTal1Ar area	0.24	0.29	0.37	0.44	0.13
	(0.04)	(0.02)	(0.02)	(0.02)	(0.03)
	(0.05-0.78)	(0.16-0.56)	(0.15-0.57)	(0.31-0.68)	(0.04-0.19)
FiLipAr area / TotFibTalAr area	1.64	1.12	1.78	0.82	1.35
	(0.18)	(0.15)[5]	(0.15)	(0.09)[7]	(0.14)
	(0.64-3.60)	(0.35-4.08)	(0.83-3.65)	(0.46-1.29)	(1.02-1.70)
FiTalTH1[2]	19.04	24.86	21.00	9.07	17.20
	(1.09)	(1.24)	(1.37)[6]	(0.82)[8]	(2.46)
	(6.00-25.80)	(13.3-35.2)	(10.00-32.30)	(3.00-19.00)	(9.00-23.00)
FiTalTH2[2]	43.07	63.16	59.76	38.43	55.60
	(1.37)[3]	(1.60)	(1.34)[6]	(1.43)[8]	(4.82)
	(32.00-59.00)	(48.0-78.9)	(50.13-76.10)	(26.00-52.00)	(40.00-70.00)
FiTalTH3[2]	48.10	48.33	57.45	34.79	37.63
	(1.77)[4]	(2.07)	(2.54)	(0.90)[8]	(1.67)
	(42.20-54.70)	(29.40-64.70)	(42.60-70.22)	(28.00-46.00)	(33.53-42.55)

[1] See Table 2 for abbreviations. Variables are explained in the text. All variables were natural log-transformed, e.g., ln (FiTal2Ar area / FiTal1Ar area).

[2] Angles expressed in degrees.

[3] *n* = 23; [4] *n* = 9; [5] *n* = 26; [6] *n* = 24; [7] *n* =10; [8] *n* = 28.

Table 5 – Varimax rotated component matrix of the variables (ln transformed) used in the principal component analysis.

Variable	PC1	PC1
FiTal2Ar area / FiTal1Ar area[1]	-0.016	-0.978
FiLipAr area / TotFibTalAr area	0.580	0.040
FiTalTH1	0.774	0.289
FiTalTH2	0.806	-0.138
FiTalTH3	0.773	-0.014

[1] See Table 2 for abbreviations. Variables are explained in the text.

Table 6 - Results of Tukey tests for interspecific comparisons of fibulotalar surface area ratios (FiTal2Ar area / FiTal1Ar area and FiLipAr area / TotFibTalAr area), and fibulatalar surface angles (FiTalTH1, FiTalTH2 and FiTalTH3) on the extant sample.

Variables[1]	*Pongo* (SD) *n* = 24	*Pan* (SD) *n* = 27	*Gorilla* (SD) *n* = 27	*Homo* (SD) *n* = 29
FiTal2Ar area / FiTal1Ar area	-1.68_{PGH}[2]	-1.30_{O}	-1.04_{O}	-0.85_{O}
	(0.75)	(0.31)	(0.33)	(0.22)
FiLipAr area / TotFibTalAr area	0.36_{GH}	-0.04_{G}	$0.49_{P,H}$	$-0.25_{O,G}$
	(0.52)	(0.52)[5]	(0.43)	(0.34)[8]
FiTalTH1	2.90_{H}	3.17_{H}	2.99_{H}	$2.09_{O,P,G}$
	(0.35)	(0.29)	(0.35)[7]	(0.51)[9]
FiTalTH2	$3.75_{P,G}$	$4.14_{O,H}$	$4.08_{O,H}$	$3.63_{P,G}$
	(0.16)[3]	(0.14)	(0.11)[7]	(0.21)[9]
FiTalTH3	3.87_{H}	$3.86_{G,H}$	$4.04_{P,H}$	$3.54_{O,P,G}$
	(0.11)[4]	(0.18)[6]	(0.14)[8]	(0.14)[9]

[1] See Table 2 for abbreviations. Variables are explained in the text. All variables were natural log-transformed, e.g., ln (FiTal2Ar area / FiTal1Ar area).

[2] Subscripts indicate statistical significance from *Pongo* = O, *Pan* = P, *Gorilla* = G and *Homo* = H using Tukey multiple-comparisons tests.

[3] *n* = 23; [4] *n* = 9; [5] *n* = 27; [6] *n* = 16; [7] *n* = 24; [8] *n* = 10; [9] *n* = 28.

Table 7 –Ln transformed fibulotalar surface area ratios (FiTal2Ar area /FiTal1Ar area and FiLipAr area / TotFibTalAr area), and fibulotalar surface angles (FiTalTH1, FiTalTH2 and FiTalTH3) of the *A. afarensis* specimens.

