

 Open access • Journal Article • DOI:10.1111/JOA.13359

Effect of mass and habitat on the shape of limb long bones: A morpho-functional investigation on Bovidae (Mammalia: Cetartiodactyla) — [Source link](#)

Cyril Etienne, Andréa Filippo, Raphaël Cornette, Alexandra Houssaye

Institutions: Centre national de la recherche scientifique

Published on: 01 Apr 2021 - Journal of Anatomy (John Wiley & Sons, Ltd)

Topics: Cursorial

Related papers:

- [Morphology and locomotor adaptations of the bovid femur in relation to habitat.](#)
- [Influence of body mass on the shape of forelimb in musteloid carnivorans](#)
- [Do constraints associated with the locomotor habitat drive the evolution of forelimb shape? A case study in musteloid carnivorans](#)
- [Thinking Inside the Box: Comparative Limb Bone Shape in Emydid Turtles](#)
- [Functional inferences on the long bones of ischyrictis zibethoides \(Blainville, 1841\) \(carnivora, mustelidae\) from the middle miocene locality of sansan \(Gers, France\)](#)

Share this paper:    

View more about this paper here: <https://typeset.io/papers/effect-of-mass-and-habitat-on-the-shape-of-limb-long-bones-a-4h8vz9riux>



HAL
open science

Effect of mass and habitat on the shape of limb long bones: A morpho-functional investigation on Bovidae (Mammalia: Cetartiodactyla)

Cyril Etienne, Andréa Filippo, Raphael Cornette, Alexandra Houssaye

► To cite this version:

Cyril Etienne, Andréa Filippo, Raphael Cornette, Alexandra Houssaye. Effect of mass and habitat on the shape of limb long bones: A morpho-functional investigation on Bovidae (Mammalia: Cetartiodactyla). *Journal of Anatomy*, Wiley, 2021, 238 (4), pp.886-904. 10.1111/joa.13359 . hal-03159183

HAL Id: hal-03159183

<https://hal.archives-ouvertes.fr/hal-03159183>

Submitted on 4 Mar 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

13 **Abstract**

14 Limb long bones are essential to an animal's locomotion, and are thus expected to be heavily
15 influenced by factors such as mass or habitat. Because they are often the only organs preserved
16 in the fossil record, understanding their adaptive trends is key to reconstructing the
17 palaeobiology of fossil taxa. In this regard, the Bovidae has always been a prized group of
18 study. This family is extremely diverse in terms of both mass and habitat, and it is expected that
19 their bones will possess adaptations to both factors. Here we present the first 3D geometric
20 morphometric study focusing on bovid limb long bones. We used anatomical landmarks as well
21 as curve and surface sliding semi-landmarks to accurately describe the stylopod and zeugopod
22 bones. We included 50 species from ten of the twelve currently recognized tribes of bovids,
23 ranging from 4.6 to 725 kg, and living in open plains, forests, mountains or anywhere in-
24 between. Shape data were correlated with the mean mass of the species and its habitat, even
25 when taking into account the phylogenetic history of our sample. Bones pertaining to heavy
26 species are more robust, adapted for a better repartition of stronger forces. Articulations are
27 especially affected, being proportionally much larger in heavier species. Muscle insertion areas
28 are unevenly affected. Insertion areas of muscles implied in body support and propulsion show
29 a strong increase in their robustness when compared to insertion areas of muscles acting on the
30 limb mostly when it is off the ground. Habitat influences the shape of the humerus, the radius-
31 ulna, and the femur, but not of the tibia, whether the phylogeny is taken into account or not.
32 Specific habitats tend to be associated with particular features on the bones. Articulations are
33 proportionally wider in open-habitat species, and the insertion areas of muscles involved in
34 limb extension and propulsion are wider, reflecting the fact that open habitat species are more
35 cursorial and rely on fast running to avoid predators. Forest and mountain species generally
36 present similar adaptations for increased manoeuvrability, such as a round femoral head, and
37 generally have more gracile bones.

38 Key words: limb long bones - functional morphology – body mass - habitat – phylogeny -
39 geometric morphometrics – Bovidae

40

41 Introduction

42 In most terrestrial vertebrates, limb long bones are essential to locomotion. They provide
43 support for the weight of the animal, and a rigid attachment point for the muscles also
44 responsible for body support and movement (Hildebrand, 1982; Hildebrand et al., 1985).
45 Several factors are expected to exert a strong selective pressure on the shape of these bones.
46 Mass is among the strongest of those factors, if not the strongest one (Biewener, 1989;
47 Hildebrand, 1982; Polly, 2008). This is because the ability of bones to resist forces depends on
48 their cross-sectional area, whether the forces are expected to be proportional to the animal's
49 weight, a volume (Biewener, 1989). This means that the stresses, i.e. the forces per unit area
50 the bones are subject to, should increase proportionally to the animal's weight. In order to avoid
51 this, heavier animals typically run with a more upright posture of their limbs. This increases the
52 mechanical advantage of the lever systems of the limbs, allowing larger animals to move by
53 using weaker than expected muscles, exerting lower stresses on the bones (Biewener, 1989,
54 Biewener & Patek, 2018). Past a certain mass however (Biewener, 1989, 2005 proposes around
55 300 kg), a threshold is reached where it becomes difficult for the limb to straighten up any
56 further. Therefore, in order for the stresses in the bones to remain constant, locomotor
57 performances will decline, and bone shape will undergo more extreme changes (Biewener,
58 1989; Bertram and Biewener, 1990; Christiansen, 1999a). When mass increases, the most
59 obvious change in bone shape generally observed is an increase in robustness, i.e. diameter
60 relative to length (Schmidt-Nielsen, 1984). Additionally, muscle insertion areas will become
61 larger, presumably accommodating for stronger muscles (see e.g. Doube et al., 2009; Walmsley
62 et al., 2012; Mallet et al., 2019; Martin et al., 2019). This is of course also influenced by
63 phylogenetical factors (Biewener & Patek, 2018). Adaptations to a heavy weight can differ
64 markedly between taxa with a similar weight; e.g. hippos which possess very stout limbs and
65 cannot gallop or trot, and rhinos which have more elongate limbs and are able of galloping
66 (Wilson and Mittermeier, 2011).

67 Another factor strongly influencing bone shape is the habitat in which a species lives
68 (Kappelman, 1988; Polly, 2008; Curran, 2012; Dunn, 2018). Terrestrial mammals obviously
69 present a very different skeleton from that of aquatic ones (Hildebrand, 1982; Hall, 2008). More
70 subtly, species living in open, plains habitats present specific adaptations that differ from those
71 of species living in closed, forested habitats (see e.g. Kappelman, 1988; Plummer et al., 2008;
72 Curran, 2012, 2018; Barr, 2014). This is notably due to differences in the substrate in which the
73 animals move (e.g. the flat, two-dimensional ground of a savannah versus the complex, almost

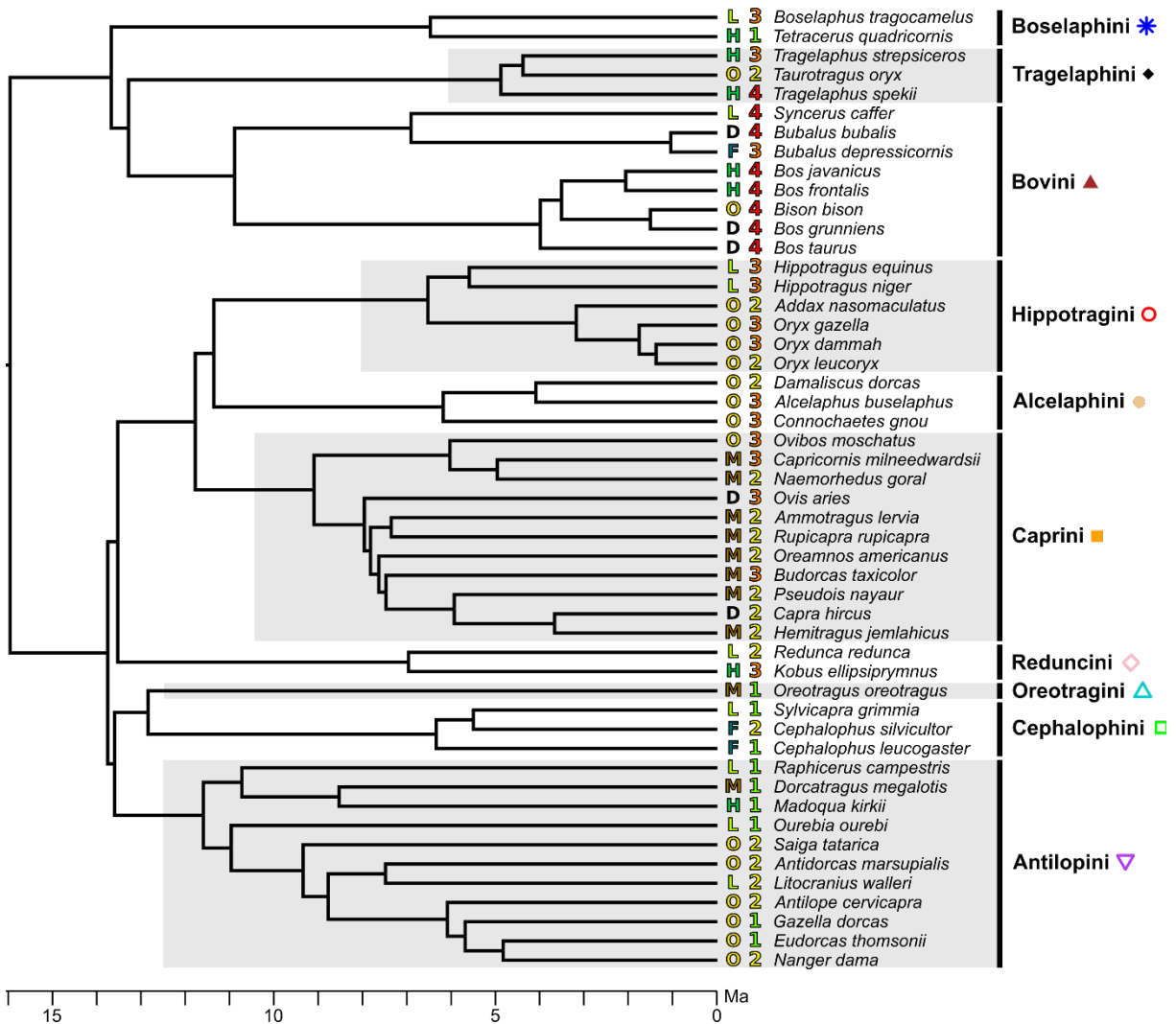
74 three-dimensional system of bushes and roots in a forest; Kappelman, 1988). Another reason
75 will be differences in predator-avoidance strategies. Open-habitat species must be fast and agile
76 runners capable of outrunning or exhausting potential predators on a mostly even ground,
77 whereas closed-habitat species presumably rely more on camouflage, and have to navigate on
78 a very complex substrate if they do have to flee (Kappelman, 1988; Kappelman et al., 1997;
79 Plummer et al., 2008). Identifying precisely the adaptations of the shape of the long bones
80 associated with a particular mass and habitat could therefore be extremely helpful in order to
81 reconstruct the paleobiology and paleoenvironment of extinct animals.

82 To study the morphological features of the limb long bones linked to habitat and mass,
83 Bovidae have always been a prized group. They are the most diverse family of large mammals
84 on earth today, comprising 279 species spread out in twelve different tribes (Castelló, 2016).
85 Bovids vary greatly in terms of mass, the smallest species (the royal antelope, *Neotragus*
86 *pygmaeus*) weighing only two kilograms whereas the heaviest one (the Asian wild water
87 buffalo, *Bubalus arnee*) can weigh up to 1200 kg (Castelló, 2016). They also vary in terms of
88 habitat, and can be found in open savannahs, dense rainforests, steep mountains, or snowy
89 environments. For all these reasons, bovid limb bones have been extensively studied, in various
90 domains such as functional morphology, zooarchaeology and palaeoecology. For instance,
91 numerous studies have tried to use bovid bones to predict paleoenvironments. DeGusta and
92 Vrba (2003) and Plummer et al. (2008, 2015) have used linear measurements on the astragalus
93 to predict a bovid's habitat, and Barr (2014) showed that this relationship holds even when
94 controlling for phylogenetic signal and size effect. Kappelman (1991, 1988) and Kappelman et
95 al. (1997) have studied the bovid femur using linear measurements, areas and ratios. They
96 determined, for instance, that bovids living in an open, plains habitat presented a cylindrical
97 femoral head that help stabilize the hip joint, whereas bovids living in closed, forested habitats
98 presented a spherically-shaped femoral head better suited for axial rotation of the femur,
99 adduction and abduction, and overall, manoeuvrability. They were able to use this to reconstruct
100 the habitat of early hominids. Several studies have examined the allometry in the limb bones.
101 Scott (1985) has studied an extensive sample of bovids and concluded that bones become much
102 thicker in heavier species, with also a relative shortening of the limb. Mendoza and Palmqvist
103 (2006) showed that body mass is highly correlated with the width of the proximal articular
104 surface of the radius, as well as the other articular surfaces in general, particularly those of the
105 elbow and the knee.

106 Our study focuses on characterising the shape of each of the limb long bones of bovids
107 (stylopodium and zeugopodium), and associating different habitats and extremes of masses
108 with a particular shape. This is conducted using a 3D geometric morphometric study (Zelditch
109 et al., 2012; Adams et al., 2013), the first to our knowledge performed on bovid limb long
110 bones. Based on previous studies, we expect both mass and habitat to have a strong impact on
111 the shape of long bones. We expect bones of more massive species to be more robust in shape,
112 with relatively larger articular facets and muscle insertion areas, and a relatively wider
113 diaphysis. We expect bones of species living in open habitats to present adaptations for a high
114 degree of cursoriality, and bones of species living in closed or mountain habitats to present
115 adaptations for better manoeuvrability. We expect that the 3D shape comparison approach
116 permitted by geometric morphometrics will enable a better characterization and quantification
117 of shape variations linked to mass and habitat across bovids, as well as confirm and expand
118 previous results found in bovids with other techniques. This would increase our understanding
119 of the link between form and function in bone morphology, and especially of the impact of mass
120 and habitat on skeletal architecture.

121 **Material and methods**

122 **Material**



123

124 **Figure 1.** Phylogenetic tree used in this study, modified from Bibi (2013), with indications of habitat
 125 and mass for each species. **O**: open habitat; **L**: light cover habitat; **H**: heavy cover habitat; **F**: forest
 126 habitat; **M**: mountain habitat; **D**: domesticated species. **1**: mean mass under or equal to 20 kg; **2**: mean
 127 mass from 21 to 100 kg; **3**: mean mass from 101 to 300 kg; **4**: mean mass above 300 kg.

128 **Table 1.** Number of bones studied per tribe.

Tribe	Humerus	Femur	Tibia	Radius-ulna	Total
Alcelaphini	6	6	6	4	22
Antilopini	13	16	13	7	49
Boselaphini	4	4	4	3	15
Bovini	15	14	14	13	56
Caprini	18	20	15	15	68
Cephalophini	1	3	2	1	7
Hippotragini	9	10	10	9	38
Oreotragini	2	2	2	0	6

Reduncini	4	4	2	3	13
Tragelaphini	3	4	4	3	14
Total	75	83	72	58	288

129

130 We studied a total of 288 stylopod and zeugopod bones from 50 species among ten of the
131 twelve currently recognized tribes of bovids (see Fig. 1, Table 1, and Table S1 for the list of all
132 specimens). Specimens were chosen pending on availability and with the aim of obtaining a
133 representative sample of the bovid family in terms of mass, habitat and phylogeny. Neotragini
134 and Aepycerotini are the only tribes for which we did not find any member in the collections
135 we visited. Specimens come from the collections of the Muséum National d’Histoire Naturelle
136 (MNHN, Paris, France), and the Museum für Naturkunde (ZMB, Berlin, Germany). The
137 taxonomy of the family follows Castelló (2016). All bones belong to adult or subadult
138 specimens, as indicated by the complete fusing of their epiphyses to their diaphyses. We tried
139 to get two specimens by species when possible, depending on material available. Per bone, our
140 sample includes 43 species for the humerus (32 for which we have two specimens), 38 species
141 for the radius-ulna (20 with two specimens), 48 species for the femur (35 with two specimens)
142 and 45 species for the tibia (27 with two specimens). The anatomical nomenclature follows De
143 Iuliis & Pulerà (2011) as well as anglicised terms from (Barone, 1999, 2010).

144 Mass and habitat attribution

145 Mass estimates were retrieved from Castelló (2016). Usually, two ranges of mass are
146 available, one for each sex. The sex of the specimens sampled was usually unknown;
147 considering the need of a unique value for the analyses, we used the mean of the lowest and
148 highest values provided for the whole species. The average species masses range from 4.6 kg
149 for the lightest species (Kirk’s dik-dik, *Madoqua kirkii*) to 725 kg for the heaviest one (the
150 domestic cow, *Bos taurus*, Table 2). For the scimitar oryx (*Oryx dammah*), the mass range is
151 taken from Mungall (2007) since the value given by Castelló (2016) is for males only. For the
152 hartebeest (*Alcelaphus buselaphus*), Castelló (2016) considers that it should be split into seven
153 independent species and reports separate mass values for each of them. Given that we were
154 unable to reassign the specimens we studied to one of those species, the range of mass used is
155 that of all the species that were once regrouped under *A. buselaphus*.

156 Habitat attribution follows the categories initially proposed by Kappelman *et al.* (1997),
157 adding a mountain category as proposed by Scott & Barr (2014). We used an additional separate
158 category for the domesticated species since they have undergone artificial selective pressures

159 that could alter their bone shape and are kept in enclosures that do not necessarily reflect their
 160 original habitat. We used the species assignments to habitat categories of DeGusta & Vrba
 161 (2003), Plummer *et al.* (2008) and Scott & Barr (2014). When a species of our sample had not
 162 been assigned to a habitat category by any of them, or when two publications disagreed on the
 163 category one species should be classified into, we assigned the species to a habitat category
 164 ourselves based on Castelló (2016). Five species are classified as domesticated species, three
 165 as forest-dwellers, seven as heavy cover species, nine as light cover species, ten as mountain
 166 species and 16 as open-habitat species (Table 2).

167
 168 **Table 2.** Mass and habitat assigned to each of our species, based on DeGusta & Vrba (2003), Plummer
 169 *et al.* (2008), Scott & Barr (2014), and Castelló (2016) for habitat, and Castelló (2016) for masses.

