

# Comparative morphometric analysis of the proximal femur of African hominids and felids

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Size and shape of the mammalian proximal femur and taxon-specific distinctions in the relative proportions of the proximal articulation, the femoral neck and the proximal femoral diaphysis, are critical determinants in its adaptation to differential biomechanical stresses and observed locomotor habitus in different taxa. The morphometrics of the proximal femur are considered equally critical in the assessment of locomotor habitus of extinct fossil mammals, particularly extinct Miocene anthropoids and Plio-Pleistocene hominins. Analyses of size and shape of  $k=10$  dimensions of the proximal femur were undertaken for a large sample series of two extant mammal families – the Felidae and Hominidae – using conventional multivariate statistical procedures, commonly used size-correction methods, and post-hoc tests of significance. While significant differences in form do exist, there are equally striking convergences in the functional morphology of extant hominid and felid taxa. Multivariate and bivariate allometric analyses confirm that the proximal femur of these two mammalian families share a common underlying structure manifest in a shared first common principal component. Nevertheless, while considerable convergences in general form of the proximal femur of African hominids and large-bodied felids are apparent, there exist equally discreet distinctions which are consistent with the differential structural demands imposed by their distinct locomotor and behavioural habitus.

## Introduction

The proximal femur of mammals is extremely generalised in its external and internal form<sup>1-3</sup>, yet the unique mode of posture and progression in living humans and their extinct Plio-Pleistocene relations is manifest as a suite of consistent structural modifications<sup>4-6</sup>. The principles of osteonal remodelling, and that of its cartilaginous precursors, are universally accepted<sup>7-9</sup> and the adult form of the proximal femur retains considerable potential as a source of quantitative evidence concerning taxonomy, function and phylogeny.<sup>4-6,10</sup>

All quadrupedal vertebrates are essentially hindlimb driven and, the unusual 'diagonal sequence' gait typical of primates notwithstanding, hindlimb drive is employed in recognition of the simple fact that the pelvic and proximal hindlimb musculature is the primary source of initial power input at commencement of the gait cycle from a static position of rest.<sup>11-14</sup> The principal function of the musculoskeletal components of the hip joint are akin to the stroke cycle of a piston rod (or main rod) which powers the main driving wheels in the propulsion of steam-powered locomotives.<sup>15,16</sup> Cyclical rotations and angular excursions of the spherical femoral head within its ball-and-socket joint and the shaft of the femur during contact phases of gait, particularly at optimal and peak velocities, are critical in maintaining momentum and direction of the centre of mass.<sup>14,17,18</sup> From dynamic and static perspectives, the mammalian proximal femur differs from the main rod of a steam locomotive in that it must be 'engineered', for want of a more appropriate descriptor, to withstand potentially critical stresses induced by ground reaction forces which exceed body mass by a considerable magnitude at peak velocities.<sup>9,19</sup>

The femoral neck of mammals varies in its absolute (anatomical) length, its superoinferior angulation, and its degree of anteroposterior anteversion, yet despite observed intraspecific and interspecific functional variance in these parameters, it is generally accepted that the femoral neck performs the function of a cantilever subject to bending in the superoinferior plane.<sup>20-23</sup> These stresses are greatest at the locus of the neck-shaft junction and are structurally mediated by the overall length of the cantilever (anatomical/functional length), its proportions in the primary plane of bending and in the orthogonal neutral axes ( $x,y$ ) and, by extension, its geometric conformity.<sup>6,21,22,24</sup>

The primary function of the proximal femoral articulation in terrestrial vertebrates lies in the transfer of force, propulsive and reactive, engendered by mass of the organism during posture and ambulation and, to a greater degree, during high-energy ground contact at moderate-to-peak velocities of the gait cycle.<sup>12,19,25,26</sup> The magnitude of these forces ultimately determines the absolute and relative size of the articular surface, which is greater in terrestrial bipeds.<sup>21,27</sup> Absolute length of the neck is a critical determinant of the lever arm of the external and intrinsic hip musculature in quadrupeds and bipeds<sup>5,21</sup> and in terrestrial hominins the neck-shaft junction is subject to considerably elevated compressive stresses compared with those of more arboreal species like *Gorilla* and *Pan*<sup>8,10</sup>. Proportions of the proximal and distal osseous components of the limbs and the digits (manus and pes) attest to considerable modifications to habitual structural demands, whether as levers increasing mechanical efficiency with respect to specific functional demands (i.e. suspension versus support; increased inertia in specialised high-velocity taxa), or in resistance to flexure and ultimate failure during peak loading cycles.<sup>13,28-30</sup>

The extant African hominids (*Gorilla*, *Pan* and *Homo*) and large-bodied felids (*Panthera* and *Acinonyx*) offer a unique prospectus to assess patterns of variance in the general morphology of the proximal femur and its modification to disparate structural demands. Both mammalian families exhibit considerable size variance that was likely exceeded in some extinct Plio-Pleistocene representatives<sup>31,32</sup> and both include one highly specialised extant taxon, namely *Homo* and *Acinonyx*. However, there is good reason to designate the fore- and hindlimb anatomy of *Acinonyx* to being merely functionally derived, rather than unique, whereas the lower limb of *Homo* has no true extant comparator. Living humans were thus excluded from this analysis, which was focused upon the elucidation of distinctions and general underlying convergences in the proximal femoral morphology of other hominids and felids.

This contribution explicitly assesses patterns of underlying convergences and disparities in proximal femoral form of these two phylogenetically discrete families of extant African mammals. If the proximal femur of mammals is conservative in its general form, it follows logically that extant African hominids and large-bodied African felids will share a common generalised vector of size and shape ( $H_0: 1$ ). However, given the distinct postural repertoires and locomotor modes of extant African hominids and large-bodied felids, whereby the total mass of the individual is supported to a greater extent by the proximal femoral articulation in the former, an equally logical expectation is that any discrete morphometric distinctions of the proximal femur will be consistent with the mechanical demands of their observed disparate posture and locomotor modes.

