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# 1 New insights into patterns of integration in the femur 2 and pelvis among catarrhines

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## 15 Abstract

### 16 Objectives

17 Integration reflects the level of coordinated variation of the phenotype. The integration of  
18 postcranial elements can be studied from a functional perspective, especially with regards to  
19 locomotion. This study investigates the link between locomotion, femoral structural properties  
20 and femur-pelvis complex morphology.

### 21 Material and Methods

22 We measured (1) morphological integration between femoral and pelvic morphologies using  
23 geometric morphometrics, and (2) covariation between femoral/pelvic morphologies and  
24 femoral diaphyseal cross-sectional properties, which we defined as morpho-structural  
25 integration. Morphological and morpho-structural integration patterns were measured among  
26 humans (n=19), chimpanzees and bonobos (n=16), and baboons (n=14), whose locomotion are  
27 distinct.

### 28 Results

29 Baboons shows the highest magnitude of morphological integration and the lowest of morpho-  
30 structural integration. Chimpanzees and bonobos show intermediate magnitude of  
31 morphological and morpho-structural integration. Yet, body size seems to have a considerable  
32 influence on both integration patterns, limiting the interpretations. Finally, humans present the  
33 lowest morphological integration and the highest morpho-structural integration between  
34 femoral morphology and structural properties but not between pelvic morphology and femur.

### 35 Discussion

36 Morphological and morpho-structural integration depict distinct strategies among the samples.  
37 A strong morphological integration among baboon's femur-pelvis module might highlights  
38 evidence for long-term adaptation to quadrupedalism. In humans, it is likely that distinct  
39 selective pressures associated with the respective function of the pelvis and the femur tend to  
40 decrease morphological integration. Conversely, high mechanical loading on the hindlimbs  
41 during bipedal locomotion might result in specific combination of structural and morphological  
42 features within the femur.

43 **Keywords:** morpho-structural integration, biomechanics, locomotion, primates

## 44 1 Introduction

45 The tendency of morphological traits to exhibit coordinated variation is defined as  
46 morphological integration (Olson & Miller, 1958). Its study provides insights into a range of  
47 evolutionary trajectories of the phenotype (Ackermann, 2009; Goswami, Smaers, Soligo, &  
48 Polly, 2014; Anjali Goswami & Polly, 2010). Over the last few decades, this approach has been  
49 widely applied to investigate the link between skeletal morphological adaptations and  
50 locomotion. Among primates, integration of postcranial skeletal elements is more prominent in  
51 quadrupeds than in climbers and hominoids (Agosto & Auerbach, 2022; Jung, Simons, &  
52 Cramon-Taubadel, 2021; Villmoare, Fish, & Jungers, 2011). This is particularly apparent in the  
53 appendicular skeleton, either between homologous forelimb and hindlimb elements (humerus-  
54 femur), or between articulated elements within a limb (humerus-ulna / femur-tibia) (Conaway  
55 & von Cramon-Taubadel, 2022; Young, Wagner, & Hallgrímsson, 2010). The relatively low  
56 integration within the postcranial skeleton in hominoids has been interpreted as the result of  
57 functional dissociation between the lower and upper limbs during locomotion (Young et al.,  
58 2010). This independent variation of skeletal elements reflects some phenotypic plasticity  
59 among hominoids (Hansen & Houle, 2008; Wagner, Pavlicev, & Cheverud, 2007).

60 Generally, morphological integration defines semi-autonomous units, or modules, that are parts  
61 of an organism that present higher magnitude of integration between themselves than with other  
62 parts of the organism (Cheverud, 1996; Wagner, 1996; Wagner et al., 2007). Although there  
63 are many kinds of module (e.g. variational, anatomical, developmental, functional, see for  
64 examples Hallgrímsson et al., 2009; Klingenberg, 2008; Wagner et al., 2007), if one want to  
65 focus on the study of locomotion, there is a need to identify functional modules, meaning a  
66 module composed of features that act together to perform a specific function. Due to the shared  
67 muscles, ligaments or articular surfaces, it is generally considered that morphological  
68 integration between bones in the same joint chain results from functional interactions (Fabre,  
69 Goswami, Peigné, & Cornette, 2014; Hallgrímsson, Willmore, & Hall, 2002; Hanot, Herrel,  
70 Guintard, & Cornette, 2018; Klingenberg, 2009). From this perspective, the femur-pelvis  
71 module can be considered as functional module in which all elements are intimately linked to  
72 the locomotor function.

73 The degree of integration within the femur-pelvis module as a functional one was measured  
74 from geometric morphometrics data based on 3D anatomical landmarks among crab-eating  
75 macaques (*Macaca fascicularis*) and compared to other anatomical modules (Conaway,  
76 Schroeder, & von Cramon-Taubadel, 2018). The results of this study indicate greater  
77 integration within the femur-pelvis module than the humerus-scapula module. To our

78 knowledge, there has been no interspecies comparison of morphological integration within the  
79 femur-pelvis module that considers the overall morphology of both bones.

80 This study therefore proposes to measure morphological integration between the femur and  
81 pelvis among groups of primates with distinct positional repertoires. We furthermore propose  
82 an exploratory approach that incorporates bone structural properties, which are also related to  
83 locomotion. Integration is here a tool to quantify and assess the coordination of morphological  
84 and structural variation in the femur-pelvis module. Our aim is to investigate whether there are  
85 different levels of coordination in external morphology, and whether there is another facet of  
86 integration that do not only rely on external morphology within the femur-pelvis module.

## 87 1.1 Morpho-structural integration

88 The external morphology refers to the form and shape of bones (*i.e* its architecture) that can be  
89 measured morphometrically. This morphology is integrated and is primarily the result of long-  
90 term changes linked to the evolutionary trajectories at a species level, and largely influenced  
91 by its ancestral state. In the other hand, the internal structure on bones refers to both the  
92 trabecular organization (anisotropy of the network, thickness of the trabeculae, BV/TV) and  
93 cortical bone distribution (cortical thickness and orientation). The internal structure is manly  
94 considered to reflect the actual behaviours at an individual's level (Ruff, Holt, & Trinkaus,  
95 2006). Because of bone plasticity and remodelling process, the internal structure of long bones  
96 is a biomechanical indicator related to the stresses experienced by the skeleton, of which  
97 locomotion is a primary source (Biewener & Taylor, 1986; Lanyon & Rubin, 1984; Rubin &  
98 Lanyon, 1982). Concerning the cortical bone, the analysis of the cross-sectional geometric  
99 parameters of the diaphyseal sections (CSG) accounts theoretically for the structural response  
100 of the bone to mechanical loading due to locomotion (Burr, Ruff, & Johnson, 1989; Demes,  
101 Jungers, & Selpien, 1991; Lieberman, Polk, & Demes, 2004; Ruff, 2002a). In a palaeontological  
102 context, analysis of femoral diaphyseal CSG allows assumptions as to specific locomotor  
103 behaviours in specific environments (Daver et al., 2022; Marchi et al., 2016; Rodríguez,  
104 Carretero, García-González, & Arsuaga, 2018; Ruff, Burgess, Ketcham, & Kappelman, 2016).

105 However, this opposition between an external morphology as a result of long-terms changes at  
106 the species level and an internal structure as a result of short-term changes at the individual  
107 level should be tempered. For instance, the external morphology of hindlimb also undergo  
108 development throughout an individual's life. A notable example is the bicondylar angle in the  
109 distal femur in humans, which changes with age under the influence of mechanical stimuli  
110 linked to the initiation of a bipedal gait (Tardieu & Damsin, 1997; Tardieu, 1994). In hominins,  
111 the external morphology of the hindlimb is both driven by (phylo)genetic and mechanical  
112 influence to fulfill a given locomotion (Shefelbine, Tardieu, & Carter, 2002; Tardieu, 1999). It  
113 should be the same among other primate species. Also, the internal structure is also driven by  
114 genetic process since the cross-sectional shape and cortical distribution appear to be shared by  
115 individuals with distinct positional behavior and loading regime at both intra- (Cosnefroy et al.,  
116 2022; Hansen, Bredbenner, Nicolella, Mahaney, & Havill, 2009; Morimoto, De León, &  
117 Zollikofer, 2011) and inter (Morimoto, Nakatsukasa, Ponce de León, & Zollikofer, 2018;  
118 Morimoto, Zollikofer, & Ponce de León, 2012) specific levels among primates.