Variables[1]	A.L. 288-1at	A.L. 333-9a	A.L. 333-9b	A.L. 333-85	A.L. 333w-37
FiTal2Ar area / FiTal1Ar area	-3.297	-1.655	-1.682	-2.216	-1.917
FiLipAr area / TotFibTalAr area	0.015	0.328	0.029	0.532	0.484
FiTalTH1	3.135	2.890	3.045	2.197	2.708
FiTalTH2	4.060	4.248	3.689	3.970	4.043
FiTalTH3	3.751	3.605	3.512	3.555	3.696

[1] See Table 2 for abbreviations. Variables are explained in the text. All variables were natural log-transformed, e.g., ln (FiTal2Ar area / FiTal1Ar area).

Table 8 - Distance of *A. afarensis* from extant species [number of SD from the species mean = (fossil - extant) / SD)]. Negative values mean the fossil value is smaller than the extant species. In bold values lower than or equal to 1.0 standard deviation.

Fossil	**Properties**	***Pongo***	***Pan***	***Gorilla***	***Homo***
A.L. 288-1at	FiTal2Ar area / FiTal1Ar area[1]	-2.2	-6.4	-6.8	-11.1
	FiLipAr area / TotFibTalAr area	**-0.7**	**-0.1**	-1.1	**0.8**
	FiTalTH1	**0.7**	**-0.1**	**0.4**	2.0
	FiTalTH2	1.9	**-0.6**	**-0.2**	2.0
	FiTalTH3	-1.1	**-0.6**	-2.1	1.5
A.L. 333-9a	FiTal2Ar area / FiTal1Ar area	**0.0**	-1.1	-1.9	-3.7
	FiLipAr area / TotFibTalAr area	**-0.1**	**0.6**	**-0.4**	1.7
	FiTalTH1	**-0.0**	**-0.9**	**-0.3**	1.6
	FiTalTH2	3.1	**0.8**	1.5	2.9
	FiTalTH3	-2.4	-1.4	-3.1	**0.5**
A.L. 333-9b	FiTal2Ar area / FiTal1Ar area	**0.0**	-1.2	-1.9	-3.8
	FiLipAr area / TotFibTalAr area	**-0.6**	**0.1**	-1.1	**0.8**
	FiTalTH1	**0.4**	**-0.4**	**0.2**	1.9
	FiTalTH2	**-0.4**	-3.2	-3.4	**0.3**
	FiTalTH3	-3.3	-1.9	-3.8	**-0.2**
A.L. 333-85	FiTal2Ar area / FiTal1Ar area	**-0.7**	-3.0	-3.6	-6.2
	FiLipAr area / TotFibTalAr area	**0.3**	1.1	**0.1**	3.0
	FiTalTH1	-2.0	-3.4	-2.3	**0.2**
	FiTalTH2	1.4	-1.2	**-1.0**	1.6
	FiTalTH3	-2.9	-1.7	-3.5	**0.1**
A.L. 333w-37	FiTal2Ar area / FiTal1Ar area	**0.3**	-2.0	-2.7	-4.9
	FiLipAr area / TotFibTalAr area	**0.2**	1.1	**0.0**	2.2
	FiTalTH1	**-0.5**	-1.6	**-0.8**	1.2
	FiTalTH2	1.8	**-0.7**	**-0.3**	2.0
	FiTalTH3	-1.6	**-0.9**	-2.5	1.1

[1] See Table 2 for abbreviations. Variables are explained in the text.