## Materials and methods

A total of 213 specimens of African hominid species and sub-species of the extant genera *Gorilla* (gorillas) and *Pan* (chimpanzees and bonobos) were included in the analysis (Supplementary table 1 of the online supplementary material). The extant large-bodied felid samples included *Panthera* – *Panthera tigris* (tigers), *Panthera leo* (lions) and *Panthera pardus* (leopards) – and *Acinonyx* (*Acinonyx jubatus*; cheetahs) and comprised 69 individuals. Only adult specimens evidencing complete fusion of the postcranial epiphyses were used in this study. A series of  $k=10$  linear dimensions of the proximal femur used in conventional appraisals of the taxonomic and functional affinities of extinct Plio-Pleistocene hominin genera (*Australopithecus*, *Paranthropus* and early *Homo*)<sup>33</sup> were taken using a pair of Mitutoyo™ digital calipers (Figure 1). As can be seen, these linear dimensions effectively describe the general form (form = size + shape)<sup>34</sup> of the proximal articulation (superoinferiorly, anteroposteriorly, mediolaterally), the proportions of the femoral neck and proximal femoral diaphysis (mediolaterally and anteroposteriorly).

All linear data were log-transformed (base  $e$ ) in MS Excel and subsequently size corrected using the approach outlined by Mosimann<sup>35</sup>, whereby each individual  $k$  linear dimension for a particular specimen is expressed as a proportion (not a percentage) of the geometric mean of all  $k=10$  dimensions. The variates generated using this approach are effectively uncorrelated with size and facilitate both bivariate and multivariate perspectives on relative size distinctions between series of forms.<sup>35</sup> Following the rationale of Jolicoeur, the most appropriate mathematical descriptor of size and shape is the first principal component (PC) of a log-transformed covariance matrix.<sup>35,36</sup> If size is dominant, then the first PC (PC1) should account for an overwhelming proportion of the total observed variance, leaving little residual variance assigned to successive orthogonal (and uncorrelated) PC axes.<sup>37,38</sup> If this prospectus holds, then the loadings of individual  $k$  variates on this axis can be expressed as multivariate allometry coefficients standardised around a value of 1, the theoretical coefficient of isometry.<sup>34-36</sup> This is simply calculated

as  $1/\sqrt{k}=0.316$  in the case of our  $k=10$  dimensions and all log-transformed raw variates should yield positive scores on the first PC.

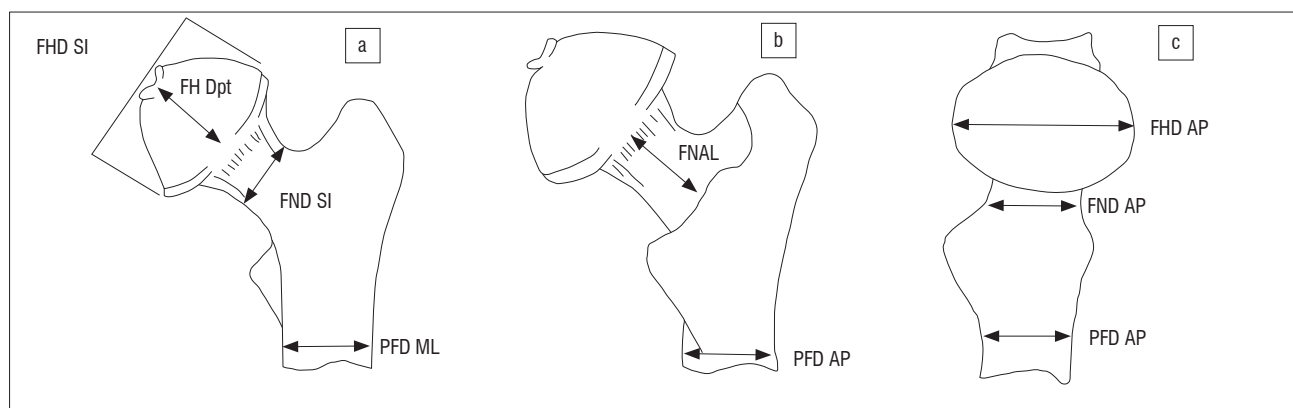
All principal components analyses (PCA) were performed on the variance-covariance matrix (hereafter VCV), as opposed to the correlation matrix, using PAST version 3<sup>39</sup>, which extracts a series of components commensurate to the  $k$ -variate series,<sup>37,38</sup> irrespective of the magnitude of the variance explained by successive PCs, that effectively diminish to a total cumulative 100%. If PC1 does constitute a 'generalised size and shape vector', then successive PCs may be effectively negligible.<sup>34-38</sup> In the first instance, PCAs were performed on the log-transformed raw data of the total sample (pooled hominid and felid) and on the individual family series of hominids and large-bodied felids. Jolicoeur multivariate allometry coefficients were subsequently calculated for the component loadings of the  $k=10$  linear variate series on PC1 alone.<sup>35,36</sup>

While the derivation of Jolicoeur multivariate allometry coefficients provides a computationally effective means of assessment of distinctions in  $n=2$  (or  $n>2$ ) samples for a given battery of  $k$  linear dimensions, explicit tests of underlying structural commonalities in sample-specific VCV matrices were explored via the Flury hierarchy of common principal components analysis which assesses for equality, proportionality and sequential shared common PCs.<sup>40,41</sup> The common principal components hierarchy is an effective test of underlying correspondences and disparities in matrix structure beyond a simple test of equality of  $n$ -group matrices. These tests were performed using the program written in MS Dos for Windows by Dr Patrick C. Phillips.

A second PCA was performed on the total series data set using the Mosimann shape variates of the  $k=10$  dimensions in order to explicitly examine patterns of relative size disparities in the proximal femur of African hominids and large-bodied felids. Model II (reduced major axis) bivariate allometric equations were calculated in post-hoc assessments either as sample-specific (i.e. hominid or felid) or total-sample models using PAST v.3. Post-hoc significance tests of estimates of  $\gamma$  (the dependent variate) on  $x$  (the geometric mean) were determined via Fisher's paired randomisation test performed in Rndom Projects 2.<sup>42,43</sup>

## Results

Summary data for the PCAs of the total and individual sample series, PC loadings and multivariate allometry coefficients for the total sample series are given in Tables 1 and 2. The PC loadings and multivariate allometry coefficients for the individual series (African hominid, large-bodied felid) are given in the online supplementary material (Supplementary tables 2 and 3). In the three analyses of the log-transformed raw data, the first PC is a generalised size vector accounting for about 88% and 96% of the total variance and is greater in felids than in hominids (Table 1). Pearson's  $r$  between the PC1 scores and geometric means of the  $k=10$  linear variates is perfect in both felids and hominids ( $r=1.000$ ;



FHD SI/AP, superoinferior/anteroposterior diameter of the proximal articulation; FH Dpt, mediolateral diameter of the proximal articulation; FND SI/AP, superoinferior/anteroposterior diameter of the femoral neck; PFD ML/AP, mediolateral/anteroposterior diameter of the proximal diaphysis (distal to the lesser trochanter); FNAL, anatomical length of the femoral neck.