119 The changes in internal structure of long bones during the individual's life are the results of  
120 combined external and internal forces that are influenced by a multitude of factors, including  
121 body size and shape, sex, age, hormones, phylogeny, and biomechanical loading (Cowgill,

122 Harrington, MacKinnon, & Kurki, 2023; Frost, 2001; Libanati, Baylink, Lois-Wenzel,  
123 Srinivasan, & Mohan, 1999; Parfitt, 2002; Ruff et al., 2006). The CSG therefore may vary  
124 between species with a given locomotion. This applies particularly to humans in which  
125 differences in taxonomy (Puymeraill et al., 2012; Trinkaus & Ruff, 2012) or lifestyle (Marchi,  
126 2008; Saers et al., 2021; Shaw & Stock, 2013; Villotte, Samsel, & Sparacello, 2017) affect the  
127 geometry of the femoral diaphyseal section. Thus, the same CSG that are used to discriminate  
128 between locomotor modes (especially second moment of area) can be used to identify activity  
129 patterns within the same mode (Ruff, 2018). Conversely, some primates with different  
130 positional repertoires exhibit comparable CSG diaphyseal properties, both intra-specifically  
131 and inter-specifically (e.g. Cosnefroy et al., 2022; Nadell, Elton, & Kovarovic, 2021). As  
132 hypothesized by Carlson and colleagues, it is also likely that some locomotor modes do not  
133 meet the mechanical requirements to significantly modify the shape of diaphyseal sections  
134 (Carlson et al., 2006). Although CSG remain reliable tool for inferring bone loading (Pearson  
135 & Lieberman, 2004; Ruff, Holt, & Trinkaus, 2006), strict equivalence between CSG and  
136 positional repertoire remain discussed (Morimoto et al., 2011).

137 Thus, it appears that the phenotype adaptations to positional behaviours are reflected by both  
138 the in the external morphology and internal structure; under the combined influence of both  
139 long-term (phylo)genetic and short-term mechanical constraints. One may therefore ask how  
140 these external and internal features are combined to achieve a morpho-structural adaptation.  
141 However, only a few studies have explored so far the link between internal structure and  
142 morphological features. For example, Kubicka and Myszka have shown that there is no  
143 correlation between the CSG of the humeral diaphysis and the strength of the entheses of the  
144 upper limb in humans (Kubicka & Myszka, 2020). In addition, comparison between the CSG  
145 and the bi-acetabular width or neck anteversion angle has shown that the mediolateralization of  
146 cortical bone distribution across the femoral shaft in hominins may be a structural response to  
147 the lateral tilt of the centre of gravity associated with pelvic enlargement during bipedal walking  
148 (Ruff, 1995).

149 The relationship between morphological and structural variations and their connection with  
150 locomotion is still not well understood. To better assess this relationship in the context of an  
151 exploratory study, it is necessary to combine analyses that optimally quantify morphology and  
152 structure. In order to quantify morphology of the pelvis and the femur, we used landmark-based  
153 geometric morphometrics. Geometric morphometrics is an approach based on coordinates from  
154 homologous landmarks that are taken on specific structures which enables statistical  
155 comparison of their morphology (Bookstein, 1996; Mitteroecker & Gunz, 2009). This approach  
156 has been broadly used in biological anthropology to describe and quantify morphology of  
157 several anatomical features (for a review see Mitteroecker & Schaefer, 2022). Furthermore, the  
158 use of geometric morphometrics datasets is common in the study of integration (Agosto &  
159 Auerbach, 2022; Hanot et al., 2018; Klingenberg, 2009; Komza, Viola, Netten, & Schroeder,  
160 2022; Neaux et al., 2017; Torres-Tamayo et al., 2020).

161 We applied three-dimensional landmark geometric morphometrics to provide quantitative  
162 morphological data from the pelvis and femur. We statistically compared these quantitative  
163 morphological data to CSG from the femoral diaphysis, which are also quantitative structural  
164 data. This allows us to assess covariation between femoral or pelvic morphology and the  
165 structural properties of the femoral shaft in order to describe what we call morpho-structural

166 integration. In this study, this refers to the evaluation of covariation between the morphology  
167 of the femur or pelvis, and the structural properties of the femoral shaft.

## 168 1.2 Object and aims of the study

169 The purpose of this study is to explore the morphological and morpho-structural integration  
170 within the femur-pelvis module and their relation to the positional repertoire (*i.e* posture and  
171 locomotion) in primates. To do so we use three models of primates that exhibit distinct  
172 positional repertoires (Table 1): (1) humans (*Homo sapiens*) of which the positional repertoire  
173 is almost restricted to bipedalism with a fully orthograde posture in adults (but see  
174 Venkataraman, Kraft, & Dominy, 2013); (2) olive baboons (*Papio anubis*) considered as mainly  
175 terrestrial and quadrupedal with a pronograde posture in adults (Druelle, Aerts, & Berillon,  
176 2017; Hunt, 2016; Rose, 1977); (3) chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*)  
177 that exhibit a wider positional repertoire (*i.e* more diversity) than humans and baboons,  
178 including knuckle-walking, arboreal climbing and suspensory behaviours and both orthograde  
179 and pronograde posture (Doran, 1992; Hunt, 1992; Williams, Prang, Russo, Young, & Gebo,  
180 2023). For each three models, we explore potential patterns of integration at three levels:

- 181 - the magnitude of morphological integration between the external morphology of the  
182 pelvis and that of the femur. This allows us to test if morphological integration in the  
183 femur-pelvis module is common or differ between these models and if it is linked to  
184 their positional repertoire' characteristics.  
185
- 186 - the magnitude of morpho-structural integration between the CSG of the femoral  
187 diaphysis and the external morphology of the femur. This allows us to test if morpho-  
188 structural integration within the femur is common or differ between these models and if  
189 it is linked to their positional repertoire' characteristics.  
190
- 191 - the magnitude of morpho-structural integration between the CSG of the femoral  
192 diaphysis and the external morphology of the pelvis. This allows us to test if morpho-  
193 structural integration between the femur and the pelvis is common or differ between  
194 these models and if it is linked to their positional repertoire' characteristics.  
195

196 Uncovering these patterns of integration would enable the detection and description of complex  
197 adaptations to positional repertoires that are based on potentially integrated morphological and  
198 structural variations of the postcranial skeleton, using three primate models with distinct  
199 behaviours.

## 200 2 Material and methods

### 201 2.1 Material

202 The sample contains 55 femora and right hemi-pelves from individuals of the genera *Homo*,  
203 *Pan*, and *Papio*. The bones were either reconstructed from surface scans or segmented from  
204 CT-scans. The humans sample consists in CT-scans of hospital patients living in Marseille were  
205 collected from the PACS (Picture Archiving and Communication System, McKesson Medical  
206 Imaging Group, Richmond, BC, Canada) of the Assistance Publique des Hôpitaux de Marseille  
207 (AP-HM). All CT images and personal patient information were anonymized before collection

208 following the personal privacy standards of the French National Ethical Committee and the  
 209 Helsinki Declaration of 1975, revised in 1983. This procedure is the standard protocol for  
 210 retrospective research studies involving medical images. The baboon sample encompasses CT-  
 211 scan of adults specimens in captivity (< 4.5 years old) all originating from a single population  
 212 housed at the Station de Primatologie of the Centre national de la Recherche Scientifique at  
 213 Rousset-sur-Arc, France (see more information about this population in former publications:  
 214 e.g. Berillon et al., 2010; Boulinguez-Ambroise et al., 2021; Cosnefroy et al., 2022; Druelle,  
 215 Aerts, D’Août, Moulin, & Berillon, 2017). Finally, the chimpanzees and bonobos sample  
 216 contains both surface scan (for the pelvis only) and CT-scans (for both the pelvis and the femur)  
 217 that were obtained from open online databases or originating from the Musée Royal de  
 218 l’Afrique Centrale of Tervuren, Belgium (see more individual information in supplementary  
 219 material).

220 We only include adults and both sexes are considered. In order to avoid juveniles in non-human  
 221 primates samples for which we do not have precise age (*i.e* the *Pan* specimens), only specimens  
 222 that present a fully erupted third molar to the occlusal surface on their associated cranial remain  
 223 were considered. Common chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) are  
 224 combined into a single group to enable more robust statistical analyses, and because of the  
 225 slight locomotor differences between the two species documented repertoire (D’Aout et al.,  
 226 2004; Perrot, Narat, & Druelle, 2022).

227 Surface scan acquisitions were performed by the authors using EinScan Pro Fixed Scan with  
 228 turntable and 0.04 mm of accuracy, and the segmentations from CT-scans were performed with  
 229 Avizo 7.1 (Thermo Fisher Scientific).

