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1 Shape variation in the limb long bones of modern  
2 elephants reveals adaptations to body mass and habitat

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## 25 ABSTRACT

26

27 During evolution, several vertebrate lineages have shown trends toward an increase of mass. Such a  
28 trend is associated with physiological and musculoskeletal changes necessary to carry and move an  
29 increasingly heavy body. Due to their prominent role in the support and movement of the body, limb  
30 long bones are highly affected by these shifts in body mass. Elephants are the heaviest living terrestrial  
31 mammals, displaying unique features allowing them to withstand their massive weight, such as the  
32 columnarity of their limbs, and as such are crucial to understand the evolution toward high body mass  
33 in land mammals. In this study, we investigate the shape variation of the six limb long bones among  
34 the modern elephants, *Elephas maximus* and *Loxodonta africana*, to understand the effect of body  
35 mass and habitat on the external anatomy of the bones. To do so, we use three-dimensional geometric  
36 morphometrics (GMMs) and qualitative comparisons to describe the shape variation, at both the  
37 intraspecific and interspecific levels. Our results reveal that the two species share similar negative  
38 ontogenetic allometric patterns (i.e., becoming stouter with increased length) in their humerus and  
39 femur, but not in the other bones: the proximal epiphyses of the stylopod bones develop considerably  
40 during growth, while the distal epiphyses, which are involved in load distribution in the elbow and knee  
41 joints, are already massive in juveniles. We attribute this pattern to a weight-bearing adaptation  
42 already present in young specimens. Among adults of the same species, bone robustness increases  
43 with body mass, so that heavier specimens display stouter bones allowing for a better mechanical load  
44 distribution. While this robustness variation is significant for the humerus only, all the other bones  
45 appear to follow the same pattern. This is particularly visible in the ulna and tibia, but less so in the  
46 femur, which suggests that the forelimb and hindlimb adapted differently to high body mass support.  
47 Robustness analyses, while significant for the humerus only, suggest more robust long bones in Asian  
48 elephants than in African savanna elephants. More specifically, GMMs and qualitative comparisons  
49 indicate that three bones are clearly distinct when comparing the two species: in *E. maximus* the  
50 humerus, the ulna and the tibia display enlarged areas of muscular insertions for muscles involved in  
51 joint and limb stabilization, as well as in limb rotation. These results suggest a higher limb compliance  
52 in Asian elephants, associated with a higher dexterity, which could be linked to their habitat and  
53 foraging habits.

54

55

56 Key-words: Elephants; Bone External Anatomy; 3D Geometric Morphometrics; Functional Morphology

## 57 INTRODUCTION

58

59 Throughout time, several vertebrate lineages have shown trends toward an increase of mass (Depéret,  
60 1907; Raia *et al.*, 2012; Baker *et al.*, 2015; Bokma *et al.*, 2016), which comes with numerous benefits,  
61 such as an increased defense against predation and/or an extended longevity (Clauss *et al.*, 2013; Hone  
62 & Benton, 2005), and associated trade-offs, such as reduced athleticism (Hutchinson *et al.*, 2003, 2006)  
63 and/or increased need for food and water (Demment & Van Soest, 1985). This evolutionary trend is  
64 associated with physiological and musculoskeletal changes necessary to accommodate an increase in  
65 size and mass (Kleiber, 1961; Biewener, 1989b; Nielsen, 1997; Campione & Evans, 2012), notably to  
66 carry and move their heavy body.

67 If animals displaying these traits are said to be ‘graviportal’ (Hildebrand, 1974), the concept of  
68 graviportal, introduced by Gregory (1912) and Osborn (1929), remains debated (Mallet *et al.*, 2019).  
69 Indeed, graviportal is defined by several anatomical and locomotion criteria: in addition to having a  
70 body mass of several hundreds of kilograms, graviportal taxa are supposed to display columnar limbs,  
71 associated with a relative lengthening of the stylopod and shortening of the autopod, and robust bones  
72 (i.e., larger shaft for a given length). Other criteria include large feet with enlarged adipose cushions,  
73 shorter phalanges, and long strides associated with the inability to gallop (Gregory, 1912; Osborn,  
74 1929; Coombs, 1978). However, while some modern taxa display several combinations of these  
75 criteria, few of them meet the entirety of the graviportal characteristics: rhinoceroses, while being the  
76 second heaviest land mammals after elephants and displaying specific skeletal adaptations to body  
77 weight support (Alexander & Pond, 1992; Mallet *et al.*, 2019), are able to gallop, and do not meet the  
78 weight expectations for some of the earliest authors, so that Gregory (1912) and Osborn (1929)  
79 considered them as mediportal, although they were later considered as graviportal in several studies  
80 (Prothero & Sereno, 1982; Eisenmann & Guérin, 1984). Similarly, hippos have alternatively been  
81 considered as mediportal (Coombs, 1978; Ross, 1984) or graviportal (Alexander & Pond, 1992; Carrano,  
82 1999; MacFadden, 2005; Stilson, Hopkins & Davis, 2016). Elephants, on the other hand, are the perfect  
83 example of the graviportal form, fulfilling all the criteria (Coombs, 1978; Alexander & Pond, 1992;  
84 Langman *et al.*, 1995). However, despite their massive appearance and their inability to gallop, the  
85 kinematics of the elephants’ running defies the traditional graviportal view of rigid limbs joints,  
86 displaying instead a surprising limb compliance (Hutchinson *et al.*, 2008; Ren *et al.*, 2008, 2010); thus  
87 indicating that their skeletal architecture is adapted to support a massive weight while allowing a  
88 certain flexibility.

89 Elephants are the only living representatives of the order Proboscidea, which conversely includes  
90 numerous extinct graviportal taxa (e.g., *Deinotherium*, *Mammut*, *Mammuthus*; see Gheerbrant &

91 Tassy (2009)). At a larger taxonomic and evolutive scale, proboscideans were not the first to display  
92 fully graviportal bodies: sauropod dinosaurs were obligatory quadrupeds sharing a general graviportal  
93 form (Rauhut *et al.*, 2011; Sander *et al.*, 2011; Lefebvre *et al.*, 2022). Their diversification towards a  
94 range of extreme gigantism was made possible by the acquisition of columnar limbs (straighter and  
95 positioned almost vertically), allowing to support a multi-tons' body mass (Hildebrand, 1982). This  
96 specific 'columnar' architecture was convergently acquired in proboscideans, and can now be found in  
97 the elephant limbs only, making it a unique feature among extant vertebrates. Elephants display  
98 unique postural and locomotor adaptations which are reflected in their skeleton (Christiansen, 2007;  
99 Kokshenev & Christiansen, 2010), they are thus a particularly interesting group to analyse limb bone  
100 adaptation to heavy weight support.

101 Long bones provide a rigid frame on which muscles attach; as such, they play a prominent role in both  
102 the movement and the support of the body. Like all biological structures, limb anatomy results from  
103 the conjoined effects of phylogenetic, structural and functional constraints (e.g., Gould, 2002; Cubo,  
104 2004; Seilacher, 1970). Among those, body mass is known to strongly affect limb bones and joints, so  
105 that their anatomy is highly impacted by shifts in body mass during evolution (Hildebrand, 1982;  
106 Biewener, 1989; Smuts & Bezuidenhout, 1994; Polly, 2008). Several studies on taxa that are considered  
107 graviportal have shown specific adaptations in the external anatomy of limb long bones in heavy  
108 mammalian taxa (MacLaren & Nauwelaerts, 2016; MacLaren *et al.*, 2018; Mallet *et al.*, 2019, 2020;  
109 Etienne *et al.*, 2020). However, they also highlighted that limb adaptation to high body mass can differ  
110 considerably between species of similar weight, so that even among species that are considered  
111 graviportal, graviportalness is not expressed in the same way: for example, hippos display stout limbs  
112 associated with the inability to trot or gallop, while rhinos possess more elongated limbs and are able  
113 of galloping (Wilson, Mittermeier & Altrichhter, 2011).

114 Among morphological adaptations to heavy weight, bone robustness is of particular interest. Indeed,  
115 limb bone robustness increases at a higher rate than body mass (Campione & Evans, 2012) so that  
116 heavy taxa display overall larger and stouter bones than smaller taxa, in order to withstand their  
117 increased weight. Consistently with the high body mass of proboscideans, their limb bones display a  
118 massive morphology (Christiansen, 2007).

119 The three extant species of elephants are geographically and taxonomically divided into the Asian  
120 genus *Elephas*, represented by a single species (*Elephas maximus*, the Asian elephant), and the African  
121 genus *Loxodonta*, represented by two species (*Loxodonta africana* and *Loxodonta cyclotis*, the African  
122 savanna and forest elephants). While the Asian elephant (*E. maximus*) can be found throughout the  
123 Indian subcontinent and Southeast Asia, the African savanna elephant (*L. africana*) occurs in Sub-  
124 Saharan Africa in a variety of habitats, sometimes in subtropical and temperate forests but mostly

125 desert and semi-desert areas, whereas the African forest elephant (*L. cyclotis*) has a much more limited  
126 distribution, restricted almost exclusively to the rainforests of Cameroon, Democratic Republic of  
127 Congo and Gabon (Barnes *et al.*, 1997; Blake *et al.*, 2008).

128 Modern elephant species display a strong variation of size and body mass. Both *Loxodonta* species  
129 represent the extremes of height and mass: *Loxodonta africana* exhibits the most massive forms,  
130 reaching up to 8000 kilograms and 4 meters at the shoulder; at the opposite, *Loxodonta cyclotis* is the  
131 smallest extant elephant, with a body mass reaching up to 4000 kilograms and a shoulder height of 3  
132 meters. *Elephas maximus* displays an intermediate weight (up to 6000 kilograms) and height (3.5  
133 meters), although its morphology cannot be confused with the two *Loxodonta* species: the Asian  
134 elephant is easily distinguishable from the African species, with its small, rounded ears and its twin-  
135 domed head, among other features. While it is possible to distinguish between Asian and African  
136 elephant species using the shape of their spine (*E. maximus* having a more convex back than *L.*  
137 *africana*) or their autopod (differing number of toenails), their limb long bones are not known to bear  
138 specific morphological features that would allow species distinction (West, 2006; Todd, 2010 and  
139 references therein). However, given the mass discrepancy between the species, we could expect to  
140 observe a shape variation between the limb bones of Asian and African savanna elephants.

141 While limb long bones share a function of weight support, they do not participate equally: unlike most  
142 quadrupedal mammals, the ulna plays a major role in weight bearing compared to the radius (Bertram  
143 & Biewener, 1992; Smuts & Bezuidenhout, 1993); similarly, the tibia is the main weight bearer in the  
144 hindlimb zeugopod, while the fibula is reduced (Smuts & Bezuidenhout, 1994). Due to their position  
145 closer to the trunk, bones of the stylopod bear more muscular insertions with the pectoral and pelvic  
146 girdles than do bones of the zeugopod (Shindo & Mori, 1956a, 1956b) and thus face different  
147 constraints. The six bones might then be affected differently by body mass variations, so that we could  
148 expect to observe varying degrees of shape variation linked to heavy weight support among them.  
149 Additionally, like in most quadrupedal mammals the center of mass in elephants is closer to the  
150 forelimb than to the hindlimb, so that the forelimb elements carry more weight (60% of the body mass)  
151 than the hindlimb elements (Lessertisseur & Saban, 1967; Hildebrand, 1974; Polly, 2008, Ren *et al.*,  
152 2010; Etienne *et al.*, 2020). We could thus expect to see more shape variation linked to heavy weight  
153 support in the bones of the forelimb than in bones of the hindlimbs.

154 While several studies have described the limb muscular (Eales, 1925; Shindo & Mori, 1956a, 1956b ,  
155 Weissengruber & Forstenpointner, 2004) and skeletal anatomy (Eales, 1925; Smuts & Bezuidenhout,  
156 1993, 1994; Weissengruber *et al.*, 2006a, 2006b; Hutchinson *et al.*, 2008) of elephants, as well as their  
157 locomotor kinematics (Langman *et al.*, 1995, 2012; Hutchinson *et al.*, 2006; Ren *et al.*, 2008, 2010), to  
158 our knowledge no study has yet investigated the shape variation of the six limb long bones conjointly.

159 3D GMMs have been proven extremely useful to characterize shape variation on such bones. They  
160 have been used to study the influence of locomotion and body mass in small carnivorans (Fabre *et al.*,  
161 2013a, b, Martin-Serra *et al.*, 2014; Fabre *et al.*, 2015; Figueirido *et al.*, 2015), rodents (Alvarez, Ercoli  
162 & Prevosti, 2013; Wölfer *et al.*, 2019), xenarthrans (Alfieri *et al.*, 2022) and primates (Botton-Divet &  
163 Nyakatura, 2022), as well as in heavier taxa like Suidae (e.g., Harbers *et al.*, 2020). Similarly, they have  
164 been used to study the effect of high body mass in mammals (Mallet *et al.*, 2019) and reptiles (Pintore  
165 *et al.*, 2021; Lefebvre *et al.*, 2022), but not on proboscideans bones.

166 In addition to linear measurements of the robustness of the shaft, 3D GMMs will allow a more precise  
167 quantification of the shape (variation) along the whole bone. Additionally, since the diaphyseal  
168 circumference cannot not be obtained for the radius and ulna, 3D GMMs will compensate for the  
169 absence of robustness calculations for these bones.

170 We link here the shape of the bones to their function of weight support in a graviportal species. While  
171 body mass data was not available, the link between size (centroid size and diaphyseal circumference)  
172 and mass has previously been established in numerous species, including elephants (Campione &  
173 Evans, 2012) and other heavy taxa such as tapirs and rhinos (MacLaren *et al.*, 2018; Mallet *et al.*, 2019).  
174 Thus, we chose to use the various size measurements as proxies to infer mass variation in our sample.  
175 Our study aims to determine the adaptations of the limb long bones to a heavy weight in elephant  
176 species as a whole, so that the body mass inferences from bone size will allow us to describe bone  
177 shape adaptations reflecting the generally massive weight of the species.

178 Here we propose to analyze the external morphology of the limb long bones in a sample of modern  
179 elephants: we quantify the intraspecific and interspecific shape and robustness variations in *Loxodonta*  
180 *africana* and *Elephas maximus*, and interpret them in relation to their relative body mass and habitat.  
181 In order to do so, (1) we first investigate the morphological variation of the six long bones at the  
182 intraspecific level, estimating the potential effect of ontogeny on bone shape allometry using a small  
183 sample of juvenile specimens, (2) then we explore the interspecific shape variation between the two  
184 species, taking their body proportions, habitat and locomotor behavior into account, and (3) we  
185 compare the amount of shape variation in the six bones, investigating which part(s) of the limbs are  
186 most affected by body mass and habitat.

187

## 188 MATERIAL AND METHODS

### 189 Sample

190 We selected a total of 97 bones from 32 elephant specimens from several European and American  
191 institutions, belonging to the three extant elephant species. While the distinction between the  
192 *Loxodonta* and *Elephas* genera in museum's collections is reliable (based on the country of origin and  
193 the shape of the skull when it is present), the distinction between the African species *L. africana* and  
194 *L. cyclotis* is generally not possible: the separation of the *Loxodonta* genus into two species is very  
195 recent (Roca *et al.*, 2001; Rohland *et al.*, 2010), so that most specimens originating from Africa are  
196 registered as *L. africana* in collections. Each specimen of this species is thus susceptible to have been  
197 incorrectly diagnosed as *L. africana* and to actually belong to the *L. cyclotis* species, with the exception  
198 of two specimens (MNHN-ZM-AC-1907-49 and MNHN-ZM-AC-1938-375) from which DNA samples  
199 have been obtained and analysed in an unrelated study (R. Debruyne, pers. comm.). However, since  
200 African forest elephants are assumed to be less easily and thus less often hunted (BYH: Forest  
201 elephant... c2015-2022), we assumed that the specimens of this sample were correctly attributed,  
202 although genetic analyses or identifications using cranio-dental characteristics might prove otherwise  
203 (Table 1). We thus kept each museum's species diagnosis, resulting in a sample containing a vast  
204 majority of specimens from the *L. africana* and *E. maximus* species, and a single official *L. cyclotis*  
205 specimen.

206 Our sample was composed of 18 humeri, 14 radii, 14 ulnae, 26 femora, 13 tibiae and 12 fibulae,  
207 depending on availability (Table 1). Nine femora were not diagnosed. Those specimens were  
208 referenced in the archives of the Muséum national d'Histoire Naturelle (MNHN) as a set of  
209 undetermined femora marked with a Chinese character (translated to "profit"), which indicates a  
210 probable Asian origin. However, their actual determination being uncertain, analyses were performed  
211 in order to ascertain to which species they could belong, and all analyses on the femur were performed  
212 twice: once with these specimens considered as Asian elephant, and once without these specimens.

213 Age determination was provided by the institutions in some cases. When no data on the age of the  
214 specimens was available, we determined the ontogenetic stage (juvenile, subadult, adult) based on  
215 the level of fusion and development of the epiphyses (juvenile: unfused epiphyses, subadult: visible  
216 epiphyseal plate line, adult: fully fused epiphyses). The sex of the specimens, as well as their exact  
217 origin and captivity state, were generally unknown. As such, we could not account for these  
218 parameters in our analyses.

219

## 220 3D imaging

221 A large part of the sample (61 bones) was digitized using a structured-light three-dimensional scanner  
222 (Artec Eva) and reconstructed with Artec Studio Professional software (version 12.1.6.16, Artec 3D,  
223 2016). Complementarily, 25 bones were digitized using photogrammetry, following Mallison & Wings  
224 (2014) and Fau et al. (2016). Pictures were taken with a digital camera (Nikon D5500, Nikon Inc., 50  
225 mm lens) all around each bone and aligned to create a 3D model using Agisoft Photoscan software  
226 (version 1.4.0.5076, Agisoft, 2017).

227 Additionally, three bones were CT-scanned for a later study; they were scanned using high resolution  
228 computed tomography at the AST-RX platform (UMS 2700, Muséum National d'Histoire Naturelle,  
229 Paris) with reconstructions performed using X-Act (RX-Solutions). Voxel size varies from 86  $\mu\text{m}$  to 330  
230  $\mu\text{m}$  depending on specimen size. The external surface of these bones was segmented and  
231 reconstructed in VGStudio MAX software (version 2.2, Volume Graphics GmbH, 2016). Each mesh was  
232 decimated to reach 250,000 vertices and 500,000 faces using MeshLab software (version 2020.07,  
233 Cignoni *et al.*, 2008). Finally, 3D models from the specimen IMNH-1486 were obtained from  
234 MorphoSource (6 bones); they had been created using a laser scanner (Faro Edge Arm, Idaho  
235 Virtualization Lab).

236 Previous research on similarly sized bones has found no major differences in 3D models created using  
237 these two methods (Petti *et al.*, 2008; Remondino *et al.*, 2010; Fau *et al.*, 2016, Soodmand *et al.*, 2018;  
238 Díez Díaz *et al.*, 2021; Waltenberger *et al.*, 2021).

239

240 The right bones were symmetrized arbitrarily on the left side for the purpose of the analyses using  
241 Meshlab software.

242

## 243 Geometric morphometrics

### 244 Landmark digitization

245 We defined the shape of the bones using anatomical landmarks, and curve and surface sliding semi-  
246 landmarks, as described by Gunz, Mitteroecker & Bookstein (2005), Gunz & Mitteroecker (2013), and  
247 Botton-Divet *et al.* (2016). We used 14 anatomical landmarks for the humerus, 12 for the radius, 15  
248 for the ulna, 16 for the femur, 18 for the tibia and 10 for the fibula (Supplementary Fig. 1-6; Tables S1-  
249 6). Each curve is bordered by anatomical landmarks as recommended by Gunz & Mitteroecker (2013).  
250 All landmarks and curves were placed using the IDAV Landmark software (version 3.0, Wiley *et al.*,  
251 2005).

252 For some specimens, the radius and ulna could not be separated because the two bones were fused  
253 together, so that we could not access the surface of contact between them. In order to place  
254 homologous landmarks on the entire sample of radius and ulna, we placed curves around the contact  
255 zones to delimit the surface of each bone, so that semi-landmarks could not slide out of the defined  
256 area. We placed the same curves on isolated radii and ulnae so that all surfaces considered were  
257 homologous (Supplementary Fig. 2, 3). These curves were removed after the sliding landmark  
258 procedure and before performing the shape analysis, so that they are not included in our analyses,  
259 following Pintore *et al.* (2021).

260 For each bone, surface semi-landmarks were manually placed on a template, created from a single  
261 specimen selected beforehand for its mean conformation with the 'findMeanSpec' function of the  
262 geomorph package (Adams and Otárola-Castillo, 2013) of R (R Core Team, 2020, version 4.0.2), using  
263 RStudio (RStudio Team, 2020, version 1.3.959–1). Each bone template was then used to project the  
264 semi-landmarks onto the surface of the other specimens of the dataset using the 'placePatch' function  
265 of the Morpho package (Schlager, 2017). Projection was followed by a relaxation step to ensure that  
266 the projected points matched the actual surface of the mesh. The curve and surface semi-landmarks  
267 were slid using the minimizing bending energy algorithm (Bookstein, 1998). The landmarks and semi-  
268 landmarks could therefore be treated as geometrically homologous from one bone to the next.

269

## 270 Generalized Procrustes analyses

271 Following the sliding of all semi-landmarks, all the specimens were superimposed using a Generalized  
272 Procrustes Analysis (GPA) (Rohlf & Slice, 1990; Bookstein, 1991) to remove the effects of position,  
273 orientation and size and to isolate the shape information (3D landmarks coordinates). Additionally,  
274 GPA produces centroid size (Cs), defined as the square root of the summed squared distances of each  
275 landmark and the centroid of the landmarks' configuration. We used PCA to visualize the specimen  
276 distribution in the morphospace.

277 For each bone, the error in digitizing the landmarks was assessed by a repeatability test. Ten recordings  
278 of anatomical landmarks were made on three visually similar specimens of the same species and  
279 analysed by principal component analysis (PCA). In order to maximize human variation, the landmarks  
280 were placed in two sessions of five measurements separated by several days (the landmarks were  
281 placed first on one bone, followed by the second and the third, for each iteration). All repeated  
282 measurements produced three well-separated clusters on the first two Principal Components (PCs),  
283 indicating that measurement error was negligible compared to the biological differentiation among  
284 the three specimens.

285 Patterns of shape variation for were visualized using PCAs, computed on each type of bone. In order  
286 to display shape deformation along the principal axes, we computed theoretical consensus shapes of  
287 our sample and used it to calculate TPS deformation of the template meshes. We then used this newly  
288 created consensus mesh to compute theoretical shapes associated with the maximum and minimum  
289 of both axes of each PCA, as well as mean shapes of each bone for each species. To compare adult and  
290 juvenile specimens of *E. maximus*, mean shapes of adult and juveniles were computed separately. To  
291 compare adult specimens of *E. maximus* and *L. africana*, mean shapes of the adult specimens of *L.*  
292 *africana* were additionally computed (the mean shape of adult *E. maximus* being the same as used  
293 previously). The *L. cyclotis* specimen was included in the PCAs to assess its position within the shape  
294 variation of the whole sample; qualitative comparisons were made using the meshes of the six bones.  
295 GMM procedures were performed with the 'geomorph' (version 3.0.7, Adams & Otárola-Castillo, 2013;  
296 Schlager, 2018) functions and the 'Morpho' (version 2.6) packages of R software (4.0.2, R Core Team).  
297 To visualize patterns of shape similarities among our sample, we performed Neighbour-Joining trees  
298 on each type of bone, using the Euclidean distances between each specimen's bone shape computed  
299 from their PCA scores using the 'ape' package (Paradis & Schliep, 2019).