**Figure 1:** Linear dimensions taken on the proximal femur in (a) anterior, (b) posterior and (c) medial views.

Supplementary figure 1). Nevertheless, subtle distinctions do exist in the sample-specific multivariate allometry coefficients, particularly in dimensions reflecting absolute size of the proximal femur, proximal femoral diaphysis and femoral neck. Yet in both hominids and felids, the articulation is approximately isometric and is greater in the superoinferior plane (Supplementary tables 2 and 3).

As can be seen in Figure 2a, significant contrasts exist in the proximal femur of hominids and large-bodied felids on PC2, which primarily reflects differential loadings of the femoral head on the one hand and dimensions of the neck on the other. An interesting point of note is that the proximal femur of *Pn. paniscus* (bonobos) appears to be intermediate in form between extant felids and the main scatter of *Pn. troglodytes* (chimpanzees) and *Gorilla* on axis 2, reflecting correspondences

in the general form of the femoral neck. The anatomical length, the superoinferior height and anteroposterior depth, load positively on this axis and are greater in felids than in hominids. An explicit assessment of commonality of underlying structure in the VCV matrices of log-transformed raw data using the Flury hierarchy confirms that both series share a first, but not a second, common PC. The VCV matrices are neither equivalent nor proportional, and significant contrasts in proximal femoral morphology in hominids and large-bodied felids are confirmed, irrespective of whether the 'jump-up' or 'step-up' approach is preferred (Supplementary tables 4 and 5).<sup>41</sup>

The observed contrasts in the proximal femur of extant African hominids and large-bodied felids on the one hand, and *Pn. paniscus* on the other, are further exemplified in multivariate analyses of the Mosimann

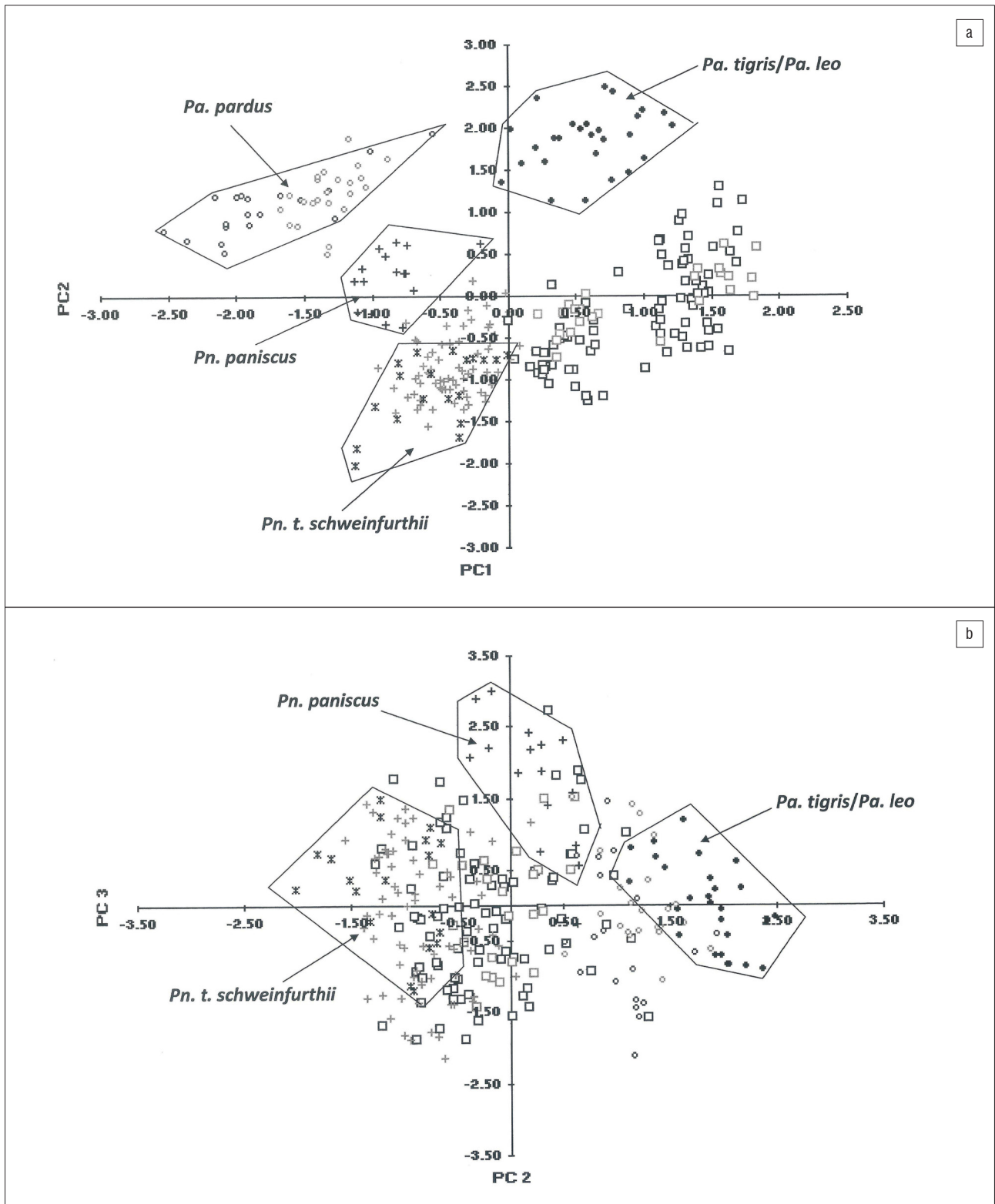
**Table 1:** Summary statistics for the principal components (PC) analysis: raw data

Total			
PC	Eigenvalue	% Variance	% Cumulative
1	0.5101	87.77	87.77
2	0.0358	6.16	93.93
3	0.0168	2.89	96.82
Hominid			
PC	Eigenvalue	% Variance	% Cumulative
1	0.3684	88.72	88.72
2	0.0199	4.79	93.51
3	0.0119	2.86	96.37
Felid			
PC	Eigenvalue	% Variance	% Cumulative
1	0.6449	95.73	95.73
2	0.011	1.64	97.37
3	0.0051	0.76	98.13

