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Calcar femorale variation in extant and fossil hominids: Implications for identifying bipedal locomotion in fossil hominins.

Abstract

The calcar femorale is an internal bony structure of the proximal femur considered to be functionally related to bipedal locomotion. Among extant primates, the presence of a calcar femorale has been so far documented in extant humans and *Pan* and, among extinct hominins, in the late Miocene *Orrorin tugenensis*, in a Pliocene *Australopithecus*, and in a Middle Pleistocene *Homo* specimen. Using high-resolution microcomputed tomography, we investigated the occurrence, 3D morphology, and size variation of the calcar femorale in an adult sample of extant humans, *Pan troglodytes*, *Gorilla gorilla*, *Pongo* sp., and *Papio ursinus*. We also investigated the occurrence of a calcar femorale for the first time in the adult proximal femoral remains of a late Miocene great ape (*Rudapithecus*) and five Plio-Pleistocene hominins from Southern and Eastern Africa (*Australopithecus* and *Paranthropus*). We took four measurements: periosteal-to-tip maximum length; maximum length excluding cortical thickness; maximum vertical height; and the distance between the most anterior and posterior limits of the root. To allow for intergeneric comparisons, estimated body size was used to standardize all measurements. Nine of 10 extant humans have a well-developed calcar femorale. Among the African apes, 6/10 *Pan* and 6/10 *Gorilla* also show a distinct calcar femorale. In *Pongo* (*n* = 9), it is only present in one captive individual. none of the five investigated *Papio* specimens show any trace of this structure. Only calcar femorale height, which is systematically taller and extends into the lower part of the lesser trochanter, discriminates humans from extant great apes, except for one *Gorilla*. The calcar femorale was absent in one *Paranthropus robustus* and variablydeveloped in all other investigated fossils. These results indicate that this structure cannot be considered as a diagnostic feature of habitual bipedal locomotion and emphasizes the need for further investigations on its functional role.

Keywords: Proximal femur; Extant great apes; Fossil hominins; X-ray microtomography; Internal bone structure

1. Introduction

The calcar femorale (CF) is an osteological feature described in a typical, healthy human femur as a vertical to slightly oblique spur of thickened bone within the femoral neck (Fig. 1). It extends typically from the inferolateral endosteal margin of the femoral neck, posterior to the neutral axis, laterally and distally towards the greater trochanter (Griffin, 1982; Adam et al., 2001; Le Corroller et al., 2011). The CF was illustrated for the first time in a mid-19th century human anatomical atlas (Pirogovs, 1853, cited by Glinkowski and Ciszek, 1989). Since then, the gross morphology and possible functional significance of the CF, especially in relation to bipedalism, have been discussed in several anatomical studies (e.g., Merkel, 1874; Bigelow, 1875; Dixon, 1910; Harty, 1957; Griffin, 1982; Stiles et al., 1990; Hammer, 2019) and increasingly considered in clinical research, particularly in relation to osteoporosis and osteoarthritis (e.g., Le Corroller et al., 2011; Thakkar et al., 2015; Tetsunaga et al., 2017; Sas et al., 2019; Zha et al., 2019).

The CF is thought to be related to the load created by the insertion of the iliopsoas tendon on the lesser trochanter (Cunningham et al., 2016) and experimental and clinical studies have identified that it provides additional mechanical strength for weight transmission (Li and Aspden, 1998; Zhang et al., 2009). The CF is proximally rooted at the region of bending of the neck-shaft arch and therefore is thought to act as a transitional structure for load transfer through the hip joint and to prevent the posterior and medial regions of the proximal femur from suffering overload (Farkas et al., 1948; Li and Aspden, 1997, 1998; Gao et al., 1999; Wang et al. 2005; Zhang et al., 2009; Hammer, 2019). In addition, it is architecturally connected with the vertical and the trochanteric trabecular bundles (Aiello and Dean, 1990). The vertical bundle arises from the superior aspect of the head and radiates inferolaterally towards the inferior cortex of the femoral neck, while the trochanteric bundle radiates towards the medial cortex of the shaft by forming a ‘Gothic arch’ at the intersection with the arcuate bundle (see Cazenave et al., 2021: Figure 6; Kapandji, 2006). These bundles reflect compressive and tensile stress trajectories through the human femoral neck created by axial compressive and bending loads (Kapandji, 2006; Levangie and Norkin, 2011). it is thought that the presence of a CF connected to the two bundles contributes to the strength of the base of the femoral neck in resisting these loads (Newell, 1997; Wroblewski et al., 2000; Hammer, 2010, 2019; Cunningham et al., 2016). However, morphostructural variability in the CF in extant humans has been reported across multiple age cohorts. In addition to the occasional absence of this spur of thickened bone in both adult males and females, the CF can vary in shape and dimension, most notably in how far it penetrates within the lesser trochanter and the degree of intra-individual bilateral asymmetry (e.g., Thompson, 1907; Garden, 1961; Kuperavage, 2009; Hammer, 2010, 2019; Le Corroller et al., 2011; Kuperavage et al., 2018).

