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Phylogenetic and biomechanical influences in the structural pattern of the femoral diaphysis among catarrhines

Influences phylogénétiques et biomécaniques sur l'organisation structurelle de la diaphyse fémorale chez les catarrhiniens

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EDITOR'S NOTE

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1 Introduction

1.1 Locomotion and bone structure

- 1 Mechanical loads applied to the skeleton during locomotion are key factors in the bone modeling process (Rubin & Lanyon, 1982; Lanyon & Rubin, 1984; Biewener & Taylor, 1986; Ruff *et al.*, 2006; Barak, 2020). These loads are particularly present in the long bones diaphysis and are known to affect their structural properties (Ruff, 1989; Ruff *et al.*, 1993; Lieberman *et al.*, 2004). Cross-sectional geometry is a common approach to investigate the influence of mechanical loading on bone (Ruff & Hayes, 1983; Demes *et al.*, 1991; Lieberman *et al.*, 2004). It involves generating cross-sections in the diaphysis of long bones and analyzing their geometrical properties (CSG). Theoretically,

compressive loads that spread along the longitudinal axis of a long bone tend to increase the cortical area in the diaphysis (Ruff *et al.*, 1993). Similarly, bending and torsional loads cause changes in the distribution of cortical bone and affect the cortical distribution within the cross-sections (Ruff & Hayes, 1983; Ruff *et al.*, 1993; Macdonald *et al.*, 2009). In a paleoanthropological framework, such an approach enables hypotheses on the biomechanics of hominin locomotion (e.g. Puymerail *et al.*, 2012a ; Trinkaus & Ruff, 2012; Ruff *et al.*, 2016; Marchi *et al.*, 2017; Rodríguez *et al.*, 2018; Daver *et al.*, 2022; Chevalier & de Lumley, 2022). With regard to bipedalism evolution, the study of the femoral cross-sectional properties is of particular interest since all the loadings generated during bipedal locomotion are transmitted through it (e.g. Ruff, 1995; Chevalier, 2013; 2022). However, a good understanding of the link between femoral CSG and actual behaviors performed during an individual's life is needed to strengthen paleoanthropological interpretations. This can be studied among living primates, which exhibit a very large diversity of locomotor behaviors.

- 2 Several studies have previously assessed femoral CSG in living primates. For example, in cercopithecoids, leapers exhibit stronger anteroposterior bending rigidity and torsional resistance than climbers (Burr *et al.*, 1981; 1989; Ruff, 2002a; Ruff *et al.*, 2019), while terrestrial quadrupeds seem to present more balanced anteroposterior vs mediolateral values (e.g. Ruff, 2003; Puymerail, 2011; Cosnefroy *et al.*, 2022). Concerning hominoids, non-human apes generally display increased femoral mediolateral (ML) bending rigidity (e.g. Puymerail, 2011; Nadell & Shaw, 2016; Sarringhaus *et al.*, 2022). Conversely to other hominoids, humans present an increased femoral anteroposterior (AP) bending rigidity, particularly at midshaft (see Ruff, 2018 for a recent review of modern humans). However, it is noteworthy that the orientation of cross-sectional shape and cortical distribution are difficult to correlate to the principal axis of loading (Lieberman *et al.*, 2004) and thus, AP or ML bending rigidity are therefore difficult to relate to specific behaviors (Carlson *et al.*, 2006). For example, it is difficult to relate ML femoral bending rigidity of gorillas and chimpanzees to knuckle-walking dominance or more generally to terrestrial quadrupedalism, since it is also described among suspensory apes like orangutans (Nadell *et al.*, 2021). Furthermore in humans, lifestyle and levels of physical activity also largely influence the femoral CSG within the frame of bipedalism (e.g. Marchi, 2008; Shaw & Stock, 2013; Villotte *et al.*, 2017; Saers *et al.*, 2021). Other studies also pointed out the potential (phylo)genetic signal that is reflected by femoral CSG, irrespectively of the locomotion at both intra (e.g. Hansen *et al.*, 2009; Morimoto *et al.*, 2011b; Cosnefroy *et al.*, 2022) and inter-specific level (Morimoto *et al.*, 2012; 2018; but see Ruff *et al.*, 2018).
- 3 There is therefore no consensus yet on a potential direct reflection of locomotor behaviors in femoral CSG, since the latter seem to be influenced by several factors. In a paleoanthropological perspective, the relevance of femoral CSG as a proxy to infer fossil behaviors can be questioned. However, while there is evidence for distinction to loading between distal and proximal diaphysis within a single bone (Mongle *et al.*, 2015), most of the studies focus on the midshaft cross-section (e.g. Ruff, 2003; Hansen *et al.*, 2009; Sparacello & Pearson, 2010). A more comprehensive analysis of femoral CSG seems therefore welcome to further address the link between structural properties of the femoral diaphysis and locomotion.

1.2 Aims and predictions

- 4 In this study we address the structural properties of the femur as a proxy for reconstructing past locomotion. To this purpose we (re)evaluate the relation between these structural properties and locomotor behaviors in extant primates: we measure the degree of similarity/distinctions in the femoral structural properties in relation to locomotor modes and to phylogenetic relationships. This contrasts with the previous approaches by investigating the entire femoral diaphysis and not a specific location such as midshaft (see also Puymeraul, 2011). To do so, we compare femoral structural properties through femoral diaphyseal CSG and cortical thickness maps among (Table 1):
- 5 - Chimpanzees and bonobos (*Pan troglodytes*, *P. paniscus*), which are predominantly knuckle-walkers associated with arboreal behaviors (e.g. Doran, 1992; Hunt, 1992; Carlson *et al.*, 2006; Sarringhaus *et al.*, 2014; Perrot *et al.*, 2022);
 - 6 - Gorillas (*Gorilla gorilla*, *G. beringei*), which are predominantly knuckle-walkers with lower amount of arboreal behaviors when compared to *Pan* genus (e.g. Doran, 1996; 1997; Doran & McNeilage, 1998);
 - 7 - Olive baboons (*Papio anubis*), which are quadruped almost exclusively terrestrial (e.g. Rose, 1977; Berillon *et al.*, 2010; Druelle *et al.*, 2017);
 - 8 - Rhesus macaques (*Macaca mulatta*), which are also quadruped but which engage in greater variety of locomotor modes than baboons, related to different substrates (e.g. Wells & Turnquist, 2001; Hunt, 2016);
 - 9 - Humans (*Homo sapiens*), which practice exclusively bipedalism (but see Venkataraman *et al.*, 2013);
 - 10 - Hylobatids (*Hylobates* genus), which engage in brachiation combined with other locomotor modes related to the arboreal environment (e.g. Chivers, 1972; Fleagle, 1976; Gittins, 1983; Srikosamatara, 1984; Fan *et al.*, 2013).
- 11 Generally, if the structural properties of the femoral diaphysis represent a good proxy for reconstructing locomotion, then these properties should be more similar among taxa with similar locomotor behaviors. Similarly, the more different the modes in which specimens engage in, the greater the differences in structural properties of their femoral diaphysis should be. Considering the distinctions and similarities in the main locomotor modes within our comparative sample, our predictions are as follows:
- 12 (1) The femoral structural properties of quadrupeds (*Pan*, *Gorilla*, *Papio* and *Macaca* genera), bipeds (humans) and brachiators (hylobatids) are distinctive.
 - 13 (2) Within quadrupeds, the structural properties of *Pan* and *Gorilla*, which are knuckle-walkers, are expected to be distinct from *Papio* and *Macaca*, which are plantigrade quadrupeds. Differences are also expected within knuckle-walkers between *Gorilla* and *Pan* with the latter being more arboreal, and within quadrupedal cercopithecoids between *Papio* and *Macaca* with the latter having a greater locomotor and substrate used variety.
- 14 In addition, distinctions in femoral structural properties between cercopithecoids (*Macaca* and *Papio* genera) and hominoids (*Homo*, *Pan*, *Gorilla* and *Hylobates* genera) irrespectively from their locomotor behaviors, could be interpreted as a phylogenetic signal.