**Table 2:** Component loadings for the principal components (PC) analysis of the proximal femur: pooled-sample raw data

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	JIC
FHD SI	0.353	-0.206	0.123	-0.193	0.065	-0.076	-0.082	-0.482	-0.175	-0.708	1.115
FHD AP	0.347	-0.214	0.139	-0.227	0.110	-0.073	-0.147	-0.461	-0.132	0.703	1.096
FH Dpt	0.332	-0.120	0.106	-0.432	0.015	0.008	0.743	0.352	-0.034	0.019	1.049
PFB	0.321	-0.007	0.084	-0.239	-0.095	0.184	-0.322	0.137	0.815	-0.045	1.016
FBNL	0.317	0.028	0.013	-0.140	-0.188	0.303	-0.477	0.494	-0.530	-0.009	1.001
PFD ML	0.331	-0.212	-0.100	0.605	-0.253	0.553	0.263	-0.168	0.036	0.036	1.046
PFD AP	0.352	-0.325	-0.001	0.451	0.045	-0.670	-0.091	0.322	0.057	-0.001	1.114
FNAL	0.299	0.294	-0.875	-0.089	0.201	-0.066	0.017	-0.071	0.006	0.006	0.945
FNM SI	0.257	0.688	0.223	0.077	-0.540	-0.276	0.097	-0.160	-0.029	0.030	0.812
FNM AP	0.232	0.432	0.348	0.255	0.735	0.165	0.013	0.073	-0.008	-0.018	0.732

JIC, Jolicoeur multivariate allometry coefficients; FHD SI/AP, superoinferior/anteroposterior diameter of the proximal articulation; FH Dpt, mediolateral diameter of the proximal articulation; PFB, total mediolateral breadth of the proximal femur; FBNL, biomechanical length of the femoral neck; PFD ML/AP, mediolateral/anteroposterior diameter of the proximal diaphysis (distal to the lesser trochanter); FNAL, anatomical length of the femoral neck; FNM SI/AP, superoinferior/anteroposterior diameter of the femoral neck.



Open black squares, *Gorilla g. gorilla*; open grey squares, *G. b. graueri*/*G. b. beringei*; black crosses, *Pan paniscus*; grey crosses, *Pn. t. troglodytes*; black asterisks, *Pn. t. schweinfurthii*; filled black circles, *Panthera tigris/Pa. leo*; open black circles, *Pa. pardus*; open grey circles, *A. jubatus*.

**Figure 2:** Principal components (PC) analysis of the pooled sample raw data: (a) PC2 to PC1 and (b) PC3 to PC2.

shape variates (Figure 3). As size has been effectively removed, five PCs are required to account for approximately 93% of the total variance and component loadings of the  $k=10$  variates range from negative to positive (Tables 3 and 4; Figure 3). Clear distinctions exist between felids (+ scores) and hominids (- scores) on the first, but not the second, PC axis, which reflects contrasts in the relative proportions of the proximal articulation and proximal diaphysis, which are greater in *Gorilla* and *Pan*, and the femoral neck (Table 4). As in the PCA of the raw data series, the principle morphometric distinctions in the femoral neck of felids and hominids lie in the proportions of the femoral neck, particularly its relative area (superoinferior and anteroposterior diameters). The striking convergence in proximal femoral morphology of *Pn. paniscus* and large-bodied felids is equally apparent in Figure 3a, yet in Figure 3b the equally stark contrasts in absolute size of the head and total and functional length of the proximal femur are demonstrable (Table 4; Figure 3).

In order to further assess the significance of the observed distinctions in relative proportions of the proximal femur in African hominids and large-bodied felids, reduced major axis regression solutions were derived for either pooled-sample or family-specific models, depending upon expectations of a single or independent allometric trend. The geometric mean of the  $k=10$  dimensions was used as the independent ( $x$ ) variate in all comparisons with the exception of the proportions of the neck and proximal diaphysis, in which contrasts in relative anteroposterior/mediolateral proportions were considered (Table 5). With few exceptions, the linear variates of the proximal femur attest to positive allometry in hominids and felids. Bivariate scatter plots of three variates that

apparently contribute to effective discrimination of the proximal femur of hominids and large-bodied felids in multivariate space are shown in Figure 4. Only the absolute size of the proximal articulation exhibits a sound bivariate relationship with minimal scatter in the data and further attests consistent proportional distinctions between felids and hominids (Figure 4a). Although there is a general tendency for *Pa. pardus* and *A. jubatus* proximal femoral diaphyses to fall outside the ranges of *Pan* with respect to their femoral neck anteroposterior/mediolateral diaphyseal proportions in their lower size ranges, this tendency is less consistent in their upper ranges and scarcely holds for *Pa. leo* and *Pa. tigris* with *Gorilla* (Figure 4b,c). Despite its functional significance and consistency in the multivariate analyses, relative anatomical length of the neck exhibits inordinate variance. Data in Figure 4c confirm that the major difference in the proximal femur of *Pn. paniscus* compared with *Pn. troglodytes* and *Gorilla* lies in their proportionally shorter, rather than elongate, femoral neck.

A similar overlap is observed in a great majority of other variates regressed against the geometric mean (GM), yet there is some consistency in *Pa. leo* and *Pa. tigris* in the relative proportions of the proximal femoral diaphysis compared with gorillas of equivalent size (Supplementary figures 2–4). These data are generally consistent with post-hoc tests (Table 6) which confirm general distinctions in the relative size of the proximal articulation between hominids and felids and in the proportions of the femoral neck and proximal diaphysis. Nevertheless, comparisons of observed and expected series in felids (medians are presented as a guide) reveal subtle distinctions in the proximal femur of

