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1 **A first glimpse at the influence of body mass in the morphological integration**
2 **of the limb long bones: an investigation in modern rhinoceroses**

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15

16 **Abstract**

17 The appendicular skeleton of tetrapods is a particularly integrated structure due to the shared
18 developmental origin or similar functional constraints exerted on its elements. Among these
19 constraints, body mass is considered as strongly influencing its integration but its effect on shape
20 covariation has rarely been addressed in mammals, especially in heavy taxa. Here we propose to
21 explore the covariation patterns of the long bones in heavy animals and their link to body mass. We
22 investigate the five modern rhinoceros species, which display an important range of body weight. We
23 used a 3D geometric morphometric approach to describe the shape covariation of the six bones
24 composing the stylopodium and zeugopodium both among and within species. Our results indicate
25 that the appendicular skeleton of modern rhinos is a strongly integrated structure. At the
26 interspecific level, the shape covariation is roughly similar between all pairs of bones and mainly
27 concerns the muscular insertions related to powerful flexion and extension movements. The forelimb
28 integration appears higher and more related to body mass than that of the hind limb, suggesting a
29 specialization for weight support. The integration of the stylopodium elements does not seem to
30 relate to body mass in our sample, which suggests a higher effect of shared developmental factors.
31 Conversely, the covariation of the zeugopodium bones seems more associated with body mass,
32 particularly for the radius-ulna pair. The fibula appears poorly integrated with other bones, especially
33 within non-*Rhinoceros* species, which may represent a case of parcellation due to a functional
34 dissociation between the hind limb bones. The exploration of the integration patterns at the
35 intraspecific level also highlights a more prominent effect of age over individual body mass on shape
36 covariation within *C. simum*. This study lends support to previous hypotheses indicating a link
37 between high body mass and high integration level, highlighting that one single constraint – body
38 mass – can lead to different covariation patterns even between closely-related taxa.

39 **Keywords**

40 Rhinocerotidae; geometric morphometrics; functional morphology; appendicular skeleton;
41 locomotion; morphological integration; body mass

42 **Introduction**

43 The morphology of the different anatomical parts constituting organisms are known to be influenced
44 by interactions between these parts due to shared developmental origin, phylogenetic legacy,
45 functional constraints or structural requirements (Olson & Miller 1958; Van Valen 1965; Cheverud
46 1982; Gould 2002; Hallgrímsson et al. 2002; Cubo 2004; Goswami & Polly 2010; Goswami et al. 2014).
47 The tendency of morphological traits to covary under the influence of these factors is known as
48 morphological integration (Olson & Miller 1958; Van Valen 1965). These factors can indeed increase
49 morphological integration of the whole body or parts of it, but they can also act locally to produce
50 stronger covariation within parts than with other units (e.g. modules – Hallgrímsson et al. 2002;
51 Young & Hallgrímsson 2005; Klingenberg 2008; Goswami et al. 2014). Morphological integration is
52 therefore classically explored through the study of covariation between sets of linear measurements
53 or shape data (Van Valen 1965; Klingenberg 2008; Goswami & Polly 2010; Bookstein 2015).

54 Among tetrapods, the appendicular skeleton is a particularly integrated structure due to the common
55 developmental origin of its parts (serial homology – Young & Hallgrímsson 2005; Bininda-Emonds et
56 al. 2007; Sears et al. 2015) and shared functional constraints linked to locomotion and ecology
57 (Hallgrímsson et al. 2002; Young & Hallgrímsson 2005; Goswami et al. 2014; Martín-Serra et al. 2015;
58 Botton-Divet et al. 2018). In this framework, it has been hypothesized that the functional
59 specialization of the appendicular skeleton is associated with a decrease of the integration level
60 between limbs and serially homologous elements, and an increase of the within-limb integration
61 (Hallgrímsson et al. 2002; Young & Hallgrímsson 2005). This has been particularly observed for some
62 extreme locomotor adaptations like flight in bats or bipedal locomotion in hominoids, which led to a
63 strong specialization of a specific part of the appendicular skeleton and consequently to a decrease
64 of the general integration (Young & Hallgrímsson 2005; Young et al. 2010; Bell et al. 2011). Moreover,
65 among quadrupedal mammals, the loss of the clavicle allows a greater mobility of the scapula,
66 playing an active role in locomotion (Gasc 2001; Schmidt & Fischer 2009). This led to a shift in the
67 functional relations between limb parts, where the serially homologous elements are not functionally
68 analogous anymore (Gasc 2001; Schmidt & Fischer 2009) (Figure 1). At the interspecific level (e.g.
69 evolutionary integration – Klingenberg 2014), it has been shown that many terrestrial taxa (equids,
70 carnivorans, marsupials) present a strong general integration among all their limb long bones
71 (Bennett & Goswami 2011; Kelly & Sears 2011; Fabre et al. 2014; Martín-Serra et al. 2015; Hanot et
72 al. 2017, 2018, 2019; Botton-Divet et al. 2018; Martín-Serra & Benson 2019), with a covariation
73 mainly linked to the locomotion and shared phylogenetic history. But few studies explored the
74 patterns of morphological integration of the appendicular skeleton among mammals at the
75 intraspecific level (e.g. static or developmental integration – Klingenberg 2014) and tempted to

76 compare them with the patterns observed at the interspecific level (Young et al. 2010; Hanot et al.
77 2017, 2018, 2019).

78 The support of a heavy mass is likely an important factor influencing the shape and integration of the
79 appendicular skeleton. Among mammals, many lineages displayed an increase of their body mass
80 along their evolutionary history (Depéret 1907; Raia et al. 2012; Baker et al. 2015; Bokma et al.
81 2016). Biomechanical studies indicate that the shape of the limb bones should be driven by stress
82 linked to mass support during the stance and the displacement of the animal (Hildebrand 1974;
83 Biewener 1983, 1989a,b). However, few studies have explored the precise role exerted by body mass
84 on the shape variation of the limb bones (Biewener 1983; Bertram & Biewener 1992; Fabre et al.
85 2013; Mallet et al. 2019). Likewise, the influence of body mass on integration patterns among limb
86 bones is poorly known. Previous studies on relatively light taxa indicated a limited effect of body
87 mass on integration patterns, overcome by other factors such as locomotor ecology (Martín-Serra et
88 al. 2015; Botton-Divet et al. 2018; Martín-Serra & Benson 2019). At the opposite, other works
89 proposed that body mass may still have an impact on the shape covariation of the limb long bones
90 (Hanot et al. 2017; Randau & Goswami 2018), possibly more pronounced for heavier species
91 (Schmidt & Fischer 2009). Drawing on this, we chose to explore the integration patterns among
92 modern rhinoceroses, constituting the second heaviest terrestrial group after elephants among
93 modern mammals (Alexander & Pond 1992). Whereas body size and mass poorly vary among the
94 three species of elephants, the five modern species of rhinos surviving nowadays display a wide
95 range of body mass (BM): *Dicerorhinus sumatrensis* (Fischer, 1814) – mean BM: 775 kg; *Diceros*
96 *bicornis* (Linnaeus, 1758) – mean BM: 1,050 kg; *Rhinoceros sondaicus* Desmarest, 1822 – mean BM:
97 1,350 kg; *Rhinoceros unicornis* Linnaeus, 1758 – mean BM: 2,000 kg; and *Ceratotherium simum*
98 (Burchell, 1817) – mean BM: 2,300 kg (Dinerstein 2011). This range of body mass can be highly
99 variable within each species due to sexual dimorphism or between wild and captive specimens: 600 –
100 950 kg for *Ds. sumatrensis*; 800 – 1,300 kg for *Dc. bicornis*; 1,200 – 1,500 kg for *R. sondaicus*; 1,270 –
101 2,800 kg for *R. unicornis*; 1,350 – 3,500 kg for *C. simum* (Zschokke & Baur 2002; Dinerstein 2011).
102 *Ceratotherium simum* and *Dc. bicornis* are present in Africa while the three other species only live in
103 Asia. While a few studies have explored the shape variation of their long bones in relation to the
104 ecology, phylogeny and functional constraints, such as body mass (Guérin 1980; Eisenmann & Guérin
105 1984; Mallet et al. 2019), no work has focused on the integration of their appendicular skeleton and
106 its relationship to these factors. The aim of this study is thus to explore shape covariation patterns
107 among limb long bones within and between species in order to highlight potential influence of body
108 mass.

109 Here we propose to investigate the integration patterns of the shape of the limb long bones among
110 the five species of modern rhinos, to quantify the integration level within and between limbs and to
111 explore whether body mass could influence covariation patterns. In order to describe precisely the
112 shape covariations by taking into consideration the whole shape of the bones in three dimensions,
113 our analyses were done using 3D geometric morphometrics. They were performed at both
114 interspecific and intraspecific levels, taking phylogenetic relationships into account where necessary.
115 Although phylogeny is still debated among rhinos, notably regarding the position of *Ds. sumatrensis*,
116 the monophyly of the African rhinos (*Ceratotherium* and *Diceros*) and the one of *Rhinoceros* species
117 are considered as consensual (Antoine 2002; Willerslev et al. 2009; Gaudry 2017; Cappellini et al.
118 2019). In accordance with previous works, we hypothesize that the shape of limb long bones among
119 rhinos should be: 1) strongly integrated as in other quadrupedal mammals at both interspecific and
120 intraspecific levels (Hanot et al. 2017); 2) relatively homogenous between fore- and hind limbs as in
121 other quadrupedal mammals (Martín-Serra et al. 2015; Hanot et al. 2017); 3) more strongly
122 integrated than in lighter mammal species (Schmidt & Fischer 2009); 4) showing similar patterns of
123 shape covariation at both interspecific and intraspecific levels (Klingenberg 2014). This will allow us
124 to emphasize how body mass could influence the structure of the limb long bones among rhinos.

125 **Material and Methods**

126 **Studied sample**

127 The dataset was composed of 50 complete skeletons housed in different European and American
128 museums and belonging to the five extant rhino species: *Ceratotherium simum* (15 specimens),
129 *Dicerorhinus sumatrensis* (9 specimens), *Diceros bicornis* (10 specimens), *Rhinoceros sondaicus* (7
130 specimens) and *Rhinoceros unicornis* (9 specimens) (Table 1). We considered individuals with fully
131 fused epiphyses (adults) or individuals where the line of the epiphyseal plates was still visible on
132 some bones (subadults). Bones with breakages or unnatural deformations were not selected. The
133 sample involved males, females and specimens without sex information, as well as captive and wild
134 specimens. All anatomical terms follow classic anatomical and veterinary works (Guérin 1980;
135 Federative Committee on Anatomical Terminology 1998; Antoine 2002; Barone 2010) and are given
136 in Supplementary Figure S1.

137 **3D models**

138 Most of the bones were digitized using a structured-light three-dimensional scanner (Artec Eva) and
139 reconstructed with Artec Studio Professional software (v12.1.1.12—Artec 3D, 2018). Twelve bones
140 were digitized with a photogrammetric approach, following Mallison & Wings (2014) and Fau,
141 Cornette & Houssaye (2016). Sets of photos were used to reconstruct 3D models using Agisoft
142 Photoscan software (v1.4.2—Agisoft, 2018). Each mesh was decimated to reach 250,000 vertices and
143 500,000 faces using MeshLab software (v2016.12—Cignoni et al., 2008). Only left bones were
144 selected for digitization; when left sides were not available, right bones were selected instead and
145 mirrored before analysis.

146 **3D geometric morphometrics**

147 The shape covariation was analysed using a 3D geometric morphometrics approach. This widely-used
148 methodology allows to quantify the morphological differences between objects by comparing the
149 spatial coordinates of points called landmarks (Adams et al. 2004; Zelditch et al. 2012). This method
150 can also be easily extended to the study of shape covariation (Goswami & Polly 2010; Bardua et al.
151 2019). Bone shape was quantified by placing a set of anatomical landmarks and curve and surface
152 sliding semi-landmarks on the meshes, following Gunz & Mitteroecker (2013), Botton-Divet et al.
153 (2016) and Mallet et al. (2019). We placed all landmarks and curves using the IDAV Landmark
154 software (v3.0—Wiley et al., 2005). We created a template to place surface semi-landmarks for each
155 bone. We used the same number and position for anatomical landmarks and curve sliding semi-
156 landmarks than in the protocol described in Mallet et al. (2019) but the number of surface sliding

157 semi-landmarks was reduced for all the bones – except the fibula – to improve the computation
158 duration (see Supplementary Information Data S2). The specimen *C. simum* RMCA 1985.32-M-0001
159 was arbitrarily chosen to be the initial specimen on which all anatomical landmarks, curve and
160 surface sliding semi-landmarks were placed. This specimen was then used as a template for the
161 projection of surface sliding semi-landmarks on the surface of all other specimens. Projection was
162 followed by a relaxation step to ensure that projected points matched the actual surface of the
163 meshes. Curve and surface sliding semi-landmarks were then slid to minimize the bending energy of
164 a thin plate spline (TPS) between each specimen and the template at first, and then four times
165 between the result of the previous step and the Procrustes consensus of the complete dataset.
166 Therefore, all landmarks can be treated at the end as geometrically homologous (Gunz, Mitteroecker
167 & Bookstein, 2005). After the sliding step, we performed a Generalized Procrustes Analysis (GPA) to
168 remove the effect of size, location and orientation of the different landmark conformations (Gower
169 1975; Rohlf & Slice 1990). Projection, relaxation, sliding processes and GPA were conducted using the
170 “Morpho” package (v2.7) in the R environment (v3.5.1—R Core Team, 2014). Details of the process
171 are provided in the documentation of the package (Schlager 2017).