300 In order to assess whether femoral shape could be as good indicator of species determination, we used  
301 the k-Nearest-Neighbour (k-NN) algorithm (Venables & Ripley, 2002; Ripley, 2007) in the 'class'  
302 package (Venables & Ripley, 2002). This nonparametric method consists of classifying an object into a  
303 predefined group according to its Euclidean distance with its k-NN (k being a natural number). We  
304 tested with k ranging from 1 to n-1, n being the smallest number of individuals within a group, then  
305 calculated the mean of the values obtained. The single *L. cyclotis* specimen was not included in the k-  
306 NN analyses for obvious reasons of sample size.

307

### 308 Robustness parameters

309 In order to assess the robustness of the bones, we measured the circumference of the diaphyses at  
310 their thinnest part ( $C_i$ ), and the maximal length (MaxL) of the bones. Bones were aligned along their  
311 longitudinal axis following Ruff (2002). Circumferences were obtained using the CloudCompare  
312 software (version 2.12.0, <http://www.cloudcompare.org>) for each bone except for the radius and ulna,  
313 which could not be separated in several specimens. Radius and ulna were thus excluded from analyses  
314 using circumference as a parameter. Bone maximal length was obtained virtually by placing reference  
315 points on the 3D models and measuring the distance between them using the Landmark software.  
316 Robustness ( $R_b$ ) was defined as the ratio of minimal diaphyseal circumference to maximal length of  
317 the bones ( $C_i/\text{MaxL}$ ). The difference in adult bone length, circumference and robustness between  
318 species were tested by performing t-tests.

319

## 320 Statistics

321 Allometry can be defined as the covariation of size with shape (Gould, 1966; Klingenberg, 2016). In  
322 order to investigate the morphological variation of the six long bones at the intraspecific level, we  
323 checked for allometry among the *E. maximus* sample: we tested the ontogenetic allometry (covariation  
324 of size with shape during growth) and the static allometry (covariation of size with shape between  
325 individuals of the same age) with Procrustes Analyses of Variance (Procrustes ANOVAs; allowing the  
326 use of morphometric shape data) using the `procD.lm` function in the 'geomorph' library (Klingenberg,  
327 2016). The intraspecific morphospaces of each bone were visualized using PCAs.

328 At the interspecific level, allometry can be studied between different species or clades (evolutionary  
329 allometry). Here we checked for shape variation and centroid size difference between *E. maximus* and  
330 *L. africana*, as well as for the eventual presence of an interspecific variation, using Procrustes ANOVAs  
331 (Klingenberg, 2016) on the adult sample. We tested the effect of size and robustness within the PCAs  
332 using linear regressions on the first two PCs with  $\log(C_s)$ ,  $C_i$ , and  $MaxL$ , respectively, as size estimates.  
333 Maximal length, minimum diaphyseal circumference and robustness differences between *E. maximus*  
334 and *L. africana* individuals were tested with ANOVAs on adult specimens. The morphospaces were  
335 visualized using PCAs, and theoretical shapes at the first two PCs minimum and maximum were  
336 computed in order to explore the morphological variations between the two species.

337 In the specific case of the undetermined femora, the ANOVAs on centroid size and shape variation  
338 were associated with pairwise comparisons (Collyer *et al.*, 2015) in order to assess whether these  
339 bones could be distinguished into the two genera.

340

341 Finally, we compared the amount of shape variation in the six bones using the mean shapes  
342 visualizations of each sample (adults of each species, juveniles of *E. maximus*) and results of the  
343 aforementioned Procrustes ANOVAs and ANOVAs performed on shape and robustness data.

344

## 345 RESULTS

### 346 Intraspecific variation

#### 347 Ontogenetic allometry

348 Since there was no juvenile specimen of *L. africana* in our sample, all analyses of the shape variation  
349 during ontogeny were performed on the *E. maximus* specimens. To obtain an adult-only sample,  
350 subadults specimens were grouped with the juvenile specimens in our analyses.

351 Procrustes ANOVAs on the shape data of the *E. maximus* sample indicated a significant variation of  
352 humeral and femoral shape with centroid size, i.e. during growth (Table 2). Consistently, there was a  
353 significant difference of shape for the humerus and femur between non-adult and adult specimens but  
354 not for the other bones.

355 In the Asian elephant (*Elephas maximus*), the morphological variation of the humerus during ontogeny  
356 is characterized by the development of the epiphyses from ill-defined bulbous shapes into well-defined  
357 structures, forming the head, the greater tubercle and the condyles. In the proximal epiphysis, the  
358 greater tubercle forms a thin crest in non-adult specimens, then grows into a larger, wider and more  
359 rounded form (Fig. 1A, C). The neck of the humerus becomes more defined, with a clear delimitation  
360 with the humeral head. Additionally, the angle formed by the humeral head and the greater tubercle  
361 widens; this is accompanied by a thickening of the humeral crest and of the deltoid tuberosity, as well  
362 as a deepening of the intertubercular groove. In the distal epiphysis, the medial and lateral condyles  
363 grow more defined with age, forming a smooth structure with clear delimitations. The olecranon fossa  
364 gets deeper, while the trochlea is also more defined on both the medial and lateral sides. The  
365 supracondylar crest appears steeper in adult specimens, forming a sharper angle with the lateral  
366 epicondyle. The proximal epiphysis grows larger during ontogeny, so that it reaches approximately the  
367 same width as the distal epiphysis during growth.

368 Similarly as for the humerus, the morphological variation of the femur during ontogeny is characterized  
369 by the development of both epiphyses. In the proximal epiphysis, the greater trochanter grows into a  
370 large and rounded structure under which the trochanteric fossa deepens (Fig. 1B, D). The femoral neck  
371 gets proportionally thinner and longer, while the femoral head appears to retain its shape. The lesser  
372 trochanter is almost undiscernible in non-adult specimens, and develops into a small protuberance on  
373 the medial side of the diaphysis. Additionally, the central part of the diaphysis is proportionally larger  
374 in adult specimens, closer to the width of the distal epiphysis than in non-adult specimens. The patellar  
375 surface is not visible on the non-adult specimens; it develops with age, forming a smooth and well-  
376 defined articular surface on the caudal side (Fig. 1B, D). On the caudal side of the distal epiphysis, both

377 condyles are already visible in non-adult specimens; they grow proportionally bigger and form a  
378 narrow opening on the intercondylar fossa.

379

### 380 Sexual dimorphism

381 Sexual dimorphism could not be tested quantitatively since the sex of most specimens was unknown.  
382 In an attempt to evaluate sexual dimorphism, we computed the mean shapes of the six bones of male  
383 and female specimens of *E. maximus* when the sex groups were represented by 2 specimens or more,  
384 and used the unmodified 3D models of bones for which only one specimen of known sex was available.  
385 There was no adult female in the *L. africana* sample so that we could not evaluate the sexual  
386 dimorphism qualitatively. Here we describe the mean shape variation of the humerus of *E. maximus*,  
387 which was the only bone displaying a clear morphological variation pending on sex attribution.

388

389 The mean shape of the male specimens shows a massive morphology with a thick diaphysis and large  
390 epiphyses. The greater tubercle is rounded and extends as far as the humeral head proximally. The  
391 lesser tubercle is not prominent, so that the intertubercular groove forms an open angle. The trochlea  
392 is large and angled in the cranial direction, forming a marked concavity on the coronoid fossa. The  
393 mean shape of the female specimens shows a thinner shape, with narrower epiphyses. The greater  
394 tubercle is thin and extends farther than the humeral head proximally. The lesser tubercle is sharp and  
395 angled in the medial direction; the intertubercular groove forms a rounded, closed angle. The deltoid  
396 tuberosity is more prominent than in males, forming a sharper angle with the humeral crest. While the  
397 distal epiphysis is narrower than in males, the lateral condyle of the trochlea appears bigger and more  
398 elongated mediolaterally.

399

### 400 Static allometry

401 Results of the Procrustes ANOVA on the shape data with the centroid size as an independent variable  
402 show a significant allometry within the adult samples of *E. maximus* and *L. africana*, respectively, for  
403 the humerus only (Table 3): In the African elephant, the difference between smaller and larger adult  
404 specimens is expressed through a general thickening of the humerus in both cranio-caudal and medio-  
405 lateral directions, particularly visible on the deltoid tuberosity and on the supracondylar crest. In larger  
406 specimens, the greater tubercle is more rounded and extends further in the lateral direction (Fig. 2).  
407 This pattern of morphological variation is similar for the humerus of the Asian elephant; with the  
408 additional difference of the supracondylar crest, which forms a larger prominence angled toward the  
409 caudal direction in larger specimens. This larger crest is associated with a deeper olecranon fossa,

410 beginning more proximally under the supracondylar crest.  
411 Overall, larger specimens appear stouter and more robust than smaller specimens in both species, with  
412 proximal and distal epiphyses becoming similarly larger. Results of the correlation tests between the  
413 size parameters and the first two PCs of the PCAs performed on humeral shape data indicate that for  
414 both *E. maximus* and *L. africana*, the first PC is significantly correlated with size (Table 4).

415

## 416 Interspecific variation

### 417 Correlation with size and robustness variables

418 No correlation is detected between the different size parameters (Cs, Ci, MaxL, Rb) and the first PCs of  
419 the PCAs performed on shape data observed at the intraspecific level is not detected when using the  
420 entire adult sample (all adult *E. maximus* and *L. africana* specimens), with the exception of the  
421 minimum diaphyseal circumference along the first axis of the PCA on fibular shape data (Table 5).

422 Although Procrustes ANOVAs testing the covariation of shape data with log-transformed centroid size  
423 within the *E. maximus* sample detected an allometry in the humerus, no allometry was not detected  
424 when testing the entire adult sample (all adults *E. maximus* and *L. africana* specimens). All the  
425 following analyses are thus performed without checking for covariation with the centroid size.

426

### 427 Size and robustness analyses

428 There was no significant difference in the centroid size, the circumference nor the length of the bones  
429 between *E. maximus* and *L. africana* (Table 6). Results of the t-tests on the robustness of the bones  
430 (Rb) indicated that *E. maximus* displayed a significantly more robust humerus than *L. africana* (Table  
431 6, Supplementary Fig. 7A, 8A). Although the t-tests indicated no significant difference, qualitative  
432 comparisons of the mean shape of the humerus, ulna and tibia revealed considerably more robust  
433 bones in *E. maximus* than in *L. africana*. Scatterplots of the length on circumference ratios were  
434 consistent with the qualitative observations: *E. maximus* displayed higher Ci/MaxL ratios for each  
435 bone, i.e. a higher robustness (Supplementary Fig. 7B, C, D, 8B, C, D). The single *L. cyclotis* was included  
436 in the scatterplots, and for each bone displayed a higher robustness than *E. maximus*.

437

## 438 Shape analyses

### 439 Humerus

440 Results of the Procrustes ANOVA on the humerus shape data (Table 6) revealed a significant difference  
441 of shape between the two species ( $p=0.001$ ,  $r^2=0.26$ ). The Neighbour-Joining tree computed on adult  
442 humeral shape data confirmed a clear separation between specimens of *E. maximus* and *L. africana*,  
443 with the *L. cyclotis* specimen placed in the middle of the *E. maximus* group (Supplementary Fig. 9A).

444 The first two axes of the PCA performed on the humerus shape data express 52.3% of the global  
445 variance (Fig. 3). The first axis (which represents 31.8% of the variance) separates the African savannah  
446 elephant on the positive part and the Asian and African forest elephants on the negative part of the  
447 graph. The theoretical shape at the PC1 minimum shows a massive and stout morphology, with wide  
448 epiphyses and a thick diaphysis, while the theoretical shape at the PC1 maximum shows a thin and  
449 elongated morphology, with epiphyses extended in the cranio-caudal axis and overall less pronounced  
450 protuberances. Both *L. africana* and *E. maximus* display an important intraspecific variation along the  
451 second axis (20.5% of the variance). For *L. africana*, the intraspecific variation is expressed by the first  
452 two axes and appears to be linked to the centroid size of the specimens, with the smallest ones driving  
453 the variation toward the positive part of the first axis and the negative part of the second axis. For *E.*  
454 *maximus*, the biggest specimens appear to drive the variation toward the negative part of the two first  
455 axes. The specimens of *E. maximus* closest to the *L. africana* group are not the larger ones; size thus  
456 does not appear to drive the variation similarly for the two species along the first axis. The specimen  
457 of *L. cyclotis* is part of the *E. maximus* group. Detailed descriptions of the theoretical shapes at the PCs  
458 minimum and maximum are in Supplementary Results S1.

459 On this PCA, the female of *E. maximus* is closer to the male specimen of *L. africana* than to the males  
460 of their own species. For *E. maximus*, the only fully adult female specimen is at the extreme positive  
461 part of the hull on the first axis, while the three male specimens are at the extreme negative part. The  
462 first axis displays a gradient, from male *E. maximus*, to female *E. maximus*, then male *L. africana* and  
463 finally female *L. africana*. The mean shapes of each species logically follow the gradient observed along  
464 the first axis: *L. africana* displays a thin, elongated morphology, as opposed to the stout and massive  
465 one displayed by *E. maximus*.

466 Taking non-adult specimens into account, we observe a wide distribution of *E. maximus* along the  
467 second axis (PC2=20.22% of the variance), mainly driven by the two juvenile specimens in the negative  
468 part of the graph; the only subadult specimen of *E. maximus* is placed closer to the *L. africana* cluster  
469 along both axes (Supplementary Fig. 10). This distribution is confirmed by the Neighbour-Joining tree  
470 on the humeral shape data of the entire sample (Supplementary Fig. 9B).

471

#### 472 *Radius*

473 Results of the Procrustes ANOVA on the radial shape data (Table 6) revealed no significant difference  
474 of shape between *E. maximus* and *L. africana* ( $p=0.30$ ,  $r^2=0.11$ ). The Neighbour-Joining tree computed  
475 on radial shape data showed a clear separation between *E. maximus* and *L. africana*, with the *L. cyclotis*  
476 specimen placed closer to a *L. africana* specimen than to the rest of the sample (Supplementary Fig.  
477 9C).

478 The first two axes of the PCA performed on the radius shape data express 50.3% of the global variance  
479 (Supplementary Fig. 12). *E. maximus* displays a high intraspecific variation, occupying most of the PCA  
480 graph, while all *L. africana* specimen are grouped in the middle of the first axis and in the negative part  
481 of the second axis (PC2: 21.7% of the variance). Most of the *L. africana* distribution overlaps with that  
482 of *E. maximus*, but not with *L. cyclotis*.

483

#### 484 *Ulna*

485 Results of the Procrustes ANOVA on the ulna shape data (Table 6) revealed a significant difference of  
486 shape between *E. maximus* and *L. africana* ( $p=0.02$ ,  $r^2=0.22$ ). The Neighbour-Joining tree computed on  
487 ulnar shape data showed a slight separation between *E. maximus* and *L. africana*, with the *L. cyclotis*  
488 specimen placed closer to the *E. maximus* specimens (Supplementary Fig. 9D).

489 The first two axes of the PCA performed on the ulna shape data express 54.01% of the global variance  
490 (Fig. 4). While being clearly distinct on the graph, both *E. maximus* and *L. africana* display a large  
491 intraspecific variation along the first (PC1: 37.6% of the variance) and second (PC2: 17.4% of the  
492 variance) axes. The first axis appears to be linked with the size of the specimens: larger specimens of  
493 *L. africana* are situated in the positive part of the graph, while larger specimens of *E. maximus* are in  
494 the negative part of the graph. The second axis separates *L. cyclotis*, in the negative part of the graph,  
495 from the two other species on the positive part. Detailed descriptions of the theoretical shapes at the  
496 PCs minimum and maximum are in Supplementary Results S1.

497

#### 498 *Femur*

499 Results of the Procrustes ANOVA on the femur shape data (Table 6) revealed no significant difference  
500 of shape between *E. maximus* and *L. africana* ( $p=0.16$ ,  $r^2=0.11$ ). The Neighbour-Joining trees computed  
501 on humeral shape data showed no clear separation between *E. maximus* and *L. africana*, whether  
502 considering the undetermined specimens or not (Supplementary Fig. 9E, F).

503 There was also no significant difference in shape when taking the undetermined adult specimens into  
504 account and considering them as *E. maximus* specimens ( $p=0.13$ ,  $r^2=0.08$ ). The PCA performed on the

505 shape data of this sample indicates that these specimens are closer to the *E. maximus* group, with  
506 almost no overlap, than to the *L. africana* group and the *L. cyclotis* specimen, supporting the hypothesis  
507 of this subsample belonging to the Asian elephant species (Supplementary Fig. 15).

508 However, when considering the undetermined adult specimens as a third group, we found a significant  
509 difference in shape ( $p=0.02$ ,  $r^2=0.20$ ): pairwise comparisons indicate that while *E. maximus* and *L.*  
510 *africana* did not differ significantly in their femoral shape ( $p=0.22$ ), the undetermined group did differ  
511 significantly from both *E. maximus* ( $p=0.02$ ) and *L. africana* ( $p=0.04$ ). Details of the femur anatomy are  
512 in Supplementary Figure 16.

513 The k-NN algorithm reached 66.7% of correct classification when predicting the three groups (*E.*  
514 *maximus*, *L. africana*, undetermined specimens), and up to 81% when considering the undetermined  
515 specimens as *E. maximus*.

516

#### 517 *Tibia*

518 Results of the Procrustes ANOVA on the tibial shape data (Table 6) revealed a significant difference of  
519 shape between *E. maximus* and *L. africana* ( $p<0.01$ ,  $r^2=0.22$ ). The Neighbour-Joining tree computed on  
520 tibial shape data showed a clear separation between *E. maximus* and *L. africana*, with the *L. cyclotis*  
521 specimen placed closer to *E. maximus* (Supplementary Fig. 9G).

522 The first two axes of the PCA performed on the tibia shape data express 50.30% of the global variance  
523 (Fig. 5). The first axis (which represents 29.9% of the variance) separates both *Loxodonta* species in the  
524 positive part of the graph, and *E. maximus* in the negative part. The theoretical shape at the PC1  
525 minimum shows a massive form, with wide epiphyses and a thick diaphysis. At the opposite, the  
526 theoretical shape at the PC1 maximum shows a more delicate morphology, with a thinner diaphysis in  
527 both mediolateral and craniocaudal axes. The *L. cyclotis* specimen is clearly separated from the *L.*  
528 *africana* group on the second axis (PC2: 20.4% of the variance). This axis appears to be linked with the  
529 centroid size of the specimens: for both *E. maximus* and *L. africana*, the larger specimens are closer to  
530 the positive part of the graph than the smaller ones. The theoretical shape at the PC2 minimum shows  
531 a thin and elongated morphology, the diaphysis and the epiphyses being reduced in both the  
532 craniocaudal and the lateromedial axes; The theoretical shape at the PC2 maximum shows a more  
533 massive morphology, with wide epiphyses and a large diaphysis.

534 The mean shapes of each species roughly correspond to the differences observed along the first axis:  
535 *L. africana* displays a thinner, elongated morphology, as opposed to the stout and massive one  
536 displayed by *E. maximus*. Detailed descriptions of the theoretical shapes at the PCs minimum and  
537 maximum are in Supplementary Results S1.

538

### 539 *Fibula*

540 Results of the Procrustes ANOVA on the fibula shape data (Table 6) revealed no significant difference  
541 of shape between *E. maximus* and *L. africana* ( $p=0.63$ ,  $r^2=0.17$ ). The Neighbour-Joining tree computed  
542 on fibular shape data showed no clear separation between the two species, with the *L. cyclotis*  
543 specimen placed in the middle of the NJ tree (Supplementary Fig. 9H). Details of the fibula anatomy  
544 are in Supplementary Figure 18.

545

### 546 *Integrative overview*

547

548 At the intraspecific level (*Elephas maximus*), only the stylopod bones showed an ontogenetic  
549 allometry. In both the humerus and femur, this allometry was characterized by a development of the  
550 proximal extremity of the bone, while the distal extremity stayed relatively similar in shape. ANOVAs  
551 testing for shape difference between male and female specimens of *E. maximus* yielded no significant  
552 difference for any of the six bones; however, qualitative comparisons of the mean shapes of male and  
553 female specimens suggested morphological variations in the humeral epiphyses. ANOVAs testing for  
554 static allometry among the adult samples detected a significant allometry for the humerus only: in  
555 both species, the humerus grows more massive and robust with increased centroid size. Robustness  
556 analyses also revealed a significant difference for the humerus only: *E. maximus* displays more robust  
557 humeri than does *L. africana*. While there was no significant difference for the other bones, qualitative  
558 comparisons of the mean shapes indicated globally more robust bones in *E. maximus* than in *L.*  
559 *africana*. ANOVAs testing for shape difference at the interspecific level revealed significant differences  
560 for the humerus, the ulna and the tibia. For each of the three bones, the morphological variation was  
561 noticeable enough to allow for species distinction based on qualitative analysis alone. Overall, the  
562 humerus is the bone showing the most variation of shape between specimens, whether at the  
563 intraspecific or interspecific level, followed by the ulna and tibia displaying clear morphological  
564 differences between the two species, whereas the femur and fibula display almost no morphological  
565 variation.

566

## 567 DISCUSSION

### 568 Morphological variation at the intraspecific level

#### 569 Shape variation during ontogeny

570 Since long bones play a prominent role in the support and movement of the body, their external  
571 morphology is expected to reflect the biomechanical demands they face (Iwaniuk *et al.*, 1999, 2000);  
572 among those, body mass in particular is a major parameter (Biewener, 1989; Hildebrand, 1982). During  
573 ontogeny, bones are thus subjected to increasing stresses, although to varying degrees depending on  
574 the considered taxa. Gracility can be defined as the inverse of robustness, i.e as the ratio of the entire  
575 bone length over the diaphyseal circumference. The gracility of bones increases during growth  
576 (considered here as positive allometry) in most taxa, with the notable exception of proboscideans  
577 (Carrier, 1990). More specifically, cursorial taxa and taxa under 20 kg display a positive allometry, while  
578 graviportal taxa (including rhinos and hippos) display a negative allometry during ontogeny (Carrano,  
579 1999; Christiansen, 2002; Kilbourne & Makovicky, 2012). We found a negative allometry in the  
580 variation of the stylopod bones during growth in *E. maximus*, partly supporting the results of  
581 Kokshenev & Christiansen (2010) stating that both *Elephas maximus* and *Loxodonta africana* share  
582 similar negative allometric patterns in their six long bones during ontogeny, growing more robust with  
583 increasing size. Here, a clear shape difference is thus observed between adult and non-adult specimens  
584 in the humerus and femur, but not for the radius, ulna, tibia and fibula, which indicates an isometric  
585 growth pattern for these bones. Thus, our results are also partly consistent with those of Kilbourne &  
586 Makovicky (2012), who studied the tibia, femur and humerus, and found an isometric growth pattern  
587 for these bones: our results are consistent with theirs regarding the isometric growth of the tibia, but  
588 not for the femur and the humerus.