Tribe	Species	Habitat	Mass (kg)
Alcelaphini	<i>Alcelaphus buselaphus</i>	Open	169 (120-218)
Alcelaphini	<i>Connochaetes gnou</i>	Open	145 (110-180)
Alcelaphini	<i>Damaliscus pygargus</i>	Open	71 (56-86)
Antilopini	<i>Antidorcas marsupialis</i>	Open	29 (20-38)
Antilopini	<i>Antilope cervicapra</i>	Open	37.5 (19-56)
Antilopini	<i>Dorcatragus megalotis</i>	Mountain	11 (9-13)
Antilopini	<i>Eudorcas thomsonii</i>	Open	19 (13-25)
Antilopini	<i>Gazella dorcas</i>	Open	19 (15-23)
Antilopini	<i>Litocranius walleri</i>	Light cover	40 (30-50)
Antilopini	<i>Madoqua kirkii</i>	Heavy cover	4.6 (2.7-6.5)
Antilopini	<i>Nanger dama</i>	Open	57.5 (40-75)
Antilopini	<i>Ourebia ourebi</i>	Light cover	12.5 (8-17)
Antilopini	<i>Raphicerus campestris</i>	Light cover	11.5 (7-16)
Antilopini	<i>Saiga tatarica</i>	Open	36 (21-51)
Boselaphini	<i>Boselaphus tragocamelus</i>	Light cover	205 (200-290)
Boselaphini	<i>Tetracerus quadricornis</i>	Heavy cover	20 (15-25)
Bovini	<i>Bison bison</i>	Open	679 (360-998)
Bovini	<i>Bos frontalis</i>	Heavy cover	455 (350-560)
Bovini	<i>Bos grunniens</i>	Domesticated	395 (197-593)
Bovini	<i>Bos javanicus</i>	Heavy cover	600 (400-800)
Bovini	<i>Bos taurus</i>	Domesticated	725 (150-1300)
Bovini	<i>Bubalus bubalis</i>	Domesticated	700 (400-1000)
Bovini	<i>Bubalus depressicornis</i>	Forest	225 (200-250)
Bovini	<i>Syncerus caffer</i>	Light cover	625 (350-900)
Caprini	<i>Ammotragus lervia</i>	Mountain	87.5 (30-145)
Caprini	<i>Budorcas taxicolor</i>	Mountain	250 (150-350)
Caprini	<i>Capra hircus</i>	Domesticated	66.5 (20-113)
Caprini	<i>Capricornis milneedwardsii</i>	Mountain	112.5 (85-140)
Caprini	<i>Hemitragus jemlahicus</i>	Mountain	85 (30-140)
Caprini	<i>Nemorhaedus goral</i>	Mountain	38.5 (35-42)
Caprini	<i>Oreamnos americanus</i>	Mountain	95 (60-130)
Caprini	<i>Ovibos moschatus</i>	Open	295 (180-410)
Caprini	<i>Ovis aries</i>	Domesticated	102.5 (45-160)

Caprini	<i>Pseudois nayaur</i>	Mountain	53.5 (32-75)
Caprini	<i>Rupicapra rupicapra</i>	Mountain	38 (14-62)
Cephalophini	<i>Cephalophus leucogaster</i>	Forest	17.5 (14-21)
Cephalophini	<i>Cephalophus silvicultor</i>	Forest	62.5 (45-80)
Cephalophini	<i>Sylvicapra grimmia</i>	Light cover	18 (10-26)
Hippotragini	<i>Addax nasomaculatus</i>	Open	92.5 (60-125)
Hippotragini	<i>Hippotragus equinus</i>	Light cover	257.5 (215-300)
Hippotragini	<i>Hippotragus niger</i>	Light cover	205 (160-250)
Hippotragini	<i>Oryx dammah</i>	Open	150.5 (91-210)
Hippotragini	<i>Oryx gazella</i>	Open	227.5 (180-275)
Hippotragini	<i>Oryx leucoryx</i>	Open	64.5 (54-75)
Oreotragini	<i>Oreotragus oreotragus</i>	Mountain	13.5 (9-18)
Reduncini	<i>Kobus ellipsiprymnus</i>	Heavy cover	217.5 (160-275)
Reduncini	<i>Redunca redunca</i>	Light cover	50 (35-65)
Tragelaphini	<i>Taurotragus oryx</i>	Open	575 (450-700)
Tragelaphini	<i>Tragelaphus spekii</i>	Heavy cover	87.5 (50-125)
Tragelaphini	<i>Tragelaphus strepsiceros</i>	Heavy cover	217.5 (120-315)

170

171 Data acquisition

172 Most of the specimens were digitized using an Artec Eva surface scanner and the Artec
 173 Studio Professional v12.1.5.1 software (Artec 3D, 2018). The smallest specimens were
 174 digitized using a Nikon D5500 camera (automatic mode, without flash, focal length 50 mm,
 175 aperture f/1.8) and the photogrammetry software Agisoft PhotoScan v1.4.0 (Agisoft LLC,
 176 2017). The 3D meshes were then exported, decimated down to 200,000 faces and mirrored to
 177 have only right side bones, using MeshLab v2016.12 (Cignoni et al., 2008).

178 Geometric morphometrics

179 **Table 3.** Number of anatomical landmarks, curve semi-landmarks and surface semi-landmarks placed
 180 on each bone.

Bone	Anatomical landmarks	Curve semi-landmarks	Surface semi-landmarks	Total
Humerus	23	160	576	759
Radius-ulna	17	208	365	590
Femur	21	186	565	772
Tibia	19	178	500	697

181

182 To analyse shape variations in our sample, we performed 3D geometric morphometrics in
 183 order to quantify the shape of each bone. Bone shape was modelled using three kinds of
 184 landmarks: anatomical landmarks, semi-landmarks sliding on curves, and semi-landmarks
 185 sliding on surfaces (Gunz et al., 2005; Gunz and Mitteroecker, 2013). Landmarks were defined

186 and placed by a single operator (Table 3, Tables S2-S5, Figs. S1-S4). Landmarks and curves
187 were placed on the meshes using the IDAV Landmark software package (Wiley, 2005). All the
188 analyses and statistical tests were run using R (R Development Core Team, 2005) and RStudio
189 (RStudio, Inc., 2018). The curves were resampled using the algorithm provided in Botton-Divet
190 *et al.* (2016), in order to reduce the number of curve semi-landmarks. The algorithm uses the
191 coordinates of the semi-landmarks of each curve to return a given number of equidistant points
192 per curve. The new curve semi-landmarks were then projected on the meshes using the
193 `closemeshKD` function of the Morpho R package (Schlager *et al.*, 2018), to ensure that each
194 curve semi-landmark was indeed placed on the surface of the mesh. The function uses the
195 coordinates of each semi-landmark to calculate its closest match on the surface of the mesh.

196 As for the surface semi-landmarks, a template was designed for each bone type. A specimen
197 was arbitrarily chosen among those assessed by eye to be the closest to the average and used to
198 design the template (*Bos taurus* MNHN 1926-302 for the humerus, *Connochaetes gnou* MNHN
199 2013-26 for the radius-ulna, and *Damaliscus pygargus* ZMB 70722 for both the femur and
200 tibia). Surface semi-landmarks were manually added to this template, in order to cover the
201 whole surface. We used this template to project automatically the surface semi-landmarks on
202 the surface of all the other specimens using the `placePatch` function of the Morpho R package
203 (see Schlager *et al.*, 2018). This was followed by a relaxation step using the `relaxLM` function,
204 to ensure that projected points were spread across the entire surface of the meshes. Curve and
205 surface sliding semi-landmarks were then slid to minimize the bending energy of a thin plate
206 spline (TPS, see Mitteroecker & Gunz, 2009; Gunz & Mitteroecker, 2013) between each
207 specimen and the template at first, and then two times between the result of the preceding step
208 and the Procrustes consensus of the complete dataset, using the `slider3d` function. All the
209 specimens were checked at each step using the `checkLM` function, to ensure that the semi-
210 landmarks were placed correctly.

211 All the landmarks were superimposed using a Generalized Procrustes Analysis (GPA (Rohlf
212 and Slice, 1990), which translates, scales and rotates each set of landmarks in order to remove
213 the information of size, position and angle and minimize the sum of the square distances
214 between landmark configurations. The aligned landmarks coordinates were then used in a
215 Principal Component Analysis (PCA) in order to reduce dimensionality of the dataset and
216 visualize the distribution of the individuals in the morphometric space. Thin Plate Splines (TPS,
217 see (Klingenberg, 2013) were used to visualize the results of our analyses: for each set of
218 landmarks on the four bones, the mean-shape generated by the GPA was mapped onto the
219 specimen closest to the mean value. Then, this mean-shaped model was deformed using TPS

220 towards the shape resulting from our analyses (*e.g.* the shape corresponding to the maximal
221 theoretical mass). This allowed us to obtain the complete 3D models of theoretical bones
222 corresponding for instance to the average heavy bovid or to the average bovid living in an open
223 habitat, according to our sample. When shape differences were subtle and not clearly visible to
224 the naked eye, colour maps were applied on the theoretical bones showing the local shape
225 deviation from a reference model, using the `meshDist` function of the `Morpho` R package. The
226 function calculates the distance between a reference mesh and another mesh along every vertex
227 of the reference mesh.

228 In order to test the repeatability of our set of landmarks, we placed each of the anatomical
229 landmarks five times on our two specimens of *Oryx leucoryx* and our two specimens of *Oryx*
230 *dammah*. We could not use specimens belonging to only one species, as we do not have any
231 species with more than two specimens. The four specimens were assessed by sight to be the
232 four morphologically closest ones, and belong to phylogenetically very close species (Fig. 1).
233 For each bone, these 20 landmarks sets were then superimposed using a GPA and visualized
234 using a PCA, to check that landmark error per specimen was smaller than inter individual
235 variation (Fig. S5).

236 Statistical analyses

237 All our tests, except the K-mult (see below), were performed on the Procrustes coordinates
238 of the specimens. When two specimens were available for a species, the average of the
239 Procrustes landmark coordinates of the two specimens was used. Three tests were performed
240 for each of the four limb long bones:

241 1. A test of phylogenetic signal in the data, using a multivariate K statistic (K-mult), based
242 on all the PC-scores. It compares the observed rate of morphological change to the expected
243 change under a Brownian motion (see Adams, 2014a; Blomberg et al., 2003). The phylogeny
244 used is the one in Figure 1. This was performed using the `K.mult` function of the `phylocurve` R
245 package (Goolsby, 2015).

246 2. A multivariate analysis of covariance (MANCOVA), against both mass and habitat, with
247 the `procD.lm` function of the `geomorph` R package (Adams et al., 2018). The logarithm of the
248 cubic root of the mass was used. This tested the influence of the species' mean mass and habitat
249 on the shape of the bones in our sample. Shape data corresponding to the minimum and
250 maximum mass and to each habitat were also extracted, if the test was significant.

251 3. A Phylogenetic Generalised Least Squares (PGLS) regression, again to test the influence
252 of mass and habitat but this time in a phylogenetic framework (Adams, 2014b). This assumes
253 a Brownian model of evolution. This was performed with the *procD.pgls* function of the
254 geomorph R package.

255 To test the independence of mass and habitat in our sample, Student's t-tests were performed
256 to assess if each habitat category had a different mean mass from the others. This was done
257 separately for each bone, as our sample differed slightly between each bone. Considering we
258 have six categories of habitat, this resulted in 15 pair-wise comparisons per bone, which may
259 make it necessary to perform statistical corrections of the p-values in order to lower the risk of
260 one or several false positives. There is, however, no consensus in the literature on whether or
261 not this should be done, as although it lowers the risk of false positives, it increases the risk of
262 false negatives (Cabin and Mitchell, 2000; Streiner and Norman, 2011). We therefore report
263 both the corrected and uncorrected p-values. We used the *p.adjust* function of the stats R
264 package, using a Benjamini-Hochberg correction (Benjamini and Hochberg, 1995).

265 Results

266 **Table 4.** Results of the K-mult test, for each bone.

Bone	K	p-value
Humerus	0.75	<0.001
Radius-Ulna	1.10	<0.001
Femur	0.73	<0.001
Tibia	0.79	<0.001

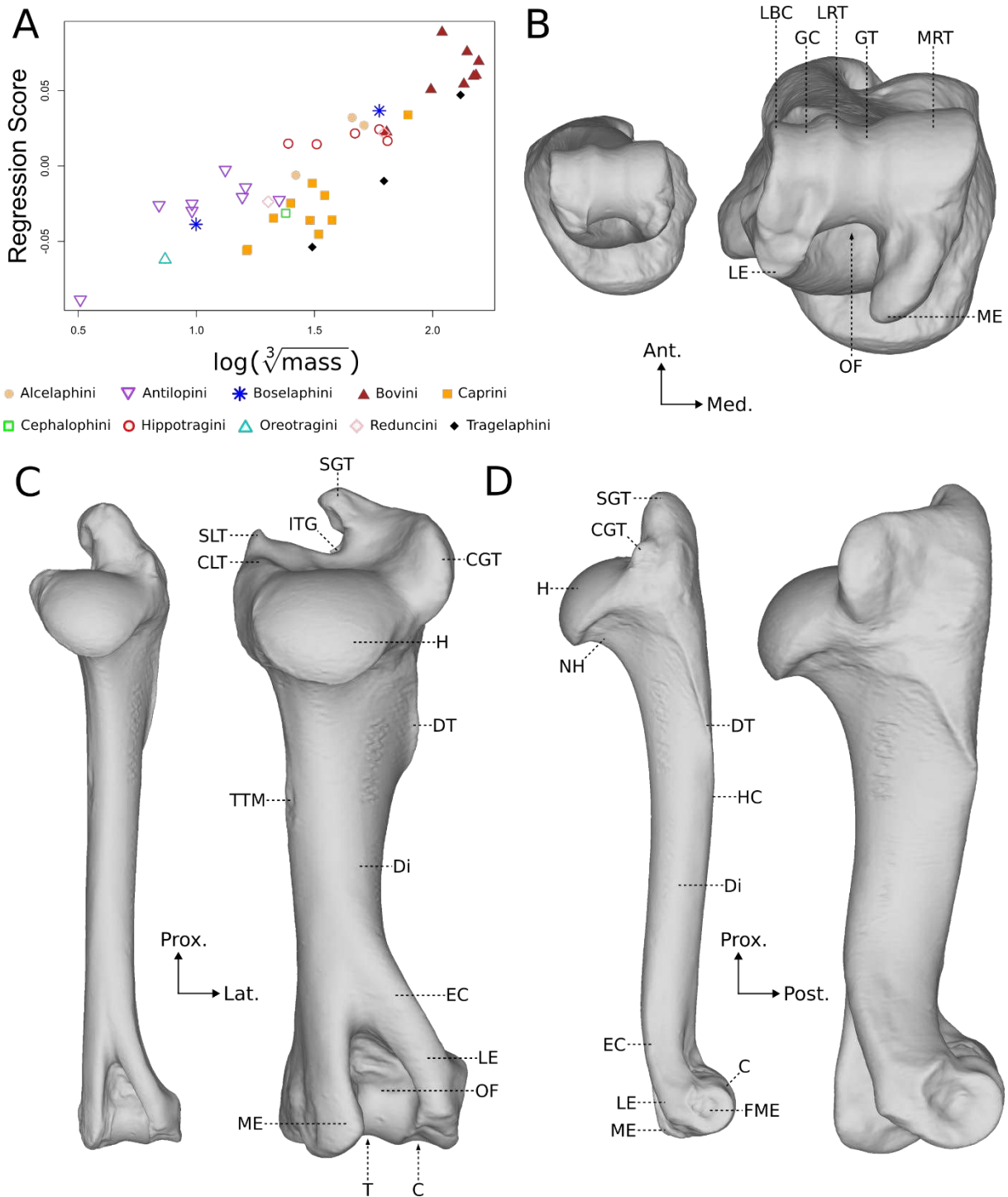
267 There is a strong phylogenetic signal in all the bones studied (Table 4). That signal is lower
268 than would be expected under a Brownian motion ($K < 1$) for the humerus, the femur and the
269 tibia. However, it is the reverse for the radius-ulna ($K > 1$).

270 The results of the Student's t-test show no statistically significant difference of mean mass
271 between species of different habitats in our sample (Fig. S6; Table S6), except for domesticated
272 species that are heavier on average than mountainous species. However, this statistically
273 significant difference of mean mass disappears when using a Benjamini-Hochberg correction
274 (Table S6).

275 **Table 5.** Results of the multivariate analyses of covariance and of the phylogenetic generalised least
276 squares regressions.

	MANCOVA						PGLS					
	Mass		Habitat		Interaction		Mass		Habitat		Interaction	
	p	R ²	p	R ²	p	R ²	p	R ²	p	R ²	p	R ²
Humerus	<0.001	0.48	<0.001	0.17	<i>0.15</i>	0.05	<0.001	0.33	<0.01	0.17	<i>0.46</i>	0.07
Radius-ulna	<0.001	0.50	<0.01	0.14	<i>0.16</i>	0.07	<0.001	0.15	<0.01	0.22	<i>0.51</i>	0.10
Femur	<0.001	0.46	<0.001	0.14	<i>0.08</i>	0.06	<0.001	0.29	<0.001	0.17	<i>0.56</i>	0.06
Tibia	<0.001	0.56	<i>0.19</i>	0.06	<i>0.11</i>	0.06	<0.001	0.26	<i>0.07</i>	0.13	<i>0.43</i>	0.08

277 Mass is statistically correlated with the shape of the bones in our sample, whether the test
278 used is a MANCOVA or a PGLS regression (see Table 5). According to the MANCOVA, mass
279 explains between 46% and 56% of the total variance of the shape of the bones. According to
280 the PGLS regression, this percentage is lower: between 15% and 33%. Habitat is statistically
281 correlated with the shape of each bone except the tibia (see Table 5). According to the
282 MANCOVA, habitat explains between 14% and 17% of the total shape variance, tibia excluded.
283 According to the PGLS, this percentage is slightly higher: between 17% and 22%. The
284 interaction between mass and habitat never shows a statistically significant influence.