Experimental analyses have demonstrated that, within the limits imposed by a phylogenetically-determined adaptive *Bauplan* and the influence of a number of biological factors (e.g., Lovejoy et al., 1999; Judex et al., 2004; Demissie et al., 2007; Havill et al., 2007, 2010; Bonewald and Johnson, 2008; O'Neill and Dobson, 2008; Cunningham and Black, 2009; Estrada et al., 2012; Reissis and Abel, 2012; Wallace et al., 2012, 2020; Medina-Gomez et al., 2018; Hou et al., 2020), cortical bone thickness distribution and trabecular structure can adapt to the site-specific mechanical loading environment to resist local stresses (e.g., Lanyon, 1973; Skerry and Lanyon, 1995; Biewener et al., 1996; Guldberg et al., 1997; Mori et al., 2003; Mittra et al., 2005; Pontzer et al., 2006; Carlson and Judex, 2007; Chang et al., 2008; Polk et al., 2008; Barak et al., 2011; Wallace et al., 2013; Cresswell et al., 2015; Vera et al., 2020). Importantly, several studies have found that variation in cortical and/or trabecular bone structure at different skeletal sites is consistent with predicted differences in locomotor-related loadings in humans and other primates. Indeed, although the link between the endostructural architecture of the proximal femur and the load transfer and dissipation is more complex than assumed by the first mechanical models (e.g., Fajardo et al., 2007; Ryan and Walker, 2010; Shaw and Ryan, 2012), trabecular bone variation in the primate femoral head has provided evidence for structural differences across locomotor groups and has identified unique features in humans related to habitual bipedalism (Fajardo and Müller, 2001; MacLatchy and Müller, 2002; Ryan and Ketcham, 2002a, b, 2005; Ryan and Krovitz, 2006; Saparin et al., 2011; Ryan and Shaw, 2012, 2015; Raichlen et al., 2015; Ryan et al., 2018; Tsegai et al., 2018a; Georgiou et al., 2019). Similarly, the asymmetrical distribution of cortical bone thickness within the femoral neck compartment, resulting from an absolutely thinner superior cortex and a thicker inferior cortex, has been shown to characterize bipedal humans and quadrupedal primates, reflecting their distinct stereotypical loadings at the hip joint (Lovejoy, 1988, 2005; Ohman, 1993; Ohman et al., 1997; Rafferty, 1998; Lovejoy et al., 2002; Ruff and Higgins, 2013; Ruff et al., 2016; Cazenave et al., 2019; Pina et al., 2019). However, compared to the femoral head and neck, other anatomical regions of the proximal femur have received far less attention in extant humans and other primates (Miller et al., 2002; Cazenave et al., 2021).

In nonprimate animals, the CF was found to be absent in small samples of hens, dogs, and pigs (Glinkowski and Ciszek, 1989). Among primates, the presence of a CF has so far only been investigated in a sample of 10 rhesus macaques, where it was reportedly absent in all individuals (Glinkowski and Ciszek, 1989), and in chimpanzees, where it was identified in 7/10 individuals (Kuperavage et al., 2018). However, in chimpanzees, the CF was found to be distinguishable from the human condition both because of its lower occurrence and because of its more limited vertical extension within the femoral neck (Kuperavage et al., 2018). Recently, it has been reported that "some *Gorilla* specimens at least also exhibit a calcar femorale (e.g., KUPRI 1492 on the Kyoto University Digital Morphology Museum site [pers. commun. to R.H.C. from Adam Kuperavage])" (Crompton et al., 2021, in press), but neither quantitative evidence nor images have been provided.

Because of the presumed mechanical relationship of the CF to bipedalism, its occurrence has also been investigated in some early fossil hominins (White, 1984; Grine et al., 1995; Kuperavage et al., 2018). The presence of a CF was reported in the late Miocene *Orrorin tugenensis* (BAR 1002'00 and 1003'00; Kuperavage et al., 2018) and, because of its relative vertical extension, has been invoked to support the inference of bipedal locomotion in this taxon (Senut et al., 2001; Pickford et al., 2002). A CF has also been identified in an *Australopithecus* specimen (MAK-VP-1/1; White, 1984; see also Reed et al., 1993) and in a Middle Pleistocene *Homo* specimen (Berg Aukas; Grine et al., 1995). However, no study has yet evaluated the occurrence (i.e., presence or absence) of the CF in any extinct nonhuman hominid.

Given the variability in occurrence and morphology, and dimension of the CF observed in extant humans, the very limited data for extant nonhuman primates, and the lack of information on this feature in extinct hominids, a more detailed consideration of the CF in extant and fossil primates may provide greater clarity on its functional significance and whether there are unique aspects of this feature that could potentially be related to bipedalism.

To address these knowledge gaps, we use high-resolution microcomputed tomography (μCT) to evaluate and compare CF occurrence and 3D morphology (i.e., shape, location, extension within the lesser trochanter, absolute and standardized vertical height and horizontal length, and root width) in adult femora representing extant humans, extant great apes (*Pan*, *Gorilla*, and *Pongo*), and one species of cercopithecine monkey (*Papio*). We then evaluate CF occurrence and morphology in the adult femoral remains of a late Miocene great ape (*Rudapithecus*) and five Plio-Pleistocene hominins from Southern and Eastern Africa representing *Australopithecus* and

Paranthropus. We expand on previous studies by not only assessing CF occurrence and morphology in a broader taxonomic primate sample, but also by quantifying additional aspects of the CF, i.e., CF length excluding the cortex to assess the influence of variation in cortical bone thickness, and CF maximum vertical height and root thickness to determine whether the degree of expression of such parameters is unique to habitual bipeds. Based on the body of evidence available so far, we hypothesize that (i) extant humans and great apes differ in CF occurrence and morphology, and both differ from the pattern observed in *Papio*; (ii) extinct hominins are more similar in CF occurrence and morphology to that of extant humans compared with other extant apes, and (iii) the Miocene ape *Rudapithecus* is most similar to the CF morphology to extant nonhuman apes. Below we outline our predictions.

Assuming the CF is primarily, though not necessarily uniquely, related to mechanical loading during (whatever form of) bipedal locomotion (Farkas et al., 1948; White, 1984; Reed et al., 1993; Grine et al., 1995: Kuperavage et al., 2018; Hammer, 2019), and given the results of human and *Pan* comparisons presented in Kuperavage et al. (2018), we predict that the CF will be more frequently expressed, absolutely and relatively longer, more vertically extended and characterized by a thicker root in our sample of extant humans compared to the extant ape samples.