230

231 *Table 1 : Study sample description. Percentages are average values of locomotor bouts. †Climbing bouts can also be*  
 232 *considered at the species level (Kraft, Venkataraman, & Dominy, 2014; Venkataraman et al., 2013); ‡data for Pan: (Doran,*  
 233 *1992, 1997; Hunt, 1992; Sarringhaus et al., 2014) ; §data for Papio: (Druelle et al. 2017; Hunt, 2016; Rose, 1977).*

<i>Genera</i>	<i>species</i>	<b>Number of specimens (F/M/Indet)</b>	<b>Positional repertoire</b>
<i>Homo</i>	<i>sapiens</i>	19 (9/10/0)	Bipedalism (almost 100%) <sup>†</sup>
<i>Pan</i>	<i>troglodytes,</i> <i>paniscus</i>	16 (6/6/4), 6 (2/4)	Knuckle-walking (mean 83%), vertical climbing (mean 8,5%), bipedalism (mean 1,2%), others (mean 7,3%) <sup>‡</sup>
<i>Papio</i>	<i>anubis</i>	14 (12/2/0)	Quadrupedalism (mean 98,7%), vertical climbing (mean 1%), others (mean 0,3%), <sup>§</sup>

234

## 235 2.2 Methods

### 236 2.2.1 Geometric morphometrics

237 The external morphology of both the femur and the pelvis are assessed in each sample by  
238 landmark-based geometric morphometrics. For each specimen, the landmark datasets consist  
239 of 27 femoral and 34 pelvic landmarks of type I (true anatomical) and II (reproducible). Type  
240 I landmarks are derived from the set proposed by Weaver which serve as published reference  
241 for anatomical landmarks used to compare external morphology and cross-sectional geometry  
242 (see Weaver, 2003). From this basis 250 surface semi-landmarks are projected on the femoral  
243 surface, and 217 curve semi-landmarks and 50 surface semi-landmarks on the pelvic surface  
244 (Figure 1). Pelvic landmarks are generated with Viewbox 4.1 (dhal.com) and femoral  
245 landmarks with the *Morpho* R-package v2.9 (Schlager, 2017). Once set, the semi-landmarks  
246 are slid using the least squares method to maximize the homology between individuals  
247 landmark configurations (Gunz, Mitteroecker, & Bookstein, 2005). For each group, we then  
248 perform Generalized Procrustes analysis (GPA) on the landmarks configurations to separate  
249 shape from overall size, position and orientation (Bookstein, 1996, 2017; Rohlf & Slice, 1990).  
250 The Procrustes coordinates that result from this analysis are used to assess both morphological  
251 and morpho-structural integration.

252 All statistical analyses are performed using Morpho J (Klingenberg, 2011), *geomorph* v4.0.2  
253 (Adams, Collyer, Kaliontzopoulou, & Sherratt, 2016; Baken, Collyer, Kaliontzopoulou, &  
254 Adams, 2021) and *Morpho* v2.9 (Schlager, 2017) R packages.

### 255 2.2.2 Allometry

256 The variation in body size and mass, mainly due to sexual dimorphism in primates, can  
257 influence both external morphology and internal structure and lead to overestimate phenotypic  
258 variation (e.g. Bastir et al., 2017; Carlson, 2005; Klingenberg & Marugán-Lobón, 2013;  
259 Lacoste Jeanson, Santos, Villa, Banner, & Brůžek, 2018; Ruff, 2002b). In our study, body mass  
260 and size should therefore influence magnitude of morphological and morpho-structural  
261 integrations. We evaluate the impact of body mass and size in both by using allometry in  
262 external morphological data. To do so, we create another dataset of geometric morphometrics  
263 from which allometry has been removed. To remove allometry, we calculate the centroid size  
264 and extract residuals from multivariate regressions of Procrustes coordinates on the logarithm  
265 of the centroid size for each landmark conformation (Monteiro, 1999). The centroid size is a  
266 measure of scale for landmark configurations classically used to assess allometry in geometric  
267 morphometrics analyses (Bookstein, 1992; Mitteroecker and Gunz, 2009). Here, the centroid-  
268 size is calculated from the entire landmark configuration encompassing both anatomical and  
269 semi-landmarks. Allometric residuals are used in addition to Procrustes coordinates to assess  
270 both morphological and morpho-structural integration.

### 271 2.2.3 Morphological integration

272 The magnitude of morphological integration is assessed by the Covariance Ratio (CR) using  
273 the *modularity.test* function in *geomorph* (Adams, 2016). The CR compares the ratio of the sum  
274 of squared covariances within a set of variables to that between different sets of variables ( $S_1$   
275 and  $S_2$ ) in order to quantify the modular structure of the whole (Adams, 2016).

276 The CR of datasets  $S_1$  and  $S_2$  is calculated as follows:



277

$$CR = \sqrt{\frac{\text{trace}(S_{12}S_{21})}{\sqrt{\text{trace}(S^*_{11}S^*_{11})\text{trace}(S^*_{22}S^*_{22})}}}$$

278 Where  $S^*_{11}$  and  $S^*_{22}$  are the covariance matrices within  $S_1$  and  $S_2$  respectively, and  $S_{12}$  and  $S_{21}$   
279 the covariance matrices between  $S_1$  and  $S_2$  respectively. In this study, we consider the Procrustes  
280 coordinates (or allometric residuals) from the pelvis as the first set ( $S_1$ ), and the landmark  
281 Procrustes coordinates (or allometric residuals) from the femur as the second set ( $S_2$ ). The CR  
282 is calculated within each sample (Table 2). Unlike other integration measures (e.g. Escoffier's  
283 RV coefficient), the CR is less sensitive to the sample size and number of variables and is  
284 therefore suited to geometric morphometrics datasets (e.g. Adams & Collyer, 2018; Evans et  
285 al., 2021; Janin, 2021). Higher CR values indicate higher integration (or lower modular signal)  
286 between the two sets of morphometric variables (Adams, 2016).

287 For intergroup comparisons, we used the CR effect size difference which evaluate the difference  
288 between two integration effect sizes (Adams & Collyer, 2016, 2019). This difference was  
289 assessed either based on Procrustes coordinates or allometric residuals using the *compare.CR*  
290 function in *geomorph* (Adams & Collyer, 2019). This function allows to statistically compare  
291 the modular signal between pairs of datasets (here the *Homo*, *Pan* and *Papio* samples) and is  
292 here used to determine which group present the highest magnitude of morphological integration  
293 (Table 3).

#### 294 2.2.4 Morpho-structural integration

295 To our knowledge, there have been no studies focusing on the morpho-structural integration  
296 between external morphology and internal structure by evaluating it through the covariation  
297 between landmark-based geometric morphometrics datasets and CSG of long bone. In the  
298 absence of any reference to evaluate this integration statistically, we assess morpho-structural  
299 integration using 2-block Partial Least Squares (2b-PLS). This method enables evaluation of  
300 the covariation between different types of variables, including landmark conformations (Rohlf  
301 & Corti, 2000). For each group separately, the first block of the 2b-PLS consists in external  
302 morphological variables, and the second block consists in internal structure variables.

303 The external morphology is assessed via the geometric morphometrics variables that are either  
304 the whole set of Procrustes coordinates from the GPA, or the allometric residuals from both the  
305 femur and the pelvis. To consider more localized morphological variation that can impact the  
306 morpho-structural integration with CSG, we also perform intra-group Principal Component  
307 Analysis on Procrustes coordinates and allometric residuals. The first two Principal Component  
308 that account for more than 10% of variance (meaning PC1 and PC2 for Procrustes coordinates  
309 and rPC1 and rPC2 for allometric residuals) are used to identify these specific morphological  
310 variations; and also account as external morphology variables in 2b-PLS along with CSG.

311 The internal structure is assessed via CSG of the femoral diaphysis. CSG are measured for the  
312 entire femoral shaft (61 sections from 20% to 80% of the biomechanical length), but also locally  
313 on shaft portions (15 sections at distal: 20%-35%, mid-distal: 35%-50%, mid-proximal: 50%-  
314 65%, and proximal: 65%-80%). The CSG for the femoral shaft include the ratio of second  
315 moments of area relative to the anteroposterior and mediolateral axes ( $I_x/I_y$ ) and the ratio of  
316 maximum/minimum second moments of area ( $I_{max}/I_{min}$ ). These CSG account for the  
317 distribution of cortical bone within a section (Carlson et al., 2006; Ruff, 1995; Sarringhaus,  
318 MacLachy, & Mitani, 2016), and are indicators of bending rigidity which is prevalent loading

319 during locomotion (Lieberman et al., 2004; Ruff, Trinkaus, Walker, & Larsen, 1993; Schaffler,  
320 Burr, Jungers, & Ruff, 1985). The use ratios are chosen to avoid further standardization of the  
321 CSG data. The CSG are extracted using the R *morphomap* package v1.3 (Profico, Bondioli,  
322 Raia, O’Higgins, & Marchi, 2020).