172 **Study of morphological integration**

173 We explored fifteen covariation patterns among all the possible pairs of bones (Gasc 2001; Schmidt
174 & Fischer 2009): within-limbs adjacent bones (humerus-radius, humerus-ulna, radius-ulna, femur-
175 tibia, femur-fibula and tibia-fibula), serially homologous bones (humerus-femur, radius-tibia, radius-
176 fibula, ulna-tibia and ulna-fibula) and functionally analogous bones (humerus-tibia, humerus-fibula)
177 (Figure 1). If the serial homology for the stylopodial bones seems obvious, no clear consensus exists
178 for the serial homology within the zeugopodium elements. Many studies consider the radius and the
179 tibia, and the ulna and the fibula, as serially homologous respectively (Bininda-Emonds et al. 2007;
180 Schmidt & Fischer 2009; Martín-Serra et al. 2015; Hanot et al. 2017; Botton-Divet et al. 2018),
181 unfortunately without strong developmental or genetic evidences. Recent studies tend to indicate
182 that the apparently obvious homology between fore- and hind limb segments might be much more
183 spurious than previously thought (Diogo & Molnar 2014; Sears et al. 2015). In this context, we
184 therefore tested the four possible bone combinations in the zeugopodium. As the appendicular
185 skeleton is known to be highly integrated among quadrupedal mammals (Schmidt & Fischer 2009;
186 Martín-Serra et al. 2015; Hanot et al. 2017; Botton-Divet et al. 2018), we also tested the
187 combinations involving non-homologous or analogous bones (radius-femur and ulna-femur) (Figure
188 1). Covariation patterns were investigated using Two-Blocks Partial Least Squares (2BPLS) analyses.
189 The 2BPLS method extracts the principal axes of covariation from a covariance matrix computed on

190 two shape datasets (Rohlf & Corti 2000; Botton-Divet et al. 2018; Hanot et al. 2018), allowing to
191 visualise the specimen repartition relatively to these axes and the shape changes associated.

192 Each PLS axis is characterized notably by its explained percentage of the overall covariation, its PLS
193 correlation coefficient (r_{PLS}) and its p-value, computed as a singular warp analysis as detailed in
194 Bookstein et al. (2003). The p-value was considered as significant when the observed r_{PLS} was higher
195 than the ones obtained from randomly permuted blocks (1000 permutations). When the p-value was
196 below 0.05, the PLS was considered as significant, i.e. the two considered blocks as significantly
197 integrated. We used the function “pls2b” in the “Morpho” package to compute the 2BPLS (Schlager
198 2017). To visualise these shape changes along the PLS axes, we used the function “plsCoVar” in the
199 “Morpho” package to compute theoretical shapes at two standard deviations on each side of each
200 axis (see Schlager, 2017). These theoretical conformations were then used to calculate a TPS
201 deformation of the template mesh and therefore visualise the shape changes along the PLS axes. We
202 then used the function “meshDist” in the “Morpho” package to create colour maps indicating the
203 location and the intensity of the covariation between two meshes by mapping the distance between
204 the minimum and maximum theoretical shapes along the first PLS axis (i.e. areas in red are the ones
205 showing the most of shape changes within a bone pair whereas the areas in blue are the ones
206 showing the less of shape change).

207 This procedure was performed at an interspecific level including all the 50 specimens into a single
208 GPA. We also explored the intraspecific level of covariation by performing the sliding and GPA
209 procedures on subsamples containing each different species. We then obtained five specific datasets
210 on which were performed 2BPLS analyses.

211 **Effect of the allometry**

212 It has been previously demonstrated that centroid size may be a good approximation of the body
213 mass of the specimen (Ercoli & Prevosti 2011; Cassini et al. 2012), notably among modern rhinos
214 (Mallet et al. 2019). To assess the effect of body mass on integration patterns – i.e. the effect of
215 evolutionary allometry – we computed a multivariate regression of the shape against the centroid
216 size using the function “procD.lm” in the “geomorph” package (v3.1.2—Adams & Otárola-Castillo,
217 2013). Then the residuals were used to compute allometry-free shapes, which were analysed with
218 2BPLS as described previously. Each species may have its own allometric slope, making it difficult to
219 remove the general allometry effect (Klingenberg 2016). However, considering previous results on
220 rhino long bones indicating close allometric slopes for the different species (Mallet et al. 2019) and
221 the reduced sample size inherent to studying this endangered group, we chose to provide allometry-
222 free shapes considering a single allometric component among all species (evolutionary allometry).

223 **Statistical corrections for multiple comparisons**

224 As explained above, we performed multiple pairwise comparisons when computing the different PLS.
225 Each analysis tested a different pair of bones and contained part of the data present in some other
226 analyses (e.g., landmarks of the humerus are tested for covariation with those of the radius, but also
227 in all other pairs involving the humerus). For each tested pair, the hypothesis was that of a significant
228 covariation between the shapes of the two bones. Given these settings and the exploratory approach
229 of the study, there is no common agreement in the literature regarding whether or not statistical
230 corrections for multiple comparisons should be used in the present case in order to lower the risk of
231 finding false positives (i.e. finding a significant result due to chance) (Cabin & Mitchell 2000; Streiner
232 & Norman 2011). In this context, we chose to present and discuss both uncorrected and corrected
233 analyses for multiple comparisons, especially for the analyses at the intraspecific level where the
234 correction had a higher impact (see Results). We applied a Benjamini-Hochberg correction to our
235 data (Benjamini & Hochberg 1995) as described by Randau & Goswami (2018) in a similar context of
236 covariation tests on 3D geometric morphometric data. The test was run in R using the function
237 “p.adjust” in the “stats” package. This correction was applied to all our tests at the interspecific and
238 intraspecific levels.

239

240 Results

241 Covariation at the interspecific level

242 All the first PLS axes are highly significant (p -values < 0.01 after correction – see Figures 2 and 3).
243 These first axes gather between 53% (tibia-fibula) and 90% (humerus-femur) of the total covariation.
244 Similarly, the rPLS values are high and vary between 0.72 (tibia-fibula) and 0.94 (humerus-ulna),
245 indicating a strong general integration of the limb bones (Figure 4A). Intra-limb bones covary slightly
246 more strongly in the forelimb than in the hind limb (Figure 4A). Surprisingly, the humerus and the
247 ulna covary slightly more together (rPLS = 0.94) than the radius-ulna pair (rPLS = 0.93). In the hind
248 limb, despite a high degree of covariation between the femur and the tibia (rPLS = 0.89), these two
249 bones are poorly integrated with the fibula. When looking at serially homologous bones, the
250 integration appears stronger between the humerus and the femur (rPLS = 0.93) and the ulna and the
251 tibia (rPLS = 0.92) than between the radius and the tibia (rPLS = 0.88) and the ulna and the fibula
252 (rPLS = 0.82). The radius-fibula covariation is the weakest (rPLS = 0.76) of all serially homologous
253 bones. Regarding the functionally analogous bones, the covariation between the humerus and the
254 hind limb zeugopodial bones is strong and more marked with the tibia (rPLS = 0.92) than with the
255 fibula (rPLS = 0.84). Finally, the non-homologous or functionally analogous bones reveal also a
256 stronger covariation between the ulna and the femur (rPLS = 0.90) than between the radius and the
257 femur (rPLS = 0.84). In summary, all categories of pairwise comparisons (intra-limb, serial homology,
258 functional analogy, non-homologous or analogous bones) showed high but unequal degrees of
259 covariation. The fibula particularly stands out as having relatively weak degrees of covariations with
260 other bones, being the only one not showing at least one very high covariation with another bone.

261 All plots of the first PLS axes are structured by an opposition between *Ds. sumatrensis* in the negative
262 side and *C. simum* in the positive side (Figures 2 and 3), except for the tibia-fibula pair. *Diceros*
263 *bicornis*, *R. sondaicus* and *R. unicornis* generally plot between these two extremes. All PLS plots
264 involving the humerus display a clear isolation of these three taxa around null values and poorly
265 dispersed clusters (Figure 2A-E). The clusters along the first PLS axis appear structured by a
266 distinction between Asiatic and African taxa (less marked for the humerus-radius [Figure 2A] and the
267 humerus-ulna [Figure 2E] couples) which can reflect an effect of the phylogeny (if considering African
268 and Asiatic groups as sister taxa). This separation between African and Asiatic taxa follows the
269 distribution of body mass within those groups, the lightest species showing the most negative values
270 and the heaviest ones the most positive ones within both geographic groups. For all the bone pairs
271 not involving the humerus, specimens within each species are more widely distributed in the
272 morphospace and are organized differently along the first PLS axis. The radius-ulna first axis clearly

273 expresses a sorting of the species from the lightest (*Ds. sumatrensis*) on the negative side to the
274 heaviest (*C. simum*) on the positive side (Figure 2F) independently of the phylogenetic affinities
275 between species. Although less clear, this structure also occurs for the radius-femur, radius-fibula,
276 ulna-femur, ulna-fibula and femur-tibia pairs (Figure 2G and Figure 3B, C, E, F). *Dicerorhinus*
277 *sumatrensis* is strongly isolated on the negative side on all pairs involving the femur (Figure 2C, G and
278 Figure 3C, F, G). A third pattern isolating *Ds. sumatrensis* and *Dc. bicornis* on the negative part from
279 the three other species on the positive part can be observed for the radius-tibia and ulna-tibia pairs
280 (Figure 3A, D). The only first PLS axis showing a clearly different pattern is that of the tibia-fibula pair,
281 where *R. sondaicus* is the most extreme species on the positive part and *C. simum* and *R. unicornis*
282 clusters overlap (Figure 3H).

283 The second PLS axes are significant in most of the cases, except for the humerus-radius and humerus-
284 femur pairs (p -values > 0.05 – see Supporting Information Figures S3). These second axes explain
285 between 4% (humerus-femur) and 31% (ulna-tibia) of the global covariation. Most of the PLS plots
286 indicate a separation between the genus *Rhinoceros* and the three other rhino species, with an
287 important overlapping of the clusters in many cases (see Supporting Information Figure S3). This
288 distinction is however absent for most of the plots involving the fibula, where the genus *Rhinoceros*
289 may overlap the *D.* or *D.* clusters. No clear intraspecific pattern linked to age or sex has been found
290 along these second PLS axes.

291 Colour maps computed using the theoretical shapes (available in the Supplementary Figure S4)
292 indicate that covariation associated to the first PLS axes are very similar for each bone regardless of
293 the considered pair. Eight pairs representing the four types of relation existing between bones are
294 presented in Figure 5 and 6. All other pairs are available in Supplementary Figure S5. The shape
295 changes are mainly related to an increase of the bone robustness from negative to positive values of
296 the axes, associated to a development of most of the muscular insertions (tubercles and trochanters)
297 and of articular surfaces. For the humerus, most of the shape covariation with the other bones is
298 located on muscular insertion areas, such as the lesser tubercle, the deltoid tuberosity, the lesser
299 tubercle convexity and the epicondylar crest, where insert respectively the *m. supraspinatus*, the *m.*
300 *deltoideus*, the *m. subscapularis* and the *m. extensor carpi radialis* (Figure 5A and 5D). The intensity
301 of the covariation of the deltoid tuberosity is higher with the radius than with all other bones. For the
302 radius, the strongest shape covariation with the other bones is located on the lateral insertion relief
303 where inserts the *m. extensor digitorum communis*, on the medial part of the distal epiphysis and, to
304 a lesser extent, on the radial tuberosity where inserts the *m. biceps brachii* (Figure 5B and 6A). On
305 the medial part of the distal epiphysis, the shape covariation is less intense in the humerus-radius
306 and radius-fibula couples than in the other bone pairs. For the ulna, the shape covariation with the

307 other bones is mainly located on the medial and lateral tuberosities of the olecranon (where insert
308 respectively the medial and lateral heads of the *m. triceps brachii*) and along the lateral and palmar
309 edges of the shaft, where insert most of the digit extensors (Figure 5C, 6A and 6D). The shape
310 covariation is slightly more pronounced on the olecranon tuberosity in the radius-ulna pair than in
311 the other pairs. The femur is the bone showing the most similar patterns of shape covariation
312 regardless of the bone pair. The strongest shape covariation with all other bones is located on the
313 third tubercle and corresponds to the insertion of the *m. gluteus superficialis*. Other strong shape
314 covariations between the femur and the other bones are located on the greater trochanter convexity
315 where inserts the *m. gluteus accessorius*, and from the *fovea capitis* to the lesser tubercle where
316 insert both the *mm. psoas major* and *iliacus* as well as the joint capsule of the hip (Figure 5A, 6B and
317 6D). Unlike the femur, the patterns of shape covariation for the tibia are highly variable depending of
318 the considered bone pair. For the radius-tibia and the ulna-tibia pairs, the strongest shape
319 covariation is mainly located on the tibial tuberosity (where insert notably the medial, intermediate
320 and lateral patellar ligaments, the patellar fascia and the *fascia lata*), the tibial crest, the area located
321 distally to the medial condyle of the tibia where inserts the *m. popliteus*, and on the cranial and
322 caudal sides of the distal part of the shaft (Figure 5B). The shape covariation is located in the same
323 areas but with less intensity for the femur-tibia and tibia-fibula pairs (Figure 6B and 6C). The intensity
324 of the shape covariation is minimal for the humerus-tibia pair, except for the insertion of the *m.*
325 *popliteus* (Figure 5D). Finally, for the fibula, the shape covariation with the other bones is mainly
326 located on the cranial part of the head of the fibula, on the distal part of the cranial crest and on the
327 caudal crest along the shaft, where insert notably the digit extensors (Figure 5C and 6C).