2 Material and Methods

- 15 We study 127 femurs from adult catarrhine primates of 6 genera and 10 species (Table 1, see also sample details in supplementary Table 1). Hylobatids represent an interesting group to test our hypotheses since they share phylogenetic relationship with other hominoids and because of their unique repertoire among the sample. However, considering their sample size, they are excluded from statistical analyses.

Table 1

Genera	species	N (♀/♂/ND)	Positional repertoire	Locomotor group
<i>Homo</i>	<i>sapiens</i>	32 (17/15/0)	Bipedalism (100%)	Bipeds
<i>Pan</i>	<i>paniscus</i> , <i>trogloodytes</i>	28 (10/14/4)	Knuckle-walking (mean 83%), vertical climbing (mean 8.5%), bipedalism (mean 1.2%), others (mean 7.3%) ^{1,3,4,11*}	Quadrupeds (knuckle-walkers)
<i>Gorilla</i>	<i>gorilla</i> , <i>beringei</i>	10 (3/7/0)	Knuckle-walking (mean 96.5%), bipedalism (mean 1.5%), vertical climbing (mean 1.3%), others (mean 0.7%) ^{2,11*}	Quadrupeds (knuckle-walkers)
<i>Hylobates</i>	<i>lar</i> , <i>agilis</i> , <i>hoolock</i>	4 (1/3/0)	Brachiation (mean 62.3%), leaping (mean 18.9%), vertical climbing (mean 14.3%), bipedalism (mean 1.4%), quadrupedalism (mean 1.2%), other (mean 1.9%) ^{5,6,7,8,9}	Brachiators
<i>Papio</i>	<i>anubis</i>	38 (29/9/0)	Quadrupedalism (mean 98.7%), vertical climbing (mean 1%), others (mean 0.3%) ^{10,11}	Quadrupeds (plantigrade)
<i>Macaca</i>	<i>mulatta</i>	15 (9/6/0)	Quadrupedalism (mean 80%), vertical climbing (mean 15%), bipedalism (mean 2.7%), leaping (mean 1.7%), others (mean 0.6%) ¹²	Quadrupeds (plantigrade)

Study sample. Percentages are averages of locomotor bouts from: ¹Doran, 1996; ²Doran, 1997; ³Hunt, 1992; ⁴Sarringhaus *et al.*, 2014; ⁵Gittins, 1983; ⁶Srikosamatara, 1984; ⁷Fleagle, 1976; ⁸Fan *et al.*, 2013; ⁹Chivers, 1972; ¹⁰Rose, 1977; ¹¹Hunt, 2016; ¹²Turnquist & Wells, 1994. *data for chimpanzees and bonobos are averaged as well as for mountain and lowlands gorillas.

- 16 We measure cross-sectional geometry parameters (CSG) on 61 sections that range each percent from 20% to 80% of femoral biomechanical length (see Ruff & Hayes 1983; Ruff, 2002 for definition). These parameters include: sectional percentage cortical area (%CA) which is related to axial loads; the ratios of anteroposterior to mediolateral (I_x/I_y) and maximal to minimal (I_{max}/I_{min}) second moments of area, which indicate whether the cortical distribution is oriented along a preferential axis ($I_x > I_y$ for an anteroposterior distribution, $I_x < I_y$ for a mediolateral distribution) and whether this distribution is circular ($I_{max} \sim I_{min}$) or asymmetric ($I_{max} \gg I_{min}$). The second moments of area are

proportional to bending rigidity and, in the case of I_{max}/I_{min} , provide a good indicator of cross-sectional shape (Carlson, 2005). The use of ratios controls for the effect of body size on individual. The approach used to calculate the CSG is identical to that presented in a previous study (see Cosnefroy *et al.*, 2022). For each 5% of length, every parameter is compared between pairs of samples (except hylobatids whose sample is reduced) using a Wilcoxon-Mann-Whitney test (Tables 2, 3 and 4).

- 17 For each individual, we generate cortical thickness maps that present the overall cortical distribution within the diaphysis (Bondioli *et al.*, 2010; Profico *et al.*, 2020). These maps are derived from the Generalized Additive Models method (GAM; see Wood, 2006). They represent cortical thickness variations on an individual-specific standardized scale from 0 (minimum thickness in blue) to 1 (maximum thickness in red). This approach enables identical dimensional mappings to be made from which thickness data are extracted and make an inter-individual comparison possible. The aim of this analysis is to compare patterns of relative cortical thickness variations, emphasizing the similarities and differences in cortical distribution rather than absolute thickness measurements. All the individual cortical thickness maps are presented in the supplementary Figure 1. This approach therefore emphasizes on the potential heterogeneity of the structural organization of the cortical thickness, rather than on its magnitude. We perform this comparison via a principal component analysis (PCA). We also generate consensus maps for each group. These maps are realized by combining all the individual information into a single data set. Indeed, since the individual maps are of the same size, it is possible to overlay them and calculate the consensus regression surface to the individuals in a group (see method in Bondioli *et al.*, 2010; Puymerail, 2011). CSG and cortical thickness maps are obtained using the R package *morphomap* (Profico *et al.*, 2020).

3 Results

- 18 Results on intra-genus differences and sexual dimorphism are not the primary focus of this study, which aims to evaluate distinctions in femoral structure between groups that differ in both locomotion and phylogeny. However, these intra-genus differences and aspects of sexual dimorphism are detailed in the supplementary material (see Figure 1, supplementary Tables 2 and 3).