589 Most interestingly, while the limb long bones of elephants do not share the allometric trend observed  
590 in most quadrupeds, bones of their autopods do: most bones of the manus and pes display an isometry  
591 or a positive allometric pattern in Asian elephants (Main & Biewener, 2004; Miller *et al.*, 2008). This  
592 variation in allometric patterns highlights how differences in functional constraints (e.g., in relation to  
593 the position within the limb, proximity to the footpad) between limb long bones and bones of the  
594 autopod might affect how they respond to mass increase during growth.

595 The visible effect of ontogeny on the stylopod but not on the zeugopod might be linked to the  
596 anatomical position of the bones within the limb, and thus the different structural strains they face:  
597 the zeugopod bones are “more columnar” (i.e., positioned more orthogonally to the ground) than the  
598 stylopod bones (Larramendi, 2016), so we can hypothesize that they are more parallel to the weight  
599 and ground reaction forces. Their shape would thus be primarily adapted to these forces, and thus  
600 need to be stay stable during ontogeny. In the stylopod bones, the proximal epiphysis develops

601 proportionally more than the distal epiphysis during growth, roughly doubling its width. This difference  
602 in shape variation along the proximo-distal axis is consistent with the idea of a distal part of the limb  
603 more adapted to weight bearing in an orthogonal position to the ground: we found that the distal  
604 epiphyses, part of the elbow and knee joints respectively, display a more stable shape through  
605 ontogeny. In elephants, these joints play a specific role in supporting the body mass by distributing the  
606 load on the entirety of the articular surface (Weissengruber *et al.*, 2006). Even the youngest elephants  
607 display this pattern; since elephant calves weight around 90 to 100 kg at birth, we can propose that it  
608 allows them to withstand a high body mass from the earlier stages of life. The shape variation of the  
609 proximal epiphyses during growth suggests that the proximal part of the stylopods are not similarly  
610 adapted to weight-bearing in young individuals. Kilbourne & Makovicky (2012) suggested that a larger  
611 sample size might reveal isometric growth pattern in bones of the stylopod. However, the general  
612 trend here indicates a clear allometric growth pattern in both the femur and the humerus, consistent  
613 with the results of Kokshenev & Christiansen (2010); as such, an isometric growth pattern in the  
614 stylopod bones of elephants would be very surprising.

615

#### 616 [Static allometry and sexual dimorphism](#)

617 We observed a global pattern of increased robustness (i.e., ratio of circumference to bone length) at  
618 the intraspecific level in both *E. maximus* and *L. africana*, with larger specimens being more robust  
619 than smaller specimens. This is consistent with what is generally observed in heavier mammalian  
620 clades, in which an increase in body size and mass is generally associated with a global broadening of  
621 the limb long bones, with an enlargement of both the diaphysis and epiphyses (Bertram & Biewener,  
622 1990, 1992; Christiansen, 1999; Kilbourne & Makovicky, 2012; Mallet *et al.*, 2019)

623 Despite the qualitative observations of increased robustness in all the bones, the shape variation  
624 within the adult sample of each species indicated a significant negative allometry in the humerus only:  
625 larger specimens exhibited stout and robust humeri while their smaller counterparts exhibited more  
626 gracile and elongated ones; this is consistent with the fact that the humerus is the bone displaying the  
627 most shape variation linked to mass increase in our analyses. In quadruped mammals, the centre of  
628 mass is typically closer to the forelimb than to the hindlimb, so that forelimb elements bear more  
629 weight than hindlimb ones (Lessertisseur & Saban, 1967; Hildebrand, 1974; Polly, 2008, Etienne *et al.*,  
630 2020). Elephants are no exception to this rule (Ren *et al.*, 2010), their forelimb supporting around 60%  
631 of the total weight (Henderson *et al.*, 2006). The ground reaction forces as well as the weight-bearing  
632 forces are thus higher in the forelimb than in the hindlimb, increasing the mechanical load on the bones  
633 and on their associated shape variation; this would explain the presence of a negative allometry in the  
634 forelimb only. The negative allometry observed in the humerus only is consistent with previous works

635 stating that the effect of a high body mass would be more pronounced on the stylopod than on the  
636 zeugopod (Biewener, 1989; Campione & Evans, 2012, Mallet *et al.*, 2019).

637

638 In elephants, body size and mass can vary considerably depending on the sex of the animal, so that we  
639 might expect to observe more robust bones in the larger, heavier male specimens. Among the  
640 specimens for which the sex was known, we observed more robust humeri in male specimens, which  
641 displayed wider epiphyses than females. This shape variation might be directly linked to differences in  
642 body mass and body mass distribution between the sexes: since weight is expected to scale with linear  
643 dimensions cubed, even a small increase in body height results in a large variation in mass. On average,  
644 male African savanna elephants display 3.2m height at the shoulder, which is about half a meter more  
645 than their female counterparts; as a result, they can weight more than twice their body mass (Wilson,  
646 Mittermeier & Altrichhter, 2011). These size and mass differences between males and females are  
647 similar in Asian elephants (Wilson, Mittermeier & Altrichhter, 2011). Additionally, males can grow tusks  
648 in both species. Female Asian elephants do not grow tusks (Sukumar, 1989), and although both sexes  
649 can have tusks in *L. africana*, they are generally bigger in males (Elder, 1970; Smith & Fisher, 2013). As  
650 a result, there might be a big difference in weight distribution between male and female specimens  
651 (albeit more pronounced in *E. maximus* than in *L. africana*). Since we observed this robustness  
652 variation between males and females in the humerus only, we could propose that the humerus plays  
653 a role in the accommodation of the increased weight of the head linked to the presence of heavier  
654 tusks and a generally higher body mass supported by the forelimb. However, the subsample of  
655 specimens for which the sex was known is too small to state on the sexual dimorphism in bone  
656 robustness, and a larger sample might reveal shape and robustness difference in limb bones other than  
657 the humerus, or conversely, show that there is not consistent variation linked to sex in the external  
658 morphology of the bones.

659

## 660 [Morphological variation at the interspecific level](#)

### 661 [Adaptation to weight bearing](#)

662 While still gigantic compared to the majority of quadrupedal mammals, the Asian elephant is smaller  
663 in height and body mass than its African savanna counterpart (Mittermeier & Altrichhter, 2011).  
664 However, at equal shoulder-height the two species do not differ in weight (Larramendi, 2014). In our  
665 sample, we found no evidence for a statistically significant size difference in the length of the limb long  
666 bones between the two species. This could arguably be due to a small sample size, or the missing  
667 information regarding the sex of our specimens, leading to a biased sample and an overlapping of male

668 Asian elephants and female African elephants, closer in size and mass. In any case, the absence of  
669 species-specific size difference in our sample, as well as the similar variance in the size distribution of  
670 the two species indicate that in our sample all the adult specimens of both *L. africana* and *E. maximus*  
671 share the same approximate height, so that we can assume that our sample is composed of specimens  
672 sharing globally similar body masses. This enables us to investigate how the two species adapt to a  
673 similar body weight.

674 We observed a clear morphological variation in the long bones of the two species: *L. africana* typically  
675 has long and gracile bones, when *E. maximus* exhibits stouter, more robust ones. While this global  
676 shape difference is qualitatively considerable for all bones with the exception of the fibula, we found  
677 that only three bones displayed a significant shape difference: the humerus, ulna and tibia; this is  
678 consistent with our qualitative observations in which they displayed a greater variation than the  
679 other bones. The humerus of the Asian elephant was overall enlarged in both cranio-caudal and medio-  
680 lateral directions, with larger epiphyses. In the African savanna elephant, both the shaft and the  
681 epiphyses appeared narrower, with a greater tubercle considerably elongated in the proximal  
682 direction. The greater tubercle bears the insertions of the supraspinatus and infraspinatus muscles,  
683 which play a prominent role in the shoulder joint stabilization, as well as a role in humeral abduction.  
684 This might indicate different adaptations to weight support in the two species, with the Asian elephant  
685 relying on enlarged elbow and shoulder joints to distribute the mechanical load. This may be linked to  
686 differences in skull size and relative position between Asian and African elephants: the skull of *E.*  
687 *maximus* is indeed relatively larger and positioned higher than in African species (Marchant &  
688 Shoshani, 2007; Larramendi, 2014), resulting in a stronger mechanical load on the forelimb. However,  
689 male *E. maximus* specimens display smaller (and thus lighter) tusks than do *L. africana* specimens, and  
690 female *E. maximus* specimens do not have tusks, so that the supposedly relative increased weight of  
691 the head in *E. maximus* might be counterbalanced by the reduced/absent tusks, compared to *L.*  
692 *africana*. The relative mass of the head compared to the body is thus difficult to ascertain. Despite this  
693 possible balance between the two species (heavier tusks vs. higher and heavier skull), it is worth noting  
694 that Marchant & Shoshani (2007) described an additional muscle in the neck of *E. maximus* (*m. splenius*  
695 *superficialis*), interpreted as an additional muscular support of the weight of the head. Larramendi &  
696 Asier (2015) hypothesized that this muscle was heavily involved in the support of the head and was  
697 present in all *Elephas* species as well as in several other extinct proboscideans. The secondary loss of  
698 this muscle in *L. africana* may be linked to the reduced size of the cranial dome, on which it inserts,  
699 although it is uncertain which led to the other. This difference in the neck musculature between  
700 *Elephas* and *Loxodonta* indicates that the two species adapted in a different manner to support the  
701 weight of the head; it is thus logical to expect other accompanying anatomical differences, as observed

702 here in the humerus. However, quantitative biomechanical comparisons of the weight distribution  
703 between the two species, taking tusks weight into consideration, are needed to better understand how  
704 head weight and head position relative to the body may influence the shape of limb long bones.

705 In our shape analyses of the humerus, both species were clearly separated, and we observed a  
706 distribution linked with size. However, the size distribution was almost opposite for the two species,  
707 indicating different growth patterns (Fig. 3). While we found a significant static allometry in both  
708 species, the interspecific variation was stronger, again indicating different adaptations of the humeral  
709 shape to size increase. Female Asian elephants, more gracile, were closer to the males of the African  
710 elephant than to the males of their own species in our shape analysis; the two species were separated  
711 in the morphospace, with male and female specimens positioned at the extremities, indicating a  
712 possible gradient ranging from the more robust bones (male *E. maximus* specimens) to the more  
713 gracile ones (female *L. africana* specimens). However, this morphological distribution linked to sex  
714 stays hypothetical, as the sex of most specimens was unknown.

715

716 The role of the radius in weight-support has been highlighted among a wide sample of quadrupedal  
717 mammals (Bertram & Biewener, 1992), including heavy taxa such as rhinoceroses (Mallet *et al.*, 2019;  
718 Etienne, 2020) and hippopotamuses (Fisher *et al.*, 2007). Proboscideans are an exception to this  
719 pattern: in elephants, the ulna plays a more important role in the support of the body mass than the  
720 radius, which is reduced in size (Smuts & Bezuidenhout, 1993). The restricted role of the radius in body  
721 mass support could explain the absence of a morphological variation between Asian and African  
722 savanna elephants.

723

724 In elephants, the columnarity of the forelimb is partly achieved by the reorientation of the trochlear  
725 notch in the dorsal direction (Christiansen, 1999). The ulna is parallel to the weight and ground reaction  
726 forces during static weight bearing, and as such allows an efficient support and distribution of the  
727 mechanical load to the humerus. The main extensor of the forearm is the triceps brachii, which inserts  
728 on the extremity of the olecranon (Fisher *et al.*, 2007; Barone, 2010). In heavier taxa, the olecranon is  
729 wider and longer, especially in the anteroposterior direction, which corresponds with the increased  
730 strain exerted by this muscle to maintain an erect posture (Etienne *et al.*, 2020). Etienne *et al.* (2020)  
731 stated that a longer olecranon relative to the length of the ulna, as well as a more posterior position  
732 of the olecranon, would allow a more open angle when the elbow is in extension, as well as a longer  
733 lever arm. Here, we found that the olecranon was thin and elongated in the craniocaudal direction in  
734 the African savanna elephant, whereas it was rounder and wider in the mediolateral direction in the  
735 Asian elephant. This might indicate a higher stress exerted by the long head of the triceps brachii (the  
736 most powerful part of the muscle) in the African elephant, opposed to a higher strain exerted by the

737 lateral and medial heads (accessories to the long head, inserting on the medial and lateral sides of the  
738 humerus) in the Asian elephant. These muscular insertions could play a role proximally in the global  
739 thickening of the diaphysis we observed in the humerus of the Asian elephant. We observed no clear  
740 difference in the relative length of the olecranon between the Asian and African savanna elephant  
741 species, indicating that they do not differ in elbow position nor in lever arm efficiency.

742 We found no significant variation of shape between the femur of the *E. maximus* and *L. africana*. In  
743 quadrupedal mammals, the forelimb and the hindlimb ensure different function in locomotion: the  
744 forelimb plays an additional role in braking during locomotion, while the hindlimb plays a prominent  
745 role in the propulsion of the body (Dutto *et al.*, 2006). As a result, we expect them to react differently  
746 to increases in body mass, as it was shown in rhinos (Mallet, 2019; Etienne, 2020). But, while the  
747 functional distribution of weight-bearing is similar in elephants (Schmidt-Burbach & Eulenberger, 2008;  
748 Panagiotopoulou *et al.*, 2012), it is not the case for the locomotor functions: Ren *et al.* (2010) compared  
749 the elephant forelimb and hindlimb to a four wheeled vehicle, in which the propulsion and braking  
750 roles are equally shared by the limbs. Since the forelimb bears more weight than the hindlimb, we infer  
751 that the bones of the hindlimb are subjected to less stress than bones of the forelimb, so that they  
752 would be less prone to morphological variation; however, the considerable shape variations observed  
753 in the tibia suggest that weight constraints vary greatly between the stylopod and the zeugopod. Since  
754 we found no difference between the shape of the femur between the two species, we were not able  
755 to diagnose the undetermined femora. They appeared closer to the Asian species than to the African  
756 ones in the shape analyses, although there was no clear differentiation. These bones might belong to  
757 the African forest elephant; conversely, their reduced size might indicate that they all belong to female  
758 specimens, in which case their distribution (slight separation on the NJ-tree) might indicate a sexual  
759 dimorphism in the femur of *E. maximus*.

760 The tibia is the main weight bearer in the hindlimb zeugopod, due to its large surface of articulation  
761 with the bones of the autopod, and its orthogonal position to the ground. We found that the  
762 hyperventricity of the hindlimb was reflected in the shape of the tibia that in elephants is distinctly  
763 different from that of other quadrupedal mammals, even when compared with heavier taxa (Smuts &  
764 Bezuidenhout, 1994; Barone, 2010; Etienne, 2021). A particular feature is the markedly concave  
765 articular surface of the tibia, corresponding with the femoral condyles. This translates to a higher  
766 congruence of the knee joint, allowing the weight to be distributed more efficiently onto the femur  
767 (Weissengruber *et al.*, 2006). Bertram & Biewener (1992) noted a decrease of the tibial curvature  
768 associated with an increase in body mass among terrestrial mammals. This is particularly visible in our  
769 sample since the shaft is straight in all specimens, although it is more pronounced in *L. africana*  
770 specimens. While they both share a morphology adapted to the near-columnarity of the limb, we

771 observed a clear difference in the tibial global shape of the two species.  
772 In *E. maximus*, the tibia was stouter and more massive than in *L. africana*, with thicker condyles in the  
773 proximal epiphysis. The lateral condyle in particular was wider along the dorsoventral axis, and was  
774 elongated in the caudal direction. This condyle bears the insertion of muscles involved in the extension  
775 of the hip and of the knee, as well as the abduction and the external rotation of the ankle. These  
776 enlarged areas for muscles involved in joint flexion and rotation suggest a higher compliance in *E.*  
777 *maximus*, which is consistent with the higher limb compliance in the elbow and knee of the Asian  
778 elephant as compared to the African savanna elephant described by Kokshenev & Christiansen (2010)  
779 based on limb bone scaling. In elephants, the large, prominent tibial crest bears the insertion of the  
780 *biceps femoris* muscle, a powerful extensor of the hip and knee. This muscle originates on the ischium,  
781 preventing its elevation under the effect of body weight, and contributes to keeping the pelvis upright  
782 (Shindo & Mori, 1936; Barone, 2010), so that its enlarged area of attachment suggests a high muscular  
783 strain, which is consistent with the need to counterbalance the massive weight of the animal. In both  
784 *Loxodonta* and *Elephas*, the tibial crest is prominent and placed more medially than in most taxa,  
785 delimitating a wide, concave surface on the cranial side, and ends distally in a rough area for muscular  
786 attachment (Smuts & Bezuidenhout, 1994). This cranial, concave area provide a wide zone of insertions  
787 for patellar ligaments, which are the continuation of the various heads of the *quadriceps femoris*  
788 muscle, a powerful knee extensor, allowing the stabilizing of the knee. Additionally, one of the heads  
789 of the *quadriceps femoris* muscle inserts via a separate tendon onto the tibial tuberosity instead of  
790 stopping on the patella (Weissengruber *et al.*, 2006). This is not the case in other heavy taxa such as  
791 rhinos (Etienne *et al.*, 2020) and hippos (Fisher *et al.*, 2010); we conclude that this tibial crest  
792 development is linked to a high muscular strain, and thus that this adaptation is specific to weight-  
793 support in elephants by increasing the knee-joint stability.  
794 *E. maximus* displayed wider epiphyses than *L. africana*, with an enlarged tibial crest. This mediolateral  
795 widening was associated to a larger concave area on the cranial side. This area forms a triangle,  
796 delimited proximally by the condyles, laterally by the tibial crest and medially by a rough ridge  
797 connecting the distal limit of the tibial crest and the most cranial part of the medial condyle. Several  
798 muscles and ligaments involved in hip adduction and ankle flexion insert in this area. Under those,  
799 several digital flexors insert directly on the concave area (Shindo & Mori, 1936). In *E. maximus*, this  
800 area reached more distally on the shaft of the tibia, indicating relatively larger areas of muscular  
801 attachment. This might indicate that the Asian elephant relies more than the African savanna elephant  
802 on the stabilizing power of the hindlimb muscles to maintain an erect posture.

803

804 Changes in robustness

805 Several studies have investigated bone robustness in proboscidean limb bones, with sometimes  
806 contradicting results: based on linear measurements, Christiansen (2007) originally stated that there  
807 was no difference in robustness between the stylopod bones of *E. maximus* and *L. africana*, but in a  
808 later study (also based on linear measurements) Kokshenev & Christiansen 2010 found that the six  
809 bones were significantly more robust in Asian elephants than in African savanna elephants. Our results  
810 are consistent with the latter: although the interspecific robustness difference was significant for the  
811 humerus only, all the other bones displayed a similar trend that might prove significant based on a  
812 greater sample.

813 Various trends of robustness can be observed among terrestrial quadrupeds, with equally various  
814 explanations as to their biomechanical consequences. Numerous attempts to formulate generally  
815 applicable allometric laws using body mass, bone length and bone circumference have been proposed,  
816 and have been subject to several decades of debates (Alexander, 1977; Alexander *et al.*, 1979;  
817 Biewener, 1983, 2005; Bertram & Biewener, 1990; Christiansen, 1999, 2002, 2007, Kokshenev *et al.*,  
818 2003; Kokshenev, 2007; McMahon, 1973, 1975a, b). Using three of the most common allometric  
819 models, Kokshenev & Christiansen (2010) concluded that the bones of the Asian elephant, more  
820 robust, were more adapted to resist the bending and torsion forces exerted by the muscles (bending-  
821 torsion model), while the bones of the African savanna elephant, more gracile, were optimized to resist  
822 gravitational forces (buckling model). However, this raises the question of the underlying causes  
823 behind this species-specific adaptation.

824 This morphological divergence between *E. maximus* and *L. africana* could be linked with human  
825 activity: Asian elephants have a long history of being used by humans for various tasks, ranging from  
826 field work and military use to modern days tourism and circus shows. However, despite this extensive  
827 human exploitation, elephants were never domesticated, so that elephant breeding was never fully  
828 controlled by humans. We can thus exclude the possibility of an anthropic selection toward more  
829 robust individuals, or of a by-product of domestication. Another explanation could be a difference in  
830 locomotor mode between the two species: there is a widely-spread belief that African savanna  
831 elephant can reach higher running speed than Asian elephants. Several studies reported high speeds  
832 in African savanna elephants (Andrews, 1937; Garland, 1983; Le Rue, III, 1994; Iriarte-Díaz, 2002), that  
833 were then attributed to high error rates in measurements taken from automobile speedometers, as  
834 well as human error due the excitement of witnessing a charging wild elephant (Hutchinson *et al.*,  
835 2006). As such, they consider these values to be exaggerations, and based on their own measurements  
836 and predictive models state that both elephant species can reach the same maximal speed.

837 In addition to sharing the same running speed, both species share a similar walking gait (Ren *et al.*,  
838 2010; Langman, 2012), so that we conclude that the robustness difference does not result from a

839 variation in speed nor gait. Asian and African savanna elephants share similar locomotor mechanics  
840 (Hutchinson *et al.*, 2006; Ren *et al.*, 2008), and the differences in their foot anatomy are minor (Miller  
841 *et al.*, 2008); additionally, the ground reaction forces are distributed similarly in the foot pad of both  
842 species (Panagiotopoulou *et al.*, 2016). These results suggest that there is no postural difference that  
843 could explain the robustness variation.

844 However, *E. maximus* and *L. africana* occur in different types of habitat, so that they walk on different  
845 types of substrates and terrains. Asian elephants mostly walk on soft and yielding surfaces in humid  
846 forests and jungles, while African savanna elephants roams on savanna grasslands and sandy plains, as  
847 well as the hard, dry surfaces of semiarid deserts (Roocroft & Oosterhuis, 2001; Wilson, Mittermeier  
848 & Altrichhter, 2011). For obvious practical reasons, all studies performed on elephant gait, running  
849 speed and weight distribution have been conducted on hard and artificial surfaces; we could  
850 hypothesize that while they found no difference in force distribution nor in locomotion patterns, the  
851 results might have been different if the analyses had been conducted in the natural habitat of the  
852 animals. Asian elephants might require more stabilizing while walking on uneven and soft ground, as  
853 well as greater dexterity when navigating in densely forested areas. Furthermore, *E. maximus* and *L.*  
854 *africana* have evolved different foraging habits: African savanna elephants are browsers, using their  
855 trunk rather than their feet when foraging. Asian elephants, however, use their forefeet to scrape and  
856 dig deep into the soil (Roocroft & Oosterhuis, 2001), and have been reported to use their forelimbs to  
857 secure fallen trees and tear away at the tree bark and root system, or to strike down bamboo and tall  
858 grass (Buckley, 2008). This larger range of limb movement observed in *E. maximus* may also result in  
859 higher muscular strains and thus explain the stouter morphology we observed in the humerus.