Although extant nonhuman great apes differ in their type and frequency of locomotor and postural behaviors (primarily knuckle walking in the African apes vs. specialized suspensory behaviors in orangutans; e.g., Hunt, 1991; Doran, 1996; Thorpe and Crompton, 2006; see also for a review), they share a higher degree of hip joint mobility with enhancement of abduction and lateral rotation movements (Isler and Thorpe, 2003; Hammond, 2013; Finestone et al., 2018). Moreover, nonhuman great apes show similar patterns of trabecular bone distribution within the femoral head (Ryan and Shaw, 2012; Georgiou et al., 2019) and of cortical and trabecular bone arrangement at the neck/shaft junction that *Pan*, *Gorilla*, and *Pongo* experience generally comparable load transfer at the hip joint (Rafferty, 1998; Cazenave et al., 2019; Pina et al., 2019). We therefore predict a similar degree of development of the CF (i.e., occurrence, shape, extension into the lesser trochanter, absolute and relative vertical height, length and root width) within the three nonhuman great apes. In contrast, *Papio*, which engages primarily in terrestrial, pronograde quadrupedal walking and running (Rose, 1977) has a lower hip joint mobility than that of great apes (Hammond, 2013), which is reflected in a more asymmetrical femoral neck cortical distribution (Rafferty, 1998; Pina et al., 2019). Thus, we predict that the CF should not be present in *Papio.*

Australopithecines are considered habitual bipeds when terrestrial (Ward, 2013) and, although likely somewhat distinct from humans in their bipedal biomechanics and loading environment at the hip joint (e.g., Ruff and Higgins, 2013; Ryan et al., 2018; Cazenave et al., 2019, 2021), are thus expected to express a CF configuration (i.e., occurrence, shape, extension into the lesser trochanter, absolute and relative vertical height, length and root width) similar to the extant human condition. In contrast, *Rudapithecus*, the only fossil ape representative analyzed in this study, has postcranial morphology suggesting frequent use of forelimb-dominated suspensory behaviours (Morbeck, 1983; Begun, 1993; Kivell and Begun, 2009; Ward et al., 2019; Almécija et al., 2021). Thus, if a CF is present in *Rudapithecus*, we expect its morphology to be most similar to that of extant nonhuman great apes.

2. Materials and methods

2.1. Samples

Our extant primate sample consists of 44 femora from adult males and females of modern humans (*n* = 10), *Pan troglodytes* (*n* = 10), *Gorilla gorilla* (*n* = 10), *Pongo* sp. (*n* = 9), and *Papio ursinus* (*n* = 5). All specimens were free from obvious signs of pathology. All nonhuman primate specimens were wildcaught, with the exception of two captive *Pongo* specimens. six *P. troglodytes* and one *Pongo* specimens were of unknown provenance. Details of the extant sample composition are provided in Supplementary Online Material (SOM) Table S1.

We included one fossil great ape specimen representing *Rudapithecus hungaricus* (RUD 234) from the late Miocene site of Rudabánya (Hungary), housed at the Mining and Geological Survey of Hungary, Budapest (Begun et al., 2012; Ward et al., 2019; SOM Table S2). The Plio-Pleistocene hominin sample includes the following specimens: StW 99 and 367 from Sterkfontein Member 4, South Africa, both attributed to *Australopithecus africanus* and curated at the Evolutionary Studies Institute of the University of the Witwatersrand, Johannesburg, South Africa (Harmon, 2009; Ruff and Higgins, 2013; Zipfel et al., 2020; Pickering et al., 2021); SK 97 from Swartkrans Member 1, South Africa representing *Paranthropus robustus* curated at the Ditsong National Museum of Natural History, Pretoria, South Africa (Robinson, 1972; Susman et al., 2001; Cazenave et al., 2019, 2021); and KNM-ER 738 and 1465 from Koobi Fora, Kenya, both likely representing *Paranthropus boisei* curated at the National Museums of Kenya, Nairobi (Wood and Costantino, 2007; Wood and Leakey, 2011; Ward et al., 2015; Ruff et al., 2016; SOM Table S2). We also assessed additional fossil specimens including four Miocene apes (including one *Dryopithecus fontani*, two *Hispanopithecus laietanus* and another *R. hungaricus* femora) and five Plio-Pleistocene hominins (representing three additional *A. africanus*, one *P. robustus* and one *P. boisei* or *Homo* sp.); however, their poor internal preservation prevented the possibility to reliably quantify potential CF morphology (SOM Table S2; SOM Fig. S1).

2.2. Microcomputed tomography

Details on the different microtomographic (µCT) equipment and the scanning resolutions are provided in SOM Tables S1 and S2 for the extant and the fossil specimens, respectively. Four individuals of the extant human sample and one *Pan* femur were scanned using a Nikon XT H225/320L industrial XCT system at the Evolutionary Studies Institute of the University of the Witwatersrand (Johannesburg, South Africa) using 70 kV, 120 µA, and 2000 projections. The remaining human specimens and one *Papio* specimen were scanned at the microfocus X-ray tomography facility (MIXRAD) of the South African Nuclear Energy Corporation SOC Ltd (Necsa, Pelindaba), using a Nikon XTH 225 ST (Metris) equipment and 100 kV, 100 µA, and 1000–2000 projections. Seven *Pan* specimens were scanned at the AST-RX: X-ray tomography technical platform by the v|tome|x L 240–180 equipment housed at the Muséum National d'Histoire Naturelle (Paris, France) using 100 kV, a current ranging from 500 to 610 µA, and 2400–2900 projections. The two remaining *Pan* specimens, the *Pongo* sample, and all fossil specimens were scanned with the BIR ACTIS 225/300 industrial microfocus X-ray tomography scanner at the Department of Human Evolution in the Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany), using 130–140 kV, 100–140 µA, and 2500–2790 projections. the *Gorilla* sample was scanned with a Nikon XT 225 ST Metris scanner at the Cambridge Biotomography Centre of the Department of Zoology, University of Cambridge (Cambridge, UK) at 145–170 kV, 110–160 µA, and 2000 projections. Details about the scanning procedures used to image the additional nine fossil specimens that were excluded from the study due to poor preservation are provided in SOM Table S2.

Femur size varied greatly across our comparative sample, ranging from the smallest *Papio* to the largest *Gorilla*. thus, scan resolution varied as well due to the constraints of the μCT systems and taking into account the specific geometric characteristics of the analytical platforms. The resolution range for each taxonomic sample was as follows: humans, 50–70 μm; *Pan*, 30–80 μm; *Gorilla*, 45–75 μm; *Pongo*, 28–29 μm; *Papio*, 45–67 μm. The fossil specimens were scanned at resolutions ranging from 30 to 91 μm (SOM Table S2).