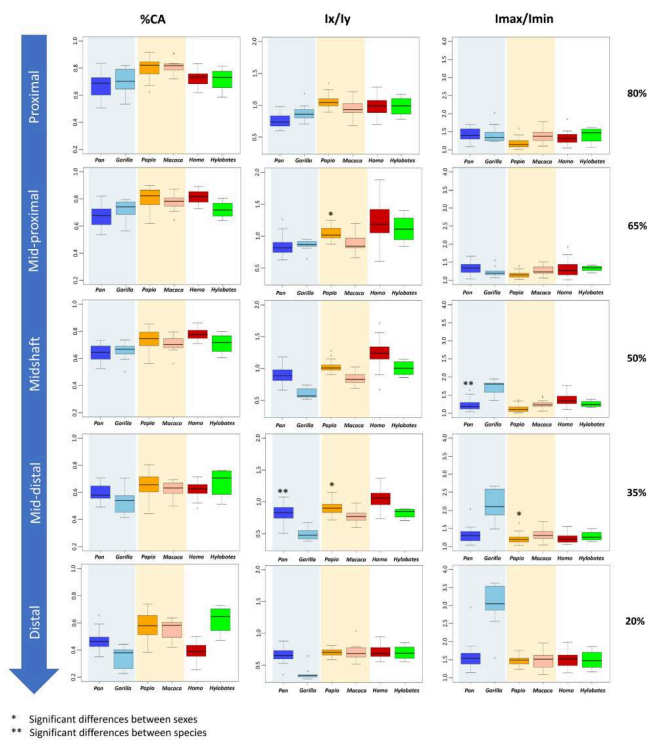
3.1 Cross-sectional geometry

3.1.1 Relative cortical area

- 19 Concerning %CA, our results indicate an increase from the distal to proximal diaphysis in all groups (Figure 1, Table 2). In quadrupeds, both African ape groups present lower %CA than both baboons and macaques in the entire diaphysis (Figure 1, Table 2). In comparison to quadrupeds, humans present higher %CA than both African apes in the entire diaphysis (except proximal extremity within Gorilla, see Table 2 and Figure 1). When compared to cercopithecoids, humans present lower %CA than both baboons and macaques in the distal diaphysis (20-30%, Table 2, Figure 1) but higher %CA at midshaft. Humans have higher %CA than macaques but do not differ from baboons in the mid-proximal diaphysis (55-70%, Table 2, Figure 1), and have lower %CA than both baboons and macaques in the distal diaphysis (Figure 1). Hylobatids have higher %CA than both

African apes and fall in the range of baboons from distal diaphysis to midshaft (Figure 1). Then they fall in the range of gorillas and have lower %CA than baboons and macaques in the mid-proximal and proximal diaphysis (Figure 1). Hylobatids have higher %CA than humans in the distal diaphysis, lower at midshaft and in the mid-proximal diaphysis, while both groups fall in the same range in the mid-distal and proximal diaphysis (Figure 1).

Figure 1



CSG measured on discrete femoral cross sections for genera. %CA: percentage of cortical area per section. Ix/Iy: ratio of the second moments of areas relative to the mediolateral and anteroposterior axes. Imax/Imin: ratio of the maximum and minimum second moments of areas. Boxplots : min, Q1, average, Q3, max.

- 20 Within knuckle-walkers, *Pan* genus exhibits higher %CA than gorillas in the distal and mid-distal diaphysis (20-35%, Table 2, Figure 1), but they do not differ significantly in the mid-and proximal diaphysis (Table 2). Within quadrupedal cercopithecoids, baboons have higher %CA than macaques in the mid-proximal diaphysis (50-65%, Table 2, Figure 1), but both groups fall closer in both distal and proximal extremities (Table 2).

Table 2

% of length	%CA			
	<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Papio</i>
20%	X	X	X	X

	<i>Pan</i>	1.55E-05	X	X	X
	<i>Gorilla</i>	2.13E-01	3.68E-06	X	X
	<i>Papio</i>	2.41E-11	6.08E-07	2.81E-06	X
	<i>Macaca</i>	5.52E-09	1.18E-04	1.22E-06	2.65E-01
25%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.12E-03	X	X	X
	<i>Gorilla</i>	2.13E-01	7.17E-05	X	X
	<i>Papio</i>	7.35E-09	1.20E-04	1.34E-05	X
	<i>Macaca</i>	8.22E-07	5.19E-03	7.34E-06	3.00E-01
30%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	3.42E-01	X	X	X
	<i>Gorilla</i>	3.59E-02	4.32E-03	X	X
	<i>Papio</i>	1.64E-05	1.32E-03	2.44E-04	X
	<i>Macaca</i>	2.44E-03	2.29E-02	6.94E-04	2.32E-01
35%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	3.95E-02	X	X	X
	<i>Gorilla</i>	2.05E-03	3.09E-02	X	X
	<i>Papio</i>	5.85E-02	6.92E-04	9.23E-04	X
	<i>Macaca</i>	6.60E-01	3.01E-02	5.43E-03	2.25E-01
40%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	4.20E-06	X	X	X
	<i>Gorilla</i>	1.83E-04	3.17E-01	X	X
	<i>Papio</i>	8.74E-01	5.31E-05	7.69E-04	X

	<i>Macaca</i>	5.03E-02	1.37E-02	7.99E-03	8.06E-02
45%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.06E-10	X	X	X
	<i>Gorilla</i>	8.94E-07	9.35E-01	X	X
	<i>Papio</i>	1.39E-01	6.94E-06	7.01E-04	X
	<i>Macaca</i>	1.84E-04	1.27E-02	7.99E-03	7.72E-02
50%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	9.80E-15	X	X	X
	<i>Gorilla</i>	1.89E-07	6.83E-01	X	X
	<i>Papio</i>	2.47E-02	1.54E-07	7.01E-04	X
	<i>Macaca</i>	3.61E-05	1.90E-03	4.13E-02	4.95E-02
55%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	5.25E-15	X	X	X
	<i>Gorilla</i>	2.64E-07	1.72E-01	X	X
	<i>Papio</i>	7.41E-02	9.40E-09	1.32E-03	X
	<i>Macaca</i>	6.30E-06	6.13E-04	1.96E-01	9.97E-03
60%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	2.26E-13	X	X	X
	<i>Gorilla</i>	2.64E-07	2.30E-01	X	X
	<i>Papio</i>	4.47E-01	8.06E-09	5.82E-04	X
	<i>Macaca</i>	8.40E-05	2.47E-04	1.15E-01	6.24E-03
65%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X

	<i>Pan</i>	3.42E-12	X	X	X
	<i>Gorilla</i>	1.83E-04	1.61E-01	X	X
	<i>Papio</i>	1.00E+00	4.01E-09	1.21E-03	X
	<i>Macaca</i>	1.70E-02	1.71E-05	5.45E-02	3.38E-02
70%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	2.11E-09	X	X	X
	<i>Gorilla</i>	7.43E-03	2.30E-01	X	X
	<i>Papio</i>	1.16E-01	3.71E-09	1.57E-03	X
	<i>Macaca</i>	6.11E-01	3.54E-05	3.08E-02	9.52E-02
75%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	2.09E-06	X	X	X
	<i>Gorilla</i>	1.38E-01	3.34E-01	X	X
	<i>Papio</i>	3.02E-04	4.69E-09	1.01E-03	X
	<i>Macaca</i>	6.24E-02	7.85E-06	1.37E-02	2.91E-01
80%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.23E-02	X	X	X
	<i>Gorilla</i>	4.75E-01	9.35E-01	X	X
	<i>Papio</i>	9.05E-06	9.35E-08	1.32E-03	X
	<i>Macaca</i>	5.89E-05	9.61E-07	2.91E-03	8.67E-01

Wilcoxon-Mann-Whitney p-values of interspecific comparison of femoral relative cross-sectional cortical area.