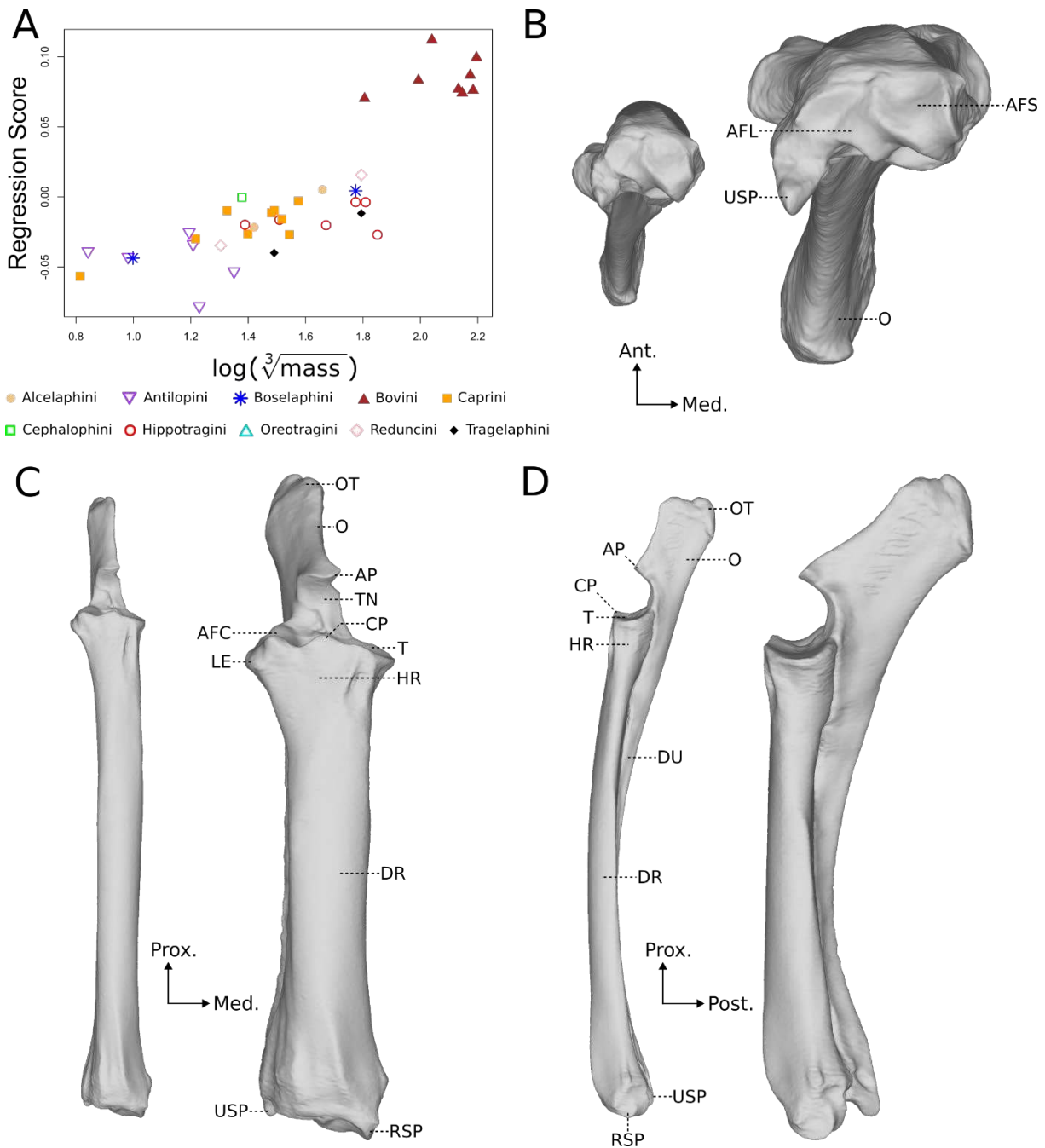


287

288 **Figure 2.** Results of the MANCOVA for the influence of the mass on the humerus. A: Regression score
 289 against the log of the cubic root of the mass of the species. B, C, D: TPS deformations of the humeri
 290 corresponding to maximal (right) and minimal (left) mass. Distal (B), posterior (C) and lateral (D)
 291 views. C: Capitulum; CGT: Convexity of the greater tuberosity; CLT: Convexity of the lesser tuberosity; Di:
 292 Diaphysis; DT: Deltoid tuberosity; EC: Epicondylar crest; FME: Fossa for the insertion of musculus

293 extensor digitorum lateralis; GC: Groove of the capitulum; GT: Groove of the trochlea; H: Head of the
294 humerus; HC: Humeral crest; ITG: Intertubercular groove; LBC: Lateral border of the capitulum; LE:
295 Lateral epicondyle; LRT: Lateral ridge of the trochlea; ME: Medial epicondyle; MRT: Medial ridge of
296 the trochlea; NH: Neck of the humerus; OF: Olecranon fossa; SGT: Summit of the greater tuberosity;
297 SLT: Summit of the lesser tuberosity; T: Trochlea; TTM: Tuberosity of the teres major.

298 The graph of the regression score against the mean mass of the species (Fig. 2A) shows that
299 the tribes Caprini and Tragelaphini have a regression score that is on average below the other
300 tribes. This means that for a given mass, an average Caprini humerus would have features
301 reminiscent of that of a lighter species, compared to an average Antilopini humerus. The most
302 obvious shape difference due to a high mass in the humerus is the increase of the overall
303 robustness of the bone (Fig. 2B-D). The diameter of the diaphysis is relatively wider in bones
304 belonging to heavy species, and the bone is also slightly less curved in heavy species. The
305 convexity of the greater tuberosity is greatly enlarged. The lesser tuberosity is more developed,
306 extending more anteriorly and proximally. Its summit rises clearly above the head of the
307 humerus and its convexity is proportionally larger antero-posteriorly. The head of the humerus
308 is relatively wider in heavy species and the deltoid tuberosity is enlarged. The two epicondyles
309 are clearly symmetrical in humeri belonging to light species, whereas in heavy species the
310 medial epicondyle is much larger than the lateral one, expanding posteriorly and distally. The
311 epicondylar crest is more robust in heavy species. The medial ridge of the trochlea is relatively
312 wider latero-medially in heavier species, being almost as wide as half the trochlea whereas it is
313 as wide as one third of the trochlea in lighter species.



315

316 **Figure 3.** Results of the MANCOVA for the influence of the mass on the radius-ulna. A: Regression
 317 scores against the log of the cubic root of the mass of the species. B, C, D: TPS deformations of the
 318 radii-ulnae corresponding to maximal (right) and minimal (left) mass. Distal (B), anterior (C) and medial
 319 (D) views. AFC: Articular facet for the capitulum; AFL: Articular facet for the lunate; AFS: Articular
 320 facet for the scaphoid; AP: Anconeal process; CP: Coronoid process; DR: Diaphysis of the radius; DU:
 321 Diaphysis of the ulna; HR: Head of the radius; LE: Lateral eminence; O: Olecranon; OT: Olecranal
 322 tuber; RSP: Radial styloid process; T: Trochlea; TN: Trochlear notch; USP: Ulnar styloid process.

323 The regression plot (Fig. 3A) shows that the Bovini tribe members possess a much higher
 324 regression score than they would if they followed the same trend as the other tribes. This means

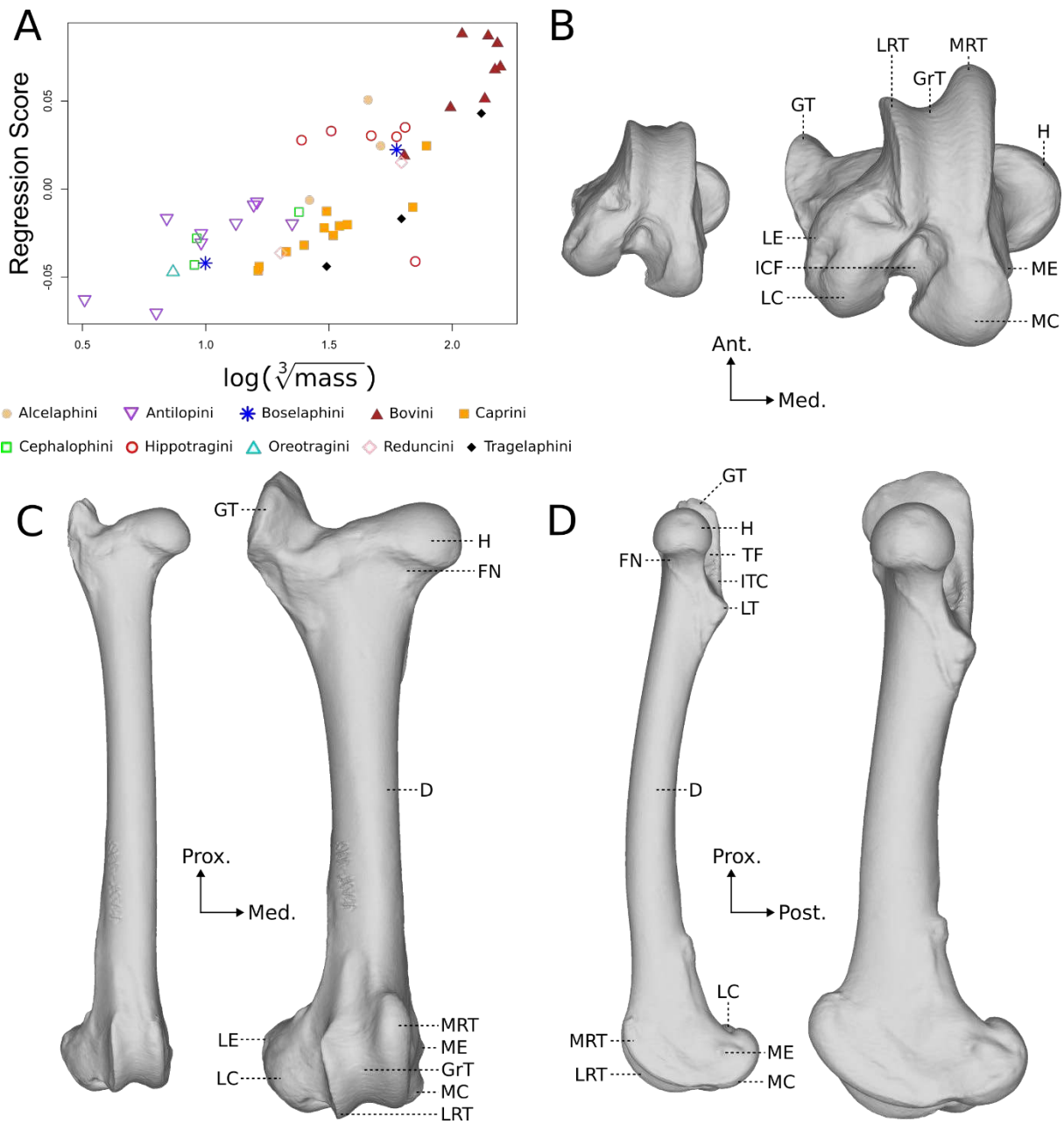
325 that their radii-ulnae possess features that would be associated with a heavier mass than their
326 actual mass, if the regression were the same as for the other bovids. The opposite is observed
327 for two species of Antilopini (*Litocranius walleri*, and *Nanger dama* in a lesser extent), which
328 possess features associated with a lighter mass than their own. In heavier species (Figs. 3B-D),
329 the bones are more robust. The radius is relatively wider at midshaft. The shaft of the ulna is
330 antero-posteriorly wider in heavier species, whereas it is much reduced in lighter species,
331 especially in the distal half. The bones are more curved longitudinally in lighter species. The
332 olecranon is antero-posteriorly wider in heavier species, and oriented more obliquely, whereas
333 in light species the olecranon is oriented almost in the same axis as the diaphysis of the ulna,
334 forming a very open angle. The olecranon is also relatively longer proximo-distally in heavier
335 species, for a given bone length. The anterior parts of the articular facets for the lunate and
336 the scaphoid are both wider medio-laterally in heavier species.

337

338

339

340

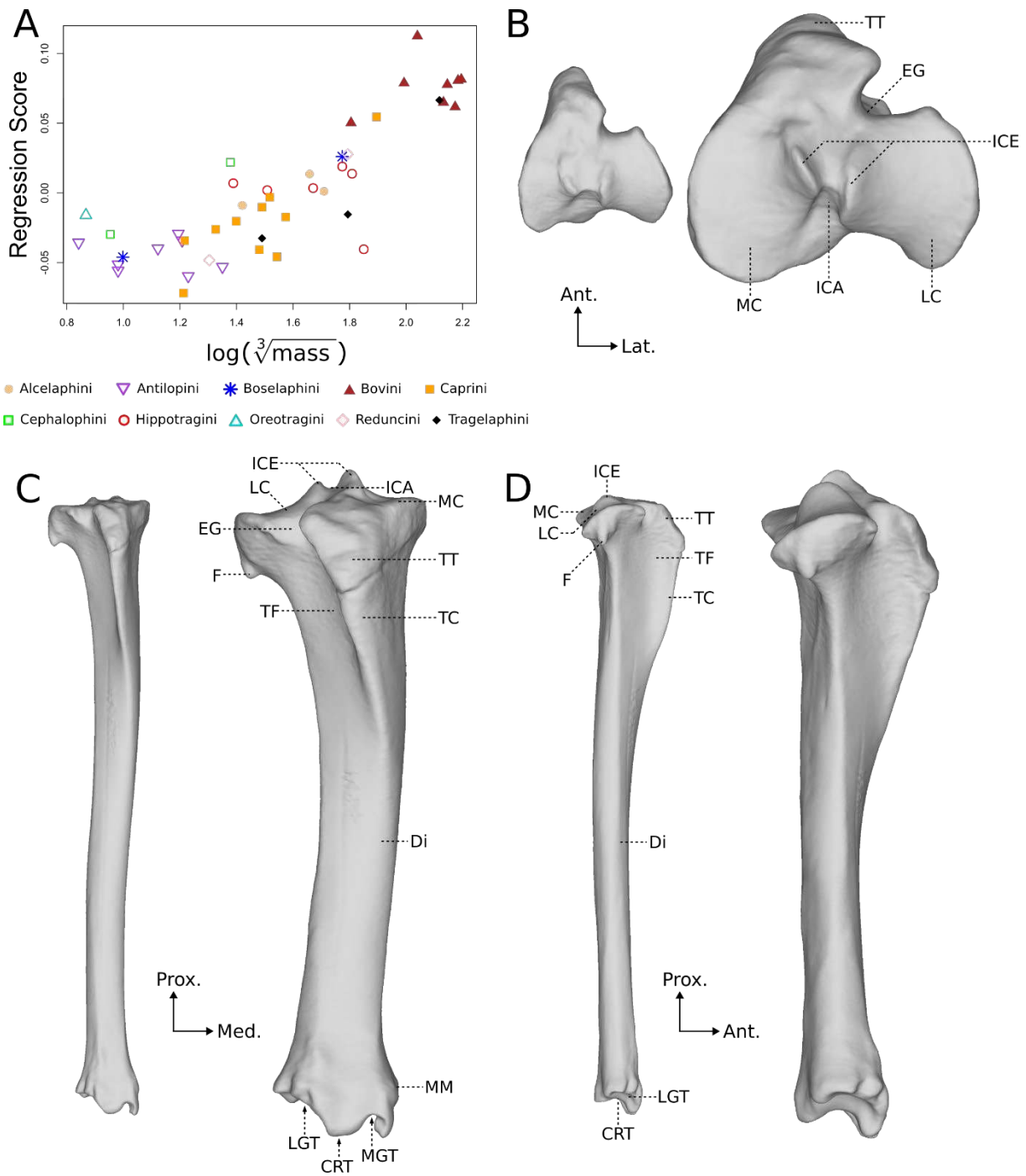


342

343 **Figure 4.** Results of the MANCOVA for the influence of the mass, on the femur. A: Regression score
 344 against the log of the cubic root of the mass of the species. B, C, D: TPS deformations of the femora
 345 corresponding to maximal (right) and minimal (left) mass. Distal (B), anterior (C) and medial (D) views.
 346 Di: Diaphysis; FN: Femoral neck; GrT: Grove of the trochlea; GT: Greater trochanter; H: Femoral head;
 347 ICF: Intercondylar fossa; ITC: Intertrochanteric crest; LC: Lateral condyle; LE: Lateral epicondyle;
 348 LRT: Lateral ridge of the trochlea; LT: Lateral tubercle; MC: Medial condyle; ME: Medial epicondyle;
 349 MRT: Medial ridge of the trochlea; TF: Trochanteric fossa.

350 The regression plot (Fig. 4A) shows again that the Caprini and Tragelaphini have a lower
 351 regression score than the other tribes, and thus present femora with more features associated to
 352 a light species than could be expected. One species of Hippotragini (*Hippotragus niger*) is very

353 noticeably below the other members of its tribe; our sample for that species consist of only one
354 specimen with no collection number reported, it may have been misidentified. Femora
355 belonging to heavy bovids (Figs. 4B-D) display again more robust shafts and epiphyses.
356 Compared to what is observed for the other bones, the femoral epiphyses are particularly
357 enlarged in heavy species, showing a greater relative increase in their medio-lateral width than
358 the diaphysis does. The distal epiphysis is extended antero-posteriorly. The bone is more curved
359 longitudinally in light species. The greater trochanter is wider in all directions, rising well above
360 the head, in heavy species. There is no clear difference in the shape of the lesser trochanter.
361 Both supracondylar tuberosities are more marked in heavy species, and the supracondylar fossa
362 is deeper. The trochlea is almost symmetrical in light species, whereas the medial ridge is bigger
363 than the lateral one in heavy species, expanding anteriorly and proximally. It is also more
364 elongated antero-posteriorly in heavy species. Both condyles are wider medio-laterally in heavy
365 species, and the intercondylar fossa is consequently reduced. The lateral epicondyle is relatively
366 bigger in heavy species, forming a bump that is not present in lighter species



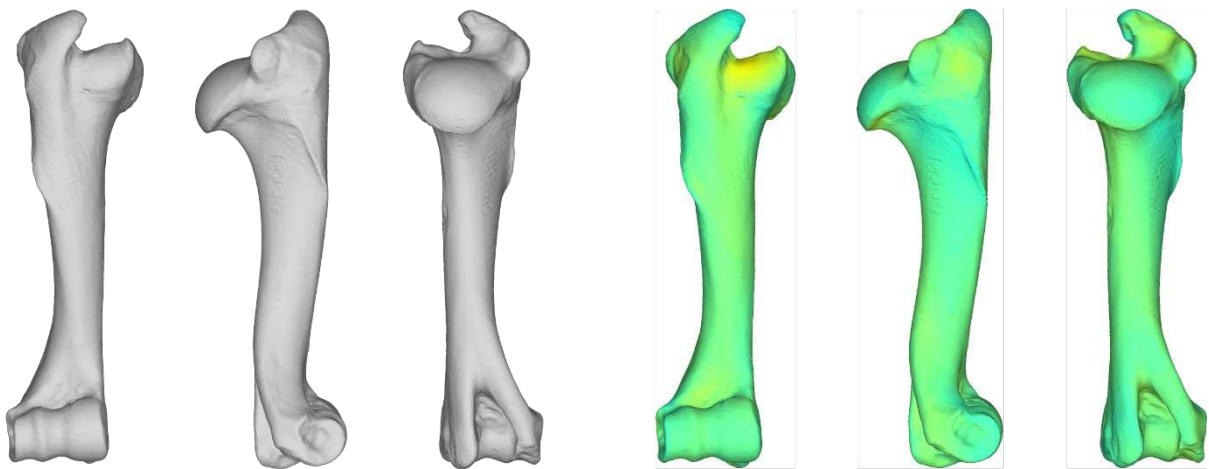
368

369 **Figure 5.** Results of the MANCOVA for the influence of the mass, on the tibia. A: Regression score
 370 against the log of the cubic root of the mass of the species. B, C, D: TPS deformations of the tibiae
 371 corresponding to maximal (right) and minimal (left) mass. Proximal (B), anterior (C) and lateral (D)
 372 views. CRT: Central ridge of the trochlea; Di: Diaphysis; EG: Extensor groove; F: Fibula; ICA:
 373 Intercondylar area; ICE: Intercondylar eminence; LC: Lateral condyle; LGT: Lateral groove of the
 374 trochlea; MC: Medial condyle; MGT: Medial groove of the trochlea; MM: Medial malleolus; TC: Tibial
 375 crest; TF: Tibial fossa; TT: Tibial tuberosity.

376 The regression plot shows again the Bovini tribe with a higher regression score than what
377 would be observed if they followed the same trend as the others (Fig. 5A). This is however less
378 marked than for the radius-ulna, and this time two non-Bovini species (*Ovibos moschatus*,
379 Caprini, and *Taurotragus oryx*, Tragelaphini) have a regression score similar to that of the
380 Bovini. Please note that we could not analyse radii-ulnae for those two species, so it is
381 impossible to know if their radii-ulnae would display the same particularity. Tibiae belonging
382 to heavy species are, again, more robust overall, with relatively wider shaft and epiphyses (Fig.
383 5B-D). The condyles are larger medio-laterally and antero-posteriorly. The intercondylar
384 eminence rises higher proximally in heavy species than in light species. The groove for the
385 extensor muscle is deeper in heavy species. Both the tibial tuberosity and the tibial crest extend
386 more distally in heavy species, and are medio-laterally larger, more robust. The trochlea for the
387 astragalus remains symmetrical in both light and heavy species.