Previous quantitative analyses of the CF in humans and *Pan* indicate that, when present, this spur of thickened bone measures several centimeters vertically and transversely (e.g., Kuperavage, 2009; Le Corroller et al., 2011; Tetsunaga et al., 2017; Kuperavage et al., 2018). Accordingly, potential measurement bias of the CF due to differences in μCT resolution or technical differences across scanning facilities is negligible (for comparative measurements of the μ-scale sized trabecular struts see Cazenave et al., 2021). For instance, if we consider a CF length of 7.76 mm in a *Pan* individual scanned with a resolution of 80 μ (i.e., the lowest resolution used in the present study), a measurement error of 1 pixel would represent only 1.03% of the length of the CF (i.e., 0.08 mm).

All specimens were virtually rotated to the same anatomical position in Avizo v. 9.0.0 (Visualization Sciences Group Inc., Bordeaux) by using the neck axis and the principal axis of the proximal shaft portion as anatomical references. Left-side specimens were flipped so all specimens were analyzed as right femora.

2.3. Measurements and analyses

To assess the occurrence and, when present, the variation in morphology of the CF across our sample, we placed a transverse cross section at the level of the upper margin of the lesser trochanter and then virtually moved proximally towards the dorsomedial neck region and distally across the lesser trochanter. When the presence of the CF was identified, we placed a parasagittal cross section at the level of the center of the lesser trochanter and virtually moved mediolaterally to delimit the extent of the CF. In the specimens showing at least a trace of the bony spur, we characterized the shape of the CF according to the three categories established by Le Corroler et al. (2011): ranging from (1) a relatively short and thick ridge-like CF; (2) a spur-type CF or, (3) a relatively thin and long septum-like CF.

To test our predictions of a longer and more vertically extended CF with a wider root in extant and fossil hominins compared with the extant and fossil great apes, and of a similar degree of development (i.e., vertical extension, absolute and relative vertical height and length, and root width thickness) among the great ape taxa, we automatically segmented the cortex from the trabecular bone using the software Dragonfly v. 2020.2.0.941 (Object Research Systems Inc., Montreal) and the method developed by Buie et al. (2007). The CF was virtually extracted from the cortex for 3D rendering. Due to preservation, the CF from fossil specimens could not be automatically segmented and was completed manually instead. We first qualitatively compared the extent of the CF into the lesser trochanter and we took the following CF measurements: maximum length, maximum vertical height and maximum root width.

We used two methods to assess CF maximum length. In all extant specimens, the distance between the periosteal surface and the most internal point (the tip) of the CF (PT MaxLength) was automatically computed using the ‘Surface Distance’ module in Avizo v. 9.0.0 and then rendered in 3D using a chromatic scale where the outer contour-tip distance increases from dark blue (thin) to red (thick; Fig. 2a). However, for the six fossil specimens, we could not automatically quantify the distance from the periosteal surface due to poor preservation. In these specimens, we used a second method and manually measured CF maximum length (CF MaxLength) from the base lying on the endosteal contour (the root) to the tip of its most lateral extension, thus excluding the cortical thickness (Fig. 2b). Given that multiple factors have been shown in humans to affect cortical thickness variation through life (e.g., Gocha and Agnew, 2016), we also quantified the CF MaxLength (length excluding the cortical bone) in all extant specimens for direct comparison with the fossil specimens. We found a high Spearman's rank correlation coefficient between PT MaxLength and CF MaxLength across the extant sample ($r = 0.91$, $p < 0.0001$).CF maximum vertical height (CF MaxHeight) was measured as the projective maximum distance between the uppermost and lowest extracted slices bearing evidence of a CF-related spur of thickened bone, i.e., between the parallel planes orthogonal to the principal axis of the proximal shaft where the CF merges with the cortical bone of the posterior wall of the neck and the endosteal surface of the posterior wall of the diaphysis, respectively (Fig. 2c). Finally, in all cases where the most anterior and posterior limits of the CF root on the endosteal contour were clearly identifiable (in 18 individuals), we also measured maximum CF root width on the related transverse cross section (Fig. 2d).

To allow for comparisons among extant taxa that differ in body size, all measurements were standardized by body mass. Body mass was estimated for each extant individual using the superoinferior diameter of the femoral head and the equations provided in Ruff et al. (2018) for the extant human sample and in Burgess et al. (2018) for the extant great ape taxa. Interspecific comparisons were completed on both the absolute and standardized mean values of each taxon. However, due to poor preservation of the femoral head, measurements of the fossils could not be standardized. Thus, all fossil results are presented and compared as absolute values only.

Given that the cortical bone thickness of the base of neck in extant apes and New Word monkeys has been shown to be influenced by local loading conditions (Ohman, 1993; Ohman et al., 1997; Rafferty, 1998), we additionally tested, in the margin of our main goal, whether the size of the CF correlates with the variation in cortical thickness at this specific site. We measured cortical bone thickness (CBT) at the level of the most anterior (CBTa) and most posterior (CBTp) limits of the CF root in our extant sample (SOM Fig. S2) and used the average between the two (CBTa and CBTp) as our estimate of CBT. we tested the possible influence of CBT variation on the CF parameters (i.e., CF length, vertical height, and root width) using a partial Spearman's correlation test controlling for body mass between CBT and each CF measurement. We also tested for the human, *Pan* and *Gorilla* samples the possible influence, within each species, of the body mass on the CF length and vertical height using Spearman's correlation test. Given the sample size, we could not test the possible influence of body mass on the CF root width or on the CF parameters in *Pongo*.

All measurements used in this study were taken by one observer (M.C.). to examine the accuracy of the non-automated variables (i.e., the CF MaxLength and the CF MaxHeight) another observer measured them in 50% of the specimens and intra and interobserver tests, calculating the intraclass correlation coefficient (ICC) between the two sets of measurements, have been run. The results show an intraobserver ICC of 0.98 and 0.99 and an inter-observer ICC of 0.78 and 0.85 for CF MaxLength and CF MaxHeight, respectively, which indicate high reproducibility of the measurements. No interobserver tests were performed for CF root width, but repeated intraobserver measurements provided a highly satisfactory ICC of 0.93.

All plots and Statistical analyses were performed in RStudio v. 1.2.5033 running with R v. 3.4.4 (R Core Team, 2018). Plots were generated using ggplot2 (Wickham, 2009). Due to small sample sizes, only nonparametric tests were performed. The significance of the interspecific differences in PT MaxLength, CF MaxLength, and CF MaxHeight (both absolute and standardized values) were tested using the pairwise Wilcoxon rank sum test (level of significance defined at p-value = 0.05). Given the small sample size, interspecific differences in maximum CF root width could not been carried out and males and females have been combined for the analyses.