3.1.2 AP/ML bending rigidity

- 21 Concerning I_x/I_y and in quadrupeds, African apes present increased ML bending rigidity when compared to macaques and particularly to baboons (Figure 1). Gorillas present much more pronounced ML bending rigidity than all other group from distal to mid-shaft diaphysis and fall closer to macaques toward the proximal diaphysis (Table 3,

Figure 1). *Pan* presents higher ML bending rigidity than baboons in the entire diaphysis but fall closer to macaques at midshaft (Table 3, Figure 1). Humans only differ from gorillas in the distal diaphysis (20-25%, Table 3), and show an AP bending rigidity that distinguishes them from other groups from mid-distal to mid-proximal diaphysis (30-65%, Figure 1, Table 3). Hylobatids present balanced AP/ML bending rigidity in the entire diaphysis (Figure 1). They exhibit lower ML bending rigidity than gorillas in the entire diaphysis and fall between macaques and baboons from mid-distal to proximal diaphysis (Figure 1). They fall in the range of baboons in the distal diaphysis and in the range of humans in the proximal and distal diaphysis (Figure 1).

- 22 Within knuckle-walkers, gorillas have relatively higher ML bending rigidity than *Pan* genus from distal to mid-proximal diaphysis (20-60%, Table 3) and relatively lower ML bending rigidity at proximal extremity (80%, Table 3). Within quadrupedal cercopithecoids, macaques constantly exhibit more ML bending rigidity than baboons from the mid-distal to proximal diaphysis (30-80%, Table 3, Figure 1).

23 Table 3

% of length	Ix/Iy				
		<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Papio</i>
20%	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	7.40E-02	X	X	X
	<i>Gorilla</i>	1.89E-07	4.23E-09	X	X
	<i>Papio</i>	8.09E-01	2.61E-02	3.19E-06	X
	<i>Macaca</i>	7.44E-01	2.82E-01	6.12E-07	8.51E-01
		Homo	Pan	Gorilla	Papio
25%	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.37E-01	X	X	X
	<i>Gorilla</i>	1.63E-08	4.23E-09	X	X
	<i>Papio</i>	4.98E-01	2.51E-01	1.94E-06	X
	<i>Macaca</i>	8.92E-02	3.98E-01	6.12E-07	1.12E-01
		Homo	Pan	Gorilla	Papio
30%	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	3.21E-04	X	X	X
	<i>Gorilla</i>	1.36E-09	4.23E-09	X	X
	<i>Papio</i>	8.67E-04	1.24E-01	1.50E-06	X
		Homo	Pan	Gorilla	Papio

	<i>Macaca</i>	7.47E-05	1.92E-01	6.12E-07	1.40E-02
35%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	5.86E-09	X	X	X
	<i>Gorilla</i>	1.36E-09	4.23E-09	X	X
	<i>Papio</i>	4.91E-06	1.50E-02	1.50E-06	X
	<i>Macaca</i>	3.01E-08	1.31E-01	6.12E-07	2.91E-04
40%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	8.21E-10	X	X	X
	<i>Gorilla</i>	1.36E-09	4.23E-09	X	X
	<i>Papio</i>	1.30E-06	4.71E-04	1.50E-06	X
	<i>Macaca</i>	1.82E-09	6.81E-02	6.12E-07	6.43E-06
45%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	2.26E-10	X	X	X
	<i>Gorilla</i>	1.36E-09	4.23E-09	X	X
	<i>Papio</i>	1.50E-07	9.16E-05	1.50E-06	X
	<i>Macaca</i>	9.21E-09	9.03E-02	6.12E-07	2.74E-06
50%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.44E-10	X	X	X
	<i>Gorilla</i>	9.51E-09	2.96E-08	X	X
	<i>Papio</i>	6.05E-08	6.14E-06	1.50E-06	X
	<i>Macaca</i>	9.21E-09	2.39E-01	2.45E-06	3.32E-06
55%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X

	<i>Pan</i>	1.95E-10	X	X	X
	<i>Gorilla</i>	1.32E-07	2.09E-06	X	X
	<i>Papio</i>	4.95E-07	6.08E-07	1.50E-06	X
	<i>Macaca</i>	8.79E-08	5.88E-01	1.19E-04	9.63E-05
60%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	9.42E-10	X	X	X
	<i>Gorilla</i>	1.89E-07	8.18E-02	X	X
	<i>Papio</i>	1.32E-05	3.10E-06	2.19E-06	X
	<i>Macaca</i>	1.59E-06	7.34E-01	1.78E-01	8.78E-04
65%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.08E-08	X	X	X
	<i>Gorilla</i>	2.01E-06	4.62E-01	X	X
	<i>Papio</i>	3.96E-04	6.95E-07	9.42E-06	X
	<i>Macaca</i>	1.27E-05	2.71E-01	8.92E-01	7.08E-04
70%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.37E-08	X	X	X
	<i>Gorilla</i>	6.89E-05	1.33E-01	X	X
	<i>Papio</i>	1.18E-01	3.38E-08	5.85E-06	X
	<i>Macaca</i>	1.06E-04	3.44E-02	5.67E-01	1.98E-04
75%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.95E-08	X	X	X
	<i>Gorilla</i>	5.08E-04	7.04E-02	X	X
	<i>Papio</i>	3.49E-01	1.28E-08	2.37E-05	X

	<i>Macaca</i>	1.21E-02	8.46E-04	1.03E-01	2.28E-03
80%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	2.75E-08	X	X	X
	<i>Gorilla</i>	7.88E-02	6.60E-04	X	X
	<i>Papio</i>	3.64E-02	1.73E-11	4.38E-04	X
	<i>Macaca</i>	4.91E-01	1.71E-05	1.60E-01	2.96E-03

Wilcoxon-Mann-Whitney p-values of interspecific comparison of femoral AP/ML second moment of area.