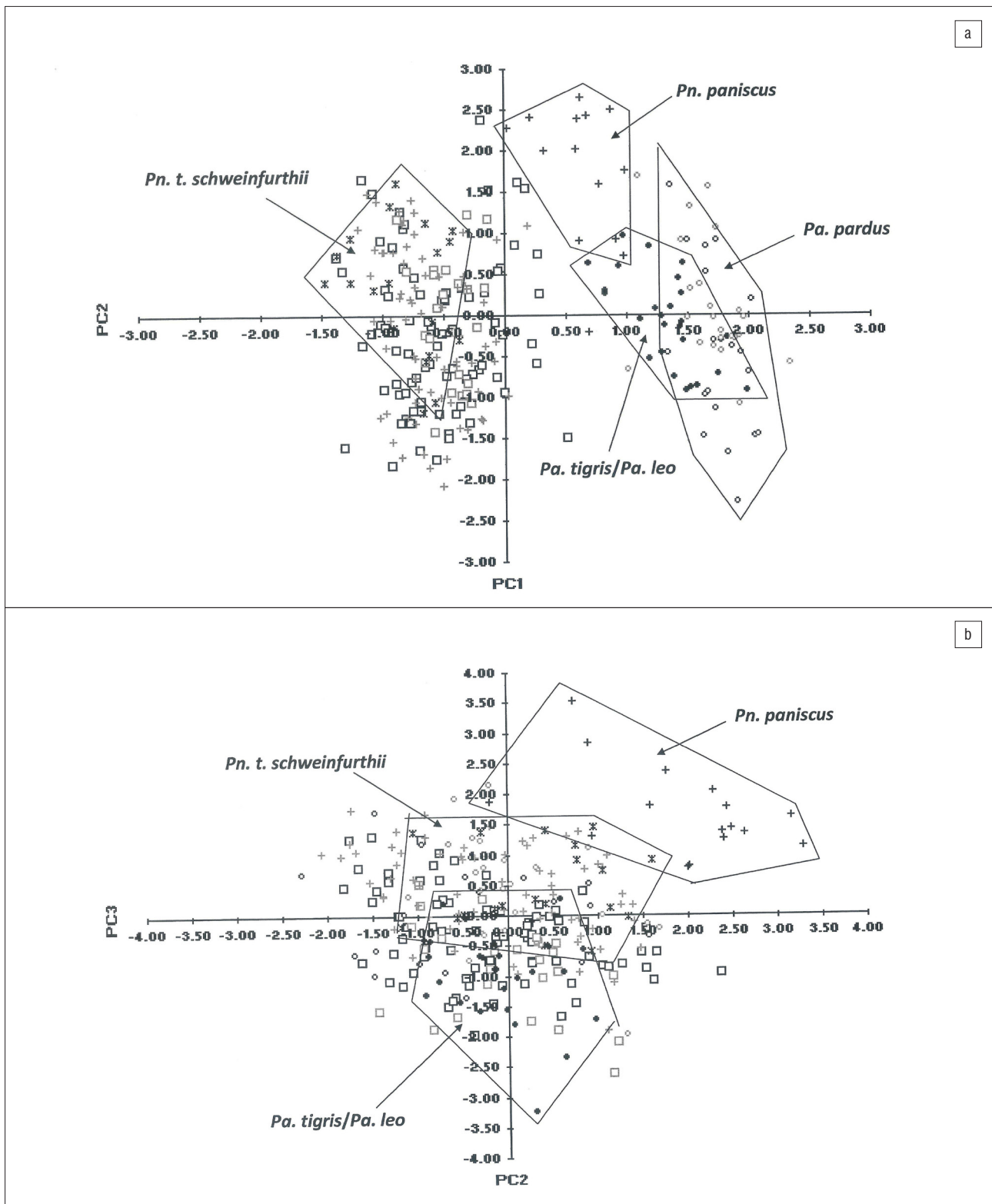
**Table 3:** Summary statistics for the principal components analysis (PCA): pooled-sample shape data

PCA			
PC	Eigenvalue	% Variance	% Cumulative
1	0.0035	52.541	52.54
2	0.0014	20.823	73.36
3	0.0006	9.378	82.74
4	0.0004	6.320	89.06
5	0.0003	4.376	93.44
6	0.0002	3.428	96.87
7	0.0001	2.045	98.91

**Table 4:** Component loadings for the principal components (PC) analysis of the proximal femur: pooled-sample shape data

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
FHD SI	-0.258	0.118	0.081	-0.219	-0.016	0.056	0.500	-0.099	-0.704
FHD AP	-0.253	0.140	0.146	-0.199	-0.061	0.113	0.492	-0.064	0.706
FH Dpt	-0.184	0.104	0.160	-0.554	0.079	-0.515	-0.500	0.004	0.025
PFB	0.050	0.112	0.510	0.283	0.075	0.175	-0.110	0.704	-0.047
FBNL	0.062	0.036	0.411	0.372	0.137	0.163	-0.247	-0.693	-0.007
PFD ML	-0.254	-0.118	-0.349	0.571	0.170	-0.566	0.139	0.065	0.042
PFD AP	-0.414	-0.027	-0.503	-0.014	-0.030	0.567	-0.386	0.064	0.002
FNAL	0.238	-0.884	0.057	-0.153	-0.176	0.030	0.058	0.023	0.010
FNM SI	0.613	0.183	-0.322	-0.174	0.582	0.090	0.102	0.023	0.032

FHD SI/AP, superoinferior/anteroposterior diameter of the proximal articulation; FH Dpt, mediolateral diameter of the proximal articulation; PFB, total mediolateral breadth of the proximal femur; FBNL, biomechanical length of the femoral neck; PFD ML/AP, mediolateral/anteroposterior diameter of the proximal diaphysis (distal to the lesser trochanter); FNAL, anatomical length of the femoral neck; FNM SI, superoinferior diameter of the femoral neck.



Open black squares, *Gorilla g. gorilla*; open grey squares, *G. b. graueri/G. b. beringei*; black crosses, *Pan paniscus*; grey crosses, *Pn. t. troglodytes*; black asterisks, *Pn. t. schweinfurthii*; filled black circles, *Panthera tigris/Pa. leo*; open black circles, *Pa. pardus*; open grey circles, *Acinonyx jubatus*.

**Figure 3:** Principal components (PC) analysis of the pooled sample Mosimann shape data: (a) PC2 to PC1 and (b) PC3 to PC2.

these taxa, irrespective of a general convergence in overall form (Tables 5 and 6; Figures 3 and 4; Supplementary figures 2–4).