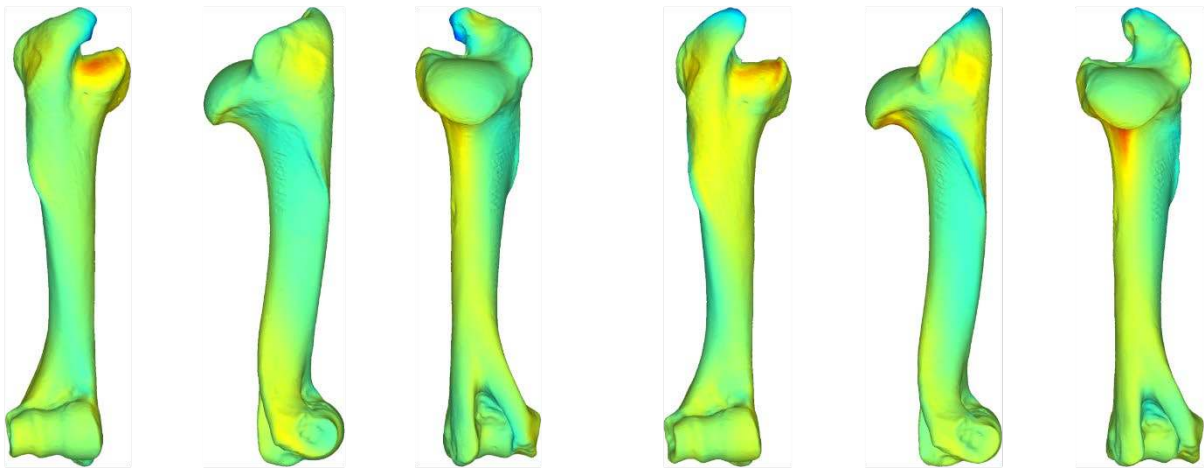
388 Influence of habitat

389 Humerus



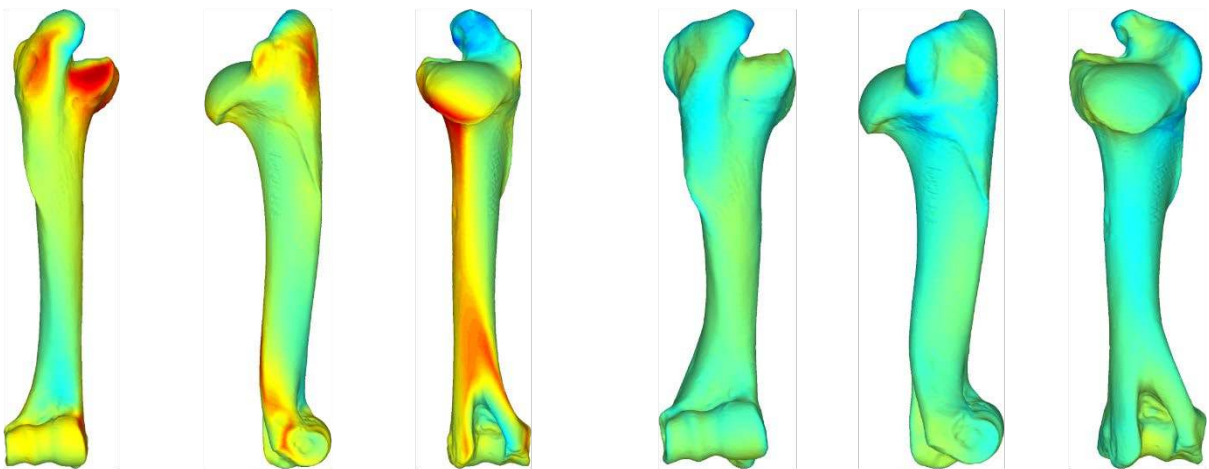
A - Open

B - Light cover



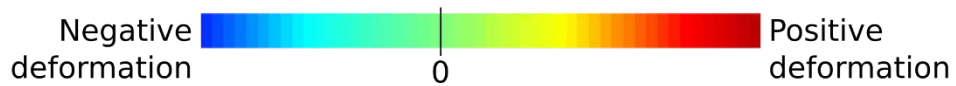
C - Heavy cover

D - Forest



E - Mountain

F - Domesticated

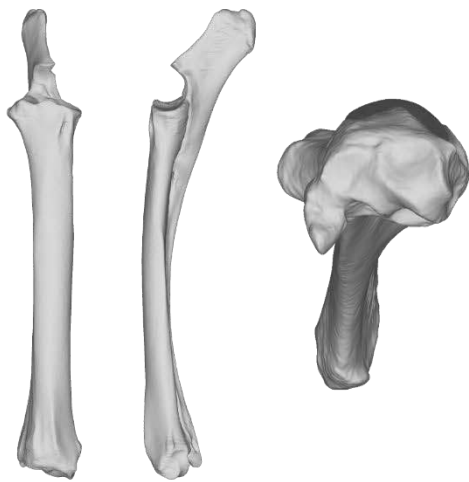


390

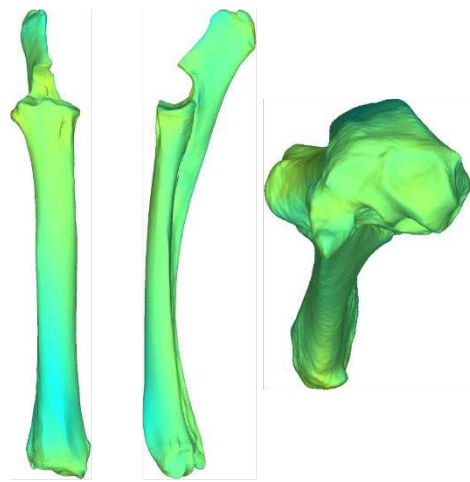
391 **Figure 6.** TPS deformations of the humeri corresponding to each habitat category. The colours
392 represent the intensity of the local shape deviation between the represented habitat and open
393 habitat; open habitats are thus not coloured. Red denotes a positive deviation of the open habitat
394 compared to the represented habitat, blue a negative deviation, light-green an absence of
395 deviation. From left to right: anterior, lateral and posterior views.

396 The results on the humerus present a continuum of shapes is generally observed between
397 the habitat categories (Fig. 6), excluding domesticated species, with, from one extreme to the
398 other: open habitat species, light cover species, heavy cover species, forest species and
399 mountain species. The bone is generally slightly more robust along the diaphysis in open habitat
400 species than in mountain species. That difference is stronger for the epiphyses. The head of the
401 humerus is clearly wider relatively, especially medially and distally, in open and light cover
402 habitat species than in the others. The convexity of the greater tuberosity is larger in open habitat
403 species, the summit of the greater tuberosity rises higher proximally in mountain and forest
404 species than in the others. The lesser tuberosity rises higher proximally in open habitat species,
405 whereas it is on the same level as the head of the humerus in mountain species. It also expands
406 much more anteriorly in open and light cover habitat species than in mountain species, with
407 heavy cover and forest species in between. Distally, the trochlea is relatively larger in open and
408 light cover habitat species than in mountain habitat species. The epicondyles are also larger in
409 open habitat species, expanding in a medio-lateral axis. We note a slight asymmetry of the
410 epicondyles, with the medial epicondyle being larger, expanding especially posteriorly in all
411 habitats, except mountain habitats. Domesticated species present characteristics reminiscent of
412 heavy weight species, e.g. a relatively more robust bone, great development of the convexity of
413 the greater trochanter, and medial epicondyle larger than the lateral one.

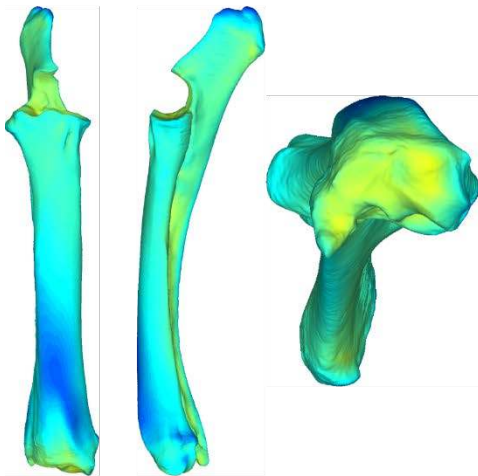
414



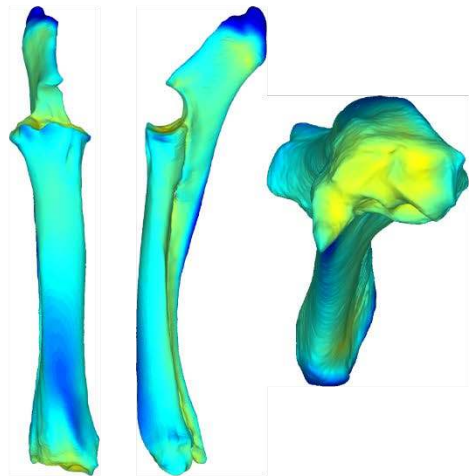
A - Open



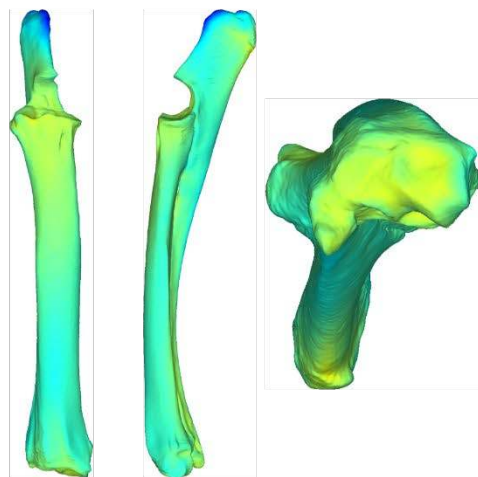
B - Light cover



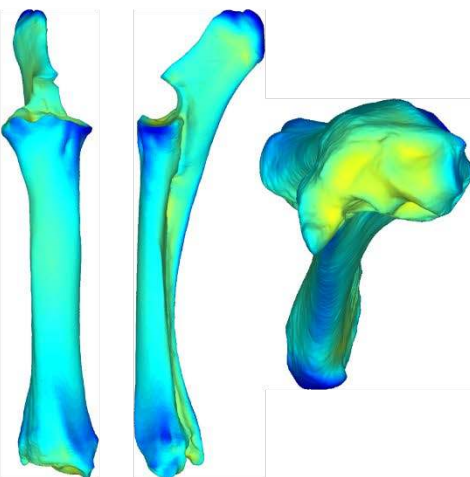
C - Heavy cover



D - Forest



E - Mountain



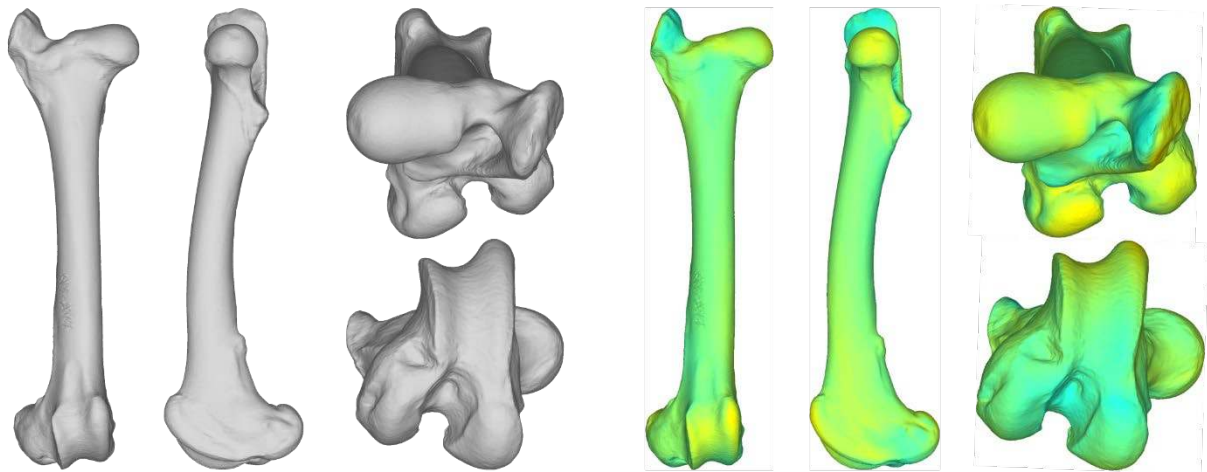
F - Domesticated



417 **Figure 7.** TPS representations of the radii-ulnae corresponding to each habitat category. The
418 colours represent the intensity of the local shape deviation between the represented habitat and
419 open habitat; open habitats are thus not coloured. Red denotes a positive deviation of the open
420 habitat compared to the represented habitat, blue a negative deviation, light-green an absence
421 of deviation. From left to right: anterior, medial and distal views.

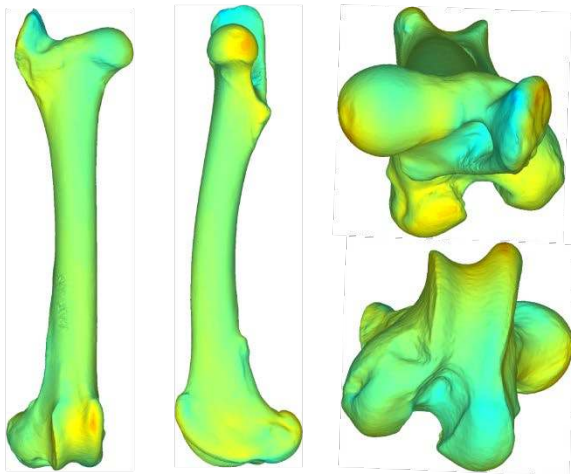
422 For the radius-ulna, the bone is overall slightly more robust in heavy cover, forest and
423 domesticated species (Fig. 7). The olecranon has a different orientation depending on the habitat
424 of the species: the angle observed between the olecranon and the diaphysis of the ulna is more
425 open in mountain species than it is in all the other habitats. This very open angle is also observed
426 qualitatively in *Oreotragus oreotragus*, and thus it is not a characteristic of the Caprini tribe,
427 whose species constitute most of our sample of mountainous species. Please note that we did
428 not include this radius-ulna of *O. oreotragus* in our geometric morphometrics sample because
429 of damages to the articular facets for the carpus. The olecranon is relatively longer relative to
430 the total length of the bone in heavy cover, forest and domesticated species than it is in light
431 cover and open habitat species. The trochlea is medio-laterally wider in domesticated, forest
432 and heavy cover species than in the three other groups. No clear variation of shape is observed
433 for the articular facets with the carpus.

434

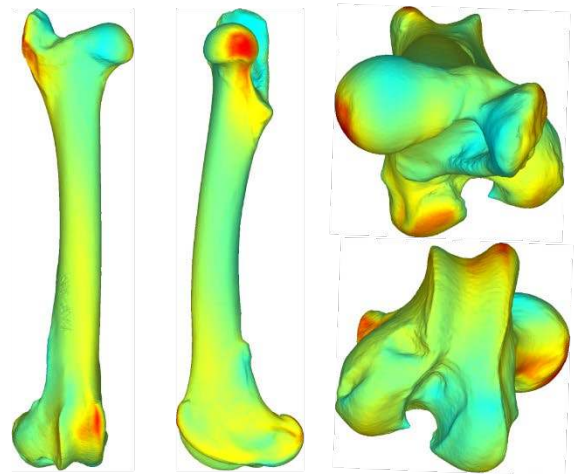


A - Open

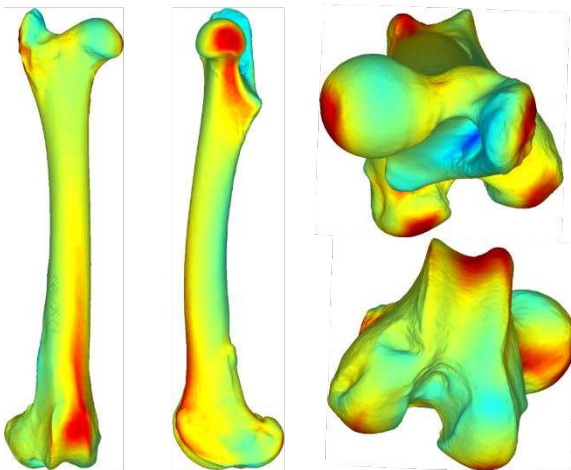
B - Light cover



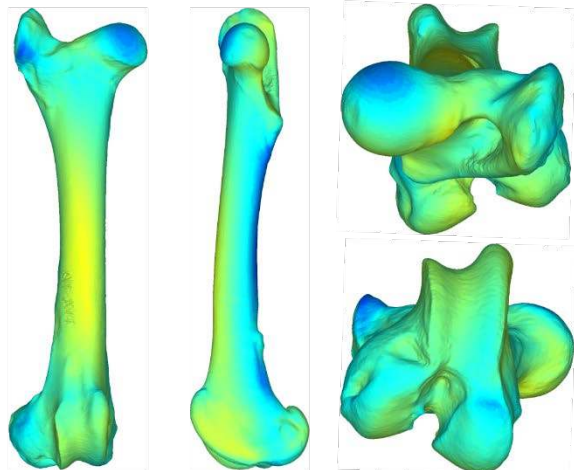
C - Heavy cover



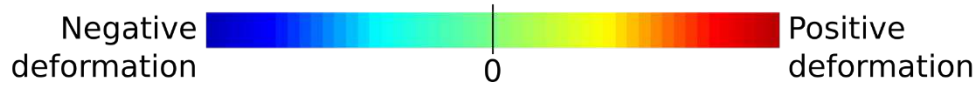
D - Forest



E - Mountain



F - Domesticated



437 **Figure 8.** TPS representations of the femora corresponding to each habitat category. The
438 colours represent the intensity of the local shape deviation between the represented habitat and
439 open habitat; open habitats are thus not coloured. Red denotes a positive deviation of the open
440 habitat compared to the represented habitat, blue a negative deviation, light-green an absence
441 of deviation. From left to right and top to bottom: anterior, medial, proximal and distal views.

442 As for the humerus, a continuum of shape is generally observed for the femur between
443 habitats (Fig. 8). From one extreme of the continuum to another, we find open habitat species,
444 light cover species, heavy cover species, forest species and mountain species. Domesticated
445 species do not place clearly on this continuum. The shaft has a very slightly wider diameter in
446 open habitat species than in mountain species, and the bones are slightly more curved
447 longitudinally. Both epiphyses are more robust in open habitat species; the proximal one is
448 larger medio-laterally, and the distal epiphysis is much larger antero-posteriorly. The greater
449 trochanter is larger in open habitat species, extending proximally and anteriorly; it is also wider
450 latero-medially, especially in the lateral direction. The lesser trochanter presents no changes in
451 shape with habitat. The head of the femur has the shape of a cylinder in open habitat species,
452 positioned along a latero-medial axis; in mountain species however, it is clearly spherical. There
453 is a clear asymmetry of the trochlea in open habitat species, the medial ridge being much wider
454 medio-laterally than the lateral one; it is also expanding much more anteriorly. That asymmetry
455 is gradually reducing in light cover, heavy cover and forest species and disappears entirely in
456 mountain species, where both ridges have globally the same shape. There is no clear variation
457 in the shape of the condyles, except that the medial condyle has a slightly more oblique
458 orientation in open habitat species than in mountain species. Both condyles are, however,
459 positioned more posteriorly in open habitat species, contributing to the antero-posterior
460 extension of the epiphysis. Domesticated species have again characteristics reminiscent of
461 heavier species, with a more robust bone, a relatively large greater trochanter and a strong
462 asymmetry of the trochlea. They also present a round head of the femur, although not as round
463 as mountain species.