328

329 **Allometry-free covariation**

330 All the first PLS axes computed on allometry-free shapes are highly significant (p-values after
331 correction < 0.01 – see Figures 7 and 8). The first PLS axes explain between 44% (ulna-fibula) and 87%
332 (humerus-femur) of the total covariation. The rPLS values remain high and range between 0.70
333 (humerus-radius) and 0.91 (humerus-femur). The rPLS values are unequally impacted by the
334 correction for allometry depending on the considered bone pair. A drop of 12 – 16% of the rPLS
335 values can be observed between raw and allometry-free shapes for some couples: two intra-limbs
336 pairs (humerus-radius, humerus-ulna) and two non-homologous or functionally analogous bones
337 (radius-femur and ulna-femur) (Figure 4B). The drop of the rPLS values is less marked for other pairs
338 and almost inexistent in the humerus-femur, humerus-fibula and ulna-fibula couples. Moreover, the

339 rPLS value is strictly the same for the radius-fibula pair. We also noticed a slight rise of the rPLS value
340 for the femur-fibula and tibia-fibula pairs by 6% and 1% respectively.

341 However, the distribution of the different species and specimens along the first PLS axes is different
342 from the previous analyses (Figures 2 and 3) when computed on allometry-free shapes (Figures 7 and
343 8). All plots involving the humerus are structured in the same way with a strong separation between
344 the three Asiatic species on the negative side and the two African species on the positive side (Figure
345 7A-E). A relatively similar structure is observed for the ulna-femur plot (Figure 8C) but the patterning
346 of the distribution for all other bone pairs distributions is far less clear. Plots for the radius-ulna and
347 the radius-tibia pairs display a similar pattern with *Dc. bicornis* and *Ds. sumatrensis* grouped together
348 on the negative side, and the three other species on the positive side (Figure 7F and Figure 8A)
349 despite some overlaps. Other plots display various patterns not distinguishing the species based on
350 either size, geography or phylogenetic relationships. We can notably see an opposition between *R.*
351 *unicornis* and *C. simum* at the positive and negative parts of the first axis respectively with *Ds.*
352 *sumatrensis* and *Dc. bicornis* overlapping around null values for the ulna-fibula pair (Figure 8E), or a
353 slight distinction between the *Rhinoceros* genus and the other species for the ulna-tibia pair, whereas
354 *Dc. bicornis* and *R. sondaicus* are strictly opposed along the first PLS axis (Figure 8D). A separation
355 between *R. sondaicus* and the other species is also clearly visible for the tibia-fibula pair (Figure 8H).
356 As for the raw data, the allometry-free shape changes along the first PLS axes mainly concern the
357 robustness of the bones and shape covariation is very similar for all the bones regardless of the
358 considered pair. All allometry-free theoretical shapes are available in the Supplementary Figure S6.

359

360 **Intraspecific covariation**

361 *Without Benjamini-Hochberg correction*

362 At the intraspecific level, rPLS values are relatively high but few first PLS axes are statistically
363 significant, even before correction (Table 2). Analyses reveal that the first PLS axis is significant for
364 five bone pairs within *C. simum* (humerus-radius, humerus-ulna, humerus-femur, radius-femur and
365 ulna-femur) and *R. sondaicus* (humerus-radius, radius-tibia, radius-fibula, humerus-tibia and ulna-
366 femur), three for *R. unicornis* (humerus-ulna, tibia-fibula and ulna-tibia), two for *Ds. sumatrensis*
367 (humerus-femur and humerus-tibia) and only one for *Dc. bicornis* (ulna-tibia). The rPLS values are
368 extremely high (from 0.89 to 0.99) for *R. sondaicus* relatively to the other species (0.72 - 0.94 for *C.*
369 *simum*, 0.66 - 0.96 for *Ds. sumatrensis*, 0.76 - 0.96 for *Dc. bicornis* and 0.79 - 0.97 for *R. unicornis*).
370 Although the covariation of some pairs may be common to some taxa (e. g. humerus-radius and ulna-
371 femur for *C. simum* and *R. sondaicus*, humerus-tibia for *Ds. sumatrensis* and *R. sondaicus*), each

372 species displays an overall different pattern of covariation. The observed lacks of significance may be
373 due to the small number of specimens per species. However, *C. simum* and *R. sondaicus* show the
374 highest percentage of significant results and are respectively represented by 15 and 7 specimens,
375 these two subsamples being not particularly more diverse than the other species (adults and
376 subadults, males and females, wild and captive specimens – see Supplementary Figure S7). This
377 indicates that the observed tendency is not only related to the sample size but may also carry some
378 biological signal. Moreover, some bone pairs show a p-value between 0.05 and 0.1 associated with a
379 high rPLS value. This is notably the case for the tibia-fibula pair in the two *Rhinoceros* species (Table
380 2). This tends to indicate that the shape covariation between the fibula and the tibia may be higher
381 for this clade than for other rhino species. In addition, the rPLS values of other pairs involving the
382 fibula are often higher in both species of *Rhinoceros* than in other species in our sample, although
383 their covariation is rarely significant.

384 For all these pairs, shape covariation involves anatomical areas which are similar within each species
385 but often different between species (see Supplementary Figure S8). However, some anatomical areas
386 appear to show high shape covariation both at the interspecific and intraspecific levels. This is
387 notably the case of the greater tubercle convexity and the deltoid tuberosity of the humerus and the
388 olecranon tuberosity of the ulna. These areas correspond to the insertion of powerful muscles for
389 flexion and extension of the forearm (respectively the *m. infraspinatus*, the *m. deltoideus* and the *m.*
390 *triceps brachii*).

391 *After Benjamini-Hochberg correction*

392 After the Benjamini-Hochberg correction of the p-values, rPLS values remain statistically significant
393 for only four bone pairs, all belonging to *C. simum*, which is the species with the highest number of
394 specimens (Table 2). In this species, the covariation is extremely strong for the humerus-radius (rPLS
395 = 0.92), the humerus-femur (rPLS = 0.93) and the ulna-femur (rPLS = 0.94) pairs, and slightly weaker
396 for the radius-femur pair (rPLS = 0.89). When looking at the first PLS axes for these four bone pairs, it
397 appears clearly that the subadults are separated from the adults, sometimes without overlap, as for
398 the ulna-femur pair (Figure 9). Contrary to the age class, the size of the individuals (expressed by the
399 sum of the centroid sizes of the two bones in each case) does not seem to follow a precise pattern
400 along the first PLS axes for these four bone pairs (Figure 9). A slight distinction between males and
401 females observed along the first PLS axes may partly account for the sexual dimorphism that exists in
402 this species (Groves 1972; Guérin 1980). However, our data are not sufficient to state on a potential
403 difference of integration level due to sexual dimorphism in *C. simum*.

404 Although not statistically significant before and after correction, similar distinctions between adults
405 and subadults have been observed on the first PLS axes for *Dc. bicornis* for some bone pairs (mainly
406 humerus-radius, humerus-ulna, humerus-femur, humerus-tibia and radius-femur). Details on age
407 class are too often missing for the three Asiatic species to state on this aspect. Shape variation
408 associated to the first PLS axes in the significant covariations after correction in *C. simum* show a
409 different tendency than at the interspecific level. The increase in robustness mainly concerns the
410 shaft of the bone, both epiphyses tending to be already very large in subadults. This is particularly
411 the case for the humerus and the femur (Figure 10). Colour maps confirm that the shape covariation
412 along the first PLS axes for *C. simum* concerns different areas than at the interspecific level, with a
413 different intensity depending on the bone pairs (Figure 10). We can notably observe that the cranial
414 side of the femur covaries strongly with the humerus and the radius, but visibly less with the ulna
415 (Figure 10B, C and D). However, some anatomical areas are similarly affected by shape covariation
416 both at the intra- and interspecific levels. This is notably the case for the lesser tubercle tuberosity on
417 the humerus (insertion of the *m. subscapularis*) (Figure 10A and B) and the greater trochanter
418 convexity on the femur (insertion of the *m. gluteus accessorius*) (Figure 10B and C).

419 **Discussion**

420 **Patterns of evolutionary integration**

421 Our results indicate that the limb long bones of modern rhino species are strongly integrated at the
422 interspecific level, confirming our first *a priori* hypothesis. This tendency has been previously observed
423 on limb bones among other terrestrial mammal groups, notably in equids (Hanot et al. 2017, 2018,
424 2019), but also in more phylogenetically distant and older clades such as carnivorans (Fabre et al. 2014;
425 Martín-Serra et al. 2015; Botton-Divet et al. 2018) and marsupials (Martín-Serra & Benson 2019). The
426 high shape covariation between functionally analogous bones (humerus-tibia) as well as between non-
427 analogous bones (ulna-femur) tends to indicate that this strong general integration may be related to a
428 highly coordinated locomotion, as observed in equids at the interspecific level (Hanot et al. 2017), which
429 is coherent with the rhino ability to gallop (Alexander & Pond 1992) and to reach high running speed
430 (Blanco et al. 2003).

431 However, contrary to our second hypothesis, this integration is unequally distributed among the tested
432 pairs of bones. The within-limb integration is slightly stronger in the forelimb than in the hind limb,
433 whereas in other taxa, the morphological integration is generally higher in the hind limb (Martín-Serra et
434 al. 2015; Hanot et al. 2017; Botton-Divet et al. 2018). The covariation is maximal for the humerus-ulna
435 and the radius-ulna couples. Although the femur and the tibia display a strong covariation with one
436 another, the fibula appears as the bone showing the lowest integration level. This is consistent with
437 previous observations on morphological variation of rhino long bones, highlighting that the shape of the
438 fibula is highly variable at the intraspecific level (Mallet et al. 2019). Therefore, the apparent lower
439 integration of the hind limb may be mainly due to the independent shape variation of the fibula. The
440 fibula appears nevertheless to be more strongly integrated with the humerus (functionally analogous)
441 and the ulna (serially homologous) than with other hind limb bones. This confirms that the shape of the
442 fibula remains covariant with other bones beyond stochastic variation, potentially driving the slightly
443 lower integration of the hind limb than of the forelimb.

444 **Body mass and evolutionary integration**

445 *Within limbs*

446 Among modern rhinos, most of the shape covariation is mainly driven by an increase in general
447 robustness and in the size of the articular surfaces and muscular insertion areas. This is coherent with
448 previous observations on other quadrupedal mammals (Martín-Serra et al. 2015; Botton-Divet et al.

449 2018; Hanot et al. 2018). The correction for allometry affects both the rhino species distribution along
450 the PLS axes and the rPLS values in a stronger way than for equids (Hanot et al. 2018), carnivorans
451 (Martín-Serra et al. 2015) or musteloids (Botton-Divet et al. 2018) at the interspecific level, confirming
452 our third hypothesis specifying that body mass has a stronger influence on the degree of integration
453 among heavy quadrupedal than in lighter mammal species. Allometry is also clearly more pronounced on
454 the forelimb than on the hind limb, as shown by the drastic reduction of the integration intensity when
455 using the allometry-free shapes. This tends to indicate that beyond the strong general integration of the
456 rhino limb bones, the overall higher integration within the forelimb might be caused by a stronger
457 allometry in these bones – and thus more strongly affected by body mass (Ercoli & Prevosti 2011; Cassini
458 et al. 2012; Mallet et al. 2019) – than the hind limb. Heavy quadrupeds bear a larger part of the body
459 weight on their forelimbs than on their hind limbs (Hildebrand 1974) and rhinos follow this body plan
460 (Regnault et al. 2013) due to their heavy head and horns and their massive trunk muscles and bones.
461 Previous observations (Schmidt & Fischer 2009; Hanot et al. 2018) led to the conclusion that body mass
462 can contribute to covariation between bones, which our data seem to confirm for rhinos. The higher
463 integration of the forelimb may thus be interpreted as a specialization linked to weight bearing (Martín-
464 Serra et al. 2015; Randau & Goswami 2018).

465 Furthermore, the covariation of the different elements composing the forelimb is probably related to a
466 complementary effect of phylogenetic relationships, developmental constraints and body mass. The
467 shape covariation between the humerus and the zeugopodium elements in the forelimb is clearly driven
468 by a distinction between Asiatic and African species, associated with a sorting linked to the mean body
469 mass within these two groups. The covariation is particularly strong between the humerus and the ulna,
470 and although it seems to be largely patterned by phylogenetic history, this is congruent with previous
471 studies indicating a high integration level between the bones involved in flexion/extension movements
472 and body stability (Fabre et al. 2014). Conversely, the interspecific covariation of the radius-ulna pair
473 seems intimately linked to the mean body mass of rhino species, with no distinct link to the phylogenetic
474 pattern. This indicates a likely major impact of mass on the zeugopodium integration coupled with a
475 common developmental origin (Young & Hallgrímsson 2005; Sears et al. 2007). These results are also in
476 good agreement with the more important impact of body mass observed on the shape of the radius and
477 ulna than on that of the humerus (Mallet et al. 2019) and the role of the zeugopodium in the support of
478 the body weight due to the alignment of this segment with pressure forces (Bertram & Biewener 1992).

479 Albeit less obvious, an effect of body mass on the hind limb interspecific integration could also exist,
480 especially between the femur and the tibia when looking at the species distribution along the first PLS
481 axis (raw shapes) and the rPLS values for allometry-free shapes. In a similar way than for the forelimb,
482 these two bones are involved in leg flexion/extension, particularly for propulsion (Hildebrand 1974;
483 Lawler 2008; Biewener & Patek 2018). Conversely, the degree of integration increases between the
484 femur and the fibula (and to a lesser extent between the tibia and the fibula) when the allometric effect
485 is removed, which is a unique phenomenon among all tested limb bone pairs. One interpretation can be
486 that the allometry effect consists in antagonistic changes between the femur and the fibula, and that the
487 fibula shape covariation at the interspecific level is poorly related to body mass. This is coherent with all
488 low rPLS drops for allometry-free shapes in all other pairs involving the fibula. This difference can also be
489 influenced by a different covariation between the femur and the fibula depending on the rhino species
490 (see below). The independence of the shape variation of the fibula relatively to the tibia also indicates
491 that, contrary to the forelimb zeugopodium, neither common developmental origin nor functional
492 requirements seem to highly constrain the covariation between the two hind limb zeugopodium bones.