3.1.3 Cross-sectional shape

- 24 Concerning I_{max}/I_{min} diaphyseal shape index, Gorillas show by far the highest values in the distal part of the diaphysis (Figure 1), they differ from all other groups from distal diaphysis to midshaft (20-55%, Table 4). In quadrupeds, *Pan* genus also presents lower cross-sectional circularity than baboons but only differ from macaques at 70% of length (Table 4). Humans only differ from gorillas in the distal diaphysis (20-30%, Table 4). Then they have lower circularity than all groups but gorillas at midshaft (Table 4, Figure 1) and differ from baboons with a lower circularity from mid-proximal to proximal diaphysis, and to both *Pan* genus (lower I_{max}/I_{min}) and baboons (higher I_{max}/I_{min}) in the distal diaphysis (Table 3). Hylobatids fall in the range of macaques and *Pan* genus in the entire diaphysis (Figure 1).
- 25 Within knuckle-walkers, *Pan* genus have a greater circularity than gorillas from distal diaphysis to midshaft (20-55%, Table 4, Figure 1), but gorillas have greater circularity at the mid-proximal diaphysis (70-75%, Table 4). Within quadrupedal cercopithecoids, macaques exhibit lower cross-sectional circularity than baboons from 35% to 80% (Table 4).

Table 4

% of length	I_{max}/I_{min}				
		<i>Homo</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Papio</i>
20%	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	2.99E-01	X	X	X
	<i>Gorilla</i>	6.71E-07	4.23E-09	X	X
	<i>Papio</i>	4.40E-01	8.33E-02	4.60E-06	X
	<i>Macaca</i>	7.44E-01	3.43E-01	6.12E-07	9.76E-01

25%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	7.97E-01	X	X	X
	<i>Gorilla</i>	4.08E-08	4.23E-09	X	X
	<i>Papio</i>	5.60E-01	3.95E-01	2.81E-06	X
	<i>Macaca</i>	6.93E-01	7.15E-01	6.12E-07	3.48E-01
30%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	1.77E-01	X	X	X
	<i>Gorilla</i>	9.51E-09	4.23E-09	X	X
	<i>Papio</i>	8.55E-01	1.55E-01	1.94E-06	X
	<i>Macaca</i>	1.13E-01	5.37E-01	6.12E-07	1.26E-01
35%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	6.05E-02	X	X	X
	<i>Gorilla</i>	2.72E-09	4.23E-09	X	X
	<i>Papio</i>	8.00E-01	2.36E-02	1.71E-06	X
	<i>Macaca</i>	2.34E-02	6.23E-01	6.12E-07	9.42E-03
40%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	6.22E-01	X	X	X
	<i>Gorilla</i>	9.51E-09	4.23E-09	X	X
	<i>Papio</i>	2.49E-03	1.51E-03	1.71E-06	X
	<i>Macaca</i>	3.03E-01	5.20E-01	6.12E-07	2.00E-03
45%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	3.67E-02	X	X	X

	<i>Gorilla</i>	2.64E-07	8.46E-09	X	X
	<i>Papio</i>	9.09E-07	2.56E-03	1.71E-06	X
	<i>Macaca</i>	3.72E-01	1.44E-01	6.12E-07	2.91E-04
50%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	9.47E-04	X	X	X
	<i>Gorilla</i>	6.89E-05	1.69E-08	X	X
	<i>Papio</i>	6.85E-09	1.45E-03	1.71E-06	X
	<i>Macaca</i>	1.70E-02	3.06E-01	2.45E-06	8.88E-05
55%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	3.12E-03	X	X	X
	<i>Gorilla</i>	8.41E-02	3.68E-06	X	X
	<i>Papio</i>	5.54E-09	2.70E-05	2.19E-06	X
	<i>Macaca</i>	1.05E-02	9.30E-01	1.84E-05	2.72E-05
60%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	2.02E-01	X	X	X
	<i>Gorilla</i>	9.42E-01	1.61E-01	X	X
	<i>Papio</i>	2.34E-07	2.25E-06	1.50E-05	X
	<i>Macaca</i>	1.19E-01	5.20E-01	7.09E-02	5.87E-05
65%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	5.61E-01	X	X	X
	<i>Gorilla</i>	1.92E-01	1.33E-01	X	X
	<i>Papio</i>	1.73E-04	5.31E-07	1.07E-01	X
	<i>Macaca</i>	4.91E-01	1.83E-01	5.67E-01	1.87E-03

70%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	6.93E-02	X	X	X
	<i>Gorilla</i>	2.48E-01	1.18E-02	X	X
	<i>Papio</i>	2.71E-02	1.06E-05	6.57E-01	X
	<i>Macaca</i>	9.91E-01	4.74E-02	2.61E-01	3.38E-02
75%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	9.47E-04	X	X	X
	<i>Gorilla</i>	6.95E-01	1.18E-02	X	X
	<i>Papio</i>	5.89E-04	3.08E-07	1.24E-02	X
	<i>Macaca</i>	9.37E-02	2.10E-01	1.44E-01	1.23E-04
80%		Homo	Pan	Gorilla	Papio
	<i>Homo</i>	X	X	X	X
	<i>Pan</i>	3.53E-02	X	X	X
	<i>Gorilla</i>	2.48E-01	4.23E-01	X	X
	<i>Papio</i>	8.03E-05	2.51E-07	2.44E-04	X
	<i>Macaca</i>	2.72E-01	3.18E-01	6.83E-01	5.87E-05

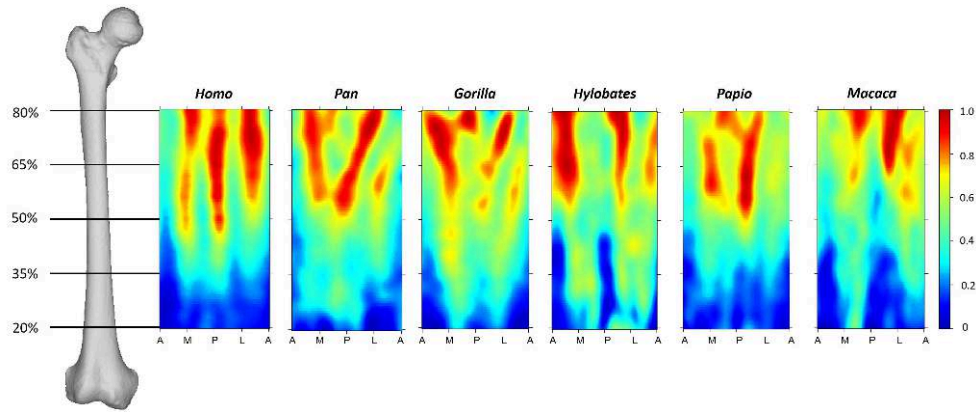
Wilcoxon-Mann-Whitney p-values of interspecific comparison of femoral max/min second moment of area.

