

Variation in tibia and fibula diaphyseal strength and its relationship with arboreal and terrestrial locomotion: extending the investigation to non-hominoid primates

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Background

The reason for investigating the relative (to the tibia) fibular diaphyseal strength follows the observation that the non-human primate fibula is more mobile, and therefore probably subjected to greater load, than the human fibula (Barnett & Napier, 1953). Hominoid and non-hominoid primates are also characterized by more mobile ankles and feet (increase in dorsiflexion/plantarflexion and inversion/eversion) than humans, a consequence of their arboreal behaviour (see Marchi, 2007). Dorsiflexion has been shown to increase torsion in the fibula (Barnett & Napier, 1952) and eversion of the foot has been shown to increase the force load on the fibula (Funk *et al.*, 2007). In addition, Barnett & Napier (1953) observed that non-human primates have in general a quite mobile fibula compared to other mammals. Finally, kinetic studies provide important clues about the role of the fibula in load bearing in non-hominoid primates. Carlson *et al.* (2005) found that during arboreal quadrupedal locomotion lemurs exerted laterally directed side-to-side forces in their limbs more frequently than when moving on the ground. Schmitt (2003) found that anthropoids more frequently exerted medially directed side-to-side forces when walking on an arboreal support than when walking on the ground.

While it has been demonstrated that relative fibular midshaft strength (where strength is intended here as cross-sectional geometric properties, CSG, of the diaphysis) is a good indicator of arboreality in hominoids (Marchi, 2007),

at present there are no studies providing information on such relationship in other primates. Because of the above mentioned experimental results (Schmitt, 2003; Carlson *et al.*, 2005), it is expected that similar relationships should be present for other primates as well. Another possible issue with previous studies conducted on the structural properties of tibia and fibula is that the relationships have been tested only at midshaft (level 50% of bone mechanical length). The midshaft is the region that has been usually considered in anthropological studies when investigating bone form/function relationships (Ruff, 1989). However, complete tibiae and fibulae (including the midshaft section) are very rare in the fossil record, while distal portions of the two bones are present (i.e. *A. sediba*, Berger *et al.*, 2010, and *A. afarensis*, Johanson & Taieb, 1976).

Here I present results of the study of relative fibular strength including cercopithecine primates (*Macaca fascicularis* and *Papio Anubis*) and measurements of the more distal aspects (20% of bone mechanical length) of both the tibia and fibula. *Papio anubis* and *M. fascicularis* were selected because they are phylogenetically distant from hominoids but closely related to each other (Perelman *et al.*, 2011) and vary in their degree of arboreal travel. Although the sample size of the cercopithecine included in this study is small ($n = 15$) the results of this study are important because they will provide for the first time a tool that can be applied to infer mobility patterns in fossil primates different from hominoids on the basis of relative fibular strength. For example, it may be

Tab. 1 – Results of Kruskal-Wallis analysis of ranks for interspecific comparison of relative fibular strength percent prediction errors (PPE) at level 50% (midshaft) and 20% (distal) of bone mechanical length.

INTERBONE COMPARISON	HOMO PPE1 (SE) (N = 26)	PAN PPE (SE) (N = 17)	GORILLA PPE (SE) (N = 17)	PONGO PPE (SE) (N = 12)	HYLOBATES PPE (SE) (N = 17)	PAPIO PPE(SE) (N = 10)	MACACA PPE (SE) (N = 5)
50% Z_p^2	2.657a,b ³ (0.68)	-2.638c,d (1.07)	0.770a,b,c (0.42)	-2.486c,d (0.82) ⁵	-4.314d (0.91)	6.583a (1.12)	-2.914b,c,d (0.76)
20% Z_p	2.353a (0.58)	-3.788b (0.98)	3.168a (0.74) ⁴	-4.181b (0.80)	-5.872b (0.67)	6.796a (0.87)	0.166a,b (2.33)

¹ PPE = (observed y - predicted y)/predicted y \times 100.