493 Following the hypotheses of Hallgrímsson et al. (2002) and Young & Hallgrímsson (2005) stating that a
494 functionally specialized part covaries less with surrounding elements, the fibula could be interpreted as a
495 highly specialized bone in some rhino species. However, as previously observed for the ulna of
496 musteloids (Botton-Divet et al. 2018), the lower integration of the fibula may be linked to a decrease of
497 the functional constraints exerted on this bone. The fibula supports the insertion of digit flexors and
498 extensors (Barone 2010) and is involved in the ankle stability and weight bearing among rhinos. However
499 the fibula shape has been proven to be poorly correlated with body mass (Mallet et al. 2019). Therefore,
500 it is likely that the fibula shape varies more independently and is less functionally constrained by body
501 mass than other limb bones in some rhino species (see below). This may be interpreted as a case of
502 parcellation (Young & Hallgrímsson 2005) due to a functional dissociation between the bones of a single
503 limb.

504 All the pairs involving the humerus seem thus more strongly impacted by phylogeny than by functional
505 constraints and, to a lesser extent, by body mass. Most of the other bone pairs rather suggest a
506 dominant effect of body mass, especially the ones involving the radius and the ulna. Although less clear,
507 similar results are obtained for the hind limb bones.

508 *Between limbs*

509 At the interspecific level, serially homologous bones are strongly integrated but their covariation is
510 differently associated with body mass, i.e. more for the zeugopodium elements than for the stylopodium
511 ones. Together with the slightly lower integration values of the zeugopodium elements relatively to the
512 stylopodium, these observations are also coherent with previous studies indicating a decrease of the
513 integration from proximal to distal parts of the limbs linked to a higher degree of specialization of distal
514 elements (Young & Hallgrímsson 2005). In addition, our results are not congruent with the strict serial
515 homology classically considered for the zeugopodium (radius-tibia and ulna-fibula) by showing a stronger
516 covariation between the ulna and the tibia than between the radius and the tibia. Similar results were
517 observed on carnivorans and interpreted as a potential functional convergence between these bones
518 (Martín-Serra et al. 2015). These results could also revive doubts on the *a priori* hypothesis of homology
519 between zeugopodium bones, which has long been debated (Owen 1848; Wyman 1867; Lessertisseur &
520 Saban 1967) and, to our knowledge, still remains unresolved although largely taken for granted (i.e.
521 Bininda-Emonds et al. 2007; Bennett & Goswami 2011; Martín-Serra et al. 2015; Botton-Divet et al.
522 2018). Only a comprehensive study of the genetic processes leading to the development of forelimb and
523 hind limb zeugopodium could clarify this aspect (Klingenberg 2014).

524 The strong integration between the humerus and the tibia (and the fibula to a lesser extent) tends to
525 confirm the functional analogy between the forelimb stylopodium and the hind limb zeugopodium (Gasc
526 2001; Schmidt & Fischer 2009). However, the shape covariation is weaker in the humerus-tibia pair than
527 in other bone pairs involving the tibia (e.g. radius-tibia and ulna-tibia), which tends to indicate that, in
528 the present case, the functional requirements linked to locomotion and body support during resting time
529 may less affect the shape covariation than the developmental constraints, contrary to what has been
530 observed in lighter taxa (Fabre et al. 2014; Hanot et al. 2017; Botton-Divet et al. 2018). Moreover, the
531 high covariation between the ulna and the femur also tackles the classic functional approach,
532 highlighting a strong integration between non-homologous or analogous bones, an observation also
533 recently revealed among marsupials (Martín-Serra & Benson 2019). Recent work using a network
534 approach on a phylogenetic matrix of characters among modern and fossil rhinos showed that
535 unexpected covariations can exist between cranial, dental and postcranial phenotypic traits in the group
536 (Lord et al. 2019). In particular, the authors observed a frequent co-occurrence of discrete traits between
537 the radius-ulna and the femur among all rhinos, which seems coherent with our results indicating a
538 strong covariation between the forelimb zeugopodium and the hind limb stylopodium. Since the
539 postcranial body plan appears to be implemented early during the Rhinoceroidea evolutionary history
540 (Lord et al. 2019) and may be less variable than in phylogenetically-close taxa like equids (McHorse et al.

541 2019), this may imply strong inherited developmental constraints within this group canalizing the shape
542 covariation (Hallgrímsson et al. 2002) even between non-homologous bones. Furthermore, the high
543 integration of non-homologous or analogous bones appears as strongly congruent with the variation in
544 body mass, lending further support to the link between heavy weight and high general integration level
545 (Schmidt & Fischer 2009; Hanot et al. 2017).

546 **Covariation at the intraspecific level: developmental integration**

547 Our exploration of integration patterns at the intraspecific level is limited by the low sample size for all
548 species and the non-significance (at $p > 0.05$) of most of the PLS axes obtained for the different pairs of
549 bones, particularly after the Benjamini-Hochberg correction. Beyond this strict non-significance (which is
550 currently criticized in favour of a more continuous approach of the p-value – see Ho et al. 2019;
551 Wasserstein et al. 2019), no clear similar pattern of integration seems to emerge between light and
552 heavy rhino species, or between African and Asiatic species. Some species share the same significant or
553 almost significant bone pairs. The covariation between the tibia and the fibula among *Rhinoceros* notably
554 seems relatively strong as compared to in other species, confirming previous results on individual shape
555 variation (Mallet et al. 2019). This aspect may indicate that the hind limb zeugopodium – and particularly
556 the fibula – is less variable among the two species of this genus, with a lesser parcellation among this
557 group.

558 The integration patterns found in *C. simum*, the species with the most specimens, reveal both similarities
559 and divergences with the patterns observed at the interspecific level (i.e. evolutionary integration, see
560 Cheverud 1996; Klingenberg 2014). All the significant PLS axes in this species concern forelimb bones and
561 indicate a very strong integration between the humerus, the radius and the ulna, as well as a high shape
562 covariation between the humerus and the femur (serial homology). The strong integration of the
563 forelimb may be partly related to the heavier and longer head of *C. simum* compared to other species
564 (Guérin 1980) and highlights different patterns of distribution of body weight among modern rhinos
565 (Antoine, pers. obs. 2020). The shape covariation among *C. simum* specimens reveals a strong effect of
566 age with a clear separation between adults and subadults in all cases. Even if this effect is not visible at
567 the interspecific level, the separation between the two age classes is the main driver of the integration
568 within this species, whereas body mass (approximately expressed through the value of the centroid size)
569 and sex do not seem to play a visible role on the covariation patterns. This tendency is associated with a
570 shape covariation on anatomical areas often different to the ones showing a strong covariation at the
571 interspecific level. Only the greater tubercle convexity and the deltoid tuberosity on the humerus, the

572 olecranon tuberosity on the ulna and the greater trochanter convexity on the femur show a high degree
573 of shape covariance both at both interspecific and intraspecific levels.

574 Within *C. simum*, developmental integration is more related to proportions between the different bone
575 parts (e.g. shaft and epiphyses) than to the development of powerful muscular insertions ensuring the
576 stability and the locomotion of the body. In the end, the global integration of the rhino limb long bones
577 results in the superposition and association of the different levels of integration (here, developmental
578 and evolutionary). These integration levels are conjointly influenced by shared phylogenetic history,
579 similar developmental origin and constraints due to both locomotion and body mass support (Cheverud
580 1996; Hallgrímsson et al. 2009; Klingenberg 2014). Investigated here among *C. simum*, the static and
581 developmental integration levels remain to be explored with a larger sample for the other rhino species
582 – which remains challenging for these endangered species. Finally, the addition of some of the numerous
583 fossil taxa belonging to the superfamily Rhinoceroidea and displaying convergent increases of body
584 mass will help testing the influence of body mass on integration patterns suggested in the present study
585 (Klingenberg 2014).

586 **Conclusion**

587 Our exploration of the integration patterns of the limb long bones among modern rhinos reveals that the
588 appendicular skeleton of these species is strongly integrated, as in other terrestrial quadrupedal
589 mammals. At the interspecific level, the forelimb appears as more covariant than the hind limb, with a
590 more apparent relation to body mass, which appears stronger than for more lightly built terrestrial
591 mammals. This can be interpreted as a higher degree of specialization of the forelimb in body weight
592 support. Proximal elements appear primarily affected by common developmental constraints whereas
593 the distal parts of the limbs seem rather shaped by functional requirements, which would confirm
594 hypotheses addressed on different mammal groups. The appendicular skeleton of rhinos appears to be a
595 compromise between the functional requirements of a highly coordinated locomotion, the necessity to
596 sustain a high body mass and important inherited developmental processes constraining shape
597 covariation – located mostly on insertion areas for powerful flexor and extensor muscles. In addition, the
598 exploration of the shape covariation at the intraspecific level reveals a prominent effect of the age class
599 in shaping the covariation patterns among *C. simum*. These results are a first step to explore further the
600 functional construction of the appendicular skeleton of modern rhinos and to extend this approach to
601 other heavy modern taxa (such as elephants or hippos). Moreover, the numerous fossil taxa composing
602 the superfamily Rhinoceroidea and showing a broad range of body mass would be a valuable group to
603 extend these results and highlight convergent patterns of shape covariation directly linked to a heavy
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621 **Author contributions**

622 C.M. designed the study with significant inputs from A.H., R.C. and G.B. C.M. did the data acquisition
623 with inputs from A.H. C.M. performed the analyses with the help of R.C and all authors interpreted the
624 results. C.M. drafted the manuscript. All authors reviewed and contributed to the final version of the
625 manuscript, read it and approved it.

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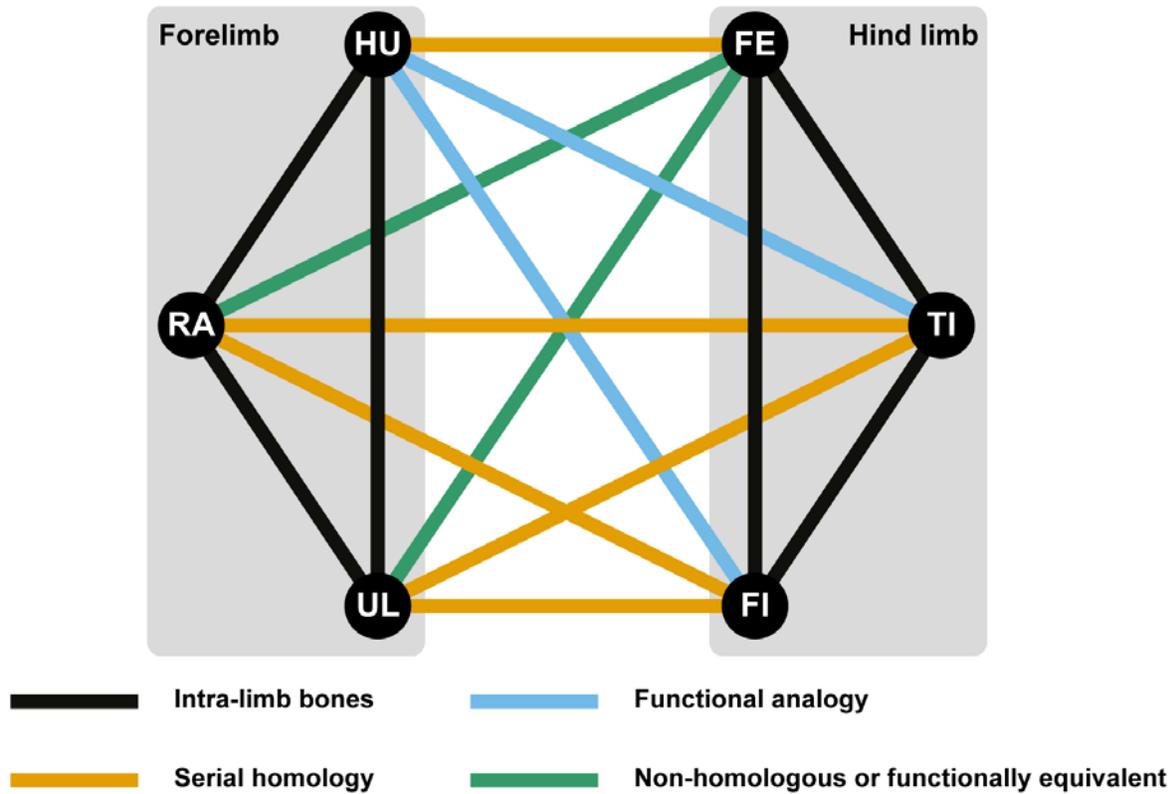
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- 834