3.2 Overall cortical distribution

- 26 Consensus maps indicate, for each group, a greater cortical thickness in the proximal than in the distal diaphysis (Figure 2). Evidence of two to three areas of high relative thickness occurs along the longitudinal axis of the diaphysis. In *Pan* genus and gorillas, two areas of high thickness in the medial and posterior region converge together towards the posteromedial axis at midshaft. In *Pan*, the area of high thickness in the posterior region is the largest, while in gorillas the area of high thickness in the antero-medial region is larger than in the posterior region (Figure 2). In baboons and macaques, the areas of high thickness are smaller than in African apes and are located in the posteromedial and posterolateral regions (Figure 2). In both cercopithecoids, the postero-lateral region is the thickest. In humans, three areas are almost parallel to the

longitudinal axis and the area of high thickness in the medial region is smaller than those from posterior and anterolateral region (Figure 2). In hylobatids, three regions are almost parallel as in humans, and the largest area of high thickness is in the antero-medial region as in gorillas (Figure 2).

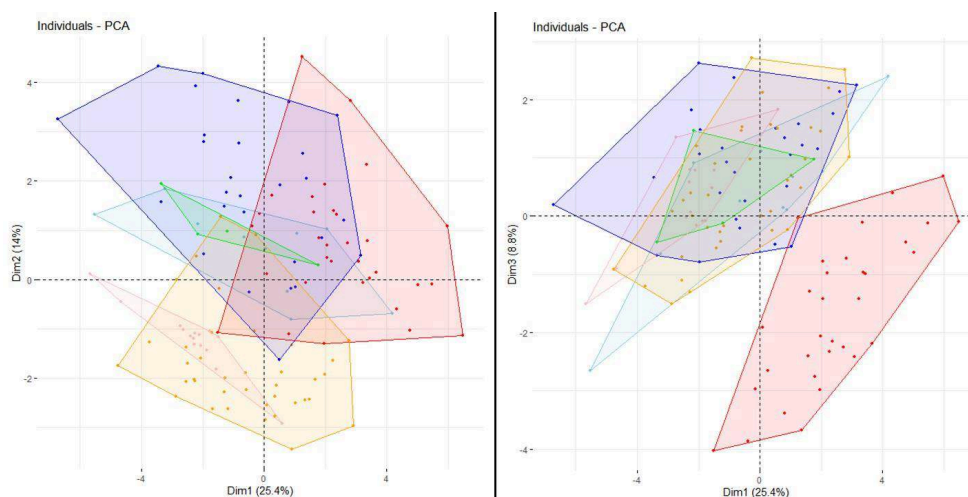
Figure 2



Consensus maps of cortical thickness distributions for genera. Orientation: A, anterior; M, medial; P, posterior; L, lateral. Thickness is represented on a standardized scale from 0 (blue) to 1 (red).

- 27 The PCA of individual maps show that all quadrupeds but macaques (and to a lesser extent baboons) have neutral positions on PC1 (25.4% of variance, Figure 3). Humans have mainly positives scores on PC1, while hylobatids are centered with quadrupeds. Concerning PC2, quadrupeds are separated with African ape knuckle-walker on positive scores and cercopithecoids on negative scores (Figure 2). On PC2, both humans and hylobatids fall in the range of African apes, forming a hominoid cluster that separate from cercopithecoids. When plotting PC1 and PC3 together (34.2% of cumulative variance, Figure 3), humans are separated from all non-human primates and form a clearly defined cluster.

Figure 3



Principal component analysis based on individual values of cortical thickness maps ($n=127$). Blue: *Pan* genus ($n = 28$), skyblue: *Gorilla* genus ($n = 10$), orange: *Papio anubis* ($n = 38$), pink: *Macaca mulatta* ($n = 15$), red: *Homo sapiens* ($n = 32$), green: *Hylobates* genus ($n=4$).

4 Discussion

4.1 Internal structure of the femoral diaphysis: locomotion or phylogeny?

4.1.1 Validating predictions

- 28 We expected that femoral structural properties of quadrupeds would differ from non-quadrupedal groups; and also that within quadrupeds, knuckle-walkers and plantigrade quadrupeds would be distinctive in their femoral structural properties. Our results on cross-sectional geometry (CSG) indicate significantly lower relative cortical area in African apes than in cercopithecoids for the entire diaphysis, while cross-sectional bending rigidity and shape only shows consistent similarities between *Pan* genus and macaques in the distal diaphysis. Interestingly, both groups engage in more arboreal behaviors such as vertical climbing compared to gorillas and baboons; this result would suggest potential functional signal associated with increased arboreal behaviors in the repertoire, as previously noted for the humerus (Patel *et al.*, 2013). However, it is difficult to conclude about the influence of the degree of arboreality in shaping the femoral CSG of quadrupeds since gorillas and baboons which are both almost fully terrestrial largely differ in all CSG. Generally, our results on CSG confirm the predominance of mediolateral bending rigidity in the femur of quadrupeds that has been stated in previous studies (e.g. Carlson *et al.*, 2006; Nadell & Shaw, 2016; Sarringhaus *et al.*, 2016; 2022). However, significant differences in bending rigidity are present between quadrupeds, between knuckle-walker and between plantigrade quadrupeds. These differences confirm that the orientation of cross-sectional shape and cortical distribution are difficult to relate to specific behaviors (Carlson *et al.*, 2006), potentially because there is a lack of correspondence between the principal axis of loading and the main axis of cortical distribution (Lieberman *et al.*, 2004).
- 29 One concern is that body size and mass can influence variation in femoral CSG. For instance, one might expect that within quadrupeds, differences in body mass and size could participate to explain the distinction in CSG between African apes and cercopithecoids. African apes are heavier and larger than cercopithecoids, and they tend to have more hindlimb dominance and a more caudally positioned center of mass compared to cercopithecoids (e.g. Schmitt, 2003; Demes & O'Neill, 2013; Demes *et al.*, 2015; Druelle *et al.*, 2019). If body size and mass were the primary factors shaping the femoral CSG, one would expect a gradual variation in CSG from the largest to the smallest group (i.e from gorillas to chimpanzees, to baboons, and finally to macaques). The results indicate that within quadrupeds, gorillas, which are distinctive in body mass and size, present the most flattened femoral diaphysis with increased mediolateral cortical distribution in the distal diaphysis compared to the whole sample. This finding likely correlates with the mediolaterally extended knee joint, which medioateral breadth has been previously reported to increase with body mass (Ruff, 2002b; Burgess *et al.*, 2018). However, this relationship does not appear to be gradual, as *Pan*, the second heaviest and largest quadruped in the study, does not differ significantly from macaques, which have the lowest body mass in the sample. Furthermore, for other diaphyseal locations and parameters, no such body-mass relation is evident. There is for instance no gradual relationship between CSG and body

mass and size is observable from largest to smallest primates, suggesting that factors other than body mass and size may play a more significant role in shaping the structural properties of these regions.