860

861 [What about the African forest elephant?](#)

862 African forest elephants are the smallest of the three living species. Our sample comprised the six  
863 bones of a single specimen, presenting no sign of aging or pathology; we included them in our shape  
864 analyses in order to see how it compared to the other species. The results are intriguing, as this  
865 specimen was clearly separated from the other species when looking at the ulna and tibia, but was  
866 included in the *E. maximus* cluster for the humerus and radius, and in the *L. africana* cluster for the  
867 femur. The fibula was also clearly separated from those of the two other species; however this result  
868 is to be considered with caution since this bone yielded minimal taxonomic signal in our study.  
869 Qualitative observations of the six bones of the *L. cyclotis* specimen are consistent with these results:  
870 overall *L. cyclotis* displayed a stouter morphology than *L. africana*, with bones of the forelimb  
871 displaying a shape closer to those of the Asian elephant, while bones of the hindlimb displayed more  
872 “in-between” shapes. The specimens to which *L. cyclotis* is closest for the bones of the forelimb are

873 not the same than for bones of the hindlimb; since bones from the same “closest” specimens were  
874 represented in analyses on both the forelimb and the hindlimb, the shape similarity of *L. cyclotis* with  
875 one species or the other depending on the bone is not due to a change in sample. Consistently,  
876 analyses on a juvenile specimen of *L. cyclotis* showed a similar pattern of morphological similarity (C.B.,  
877 pers. obs.): the humerus and ulna were closest to those of the juvenile Asian elephants, while the tibia  
878 was separated from those of both *E. maximus* and *L. africana*. The surprising pattern of shape similarity  
879 between bones of the adult *L. cyclotis* specimens and those of *E. maximus* and *L. africana* might thus  
880 be representative of this species.

881 Most interestingly, the interspecific morphological variation we describe here in modern elephants  
882 differs from other extant graviportal mammals such as rhinos. Body mass and habitat vary greatly  
883 across rhinoceros’s species (Wilson, Mittermeier & Altrichhter, 2011), the various limb bones are  
884 differently affected. In rhinoceroses, the shape variation of the humerus and the femur is mostly driven  
885 by the phylogenetic signal, while it is the radius and ulna that are mainly affected by body mass (Mallet  
886 *et al.*, 2019). Conversely, we find here a pattern of shape variation linked to the type of limb (forelimb  
887 vs. hindlimb) rather than to the limb segment (stylopod vs. zeugopod). The entire forelimb of *L. cyclotis*  
888 is morphologically closer to that of *E. maximus*, suggesting, if this specimen is indeed representative  
889 of this species, that in elephants, the forelimb bones’ morphology could be more influenced by body  
890 mass (smaller in *L. cyclotis* and *E. maximus* than in *L. africana*) and the environment (forest vs. open  
891 plains) than by the phylogenetic proximity, while it is the opposite for the hindlimb. This suggests that  
892 the adaptation of the limb bones to a high body mass does not happen in the same manner across the  
893 various “graviportal” taxa.

894

## 895 CONCLUSION

896 In both species, we observed an ontogenetic allometry in the stylopod bones due to a large growth  
897 with size of the proximal epiphyses as compared to the distal ones; this suggests that the elbow and  
898 knee joints are adapted to withstand massive weight from the earliest ontogenetic stage. The other  
899 bones follow an isometric growth pattern, indicating that the bones of the zeugopod react differently  
900 to an increase of mass. We also observed an allometry among adult specimens: bigger (and thus  
901 heavier) specimens displayed stouter, more robust bones. While this allometry was significant for the  
902 humerus only, the same trend was observed in the other bones. Limb long bones robustness thus  
903 increases with weight. While these intraspecific variations are clearly defined, their signal is masked  
904 by the more pronounced differences between the two species: our shape analyses revealed significant  
905 differences in the external morphology of the humerus, ulna and tibia between *E. maximus* and *L.*

906 *africana*: the humerus is stouter in the Asian elephant, presenting enlarged area for the attachment of  
907 muscles involved in shoulder joint stabilization and humeral abduction, indicating different  
908 adaptations to weight support in both species. The ulna, which plays an important role in the support  
909 of the body mass, displays a difference in shape and orientation of the olecranon, allowing for a wider  
910 angle of limb extension and a more efficient lever arm in *E. maximus* than in *L. africana*. The tibia  
911 displays a morphology adapted to the limb hyperventricity in both species; however, the condyle  
912 bearing muscles involved in hip and knee extension, as well as in ankle abduction and rotation, was  
913 elongated in *E. maximus*, indicating a higher limb compliance in the knee of Asian elephants.  
914 Additionally, the tibia displays enlarged muscular insertion zones for muscles involved in knee and hip  
915 stabilization, suggesting that the Asian elephant relies more than the African savanna elephant on the  
916 stabilizing power of the hindlimb muscles to maintain an erect posture. These morphological variations  
917 are strongly pronounced, allowing for species distinction based on the external shape of the humerus,  
918 the ulna and the tibia. While the difference in robustness was significant in the humerus only, our  
919 qualitative comparisons indicated an overall higher robustness in *E. maximus* than in *L. africana*. Since  
920 both species share similar walking speed and gait, these parameters do not explain this variation.  
921 However, Asian and African savanna elephants live in highly different habitats, so that the robustness  
922 difference might be linked to their walking substrate (hard and dry vs. soft, humid soil) and direct  
923 environment (open plains vs. closed forest), since navigating through the humid forests would require  
924 more stabilizing and dexterity than walking in the savanna. We also suggest that the overall robustness  
925 variation between *E. maximus* and *L. africana* is linked to their locomotor and foraging habits, since  
926 the two species also exhibit different foraging behaviors, Asian elephants being able to make raking  
927 motions with their feet, displaying a higher forelimb dexterity than African savanna elephants, which  
928 do not use their forelimbs to feed.

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956

## 957 AUTHOR’S CONTRIBUTION

958 A.H. and C.B designed the study. A.D, A.H and C.B. did the bone data acquisition. C.B. conducted the  
959 analyses and drafted the manuscript, A.H. and C.B. contributed to the final manuscript, and all authors  
960 read it and approved it.

961

## 962 CONFLICT OF INTEREST

963 The authors declare no conflict of interest.

964

965 DATA AVAILABILITY

966 The R scripts used to perform the analyses will be made available on Github.

967 3D models provided by the Idaho Museum of Natural History can be found on [www.MorphoSource.org](http://www.MorphoSource.org)

968 with the following links:

969 [ark:/87602/m4/M168768](https://doi.org/10.26434/chemrxiv-2024-87602) (IMNH 1486, humerus)

970 [ark:/87602/m4/M168870](https://doi.org/10.26434/chemrxiv-2024-87602) (IMNH 1486, radius & ulna)

971 [ark:/87602/m4/M168758](https://doi.org/10.26434/chemrxiv-2024-87602) (IMNH 1486, femur)

972 [ark:/87602/m4/M168938](https://doi.org/10.26434/chemrxiv-2024-87602) (IMNH 1486, tibia)

973 [ark:/87602/m4/M168762](https://doi.org/10.26434/chemrxiv-2024-87602) (IMNH 1486, fibula)

974 3D models obtained from MNHN specimens will be made available on [www.3dtheque.mnhn.fr](http://www.3dtheque.mnhn.fr). Most  
975 of the remaining models used in this study will be made available in their respective museum  
976 repositories and/or by curators, and unless otherwise decided, deposited on MorphoSource.

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1395 SUPPLEMENTARY MATERIAL

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1397 **Table S1:** Designation of anatomical landmarks on the humerus.

LM	Designation
1	Most disto-medial point of the greater trochanter
2	Most disto-caudal point of the greater trochanter
3	Most disto-lateral point of the border of the head
4	Most disto-medial point of the border of the head
5	Most medial point of the lesser tubercle
6	Most caudo-medial point of the intertubercular groove
7	Most caudo-medial point of the border of the head
8	Most caudo-lateral point of the border of the head
9	Most cranial point of the deltoid tuberosity
10	Most lateral point of the supracondylar crest
11	Most caudo-lateral point of the trochlea
12	Most caudo-medial point of the trochlea
13	Most cranio-medial point of the trochlea
14	Most cranio-lateral point of the trochlea

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1410 **Table S2:** Designation of anatomical landmarks on the radius.

LM	Designation
1	Most lateral point of the articular surface of the head
2	Most cranio-medial point of the articular surface of the head
3	Most lateral point of the head
4	Most disto-medial point of the head
5	Most caudal point of the epiphyseal line
6	Most medial point of the epiphyseal line
7	Most cranial point of the epiphyseal line
8	Most lateral point of the epiphyseal line
9	Most caudal point of the border of the articular surface for the carpal bones
10	Most medial point of the border of the articular surface for the carpal bones
11	Most cranio-medial point of the border of the articular surface for the carpal bones
12	Most cranial point of the border of the articular surface for the carpal bones

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1426 **Table S3:** Designation of anatomical landmarks on the ulna.

LM	Designation
1	Most cranial point of the medial condyle
2	Most cranial point of the lateral condyle
3	Maximum concavity point of the distal border of the trochlear notch articular surface
4	Most cranial point of the anconeal process
5	Most cranio-lateral point of the olecranon tuberosity
6	Most proximal point of the olecranon tuberosity
7	Most disto-cranial point of the lateral condyle
8	Most distal point of the lateral crest
9	Most disto-caudal point of the olecranon tuberosity
10	Most cranial point of the epiphyseal line
11	Most caudal point of the epiphyseal line
12	Most medial point of the epiphyseal line
13	Most proximo-caudal point of the articular surface for the carpal bones
14	Most proximo-medial point of the articular surface for the carpal bones
15	Most cranio-lateral point of the articular surface for the carpal bones

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1438 **Table S4:** Designation of anatomical landmarks on the femur.

LM	Designation
1	Most lateral point of the border of the head
2	Most medial point of the border of the head
3	Most proximo-medial part of the trochanteric fossa
4	Most disto-caudal point of the greater trochanter
5	Most proximo-medial point of the third trochanter
6	Most disto-medial point of the third trochanter
7	Most distal point of the lesser trochanter
8	Most caudal point of the medial epicondyle
9	Most lateral point of the lateral epicondyle
10	Most proximal point of the lateral lip of the trochlea
11	Most proximal point of the medial lip of the trochlea
12	Most distal point of the medial lip of the trochlea
13	Most distal point of the lateral lip of the trochlea
14	Distal maximum of curvature of the trochlear groove
15	Most proximal point of the medial condyle
16	Most proximal point of the lateral condyle

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1451 **Table S5:** Designation of anatomical landmarks on the tibia.

LM	Designation
1	Most proximal point of the medial intercondylar tubercle
2	Most proximal point of the lateral intercondylar tubercle
3	Maximum of curvature of the medial border of the medial epicondyle
4	Maximum of curvature of the caudo-lateral border of the lateral condyle
5	Most cranial point of the cranial part of the medial condyle
6	Maximum of concavity of the cranial side of the epiphyseal line
7	Most cranial point of the tibial tuberosity
8	Most cranial point of the cranial border of the tibia
9	Most lateral point of the articular surface for the fibula
10	Most caudal point of the caudal side of the medial epicondyle
11	Most caudo-medial point of the malleolar sulcus
12	Most lateral point of the diaphysis
13	Most cranio-medial point of the border of the cochlea
14	Most caudo-medial point of the border of the cochlea
15	Most caudal point of the limit between the cochlea and the fibular notch
16	Most cranial point of the limit between the cochlea and the fibular notch
17	Most lateral point of the fibular notch
18	Most distal point of the malleolus

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1463 **Table S6:** Designation of anatomical landmarks on the fibula.

LM	Designation
1	Most cranio-medial point of the head
2	Most disto-cranial point of the articular facet of the malleolus
3	Most proximal point of the head
4	Most medial point of the head
5	Proximo-lateral limit of the articular facet for the talus and calcaneus
6	Most medial point of the articular facet for the talus and calcaneus
7	Most disto-medial point of the articular facet for the talus and calcaneus
8	Most lateral point of the articular facet for the talus and calcaneus
9	Proximo-lateral limit of the articular facet for the talus and calcaneus
10	Most proximal point of the epiphyseal line

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## 1481 TABLES

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1483 **Table 1:** Sample studied. H, humerus; R, radius; U, ulna; Fe, femur; T, tibia; Fi, fibula. Sex: F, female; M, male; NA, not available.  
 1484 Age: J, juvenile, S, subadult, A, adult. AM, acquisition mode: P, photogrammetry; SS, surface scanner; CT, CT-scan; LS, laser  
 1485 scanner. Institutional codes: IMNH, Idaho Museum of Natural History, Pocatello (USA); MNHN, Muséum national d'Histoire  
 1486 Naturelle, Paris (France); NHMW, Naturhistorisches Museum Wien, Vienna (Austria); RBINS, Royal Belgian Institute of Natural  
 1487 Sciences, Brussels (Belgium); ZSM, Zoologische Staatssammlung München, Munich (Germany).

Taxon	Institution	Specimen number	H	R	U	Fe	T	Fi	Sex	Age	AM
<i>Elephas maximus</i>	IMNH	1486	X	X	X	X	X	X	NA	A	LS
<i>Elephas maximus</i>	MNHN	ZM-AC-1883-1786				X			NA	A	CT
<i>Elephas maximus</i>	MNHN	ZM-AC-1896-17	X	X	X	X	X		M	A	SS
<i>Elephas maximus</i>	MNHN	ZM-AC-1896-19	X	X	X	X			M	A	SS
<i>Elephas maximus</i>	MNHN	ZM-AC-1907-263	X	X					F	S	SS
<i>Elephas maximus</i>	MNHN	ZM-AC-1936-280					X		M	S	CT
<i>Elephas maximus</i>	MNHN	ZM-AC-1983-082	X	X	X	X	X	X	F	A	SS
<i>Elephas maximus</i>	MNHN	ZM-AC-1998-6	X	X	X	X	X	X	M	A	SS
<i>Elephas maximus</i>	NHMW	2526	X			X			NA	J	P
<i>Elephas maximus</i>	NHMW	2828				X	X	X	NA	J	P
<i>Elephas maximus</i>	NHMW	4012	X			X			NA	A	P
<i>Elephas maximus</i>	ZSM	1953/153	X	X	X	X	X	X	NA	A	SS
<i>Elephas maximus</i>	ZSM	1962/340	X	X	X				NA	J	P
<i>Elephas maximus</i>	ZSM	unnumbered	X	X	X	X	X		NA	A	P
<i>Elephas maximus</i>	NHMB	936						X	NA	A	P
<i>Elephas maximus</i>	NHMB	46024						X	NA	A	P
<i>Loxodonta africana</i>	MNHN	ZM-AC-1855-11						X	NA	A	SS
<i>Loxodonta africana</i>	MNHN	ZM-AC-1907-49	X		X	X	X	X	M	A	SS
<i>Loxodonta africana</i>	MNHN	ZM-AC-1938-375	X	X					NA	A	SS
<i>Loxodonta africana</i>	MNHN	ZM-AC-1986-060	X						F	A	CT
<i>Loxodonta africana</i>	NHMW	unnumbered	X		X	X	X		NA	A	P
<i>Loxodonta africana</i>	RBINS	10858	X	X	X	X		X	NA	A	SS
<i>Loxodonta africana</i>	ZSM	1962/252		X	X	X	X		NA	A	P
<i>Loxodonta africana</i>	ZSM	1978/182	X	X	X	X	X	X	NA	A	SS
<i>Loxodonta cyclotis</i>	RBINS	12677	X	X	X	X	X	X	NA	A	SS
NA	MNHN	ZM-AC-1977-30D				X			NA	A	SS
NA	MNHN	ZM-AC-1977-30E				X			NA	A	SS
NA	MNHN	ZM-AC-1977-30F				X			NA	A	SS
NA	MNHN	ZM-AC-1977-30G				X			NA	A	SS
NA	MNHN	ZM-AC-1977-30H				X			NA	A	SS
NA	MNHN	ZM-AC-1977-30I				X			NA	A	SS
NA	MNHN	ZM-AC-1977-30J				X			NA	S	SS
NA	MNHN	ZM-AC-1977-30K				X			NA	S	SS
NA	MNHN	ZM-AC-1977-30M				X			NA	A	SS

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1489 **Table 2:** Results of Procrustes ANOVAs testing for 1) shape difference between adult and juvenile specimens and 2)  
 1490 correlations between shape data and log-transformed centroid size among the *E. maximus* sample. Cs, Centroid size; p, p-  
 1491 value;  $r^2$ , determination coefficient value. Significant results are in bold.

		Age (shape~age)	Allometry (shape~Cs)
Humerus	n=18	<b>p&lt;0.01, r<sup>2</sup>=0.38</b>	<b>p&lt;0.01, r<sup>2</sup>=0.28</b>
Radius	n=14	P=0.70, r <sup>2</sup> =0.21	p=0.31, r <sup>2</sup> =0.14
Ulna	n=14	P=0.09, r <sup>2</sup> =0.29	p=0.05, r <sup>2</sup> =0.26
Femur	n=17	<b>p=0.01, r<sup>2</sup>=0.32</b>	<b>p&lt;0.02, r<sup>2</sup>=0.27</b>
Tibia	n=13	p=0.10, r <sup>2</sup> =0.38	p=0.17, r <sup>2</sup> =0.18
Fibula	n=10	p=0.63, r <sup>2</sup> =0.42	p=0.06, r <sup>2</sup> =0.44

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1511 **Table 3:** Results of the Procrustes ANOVA testing for correlations between shape data and log-transformed centroid size in  
1512 adult specimens. Significant results are in bold.

	<i>Elephas maximus</i>	<i>Loxodonta africana</i>
Humerus	<b>p&lt;0.02, r<sup>2</sup>=0.30</b>	<b>p&lt;0.02, r<sup>2</sup>=0.36</b>
Radius	p=0.49, r <sup>2</sup> =0.16	p=0.19, r <sup>2</sup> =0.54
Ulna	p=0.95, r <sup>2</sup> =0.10	p=0.06, r <sup>2</sup> =0.44
Femur	p=0.25, r <sup>2</sup> =0.15	p=0.08, r <sup>2</sup> =0.54
Tibia	p=0.11, r <sup>2</sup> =0.28	p=0.95, r <sup>2</sup> =0.24
Fibula	p=0.11, r <sup>2</sup> =0.15	p=0.59, r <sup>2</sup> =0.31

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1533 **Table 4:** Results of the correlation tests between the size parameters and the two first principal components of the Principal  
1534 Components Analyses computed using the shape data of the adult specimens of *Elephas maximus* and *Loxodonta africana*.  
1535 Ci, smallest diaphyseal circumference; Cs, Centroid size; MaxL, maximum length of the bone; NA, not available since we could  
1536 not measure the circumference in the radius and ulna; p, p-value;  $r^2$ , determination coefficient value. Significant results are  
1537 in bold.

		<i>Elephas maximus</i>				<i>Loxodonta africana</i>			
Bone	Component	Cs	Ci	MaxL	Rb	Cs	Ci	MaxL	Rb
Humerus	PC1	<b>p=0.017,</b> <b>r<sup>2</sup>=0.60</b>	p=0.44, r <sup>2</sup> =0.1	<b>p=0.014,</b> <b>r<sup>2</sup>=0.65</b>	p=0.27, r <sup>2</sup> =0.18	<b>p=0.01,</b> <b>r<sup>2</sup>=0.8</b>	<b>p=0.02,</b> <b>r<sup>2</sup>=0.71</b>	<b>p=0.02,</b> <b>r<sup>2</sup>=0.78</b>	p=0.14, r <sup>2</sup> =0.46
	PC2	p=0.317, r <sup>2</sup> =0.18	p=0.14, r <sup>2</sup> =0.33	p=0.35, r <sup>2</sup> =0.15	p=0.34, r <sup>2</sup> =0.16	p=0.8, r <sup>2</sup> =0.01	p=0.44, r <sup>2</sup> =0.11	p=0.7, r <sup>2</sup> =0.02	p=0.23, r <sup>2</sup> =0.41
Radius	PC1	p=0.89, r <sup>2</sup> <0.01	NA	p=0.78, r <sup>2</sup> =0.01	NA	p=0.19, r <sup>2</sup> =0.94	NA	p=0.23, r <sup>2</sup> =0.92	NA
	PC2	p=0.16, r <sup>2</sup> =0.37	NA	p=0.20, r <sup>2</sup> =0.31	NA	p=0.89, r <sup>2</sup> =0.02	NA	p=0.86, r <sup>2</sup> =0.03	NA
Ulna	PC1	p=0.79, r <sup>2</sup> =0.01	NA	p=0.84, r <sup>2</sup> <0.01	NA	p=0.05, r <sup>2</sup> =0.68	NA	p=0.09, r <sup>2</sup> =0.67	NA
	PC2	p=0.61, r <sup>2</sup> =0.05	NA	p=0.44, r <sup>2</sup> =0.13	NA	p=0.88, r <sup>2</sup> =0.02	NA	p=0.75, r <sup>2</sup> =0.04	NA
Femur	PC1	p=0.28, r <sup>2</sup> =0.15	p=0.96, r <sup>2</sup> <0.001	p=0.27, r <sup>2</sup> =0.16	p=0.15, r <sup>2</sup> =0.27	p=0.15, r <sup>2</sup> =0.58	<b>p=0.04,</b> <b>r<sup>2</sup>=0.75</b>	p=0.10, r <sup>2</sup> =0.65	p=0.63, r <sup>2</sup> =0.07
	PC2	p=0.14, r <sup>2</sup> =0.29	p=0.30, r <sup>2</sup> =0.17	p=0.12, r <sup>2</sup> =0.33	p=0.80, r <sup>2</sup> <0.01	p=0.30, r <sup>2</sup> =0.39	p=0.38, r <sup>2</sup> =0.23	p=0.33, r <sup>2</sup> =0.31	p=0.20, r <sup>2</sup> =0.43
Tibia	PC1	p=0.54, r <sup>2</sup> =0.09	p=0.87, r <sup>2</sup> <0.01	p=0.53, r <sup>2</sup> =0.09	p=0.34, r <sup>2</sup> =0.21	p=0.94, r <sup>2</sup> <0.001	p=0.97, r <sup>2</sup> =0.08	p=0.94, r <sup>2</sup> <0.01	p=0.11, r <sup>2</sup> =0.87
	PC2	<b>p=0.02,</b> <b>r<sup>2</sup>=0.78</b>	p=0.11, r <sup>2</sup> =0.70	<b>p=0.03,</b> <b>r<sup>2</sup>=0.70</b>	p=0.83, r <sup>2</sup> <0.01	p=0.35, r <sup>2</sup> =0.40	p=0.43, r <sup>2</sup> =0.27	p=0.35, r <sup>2</sup> =0.37	p=0.83, r <sup>2</sup> =0.20
Fibula	PC1	<b>p=0.04,</b> <b>r<sup>2</sup>=0.66</b>	p=0.17, r <sup>2</sup> =0.38	<b>p=0.02,</b> <b>r<sup>2</sup>=0.70</b>	p=0.99, r <sup>2</sup> <0.0001	p=0.77, r <sup>2</sup> <0.01	p=0.54, r <sup>2</sup> =0.22	p=0.89, r <sup>2</sup> <0.01	p=0.14, r <sup>2</sup> =0.68
	PC2	p=0.85, r <sup>2</sup> <0.01	p=0.34, r <sup>2</sup> =0.21	p=0.93, r <sup>2</sup> <0.01	p=0.24, r <sup>2</sup> =0.32	p=0.07, r <sup>2</sup> =0.96	p=0.19, r <sup>2</sup> =0.78	<b>p=0.02,</b> <b>r<sup>2</sup>=0.96</b>	p=0.53, r <sup>2</sup> =0.25

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1541 **Table 5:** Results of the correlation tests between the size parameters and the two first principal components of the Principal  
 1542 Components Analyses computed using the shape data of the entire adult sample for each bone. Ci, smallest diaphyseal  
 1543 circumference; Cs, Centroid size; MaxL, maximum length of the bone; NA, not available since we could not measure the  
 1544 circumference in the radius and ulna; p, p-value;  $r^2$ , determination coefficient value. Significant results are in bold.