323 To resume, in both the femur and the pelvis the morpho-structural integration is analysed  
324 through 2b-PLS of (Tables 4 and 5):

- 325 - Block 1: Procrustes coordinates/Allometric residuals (whole set) vs Block 2: Ix/Iy on  
326 the entire diaphysis (61 sections)
- 327 - Block 1: Procrustes coordinates/Allometric residuals (whole set) vs Block 2: I<sub>max</sub>/I<sub>min</sub>  
328 on the entire diaphysis (61 sections)
- 329 - Block 1: Procrustes coordinates/Allometric residuals (whole set) vs Block 2: Ix/Iy on  
330 shaft portions (15 sections)
- 331 - Block 1: Procrustes coordinates/Allometric residuals (whole set) vs Block 2: I<sub>max</sub>/I<sub>min</sub>  
332 on shaft portions (15 sections)
- 333 - Block 1: PC1/rPC1 vs Block 2: Ix/Iy on the entire diaphysis (61 sections)
- 334 - Block 1: PC1/rPC1 vs Block 2: I<sub>max</sub>/I<sub>min</sub> on the entire diaphysis (61 sections)
- 335 - Block 1: PC1/rPC1 vs Block 2: Ix/Iy on shaft portions (15 sections)
- 336 - Block 1: PC1/rPC1 vs Block 2: I<sub>max</sub>/I<sub>min</sub> on shaft portions (15 sections)
- 337 - Block 1: PC2/rPC2 vs Block 2: Ix/Iy on the entire diaphysis (61 sections)
- 338 - Block 1: PC2/rPC2 vs Block 2: I<sub>max</sub>/I<sub>min</sub> on the entire diaphysis (61 sections)
- 339 - Block 1: PC2/rPC2 vs Block 2: Ix/Iy on shaft portions (15 sections)
- 340 - Block 1: PC2/rPC2 vs Block 2: I<sub>max</sub>/I<sub>min</sub> on shaft portions (15 sections)

### 341 3 Results

342 The detailed results from the geometric morphometrics analyses and the CSG values are  
343 presented in the supplementary material.

#### 344 3.1 Morphological integration in the femur-pelvis module

345 CR analysis from Procrustes coordinates reveal the lowest value in humans and the highest  
346 value in baboons (Table 2, Figure 2). Between taxa, humans show significant differences with  
347 baboons and chimpanzees (Table 3). The CR effect size between baboons and chimpanzees is  
348 not statistically significantly different (Table 3).

349 Analysis of CR from allometric residuals again produces the lowest values in humans and  
350 higher values in baboons and chimpanzees (Table 2, Figure 2). Here, humans show significant  
351 differences with baboons but not with chimpanzees and the CR effect size between baboons  
352 and chimpanzees differs significantly (Table 3).

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Table 2: Covariance Ratio based on data on the morphometric shape of the femur and the pelvis in each dataset. First line: CR based on Procrustes coordinates; second line in parentheses: CR based on allometric residuals.

Group	CR	p-value	Confidence Interval		CR effect size
<i>Homo</i>	0.5525 (0.573)	0.001 (0.001)	0.5694 (0.5756)	0.7919 (0.807)	-28.6216 (-28.6743)
<i>Papio</i>	0.7179 (0.7106)	0.001 (0.001)	0.7132 (0.71)	0.9307 (0.9079)	-24.9152 (-27.0324)
<i>Pan</i>	0.6758 (0.6422)	0.001 (0.001)	0.6476 (0.6219)	0.8647 (0.8409)	-26.7606 (-26.3538)

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Table 3: CR effect size difference obtained for each pair of samples. First line: CR effect size difference from CR based on Procrustes coordinates; second line in parentheses: CR effect size difference from CR based on allometric residuals.

Pairs of samples	CR effect size difference	p-value
<i>Homo-Pan</i>	1.880 (0.186)	0.04 (0.853)
<i>Homo-Papio</i>	2.916 (2.6029)	0.004 (0.0092)
<i>Pan-Papio</i>	1.063 (2.305)	0.288 (0.021)

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360

## 361 3.2 Morpho-structural integration

### 362 3.2.1 *Homo*

363 In humans, femoral morphology (entire set of Procrustes coordinates) covaries with Ix/Iy taken  
364 from the entire diaphysis (Table 4). The femoral morphology also covaries with Ix/Iy locally in  
365 the mid-distal and mid-proximal portions and with I<sub>max</sub>/I<sub>min</sub> locally in the proximal portion  
366 (Table 4). When allometry is corrected, the integration between femoral morphology (entire set  
367 of allometric residuals) and CSG is similar to that without correction (Table 4), since allometry  
368 do not significantly affect femoral morphological variation in our human sample (predicted:  
369 2.27%,  $p = 0.87$ ). The morphology captured by the PC2 (not PC1) of the femoral morphometric  
370 analysis covaries with both Ix/Iy and I<sub>max</sub>/I<sub>min</sub> taken from the entire diaphysis (Figure 2, Table  
371 4). PC2 of the femur also covaries with Ix/Iy locally in the mid-distal, mid-proximal and  
372 proximal portions and with I<sub>max</sub>/I<sub>min</sub> locally in the distal portion (Figure 2, Table 4). The PC2  
373 of the femur represents variations in the neck-shaft angle, projection of the greater trochanter,  
374 mediolateral curvature of the diaphysis and posterolateral projection of the lateral condyle  
375 (Figure 2). When allometry is corrected, the integration between rPC2 and CSG is similar to  
376 that with PC2 which captured the same morphology (Figure 2, Table 4).

377 Concerning the pelvis, pelvic morphology and pelvic morphology principal components do not  
378 covary with any CSG, whether allometry is corrected or not (Table 5).

### 379 3.2.2 *Pan*

380 In *Pan* genus, femoral morphology does not covary with any CSG, whether the allometry is  
381 corrected or not (Table 4). Conversely, PC1 of the femoral morphometric analysis covaries with  
382 Ix/Iy taken from the entire diaphysis (Figure 2, Table 4). PC1 of the femur represents variation  
383 in the superior-inferior projection of the epiphyses and height of the greater trochanter (Figure  
384 2). When allometry is corrected (predicted: 2.90%,  $p = 0.72$ ), the integration between rPC1 and  
385 CSG is similar to that with PC1 which captured the same morphology (Figure 2). Additionally,  
386 PC2 of the femoral morphometric analysis covaries with I<sub>max</sub>/I<sub>min</sub> when taken locally in the  
387 mid-distal diaphysis (Figure 2, Table 4). PC2 of the femur represents variation in the femoral  
388 head dimensions, anteroposterior and mediolateral curvatures, mediolateral width of the distal  
389 epiphysis (Figure 2). When allometry is corrected, the integration between rPC2 and CSG is  
390 similar to that with PC2 which captured the same morphology (Figure 2, Table 4).

391 Concerning the pelvic morphology, it covaries with I<sub>max</sub>/I<sub>min</sub> taken from the entire diaphysis  
392 (Table 5). Allometry had a significant impact on pelvic morphology variation in the *Pan* sample  
393 (predicted: 10.60%,  $p = 0.007$ ). When allometry is corrected, the pelvic morphology does not  
394 covary with any CSG when taken from the entire diaphysis (Table 5). Conversely, pelvic  
395 morphology covaries with Ix/Iy when taken locally in the mid-distal diaphysis whether the  
396 allometry is corrected or not. The PC1 of the pelvic morphometric analysis covaries with Ix/Iy  
397 when taken from the entire diaphysis (Figure 3, Table 5). PC1 of the pelvis also covaries with  
398 Ix/Iy locally in the mid-proximal and proximal portions and with I<sub>max</sub>/I<sub>min</sub> in the mid-  
399 proximal diaphysis (Figure 3, Table 5). The PC1 of the pelvis represents variation in the  
400 acetabulum width, length of the lower pubic ramus and width of the ilium (Figure 3). When  
401 allometry is corrected, rPC do not covary with any CSG (Figure 3, Table 5).