- 30 Concerning the overall cortical thickness distribution depicted by the thickness maps, African apes seems to share a cortical reinforcement on three locations in the proximal diaphysis with hylobatids but not with quadrupedal cercopithecoids. Then, the PCA of individuals' maps indicates that African apes are separated from macaques while they partially overlap with baboons on the first principal component. While all quadrupeds are grouped together when considering the second and third components of the PCA, the cluster they form also contains the hylobatids, restricting the functional interpretation. Finally, our results on both CSG and overall thickness distribution indicate that quadrupeds do not form a homogenous group in terms of femoral structural properties, contradicting our first prediction. Furthermore, distinctions within knuckle-walkers and plantigrade quadrupeds invalidate our second prediction as well.
- 31 In humans, our results on CSG indicate that bending rigidity and shape (but not particularly %CA) appear to be differentiated from all other groups as predicted, particularly at midshaft, by being anteroposteriorly oriented. However, while anteroposterior cortical reinforcement is documented in all extant humans of all chronological periods (Ruff, 2018), it is absent in other bipedal groups such as Neanderthals and other Pleistocene hominins (e.g. Trinkaus & Ruff, 2012; Puymerail *et al.*, 2012b; 2013; Rodríguez *et al.*, 2018; Chevalier & de Lumley, 2022). Thus, it is also difficult to directly link anteroposterior bending rigidity in humans to their bipedal locomotion alone (as it is for mediolateral bending rigidity among quadrupeds). It is even possible that this trait is a peculiarity of *Homo sapiens* within human and non-human primates. Concerning the pattern of cortical distribution depicted by the thickness maps, humans also clearly differ from all non-human primates of the sample, probably impacted by a prominent linea aspera and a true pilaster. These features considerably contribute to shape the posterior diaphysis particularly by increasing anteroposterior bending rigidity. Finally, our results confirm our prediction of a biomechanical specificity of the human femoral diaphysis, which is the only biped sample and whose structural properties are distinct from all other groups, although this feature may not be directly related to bipedalism.
- 32 Concerning the hylobatids, the structural properties of their femoral diaphysis share similarities with all the other primates in the sample, regardless of their locomotor behavior. Our results, both in terms of CSG and overall cortical distribution pattern, invalidate our prediction of distinct structural properties among brachiators. According to Carlson and colleagues (2006), it is possible that the orientation of cross-sectional cortical distribution and the cross-sectional shape need a certain amount of mechanical stimuli to be significantly modified and that some specific locomotor modes may not reach these requirements. In the case of hylobatids, one can argue that the mechanical demands associated with brachiation and suspensory behaviors that predominantly load the upper limb may not reach the level of stress required to significantly alter the structural properties of the femur. This would result in a circular femoral diaphysis with little distinguishable internal structure and intermediate characteristics, as our results seem to indicate. However, previously published data on *Pongo*, which also engage mainly in brachiation and suspensory behaviors (e.g.

Sugardjito & Van Hooff, 1986; Thorpe & Crompton, 2006), indicate increased mediolateral bending rigidity and not intermediate values as in hylobatids (Nadell, 2017; Nadell *et al.*, 2021). As mentioned by Nadell and colleagues (2021), it seems therefore challenging to conclude about a significant role of locomotion in shaping the femoral structural properties in arboreal apes.

4.1.2 Cortical thickness distribution: a phylogenetic partition in non-human primates?

- 33 Both CSG and overall cortical bone distribution pattern depict a separation between humans and non-human primates. Thus, the locomotor signal might seem predominant in humans, as they are the only biped group, although this interpretation tends to be tempered by the structural differences between the femora of *Homo sapiens* and those of other bipedal hominins. However, in non-human primates, the locomotor signal seems far from evident. It is therefore likely that the biomechanical signal associated with quadrupedalism or with suspensory behaviors is relatively low in shaping femoral structural properties. Within the non-human primates, the analysis of overall cortical thickness distribution groups cercopithecoids on the one hand and hominoids on the other. This distinction can be interpreted as a phylogenetic signal rather than a functional one, since the hominoid cluster gathers both knuckle-walkers and brachiators.
- 34 Previous studies have already proposed that femoral biomechanical properties are largely dependent on non-functional factors and have particularly highlighted the genetic influence on the structural properties of long bones. For instance, Hansen and colleagues (2009) stated that genetics accounts for 15% to 23% of the total phenotypic variance in baboon femoral CSG at midshaft. Other studies by Morimoto and colleagues depicted that chimpanzees exhibit more similarities in their femoral shaft structure and morphology with humans than with gorillas, and claimed for a strong phylogenetic signal (Morimoto *et al.*, 2011a; 2012). They stated that "caution is thus warranted when inferring locomotor behavior from the surface topography of the proximal femur of fossil hominins, as the morphology of this region may contain a strong phyletic signal that tends to blur locomotor adaptation". Concerning our study, it is not clear if chimpanzees exhibit more similarities with humans than with gorillas. However, it is likely that phylogeny impacts the cortical thickness distribution at least in non-human primates and "tends to blur locomotor adaptation" (Morimoto *et al.*, 2011a).

4.2 An approach on the entire diaphysis

4.2.1 Advances

- 35 Our approach aimed to compare the CSG on the entire diaphysis rather than on few discrete locations. For instance between *Pan* and *Gorilla* genera, our results confirm previous results about distinctions in bending rigidity and shape in the mid-distal and midshaft regions (Carlson, 2005; Nadell *et al.*, 2021), but also add that these distinctions extend until the mid-proximal region. Concerning the distinction between hominoids and cercopithecoids, some previous work indicated that femoral CSG in gorillas overlap extensively with monkeys at midshaft (Ruff, 2002a), while others pointed out significant distinctions between macaques and all hominoids in femoral distal and

midshaft (Nadell *et al.*, 2021). Our results demonstrate that the values of I_x/I_y , depicting femoral bending rigidity orientation in *Gorilla* but also in *Pan* is closer to those observed in macaques depending on which diaphyseal region is considered (distal for *Gorilla*, midshaft for *Pan*), but not with those of baboons. Although they can generally be considered as quadrupeds, our approach highlights that cercopithecoids do not form a homogeneous group in terms of CSG, as shown by the differences we observe between baboons and macaques.