3. Results

3.1. Calcar femorale in The extant primate sample

Nine of the 10 extant humans (3 males and 6 females) showed the presence of a thick, ridge-like CF; a CF was absent in a 30–49 -year-old male (Fig. 3a). Among the great apes, 6/10 *Pan* (4 males and 2 females) and 6/10 *Gorilla* (4 males and 2 females) expressed a bony spur ranging from just a ridge-like trace of this spur to a distinct septum-like structure . In *Pongo*, a CF was unambiguously found in one of the two captive males (Fig. 3e; SOM Table S1) and A CF ridge-like structure was also present in one wild *Pongo* female (Fig. 3e). In contrast, none of the *Papio* specimens showed a CF or a CF-like structure (Fig. 3; SOM Fig. S3).

in all cases and taxa where the CF was present, the CF was located within the region spanning from the posteroinferior surface of the femoral neck to the lesser trochanter (Fig. 4). However, we observed intra- and interspecific variation in CF size, shape, and extent (both mediolateral and proximodistal). In nearly all cases, the CF progressively thinned medially towards the tip, where it merged into the surrounding trabecular network with a tree-like pattern (SOM Fig. S3). However, CF thickness and density were variable, with some individuals, most notably in humans, displaying a plate-like structure resulting from the merging of thickened trabeculae rather than a true spur of dense bone. In no case in our human sample did the CF extend to the posterior wall of the greater trochanter (Fig. 3; SOM Fig. S3). In some *Pan* and *Gorilla* (SOM Fig. S4), as well as in the *Pongo* individual displaying the CF (Fig. 3e), a variably-developed bone reinforcement emerging from the lateral margin of the lesser trochanter radiating medially towards the CF was observed in the transverse slices. We did not observe a similar feature in our sample of human femora.

In extant humans the CF systematically extended into the distal part of the lesser trochanter (Fig. 3). By contrast, in all *Pan*, 5/6 *Gorilla* and in the *Pongo* individual where it was unambiguously expressed, the distal end of the CF was typically confined to the proximal half of the lesser trochanter compartment, or occasionally near its middle portion. However, a typically human-like condition was found in one female *Gorilla*, whose distal extension was deep within the lesser trochanter (Fig. 3a; SOM Fig. S5).

Quantitative analyses revealed that humans had the absolutely greatest PT MaxLength, CF MaxLength, and CF MaxHeight (Fig. 5; Table 1). However, for PT MaxLength and CF MaxLength, *Gorilla* showed the greatest range of variation and also had the highest individual values. For all three variables, the differences between humans and *Pan* were statistically significant, while humans and *Gorilla* differed significantly only in CF MaxHeight (Fig. 5; SOM Table S3). *Pan* and *Gorilla* also differed significantly only in CF MaxHeight (Fig. 5; Table 1; SOM Table S3). Relative to body size, humans had significantly larger PT MaxLength and CF MaxLength compared with *Pan* and *Gorilla*, and significantly higher CF MaxHeight compared to *Gorilla* as well. The *Pongo* specimen values were closer to those of *Gorilla* or intermediate between *Pan* and *Gorilla* (Fig. 5; Table 1). Calcar femoral root width was absolutely larger in *Gorilla* (Fig. 2c) and narrower in the captive *Pongo* individual, the latter falling below the ranges of the other three taxa. However, the three great ape genera overlapped in both absolute and standardized values, with extant humans and *Gorilla* showing the greatest degree of overlap (SOM Table S4).

Spearman's correlation results revealed that PT MaxLength, CF MaxLength, CF MaxHeight, and CF root width were uncorrelated with CBT when controlling for body mass (SOM Fig.S3; SOM Table S5 and S6). PT MaxLength, CF MaxLength, and CF MaxHeight were also uncorrelated with estimated body mass (SOM Table S7) in extant humans, *Pan*, and *Gorilla*. There was however a significant positive correlation between CBT and PT MaxLength, which is not surprising given that this measurement includes the cortical thickness (SOM Table S6).

3.3. Calcar femorale occurrence in the fossil hominid sample

The CF was present in five of the six specimens comprising our fossil sample: RUD 234 (*Rudapithecus*), StW 99 and 367 (*A. africanus*), and KNM-ER 738 and 1465 (likely *P. boisei*; Fig. 6). Conversely, we observed no trace of a CF on the endosteal contour of SK 97 (*P. robustus*), although possible strengthening of the trabeculae projecting towards the greater trochanter could not be confidently ascertained because of the incomplete preservation in this specimen (Fig. 6;

SOM Fig. S6). Due to preservation quality, 3D rendering of the CF was possible only in RUD 234 and KNM-ER 738 (Fig. 7).

3.4. Comparison of the calcar femorale between the extant and fossil samples

In the five fossils exhibited a CF, the CF root width was broad, particularly in the two *A. africanus* specimens, overlapping with the *Pan* and *Gorilla* and broader than that of our extant human sample (SOM Fig. S7). Conversely, none of the fossils showed distinct evidence of a bony reinforcement at the lateral margin of the lesser trochanter comparable to that found in some *Pan* and *Gorilla* specimens, and in the *Pongo* individual displaying the CF (Fig. 3 and SOM Fig. S4).

RUD 234 showed a well-developed CF (Figs. 6 and 7), similar in structure to some *Pan* (Fig. 3; SOM Fig. S3) but extended more transversely. Indeed, CF MaxLength in RUD 234 slightly exceeded that of the CF in *Pongo* and fell within the upper end of the interquartile range of the *Gorilla* sample, outside of the range and well above *Pan*, and in the lower range of humans (Fig. 5; SOM Table S8). RUD 234 also had a longer CF MaxLength relatively to the other fossils. Its CF MaxHeight was found in the upper interquartile range of *Pan*, and was lower than the range of variation found in *Gorilla* and *Pongo*, as well as the other three fossils for which CF MaxHeight could be assessed (Fig. 5; Table 2; SOM Table S8).