835 **Figures**

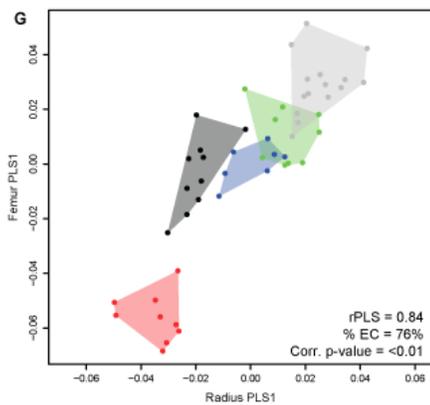
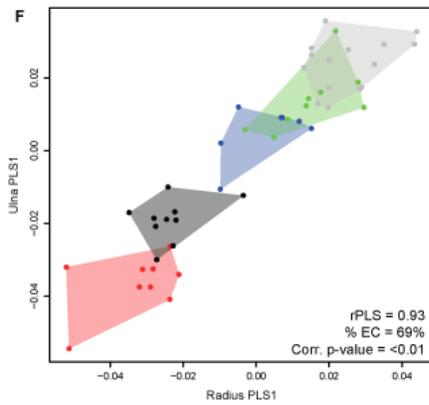
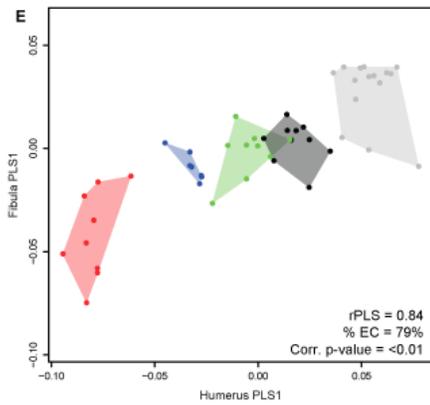
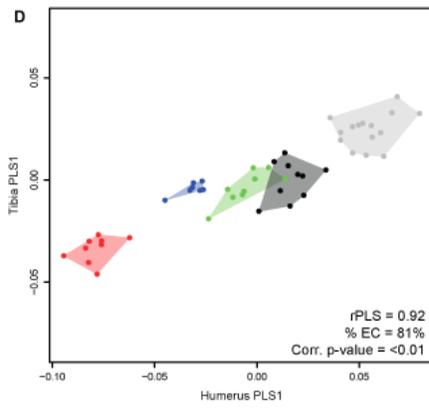
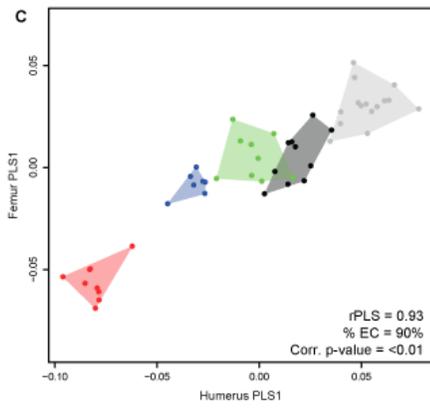
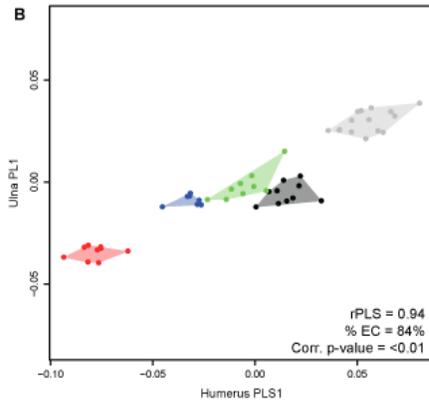
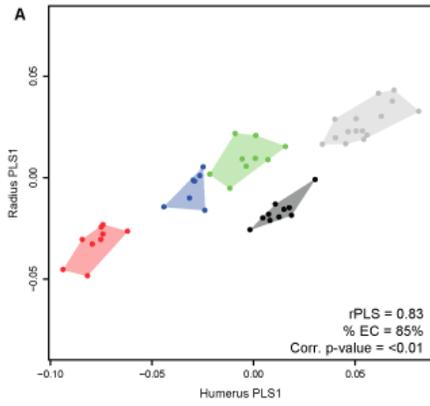
836 **Figure 1:** Graphic model showing the hypotheses of morphological integration tested in this study on the
837 appendicular skeleton of the five modern rhino species. Hu: Humerus; Ra: Radius; Ul: Ulna; Fe: Femur; Ti:
838 Tibia; Fi: Fibula.



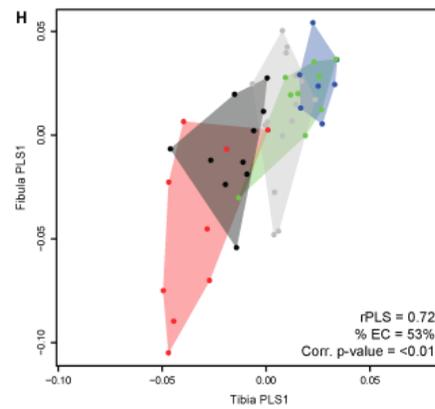
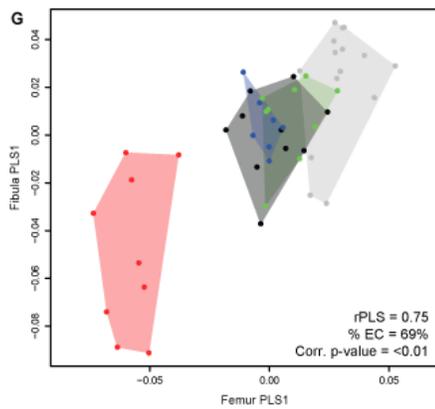
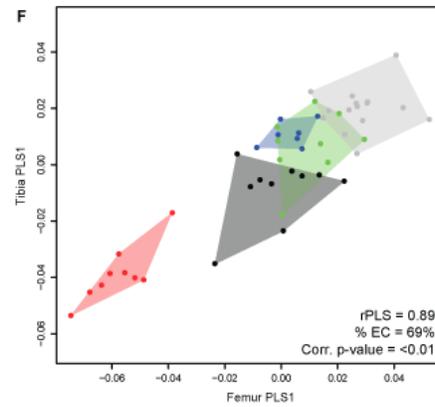
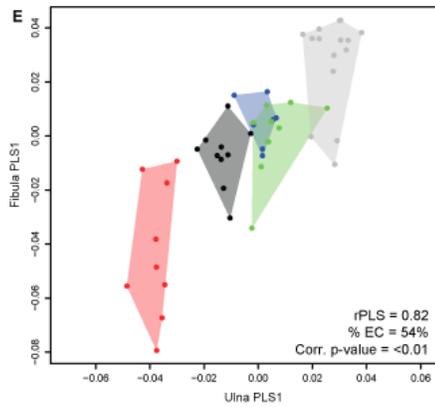
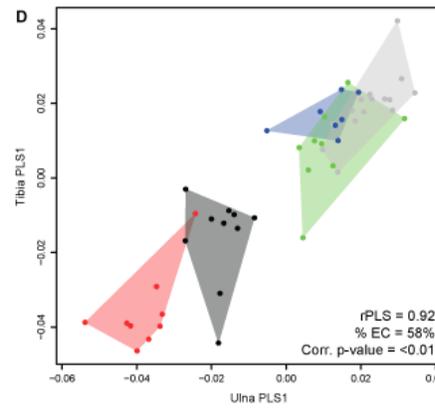
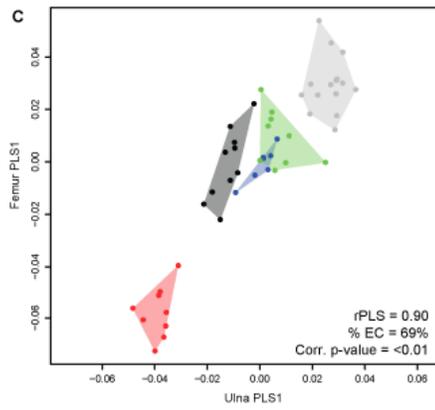
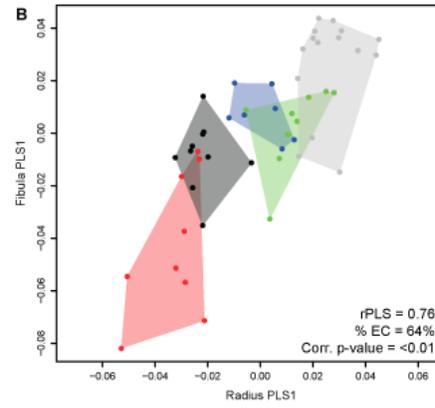
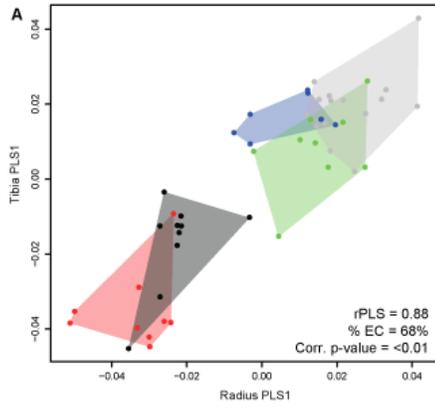
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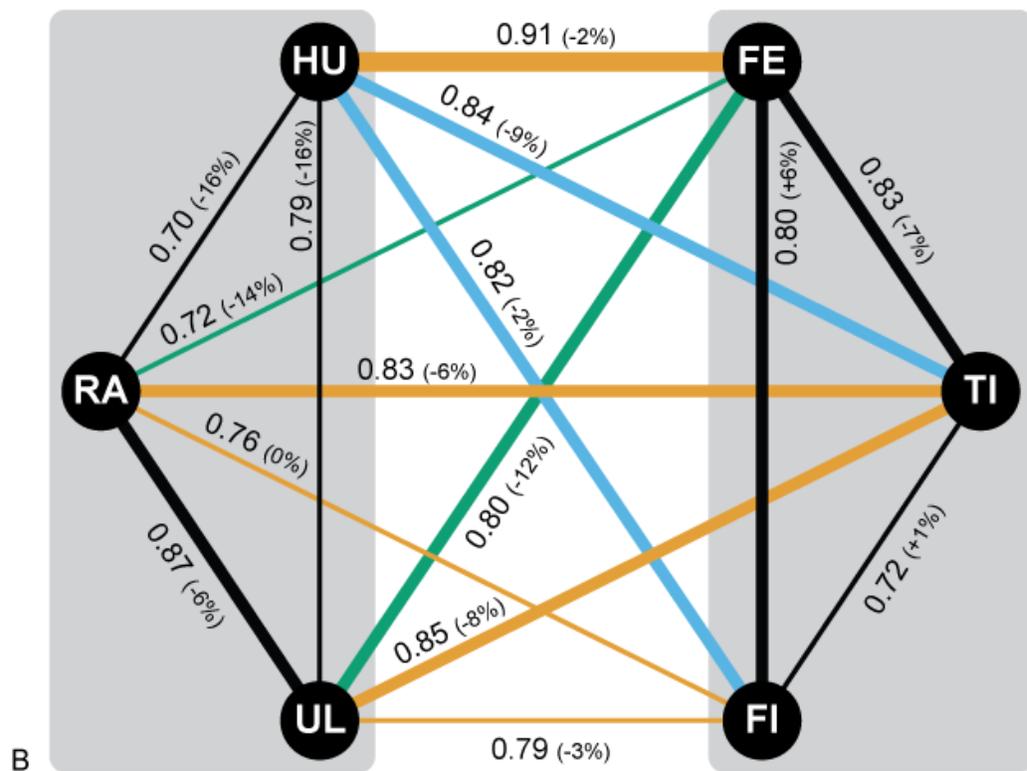
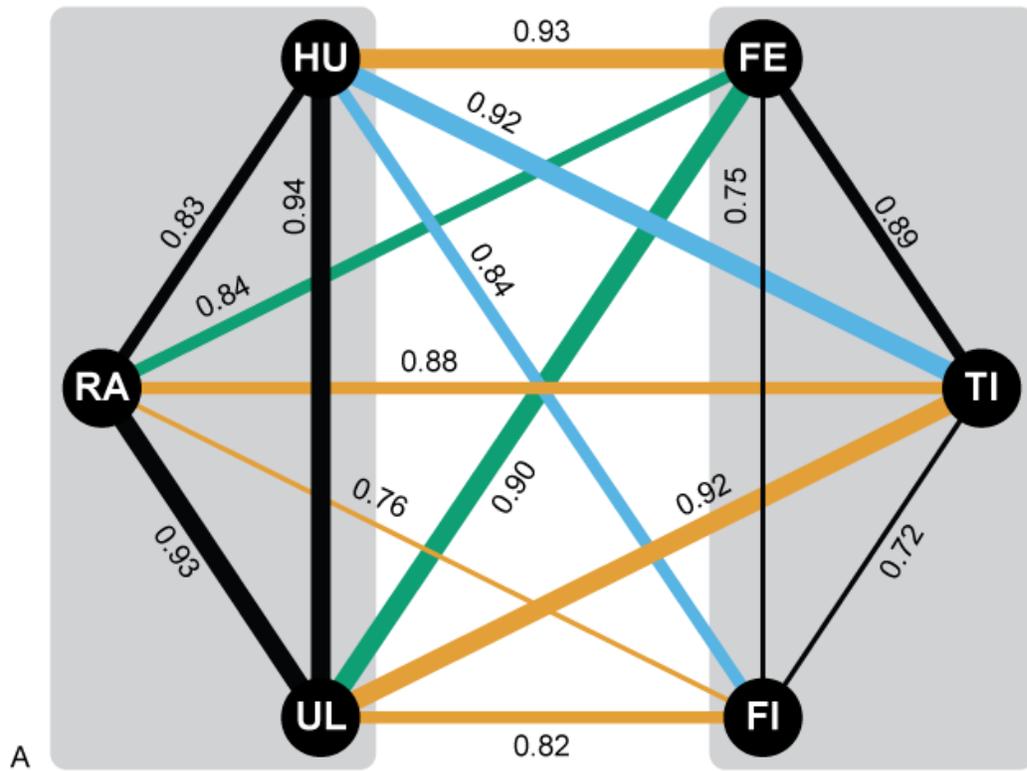
841 **Figure 2:** Plots of the first PLS axes computed on raw shapes. A: humerus-radius; B: humerus-ulna; C:
842 humerus-femur; D: humerus-tibia; E: humerus-fibula; F: radius-ulna; G: radius-femur. rPLS: value of the
843 PLS coefficient; % EC: percentage of explained covariation; Corr. p-value: corrected p-value using a
844 Benjamini-Hochberg correction. The phylogenetic tree displays a polytomy because of the absence of
845 consensus regarding the relationships of the five modern rhinos.