Bone	Component	Cs	Ci	MaxL	Rb
Humerus	PC1	p=0.60, $r^2=0.02$	p=0.41, $r^2=0.05$	p=0.61, $r^2=0.01$	<b>p=0.01,</b> <b><math>r^2=0.37</math></b>
	PC2	p=0.97, $r^2<0.01$	p=0.43, $r^2=0.05$	p=0.96, $r^2<0.01$	p=0.12, $r^2=0.18$
Radius	PC1	p=0.85, $r^2<0.01$	NA	p=0.96, $r^2<0.01$	NA
	PC2	p=0.59, $r^2=0.03$	NA	p=0.67, $r^2=0.02$	NA
Ulna	PC1	p=0.05, $r^2=0.31$	NA	p=0.05, $r^2=0.31$	NA
	PC2	p=0.52, $r^2=0.03$	NA	p=0.59, $r^2=0.02$	NA
Femur	PC1	p=0.30, $r^2<0.01$	p=0.37, $r^2=0.06$	p=0.24, $r^2=0.11$	p=0.43, $r^2=0.05$
	PC2	p=0.22, $r^2=0.11$	p=0.92, $r^2<0.01$	p=0.37, $r^2=0.06$	p=0.11, $r^2=0.17$
Tibia	PC1	p=0.96, $r^2<0.01$	p=0.35, $r^2=0.11$	p=0.95, $r^2<0.01$	p=0.33, $r^2=0.11$
	PC2	p=0.89, $r^2<0.01$	p=0.85, $r^2<0.01$	p=0.86, $r^2<0.01$	p=0.12, $r^2=0.26$
Fibula	PC1	p=0.14, $r^2=0.23$	<b>p=0.04,</b> <b><math>r^2=0.38</math></b>	p=0.11, $r^2=0.28$	p=0.39, $r^2=0.07$
	PC2	p=0.56, $r^2=0.04$	p=0.72, $r^2=0.02$	p=0.52, $r^2=0.05$	p=0.91, $r^2<0.01$

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1549 **Table 6:** Results of ANOVAs testing for size and shape variation between the species. Ci, smallest diaphyseal circumference;  
 1550 Cs, Centroid size; MaxL, maximum length of the bone; Rb, robustness; NA, not available since we could not measure the  
 1551 circumference in the radius and ulna; p, p-value; r<sup>2</sup>, determination coefficient value. Significant results are in bold.

	Cs	Ci	MaxL	Rb	Shape
Humerus	p=0.25, r <sup>2</sup> =0.20	p=0.99, r <sup>2</sup> <0.01	p=0.16, r <sup>2</sup> =0.16	<b>p&lt;0.02,</b> <b>r<sup>2</sup>=0.40</b>	<b>p=0.001, r<sup>2</sup>=0.26</b>
Radius	p=0.86, r <sup>2</sup> =0.02	NA	p=0.68, r <sup>2</sup> =0.02	NA	p=0.30, r <sup>2</sup> =0.11
Ulna	p=0.35, r <sup>2</sup> =0.17	NA	p=0.25, r <sup>2</sup> =0.12	NA	<b>p=0.02, r<sup>2</sup>=0.22</b>
Femur	p=0.21, r <sup>2</sup> =0.21	p=0.7, r <sup>2</sup> =0.07	p=0.11, r <sup>2</sup> =0.20	p=0.15, r <sup>2</sup> =0.15	p=0.16, r <sup>2</sup> =0.11
Tibia	p=0.71, r <sup>2</sup> =0.09	p=0.99, r <sup>2</sup> <0.01	p=0.45, r <sup>2</sup> =0.07	p=0.09, r <sup>2</sup> =0.37	<b>p=0.002, r<sup>2</sup>=0.22</b>
Fibula	p=0.40, r <sup>2</sup> =0.20	p=0.78, r <sup>2</sup> =0.07	p=0.50, r <sup>2</sup> =0.16	p=0.17, r <sup>2</sup> =0.34	p=0.63, r <sup>2</sup> =0.17

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1571 **FIGURE LEGENDS**

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1573 **Figure 1:** Visualizations of the mean shapes of the (A, C) humerus and (B, D) femur of (A, B) non-adult  
1574 and (C, D) adult specimens of *E. maximus* in a) cranial, b) lateral, c) caudal and d) medial views.

1575 **Figure 2:** Visualizations of the humeral shapes associated with (A, B) the minimum and (C, D) the  
1576 maximum of allometric regression analysis performed on adult specimens of (A, C) *L. africana* and (B,  
1577 D) *E. maximus* in a) cranial, b) lateral, c) caudal and d) medial views.

1578 **Figure 3:** Results of the PCA performed on morphometric data of the humerus of all adult specimens  
1579 along with the visualizations of the theoretical shapes at the minimum and maximum of the first two  
1580 axes. The size of the points is proportional to the centroid size of the bones. D.t., deltoid tuberosity,  
1581 G.t., greater trochanter, G.t.c., greater trochanter crest, H.c., humeral crest, H.h., humeral head, H.n.,  
1582 humeral neck, H.t., humeral trochlea, I.g., intertubercular groove, L.e., lateral epicondyle, L.t., lesser  
1583 trochanter, M.e., medial epicondyle, O.f., olecranon fossa, R.f., radial fossa, S.c., supracondylar crest;  
1584 Lat., lateral, Med., medial, Prox., proximal. See Supplementary Figure 10 for anatomical details of the  
1585 humerus.

1586 **Figure 4:** Results of the PCA performed on morphometric data of the ulna of all adult specimens along  
1587 with the visualizations of the theoretical shapes at the minimum and maximum of the first two axes.  
1588 The size of the points is proportional to the centroid size of the bones. A.p., anconeal process, A.s.r,  
1589 articular surface for the radius, L.c.p., lateral coronoid process, M.c.p., medial coronoid process, O.,  
1590 olecranon, O.t., olecranon tuberosity, T.n., trochlear notch, R.no., radial notch, S.p.u., styloid process  
1591 of the ulna, U.h., ulnar head; Lat., lateral, Med., medial, Prox., proximal. See Supplementary Figure 12  
1592 & 13 for anatomical details of the ulna.

1593 **Figure 5:** Results of the PCA performed on morphometric data of the tibia of all adult specimens along  
1594 with the visualizations of the theoretical shapes at the minimum and maximum of the first two axes.  
1595 The size of the points is proportional to the centroid size of the bones. A.s.f., articular surface for the  
1596 fibula, C.b., cranial border, C.i.a., caudal intercondylar area, Fi.n., fibular notch, M., malleolus, M.c.,  
1597 medial condyle, L.c., lateral condyle, L.i.t., lateral intercondylar tubercle, T.cr., tibial crest, T.t., tibial  
1598 tuberosity; Lat., lateral, Med., medial, Prox., proximal. See Supplementary Figure 16 for anatomical  
1599 details of the tibia.

1600 **Supplementary Figure 1:** Location of anatomical landmarks (red spheres), curve sliding (blue spheres)  
1601 and surface sliding (green spheres) semi-landmarks placed on the humerus. From left to right:  
1602 proximal, cranial, lateral, caudal and medial views. Numbers refer to anatomical landmarks designation  
1603 detailed in Supplementary Table 1. Landmark n°11 situated in the olecranon fossa cannot be seen.

1604 **Supplementary Figure 2:** Location of anatomical landmarks (red spheres), curve sliding (blue spheres)  
1605 and surface sliding (green spheres) semi-landmarks placed on the radius. From left to right: cranial,  
1606 lateral, caudal and medial views. Numbers refer to anatomical landmarks designation detailed in  
1607 Supplementary Table 2.

1608 **Supplementary Figure 3:** Location of anatomical landmarks (red spheres), curve sliding (blue spheres)  
1609 and surface sliding (green spheres) semi-landmarks placed on the ulna. From left to right: caudal,  
1610 lateral, caudal and medial views. Numbers refer to anatomical landmarks designation detailed in  
1611 Supplementary Table 3.

1612 **Supplementary Figure 4:** Location of anatomical landmarks (red spheres), curve sliding (blue spheres)  
1613 and surface sliding (green spheres) semi-landmarks placed on the femur. From left to right: distal,  
1614 cranial, lateral, caudal and medial views. Numbers refer to anatomical landmarks designation detailed  
1615 in Supplementary Table 4.

1616 **Supplementary Figure 5:** Location of anatomical landmarks (red spheres), curve sliding (blue spheres)  
1617 and surface sliding (green spheres) semi-landmarks placed on the tibia. From left to right, top row:  
1618 cranial, lateral, caudal and medial views; bottom row: proximal and distal views. Numbers refer to  
1619 anatomical landmarks designation detailed in Supplementary Table 5.

1620 **Supplementary Figure 6:** Location of anatomical landmarks (red spheres), curve sliding (blue spheres)  
1621 and surface sliding (green spheres) semi-landmarks placed on the fibula. From left to right: medio-  
1622 distal, cranial, lateral, caudal and medial views. Numbers refer to anatomical landmarks designation  
1623 detailed in Supplementary Table 6.

1624 **Supplementary Figure 7:** Scatterplots of the bone maximal length (MaxL) against the least  
1625 circumference of the diaphysis (Ci), along with their regression slopes and coefficients. (A) Humerus,  
1626 (B) Femur, (C) Tibia, and (D) Fibula.

1627 **Supplementary Figure 8:** Boxplots of bone robustness (Rb) defined as the Ci/MaxL ratio for each  
1628 species. (A) Humerus, (B) Femur, (C) Tibia, and (D) Fibula.

1629 **Supplementary Figure 9:** Results of the Neighbour-Joining tree computed on Euclidean distances  
1630 between each specimen's bone shape. (A), Humerus (adults), (B), Humerus (adults and juveniles), (C),  
1631 Radius, (D), Ulna, (E), Femur (diagnosed individuals), (F), Femur (all adult individuals), (G), Tibia, (H),  
1632 Fibula.

1633 **Supplementary Figure 10:** Results of the PCA performed on morphometric data of the humerus of all  
1634 specimens along with the visualizations of the theoretical shapes at the minimum and maximum of the  
1635 first two axes. Adult specimens are visualized by circles, subadults by squares and juveniles by triangles.

1636 **Supplementary Figure 11:** Anatomy of the humerus. D.t., deltoid tuberosity, G.t., greater trochanter,  
1637 G.t.c., greater trochanter crest, H.c., humeral crest, H.h., humeral head, H.n., humeral neck, H.t.,  
1638 humeral trochlea, I.g., intertubercular groove, L.e., lateral epicondyle, L.t., lesser trochanter, M.e.,  
1639 medial epicondyle, O.f., olecranon fossa, R.f., radial fossa, S.c., supracondylar crest; Caud., caudal,  
1640 Cran., cranial, Lat., lateral, Med., medial, Prox., proximal.

1641 **Supplementary Figure 12:** Results of the PCA performed on morphometric data of the radius.

1642 **Supplementary Figure 13:** Anatomy of the radius and the ulnar epiphyses. A.c.h., articular  
1643 circumference of the head (radius), A.c.r., articular surface for the carpal bones (radius), A.c.u.,  
1644 articular surface for the carpal bones (ulna), A.h., articular surface of the head (radius), A.p., anconeal  
1645 process, L.c.p., lateral coronoid process, M.c.p., medial coronoid process, O.t., olecranon tuberosity,  
1646 R.h., radial head, R.n., radial neck, R.t., radial tuberosity, S.p.r., styloid process of the radius, S.p.u.,  
1647 styloid process of the ulna, U.n.r., ulnar notch of the radius; Caud., caudal, Cran., cranial, Lat., lateral,  
1648 Med., medial, Prox., proximal.

1649 **Supplementary Figure 14:** Anatomy of the ulna. A.p., anconeal process, A.s.r, articular surface for the  
1650 radius, L.c.p., lateral coronoid process, M.c.p., medial coronoid process, O., olecranon, O.t., olecranon

1651 tuberosity, T.n., trochlear notch, R.no., radial notch, S.p.u., styloid process of the ulna, U.h., ulnar head;  
1652 Caud., caudal, Cran., cranial, Lat., lateral, Med., medial, Prox., proximal.

1653 **Supplementary Figure 15:** Results of the PCA performed on morphometric data of the femur, including  
1654 undiagnosed specimens (NA).

1655 **Supplementary Figure 16:** Anatomy of the femur. F.h., femoral head, F.h.f., femoral head fovea, F.n.,  
1656 femoral neck, F.t., femoral trochlea, G.t., greater trochanter, I.f., intercondylar fossa, L.c., lateral  
1657 condyle, L.e., lateral epicondyle, L.t., lesser trochanter, M.c., medial condyle, M.e., medial epicondyle,  
1658 P.s., popliteal surface, T.f., trochanteric fossa, T.t., third trochanter, S.t., supracondylar tuberosity;  
1659 Cran., cranial, Lat., lateral, Med., medial, Prox., proximal.

1660 **Supplementary Figure 17:** Anatomy of the tibia. A.s.f., articular surface for the fibula, C.b., cranial  
1661 border, C.i.a., caudal intercondylar area, Fi.n., fibular notch, M., malleolus, M.c., medial condyle, M.i.t.,  
1662 medial intercondylar tubercle, L.c., lateral condyle, L.i.t., lateral intercondylar tubercle, M.s., malleolar  
1663 sulcus, T.co., tibial cochlea, T.cr., tibial crest, T.t., tibial tuberosity; Caud., caudal, Cran., cranial, Lat.,  
1664 lateral, Med., medial, Prox., proximal.

1665 **Supplementary Figure 18:** Anatomy of the fibula. A.f.h., articular facet of the head of the fibula, A.f.m.,  
1666 articular facet of the malleolus; A.t.c., articular facet for the talus and calcaneus, Fi.h., fibular head,  
1667 Fi.ne, fibular neck, M., malleolus; Cran., cranial, Lat., lateral, Prox., proximal.

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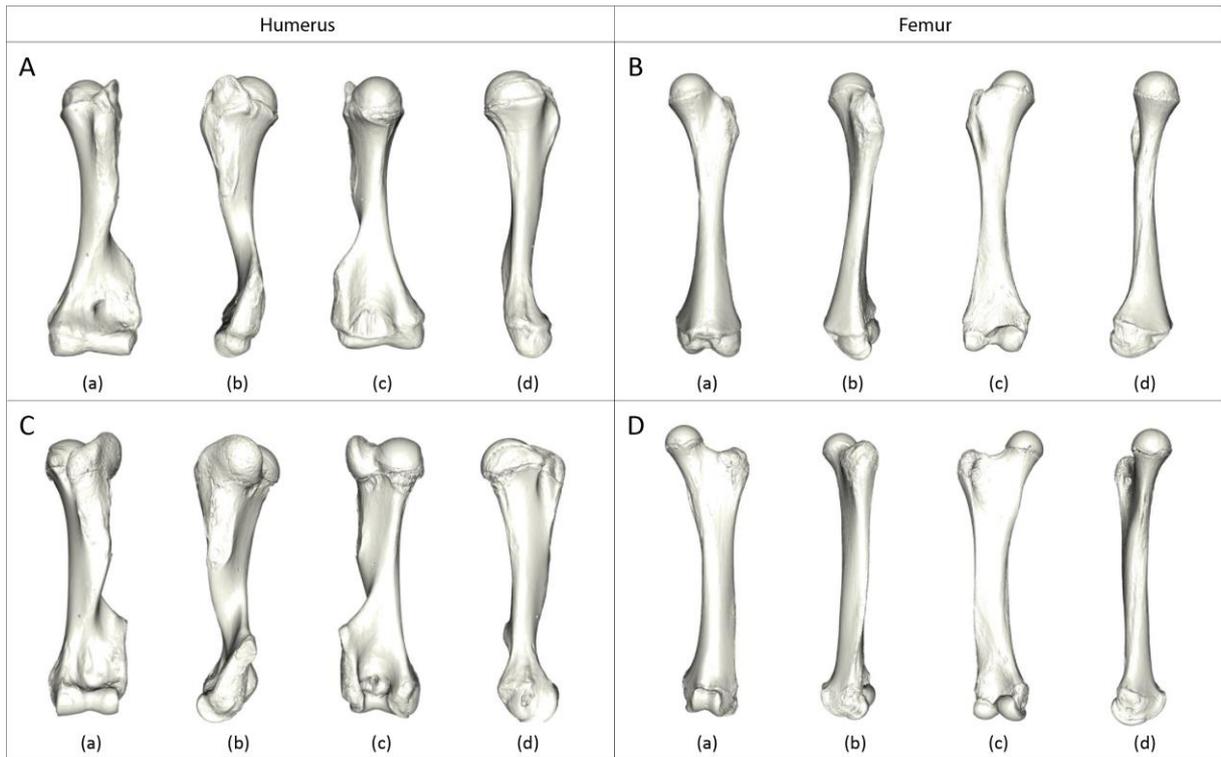
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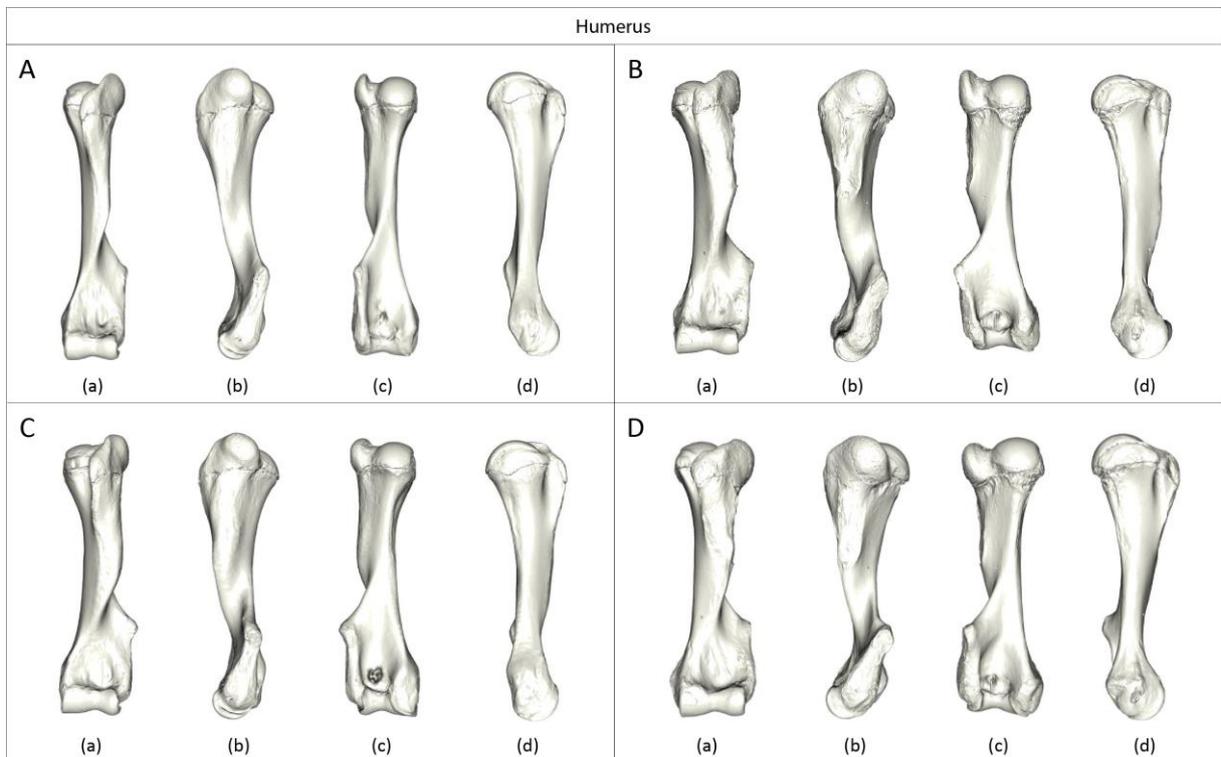
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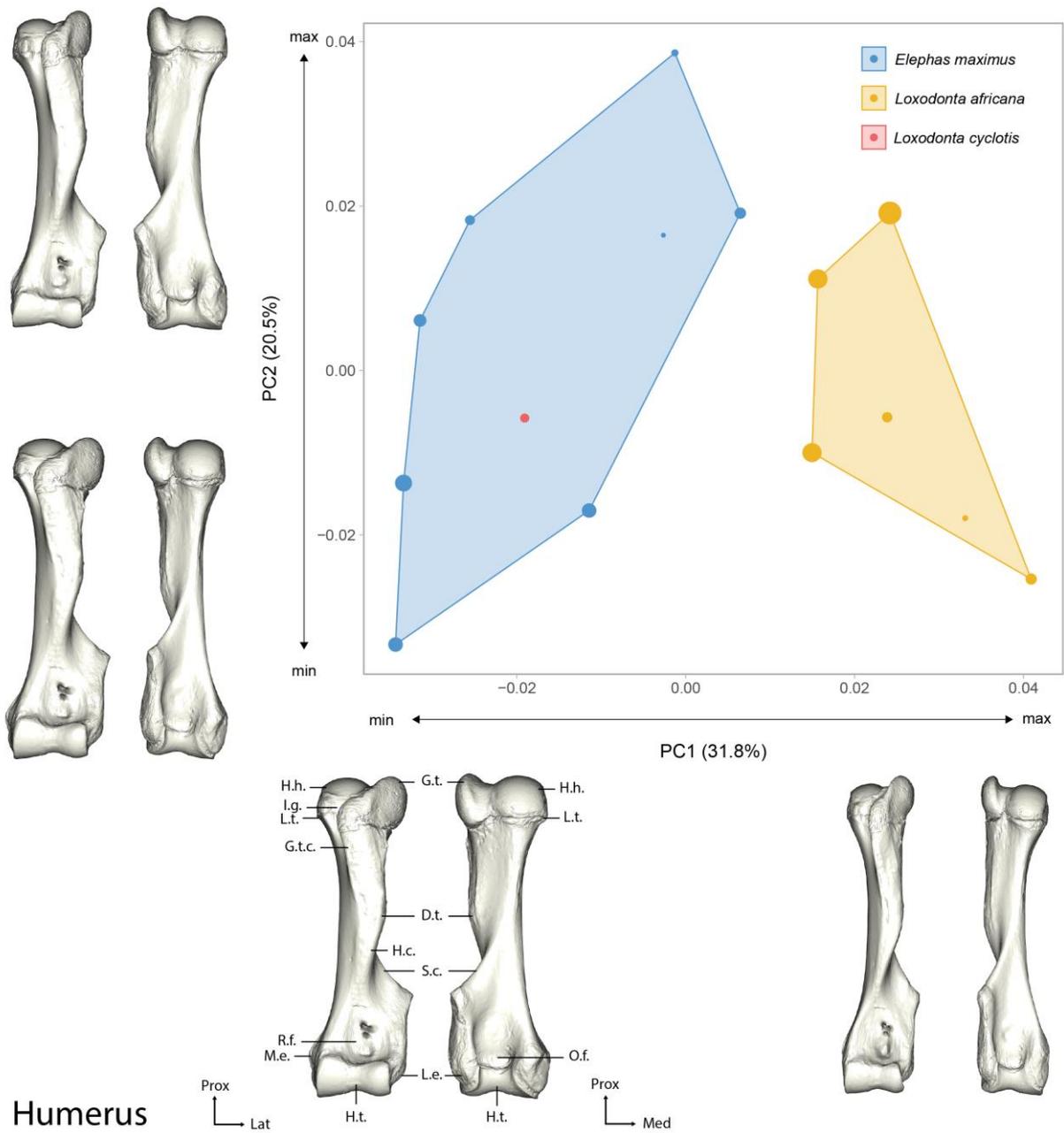
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### Humerus