## Discussion and conclusions

Segmental mass distribution in primates differs from quadrupedal mammals primarily in a proportionally greater allocation of the hindlimb musculature.<sup>12,30,44,45</sup> Nonetheless, even among living anthropoids, the terrestrial knuckle-walking gaits of *Gorilla* and *Pan* are unique in that the centre of mass is more distally located towards the hip joints than it is in terrestrial quadrupedal monkeys.<sup>12,13,30,32,45,46</sup> More crucially, irrespective of differences in absolute size, the distribution of mass during forelimb contact in the gait cycle is only marginally higher in *Gorilla* than in *Pan* and does not exceed 20%.<sup>13</sup> If large-bodied felids are accepted as suitable mammalian comparatives, then increased joint-reaction forces generated during normal posture and progression in extant African hominids is sufficient explanative for the observed proportional distinctions in their proximal femoral epiphyses.<sup>13,30,32,45,46</sup> Despite the pooled-sample least-squares regression slope of greater than 1.00, the hip joints in intraspecific comparisons of *Gorilla* and *Pan* likely approximate isometry, and the observed proportional differences between African hominids and felids cannot be simply dismissed as an allometric consequence of extreme size in *Gorilla*.

Given their immense size and exponentially increased hip joint reaction forces, gorillas might be logically expected to exhibit proportionally greater proximal femoral articulations than chimpanzees, particularly in light of the fact that their femora are proportionally shorter relative to the length of the humerus.<sup>13,28,29,32,42,47</sup> Humeral length increases isometrically with body mass ( $\alpha=0.333$ ) within the order Primates,<sup>47</sup> so the elongate humerus of *Gorilla* is entirely expected for an anthropoid of its size. Following this reasoning, the reduced length of the femur, and not the

elongation of the humerus, is imperative in their lower humero-femoral indices compared with *Pan*.<sup>13,28,29,32,47</sup> Reduction in the length of the femur in *Gorilla* and their extreme midshaft diaphyseal cross-sectional areas<sup>29,32</sup> compared with *Pan*, reflect necessary structural modifications to their increased bulk. Resultant increases in joint-reaction forces at the hip and knee of the lower limb in *Gorilla* and critical bending stresses at the femoral midshaft may be offset by a reduction in absolute and relative femur length, yet absolute length of the femur may independently mediate absolute size of the proximal and distal epiphyses in adults.<sup>29,32,33</sup>

The observed contrasts in proximal femoral morphology of *Pn. paniscus* and other extant African hominids in this analysis is deserving of consideration. The convergence in proximal femoral form of *Pn. paniscus* with the extant felids reflects subtle distinctions in the relative length and superoinferior/anteroposterior proportions of the femoral neck, which are greater than in *Pn. troglodytes* and *Gorilla*. On the one hand, these observed morphometric contrasts in the proximal femur of *Pn. paniscus* and *Pn. troglodytes* spp./*Gorilla* likely correspond with subtle, yet crucial, distinctions in extrinsic hip musculature architecture (*M. Gluteus medius*, *M. Ischiofemoralis*) and moment arms (*M. Gluteus medius*) in bonobos and their emphasis in increased hip-flexion during climbing activities, which are more influential in the bonobo's lifestyle.<sup>48,49</sup> Nevertheless, no significant contrasts in the general proportions of the neck of *Pn. paniscus* and *Pn. troglodytes* were found in previous geometric morphometric analyses<sup>50,51</sup>; the discrepancies between this analysis and that of Holliday and colleagues<sup>51</sup> may simply reflect sampling constraints (larger samples in this study). However, divergences from the results of Harmon's<sup>50</sup> findings cannot be explained by such factors and require more detailed consideration.

Traditional morphometric methods differ both qualitatively and quantitatively from geometric morphometric approaches in that size standardisation

**Table 5:** Bivariate allometry equations for the proximal femoral dimensions

Regress	Series	Model	Slope	5% Confidence interval	95% Confidence interval	Intercept	5% Confidence interval	95% Confidence interval	r	p-value
FHD SI vs GMSize	African hominids	RMA	1.048	1.025	1.070	-0.113	-0.191	-0.031	0.989	0.001
	Large-bodied felids	RMA	1.028	0.999	1.058	-0.161	-0.259	-0.066	0.993	0.001
FHD SI vs GMSize	African hominids	RMA	1.024	1.002	1.017	-0.017	-0.098	0.065	0.989	0.001
	Large-bodied felids	RMA	0.994	0.970	1.018	-0.040	-0.123	0.043	0.995	0.001
FHD Dpth vs GMSize	Total series	RMA	1.089	1.056	1.123	-0.510	-0.634	-0.388	0.967	0.001
PFB vs GMSize	Total series	RMA	1.037	1.017	1.056	0.619	0.548	0.689	0.989	0.001
FBNL vs GMSize	Total series	RMA	1.025	1.004	1.047	0.465	0.392	0.544	0.983	0.001
PFD ML vs GMSize	Total series	RMA	1.105	1.066	1.143	-0.538	-0.672	-0.400	0.948	0.001
PDF AP vs GMSize	African hominids	RMA	1.073	1.014	1.130	-0.573	-0.779	-0.354	0.942	0.001
	Large-bodied felids	RMA	1.036	0.969	1.099	-0.580	-0.793	-0.351	0.973	0.001
FNAL vs GMSize	Total series	RMA	1.108	1.037	1.177	-0.434	-0.657	-0.151	0.864	0.001
FND SI vs GMSize	African hominids	RMA	1.140	1.076	1.202	-0.767	-0.990	-0.537	0.935	0.001
	Large-bodied felids	RMA	1.004	0.955	1.050	-0.001	-0.168	0.159	0.980	0.001
FND AP vs GMSize	African hominids	RMA	0.941	0.889	0.995	-0.283	-0.481	-0.093	0.880	0.001
	Large-bodied felids	RMA	0.947	0.912	0.989	-0.129	-0.266	-0.013	0.980	0.001
PFD AP vs PFD ML	Total series	RMA	1.069	1.028	1.112	-0.413	-0.558	-0.276	0.948	0.001
FND AP vs FND ML	Total series	RMA	0.854	0.806	0.899	0.239	0.094	0.397	0.904	0.001

FHD SI, superoinferior diameter of the proximal articulation; PFB, total mediolateral breadth of the proximal femur; FBNL, biomechanical length of the femoral neck; PFD ML/AP, mediolateral/anteroposterior diameter of the proximal diaphysis (distal to the lesser trochanter); FNAL, anatomical length of the femoral neck; FND SI/AP, superoinferior/anteroposterior diameter of the femoral neck; RMA, reduced major axis.

exemplifies, rather than partitions, linear dimensions that may, or may not, approximate inter-landmark distances in 2D/3D registration space. In contrast, generalised Procrustes rotation (translation, rotation and scaling) does distort linear inter-landmark distances, which may potentially mask real morphometric distinctions in small-scale, localised regions of interest.<sup>52</sup> Further to this, direct post-hoc comparisons of Asian and African apes in Harmon's<sup>50</sup> study did reveal significant contrasts in the relative length of the femoral neck, which is proportionally greater in the former, yet no explicit post-hoc assessment of morphological distinctions in *Pan* was undertaken. At a basic level, these two methodologies are not directly comparable and any potential conflict with previously published analyses does not compromise the consistent contrasts witnessed in this study, nor their significance.