848 **Figure 3:** Plots of the first PLS axes computed on raw shapes. A: radius-tibia; B: radius-fibula; C: ulna-
849 femur; D: ulna-tibia; E: ulna-fibula; F: femur-tibia; G: femur-fibula; H: tibia-fibula. rPLS: value of the PLS
850 coefficient; % EC: percentage of explained covariation; Corr. p-value: corrected p-value using a
851 Benjamini-Hochberg correction. Colour code as in Figure 2.



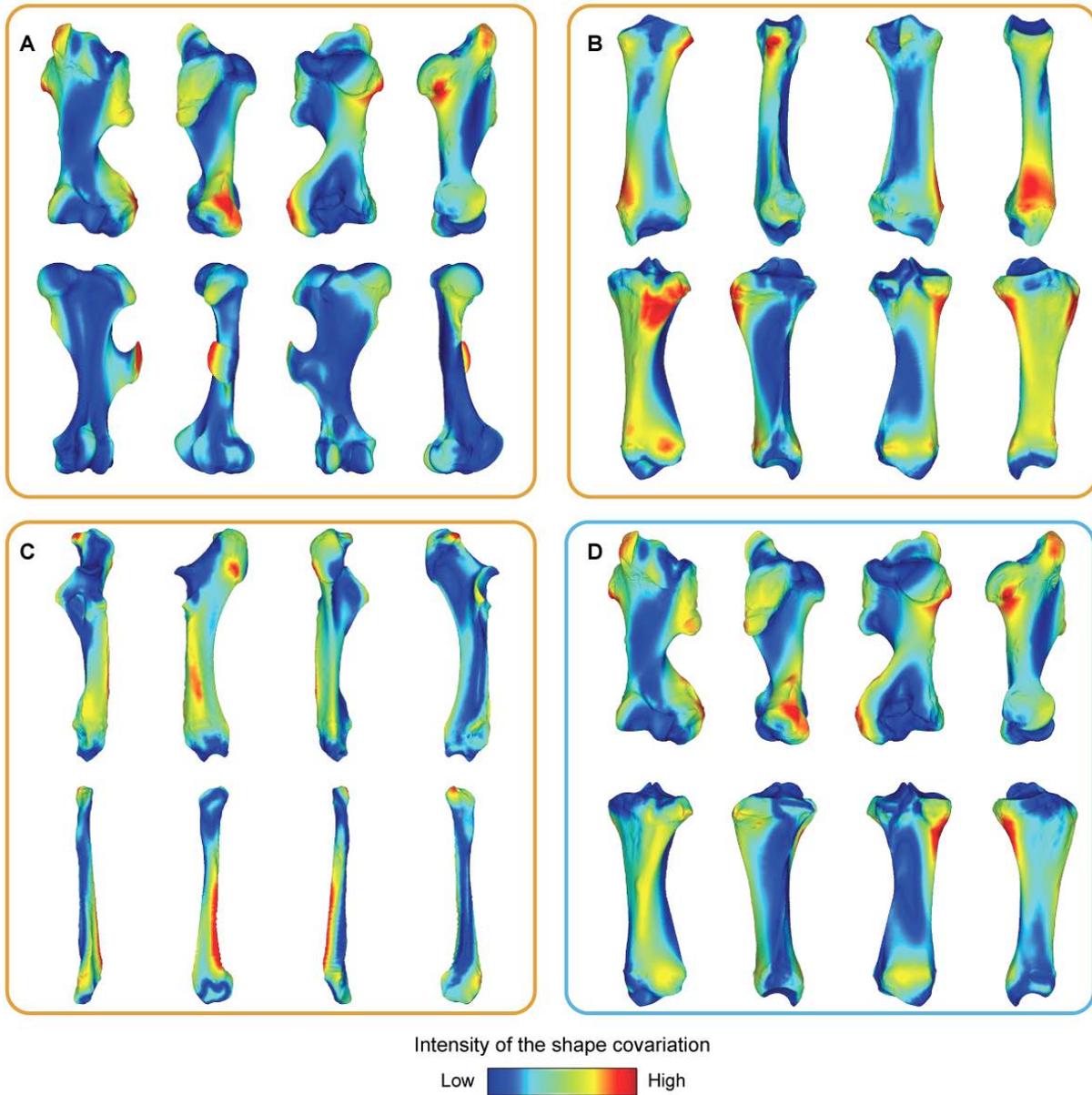
854 **Figure 4:** Graphic model of the rPLS values of the first PLS axes computed on the appendicular skeleton
855 of the five modern rhino species. The line thickness is proportional to the rPLS value. The colour code
856 expresses the type of relation between bones as described in the Figure 1. A: rPLS values obtained on
857 raw shapes. B: rPLS values obtained on allometry-free shapes. In brackets are indicated the percentages
858 of difference between rPLS obtained on raw shapes and allometry-free shapes. Hu: Humerus; Ra: Radius;
859 Ul: Ulna; Fe: Femur; Ti: Tibia; Fi: Fibula.



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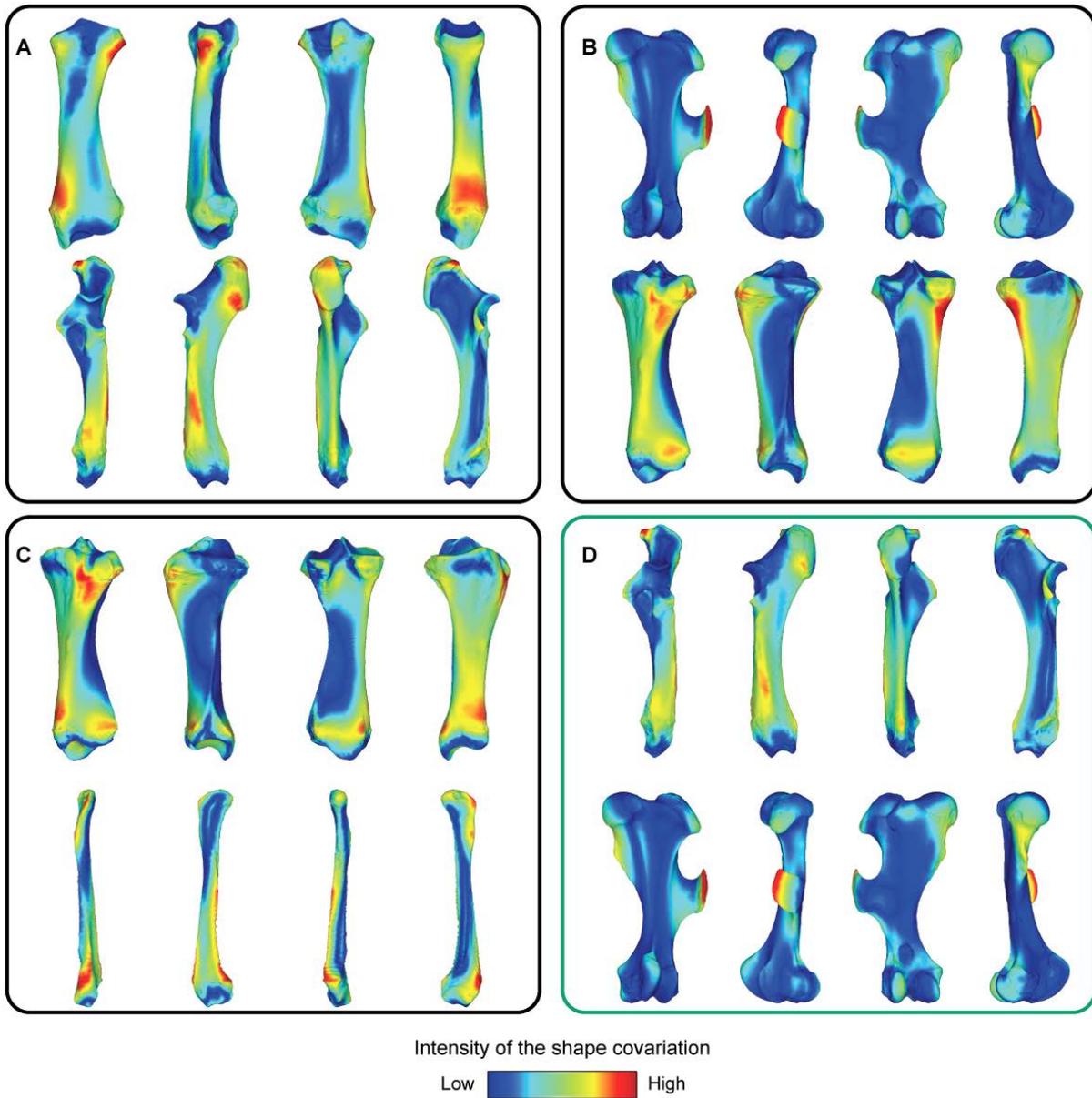
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862 **Figure 5:** Colour maps of the location and intensity of the shape deformation associated to the first PLS
 863 axes for 4 pairs of bones among the five modern species of rhinoceros. For each bone, the shape
 864 associated to the positive part of the first PLS axis was coloured depending on its distance to the shape
 865 associated to the negative part (blue indicates a low deformation intensity and red indicates a high
 866 deformation intensity). The colour code of the squares expresses the type of relation between bones as
 867 described in the Figure 1 (orange: serial homology; blue: functional analogy). A: humerus-femur; B:
 868 radius-tibia; C: ulna-fibula; D: humerus-tibia (orientation from left to right in each case: cranial,
 869 caudal and medial).



870

871 **Figure 6:** Colour maps of the location and intensity of the shape deformation associated to the first PLS
 872 axes for 4 pairs of bones among the five modern species of rhinoceros. For each bone, the shape
 873 associated to the positive part of the first PLS axis was coloured depending on its distance to the shape
 874 associated to the negative part (blue indicates a low deformation intensity and red indicate a high
 875 deformation intensity). The colour code of the squares expresses the type of relation between bones as
 876 described in the Figure 1 (black: intra-limb relation; green: non-homologous or analogous bones). A:
 877 radius-ulna; B: femur-tibia; C: tibia-fibula; D: ulna-femur (orientation from left to right in each case:
 878 cranial, lateral, caudal and medial).

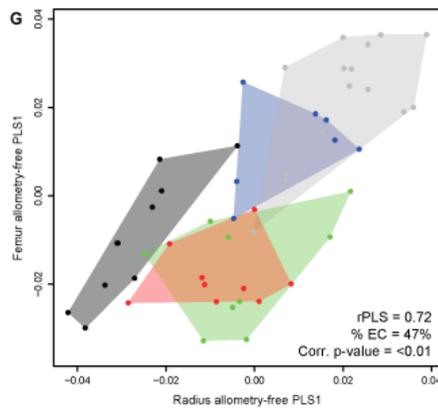
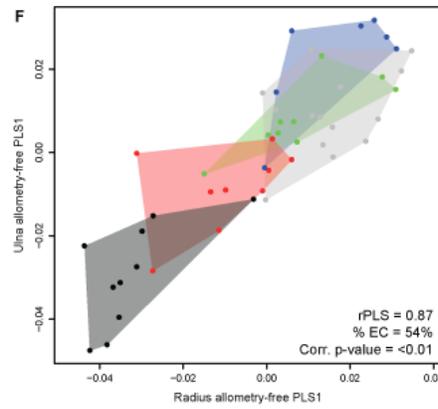
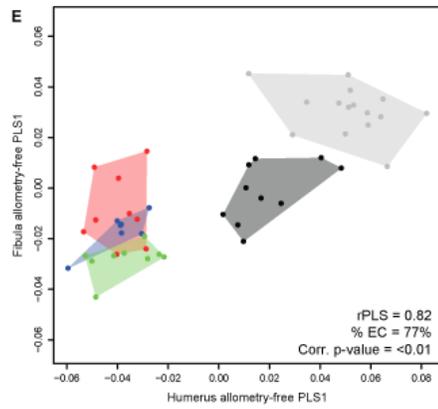
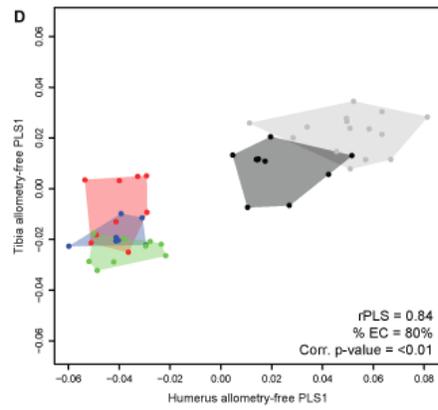
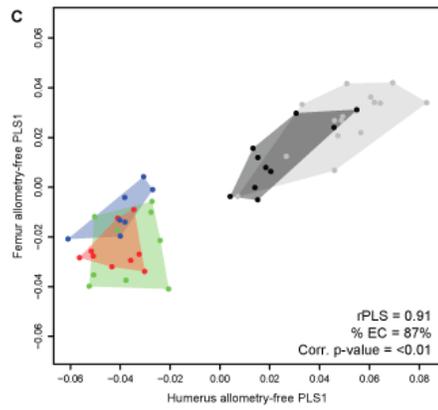
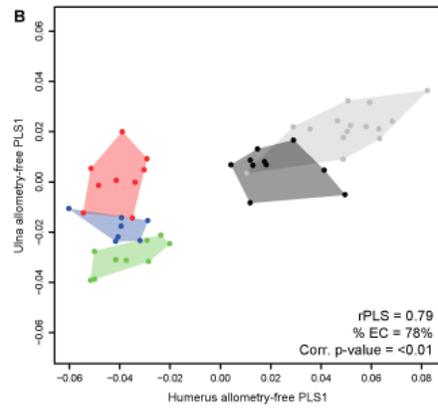
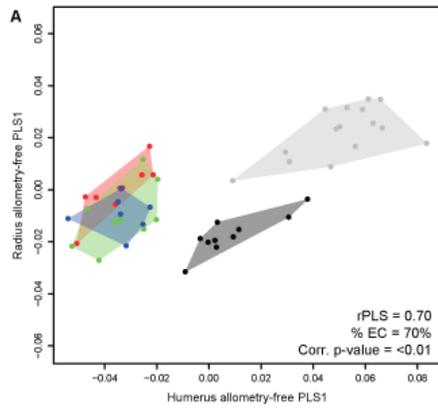