Figure 1

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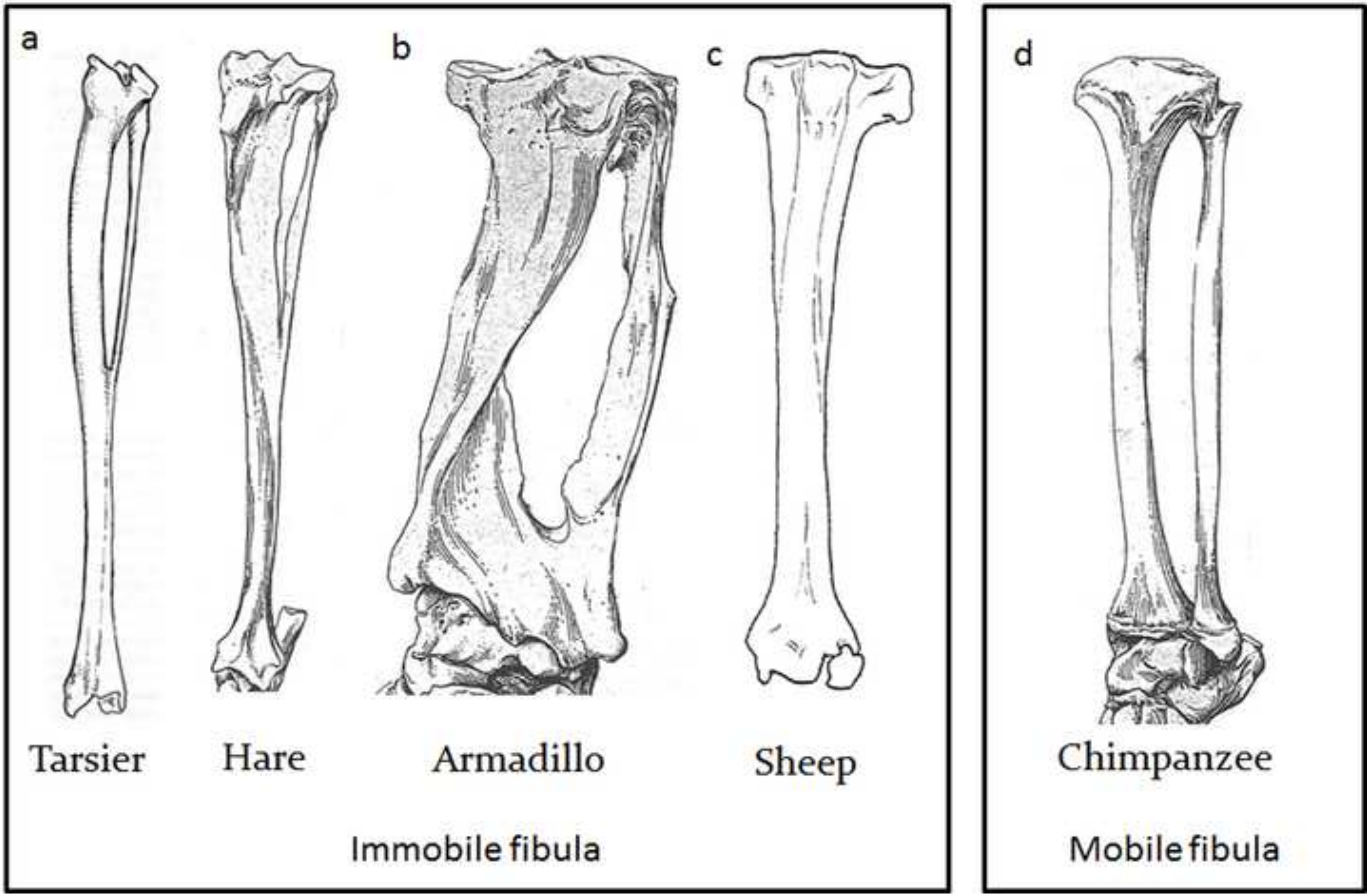
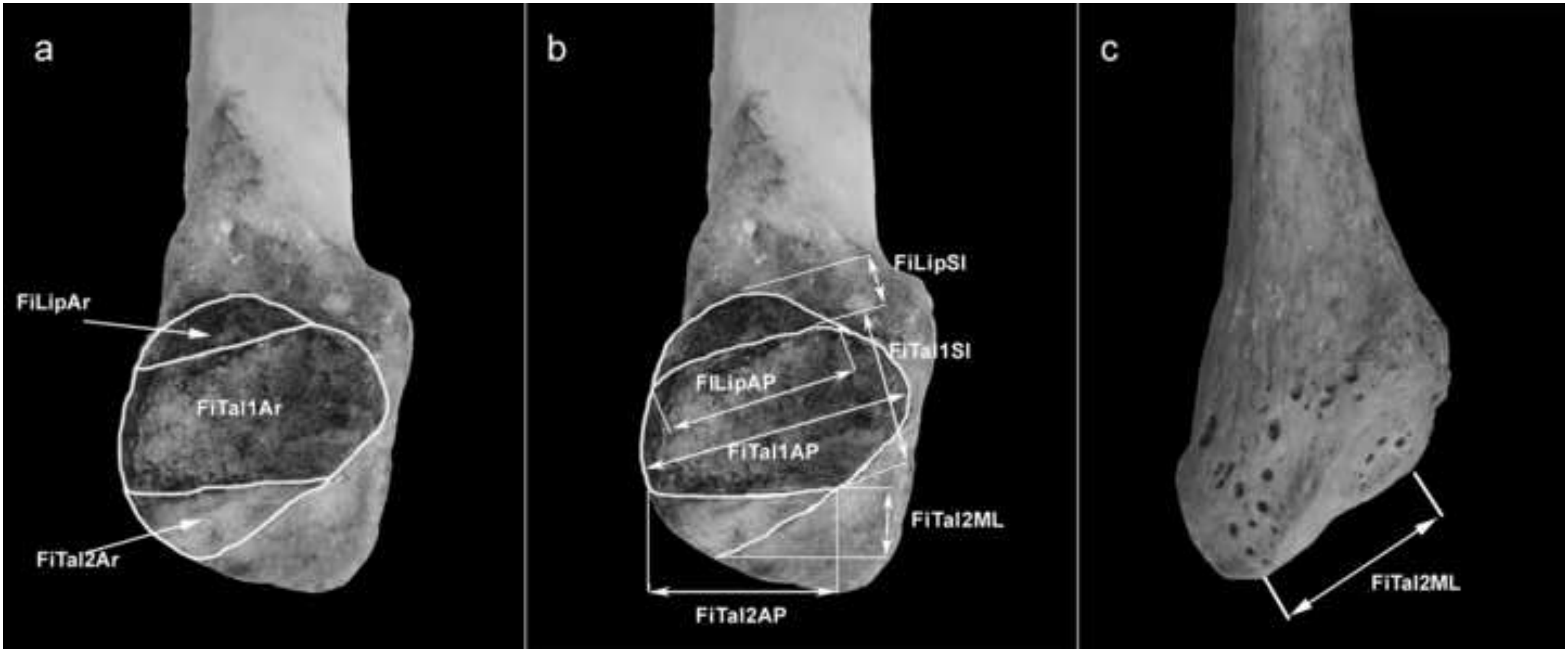