403 In olive baboons, femoral morphology and femoral morphology principal components do not  
 404 covary with any CSG, whether allometry is corrected or not (Table 4).

405 Concerning the pelvic morphology, it does not covary with any CSG, whether allometry is  
 406 corrected or not (Table 5). However, the PC1 of the of the pelvic morphometric analysis  
 407 covaries with Ix/Iy but only locally in the mid-distal portion (Figure 3, Table 5). The PC1 of  
 408 the pelvis represents the length of the inferior pubic ramus, dimensions of the acetabulum and  
 409 the relative height of the sacro-lumbar joint (Figure 3). Although allometry do not significantly  
 410 affect the morphological variation of the pelvis in our baboon sample (predicted: 8.87%, p =  
 411 0.27), this specific and localized integration between PC1 and Ix/Iy is not present with rPC1  
 412 (Figure 3, Table 5).

413 *Table 4: Detailed results of the 2b-PLS tests between femoral geometric morphometrics data and cross-sectional geometry*  
 414 *parameters, measured on the whole diaphysis (the 61 sections between 20% and 80% of the biomechanical length) and on*  
 415 *diaphyseal portions (15 sections each). The Procrustes coordinates (or allometric residuals) provide overall external femoral*  
 416 *morphology, the principal components (PC or rPC) indicate a specific morphology depicted in supplementary materials*  
 417 *figures. First line: 2b-PLS based on Procrustes coordinates; second line in parentheses: 2b-PLS based on allometric residuals.*  
 418 *Highlighted boxes show the diaphyseal stages with a significant result, bold mentions represent significant 2b-PLS.*

Morphostructural integration: FEMUR vs CSG		Entire diaphysis		20% to 35% of length		35% to 50% of length		50% to 65% of length		65% to 80% of length	
		r-PLS	p-value	r-PLS	p-value	r-PLS	p-value	r-PLS	p-value	r-PLS	p-value
Femoral Procrust coordinates (allometric residuals) vs Ix/Iy	<i>Homo</i>	<b>0.685</b> <b>(0.707)</b>	<b>0.041</b> <b>(0.024)</b>	0.507 (0.45)	0.345 (0.504)	<b>0.706</b> <b>(0.738)</b>	<b>0.031</b> <b>(0.017)</b>	<b>0.7</b> <b>(0.716)</b>	<b>0.036</b> <b>(0.02)</b>	0.59 (0.606)	0.136 (0.094)
	<i>Papio</i>	0.553 (0.546)	0.981 (0.977)	0.55 (0.567)	0.904 (0.788)	0.561 (0.558)	0.871 (0.814)	0.623 (0.61)	0.688 (0.648)	0.747 (0.65)	0.177 (0.447)
	<i>Pan</i>	0.528 (0.448)	0.374 (0.713)	0.535 (0.443)	0.335 (0.666)	0.539 (0.514)	0.335 (0.395)	0.653 (0.465)	0.062 (0.572)	0.534 (0.438)	0.355 (0.704)
Femoral Procrust coordinates (allometric residuals) vs I <sub>max</sub> /I <sub>min</sub>	<i>Homo</i>	0.635 (0.632)	0.141 (0.136)	0.497 (0.492)	0.406 (0.403)	0.488 (0.468)	0.438 (0.462)	0.438 (0.413)	0.583 (0.644)	<b>0.718</b> <b>(0.752)</b>	<b>0.044</b> <b>(0.026)</b>
	<i>Papio</i>	0.706 (0.73)	0.519 (0.34)	0.633 (0.631)	0.641 (0.545)	0.638 (0.678)	0.622 (0.36)	0.674 (0.676)	0.478 (0.366)	0.667 (0.672)	0.501 (0.39)
	<i>Pan</i>	0.589 (0.493)	0.234 (0.643)	0.545 (0.487)	0.284 (0.495)	0.599 (0.49)	0.161 (0.49)	0.511 (0.383)	0.42 (0.907)	0.557 (0.531)	0.259 (0.287)
PC1 (rPC1) FEMUR vs Ix/Iy	<i>Homo</i>	0.126 (0.125)	0.974 (0.975)	0.098 (0.237)	0.904 (0.44)	0.132 (0.075)	0.831 (0.964)	0.052 (0.059)	0.951 (0.937)	0.107 (0.104)	0.876 (0.876)
	<i>Papio</i>	0.36 (0.42)	0.849 (0.648)	0.378 (0.4)	0.276 (0.248)	0.324 (0.389)	0.376 (0.253)	0.154 (0.203)	0.98 (0.894)	0.074 (0.14)	0.954 (0.985)
	<i>Pan</i>	<b>0.546</b> <b>(0.582)</b>	<b>0.028</b> <b>(0.017)</b>	0.42 (0.407)	0.075 (0.08)	0.293 (0.268)	0.189 (0.252)	0.214 (0.195)	0.428 (0.47)	0.195 (0.246)	0.433 (0.287)

<b>PC1 (rPC1) FEMUR vs Imax/Imin</b>	<i>Homo</i>	0.566 (0.566)	0.092 (0.089)	0.437 (0.417)	0.103 (0.123)	0.481 (0.472)	0.068 (0.078)	0.1 (0.108)	0.852 (0.823)	0.139 (0.12)	0.886 (0.936)
	<i>Papio</i>	0.55 (0.601)	0.238 (0.147)	0.412 (0.456)	0.24 (0.17)	0.529 (0.573)	0.074 (0.057)	0.463 (0.51)	0.195 (0.137)	0.337 (0.364)	0.415 (0.332)
	<i>Pan</i>	0.477 (0.478)	0.157 (0.15)	0.395 (0.384)	0.128 (0.131)	0.464 (0.46)	0.053 (0.054)	0.462 (0.473)	0.082 (0.067)	0.084 (0.098)	0.963 (0.923)
<b>PC2 (rPC2) FEMUR vs Ix/Iy</b>	<i>Homo</i>	<b>0.586</b> <b>(0.585)</b>	<b>0.018</b> <b>(0.018)</b>	0.343 (0.328)	0.21 (0.241)	<b>0.604</b> <b>(0.615)</b>	<b>0.017</b> <b>(0.014)</b>	<b>0.606</b> <b>(0.605)</b>	<b>0.012</b> <b>(0.008)</b>	<b>0.466</b> <b>(0.458)</b>	<b>0.044</b> <b>(0.047)</b>
	<i>Papio</i>	0.442 (0.452)	0.529 (0.508)	0.462 (0.54)	0.157 (0.076)	0.255 (0.277)	0.532 (0.48)	0.423 (0.43)	0.231 (0.215)	0.353 (0.368)	0.437 (0.4)
	<i>Pan</i>	0.31 (0.288)	0.417 (0.492)	0.192 (0.187)	0.584 (0.592)	0.128 (0.112)	0.679 (0.742)	0.318 (0.295)	0.183 (0.765)	0.324 (0.299)	0.164 (0.215)
<b>PC2 (rPC2) FEMUR vs Imax/Imin</b>	<i>Homo</i>	<b>0.66</b> <b>(0.646)</b>	<b>0.025</b> <b>(0.025)</b>	<b>0.51</b> <b>(0.485)</b>	<b>0.043</b> <b>(0.061)</b>	0.356 (0.35)	0.261 (0.276)	0.243 (0.242)	0.37 (0.379)	0.51 (0.516)	0.113 (0.107)
	<i>Papio</i>	0.516 (0.522)	0.357 (0.343)	0.446 (0.537)	0.166 (0.077)	0.208 (0.215)	0.74 (0.723)	0.277 (0.297)	0.682 (0.627)	0.453 (0.463)	0.195 (0.181)
	<i>Pan</i>	0.425 (0.425)	0.251 (0.253)	0.26 (0.258)	0.389 (0.396)	<b>0.56</b> <b>(0.579)</b>	<b>0.01</b> <b>(0.007)</b>	0.196 (0.197)	0.664 (0.657)	0.157 (0.159)	0.714 (0.703)

419

420

421 Table 5: Detailed results of the 2b-PLS tests between pelvic geometric morphometrics data and cross-sectional geometry  
422 parameters, measured on the whole diaphysis (the 61 sections between 20% and 80% of the biomechanical length) and on  
423 diaphyseal portions (15 sections each). The Procrustes coordinates (or allometric residuals) provide overall external pelvic  
424 morphology, the principal components (PC or rPC) indicate a specific morphology depicted in supplementary materials  
425 figures. First line: 2b-PLS based on Procrustes coordinates; second line in parentheses: 2b-PLS based on allometric residuals.  
426 Highlighted boxes show the diaphyseal stages with a significant result, bold mentions represent significant 2b-PLS.