StW 99 and StW 367 (*A. africanus*) both displayed a CF whose root was thicker than those of the other fossils and near the highest values documented in the extant hominids (SOM Fig. S7). However, their CF MaxLength was short, most comparable to that of *Pan*; StW 99 fell below the 25th percentile of *Pan* and in the lower end of the interquartile range of *Gorilla* while StW 367 fell below the 25th percentile of *Pan* and *Gorilla* (Fig. 5; SOM Table S8). In CF MaxHeight, StW 99 fell well within the upper end range of variation of *Gorilla* and the lower range of extant humans but well above the range of variation found in *Pan* (Fig. 5). The distal end of the CF in StW 99 was not confined within the proximal portion of the lesser trochanter but extended at least to its mid portion, as seen in humans.

In KNM-ER 738, CF MaxHeight fell within the lower range of variation for *Gorilla* and in the upper range for *Pan* (Fig. 5). In this specimen, the CF reached the upper region of the lesser trochanter (Fig. 7), while in KNM-ER 1465 the CF was longer and extended more distally (Fig. 5; SOM Table S8) similar to the condition found in StW 99.

4. Discussion and conclusions

This study explored the occurrence and, when present, 3D morphology of the CF in extant humans, other great apes, *Papio* and a sample of fossil hominids. We found that a CF is most commonly found in extant humans, but that there was substantial variation in CF occurrence and morphology across our sample, including within humans, building on previous studies calling into question the functional significance of the CF.

4.1. Extant hominoids

Based on previous studies (Farkas et al., 1948; White, 1984; Reed et al., 1993; Grine et al., 1995: Kuperavage et al., 2018; Hammer, 2019), we predicted that, compared to great apes, the CF in humans should be more frequently present and absolutely and relatively longer and more vertically extended, with a thicker root width. However, only its higher frequency (90% in humans vs. 60–65% in the *Pan* and *Gorilla* samples) and a CF absolute and standardized average height clearly distinguished humans from other extant hominids. Indeed, contrary to our expectation, no other quantitative CF variables measured in our study unambiguously discriminate between humans and great apes. Although our hominoid sample sizes were small (n = 9-10) and larger samples may provide greater discrimination in CF morphology across taxa, it is notable that we nonetheless found substantial intraspecific variability in each hominoid taxon, including humans. In addition, the extent to which geometric differences in the proximal femur (i.e., neck shaft angle, superoinferior length of the greater trochanter, projection of the head relative to the greater trochanter; Harmon, 2007) across hominoids contribute to the distal extension of the CF in humans requires further investigation.

Whatever the cause(s) responsible for the expression of a spur of vertically and transversely thickened bone within the femoral neck, and whatever its functional significance (Farkas et al., 1948; Li and Aspden, 1997, 1998; Gao et al., 1999; Wang et al., 2005; Zhang et al., 2009; Hammer, 2019), our results make clear that presence vs. absence of a CF does not distinguish humans from other great apes. Previous research has shown that the CF can exhibit variable shape and proportions in humans, including differences between left and right femora of the same individual (Le Corroller et al., 2011), and can be poorly expressed (Kuperavage et al., 2018) or absent, even in middle-aged adults (e.g., Thompson, 1907; Glinkowki and Ciszek, 1989). Such morphological variation was also observed in our extant human sample (e.g., one individual did not show any trace of a CF).

Additional comparative research on the ontogeny of CF expression in humans and extant apes would provide much-needed information on when the CF first appears during growth and patterns of age-related strengthening, notably with respect to the onset of independent locomotion, an approach which has already provided valuable information when applied to the endostructural organization of the proximal femur (e.g., Ryan and Krovitz, 2006; Raichlen et al., 2015; Milovanovic et al., 2017; Tsegai et al., 2018b). In this context, the role of a growing iliopsoas tendon in the ontogeny of CF (Cunningham et al., 2016) should be specifically investigated given that, in humans, the CF is thought to be related to the load created by the insertion of this musculotendinous complex (Tatu et al., 2002) on the lesser trochanter (Cunningham et al., 2016) which has a fulcrum at the femoral head to increase its moment arm (Hogervorst and Vereecke, 2015).

Our second prediction was that extant great ape taxa would show a similar degree of CF occurrence given their shared high degree of hip joint mobility (Isler and Thorpe, 2003; Hammond, 2013; Finestone et al., 2018) and their similar patterns of cortical and trabecular bone distribution in the proximal femur, which suggest similar loading conditions at the hip joint (Rafferty, 1998; Ryan and Shaw, 2012; Georgiou et al., 2019; Pina et al., 2019). This prediction was partially supported by our results. Our study confirmed the frequent presence of a CF in *Pan* (Kuperavage et al., 2018) and, for the first time, also showed that a CF commonly occurs in *Gorilla* (cf. Crompton et al., 2021). However, a CF has only been identified in one captive *Pongo* (while it is absent in another captive individual from the same zoo).

Within the three nonhuman great ape taxa we also expected to detect a comparable shape, extension into the lesser trochanter, absolute and relative vertical height and length and root width of the CF. We find a similar extent of variation in *Pan* (see also Kuperavage et al., 2018) and in *Gorilla*. Compared to the more common human condition, *Pan* shows a less proximodistally developed CF. Nonetheless, Kuperavage et al. (2018) also found a degree of vertical extension comparable with the human pattern in two of seven *Pan* bearing a CF. We find that humans had the highest absolute CF values for both vertical height and transverse length, a finding that supports the results of Kuperavage et al. (2018). However, one *Gorilla* included in our sample shows a human-like CF whose distal end extends to the middle-lower part of the lesser trochanter.

Interestingly, compared to *Pan*, the *Gorilla* sample reveals a greater similarity to the human condition for the absolute values of distance between the periosteal surface and the CF's tip (PT MaxLength) and the CF MaxLength. However, when standardized by body mass, CF transversal length in humans and *Pan* overlaps, while *Gorilla* shows absolutely shorter length values compared to *Pan* and *Pongo*. In all cases, the degree of CF transverse extension does not correlate with either cortical bone thickness variation at the lesser trochanter cross-sectional level, nor with body mass.