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Figure 3

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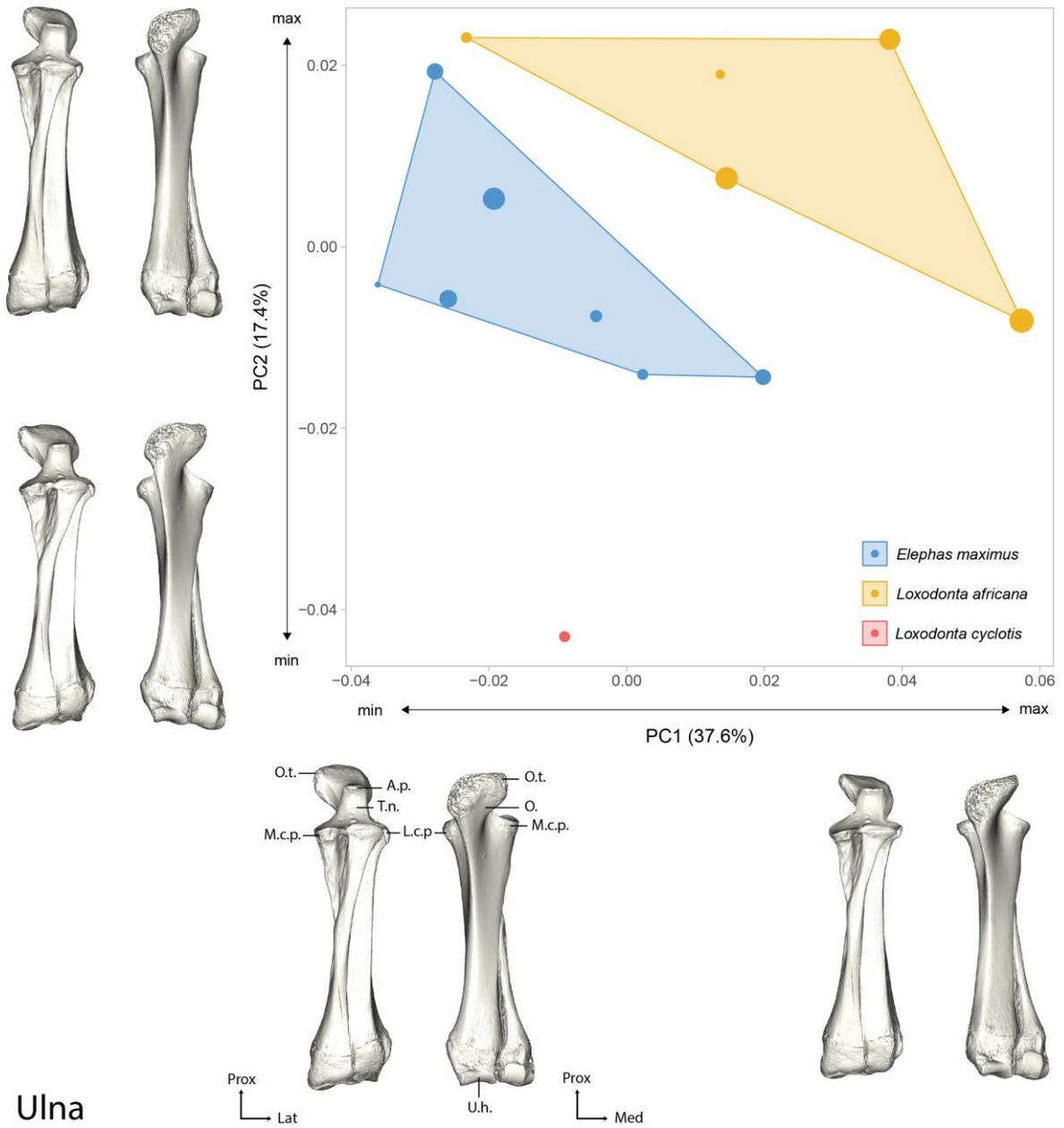
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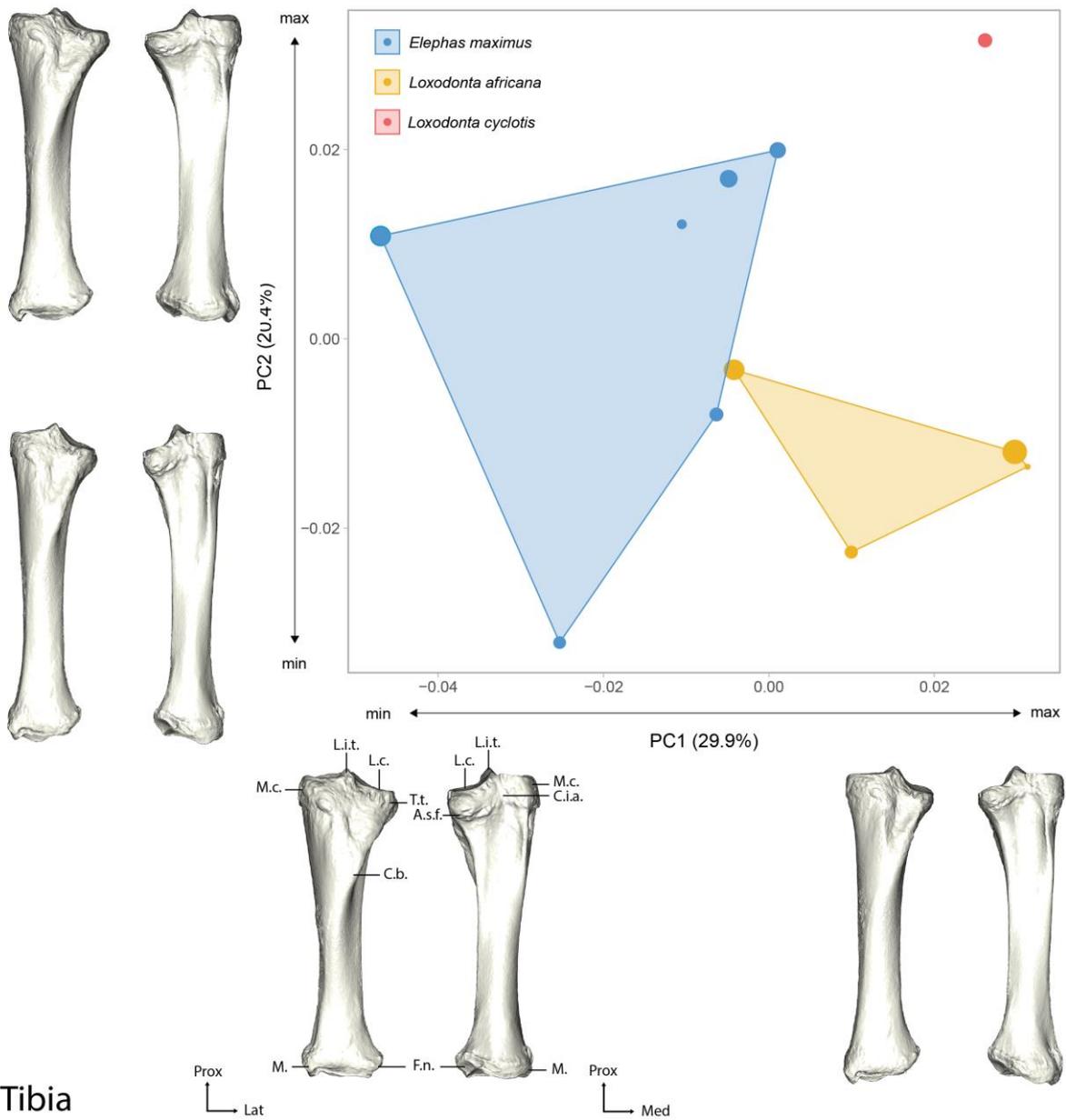
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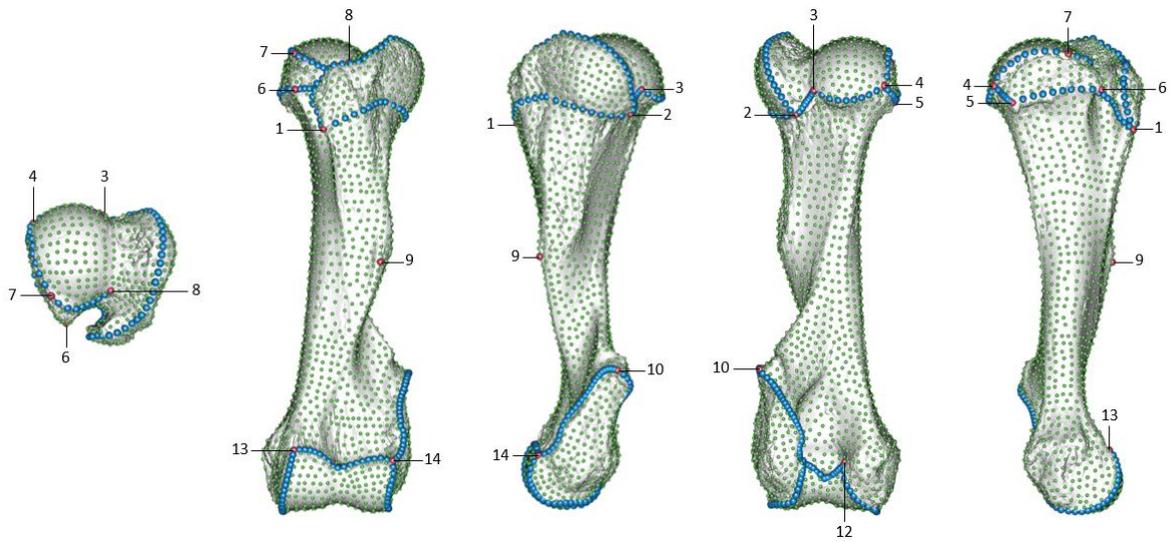
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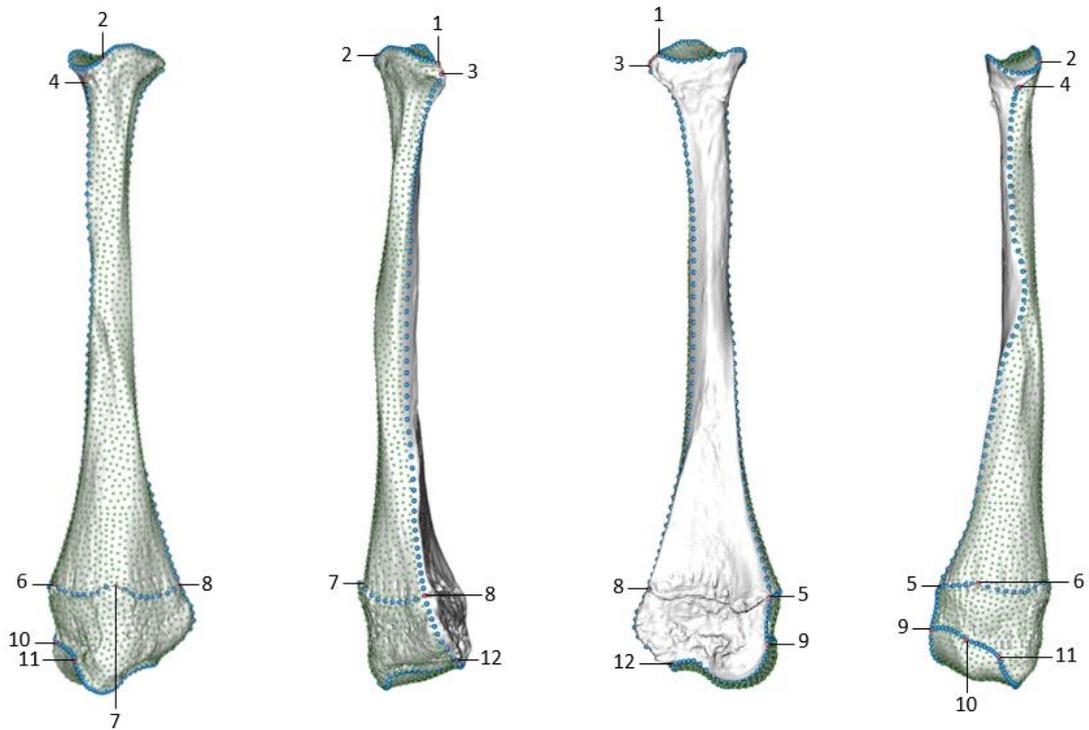
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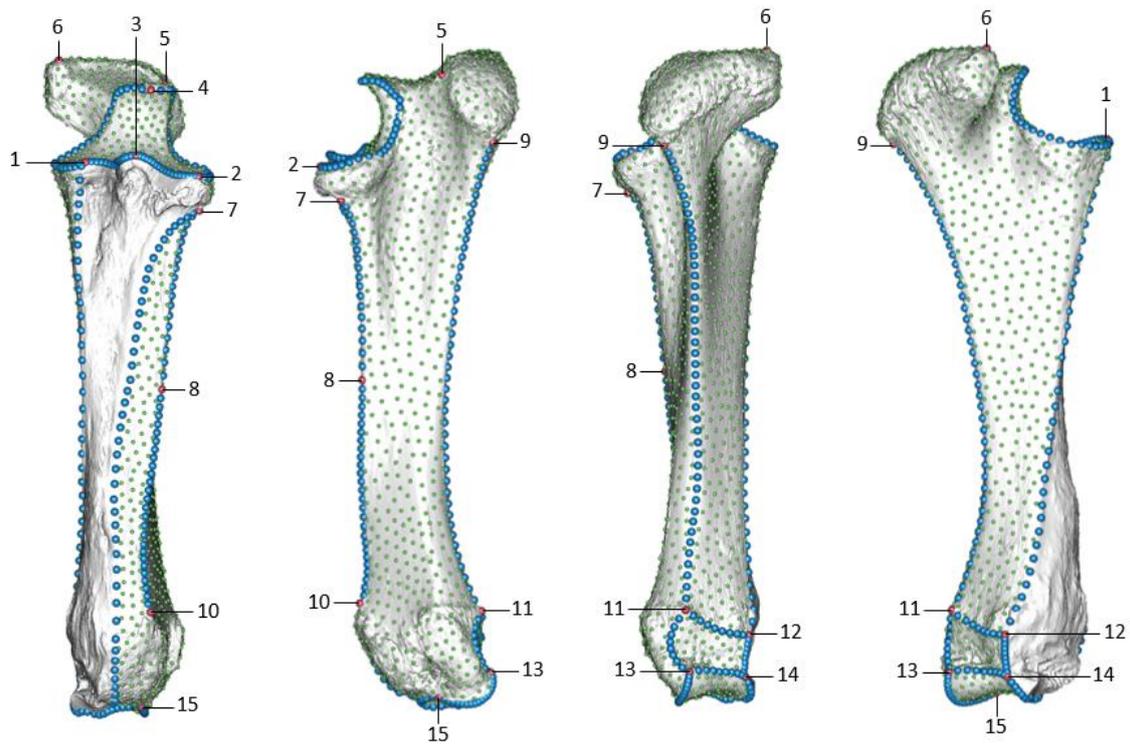
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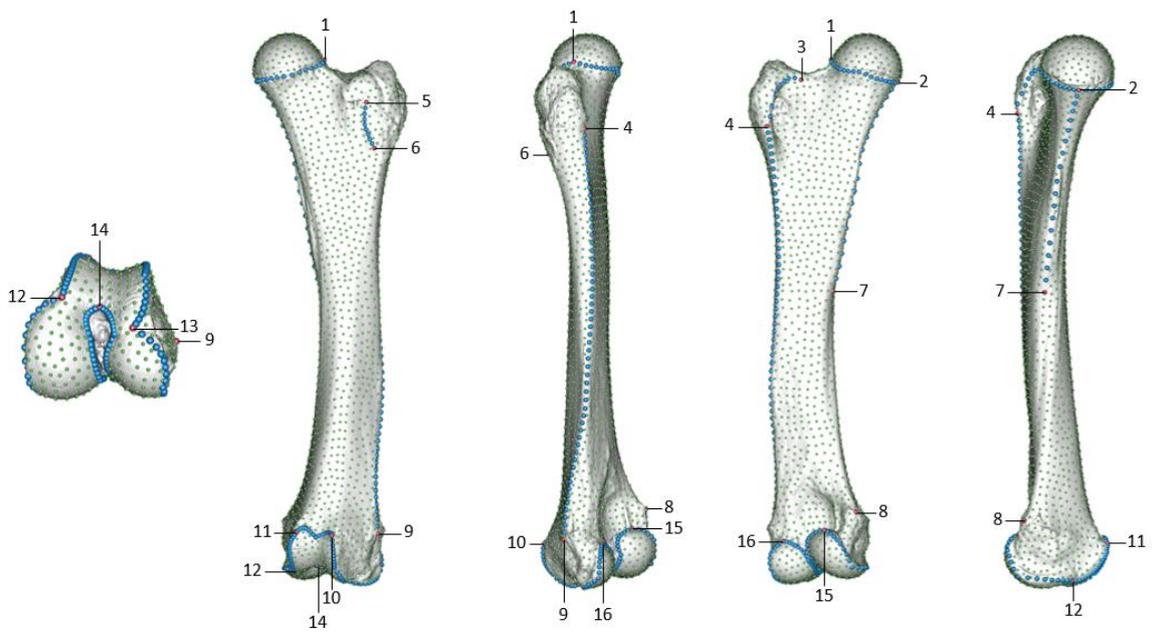


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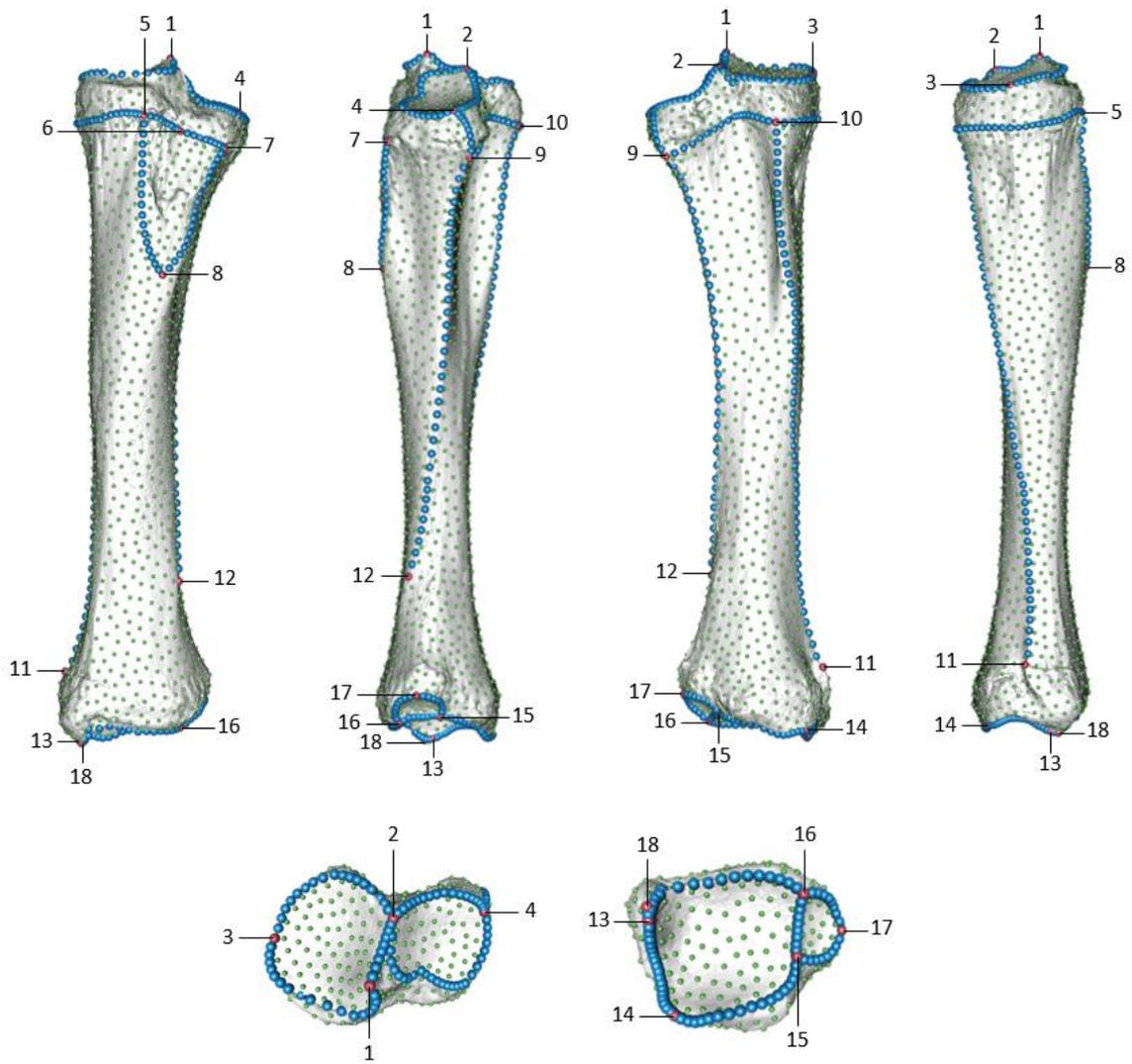


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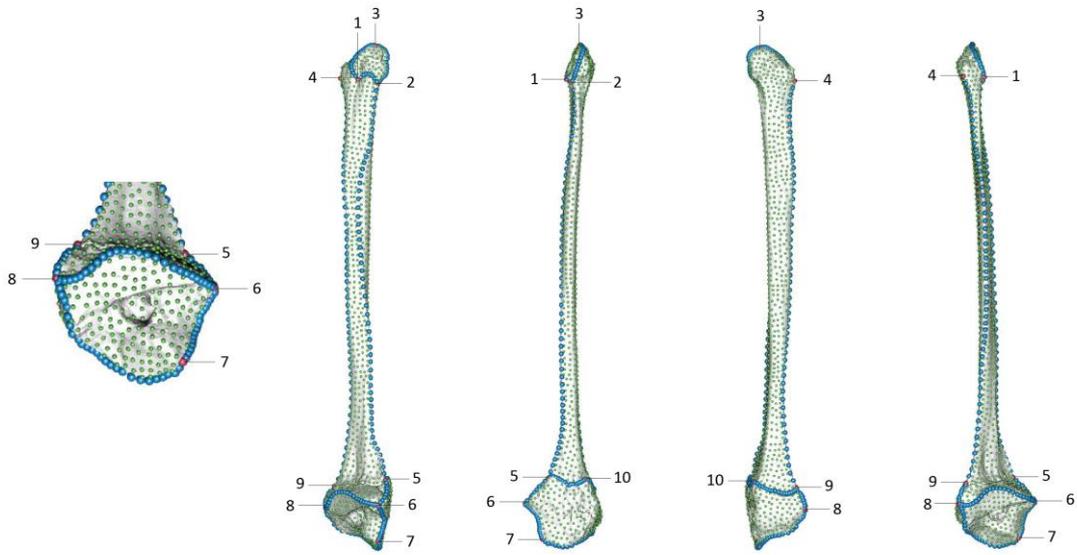