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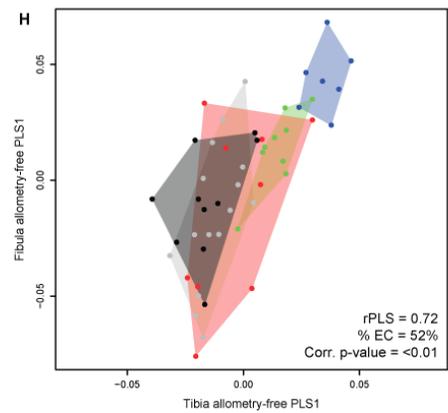
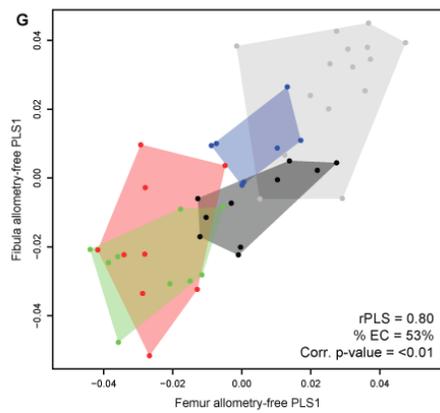
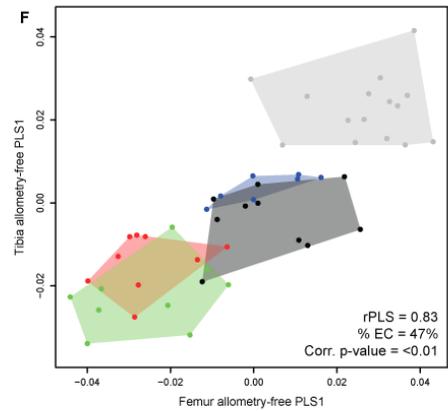
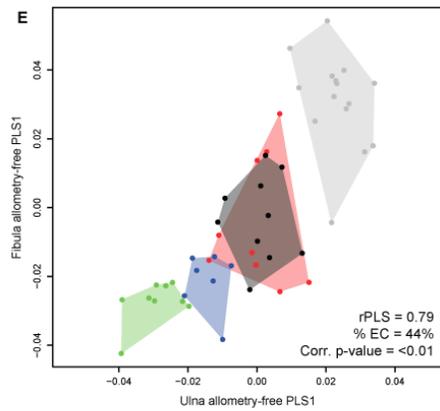
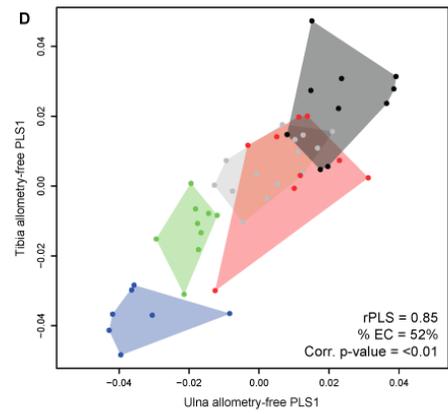
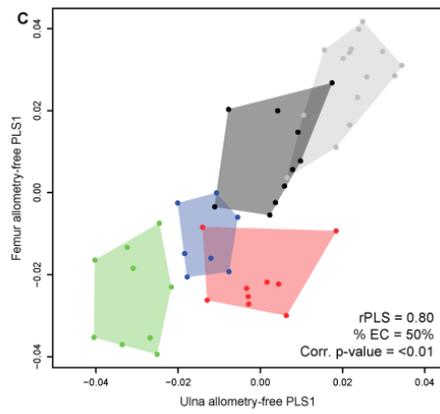
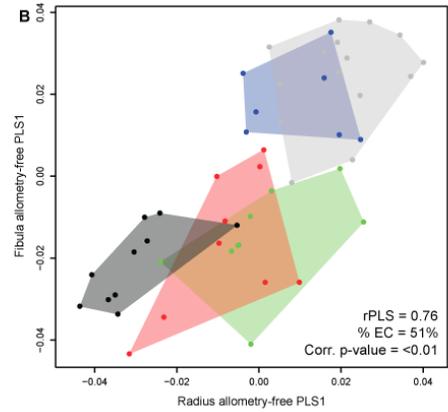
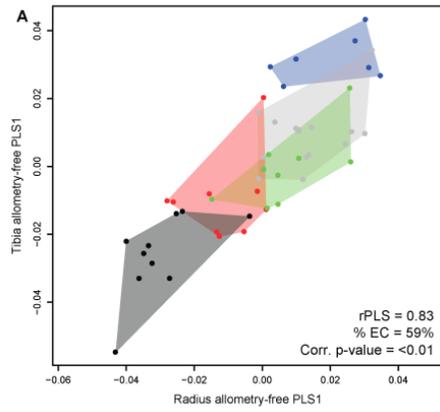
881 **Figure 7:** Plots of the first PLS axes computed on allometry-free shapes. A: humerus-radius; B: humerus-
882 ulna; C: humerus-femur; D: humerus-tibia; E: humerus-fibula; F: radius-ulna; G: radius-femur. rPLS: value
883 of the PLS coefficient; % EC: percentage of explained covariation; Corr. p-value: corrected p-value using a
884 Benjamini-Hochberg correction. The phylogenetic tree displays a polytomy because of the absence of
885 consensus regarding the relationships of the five modern rhinos.

886

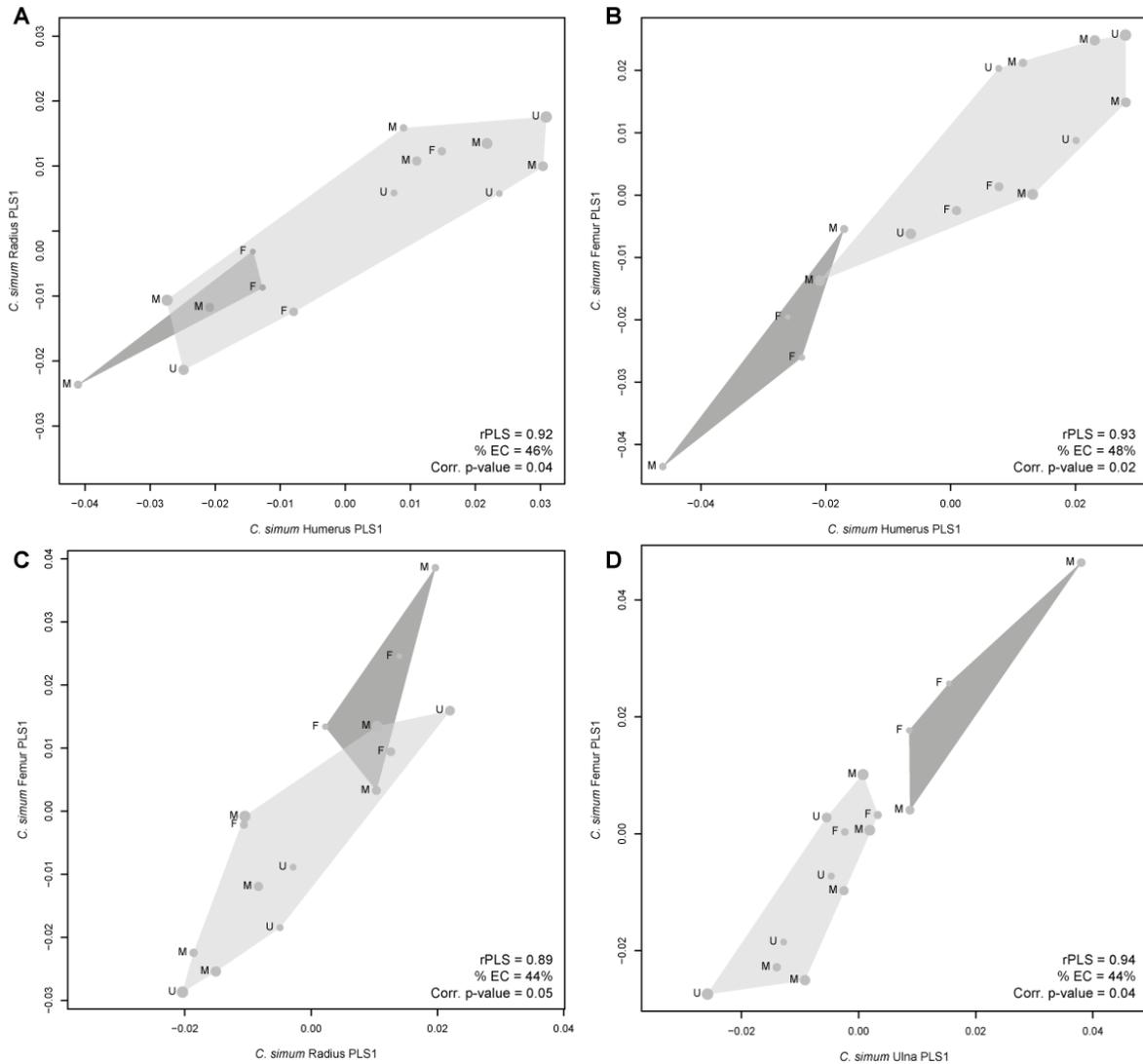


888 **Figure 8:** Plots of the first PLS axes computed on allometry-free shapes. A: radius-tibia; B: radius-fibula;
889 C: ulna-femur; D: ulna-tibia; E: ulna-fibula; F: femur-tibia; G: femur-fibula; H: tibia-fibula. rPLS: value of
890 the PLS coefficient; % EC: percentage of explained covariation; Corr. p-value: corrected p-value using a
891 Benjamini-Hochberg correction. Colour code as in Figure 6.

892



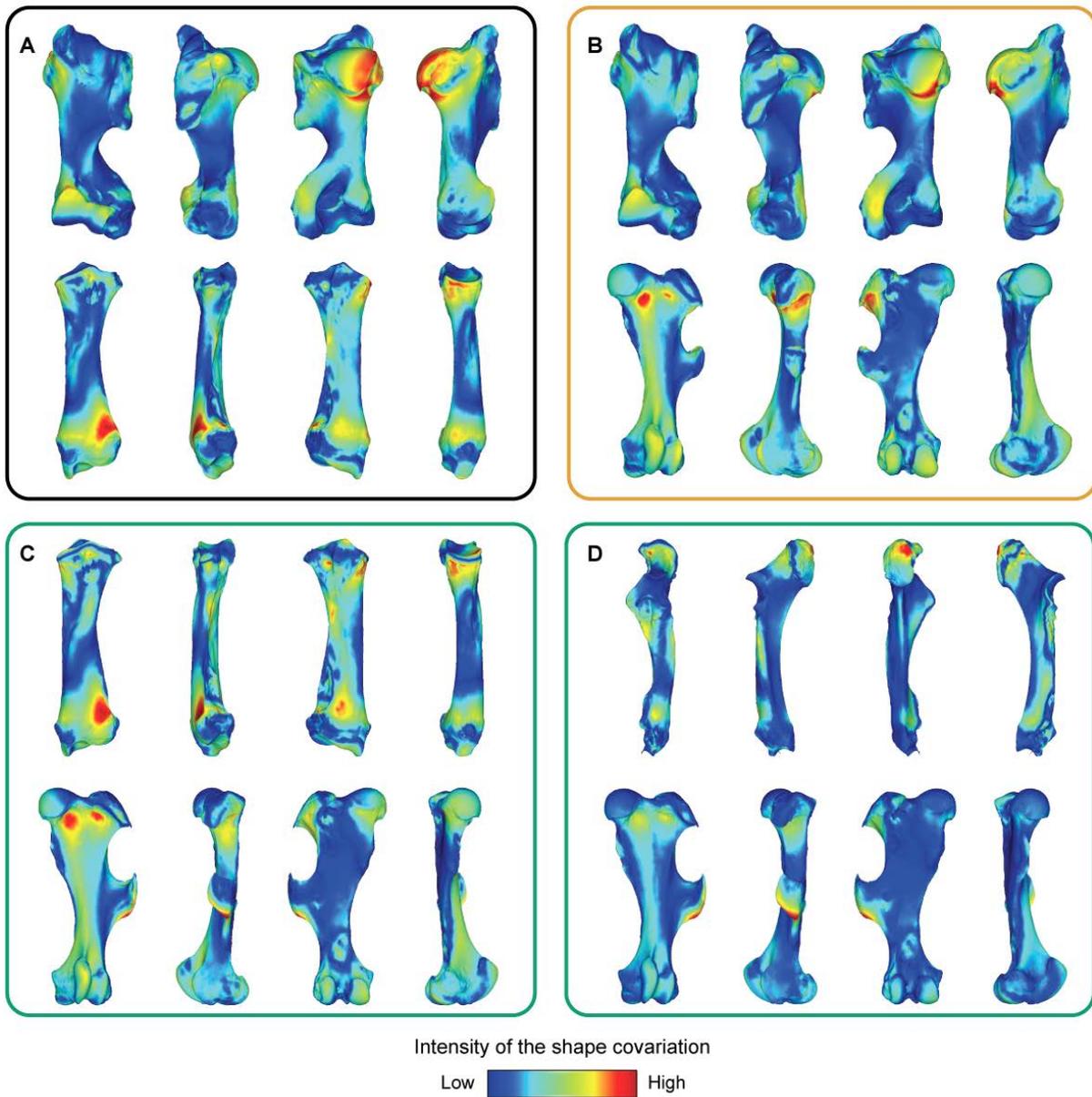
894 **Figure 9:** Plots of the first PLS axes computed on the 15 *Ceratotherium simum* specimens. Adults are
 895 highlighted in light grey and subadults in dark grey. The size of the dots is proportional to the combined
 896 value of the centroid size of the bones for each block and each specimen. A: humerus-radius; B:
 897 humerus-femur; C: radius-femur; D: ulna-femur. Sex: F: female; M: male; U: unknown; rPLS: value of the
 898 PLS coefficient; % EC: percentage of explained covariation; Corr. p-value: corrected p-value using a
 899 Benjamini-Hochberg correction.