464 **Discussion**

465 **Impact of phylogeny**

466 The K-mult tests are all significant, meaning that closely related species of our sample tend
467 to show similar morphological traits in all their limb long bones. A K-mult value inferior to 1
468 means that there are less morphological similarities than expected under a Brownian evolution

469 model, i.e. bone morphology is less restrained by phylogeny. This is what we observe for the
470 humerus, the femur and the tibia, and is consistent with what is generally found in geometric
471 morphometric studies of mammalian postcrania (e.g. Fabre et al., 2015; San Millán et al., 2015;
472 Püschel and Sellers, 2016; Etienne et al., 2020; Lewton et al., 2020). A K-mult value above 1
473 means that there are more morphological similarities between closely related species than
474 expected under a Brownian motion. This is what we observe for the radius-ulna. This could be
475 explained by the stronger than usual shape differences observed between the Bovini tribe and
476 the other bovids (Fig. 3A). One hypothesis is that the Bovini tribe underwent a rapid change of
477 morphology for their radius-ulna, which would explain the high K-mult value for these bones.

478 **Adaptations to mass**

479 Mass has a strong influence on the shape of the sampled bones. It is clearly the strongest
480 factor, whether using MANCOVA or PGLS regression. We note that the R-square is lower
481 using PGLS however, meaning that a lot of the influence of the mass is linked to the phylogeny.
482 Some monophyletic groups are indeed clearly characterized by a higher mass (e.g. Bovini,
483 Hippotragini, Fig. 1). This is consistent with the fact that mass and size are often very strong
484 factors influencing the shape of long bones and are thus expected to have a strong impact in
485 morphometric studies (Hildebrand, 1982; Biewener, 1989; Polly, 2008; Klingenberg, 2016). In
486 heavy species, we observe several likely adaptations such as an increase in the robustness of
487 the bones, with a relatively wider shaft, which can help the bones resist to the heavy weight of
488 their species by distributing the forces on a larger surface (Biewener, 1989; Currey, 2002). All
489 bones show proportionally larger epiphyses in heavy species, allowing to sustain larger articular
490 facets that permit a better dissipation of the more important forces, spreading them on a larger
491 area again. Generally, a relative increase in the size of the muscle insertion area is observed,
492 since proportionally stronger muscles are expected for animals of a greater weight (Alexander
493 et al., 1981), although this is not uniform for all muscles. All bones, except the tibia, are slightly
494 curved in light species, but straighter in heavy species, as already observed in quadrupedal
495 mammals in general (Bertram and Biewener, 1992). This could help the bones resist to bending
496 stresses, by diminishing bending moments (Biewener, 1983).

497 **Forelimb**

498 More specifically, a strong enlargement is observed for the insertion areas of the extensor
499 muscles of all three segments. Those are the most essential muscles to maintain the limb in an
500 erect posture and thus the body in a standing position, and to propel the body forward (Barone,

501 2010). In the shoulder, the supraspinatus inserts on the summits of the lesser and greater
502 tuberosities, which are both proportionally much larger in heavy species (Fig. 2C). The
503 convexity of the greater tuberosity, where the infraspinatus attaches, is also extremely enlarged.
504 This muscle is not an extensor but has an important role for the stabilization of the shoulder,
505 which is most likely very important for heavy species, especially considering that large bovids
506 are said to carry most of their weight with their forelimbs (Scott, 1985).

507 For the forearm, the main extensor is the triceps. Accordingly, the olecranon as a whole,
508 where it inserts, is wider in heavier species especially in an antero-posterior direction, which is
509 the direction of the forces exerted by the muscle (Fig. 3D). The origins of the triceps on the
510 humerus are not particularly enlarged in heavy species, but the strongest head of the triceps
511 originates on the scapula (Barone, 2010), so a stronger area of origin might be observed there.
512 The olecranon is also longer when compared to the total length of the ulna, meaning that its
513 efficiency as a lever arm must be increased in heavy species. Its more posterior orientation in
514 heavy species would permit a more open angle when the elbow is in extension. This would
515 increase the maximal stride length.

516 The extensors of the carpus and the digits also show a relatively enlarged insertion area on
517 the humerus – the epicondylar crest – in heavy bovids (Fig. 2C). Again, this is most likely useful
518 to accommodate a higher weight, which would tend to put the articulation in flexion, leading to
519 the collapse of the animal if the weight were not counterbalanced by all the extensors.

520 Most flexors do not show such increase in robustness of their insertion areas. The main
521 flexors of the arm are the teres major, the infraspinatus and the deltoideus (Barone, 2010). As
522 mentioned above, the infraspinatus has a proportionally very enlarged insertion area on the
523 humerus, but this is most likely due to its stabilization role more than its rather limited role as
524 a flexor. The tuberosity of the teres major does not show any particular enlargement in heavy
525 species (Fig. 2C). The lateral eminence of the radius, which serves as the insertion area of the
526 biceps brachii, is not particularly more robust in heavier species. Contrary to the others, the
527 flexors of the manus do show an increase in robustness of their areas of origin, particularly the
528 medial epicondyle of the humerus (Fig. 2B), which is likely due to their different role. They act
529 on the manus when it is on the ground, and thus must propel the body forward, whereas the
530 flexors of the arm and forearm have no direct role in body propulsion (Barone, 2010).

531 As for the abductors of the limb, the enlargement of the insertion area of the infraspinatus
532 could mean that large bovids need a strong abduction capacity in their forelimbs as well. The

533 deltoid tuberosity is proportionally enlarged in heavy species (Fig. 2C), but much less than the
534 tubercles, where the extensors insert. For the adductors, the insertion of the subscapularis on
535 the convexity of the lesser tubercle is very robust in heavy species, but no particular increase in
536 robustness is observed for the insertion of the teres major or the coracobrachialis. Stronger
537 adductors and abductors could help stabilize the limb during locomotion, especially against
538 medio-lateral movements. This could be important for heavy bovids, but not as important as
539 limb extension, which seems to be reflected in the lesser increase in robustness observed in the
540 insertion areas.

541 Hindlimb

542 In the proximal hindlimb, the proportionally greatly enlarged greater trochanter observed in
543 heavy species likely supports a very strong gluteus medius, which is the main muscle for
544 keeping the hip in extension and is extremely important in propelling the whole body forward
545 (Fig. 4C; Barone, 2010). The lesser trochanter does not show a particularly great enlargement
546 in heavy species. It is mainly the insertion area of the iliacus and psoas magnus, which are
547 flexors of the thigh; again, this seems to indicate that the flexors of heavy species do not need
548 an increase of their strength as great as the extensors do. Several muscles performing various
549 actions insert along the diaphysis of the femur, mainly the three vasti (lateralis, intermedius,
550 medialis; extension), the adductores (adduction) and the pectineus (adduction, flexion and
551 rotation). However, no change in shape is observed besides the increase of robustness of the
552 diaphysis, even though the vasti are the main extensors of the knee and are expected to be very
553 strong. Their very large insertion area most likely helps spread their important force along a
554 greater surface, and thus the vasti may not necessitate an insertion as strong as other extensors.

555 More distally on the limb, another important muscle for the propulsion of the body is the
556 gluteobiceps, inserting on the tibial crest, which is much enlarged in heavy species, as is the
557 rest of the proximal epiphysis of the tibia (Fig. 5C). The antero-proximal tibia is also the main
558 insertion area of the patellar ligaments, which transmit the force generated on the patella by a
559 very powerful extensor of the knee, the quadriceps femoris (Barone, 2010). The semitendinosus
560 and semimembranosus are also involved, although less strongly, in propulsion of the body. It
561 is difficult to say if this leads to an increase of robustness of their insertion areas in heavy
562 species, as they insert respectively on the diaphysis and the medial epicondyle, which are
563 enlarged anyway to allow for better dissipation of the forces inside the bone and at the
564 articulations.

565 The insertion area of the gastrocnemius and the flexor superficialis (which is a flexor of the
566 digits but an extensor of the pes; Barone, 2010), in the posterior and distal part of the femoral
567 diaphysis, does show slightly stronger reliefs in heavy species, and the diaphysis is clearly
568 enlarged in its distal part (Fig 4D). This could help sustain a stronger pull from those muscle
569 that are essential to maintaining the limb upright, but could also be linked to the general
570 enlargement of the tibiofemoral joint. An increase in robustness is observed in the lateral
571 epicondyle of the femur, below which the extensor digitorum communis and the extensor
572 digitorum medialis insert in the fossa extensoria. This could be due to an increase in strength
573 from those muscles, which are flexors of the pes but extensor of the phalanges. It could also be
574 a consequence of a probable increase in size of the lateral collateral ligament, which inserts
575 precisely where the bump observed on the lateral epicondyle is located. Both these hypotheses
576 are consistent with the overall need for a stronger articulation, firmly bound by ligaments and
577 kept open by strong muscles when standing and moving.

578 Differences in allometric trends

579 Several differences in allometric trends were highlighted in our sample. One was observed
580 on both stylopod bones, where for a given mass the Caprini and Tragelaphini tribes seem to
581 have more gracile bones than the other tribes (Figs. 2A, 4A). Our sample of Tragelaphini
582 consists of only three species, so that this trend remains to be confirmed, but our Caprini sample
583 is the most extensive one (Table 1). These two tribes have little in common (Fig. 1); they are
584 not particularly close phylogenetically, and do not share the same habitat, most Caprini living
585 in a mountain habitat. This could imply that species living in a mountain habitat necessitate less
586 robust bones (see *Adaptations to habitat*), or that the Caprini have naturally more gracile bones
587 because of historic or structural constraints.

588 The radius-ulna of the Bovini displays an interesting allometric pattern, as it is more robust
589 than expected if it followed the same allometric trend as that of the other tribes (Fig. 3A). To a
590 lesser extent, this is also true for their tibia, as well as those of our heaviest Caprini and
591 Tragelaphini (*Ovibos moschatus* and *Taurotragus oryx*, Fig. 5A). It is possible that in tribes or
592 clades characterized by an important increase of mass (i.e. above approximately 300 kg,
593 Biewener, 1989), a shift in allometric trend of the zeugopodium convergently occurred at some
594 point in their evolutionary history, enabling them to reach greater masses. Small and medium-
595 sized mammals run with a more upright posture to increase the mechanical advantage of their
596 musculoskeletal systems, and thus diminish the need for stronger muscles as mass increases

597 (Biewener, 1989; Bertram and Biewener, 1992). Massive bovids of the Bovini tribe may have
598 reached a point where they cannot run with more upright limbs, meaning this shift in allometric
599 trend was necessary for body mass to increase further. This phenomenon has already been
600 described in previous studies on mammals in general (Economos, 1983; Bertram and Biewener,
601 1990; Christiansen, 1999a, 1999b), and Bertram and Biewener (1992) do note that the radius
602 and the tibia scale with particularly strong negative allometry for species above 200 kg in mean
603 mass. Such potential shift in allometric trend is indeed not visible on the humerus nor on the
604 femur of our sample. One possibility, as suggested by Scott (1985) is that the proximal segments
605 of the limb are more constrained by the large amount of musculature inserting on them, and
606 could be limited in their potential adaptive changes as compared to more distal segments.
607 Specifically for the radius-ulna, it might have more importance in direct weight-bearing, due to
608 being generally vertical when the animal is standing, aligned with the ground reaction force
609 (Bertram and Biewener, 1992; see e.g. Fig. 9 in Castelló, 2016). All the other bones are more
610 or less tilted, and thus support will be carried more by the muscles that will keep the joints in
611 extension.

612 Adaptations to habitat

613 Habitat has a significant impact on the shape of the bones except the tibia, even when taking
614 the phylogenetic history into account. Shape variations are however more subtle than those
615 linked to body mass. A gradation is observed between the different habitats, especially on the
616 stylopod bones, along a gradient from open habitat to mountain habitat. This suggest that habitat
617 would be better represented as a continuum, with on one end open habitats, where running as
618 fast as possible is the main predator-avoidance strategy and where there is little need for
619 manoeuvrability, and on the other end closed or mountain habitats, where manoeuvrability is
620 essential in order not to trip and fall over when running (Jarman, 1974; Kappelman, 1988).

621 Specifically, for the forelimb, in open habitat species we note adaptations for more stable
622 articulations, able to sustain a greater force passing through linked to the high frequency of
623 galloping in these species. This is especially observable on the humerus whose head and
624 trochlea are wider in all directions (Fig. 6). On the medial epicondyle of the humerus, a larger
625 insertion area for the flexors of the digits is observed in open habitat species. Presumably
626 stronger flexors allow a greater propulsion that may be necessary for species galloping
627 frequently, but not for mountain-adapted species since they do not need to gallop as often. The
628 very posterior orientation of the olecranon observed in open habitat species allows a more

629 important extension of the forearm, and thus an increase in stride length during galloping, which
630 in turn leads to increased speed.

631 As for the hindlimb, the larger epiphyses in open habitat species can again be explained by
632 a need for a greater force to pass through. The larger greater trochanter can, as for species with
633 an important mass, permit a greater force to come from the gluteus medius and thus a more
634 powerful propulsion of the body (Fig. 8; Barone, 2010). The cylindrical shape of the femoral
635 head restricts movement in a parasagittal plane and stabilizes the hip joint (Kappelman, 1988;
636 Kappelman et al., 1997). Forest species present a very round femoral head, improving the
637 freedom of movement of their hip (i.e. abduction, adduction and rotation), which is necessary
638 to move in a complex system of bushes and roots. Mountain species present an even rounder
639 femoral head than forest species, illustrating the very large range of motion needed to navigate
640 in mountain habitats. Our femur sample of mountain species contains only two species that are
641 not part of the Caprini tribe (*D. megalotis* and *O. oreotragus*) but that present the same set of
642 presumed adaptations to a mountain habitat as Caprini species, indicating that they are not
643 specific to the Caprini. The asymmetry of the femoral trochlea observed in open habitat species
644 could help stabilize the stifle joint during locomotion, by preventing the medial dislocation of
645 the patella (Janis et al., 2012). Interestingly, this asymmetry is also present in forest and heavy
646 cover species, being only totally absent in mountain species. The antero-posterior extension of
647 the trochlea observed in those same species could increase the moment arm of the stifle joint,
648 and thus allow the leg to perform its propulsion role more efficiently. The femur overall presents
649 many characteristics that can link its morphology to the habitat occupied by the species, which
650 confirms that it is an excellent bone in order to reconstruct paleoenvironments in bovids.

651 Domesticated species generally present traits similar to those of heavier species. It is the
652 only habitat category in our sample that could have a significantly higher mean mass than
653 another category (mountain habitat, Fig. S6; Table S6). They might therefore be indeed slightly
654 heavier on average, which would explain their bone morphology. Alternatively, domesticated
655 species could have sustained a selective pressure for an increased amount of meat, i.e. larger
656 muscles. It is possible that this increase in muscle volume resulted in a need for stronger bones.

657 Concomitant influences of mass and habitat

658 Species living in open habitats and species having a high body mass present some
659 similarities in the morphology of their limb long bones. Most notably, they share larger
660 epiphyses, larger tuberosities and a larger medial epicondyle on the humerus, an enlarged

661 greater trochanter and an asymmetric trochlea on the femur. Considering open habitat species
662 do not have a significantly higher mass than the others species in our sample (Fig. S6; Table
663 S6), this could be due to the higher forces involved when needing to attain a greater speed or
664 move a greater mass. As a consequence, these similar anatomical features convergently result
665 from different selective pressures, which might make it difficult to decipher the paleobiology
666 of extinct species.

667 **Conclusion**

668 We provided here the first 3D geometric morphometric study focusing on the long bones of
669 bovids. Our results confirm that mass and to a lesser extent habitat strongly influence the shape
670 of stylopod and zeugopod bones, even when taking into account the phylogeny. Bones of
671 heavier species tend to be more robust, capable of resisting to the higher forces generated by
672 their own weight and their muscles' contractions. The insertion areas of the muscles that have
673 to either support the weight of the body or propel it forward (i.e. the extensors of all the limb
674 segments, and the flexors of the manus and of the digits of the hindlimb) show a greater increase
675 in proportional size than those of muscles mostly acting on the limb during the swing phase. A
676 continuum of shape is observed from open habitats to mountain habitats, going through light
677 cover, heavy cover and forest habitats. Open habitat species present clear adaptations for
678 increased cursoriality, more robust articulations and stronger insertion areas for the muscles
679 that propel the limb. Mountain and forest species present adaptations for manoeuvrability,
680 useful for navigating in a forest or on a cliff. The degree of complexity of the substrate of a
681 particular habitat (e.g. the flat substrate of a grassland vs. the steep terrain of a mountain or the
682 network of roots and bushes of a forest), and the different predator-avoidance strategies it
683 implies, seems to be a very important environmental metric influencing the shape of long bones
684 in bovids. Overall, it seems that bovids present a much conserved long bone morphology across
685 their entire family, with relatively little variation in shape, which makes it easy to identify
686 variations linked to mass or habitat. Our study helped clarify with precision how long bone
687 shape can adapt to an increase in mass or a change of habitat in ungulates. It opens new
688 perspectives of research, for instance on how to describe more precisely shifts in allometric
689 trends and associated shape variations, or on microanatomical studies to correlate internal
690 architecture with the morphology of muscle insertion areas.

691 **Acknowledgements**

692 We wish to warmly thank the curators of the collections where we digitized specimens: **J.**
693 **Lesur, C. Bens, & A. Verguin** (*Muséum National d'Histoire Naturelle*, Paris, France) and **S.**
694 **Bock** (*Museum für Naturkunde*, Berlin, Germany). We acknowledge the very helpful comments
695 of two anonymous reviewers that allowed us to improve the quality of our manuscript. This
696 work acknowledges financial support from **ERC-2016-STG GRAVIBONE** allocated to A.
697 Houssaye.

698 **Author Contribution**

699 C. Etienne designed the experiments, participated in data analyses and interpretation, wrote the
700 manuscript, and approved the final draft. A. Filippo digitized all the specimens, reviewed the
701 manuscript, and approved the final draft. R. Cornette designed the experiments, participated in
702 data analyses and interpretation, reviewed the manuscript, and approved the final draft. A.
703 Houssaye designed the experiments, participated in data analyses and interpretation, reviewed
704 the manuscript, and approved the final draft.