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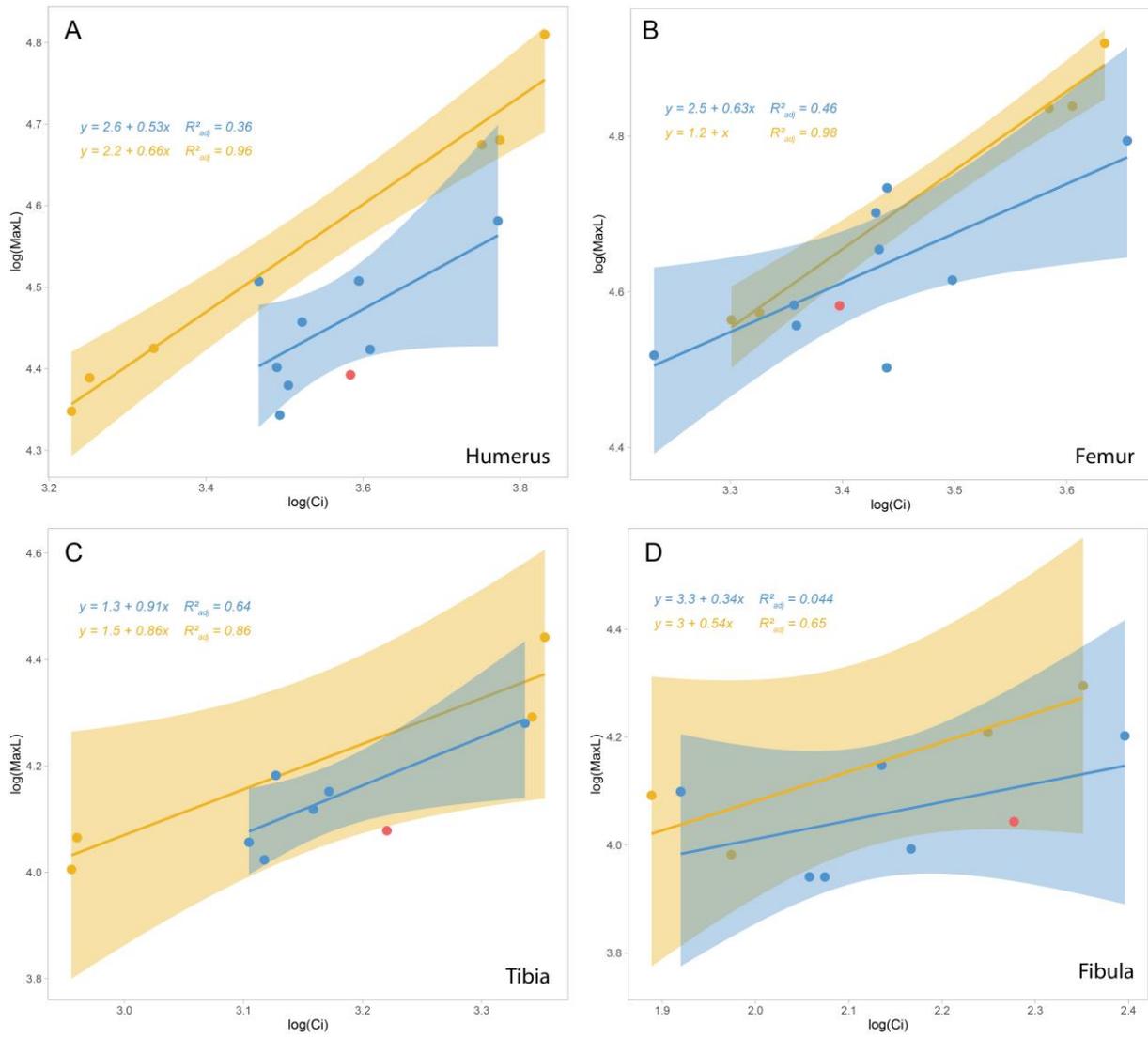


1747

1748 Supplementary figure 6

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● *Elephas maximus*   
 ● *Loxodonta africana*   
 ● *Loxodonta cyclotis*

1751

1752 Supplementary figure 7

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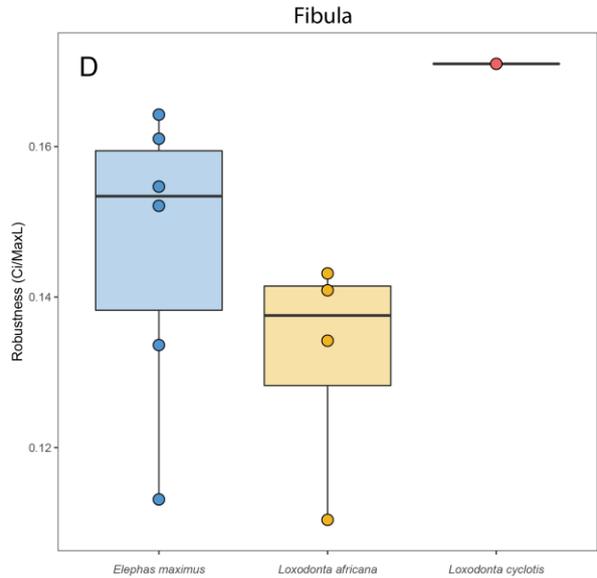
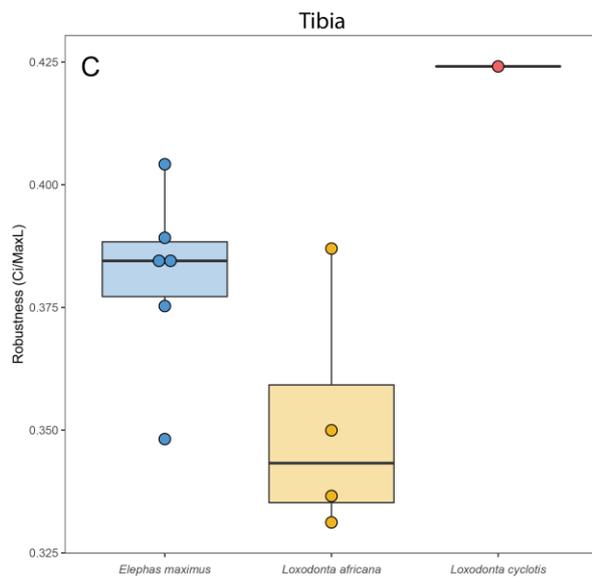
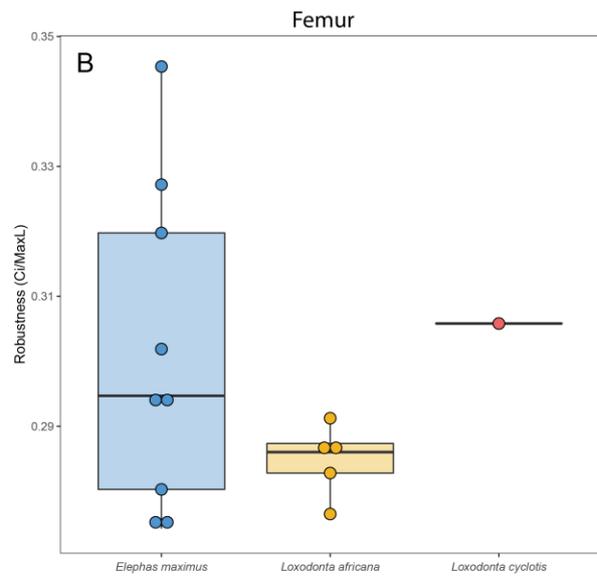
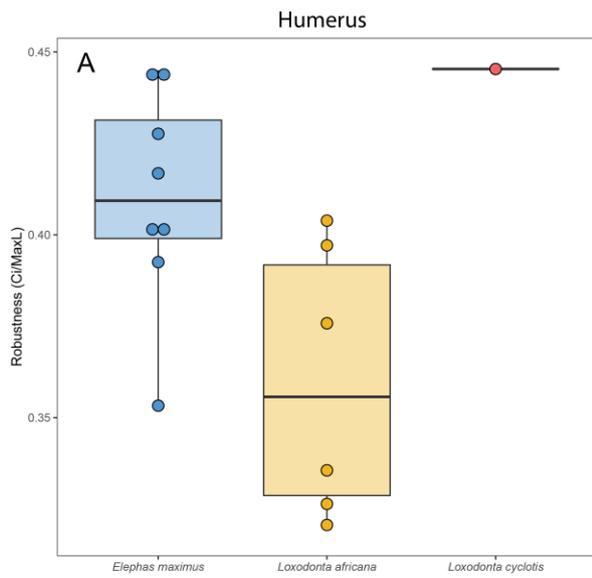
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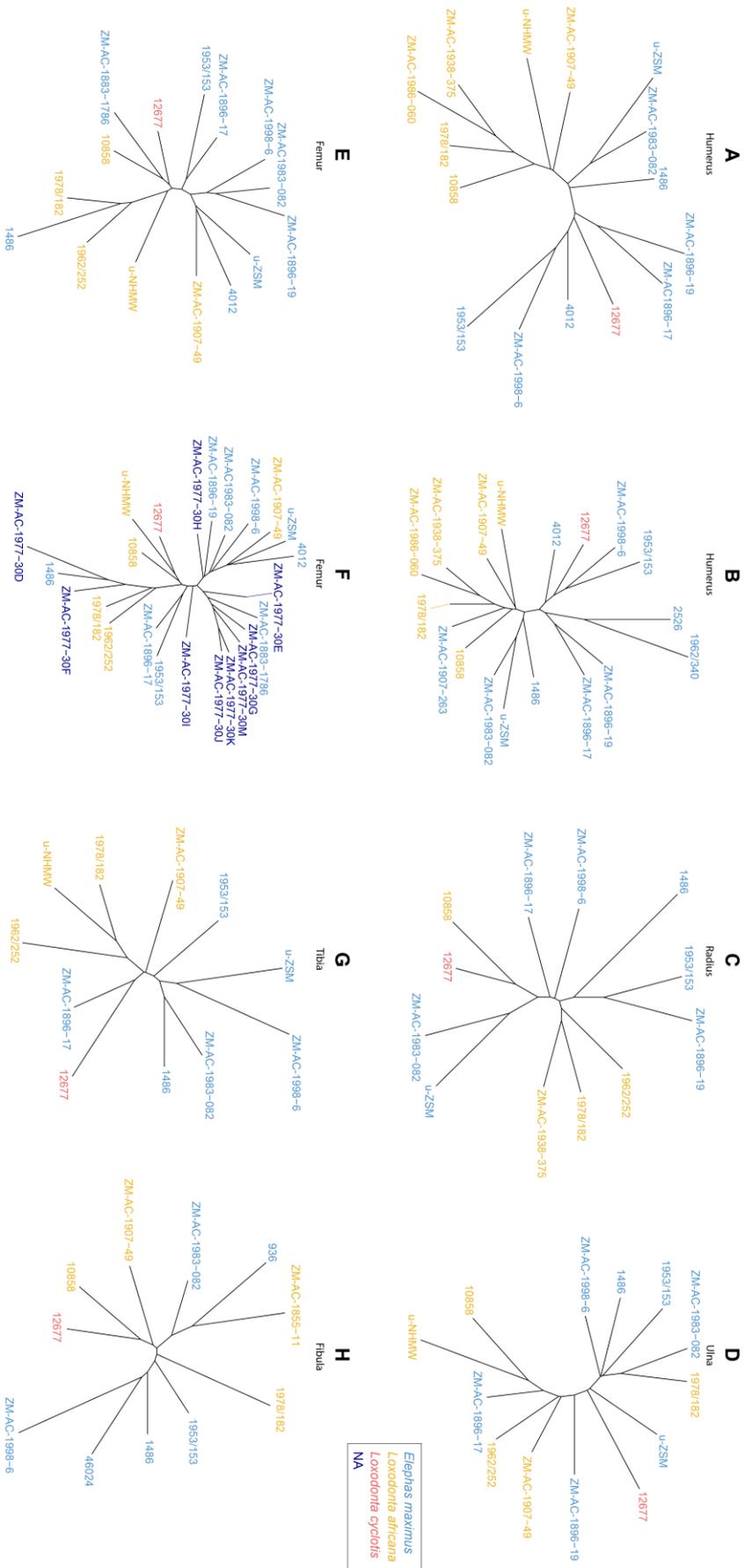


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1764 Supplementary figure 8

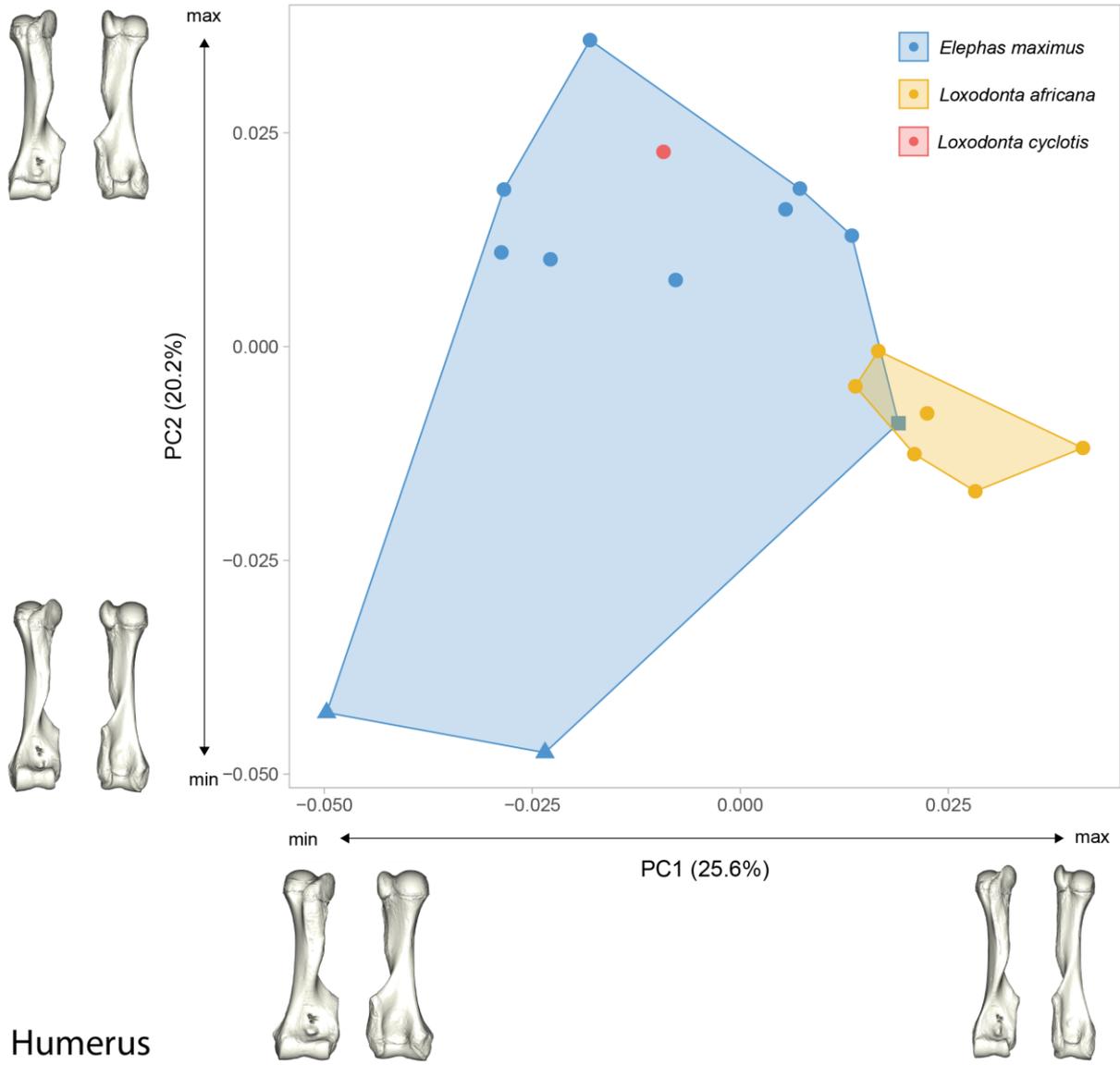
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1767

1768 Supplementary figure 9

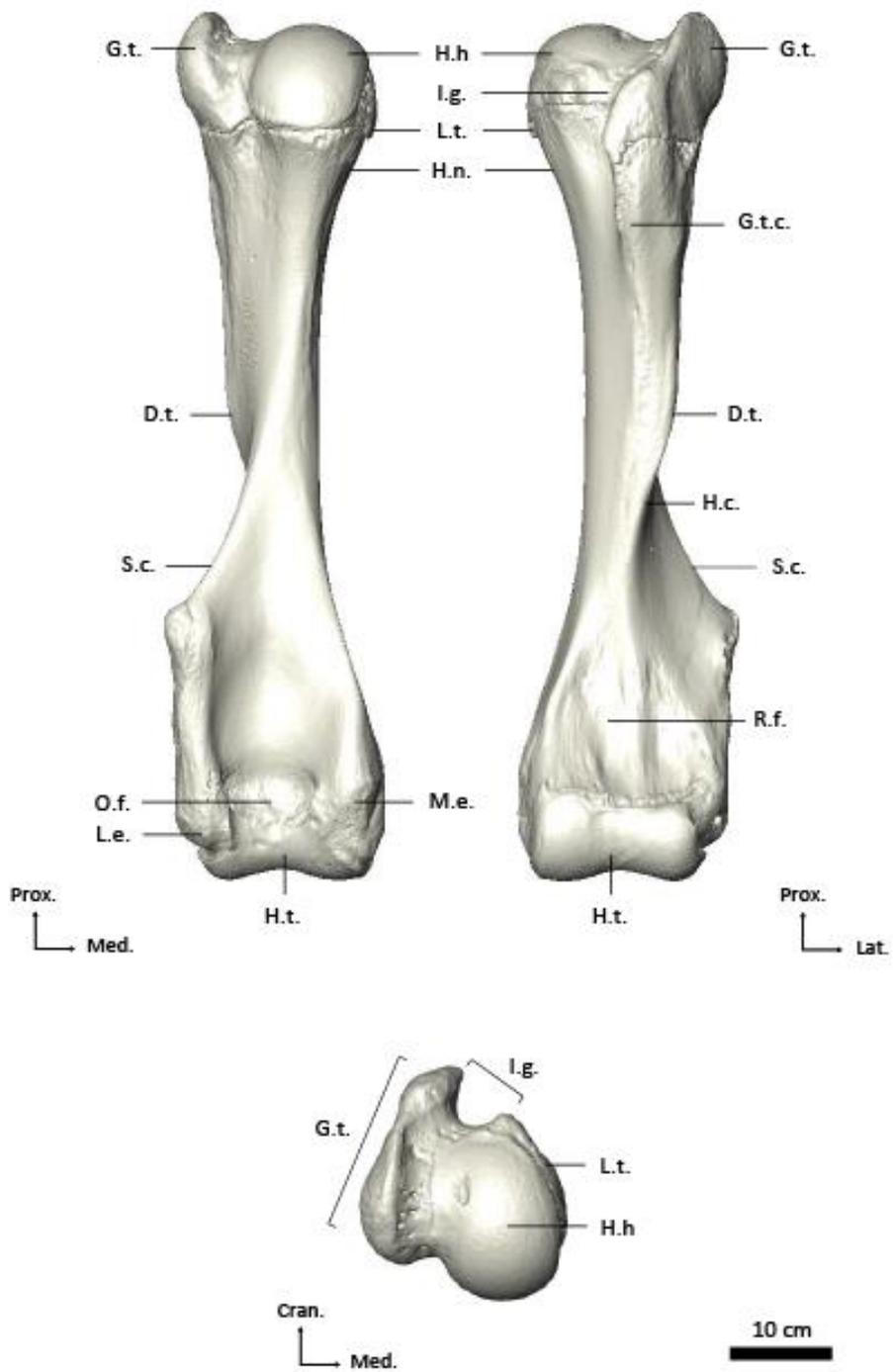


1769

Humerus

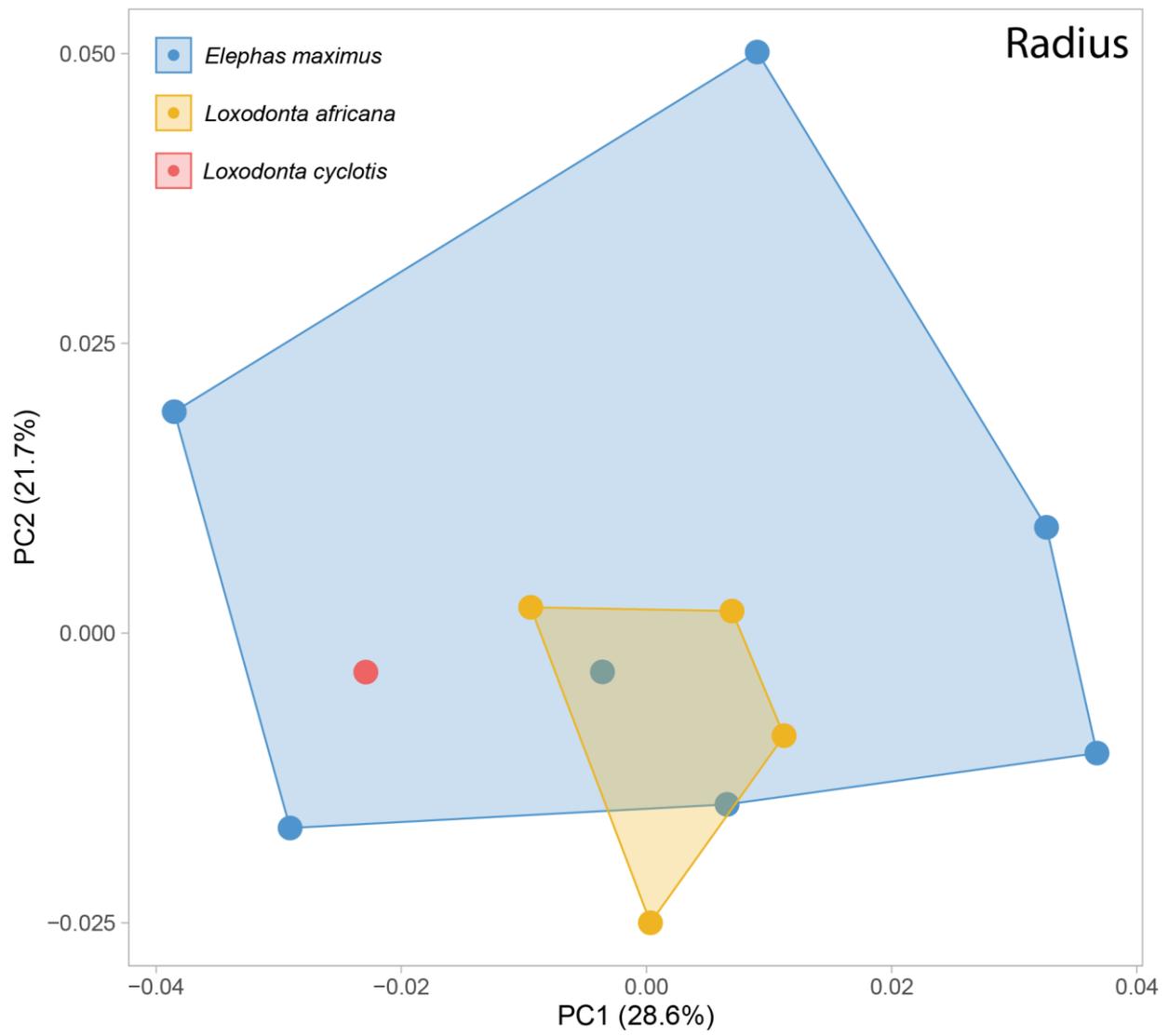
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Supplementary figure 10