Despite substantial variation in body mass (from <4 kg to nearly 200 kg), extant felids do not exhibit large-scale, size-dependent changes in either limb posture or angular joint excursion during normal progression.<sup>53</sup> Results of these analyses confirm that the

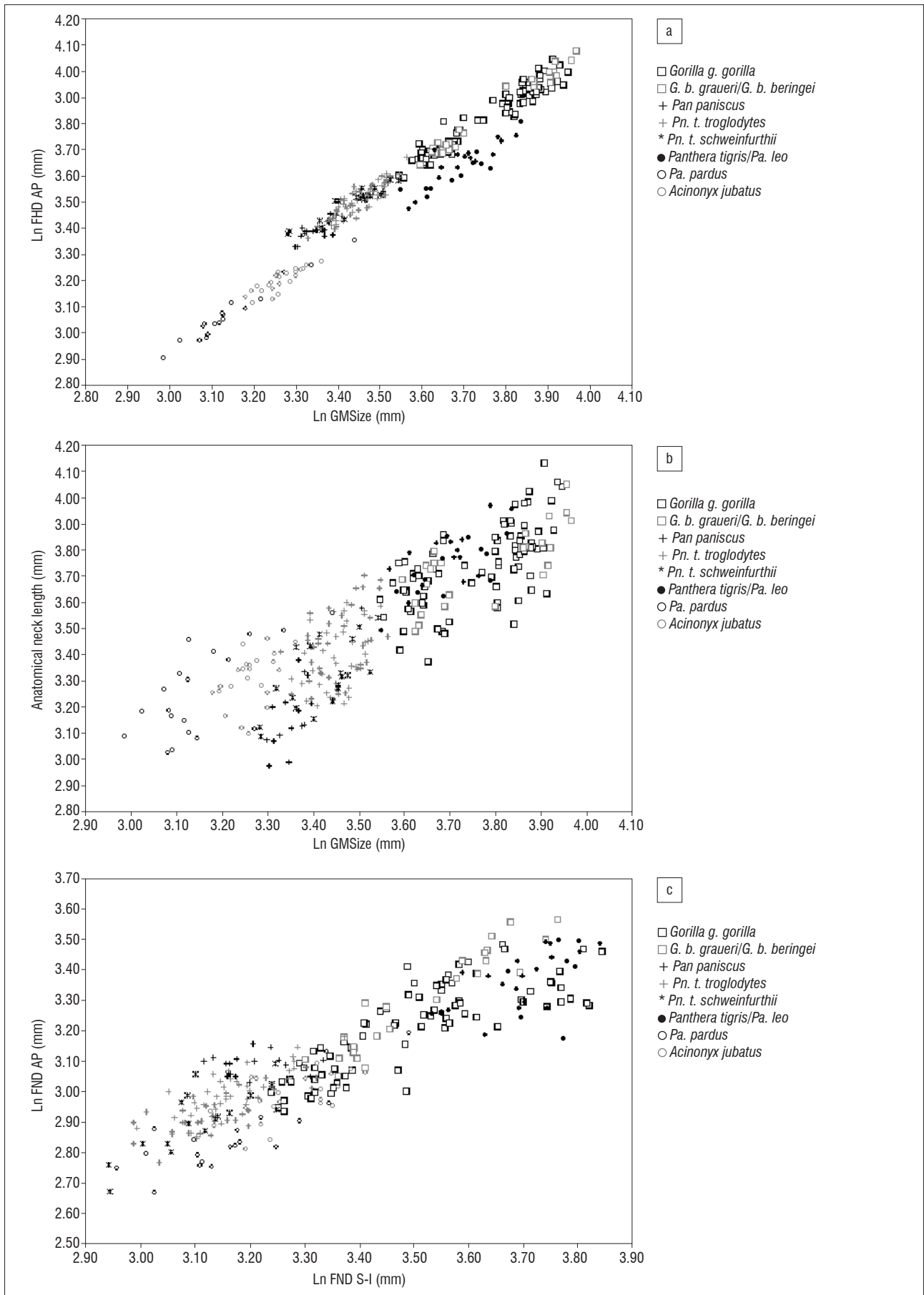
proximal femoral morphology of living large-bodied felids exhibits striking consistencies in general form, which is particularly evident in multivariate appraisals of Mosimann shape variates with considerable overlap among taxa. This finding is somewhat unexpected, given the highly specialised gait of living cheetahs (*A. jubatus*) and only the relative mediolateral proportions of the proximal diaphysis attests taxon-specific distinctions when expressed as a function of the GM. Surprisingly, it is *Pa. pardus*, rather than *Acinonyx*, which differs from the morphology of *Pa. leo* and *Pa. tigris* by virtue of their relatively broad proximal shafts in the mediolateral plane. The most logical explanation for this finding is that the elongated anatomical length of the femoral neck in *Pa. pardus* increases joint excursion and yields greater mediolateral bending moments in the proximal femoral diaphysis during normal loading<sup>20-22</sup> – a possible morphological function of increased tree-climbing behaviours observed in this species.<sup>54</sup> Compared with thoroughbred greyhounds, cheetahs evidence considerable hypertrophy and increased moment-arms of their hip-joint flexors and extensors.<sup>55-58</sup>