705 **References**

- 706 Adams, D., Rohlf, F.J., Slice, D., 2013. A Field Comes of Age: Geometric Morphometrics in
707 the 21st Century. *Hystrix* 24, 7–14. <https://doi.org/10.4404/hystrix-24.1-6283>
- 708 Adams, D.C., 2014a. A Generalized K Statistic for Estimating Phylogenetic Signal from
709 Shape and Other High-Dimensional Multivariate Data. *Syst Biol* 63, 685–697.
710 <https://doi.org/10.1093/sysbio/syu030>
- 711 Adams, D.C., 2014b. A Method for Assessing Phylogenetic Least Squares Models for Shape
712 and Other High-Dimensional Multivariate Data. *Evolution* 68, 2675–2688.
713 <https://doi.org/10.1111/evo.12463>
- 714 Adams, D.C., Collyer, M., Kaliontzopoulou, A., Sherratt, E., 2018. Geomorph : Geometric
715 morphometric analyses for 2D/3D data.
- 716 Agisoft LLC, 2017. Agisoft PhotoScan Professional.
- 717 Alexander, R.M., Jayes, A.S., Maloiy, G.M.O., Wathuta, E.M., 1981. Allometry of the leg
718 muscles of mammals. *Journal of Zoology* 194, 539–552.
719 <https://doi.org/10.1111/j.1469-7998.1981.tb04600.x>
- 720 Artec 3D, 2018. Artec Studio Professional.
- 721 Barone, R., 2010. Anatomie comparée des mammifères domestiques. Tome 2 : arthrologie et
722 myologie, 4ème édition. ed. Vigot Frères, Paris.
- 723 Barone, R., 1999. Anatomie comparée des mammifères domestiques. Tome 1: ostéologie,
724 5ème édition. ed. Vigot Frères, Paris.
- 725 Barr, W.A., 2014. Functional morphology of the bovid astragalus in relation to habitat:
726 controlling phylogenetic signal in ecomorphology. *J. Morphol.* 275, 1201–1216.
727 <https://doi.org/10.1002/jmor.20279>
- 728 Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: A Practical and
729 Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society: Series*
730 *B (Methodological)* 57, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>

- 731 Bertram, J.E.A., Biewener, A., 1990. Differential scaling of the long bones in the terrestrial
732 carnivora and other mammals. *Journal of Morphology* 204, 157–169.
733 <https://doi.org/10.1002/jmor.1052040205>
- 734 Bertram, J.E.A., Biewener, A.A., 1992. Allometry and curvature in the long bones of
735 quadrupedal mammals. *Journal of Zoology* 226, 455–467.
736 <https://doi.org/10.1111/j.1469-7998.1992.tb07492.x>
- 737 Bibi, F., 2013. A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla,
738 Ruminantia) and the importance of the fossil record to systematics. *BMC Evolutionary*
739 *Biology* 13, 166. <https://doi.org/10.1186/1471-2148-13-166>
- 740 Biewener, A., 1989. Mammalian Terrestrial Locomotion and Size. *BioScience* 39, 776–783.
741 <https://doi.org/10.2307/1311183>
- 742 Biewener, A., Patek, S., 2018. *Animal Locomotion*, 2nd edition. ed. Oxford University Press,
743 New York.
- 744 Biewener, A.A., 2005. Biomechanical consequences of scaling. *Journal of Experimental*
745 *Biology* 208, 1665–1676. <https://doi.org/10.1242/jeb.01520>
- 746 Biewener, A.A., 1983. Allometry of quadrupedal locomotion: the scaling of duty factor, bone
747 curvature and limb orientation to body size. *Journal of Experimental Biology* 105,
748 147–171.
- 749 Blomberg, S.P., Garland, T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative
750 data: behavioral traits are more labile. *Evolution* 57, 717–745.
- 751 Botton-Divet, L., Cornette, R., Fabre, A.-C., Herrel, A., Houssaye, A., 2016. Morphological
752 Analysis of Long Bones in Semi-aquatic Mustelids and their Terrestrial Relatives.
753 *Integrative and Comparative Biology* 56, 1298–1309.
754 <https://doi.org/10.1093/icb/icw124>
- 755 Cabin, R.J., Mitchell, R.J., 2000. To Bonferroni or Not to Bonferroni: When and How Are the
756 Questions. *Bulletin of the Ecological Society of America* 81, 246–248.
- 757 Castelló, J.R., 2016. *Bovids of the World: Antelopes, Gazelles, Cattle, Goats, Sheep, and*
758 *Relatives*. Princeton University Press, Princeton and Oxford.
- 759 Christiansen, P., 1999a. Scaling of mammalian long bones: small and large mammals
760 compared. *Journal of Zoology* 247, 333–348. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-7998.1999.tb00996.x)
761 [7998.1999.tb00996.x](https://doi.org/10.1111/j.1469-7998.1999.tb00996.x)
- 762 Christiansen, P., 1999b. Scaling of the limb long bones to body mass in terrestrial mammals.
763 *J. Morphol.* 239, 167–190. [https://doi.org/10.1002/\(SICI\)1097-](https://doi.org/10.1002/(SICI)1097-4687(199902)239:2<167::AID-JMOR5>3.0.CO;2-8)
764 [4687\(199902\)239:2<167::AID-JMOR5>3.0.CO;2-8](https://doi.org/10.1002/(SICI)1097-4687(199902)239:2<167::AID-JMOR5>3.0.CO;2-8)
- 765 Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., Ranzuglia, G., 2008.
766 MeshLab: an Open-Source Mesh Processing Tool. *Proceedings of the 2008*
767 *Eurographics Italian Chapter Conference* 129–136.
- 768 Curran, S.C., 2018. Three-dimensional geometric morphometrics in paleoecology, in: Croft,
769 D., Su, D., Simpson, F. (Eds.), *Methods in Paleoecology: Reconstructing Cenozoic*
770 *Terrestrial Environments and Ecological Communities*, Vertebrate Paleobiology and
771 *Paleoanthropology Series*. Springer, Cham, pp. 319–337.
- 772 Curran, S.C., 2012. Expanding ecomorphological methods: geometric morphometric analysis
773 of Cervidae post-crania. *Journal of Archaeological Science* 39, 1172–1182.
774 <https://doi.org/10.1016/j.jas.2011.12.028>
- 775 Currey, J.D., 2002. *Bones: Structure and Mechanics*. Princeton University Press.
- 776 De Iuliis, G., Pulerà, D., 2011. *The Dissection of Vertebrates*, 2nd edition. ed. Academic
777 Press.
- 778 DeGusta, D., Vrba, E., 2003. A method for inferring paleohabitats from the functional
779 morphology of bovid astragali. *Journal of Archaeological Science* 30, 1009–1022.
780 [https://doi.org/10.1016/S0305-4403\(02\)00286-8](https://doi.org/10.1016/S0305-4403(02)00286-8)
- 781 Doube, M., Conroy, A.W., Christiansen, P., Hutchinson, J.R., Shefelbine, S., 2009. Three-
782 Dimensional Geometric Analysis of Felid Limb Bone Allometry. *PLOS ONE* 4, e4742.
783 <https://doi.org/10.1371/journal.pone.0004742>
- 784 Dunn, R.H., 2018. Functional Morphology of the Postcranial Skeleton, in: Croft, D., Su, D.,
785 Simpson, F. (Eds.), *Methods in Paleoecology: Reconstructing Cenozoic Terrestrial*

786 Environments and Ecological Communities, Vertebrate Paleobiology and
787 Paleoanthropology Series. Springer, Cham, pp. 23–36.

788 Economos, A.C., 1983. Elastic and/or geometric similarity in mammalian design? *Journal of*
789 *Theoretical Biology* 103, 167–172. [https://doi.org/10.1016/0022-5193\(83\)90206-0](https://doi.org/10.1016/0022-5193(83)90206-0)

790 Etienne, C., Mallet, C., Cornette, R., Houssaye, A., 2020. Influence of mass on tarsus shape
791 variation: a morphometrical investigation among Rhinocerotidae (Mammalia:
792 Perissodactyla). *Biol J Linn Soc.* <https://doi.org/10.1093/biolinnean/blaa005>

793 Fabre, A.-C., Cornette, R., Goswami, A., Peigné, S., 2015. Do constraints associated with
794 the locomotor habitat drive the evolution of forelimb shape? A case study in musteloid
795 carnivorans. *Journal of Anatomy* 226, 596–610. <https://doi.org/10.1111/joa.12315>

796 Goolsby, E.W., 2015. Phylogenetic Comparative Methods for Evaluating the Evolutionary
797 History of Function-Valued Traits. *Syst Biol* 64, 568–578.
798 <https://doi.org/10.1093/sysbio/syv012>

799 Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and
800 surfaces. *Hystrix It. J. Mamm.* 24, 103–109. <https://doi.org/10.4404/hystrix-24.1-6292>

801 Gunz, P., Mitteroecker, P., Bookstein, F.L., 2005. Semilandmarks in Three Dimensions, in:
802 Slice, D. (Ed.), *Modern Morphometrics in Physical Anthropology, Developments in*
803 *Primatology: Progress and Prospects*. Springer, Boston, pp. 73–98.
804 https://doi.org/10.1007/0-387-27614-9_3

805 Hall, B.K., 2008. *Fins into Limbs: Evolution, Development, and Transformation*. University of
806 Chicago Press, Chicago.

807 Hildebrand, M., 1982. *Analysis of Vertebrate Structure*, 2ème édition. ed. Wiley, New York.

808 Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D., 1985. *Functional Vertebrate*
809 *Morphology*. Belknap Press of Harvard University Press, Cambridge, USA.

810 Janis, C.M., Shoshitaishvili, B., Kambic, R., Figueirido, B., 2012. On their knees: distal femur
811 asymmetry in ungulates and its relationship to body size and locomotion. *Journal of*
812 *Vertebrate Paleontology* 32, 433–445. <https://doi.org/10.1080/02724634.2012.635737>

813 Jarman, P.J., 1974. The Social Organisation of Antelope in Relation to Their Ecology.
814 *Behaviour* 48, 215–267.

815 Kappelman, J., 1991. The paleoenvironment of *Kenyapithecus* at Fort Ternan. *Journal of*
816 *Human Evolution* 20, 95–129. [https://doi.org/10.1016/0047-2484\(91\)90053-X](https://doi.org/10.1016/0047-2484(91)90053-X)

817 Kappelman, J., 1988. Morphology and locomotor adaptations of the bovid femur in relation to
818 habitat. *Journal of Morphology* 198, 119–130.
819 <https://doi.org/10.1002/jmor.1051980111>

820 Kappelman, J., Plummer, T., Bishop, L., Duncan, A., Appleton, S., 1997. Bovids as indicators
821 of Plio-Pleistocene paleoenvironments in East Africa. *Journal of Human Evolution* 32,
822 229–256. <https://doi.org/10.1006/jhev.1996.0105>

823 Klingenberg, C.P., 2016. Size, shape, and form: concepts of allometry in geometric
824 morphometrics. *Dev Genes Evol* 226, 113–137. <https://doi.org/10.1007/s00427-016-0539-2>

825

826 Klingenberg, C.P., 2013. Visualizations in geometric morphometrics: how to read and how to
827 make graphs showing shape changes. *Hystrix It. J. Mamm.* 24, 15–24.
828 <https://doi.org/10.4404/hystrix-24.1-7691>

829 Lewton, K.L., Brankovic, R., Byrd, W.A., Cruz, D., Morales, J., Shin, S., 2020. The effects of
830 phylogeny, body size, and locomotor behavior on the three-dimensional shape of the
831 pelvis in extant carnivorans. *PeerJ* 8, e8574. <https://doi.org/10.7717/peerj.8574>

832 Mallet, C., Cornette, R., Billet, G., Houssaye, A., 2019. Interspecific variation in the limb long
833 bones among modern rhinoceroses—extent and drivers. *PeerJ* 7, e7647.
834 <https://doi.org/10.7717/peerj.7647>

835 Martin, M.L., Travouillon, K.J., Sherratt, E., Fleming, P.A., Warburton, N.M., 2019.
836 Covariation between forelimb muscle anatomy and bone shape in an Australian
837 scratch-digging marsupial: Comparison of morphometric methods. *Journal of*
838 *Morphology* 280, 1900–1915. <https://doi.org/10.1002/jmor.21074>

839 Mendoza, M., Palmqvist, P., 2006. Characterizing adaptive morphological patterns related to
840 habitat use and body mass in Bovidae (Mammalia: Artiodactyla). *Acta Zoologica*
841 *Sinica* 52, 971–987.

842 Mitteroecker, P., Gunz, P., 2009. Advances in Geometric Morphometrics. *Evolutionary*
843 *Biology* 36, 235–247. <https://doi.org/10.1007/s11692-009-9055-x>

844 Mungall, D.E.C., 2007. *Exotic Animal Field Guide: Nonnative Hoofed Mammals in the United*
845 *States, Illustrated Edition*. ed. Texas A&M University Press, College Station.

846 Plummer, T.W., Bishop, L.C., Hertel, F., 2008. Habitat preference of extant African bovids
847 based on astragalus morphology: operationalizing ecomorphology for
848 palaeoenvironmental reconstruction. *Journal of Archaeological Science* 35, 3016–
849 3027. <https://doi.org/10.1016/j.jas.2008.06.015>

850 Plummer, T.W., Ferraro, J.V., Louys, J., Hertel, F., Alemseged, Z., Bobe, R., Bishop, L.,
851 2015. Bovid ecomorphology and hominin paleoenvironments of the Shungura
852 Formation, lower Omo River Valley, Ethiopia. *Journal of human evolution* 88, 108–
853 126.

854 Polly, D., 2008. Limbs in Mammalian Evolution, in: Hall, B.K. (Ed.), *Fins into Limbs:*
855 *Evolution, Development, and Transformation*. University of Chicago Press, Chicago,
856 pp. 245–268.

857 Püschel, T.A., Sellers, W.I., 2016. Standing on the shoulders of apes: Analyzing the form and
858 function of the hominoid scapula using geometric morphometrics and finite element
859 analysis. *American Journal of Physical Anthropology* 159, 325–341.
860 <https://doi.org/10.1002/ajpa.22882>

861 R Development Core Team, 2005. *R: A language and environment for statistical computing*.
862 R Foundation for Statistical Computing, Vienna, Austria.

863 Rohlf, F.J., Slice, D., 1990. Extensions of the Procrustes Method for the Optimal
864 Superimposition of Landmarks. *Syst Biol* 39, 40–59. <https://doi.org/10.2307/2992207>

865 RStudio, Inc., 2018. *RStudio*. Boston, MA.

866 San Millán, M., Kaliontzopoulou, A., Rissech, C., Turbón, D., 2015. A geometric
867 morphometric analysis of acetabular shape of the primate hip joint in relation to
868 locomotor behaviour. *Journal of Human Evolution* 83, 15–27.
869 <https://doi.org/10.1016/j.jhevol.2015.03.007>

870 Schlager, S., Jefferis, G., Dryden, I., 2018. *Morpho: a toolbox providing methods for data-*
871 *acquisition, visualisation and statistical methods related to Geometric Morphometrics*
872 *and shape analysis*.

873 Schmidt-Nielsen, K., 1984. *Scaling: Why is Animal Size So Important?* Cambridge University
874 Press, Cambridge.

875 Scott, K.M., 1985. Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the*
876 *AMNH* 179.

877 Scott, R.S., Barr, W.A., 2014. Ecomorphology and phylogenetic risk: Implications for habitat
878 reconstruction using fossil bovids. *J. Hum. Evol.* 73, 47–57.
879 <https://doi.org/10.1016/j.jhevol.2014.02.023>

880 Streiner, D.L., Norman, G.R., 2011. Correction for Multiple Testing: Is There a Resolution?
881 *Chest* 140, 16–18. <https://doi.org/10.1378/chest.11-0523>

882 Walmsley, A., Elton, S., Louys, J., Bishop, L.C., Meloro, C., 2012. Humeral epiphyseal shape
883 in the felidae: The influence of phylogeny, allometry, and locomotion. *Journal of*
884 *Morphology* 273, 1424–1438. <https://doi.org/10.1002/jmor.20084>

885 Wiley, D.F., 2005. *Landmark*. Institute for Data Analysis and Visualization.

886 Wilson, D.E., Mittermeier, R.A., 2011. *Handbook of the Mammals of the World*. Lynx
887 Edicions, Barcelona.

888 Zelditch, M.L., Swiderski, D.L., Sheets, H.D., 2012. *Geometric Morphometrics for Biologists:*
889 *A Primer*. Academic Press.

890

891 **Supplementary files**

892 **Table S1.** List of all the specimens studied. “X”; bone studied. **Hum:** humerus, **Rad:** radius-
 893 ulna, **Fem:** femur, **Tib:** tibia.

Tribe	Species	Collection number	Hum	Rad	Fem	Tib
Alcelaphini	<i>Alcelaphus buselaphus</i>	MNHN-ZM-1899-238	X			
Alcelaphini	<i>Alcelaphus buselaphus</i>	MNHN-ZM-1902-1410			X	X
Alcelaphini	<i>Alcelaphus buselaphus</i>	ZMB-71862	X		X	X
Alcelaphini	<i>Connochaetes gnou</i>	MNHN-ZM-1976-344	X	X	X	X
Alcelaphini	<i>Connochaetes gnou</i>	MNHN-ZM-2013-26	X	X	X	X
Alcelaphini	<i>Damaliscus pygargus</i>	ZMB-70722	X	X	X	X
Alcelaphini	<i>Damaliscus pygargus</i>	ZMB-71265	X	X	X	X
Antilopini	<i>Antidorcas marsupialis</i>	MNHN-ZM-1993-1670	X		X	X
Antilopini	<i>Antidorcas marsupialis</i>	MNHN-ZM-1971-89			X	X
Antilopini	<i>Antilope cervicapra</i>	MNHN-ZM-1901-174	X	X	X	X
Antilopini	<i>Antilope cervicapra</i>	MNHN-ZM-1992-618	X		X	X
Antilopini	<i>Dorcatragus megalotis</i>	MNHN-ZM-1915-32			X	
Antilopini	<i>Eudorcas thomsonii</i>	MNHN-ZM-1961-41	X			X
Antilopini	<i>Eudorcas thomsonii</i>	MNHN-ZM-1962-384	X		X	X
Antilopini	<i>Gazella dorcas</i>	MNHN-ZM-1968-803	X		X	
Antilopini	<i>Gazella dorcas</i>	MNHN-ZM-1974-113	X	X	X	X
Antilopini	<i>Litocranius walleri</i>	MNHN-ZM-1946-82		X		X
Antilopini	<i>Madoqua kirkii</i>	MNHN-ZM-1917-17			X	
Antilopini	<i>Madoqua kirkii</i>	ZMB-77194	X		X	
Antilopini	<i>Nanger dama</i>	ZMB-68971	X		X	X
Antilopini	<i>Nanger dama</i>	ZMB-83430	X	X	X	X
Antilopini	<i>Ourebia ourebi</i>	MNHN-ZM-1972-93	X	X	X	X
Antilopini	<i>Ourebia ourebi</i>	ZMB-77195	X		X	X
Antilopini	<i>Raphicerus campestris</i>	MNHN-ZM-1962-4187		X		
Antilopini	<i>Saiga tatarica</i>	MNHN-ZM-1964-313	X	X	X	X
Antilopini	<i>Saiga tatarica</i>	MNHN-ZM-1959-177			X	
Boselaphini	<i>Boselaphus tragocamelus</i>	MNHN-ZM-1864-103	X	X	X	X
Boselaphini	<i>Boselaphus tragocamelus</i>	MNHN-ZM-1907-146	X	X	X	X
Boselaphini	<i>Tetracerus quadricornis</i>	MNHN-ZM-1993-4627	X		X	X
Boselaphini	<i>Tetracerus quadricornis</i>	MNHN-ZM-1988-223	X	X	X	X
Bovini	<i>Bison bison</i>	MNHN-ZM-1885-339	X	X	X	X
Bovini	<i>Bison bison</i>	MNHN-ZM-1902-316	X	X	X	X
Bovini	<i>Bos frontalis</i>	MNHN-ZM-1970-280	X	X	X	X
Bovini	<i>Bos frontalis</i>	MNHN-ZM-1965-120	X		X	X
Bovini	<i>Bos grunniens</i>	MNHN-ZM-2008-107	X	X		X
Bovini	<i>Bos grunniens</i>	MNHN-ZM-1886-300	X	X	X	X
Bovini	<i>Bos javanicus</i>	MNHN-ZM-1944-101	X	X	X	X
Bovini	<i>Bos javanicus</i>	MNHN-ZM-1967-1689	X		X	X