Morphostructural integration: PELVIS vs CSG		Entire diaphysis		20% to 35% of length		35% to 50% of length		50% to 65% of length		65% to 80% of length	
		r-PLS	p-value	r-PLS	p-value	r-PLS	p-value	r-PLS	p-value	r-PLS	p-value
Pelvic Procrust coordinates (allometric residuals) vs Ix/Iy	<i>Homo</i>	0.66 (0.662)	0.829 (0.778)	0.769 (0.65)	0.287 (0.796)	0.673 (0.654)	0.768 (0.811)	0.623 (0.615)	0.929 (0.918)	0.708 (0.692)	0.611 (0.632)
	<i>Papio</i>	0.82 (0.734)	0.476 (0.811)	0.822 (0.816)	0.318 (0.207)	0.84 (0.646)	0.214 (0.922)	0.864 (0.746)	0.131 (0.574)	0.743 (0.738)	0.737 (0.612)
	<i>Pan</i>	0.711 (0.774)	0.307 (0.158)	0.67 (0.724)	0.473 (0.332)	<b>0.835</b> <b>(0.856)</b>	<b>0.013</b> <b>(0.007)</b>	0.714 (0.739)	0.3 (0.282)	0.719 (0.69)	0.304 (0.538)
Pelvic Procrust coordinates (allometric residuals) vs I <sub>max</sub> /I <sub>min</sub>	<i>Homo</i>	0.707 (0.696)	0.648 (0.642)	0.687 (0.67)	0.73 (0.721)	0.672 (0.687)	0.748 (0.617)	0.734 (0.702)	0.468 (0.562)	0.761 (0.717)	0.356 (0.525)
	<i>Papio</i>	0.664 (0.657)	0.987 (0.973)	0.714 (0.722)	0.873 (0.696)	0.815 (0.686)	0.352 (0.812)	0.662 (0.645)	0.967 (0.915)	0.699 (0.697)	0.905 (0.773)
	<i>Pan</i>	<b>0.81</b> <b>(0.809)</b>	<b>0.031</b> <b>(0.053)</b>	0.695 (0.702)	0.353 (0.44)	0.651 (0.756)	0.572 (0.187)	0.723 (0.764)	0.241 (0.15)	0.678 (0.722)	0.479 (0.38)
PC1 (rPC1) PELVIS vs Ix/Iy	<i>Homo</i>	0.429 (0.433)	0.141 (0.143)	0.412 (0.211)	0.105 (0.534)	0.455 (0.389)	0.073 (0.158)	0.264 (0.346)	0.272 (0.157)	0.304 (0.433)	0.257 (0.077)
	<i>Papio</i>	0.535 (0.432)	0.26 (0.561)	<b>0.577</b> <b>(0.224)</b>	<b>0.04</b> <b>(0.704)</b>	0.271 (0.209)	0.467 (0.717)	0.445 (0.284)	0.176 (0.588)	0.514 (0.569)	0.112 (0.077)
	<i>Pan</i>	<b>0.537</b> <b>(0.402)</b>	<b>0.029</b> <b>(0.166)</b>	0.213 (0.216)	0.481 (0.464)	0.225 (0.139)	0.354 (0.625)	<b>0.463</b> <b>(0.364)</b>	<b>0.031</b> <b>(0.107)</b>	<b>0.505</b> <b>(0.411)</b>	<b>0.013</b> <b>(0.076)</b>
PC1 (rPC1) PELVIS vs I <sub>max</sub> /I <sub>min</sub>	<i>Homo</i>	0.482 (0.374)	0.204 (0.558)	0.318 (0.375)	0.314 (0.197)	0.232 (0.239)	0.592 (0.564)	0.098 (0.138)	0.864 (0.732)	0.438 (0.465)	0.162 (0.115)
	<i>Papio</i>	0.484 (0.519)	0.419 (0.332)	0.232 (0.265)	0.667 (0.553)	0.412 (0.339)	0.198 (0.361)	0.431 (0.449)	0.268 (0.222)	0.404 (0.447)	0.272 (0.183)
	<i>Pan</i>	0.411 (0.415)	0.291 (0.286)	0.161 (0.238)	0.755 (0.456)	0.209 (0.08)	0.47 (0.93)	<b>0.488</b> <b>(0.34)</b>	<b>0.035</b> <b>(0.252)</b>	0.262 (0.259)	0.35 (0.334)
PC2 (rPC2) PELVIS vs Ix/Iy	<i>Homo</i>	0.286 (0.256)	0.576 (0.653)	0.449 (0.263)	0.066 (0.353)	0.209 (0.099)	0.637 (0.937)	0.173 (0.157)	0.549 (0.59)	0.201 (0.207)	0.555 (0.538)
	<i>Papio</i>	0.422 (0.423)	0.625 (0.616)	0.425 (0.426)	0.211 (0.21)	0.257 (0.267)	0.577 (0.54)	0.251 (0.253)	0.747 (0.737)	0.277 (0.278)	0.672 (0.674)
	<i>Pan</i>	0.174 (0.227)	0.841 (0.647)	0.192 (0.296)	0.542 (0.242)	0.118 (0.141)	0.725 (0.614)	0.155 (0.152)	0.65 (0.687)	0.143 (0.169)	0.63 (0.535)
	<i>Homo</i>	0.409	0.426	0.378	0.208	0.074	0.985	0.106	0.843	0.11	0.882

<b>PC2 (rPC2) PELVIS vs Imax/Imin</b>		(0.366)	(0.601)	(0.313)	(0.349)	(0.201)	(0.7)	(0.255)	(0.352)	(0.375)	(0.316)
	<i>Papio</i>	0.395 (0.39)	0.726 (0.732)	0.304 (0.306)	0.478 (0.474)	0.432 (0.423)	0.199 (0.216)	0.199 (0.2)	0.885 (0.88)	0.176 (0.257)	0.855 (0.652)
	<i>Pan</i>	0.348 (0.343)	0.496 (0.514)	0.145 (0.284)	0.808 (0.339)	0.216 (0.202)	0.415 (0.493)	0.361 (0.29)	0.195 (0.373)	0.332 (0.273)	0.165 (0.311)

427

428 Our results suggest that the magnitude of morphological integration within the femur-pelvis  
429 module is higher in baboons than in humans while intermediate in chimpanzees (Figure 4). In  
430 the latter, the magnitude of morphological integration falls closer to baboons when allometry is  
431 not corrected, and closer to humans when allometry is corrected. Morpho-structural integration  
432 is not significantly present in baboons, more often present and with higher magnitude in humans  
433 (at least concerning the femur) and appears to be intermediate in chimpanzees (Figure 4).  
434 Among the groups, different integration strategies for phenotypic variation can be depicted,  
435 depending on whether integration is more morphologically based or more morpho-structurally  
436 based: the weaker the morphological integration, the higher morpho-structural integration  
437 seems to be.

## 438 4 Discussion

### 439 4.1 Patterns of integration and positional repertoires

#### 440 4.1.1 *Papio*

441 Among baboons, the femur-pelvis module exhibits a relatively high magnitude of  
442 morphological integration. Baboons and other primates mainly engage in quadrupedal  
443 locomotion; also it is the most extensive locomotor mode among non-primate mammal species,  
444 and has been considered as ancestral locomotor mode of primates when compared to its derived  
445 form in knuckle-walking, or to other more recent locomotor behaviours such as bipedalism  
446 (Hunter, 2016; Richmond, Begun, & Strait, 2001; Simpson, Latimer, & Lovejoy, 2018;  
447 Thompson, Rubinstein, & Larson, 2018; Thorpe, Holder, & Crompton, 2007). Although  
448 quadrupedalism in primates differs from that in other mammals (e.g. diagonal gaits and  
449 compliant walk, see Shapiro and Raichlen, 2006; Schmitt, 1999), this mode is considered as a  
450 conservative locomotor mode. This conservative nature of quadrupedalism in several primate  
451 species could therefore be reflected into a highly integrated morphology in of appendicular  
452 skeleton. Conversely, morpho-structural integration within the femur-pelvis module is not  
453 statistically detected among baboons (Figure 4).