Figure 2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FiTal2ML
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c
FiTal2ML

Figure 3

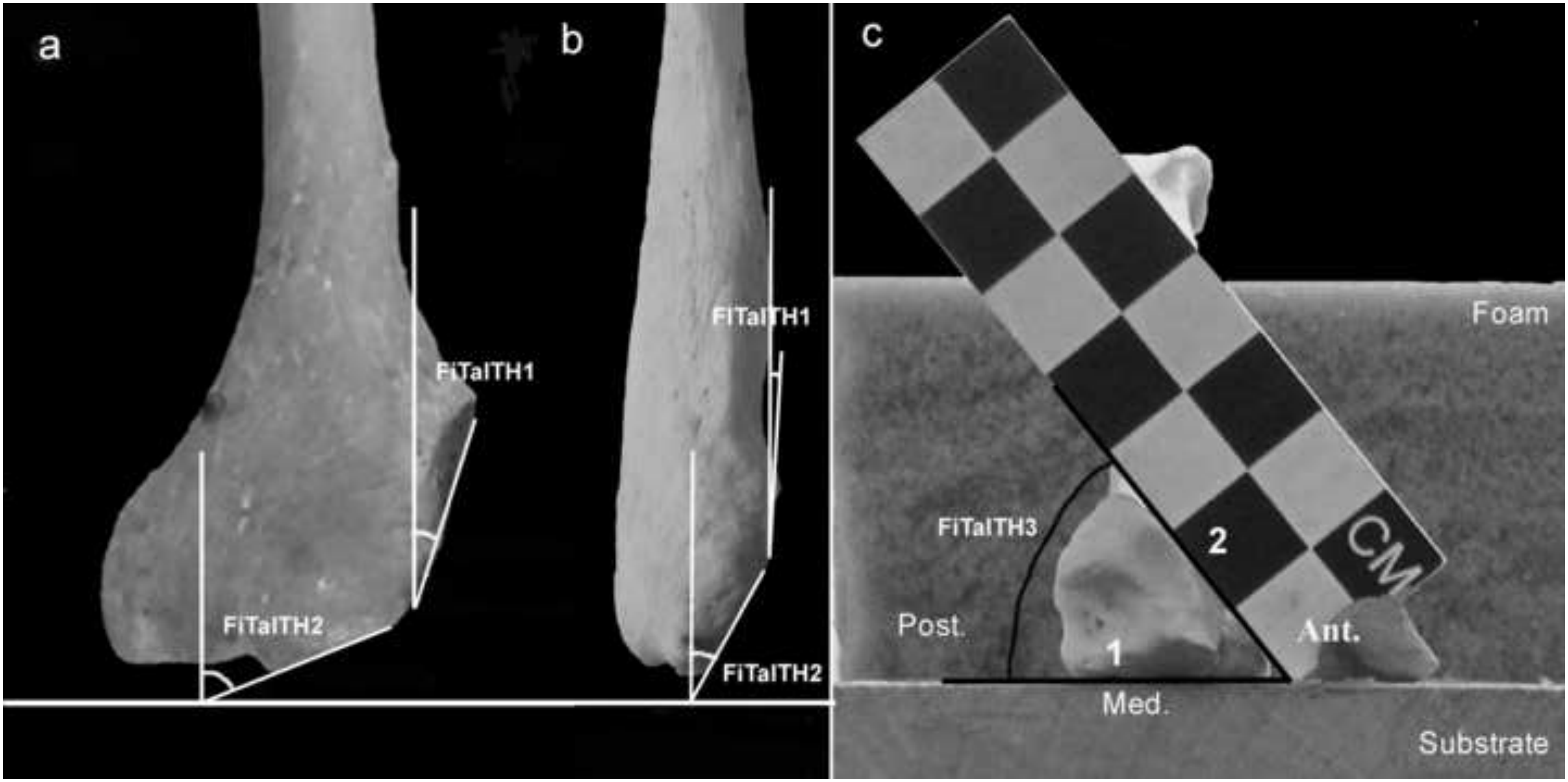
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Figure 4