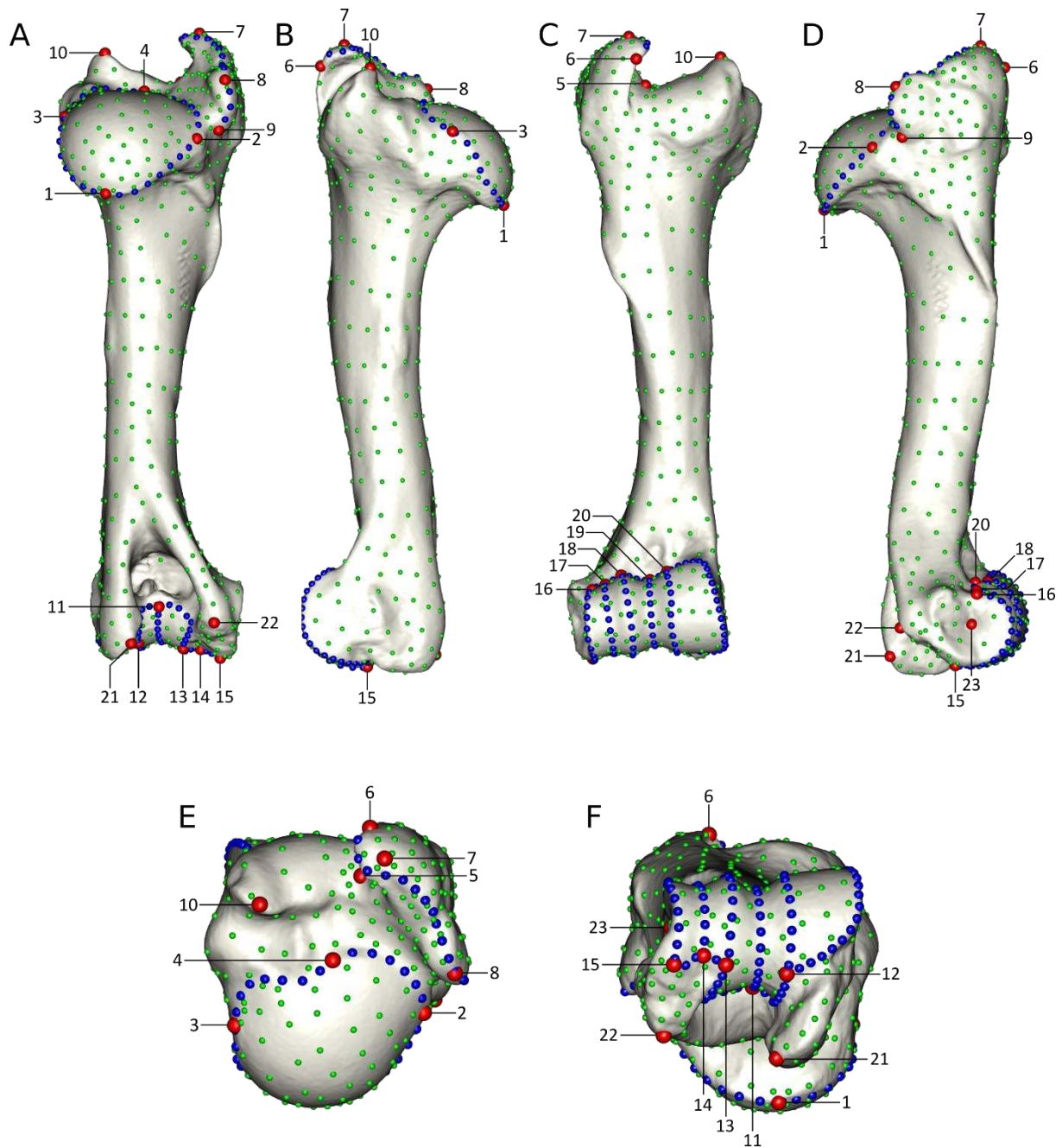
Bovini	<i>Bos taurus</i>	MNHN-ZM-A-10916	X	X	X	
Bovini	<i>Bos taurus</i>	MNHN-ZM-1926-302	X	X	X	X
Bovini	<i>Bubalus bubalis</i>	MNHN-ZM-1857-19	X	X	X	X
Bovini	<i>Bubalus bubalis</i>	MNHN-ZM-1863-65	X	X	X	X
Bovini	<i>Bubalus depressicornis</i>	MNHN-ZM-2009-421	X	X	X	X
Bovini	<i>Bubalus depressicornis</i>	MNHN-ZM-SSN	X	X	X	X
Bovini	<i>Syncerus caffer</i>	MNHN-ZM-1936-72	X	X	X	X
Caprini	<i>Ammotragus lervia</i>	MNHN-ZM-2010-643	X	X	X	X
Caprini	<i>Ammotragus lervia</i>	MNHN-ZM-1896-439	X	X	X	X
Caprini	<i>Budorcas taxicolor</i>	MNHN-ZM-2017-1199			X	
Caprini	<i>Capra hircus</i>	MNHN-ZM-2007-1349	X	X	X	X
Caprini	<i>Capra hircus</i>	MNHN-ZM-SSN	X	X	X	X
Caprini	<i>Capricornis milneedwardsii</i>	MNHN-ZM-1874-283	X	X	X	X
Caprini	<i>Hemitragus jemlahicus</i>	MNHN-ZM-1971-68	X	X	X	
Caprini	<i>Hemitragus jemlahicus</i>	MNHN-ZM-1972-133	X	X	X	X
Caprini	<i>Nemorhaedus goral</i>	MNHN-ZM-1962-153		X	X	X
Caprini	<i>Nemorhaedus goral</i>	MNHN-ZM-1963-320	X	X	X	X
Caprini	<i>Oreamnos americanus</i>	MNHN-ZM-2009-253	X	X	X	
Caprini	<i>Oreamnos americanus</i>	ZMB-67805	X	X	X	X
Caprini	<i>Ovibos moschatus</i>	MNHN-ZM-1977-43	X		X	X
Caprini	<i>Ovibos moschatus</i>	MNHN-ZM-1977-39	X		X	
Caprini	<i>Ovis aries</i>	MNHN-ZM-2000-438	X	X	X	X
Caprini	<i>Ovis aries</i>	MNHN-ZM-SSN	X	X	X	X
Caprini	<i>Pseudois nayaur</i>	MNHN-ZM-1972-92	X	X	X	X
Caprini	<i>Pseudois nayaur</i>	MNHN-ZM-1966-136	X	X	X	
Caprini	<i>Rupicapra rupicapra</i>	MNHN-ZM-1923-2326	X		X	X
Caprini	<i>Rupicapra rupicapra</i>	MNHN-ZM-1995-183	X		X	X
Cephalophini	<i>Cephalophus leucogaster</i>	MNHN-ZM-2016-2832			X	X
Cephalophini	<i>Cephalophus silvicultor</i>	MNHN-ZM-1981-1023	X	X	X	X
Cephalophini	<i>Sylvicapra grimmia</i>	MNHN-ZM-1947-871			X	
Hippotragini	<i>Addax nasomaculatus</i>	MNHN-ZM-1970-277	X	X	X	X
Hippotragini	<i>Hippotragus equinus</i>	MNHN-ZM-1995-147	X	X	X	X
Hippotragini	<i>Hippotragus equinus</i>	MNHN-ZM-1969-167	X	X	X	X
Hippotragini	<i>Hippotragus niger</i>	ZMB-SSN		X	X	X
Hippotragini	<i>Oryx dammah</i>	MNHN-ZM-1905-227	X	X	X	X
Hippotragini	<i>Oryx dammah</i>	MNHN-ZM-1972-106	X	X	X	X
Hippotragini	<i>Oryx gazella</i>	MNHN-ZM-1994-009	X	X	X	X
Hippotragini	<i>Oryx gazella</i>	MNHN-ZM-1997-009	X		X	X
Hippotragini	<i>Oryx leucoryx</i>	MNHN-ZM-1996-2101	X	X	X	X
Hippotragini	<i>Oryx leucoryx</i>	MNHN-ZM-1996-2100	X	X	X	X
Oreotragini	<i>Oreotragus oreotragus</i>	MNHN-ZM-2007-1388	X		X	X
Oreotragini	<i>Oreotragus oreotragus</i>	MNHN-ZM-SSN	X		X	X
Reduncini	<i>Kobus ellipsiprymnus</i>	MNHN-ZM-1974-112	X	X	X	
Reduncini	<i>Kobus ellipsiprymnus</i>	MNHN-ZM-1935-637	X	X	X	X
Reduncini	<i>Redunca redunca</i>	MNHN-ZM-1881-1147	X	X	X	X

894

Reduncini	<i>Redunca redunca</i>	MNHN-ZM-1923-2173	X		X	
Tragelaphini	<i>Taurotragus oryx</i>	MNHN-ZM-2013-1095			X	X
Tragelaphini	<i>Taurotragus oryx</i>	MNHN-ZM-AGA-7983	X			
Tragelaphini	<i>Tragelaphus spekii</i>	MNHN-ZM-1980-7	X	X	X	X
Tragelaphini	<i>Tragelaphus spekii</i>	MNHN-ZM-1983-126		X	X	X
Tragelaphini	<i>Tragelaphus strepsiceros</i>	ZMB-SSN	X	X	X	X

895 **Table S2.** Description of the landmarks and curves placed on the humerus.

Type	N°	Description
Landmark	1	Most distal point of the border of the humeral head.
	2	Most lateral point of the border of the humeral head.
	3	Most medial point of the border of the humeral head.
	4	Most anterior point of the border of the humeral head. If the anterior part of the head is divided by a groove, most anterior point of the lateral part.
	5	Maximum of concavity of the intertubercular groove.
	6	Anterior extremity of the summit of the greater tuberosity.
	7	Most proximal point of the greater tuberosity.
	8	Point of maximum of convexity of the greater tuberosity convexity.
	9	Most distal point of the greater tuberosity convexity.
	10	Most proximal point of the lesser tuberosity.
	11	Postero-distal extremity of the groove of the trochlea
	12	Most distal contact point between the groove and the medial ridge of the trochlea.
	13	Most distal contact point between the trochlea and the capitulum.
	14	Distal extremity of the groove of the capitulum.
	15	Distal extremity of the lateral border of the capitulum.
	16	Proximal extremity of the lateral border of the capitulum.
	17	Proximal extremity of the groove of the capitulum.
	18	Most proximal contact point between the trochlea and the capitulum.
	19	Proximal extremity of the groove of the trochlea.
	20	Most proximal contact point between the groove and the medial ridge of the trochlea.
	21	Summit of the medial epicondyle.
	22	Summit of the lateral epicondyle.
	23	Deepest point of the fossa of the musculus extensor digitorum lateralis
Curve	1	From point 2 to point 2. Border of the humeral head, beginning in the anterior direction.
	2	9 to 6. Crest of the greater tuberosity.
	3	11 to 20. Medial ridge of the trochlea.
	4	11 to 18. Lateral ridge of the trochlea.
	5	11 to 19. Groove of the trochlea.
	6	12 to 18. Medial and proximal border of the trochlea.
	7	18 to 13. Proximal, lateral and distal border of the capitulum.
	8	14 to 17. Groove of the capitulum.



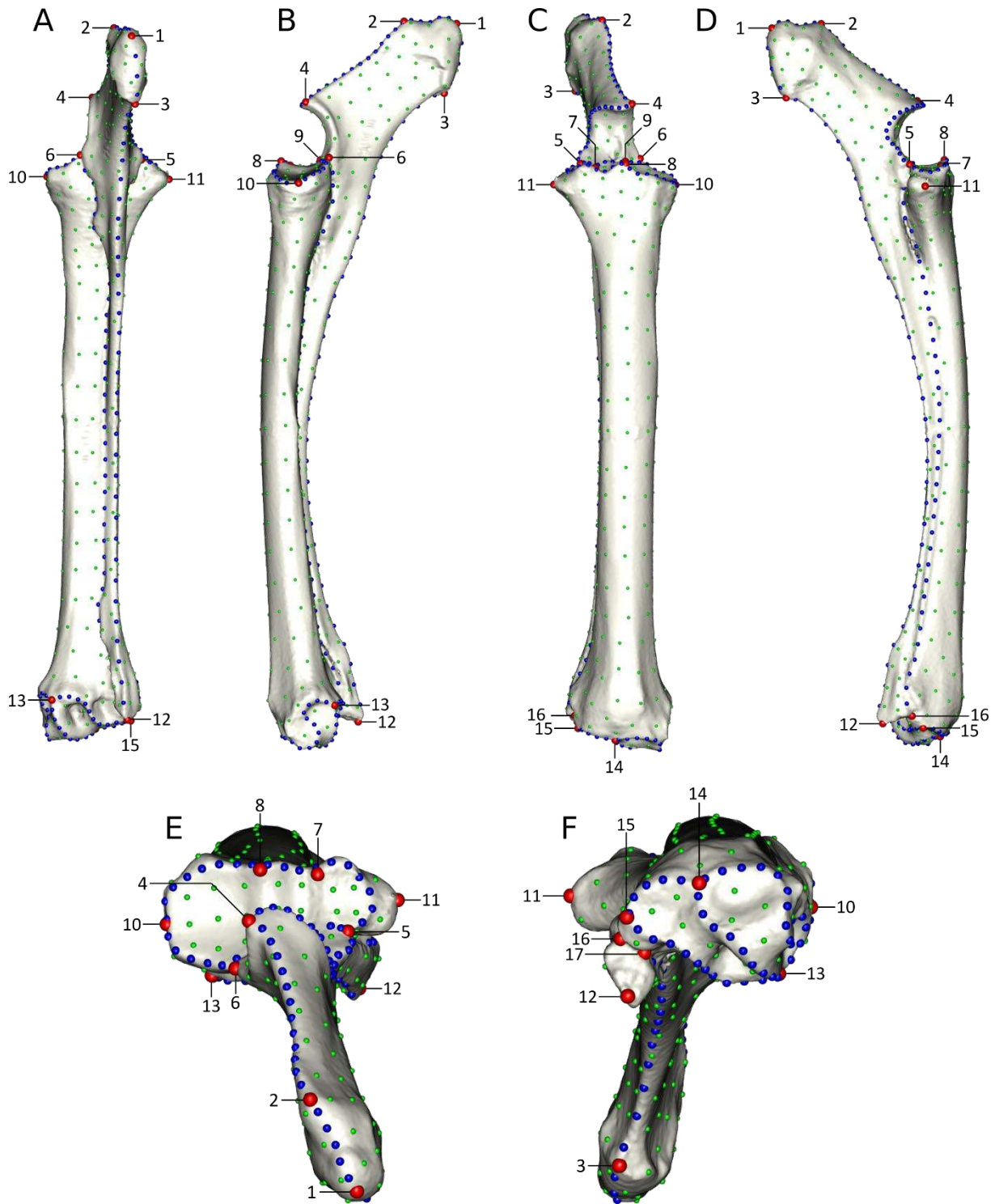
896

897 **Figure S1.** Depiction of the anatomical landmarks (red), curve semi-landmarks (blue) and
 898 surface semi-landmarks (green) placed on the humerus. Posterior (A), medial (B), anterior (C),
 899 lateral (D), proximal (E) and distal (F) views.

900 **Table S3.** Description of the landmarks and curves placed on the radius-ulna.

Type	N°	Description
Landmark	1	Most postero-proximal point of the olecranal tuber.
	2	Most antero-proximal point of the olecranal tuber.
	3	Most postero-distal point of the olecranal tuber.
	4	Anterior extremity of the anconeal process.

	5	Most proximal contact point between the ulna and the radius, on the lateral side.
	6	Most proximal contact point between the ulna and the radius, on the medial side.
	7	Most anterior contact point between the articular facet for the capitulum and the trochlea.
	8	Most anterior point of the trochlear ridge.
	9	Most posterior point of the trochlear ridge.
	10	Most medial point of the border of the trochlea.
	11	Most lateral point of the lateral eminence.
	12	Most distal point of the styloid process of the ulna.
	13	Most posterior point of the contact between the articular facet for the scaphoid and the articular facet for the lunate.
	14	Most anterior point of the contact between the articular facet for the scaphoid and the articular facet for the lunate.
	15	Most lateral point of the articular facet with the lunate.
	16	Most distal contact point between the ulna and the radius, on the lateral side.
	17	Most distal contact point between the ulna and the radius, on the medial side.
Curve	1	From point 4 to point 1. From the anconeal process to the top of the olecranon.
	2	1 to 12. From the top of the olecranon to the top of the styloid process.
	3	4 to 5. From the anconeal process to the articular facet for the capitulum.
	4	5 to 5. Border of the articular facet for the capitulum and the trochlea.
	5	5 to 16. Lateral contact line between ulna and radius.
	6	6 to 17. Medial contact line between ulna and radius.
	7	13 to 13. Border of the articular facet for the scaphoid, beginning in the medial direction.
	8	13 to 14. Border of the articular facet for the lunate (except the part in contact with the facet for the scaphoid).



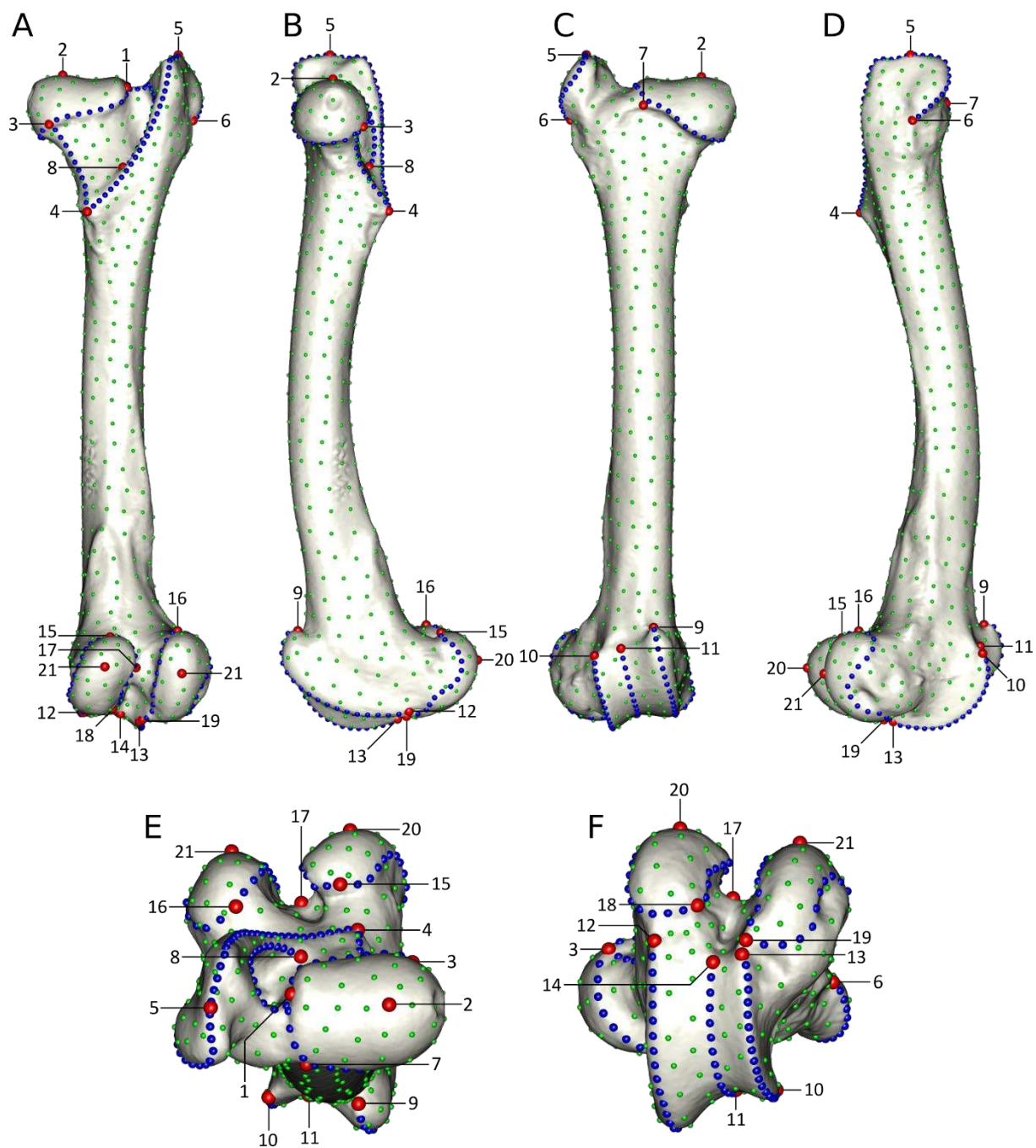
902

903 **Figure S2.** Depiction of the anatomical landmarks (red), curve semi-landmarks (blue) and
 904 surface semi-landmarks (green) placed on the radius-ulna. Posterior (A), medial (B), anterior
 905 (C), lateral (D), proximal (E) and distal (F) views.