454 In the context of a terrestrial quadrupedal primate, integration within the femur-pelvis module  
455 likely relies on the coordination of morphological variations, and not (or very little) on  
456 structural parameters. Since terrestrial quadrupedal gait in baboons leads to a balanced loading  
457 between forelimbs and hindlimbs (Druelle et al., 2019), an interesting perspective would be to  
458 also evaluate the patterns of integration in the forelimb. In comparison, macaques that are  
459 predominantly arboreal quadrupeds and which engage in more frequent leaping behaviours that  
460 predominantly load the hindlimb, present higher magnitude of morphological integration within  
461 the pelvis-femur module than within the scapula-humerus module (Conaway et al., 2018).  
462 Macaques also exhibit more pronounced femoral bending rigidity than baboons (Burr,



463 Piotrowski, & Miller, 1981; Ruff, 2003). The prevalence of hindlimb dominance in both  
464 morphological integration and internal structure in macaques suggests potential morpho-  
465 structural integration in the hindlimbs among quadrupedal primates displaying a more  
466 pronounced hindlimb dominance than baboons. However, the patterns of integration in the fore-  
467 and hind limb of more arboreal and terrestrial quadrupedal primates need to be investigated to  
468 draw further conclusions.

#### 469 4.1.2 *Pan*

470 Among chimpanzees, the magnitude of morphological integration is intermediate between  
471 baboons and humans. It is closer to baboons when allometry is present, and closer to humans  
472 when allometry is corrected. Morpho-structural integration occurs mainly between the CSG and  
473 the pelvic morphology, and most notably in the proximal  $\frac{3}{4}$  of the diaphysis, where the  
474 diaphyseal sections show much greater mediolateral cortical distribution than in baboons and  
475 humans. This means that the mediolateral orientation of the cortical bone in the femora of  
476 chimpanzees (as in other apes but not humans, e.g. Carlson et al., 2006; Nadell et al., 2021;  
477 Lauren A. Sarringhaus et al., 2016) is related to the morphology of the pelvis, more specifically  
478 to pubis length and to ilium and acetabulum width. However, these traits are highly dependent  
479 on body size and mass (Moffett, 2021). The reasons for this allometric relationship in the *Pan*  
480 genus are not necessarily related to the positional repertoire, and further investigations are  
481 needed, particularly into the possible influence of sexual dimorphism on morpho-structural  
482 integration. Some femoral traits, including the proportions of the femoral head and distal  
483 epiphysis, are also related to the CSG of the proximal diaphysis and not influenced by size. This  
484 morpho-structural integration occurs once again precisely where diaphyseal cross-sections  
485 show more prominent mediolateral cortical distribution than in baboons and humans (Figures  
486 2, 3, S1 and S2).

487 In the context of a semi-arboreal positional repertoire dominated by knuckle-walking,  
488 chimpanzees show both morphological and morpho-structural integration that includes specific  
489 femoral and pelvic morphological traits. As discussed for the baboons, the difference in limb  
490 loading can potentially explain these patterns of integration. In chimpanzees, the hindlimb is  
491 more loaded than the forelimb during knuckle-walking gait (Druelle et al., 2018; Schoonaert,  
492 D'Août and Aerts, 2007). Therefore, both external morphology and internal structure of the  
493 hindlimb might covariate to better respond to this asymmetric limb loading pattern. However,  
494 both the magnitude of morphological integration and the presence of morpho-structural  
495 integration in *Pan* are attenuated when the allometry is corrected, which greatly limits further  
496 interpretations.

#### 497 4.1.3 *Homo*

498 Among humans, the femur-pelvis module shows a relatively low magnitude of morphological  
499 integration. This is probably due to differences in the selective pressures on the pelvis and the  
500 femur. While the femoral morphology largely depends on locomotion, the pelvic morphology  
501 of modern humans is constrained by both locomotion and parturition (Frémondrière, Thollon,  
502 & Marchal, 2021; Grabowski, 2013; Huseynov et al., 2016; Ruff, 2017; Tardieu, 1994). Among  
503 primates, intra-pelvic morphological integration has been described as limited (Lewton, 2012).  
504 In humans, a low magnitude of morphological integration in the obstetric pelvis when compared  
505 to the locomotor pelvis led to interpret a low phenotypic covariation in the entire pelvis  
506 relatively to other primates (Grabowski, 2013; Ricklan, Decrausaz, Wells, & Stock, 2021). It is

507 therefore likely that pelvic morphology in humans is the product of different selection pressures.  
508 Similarly, the distinct selective pressures relative to functional distinction between the pelvis  
509 and the femur in humans probably results the reduced magnitude of morphological integration  
510 between the two elements that our results highlight. Moreover, some authors have shown that  
511 in humans, pelvic morphology displays integration with other anatomical areas. Examples  
512 include elements of the shoulder girdle and rib cage (Agosto & Auerbach, 2022; Torres-Tamayo  
513 et al., 2020), and even proposed covariation with skull size in relation to obstetrical selection  
514 pressure (Fischer & Mitteroecker, 2015). Comparable morphological integrations are not  
515 documented in chimpanzees and baboons.

516 Concerning morpho-structural integration, it occurs with high magnitude between the CSG and  
517 femoral morphology. It is particularly present in the proximal  $\frac{3}{4}$  of the diaphysis, where the  
518 CSG exhibit anteroposterior cortical distribution, a specific feature of modern humans (Ruff &  
519 Hayes, 1983; Trinkaus & Ruff, 1999, 2012). It has been hypothesized that a large biacetabular  
520 width and a long femoral neck tend to increase mediolateral cortical distribution (relatively to  
521 anteroposterior) in the femoral shaft in hominins (Ruff, 1995). Our results suggest that the  
522 anteroposterior distribution of cortical bone in the human femoral diaphysis is associated with  
523 morphological traits such as neck-shaft angle, orientation of the femoral head and diaphyseal  
524 curvature.

525 In the context of bipedal/orthograde locomotion, loads are all transmitted through the lower  
526 limb at some point. Patterns of integration within the human femur-pelvis module seem to rely  
527 more on strong coordination between variations in the internal structure and morphology of the  
528 femur, without integrating pelvic morphology.

#### 529 4.2 The significance of morpho-structural integration

530 Highlighting morpho-structural integration in groups with distinct positional repertoires  
531 enabled us to describe (1) the presence of an elaborate type of covariation that does not rely  
532 solely on morphological traits (2) different strategies producing integration patterns in the  
533 femur-pelvis module, which are strictly morphological in baboons and morpho-structural in  
534 humans, and (3) a positive correlation between the presence of morpho-structural integration  
535 and hindlimb stress during locomotion.

536 Our results suggest that morpho-structural integration is found at the mid and proximal  
537 diaphysis, which is precisely where CSG are distinctive between our groups (see Figure 2, 3  
538 and in supplementary). Conversely, the CSG of the distal diaphysis are not distinctive, either in  
539 our sample or in all catarrhines (Nadell, 2017). This suggests fewer mechanical stresses on the  
540 distal diaphysis when compared to the mid and proximal shaft. It is likely, however, that few  
541 variations in CSG or in morphology variables disabled the detection of morpho-structural  
542 integration. In baboons for example, CSG exhibit three times less variation than in humans at  
543 the mid-proximal diaphysis (see Table S1, and see also Cosnefroy et al., 2022; Puymerail,  
544 2011). A low CSG variation at intraspecies level and in some diaphyseal portions probably  
545 limits their covariation with morphometric data. As a result, morpho-structural integration is  
546 not discernible.

547 Caution might be needed in the interpretation of morpho-structural results, since this study  
548 constitutes the first attempt to measure this. For instance, the approach used to evaluate morpho-  
549 structural integration using 2b-PLS on Procrustes coordinates or allometric residuals and cross-

550 sectional properties present a high p/N ratio because of the relatively low samples size and high  
551 numbers of morphometric variables (O’Keefe, Meachen, & Polly, 2022). For example, in  
552 humans the p/N ratio is about 50.74 for the morpho-structural integration between CSG and the  
553 pelvic morphology and about 48.53 for the morpho-structural integration between CSG and the  
554 femoral morphology. However, the approach presented in this study to measure morpho-  
555 structural integration between CSG and principal component scores from the geometric  
556 morphometric analysis presents several noteworthy advantages. From a statistical perspective,  
557 this approach considerably reduces the p/N ratio (about 3.27 in humans for morpho-structural  
558 integration between CSG and a single PC/rPC, and even lower if CSG are only taken from  
559 diaphyseal portions of 15% of length). This reduction enhances the reliability of 2b-PLS results  
560 interpretation. Importantly also, employing PC/rPC scores to assess their integration with CSG  
561 provides clear and precise representation of the specific morphological variations on the  
562 skeleton associated with distinct variation in structural properties (Figures 2 and 3). Therefore,  
563 morpho-structural integration between PC/rPC and CSG represents a promising approach to  
564 understanding complex anatomical variations, offering future perspectives for a comprehensive  
565 examination of the form-function relationship (Murray, 2022).