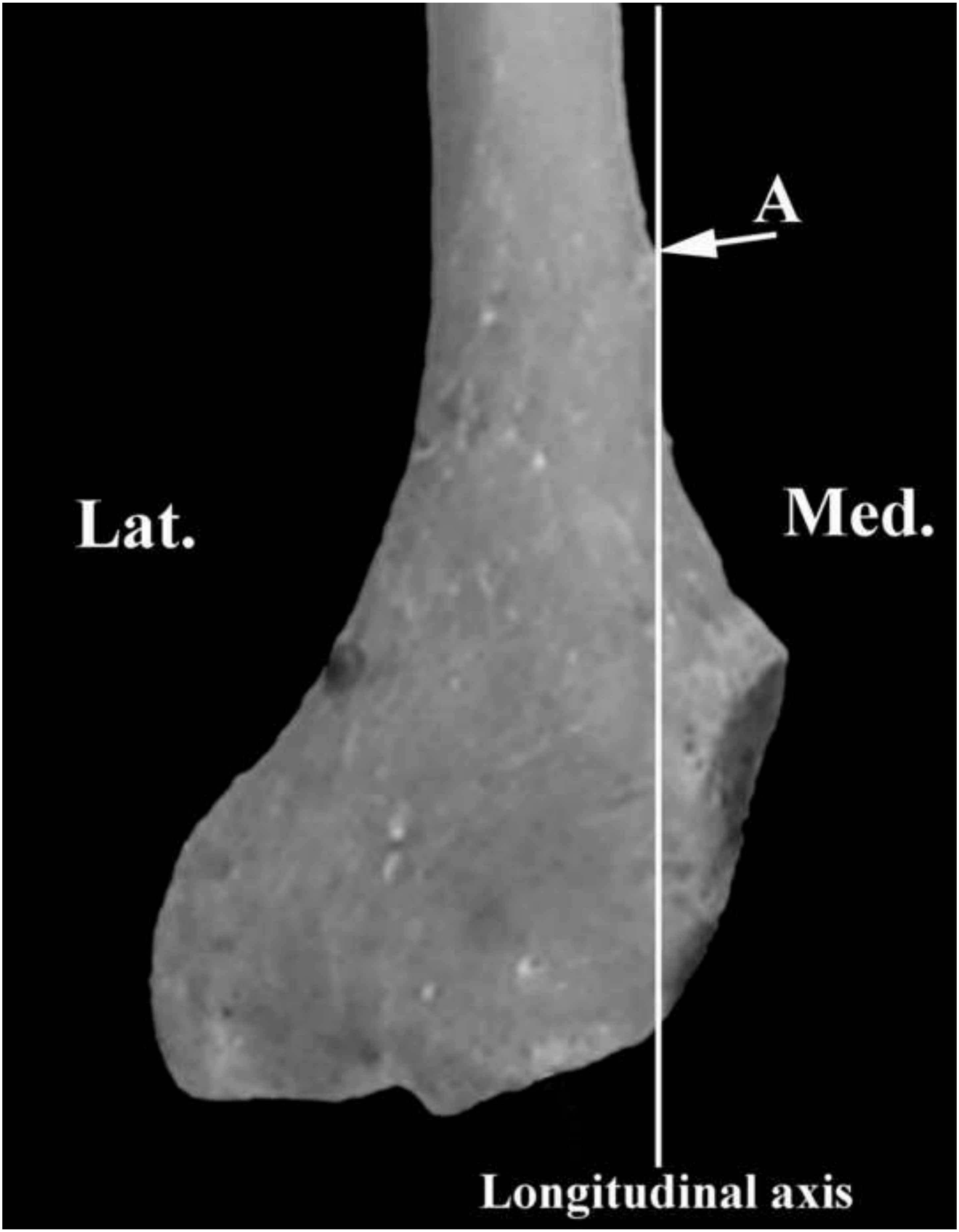
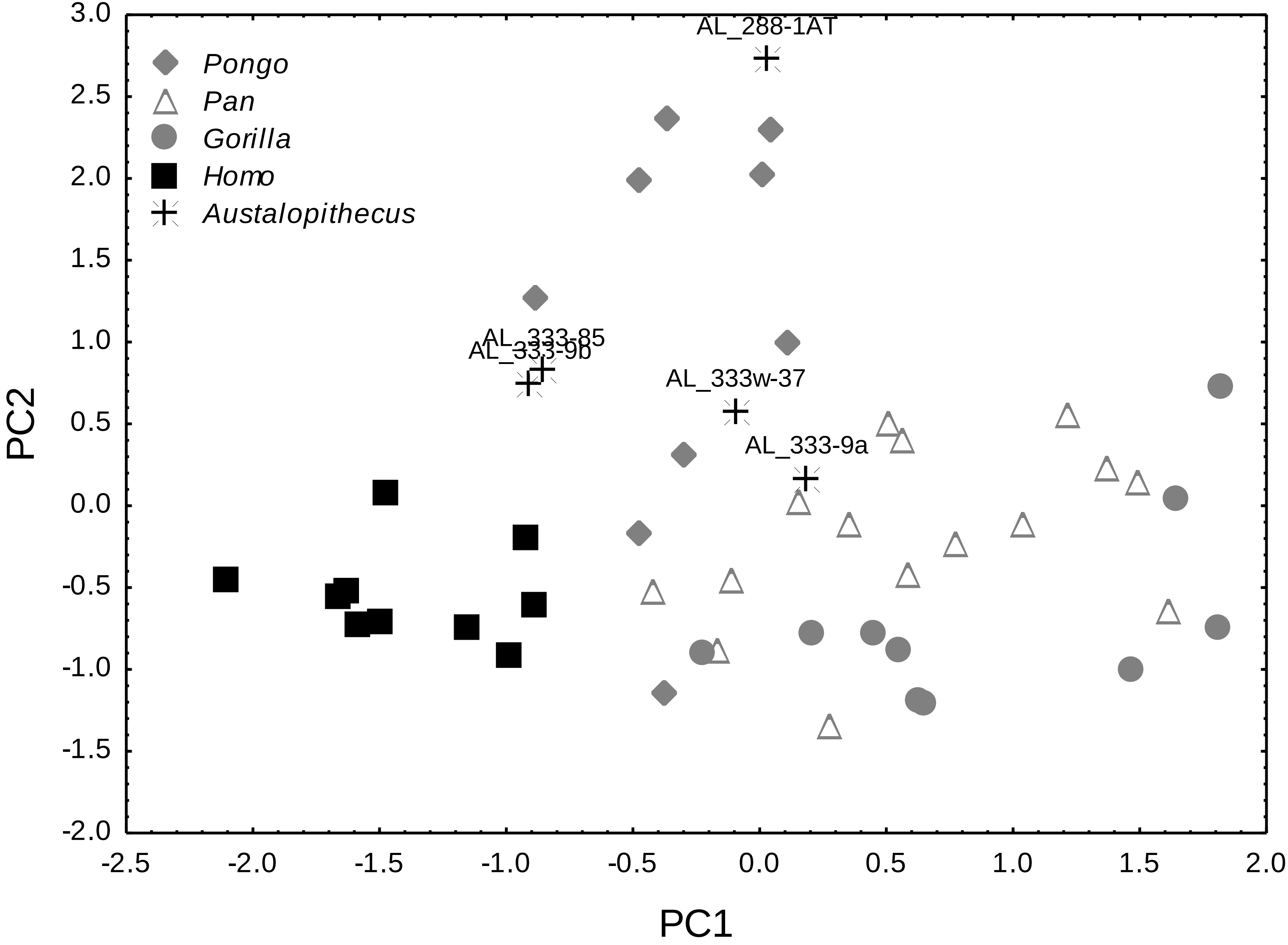