The variation in CF morphology observed between African apes and *Pongo* might reflect documented differences in climbing frequency and kinematics, in which *Pan* and *Gorilla* vertically climb and descend less frequently (Hunt, 1991; Doran, 1996; Thorpe and Crompton, 2006) and use a lower range of hip motion and external rotation (Isler, 2005; Hammond, 2013) compared with that of *Pongo*. In addition, although the cortical and trabecular distribution patterns are generally similar across great apes at the proximal femur (Ryan and Shaw, 2012; Georgiou et al., 2019, 2020), *Pongo* is distinct in having a lower trabecular bone density in the femoral head (Georgiou et al., 2019) suggesting subtle differences in loading magnitude or direction incurred at the lesser trochanteric region, which may explain variation in CF expression. If the more frequent absence of a CF in *Pongo* is related to its arboreal suspensory specializations, a similar condition should also characterize the hylobatids. We assessed two *Hylobates lar* specimens and found no evidence of a CF (SOM Fig. S8), but this hypothesis deserves further examination. The possible influence of captivity-related mechanical/environmental constraints on CF expression in extant great apes is currently unknown but the variable presence of a CF in captive *Pongo* coupled with the complete absence in wild *Pongo* individuals, as shown in this study, emphasizes the need for further investigation.

Finally, our prediction that none of the *Papio* specimens included in our sample would show evidence of a CF was supported. This results is consistent with those previously reported for rhesus macaques (Glinkowski and Ciszek, 1989). Given the absence of CF in rhesus macaques and *Papio* (and 2 hylobatids) and its clear expression in only one suspensory *Pongo*, investigating the occurrence and morphology of strepsirrhine leapers vs. non-leapers could provide us more information about the possible functional role of this feature.

Future research examining CF presence and patterns of variation in larger samples of extant apes, with special attention to the degree of expression of this feature between sister taxa that vary in the frequency of different locomotor behaviors (e.g., *P. troglodytes* vs. *Pan paniscus*; *G. gorilla* vs. *Gorilla beringei*; Hunt, 1991; Crompton et al., 2010) may shed light on the variation in CF expression and its potential functional significance. Moreover, although we did not quantitatively evaluate sex differences in the CF in this study, future investigations should also examine the possible influence of sexual dimorphism on the expression of the CF.

4.2 Fossil hominins and Rudapithecus

We predicted that the fossil hominins (*Australpithecus* and *Paranthropus*) in our sample would display a CF morphology more similar to extant humans given they are all considered habitual bipeds when terrestrial, while we expected the orthograde suspensory *Rudapithecus* to show a CF morphology more similar to that of nonhuman great apes. Both predictions were generally supported, but with some notable exceptions. Together with the evidence provided by previous studies of fossil hominin femora (White, 1984; Grine et al., 1995; Kuperavage et al., 2018), the results of our high-resolution analyses of the occurrence and 3D shape variation of the CF in a selected sample of hominid representatives (*Rudapithecus*, *Australopithecus*, *Paranthropus*) are in line with the now extended evidence available for this feature on extant hominids. Indeed, although not all CF variables could be assessed due to variablepreservation, the CF was present in all investigated fossil hominid specimens, except in SK 97 (*P. robustus*). However, s CF morphology (i.e., shape, location, extension within the lesser trochanter, absolute vertical height, absolute horizontal length, root width) in fossil hominids varied to an extent comparable to that found in the extant hominid sample used in this study and does not always fall within the human range of variation. Among the fossil hominins, a human-like CF vertical extension is found in *A. africanus* StW 99 and *P. boisei* KNM-ER 1465, with both specimens showing a CF confined within the proximal portion of the lesser trochanter, while other fossils have a shorter distal extension.

A previous study has reported the presence of a CF in the two partial femora of *Orrorin,* BAR 1002’00 and 1003’00, but it could only be quantitatively assessed in the less heavily mineralized latter specimen (Kuperavage et al., 2018). Axial virtual cross sections obtained from a medical CT scan showed a distinct CF. However, the reported absolute length of the *Orrorin* CF (1.58 cm; Kuperavage et al., 2018) is most similar to the mean values we have documented in humans and *Gorilla*. Moreover, its distal extension to the middle of the lesser trochanter (Kuperavage et al.,

2018) is intermediate between the average conditions we measured in *Pan* and humans and, most similar to the morphology displayed in a female *Gorilla* (SOM Fig. S5) and a captive male *Pongo* (Fig. 3).

The variation in CF occurrence and expression documented in the fossil hominin sample here, in combination with previous studies (i.e. *Orrorin*), may reflect variation in the biomechanics and/or frequency of bipedal (or climbing) locomotion these hominin taxa. Alternatively, this variation, including the notable absence of a CF in SK 97, may simply represent ‘normal’ variation in CF occurrence and expression that has been documented here and in previous studies (Kuperavage et al., 2018) among humans and other great apes, and further emphasises that the presence/absence of the CF is not reliable indicator of bipedalism. Extended analyses of the CF degree of development in hominin taxa that also combine cortical thickness topographic distribution and trabecular structural organization at the proximal femoral end (e.g., Ohman et al., 1997; Ruff and Higgins, 2013; Kivell, 2016; Ruff et al., 2016; Cazenave et al., 2019, 2021; Ryan et al., 2018; Georgiou et al., 2020) may reveal whether the CF variation reflects individual differences in mechanical strength across the different compartments, thus in the loading environment of the hip joint.

Importantly, we also detected a *Pan*-like CF in *Rudapithecus* RUD 234, but with a morphology more extended transversely, as observed in Gorilla. This finding is especially interesting given that short-distance bipedal walking and stance behaviors are variably displayed by all nonhuman great apes, including occasionally by *Pongo* when moving on flexible branches (Thorpe et al., 2007; Crompton, et al., 2010). In addition, the external postcranial morphology of the stem hominid dryopithecin *Danuvius guggenmosei* (Böhme et al., 2019) has been interpreted as reflecting habitual bipedal postures (but see Williams et al., 2020). Thus, the potential that *Rudapithecus* may have engaged in similar bipedal postures cannot be excluded, although bipedalism is a minor component of the *Pan* locomotor repertoire (0.4–8.0% of locomotor time; Hunt, 1991). Based on the results of our study, this suggests that the CF morphology in extant great apes and *Rudapithecus* may represent a bone functional adaptation to different orthograde locomotor behaviors likely related to a more extended hip joint such as during vertical climbing or extended-limb clambering (Isler, 2005; Böhme et al., 2019), rather than bipedalism specifically.