566 As an example, the measurement of morpho-structural integration using CSG and PC/rPC helps  
567 us to describe the potential connection between the anteroposterior reinforcement observed in  
568 the shaft and curvature in the modern human femur. This results implies that this unique  
569 structural feature of *Homo sapiens* among both extant primates and fossil hominins (e.g.  
570 Carlson et al., 2006; Ruff, 2002a; Trinkaus & Ruff, 2012) covary with the variation in femoral  
571 curvature and epiphyseal shape, which are two morphological features respectively associated  
572 with developmental loading resistance during locomotion (e.g. Bertram & Biewener, 1988; De  
573 Groote, 2011; Milne & Granatosky, 2021; Shackelford & Trinkaus, 2002) and the response to  
574 bipedal mechanical stimuli during growth (e.g. Shefelbine et al., 2002; Tardieu, 1994, 1999).  
575 This specific example of morpho-structural integration in modern humans implies a distinct  
576 adaptation and potential complex selective pressure in the human femur that might contribute  
577 to distinctive bipedal specialization.

578 Also, extending the morpho-structural integration approach to other anatomical regions, such  
579 as the scapula-humerus module, as well as to other taxa and locomotor groups, would also  
580 clarify the interpretations presented in this study.

## 581 Conclusion

582 Our study explores, for the first time, the integration between external morphology and internal  
583 structural properties in the postcranial skeleton and their link to positional repertoires. Our  
584 results corroborate the presence of stronger morphological integration of elements in the femur-  
585 pelvis module in cercopithecoids than in hominoids. In baboons, the patterns of integration  
586 appears to be based solely on morphology since morphological integration is high and while  
587 morpho-structural integration is not statistically detected. In chimpanzees, morpho-structural  
588 integration between internal structure of the femoral diaphysis and the morphology of both  
589 femur and pelvis seem to be integrated. Nevertheless, both morphological and morpho-  
590 structural integration seem to be largely related to the allometry measured within the pelvis  
591 among chimpanzees. In humans, the various selective pressures that tend to affect pelvic  
592 morphology led to a decrease in morphological integration in the femur-pelvis module.

593 Conversely, measures of morpho-structural integration reveal strong covariation between  
594 internal structure and morphology within the femur in humans. The results on morpho-  
595 structural integration in the human femur provides valuable insights and constitutes a basis for  
596 future investigations into the form-function paradigm by using a more comprehensive  
597 perspective than traditionally employed methods. Further exploration of the relationship  
598 between the internal structure and morphological traits of the femur, such as femoral curvature,  
599 would be of particular interest for studies taking an evolutionary perspective.

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## 618 Conflict of interest

619 The authors declare no competing interest.

## 620 Data availability statement

621 R-script and datasets including Procrustes coordinates, PC scores, allometric residuals, rPC  
622 scores and CSG values are available on GitHub at [https://github.com/QCosnefroy/Morpho-  
623 structural-integration](https://github.com/QCosnefroy/Morpho-structural-integration).

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1039 Table legends

1040 Table 1: Study sample description. Percentages are averages values of locomotor bouts.  
 1041 †Climbing bouts can also be considered at the species level (Kraft et al., 2014; Venkataraman  
 1042 et al., 2013); ‡data for *Pan*: (Doran, 1992, 1997; Hunt, 1992; Sarringhaus et al., 2014) ; §data  
 1043 for *Papio*: (Druelle, 2017; Hunt, 2016; Rose, 1977).

1044 Table 2: Covariance Ratio based on data on the morphometric shape of the femur and the pelvis  
1045 in each dataset. First line: CR based on Procrustes coordinates; second line in parentheses: CR  
1046 based on allometric residuals.

1047 Table 3: CR effect size difference obtained for each pair of samples. First line: CR effect size  
1048 difference from CR based on Procrustes coordinates; second line in parentheses: CR effect size  
1049 difference from CR based on allometric residuals.

1050 Table 4: Detailed results of the 2b-PLS tests between femoral geometric morphometrics data  
1051 and cross-sectional geometry parameters, measured on the whole diaphysis (the 61 sections  
1052 between 20% and 80% of the biomechanical length) and on diaphyseal portions (15 sections  
1053 each). The Procrustes coordinates (or allometric residuals) provide overall external femoral  
1054 morphology, the principal components (PC or rPC) indicate a specific morphology depicted in  
1055 supplementary materials figures. First line: 2b-PLS based on Procrustes coordinates; second  
1056 line in parentheses: 2b-PLS based on allometric residuals. Highlighted boxes show the  
1057 diaphyseal stages with a significant result, bold mentions represent significant 2b-PLS.

1058 Table 5: Detailed results of the 2b-PLS tests between pelvic geometric morphometrics data and  
1059 cross-sectional geometry parameters, measured on the whole diaphysis (the 61 sections  
1060 between 20% and 80% of the biomechanical length) and on diaphyseal portions (15 sections  
1061 each). The Procrustes coordinates (or allometric residuals) provide overall external pelvic  
1062 morphology, the principal components (PC or rPC) indicate a specific morphology depicted in  
1063 supplementary materials figures. First line: 2b-PLS based on Procrustes coordinates; second  
1064 line in parentheses: 2b-PLS based on allometric residuals. Highlighted boxes show the  
1065 diaphyseal stages with a significant result, bold mentions represent significant 2b-PLS.

## 1066 Figure legends

1067 Figure 1: template for landmarks on the pelvis and femur. Landmarks type I and II in red; curve-  
1068 landmarks in blue; surface-landmarks in green.

1069 Figure 2: Morpho-structural integration between principal component of the geometric  
1070 morphometric analysis of the femur (PC refers to Procrustes coordinates analysis, rPC to  
1071 allometric residuals analysis) and cross-sectional geometry (CSG) of the femoral diaphysis. An  
1072 arrow indicates a significant 2b-PLS between the PC/rPC and the CSG taken from the entire  
1073 diaphysis. Highlighted portions of the diaphysis indicates a significant 2b-PLS between the  
1074 PC/rPC and the CSG of the diaphyseal portion. The morphological variations depicted by the  
1075 PC/rPC are represented by landmarks projections. The deviation of the landmarks indicates its  
1076 variation on the PC/rPC score from -1 to 1. A: anterior, P: posterior, L: lateral, M: medial, S:  
1077 superior, I: inferior. When no significant 2b-PLS is found for this morpho-structural integration,  
1078 the group is not represented.

1079 Figure 3: Morpho-structural integration between principal component (PC) of the geometric  
1080 morphometric analysis of the pelvis and cross-sectional geometry (CSG) of the femoral  
1081 diaphysis. An arrow indicates a significant 2b-PLS between the PC and the CSG taken from  
1082 the entire diaphysis. Highlighted portions of the diaphysis indicates a significant 2b-PLS  
1083 between the PC and the CSG of the diaphyseal portion. The morphological variations depicted  
1084 by the PC are represented by landmarks projections. The deviation of the landmarks indicates  
1085 its variation on the PC score from -1 to 1. A: anterior, P: posterior, L: lateral, M: medial, S:

1086 superior, I: inferior. When no significant 2b-PLS is found for this morpho-structural integration,  
1087 the group is not represented.

1088 Figure 4: Patterns of morphological and morpho-structural integration. The CR value in the  
1089 dotted box indicates a test performed without allometry correction. The CR value in the hatched  
1090 box indicates a test performed with allometry correction. Double arrows indicate the presence  
1091 of a significant 2b-PLS test and therefore the presence of morpho-structural integration (see  
1092 Tables 3, 4 and SI Tables).  $\emptyset$  symbolizes the absence of significant 2b-PLS. The symbols  
1093 outside the parentheses represent the analysis taking into account all 61 diaphyseal sections;  
1094 those inside the parentheses describe the analysis taking into account diaphyseal portions  
1095 (distal, mid-distal, mid-proximal, proximal). Shaded arrows represent the presence of morpho-  
1096 structural integration only for morphological data without allometry correction; hatched arrows  
1097 represent the presence of morpho-structural integration only for morphological data with  
1098 allometry correction; solid arrows represent the morpho-structural integration present for  
1099 morphological data with and without allometry correction. The dotted clouds represent the  
1100 average conformations of the femur and pelvis from the morphometric analysis. Created with  
1101 [BioRender.com](https://www.biorender.com).