Figure 5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Homo
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AL_333-9b
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AL_333-9a
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Figure 6

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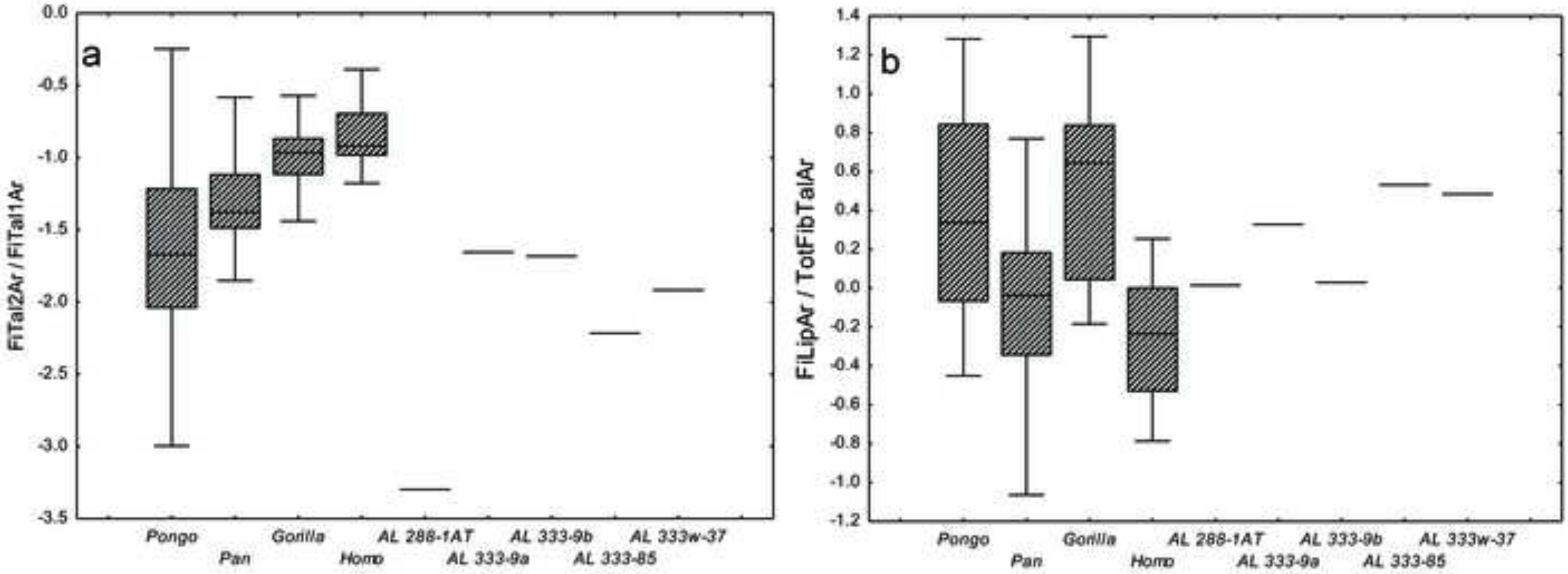
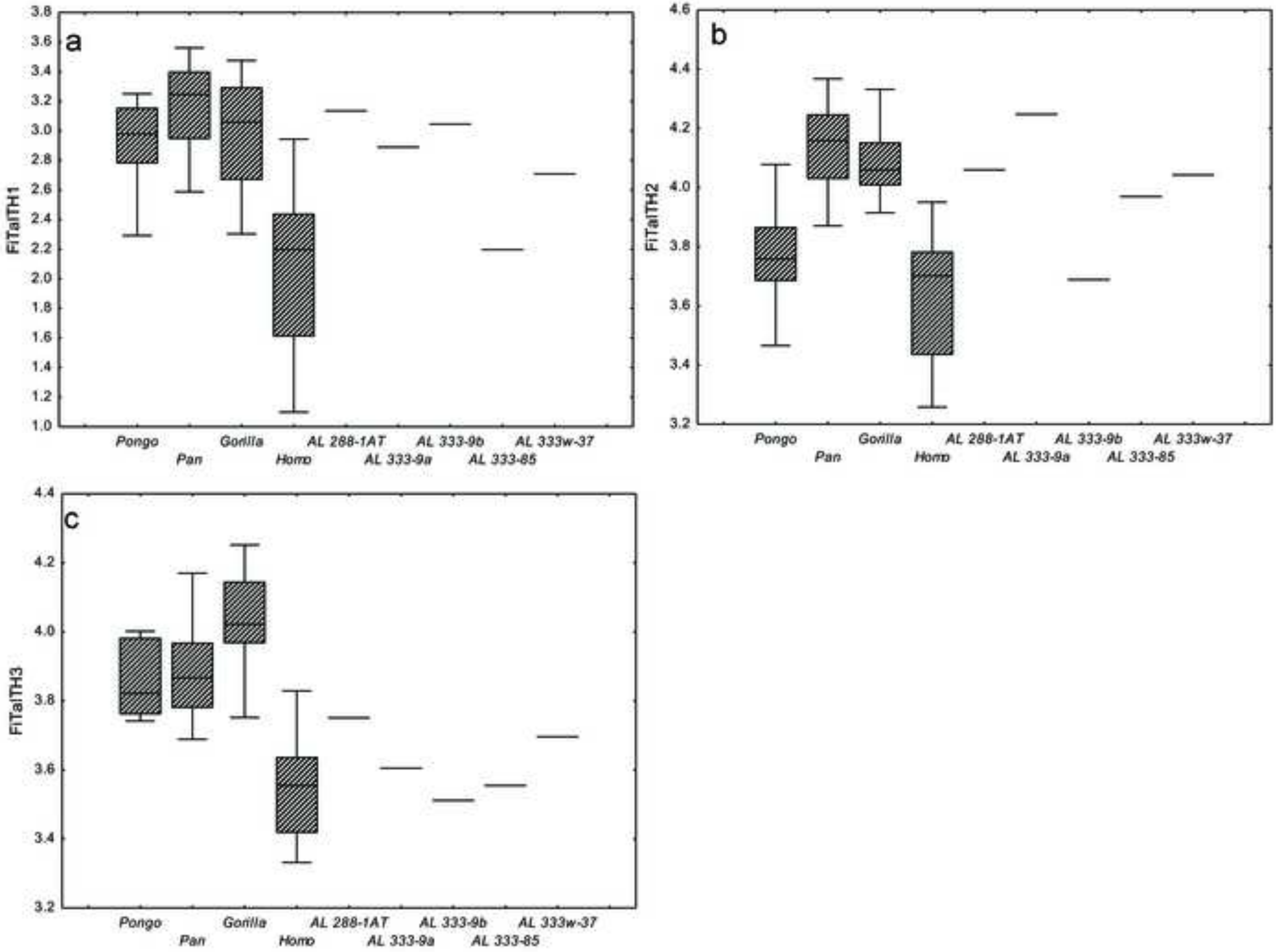


Figure 7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b
FiTalTH2
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c
FiTalTH3
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Pongo
Pan
Gorilla
Homo
AL 288-1AT
AL 333-9a
AL 333-9b
AL 333-85
AL 333w-37

Supplementary Online Material

Table 1 - Descriptive statistics for fibular angles and areas (ln transformed) of wild caught and captive chimpanzees.

	Wild caught mean (SE) n = 14	Captive mean (SE) n = 11
FiTal1Ar area / FiTal2Ar area[1]	-1.35 (0.07)	-1.21 (0.10)
FiLipAr area / TotFibTalAr area	0.08 (0.12)[2]	-0.20 (0.16)
FiTalTH1	3.14 (0.07)	3.19 (0.10)
FiTalTH2	4.12 (0.03)	4.14 (0.04)
FiTalTH3	3.77 (0.13)[3]	3.91 (0.04)

* $P < 0.05$ (Mann-Whitney U-test).