Potentially valuable information about the functional link between the CF and bipedalism could stem from the analysis of the proximal femora of Sansuke, an adult *Macaca fuscata* that regularly engaged for eight years in bipedal performance (Nakatsukasa et al., 1995). The femora of this individual have not yet been investigated for the presence of a CF, but previous research has shown that cortical bone thickness distribution and trabecular organization within the innominate, the femur, and the proximal tibia show distinct adaptive responses to the more compressive loads imposed by bipedal locomotion (Nakatsukasa and Hayama, 2003; Volpato et al., 2008; Mazurier et al., 2010). If the CF, or at least a CF-like structure plays an active role in transferring loads incurred during bipedal gait from the femoral head through the neck to the shaft (rev. in Hammer, 2019), Sansuke's proximal femora should show at least traces of a cortico-trabecular strengthening extended across this region compared to wild *M. fuscata* individuals.

In conclusion, this study demonstrated that the humans are distinguished from other extant great apes in the more frequent occurrence of a CF and a CF that is distinct in its greater proximodistal extension to within the lesser trochanter. However, an increasing body of comparative evidence from extant and extinct hominid taxa shows that the CF is a highly variable, possibly ecophenotypic (i.e, modified during life by environmental factors) structure, even in humans. As already suggested by its previous identification in some *Pan* femora (Kuperavage et al., 2018), the presence of a CF-like structure and even human-like CF in some nonhuman great apes makes clear that this feature cannot be reliably considered as a ‘magic trait’ (*sensu* Stern and Susman, 1991) to identify habitual bipedal locomotion in hominins. In light of our results, several future investigations have been suggested that may elucidate the possible functional influence on the degree of expression of the CF. Higher resolution imaging and quantitative assessment of the CF in *Orrorin* BAR 1003’00, and the analysis of the partial femora representing the late Miocene taxa *Danuvius* (Böhme et al., 2019) and *Sahelanthropus* (Macchiarelli et al., 2020) would further contribute the understanding of the evolutionary history of this trait.

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Figures captions

Figure 1. µCT-scanned transverse (upper; blue) and parasagittal (lower; yellow) virtual sections respectively, extracted at the upper margin and at the centre of the lesser trochanter showing the calcar femorale absence (a) and presence (b; arrows) in two extant human individuals.

Figure 2. µCT-based measurements (black lines) of the calcar femorale (CF) in a virtually-rendered human right proximal femur shown in semitransparency in posterior view (a, b, d) and on a virtual transverse section across the lesser trochanter of the same specimen at the level of the maximum width of the CF root (c). In all cases, medial is to the left. a) Maximum length measured as maximum distance between the periosteal contour and the CF most internal point (PT MaxLength); in the colored map, the CF increasing distance from the periosteal contour is rendered by a chromatic scale ranging from dark blue to red. b) Maximum length measured as maximum projective distance between the base of the CF root on the endosteal contour and its most internal point (CF MaxLength). c) Maximum width of the CF root. d) Maximum height measured as maximum projective distance between the uppermost (see upper view) and the lowest (see lower view) virtually extracted slices bearing evidence of a CF-related spur of thickened bone (CF MaxHeight). Scale bar = 10 mm.

Figure 3. µCT-based transverse (upper left) and parasagittal (right) virtual sections respectively extracted at the upper margin and at the center of the lesser trochanter showing the CF presence (indicated with an arrow)/absence and extension in selected proximal femora representing five extant human, *Pan, Gorilla, Pongo,* and *Papio* individuals (a–e). Independent of their original side, all specimens are imaged as right femora. See SOM Figure S3 for the additional extant specimens. Scale bar = 10 mm.

Figure 4. µCT-based 3D rendering of the CF (in red) in an extant human, a *Pan*, a *Gorilla*, and a *Pongo* right femur virtually shown in semitransparency in anterior (a), lateral (b), posterior (c), and medial (d) view. Scale bar = 10 mm.

Figure 5. Boxplots of the median (center horizontal line), interquartile range (represented by the box), maximum and minimum values of the data excluding potential outliers (vertical lines) and the potential outliers (bellow and upper 1.5 time of the interquartile range) of the absolute (upper row) and standardized (lower row) values of the variables PT MaxLength, CF MaxLength, and CF MaxHeight measured in the extant human, *Pan* and *Gorilla* samples and the values measured in one *Pongo* individual as well as the absolute individual values (upper row) of the CF MaxLength and CF MaxHeight measured in the fossil hominid specimens representing *Rudapithecus* (RUD 234), *A. africanus* (StW 99 and 367), and likely *P. boisei* (KNM-ER 738 and 1465). The asterisks indicate statistically significant inter-taxa comparisons (Pairwise Wilcoxon rank sum test); the black-closed circle (CF MaxHeight in the lower row) indicates an outlier outside 1.5 times the interquartile range. No estimate is available in StW 367 for the CF MaxHeight.

Figure 6. μCT-based transverse (upper) and parasagittal (lower) virtual sections respectively extracted at the upper margin and at the center of the lesser trochanter showing the calcar femorale (CF) presence/absence in the fossil hominid specimens representing, from left to right and top-down, *Rudapithecus* (RUD 234), *A. africanus* (StW 99 and, 367), *P. robustus* (SK 97), and likely *P. boisei* (KNM-ER 738 and 1465). The white arrows indicate the CF. We observed no trace of a CF in SK 97, although possible strengthening of the trabeculae projecting towards the greater trochanter could not be confidently ascertained because of the incomplete preservation in this specimen. Independent of their original side, all specimens are imaged as right femora (for their original side, see SOM Table S2). Scale bar = 10 mm.

Figure 7. μCT-based 3D rendering of the calcar femorale (in red) in RUD 234 (*Rudapithecus*) left femur (here imaged as right) and KNM-ER 738 (likely *P. boisei*) right femur, virtually shown in semitransparency in anterior a), lateral b), posterior c), and medial d) view in comparison to the μCT-based 3D rendering of the calcar femorale (in red) in an extant human, a *Pan*, a *Gorilla*, and a *Pongo* right femur virtually shown in semitransparency in anterior view. Scale bar = 10 mm.