- 36 Previous studies that also focused on the entire femoral diaphysis indicated limited impact of locomotor behaviors. For instance, a study of the ontogeny of the diaphyseal shape in chimpanzees and gorillas highlighted distinct ontogenetic trajectories despite similarities in locomotion during their respective development, but also a distinct trajectory in orangutans supporting a taxon-specific pattern (Morimoto *et al.*, 2018). Furthermore, the study of the entire diaphysis in captive and wild chimpanzees indicates similar CSG despite distinct locomotor behaviors (Morimoto *et al.*, 2011b), while opposite results have been highlighted when studying few discrete locations in captive and wild gorillas (Canington *et al.*, 2018). Finally, interpretations can be directly dependent on the approach, which leads to some limitations.

4.2.2 Limits

- 37 Our approach and results do not allow us to define an equivalence between specific locomotor behaviors and the structural properties of the femoral diaphysis, but highlight the wide variation in these properties between several primates, whether their locomotion is similar or not. While phylogenetic relationships seems a reliable interpretation regarding cortical thickness distribution in non-human primates, our results on CSG support a genus-specific pattern in catarrhines (see Morimoto *et al.*, 2018). Our study then brings attention to the conflicting outcomes between analysis of classic CSG parameters and cortical thickness maps analyses, notably exemplified by our results on gorillas which are in central position in the PCA and differ from all groups in terms of CSG. This contradiction suggests potential limitation in the accuracy with which CSG describe the cortical distribution in the diaphysis.
- 38 Other alternative proxies, such as the ratio of forelimb to hindlimb CSG, may provide a more suitable approach for inferring locomotor behaviors, particularly for assessing the degree of arboreal-related behaviors such as leaping or climbing at both intra- and interspecific levels (e.g. Schaffler *et al.*, 1985; Ruff, 2013; Sarringhaus *et al.*, 2016; 2022). Nevertheless, this approach suffers from limitations due the presence of topographic features of the deltoid tuberosity that disturb CSG measurements at proximal and midshaft humeral locations (Ibáñez-Gimeno *et al.*, 2013; Patel *et al.*, 2013). Furthermore from a paleoanthropological point of view, inferences from this approach on fossils are limited to very few specimens due to the lack of associated bone remains in the fossil record (e.g. Ruff, 2008; 2009; Ruff *et al.*, 2016).
- 39 Finally, the main explanation stands in that the structural properties of long bones represent only one modality of adaptation to mechanical stress. External skeletal morphology also exhibits adaptations that are strongly linked to locomotor behaviors (e.g. Nakatsukasa, 1994; Tardieu, 1994; Marchal, 2000; Berge, 2002; Nakatsukasa & Hayama, 2003; Lovejoy, 2005; Tardieu *et al.*, 2006; Kimura, 2021; Marchi *et al.*, 2022). Internal structural properties are most certainly integrated into this external

morphology that binds them and which they in turn influence (Ruff, 1995; Cosnefroy *et al.*, 2024). The study of integration of both level may be of particular interest in the evaluation of locomotor-related adaptations of the skeleton.

5 Conclusion

40 In this study, we explored the structural properties of the entire femoral diaphysis among catarrhine primates with the hypothesis that these properties would reflect the documented differences in their respective locomotion. Our results indicate that humans differ from all other non-human primates both in terms of cross-sectional properties and cortical thickness distribution. However, this singularity is difficult to interpret as a locomotor signal since it seems to be unique to bipeds considering the paleoanthropological record. In non-human primates, cross-sectional properties do not align with expectations based on locomotor behavior and depict a genus-specific pattern. Moreover, the cortical thickness distributions in non-human primates indicate that the locomotor signal seems to be overtaken by phylogenetic relationships, as knuckle-walker apes show more similarities with hylobatids than with quadrupedal cercopithecoids. We invite caution in reconstructing models of fossil locomotor behavior from the biomechanical study of the femoral diaphysis only, without integrating data from the upper limb or the morphology of the appendicular skeleton as a whole.

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Conflicts of interest

42 The authors have no conflicts of interest to declare.

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ABSTRACTS

The interpretation of hominin locomotor behaviors, which is largely based on actualism, implies a clear understanding of form-function relationship between the biomechanics of the skeleton and the locomotor behaviors of extant primates. In this study, we tested this relationship by measuring the structural properties of 127 femoral diaphyses from six genera and 10 species of catarrhine primates whose locomotor behaviors are well documented. The structural properties were assessed on the entire diaphysis via cross-sectional geometry properties including relative cortical area (%CA) and cross-sectional bending rigidity and shape (I_x/I_y and I_{max}/I_{min}), as well as the pattern of overall cortical bone distribution (cortical thickness maps). Concerning cross-sectional properties, our results highlight marked differences in CSG along the femoral diaphysis of locomotor-related groups such as knuckle-walker African apes and quadrupedal cercopithecoids. Humans seem to be distinctive in their anteroposterior bending rigidity, especially at midshaft, while brachiator hylobatids differ very little from all other groups. Concerning overall cortical bone distribution, humans differ from non-human primates. In the latter, a hominoid-cercopithecoid partition supports previously reported influence of phylogeny rather than locomotor behaviors in shaping the structural properties of the femoral diaphysis. Caution is therefore needed when inferring locomotor behavior in fossils solely based on femoral structural properties.

L'interprétation des comportements locomoteurs des hominines, largement basée sur le principe d'actualisme, implique une compréhension claire de la relation forme-fonction existant entre la biomécanique du squelette et les comportements locomoteurs des primates actuels. Dans cette étude, nous avons testé cette relation en mesurant les propriétés endostructurales de 127 diaphyses fémorales provenant de six genres et de dix espèces de primates catarrhiniens, dont les comportements locomoteurs sont documentés. Les propriétés endostructurales ont été mesurées sur la totalité de la diaphyse par le biais des paramètres de géométrie de section, notamment l'aire corticale relative (%CA), la rigidité à la flexion et la forme des sections (I_x/I_y et I_{max}/I_{min}), ainsi que le modèle de distribution de l'os cortical (cartographies d'épaisseur corticale). Concernant les paramètres de géométrie de section de la diaphyse fémorale, nos résultats mettent en évidence des différences marquées entre des groupes dont la locomotion est proche, tels que les grands-singes africains knuckle-walkers et les cercopithécoïdes quadrupèdes. Les humains semblent se distinguer par une rigidité à la flexion orientée antéropostérieurement, en particulier à mi-diaphyse, tandis que les hylobatidés brachiateurs diffèrent très peu des autres groupes. Concernant le modèle de distribution de l'os cortical, les humains diffèrent des primates non-humains. Chez ces derniers, une distinction entre hominoïdes et cercopithécoïdes confirme une influence de la phylogénie plutôt que des comportements locomoteurs dans la modulation des propriétés endostructurales de la diaphyse fémorale, comme rapporté par de précédents travaux. Il convient donc d'être prudent lorsque des comportements locomoteurs de fossiles sont déduits uniquement sur la base des propriétés endostructurales du fémur.

INDEX

Mots-clés: Géométrie de section, biomécanique, locomotion, primates

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