[1] See Table 2 in the text for abbreviations. Variables are explained in the text.

[2] n = 13; [3] n = 4.

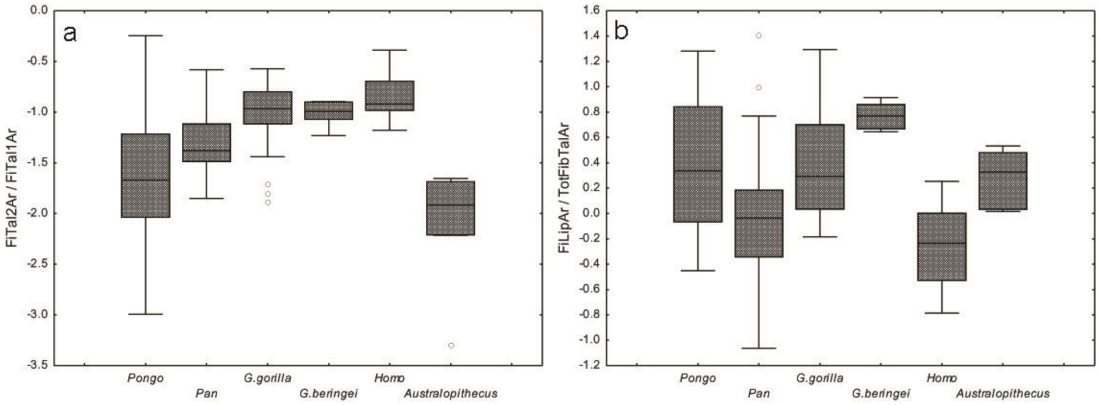

Figure 1 – Calculated area of the distal fibular articular facets in extant hominids and *A. afarensis*. (a) distal fibulotalar articular facet area (FiTal2Ar) relative to proximal fibulotalar articular facet area (FiTal1Ar) and (b) distal fibulotibial articular facet area (FiLipAr) relative to the geometric mean of distal fibular articular area (TotFibTalAr).

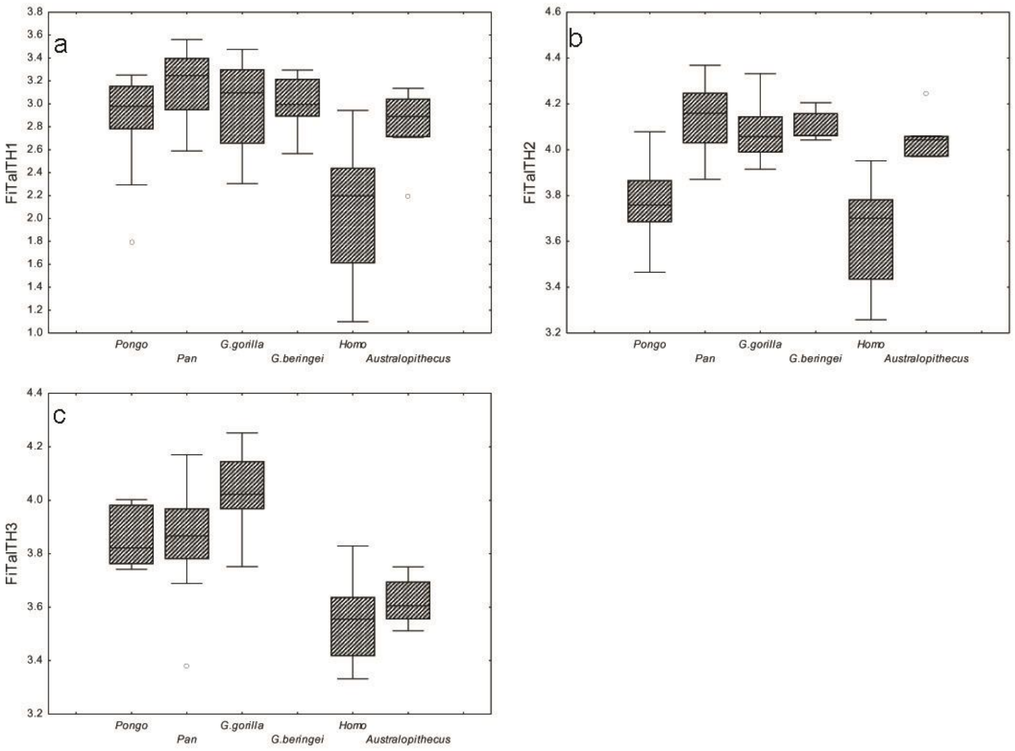

Figure 2 – Angles between the different structures of the distal fibula in extant hominids and *A. afarensis*. (a) Angle (FiTalTH1) of the proximal fibulotalar articular facet with the longitudinal axis of the fibula; (b) angle (FiTalTH2) of the distal fibulotalar articular facet with the longitudinal axis of the fibula; (c) angle (FiTalTH3) of the distal fibulotalar articular facet with the subcutaneous triangular surface.