906 **Table S4.** Description of the landmarks and curves placed on the femur.

Type	N°	Description
------	----	-------------

Landmark	1	Most proximal contact point between the head of the femur and the border of the trochanteric fossa.
	2	Most proximal point of the head of the femur.
	3	Contact point between the head of the femur and the crest connecting the lesser trochanter and the head of the femur.
	4	Most posterior point of the lesser trochanter.
	5	Most proximal point of the greater trochanter.
	6	Most distal point of the crest of the greater trochanter.
	7	Most anterior contact point between the border of the femoral head and the neck of the femur.
	8	Most distal point of the border of the trochanteric fossa.
	9	Proximal extremity of the medial ridge of the trochlea.
	10	Proximal extremity of the lateral ridge of the trochlea.
	11	Proximal extremity of the groove of the trochlea.
	12	Posterior extremity of the medial ridge of the trochlea.
	13	Posterior extremity of the lateral ridge of the trochlea.
	14	Posterior extremity of the groove of the trochlea.
	15	Most proximal point of the border of the medial condyle.
	16	Most proximal point of the border of the lateral condyle.
	17	Most posterior point of the centre of the intercondylar fossa.
	18	Most antero-lateral point of the border of the medial condyle.
	19	Most antero-medial point of the border of the lateral condyle.
	20	Most posterior point of the medial condyle.
	21	Most posterior point of the lateral condyle.
Curve	1	From point 1 to point 1. Border of the femoral head, starting in the posterior direction.
	2	1 to 8. Lateral border of the trochanteric fossa.
	3	3 to 4. Crest connecting the head of the femur to the lesser trochanter.
	4	4 to 6. Intertrochanteric crest, and crest of the greater trochanter.
	5	9 to 12. Medial ridge of the trochlea.
	6	10 to 13. Lateral ridge of the trochlea.
	7	11 to 14. Groove of the trochlea.
	8	18 to 18. Border of the medial condyle, starting in the medial direction.
	9	19 to 19. Border of the lateral condyle, starting in the medial direction.



908

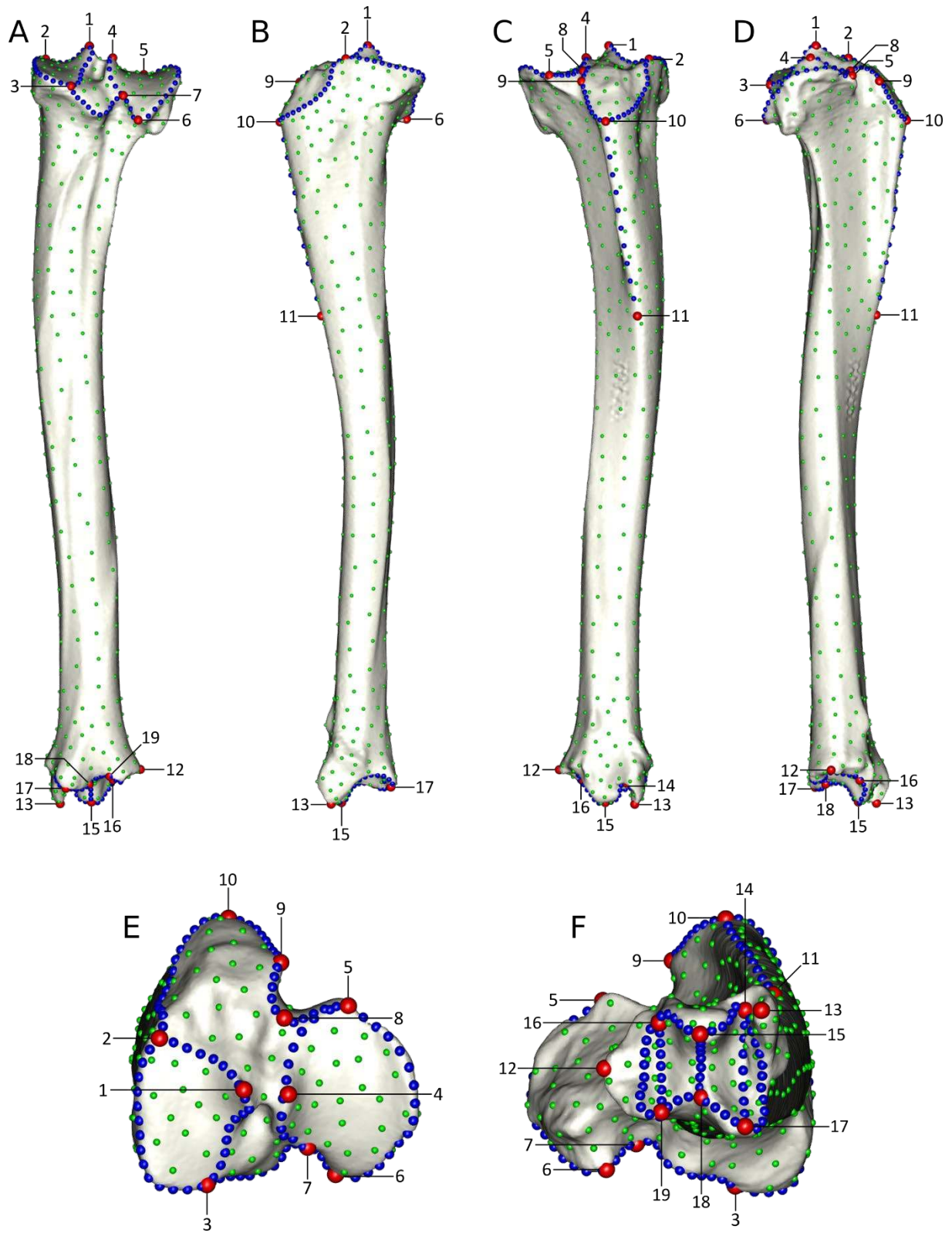
909 **Figure S3.** Depiction of the anatomical landmarks (red), curve semi-landmarks (blue) and
 910 surface semi-landmarks (green) placed on the femur. Posterior (A), medial (B), anterior (C),
 911 lateral (D), proximal (E) and distal (F) views.

912

913 **Table S5.** Description of the landmarks and curves placed on the tibia.

Type	N°	Description
Landmark	1	Most proximal point of the medial condyle.
	2	Most anterior point of the medial condyle.

	3	Posterior contact point between the medial condyle and the contour of the proximal epiphysis.
	4	Most proximal point of the lateral condyle.
	5	Most anterior point of the lateral condyle.
	6	Most distal point of the lateral condyle.
	7	Posterior contact point between the lateral condyle and the contour of the proximal epiphysis.
	8	Maximum of concavity of the proximal contour of the extensor groove.
	9	Most lateral point of the border of the tibial tuberosity.
	10	Most anterior contact point between the tibial tuberosity and the tibial crest.
	11	Most distal point of the tibial crest.
	12	Most lateral point of the distal epiphysis.
	13	Most distal point of the medial malleolus.
	14	Anterior extremity of the medial groove of the trochlea.
	15	Anterior extremity of the central ridge of the trochlea.
	16	Anterior extremity of the lateral groove of the trochlea.
	17	Posterior extremity of the medial groove of the trochlea.
	18	Posterior extremity of the central ridge of the trochlea.
	19	Posterior extremity of the lateral groove of the trochlea.
Curve	1	From point 2 to point 2. Border of the medial condyle, starting in the medial direction.
	2	5 to 5. Border of the lateral condyle, starting in the medial direction.
	3	3 to 7. Posterior part of the border on the proximal epiphysis.
	4	11 to 10. Tibial crest.
	5	10 to 5. Lateral border of the tibial tuberosity, and proximal border of the extensor groove.
	6	10 to 2. Medial border of the tibial tuberosity and contour of the proximal epiphysis, up to the medial condyle.
	7	15 to 15. Border of the trochlea for the astragalus, starting in the lateral direction.
	8	14 to 17. Lateral groove of the trochlea.
	9	15 to 18. Central ridge of the trochlea.
	10	16 to 19. Medial groove of the trochlea.

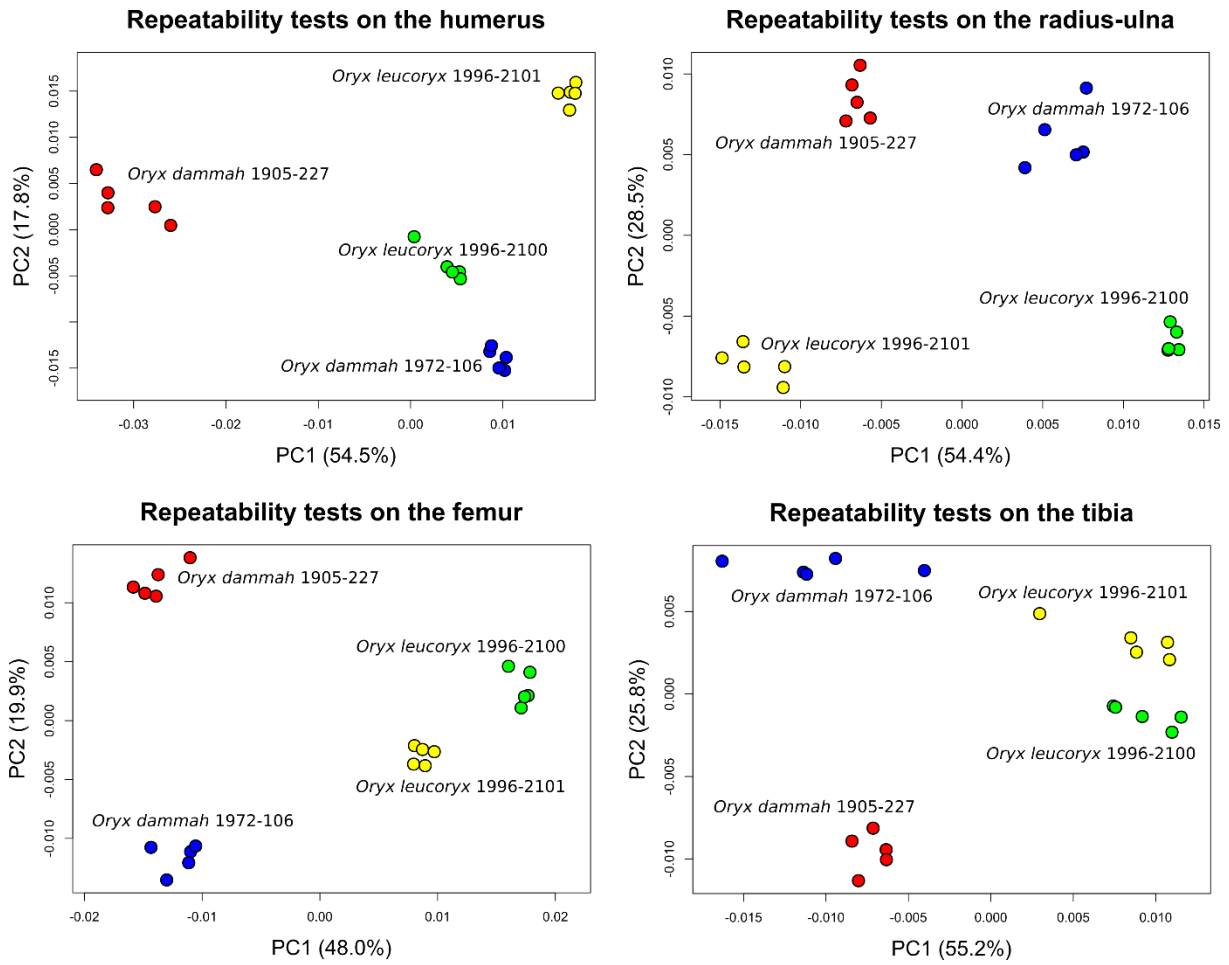


915

916 **Figure S4.** Depiction of the anatomical landmarks (red), curve semi-landmarks (blue) and
 917 surface semi-landmarks (green) placed on the tibia. Posterior (A), medial (B), anterior (C),
 918 lateral (D), proximal (E) and distal (F) views.

919

920 **Figure S5.** Results of the repeatability tests.



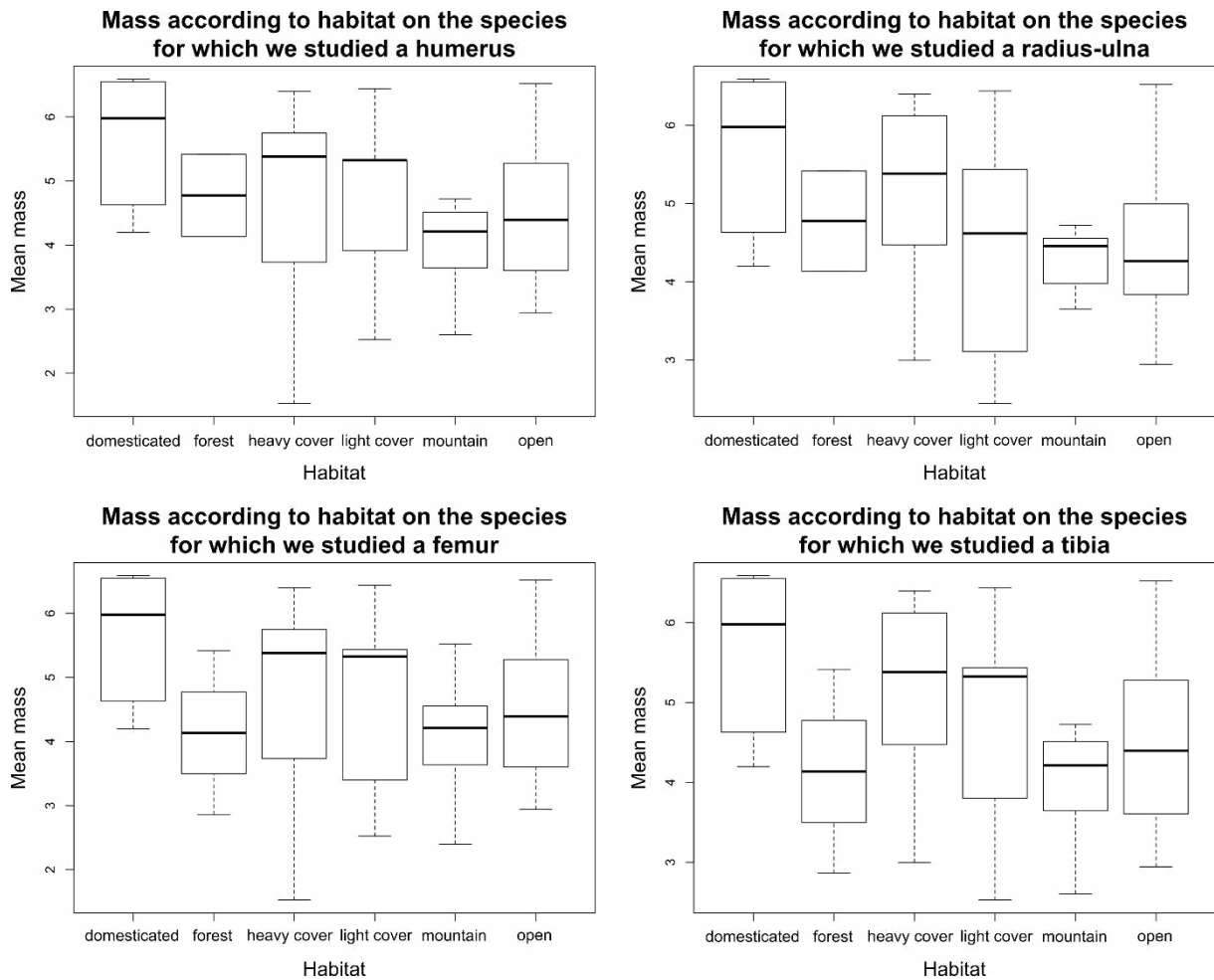
921

922 **Table S6.** Result of Student's t-tests showing which habitat categories have different mean masses. Two
 923 values are reported: one without a Benjamini-Hochberg correction for multiple pair-wise tests (A), one
 924 with the correction (B). The species sampled vary slightly for each bone (cf. Table S1), therefore the
 925 test has been done for each bone. The natural logarithm of the mass has been used. P-values below 0.05
 926 are shown in bold, p-values between 0.05 and 0.10 in italics.

A – Without Benjamini-Hochberg correction											
Humerus						Radius-Ulna					
	L	H	F	M	D		L	H	F	M	D
O	0.827	0.921	0.776	0.172	0.109	O	0.918	0.291	0.715	0.646	<i>0.093</i>
L	X	0.924	0.943	0.377	0.325	L	X	0.339	0.685	0.864	0.129
H	X	X	0.868	0.424	0.268	H	X	X	0.704	0.174	0.530
F	X	X	X	0.427	0.408	F	X	X	X	0.593	0.408
M	X	X	X	X	0.029	M	X	X	X	X	<i>0.059</i>
Femur						Tibia					
	L	H	F	M	D		L	H	F	M	D
O	0.963	0.921	0.653	0.207	0.109	O	0.810	0.338	0.653	0.172	0.109
L	X	0.960	0.665	0.393	0.201	L	X	0.549	0.577	0.266	0.231
H	X	X	0.653	0.427	0.268	H	X	X	0.332	0.086	0.530
F	X	X	X	0.873	0.181	F	X	X	X	0.880	0.181

M	X	X	X	X	0.029	M	X	X	X	X	0.029
B – With Benjamini-Hochberg correction											
Humerus						Radius-Ulna					
	L	H	F	M	D		L	H	F	M	D
O	0.943	0.943	0.943	0.712	0.712	O	0.918	0.825	0.825	0.825	0.644
L	X	0.943	0.943	0.712	0.712	L	X	0.825	0.825	0.918	0.644
H	X	X	0.943	0.712	0.712	H	X	X	0.825	0.652	0.825
F	X	X	X	0.712	0.712	F	X	X	X	0.825	0.825
M	X	X	X	X	0.436	M	X	X	X	X	0.644
Femur						Tibia					
	L	H	F	M	D		L	H	F	M	D
O	0.963	0.963	0.906	0.620	0.620	O	0.867	0.563	0.753	0.543	0.543
L	X	0.963	0.906	0.801	0.620	L	X	0.721	0.721	0.563	0.563
H	X	X	0.906	0.801	0.670	H	X	X	0.563	0.543	0.721
F	X	X	X	0.963	0.620	F	X	X	X	0.880	0.543
M	X	X	X	X	0.432	M	X	X	X	X	0.436

927



928

929 **Figure S6.** Boxplot representing the distribution of the logarithm of species' mean mass (in kg) in each
930 habitat category. The species sampled vary slightly for each bone (Table S1), therefore the graph is
931 shown for each bone.