² Z_p = \ln (tibial polar section modulus/fibular polar section modulus).

³ Letters indicate results of Kruskal-Wallis tests: possession of same letter = nonsignificant difference ($p > 0.05$) between groups; a = highest mean, b = next highest mean, etc.

⁴ n = 16; ⁵ n = 11.

particularly useful for South African sites (i.e. Cooper's Cave) where several cercopithecoid species (including *Papio*) have been recently described (DeSilva *et al.*, 2013). Moreover, the extension of the study to the distal part of the leg performed on a substantial hominoid sample (n = 89) will allow to increase the bioarchaeological/early hominin sample to which the method can be applied.

Additions to the previous study

Fifteen cercopithecines (5 *P. anubis* and 10 *M. fascicularis*) have been added for comparison [collected at the Department of Vertebrate Zoology, National Museum of Natural History (NMNH), Washington, DC] to the hominoid sample previously studied (89 individuals including *Pan*, *Gorilla*, *Pongo*, *Hylobates* and modern humans, see Marchi 2007 for a description and details of data collection). Humans, *Gorilla*, and *Papio* are referred to in this study as more terrestrial primates (TER) while *Pan*, *Pongo*, *Hylobates* and *Macaca* as more arboreal (ARB). Please refer to Marchi (2007) for a justification of locomotor categories and a full description of the methodology used. The only methodological difference with Marchi (2007) is that two cross sections, at levels equal to 20% and 50% of the tibial mechanical length, were taken instead of one at midshaft.

Cross-sectional images for the hominoid sample were obtained using external molds combined with biplanar radiographic measurement of cortical thickness (LCM method, see Marchi, 2007). For the cercopithecine sample added here, cross-sectional images were obtained through ordinary medical CT-scanning obtained at the Department of Anthropology, NMNH (Siemens Somatom Emotion Single Spiral scanner, 110 kV, 80 mA, 1 mm slice thickness). O'Neill and Ruff (2004) have shown that data obtained with the CT method and the LCM method are comparable.

Polar section modulus (Z_p), a measure of the bone's torsional and (twice) average bending strength, was measured for both the tibia and fibula at both cross-sectional locations (20 and 50% of mechanical length). Comparisons of relative fibular strengths among different species were carried out using bivariate plots. The percent prediction error [PPE = (observed value - predicted value) / predicted value \times 100] was used to compare the position of each species relative to every other species with respect to the isometric line (Marchi, 2007). Because of the small cercopithecine sample size (5 *Macaca*, 10 *Papio*) Kruskal-Wallis nonparametric tests among pairs of species means for the PPE values were performed for the comparisons at 50% and 20%. Statistical analyses were carried out with the PC program STATISTICA 7.

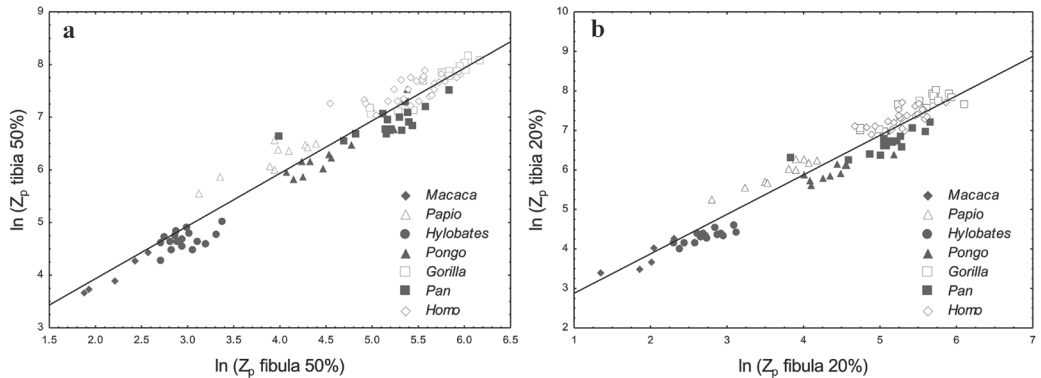


Fig. 1 - Comparison of tibial and fibular In-transformed polar section modulus (Z_p) at (a) mid-diaphysis (level 50%) and (b) distally (level 20%) in Homo, Pan, Gorilla, Pongo, Hylobates, Papio and Macaca. Polar section modulus is in mm³. The lines are isometric reference lines centered on the mean x-y of the pooled data set.