Table 6: Fisher's paired randomisation comparisons

Variable	Model	Median observed	Median predicted	Sum observed	Mean sum	5% Confidence interval	95% Confidence interval	p-value
<b>Hominids</b>								
FHD SI	RMA	3.603	3.605	0.270	0.346	0.028	0.850	0.534
FHD AP	RMA	3.614	3.615	0.262	0.347	0.030	0.851	0.550
FH Dpt	RMA	3.397	3.353	3.160	0.675	0.050	1.650	0.001
PFB	RMA	4.302	4.297	0.877	0.377	0.029	0.927	0.001
FBNL	RMA	4.119	4.101	0.807	0.480	0.041	1.159	0.182
PFD ML	RMA	3.429	3.382	1.953	0.978	0.077	2.427	0.109
PFD AP	RMA	3.252	3.233	0.192	0.820	0.060	1.992	0.852
FNAL	RMA	3.562	3.496	0.380	1.399	0.116	3.543	0.828
FNM SI	RMA	3.281	3.277	0.739	0.912	0.071	2.243	0.514
FNM AP	RMA	3.069	3.055	0.114	1.024	0.078	2.486	0.927
PFD AP	RMA	3.252	3.253	3.112	0.964	0.074	2.354	0.009
FNM AP	RMA	3.069	2.563	105.943	1.875	0.489	14.236	0.001
<b>Felids</b>								
FHD SI	RMA	3.232	3.261	1.983	0.276	0.021	0.679	0.001
FHD AP	RMA	3.249	3.240	0.041	0.159	0.013	0.387	0.838
FH Dpt	RMA	3.046	3.084	3.016	0.506	0.040	1.214	0.001
PFB	RMA	4.040	4.041	1.294	0.258	0.020	0.618	0.001
FBNL	RMA	3.865	3.847	0.310	0.289	0.024	0.706	0.393
PFD ML	RMA	3.094	3.108	2.018	0.392	0.030	0.966	0.001
PFD AP	RMA	2.841	2.839	0.063	0.400	0.031	0.983	0.897
FNAL	RMA	3.410	3.222	8.897	1.103	0.077	2.703	0.001
FNM SI	RMA	3.341	3.312	0.375	0.337	0.027	0.825	0.379
FNM AP	RMA	3.043	3.222	16.684	1.674	0.139	4.113	0.001
PFD AP	RMA	2.841	2.895	3.724	0.620	0.046	1.513	0.001
FNM AP	RMA	3.043	2.615	29.068	2.842	0.220	0.696	0.001

FHD SI/AP, superoinferior/anteposterior diameter of the proximal articulation; FH Dpt, mediolateral diameter of the proximal articulation; PFB, total mediolateral breadth of the proximal femur; FBNL, biomechanical length of the femoral neck; PFD ML/AP, mediolateral/anteposterior diameter of the proximal diaphysis (distal to the lesser trochanter); FNAL, anatomical length of the femoral neck; FNM SI/AP/ML, superoinferior/anteposterior/mediolateral diameter of the femoral neck; RMA, reduced major axis.





**Figure 4:** Bivariate scatter plots of selected parameters versus GMSize: (a) femoral head diameter (anterior to posterior); (b) anatomical neck length of the femur and (c) femoral neck (anteroposterior diameter versus superoinferior diameter).

The hypertrophied hip flexors of *Acinonyx*, and presumably of other felid taxa, are critical in the initial power input to the stroke cycle of the proximal segment of the hindlimb during deceleration of the leading limb prior to foot contact, whereas the extensors of the hip and knee ('stifle') joints are equally critical immediately after initial ground contact and the spike in the vertical component of the ground reaction force as the entire limb is extended. The extrinsic muscles of the felid hip, particularly the gluteals, have a broad insertion across the posterior aspect of the proximal femoral diaphysis,<sup>1,2,55,56,58</sup> whereas a principal intrinsic hip flexor, the *M. Psoas* muscle, is extremely well developed in *Acinonyx* compared with greyhounds. The *M. Psoas* muscle and the extrinsic hip-flexors are critical components of the accelerating leading limb during the areal phase of peak velocity galloping. Hypertrophy of the hip flexors and extensors associated with the proximal femoral diaphysis of felids, coupled with an elongate anatomical neck to increase their mechanical advantage,<sup>18,55-58</sup> would effectively reduce, rather than increase, anteroposterior bending moments in the proximal shaft and femoral neck and would account for the distinctive 'pinching' compared with the morphology of *Gorilla* and *Pan*. Functional and structural factors thus mediate the limited morphological distinctions observable in the proximal femur of these two extant mammalian families.

While the biomechanical significance of the proximal femur and its associated musculature cannot be overstated, it is equally critical to remember that osseous structures, particularly the diarthroidal joints, are neither designed nor precision engineered<sup>15,16,21,24,26,27</sup>, they emerge via a complex process of axial cellular differentiation at the growth plate<sup>7-10,59</sup>. Recent advances have shed considerable light on the developmental emergence, postnatal growth and underpinning cellular signalling mechanisms that regulate the emerging growth plate and its complexities.<sup>7,9,10,59</sup> Among living mammals, the emerging proximal femoral metaphysis comprises a singular basal growth plate, with discreet secondary ossification centres, either singular or dual, for the articulation and the greater trochanter.<sup>10,60</sup> *Pan* and *Homo* both share separate ossification centres for the articular head and greater trochanter, yet the cellular dynamics of the intervening proximal aspect of the femoral neck are subject to functionally distinct loading patterns which ultimately mediates absolute thickness of the cortex in this region.<sup>6,10</sup> The role of androgens and oestrogens in the cellular dynamics of the proximal femur are also likely critical in the observed sex-specific variance in absolute and relative neck length in humans and other mammals and, by extension, the reduced mechanical integrity and susceptibility to fracture with advanced age.<sup>59,60</sup> Results of this study suggest that the femoral neck of the living African apes is a worthy target for future research.

Results of this study confirm the prospectus that the proximal femur of two distinct families of mammals is extremely generalised in its external form; morphometric consistencies in extant African hominids and large-bodied felids considerably outweigh their observed distinctions. Further to this finding, these results underscore the necessity of a broader comparative context in understanding the nature of form and function in the mammalian postcranium. Nevertheless, where significant differences in proximal femoral form do occur – primarily in the relative size of the proximal articulation and in the anteroposterior/superoinferior and anteroposterior/mediolateral proportions of the neck and proximal diaphysis, respectively – these structural disparities are consistent with the mechanical requirements of their distinct locomotor modes and concomitant habitual stresses upon the proximal hindlimb. Further research into the morphology and functional significance of observed convergences and disparities in proximal femoral forms in other mammalian taxa can only increase our understanding of the underlying mechanisms and adaptive potential of this region of the vertebrate skeleton.

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