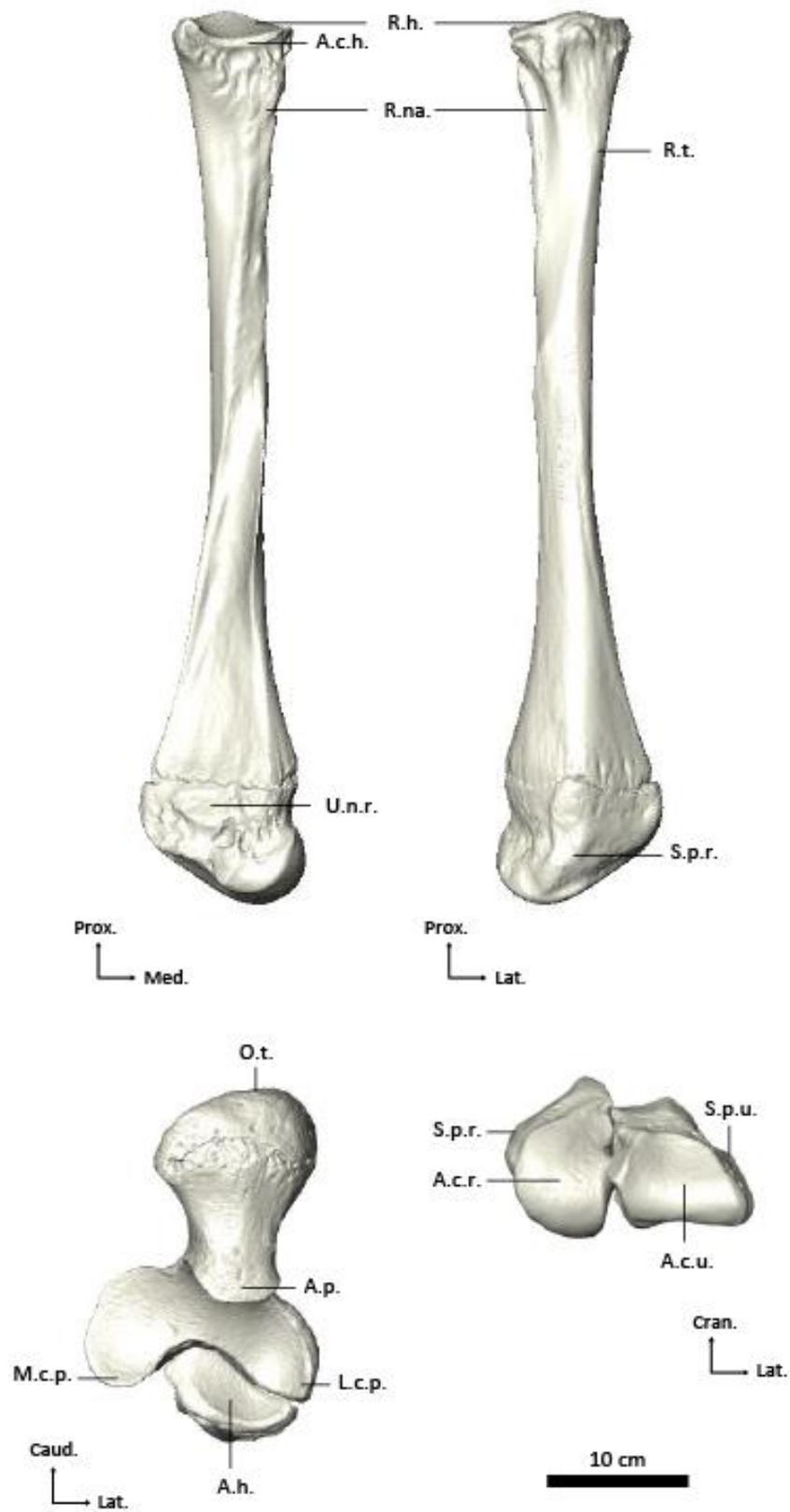
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1772 Supplementary figure 11



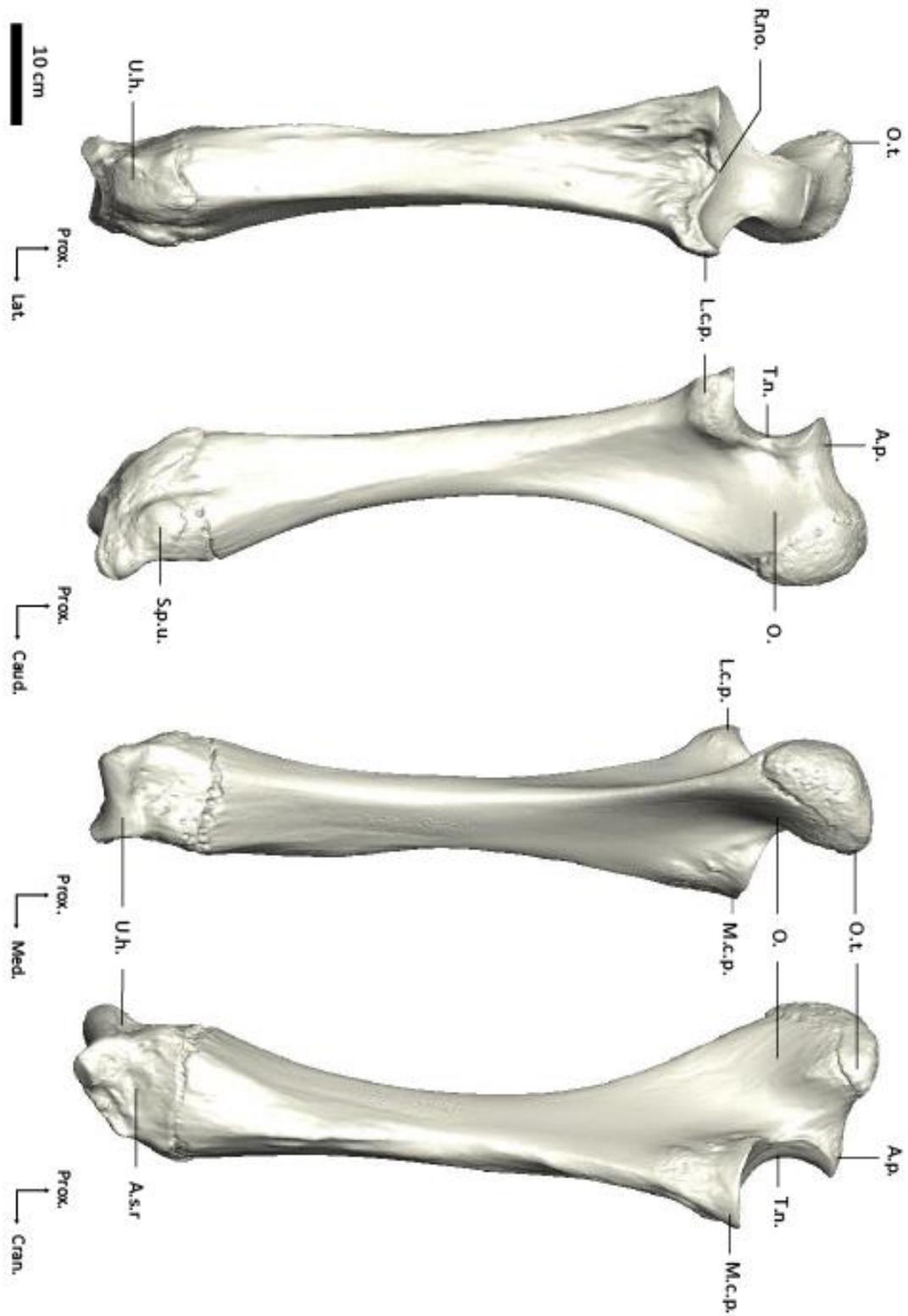
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1774 Supplementary figure 12



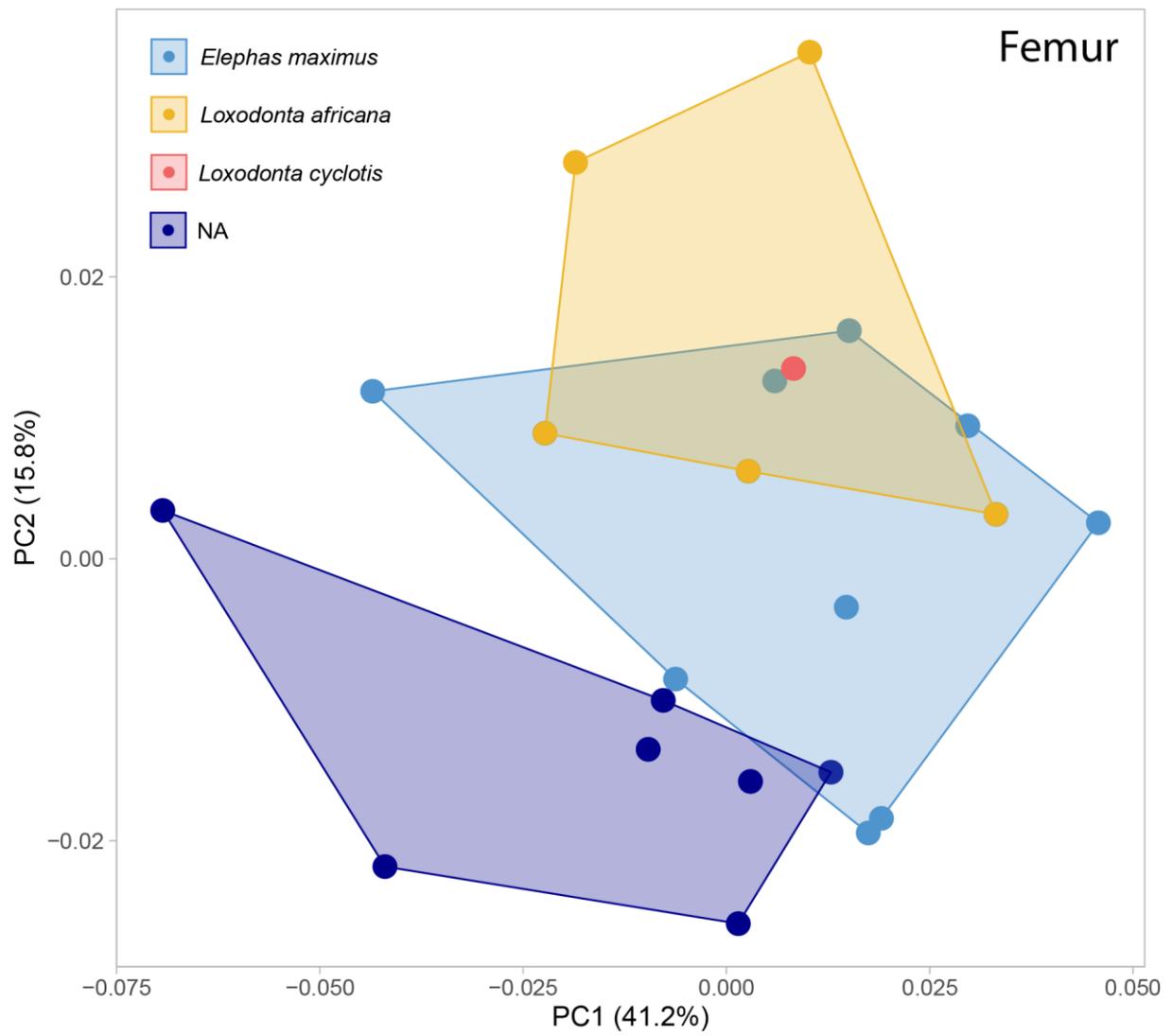
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1776 Supplementary figure 13



1777

1778 Supplementary figure 14



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1780 Supplementary figure 15

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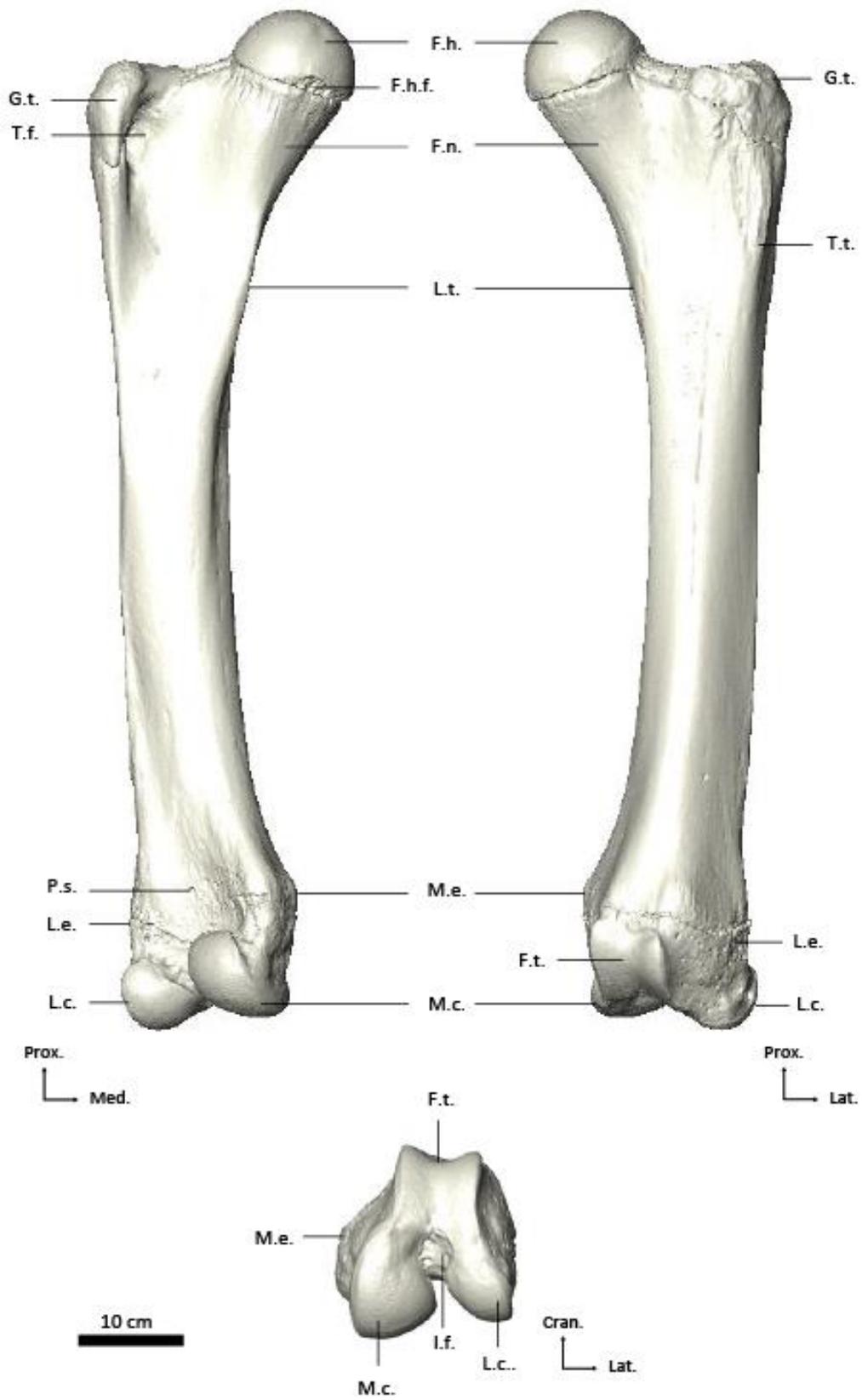
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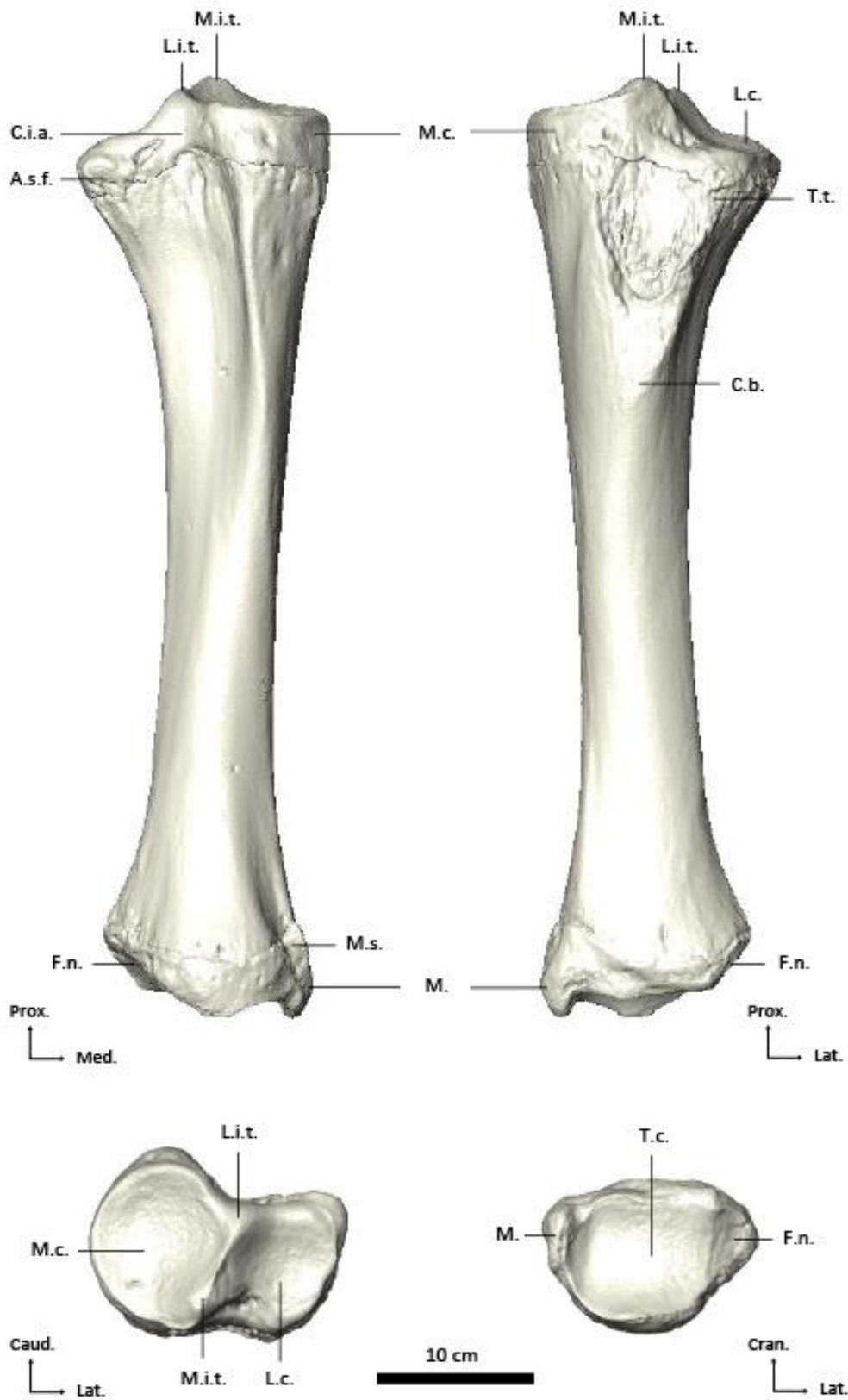
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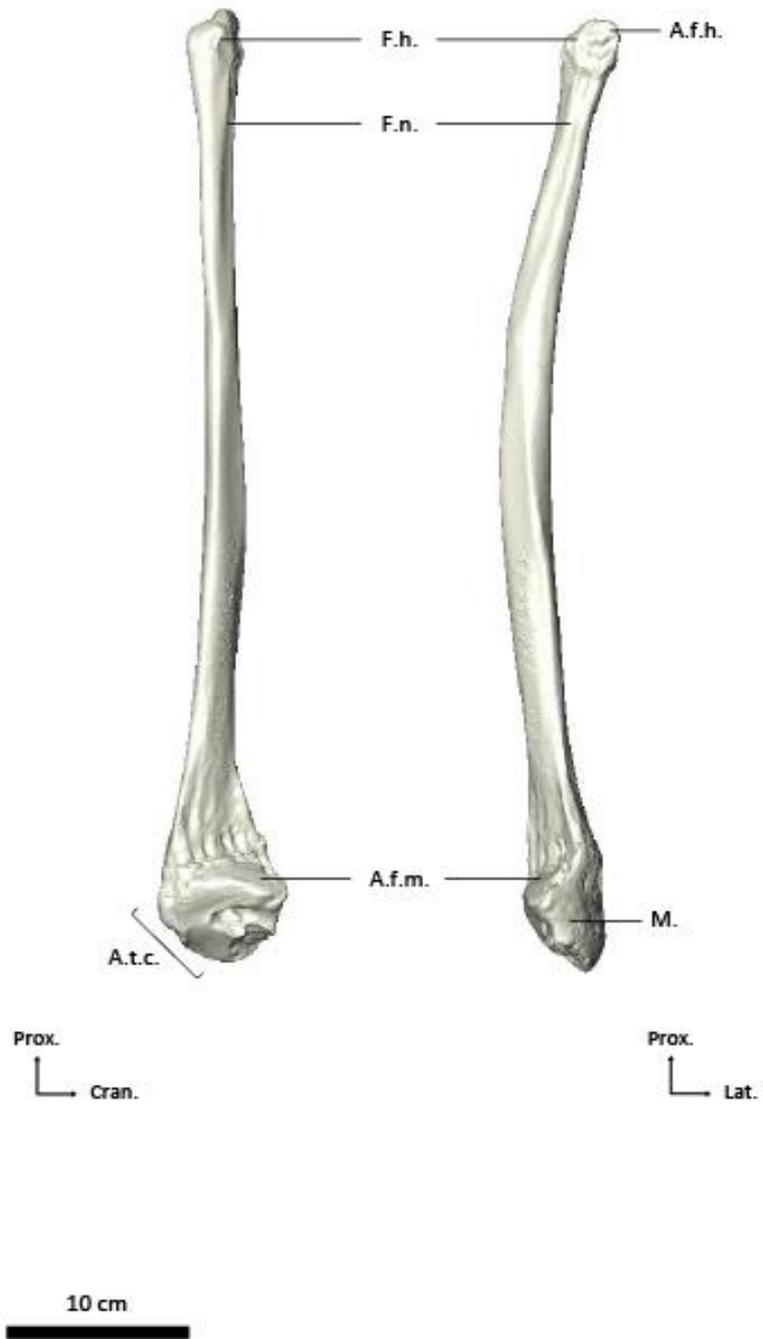
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1793 Supplementary figure 16



1794

1795 Supplementary figure 17



1796

1797 Supplementary figure 18