Table 1 and Figure 1 show that the relationships observed for hominoids between the relative fibular midshaft strength and the degree of arborescence (Marchi, 2007) appears to be valid for *M. fascicularis* and *P. anubis* too. In fact, more arboreal species group below the isometric line (higher relative fibular diaphyseal robusticity) while more terrestrial species group above the line. Distally, within hominoids more arboreal species displays higher relative fibular strength as observed at midshaft. For cercopithecines, distal diaphyseal results are not completely in agreement with those found at midshaft. In fact, while more terrestrial cercopithecines (*P. anubis*) display higher relative fibular strength as more terrestrial hominoids do, more arboreal cercopithecines (*M. fascicularis*) do not group clearly with either ARB nor TER.

Interpretation of results and future directions

Results obtained for cercopithecines distally are less clear to interpret. While *P. anubis* clearly group with TER, *M. fascicularis* grouping is less clear. Various interpretations of these results may be provided. The lack of significance of the results concerning *M. fascicularis* may be a consequence of the small sample size for this species. Table 1

shows that the standard error of the mean (SE) is quite high for *M. fascicularis* at level 20%. An increase of the sample size could decrease SE and provide more significant results. Another reason for the *M. fascicularis* results may be that although they are considered to be prevalently arboreal, they move using predominantly arboreal quadrupedalism (Cant, 1988), which is different in comparison to the characteristic torso-orthograde arboreal locomotion used by the non-human apes to which they are compared. However, also *P. anubis* when on the ground is involved in a type of quadrupedalism quite different from the one adopted by *Gorilla* (knuckle-walking), and especially different from the bipedal locomotion of *Homo*. Nevertheless, *Papio* is grouped with *Gorilla* and *Homo* in TER. It seems that the similarities found between *P. anubis* and more terrestrial hominoids are consequence of: a. the similar degree of fibular mobility, plantarflexion/dorsiflexion and inversion-eversion of the foot (Barnett & Napier, 1953); and b. ML distribution of the load (Schmitt, 2003; Carlson *et al.*, 2005) observed when moving on the ground, as previously hypothesized (Marchi, 2007). It is therefore unlikely that the different orientation of the torso between *M. fascicularis* and the most arboreal hominoids could account for the differences observed in this study. A more probable explanation of the *M. fascicularis*

results may be due to the not highly specialized arboreal habits of the species (Cant, 1988). If, as explained above, different relative fibular strengths are consequence of different loading patterns, and of fibula and ankle mobility experienced by the leg in arboreal and terrestrial environments, an animal which engages mainly in arboreal locomotion but which spend also a large amount of time on the ground (as *M. fascicularis* does) would be expected to show an intermediate expression of the trait. The inclusion of other cercopithecine species with different degrees of arboreality is needed to understand how sensitive is relative fibular strength to different degrees of arboreality.

Although the inclusion of a larger sample of cercopithecine is advisable, the present results are important because provide evidence of the relationship between relative fibular strength and degree of arboreality in non-hominoid primates and of the presence of the relationship also distally in the leg. This method can therefore be used to better understand both fossil cercopithecines (DeSilva *et al.*, 2013) and early hominin degree of arboreality. In particular, within fossil hominins the *A. afarensis* (AL 288-1, Johanson & Taieb, 1974), as well as the recently discovered *A. sediba* (MH2, Berger *et al.*, 2010) distal tibiae and fibulae can be investigated using the method presented in this paper.

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