900

901

902 **Figure 10:** Colour maps of the location and intensity of the shape deformation associated to the first PLS
 903 axes for four bones of *Ceratotherium simum*. For each bone, the shape associated to the positive part of
 904 the first PLS axis was coloured depending on its distance to the shape associated to the negative part
 905 (blue indicates a low deformation intensity and red indicates a high deformation intensity). The colour
 906 code of the squares expresses the type of relation between bones as described in the Figure 1 (black:
 907 intra-limb relation; orange: serial homology; green: non-homologous or analogous bones). A: humerus-
 908 radius; B: humerus-femur; C: radius-femur; D: ulna-femur (orientation from left to right in each case:
 909 cranial, lateral, caudal and medial).



910

911 **Tables**

912 **Table 1:** List of the studied specimens with sex, age class, condition and 3D acquisition details.

913 Abbreviations: Sex: F: female; M: male; U: unknown. Age – A: adult; S: sub-adult. Condition – W: wild; C:
914 captive; U: unknown. 3D acquisition – SS: surface scanner; P: photogrammetry. Institutional
915 abbreviations: AMNH: American Museum of Natural History, New York. BICPC: Powell Cotton Museum,
916 Birchington-on-Sea. CCEC: Centre de Conservation et d'Étude des Collections, Musée des Confluences,
917 Lyon. MNHN: Muséum National d'Histoire Naturelle, Paris. NHMUK: Natural History Museum, London.
918 NHMW: Naturhistorisches Museum Wien, Vienna. RBINS: Royal Belgian Institute of Natural Sciences,
919 Brussels. RMCA: Royal Museum for Central Africa, Tervuren. ZSM: Zoologische Staatssammlung
920 München, Munich. Specimens MNHN-ZM-AC-1885-734, NHMUK ZD 2018.143 and NHMUK ZD 1972.822
921 were previously determined or reattributed based on the analysis of the limb long bone morphology (see
922 Mallet et al. 2019).

923

| Taxon | Institution | Specimen number | Sex | Age | Condition | 3D acquisition |
|---------------------------------|-------------|------------------|-----|-----|-----------|----------------|
| <i>Ceratotherium simum</i> | AMNH | M-51854 | F | A | W | SS |
| <i>Ceratotherium simum</i> | AMNH | M-51855 | M | A | W | SS |
| <i>Ceratotherium simum</i> | AMNH | M-51857 | F | A | W | SS |
| <i>Ceratotherium simum</i> | AMNH | M-51858 | M | A | W | SS |
| <i>Ceratotherium simum</i> | AMNH | M-81815 | U | A | U | SS |
| <i>Ceratotherium simum</i> | BICPC | NH.CON.20 | M | S | W | SS |
| <i>Ceratotherium simum</i> | BICPC | NH.CON.32 | F | S | W | SS |
| <i>Ceratotherium simum</i> | BICPC | NH.CON.40 | F | S | W | SS |
| <i>Ceratotherium simum</i> | BICPC | NH.CON.110 | M | A | W | SS |
| <i>Ceratotherium simum</i> | BICPC | NH.CON.112 | M | A | W | SS |
| <i>Ceratotherium simum</i> | NHMUK | ZD 2018.143 | U | A | U | SS |
| <i>Ceratotherium simum</i> | NHMW | 3086 | U | A | W | P |
| <i>Ceratotherium simum</i> | RBINS | 19904 | M | S | W | SS |
| <i>Ceratotherium simum</i> | RMCA | 1985.32-M-0001 | U | A | W | SS |
| <i>Ceratotherium simum</i> | RMCA | RG35146 | M | A | W | SS |
| <i>Dicerorhinus sumatrensis</i> | MNHN | ZM-AC-1903-300 | M | A | W | SS |
| <i>Dicerorhinus sumatrensis</i> | NHMUK | ZD 1879.6.14.2 | M | A | W | SS |
| <i>Dicerorhinus sumatrensis</i> | NHMUK | ZD 1894.9.24.1 | U | A | W | SS |
| <i>Dicerorhinus sumatrensis</i> | NHMUK | ZD 1931.5.28.1 | M | S | W | SS |
| <i>Dicerorhinus sumatrensis</i> | NHMUK | ZE 1948.12.20.1 | U | A | U | SS |
| <i>Dicerorhinus sumatrensis</i> | NHMUK | ZE 1949.1.11.1 | U | A | W | SS |
| <i>Dicerorhinus sumatrensis</i> | NHMW | 3082 | U | A | U | P |
| <i>Dicerorhinus sumatrensis</i> | RBINS | 1204 | M | A | W | SS |
| <i>Dicerorhinus sumatrensis</i> | ZSM | 1908/571 | M | A | U | SS |
| <i>Diceros bicornis</i> | AMNH | M-81805 | U | A | U | SS |
| <i>Diceros bicornis</i> | AMNH | M-27757 | M | S | W | SS |
| <i>Diceros bicornis</i> | AMNH | M-113776 | U | A | W | SS |
| <i>Diceros bicornis</i> | AMNH | M-113777 | U | A | W | SS |
| <i>Diceros bicornis</i> | AMNH | M-113778 | U | A | W | SS |
| <i>Diceros bicornis</i> | MNHN | ZM-AC-1936-644 | F | S | U | SS |
| <i>Diceros bicornis</i> | RBINS | 9714 | F | A | W | SS |
| <i>Diceros bicornis</i> | RMCA | RG2133 | M | S | W | SS |
| <i>Diceros bicornis</i> | ZSM | 1961/186 | M | S | U | SS |
| <i>Diceros bicornis</i> | ZSM | 1961/187 | M | S | U | SS |
| <i>Rhinoceros sondaicus</i> | CCEC | 50002041 | U | A | W | SS |
| <i>Rhinoceros sondaicus</i> | MNHN | ZM-AC-A7970 | U | A | U | SS |
| <i>Rhinoceros sondaicus</i> | MNHN | ZM-AC-A7971 | U | A | W | SS |
| <i>Rhinoceros sondaicus</i> | NHMUK | ZD 1861.3.11.1 | U | S | W | SS |
| <i>Rhinoceros sondaicus</i> | NHMUK | ZD 1871.12.29.7 | M | A | W | SS |
| <i>Rhinoceros sondaicus</i> | NHMUK | ZD 1921.5.15.1 | F | S | W | SS |
| <i>Rhinoceros sondaicus</i> | RBINS | 1205F | U | S | W | SS |
| <i>Rhinoceros unicornis</i> | AMNH | M-35759 | M | A | C | SS |
| <i>Rhinoceros unicornis</i> | AMNH | M-54456 | F | A | W | SS |
| <i>Rhinoceros unicornis</i> | MNHN | ZM-AC-1960-59 | M | A | C | SS |
| <i>Rhinoceros unicornis</i> | NHMUK | ZD 1884.1.22.1.2 | F | A | W | SS |
| <i>Rhinoceros unicornis</i> | NHMUK | ZE 1950.10.18.5 | M | A | W | SS |
| <i>Rhinoceros unicornis</i> | NHMUK | ZE 1961.5.10.1 | M | A | W | SS |
| <i>Rhinoceros unicornis</i> | NHMUK | ZD 1972.822 | U | A | U | SS |
| <i>Rhinoceros unicornis</i> | RBINS | 1208 | F | A | C | SS |
| <i>Rhinoceros unicornis</i> | RBINS | 33382 | U | A | U | SS |

925 **Table 2:** Values of the rPLS for the first PLS axes for each of the five species, with respective p-values before (p) and after (p cor.) the Benjamini-
 926 Hochberg correction. Values in bold are the statistically significant ones (p or p cor. < 0.05). Abbreviations: Hum: Humerus; Rad: Radius; Uln:
 927 Ulna; Fem: Femur; Tib: Tibia; Fib: Fibula.

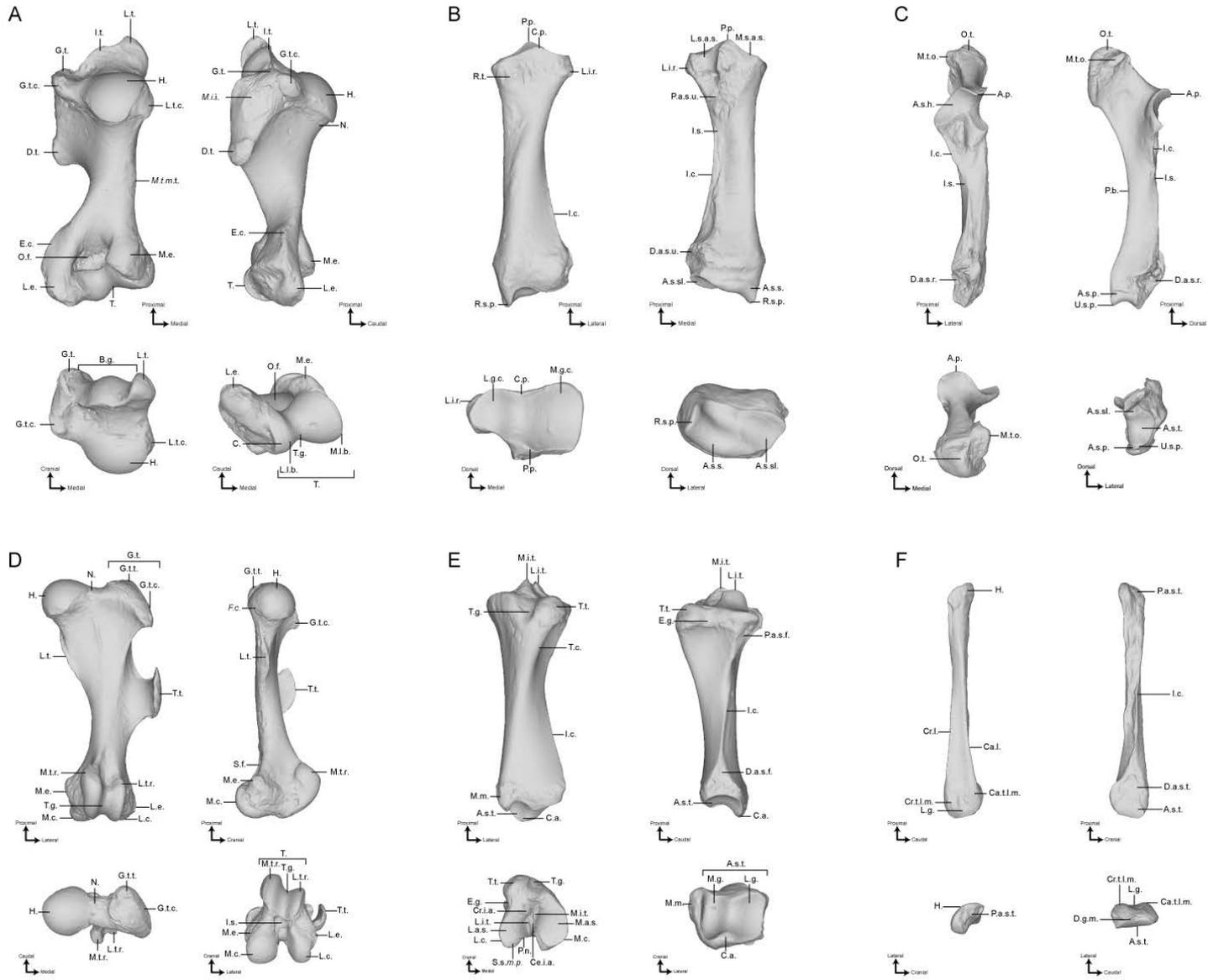
| | | <i>C. simum</i> (n=15) | | | <i>Ds. sumatrensis</i> (n=9) | | | <i>Dc. bicornis</i> (n=10) | | | <i>R. sondaicus</i> (n=7) | | | <i>R. unicornis</i> (n=9) | | |
|---|---------|------------------------|-------------|-------------|------------------------------|-------------|--------|----------------------------|-------------|--------|---------------------------|-------------|--------|---------------------------|-------------|--------|
| Paired bones | | rPLS | p | p cor. | rPLS | p | p cor. | rPLS | p | p cor. | rPLS | p | p cor. | rPLS | p | p cor. |
| Intra-limb bones | Hum-Rad | 0.92 | 0.01 | 0.04 | 0.85 | 0.40 | 0.59 | 0.89 | 0.19 | 0.55 | 0.98 | 0.01 | 0.10 | 0.90 | 0.37 | 0.59 |
| | Hum-Uln | 0.91 | 0.04 | 0.11 | 0.96 | 0.24 | 0.49 | 0.91 | 0.38 | 0.59 | 0.98 | 0.17 | 0.23 | 0.93 | 0.04 | 0.25 |
| | Rad-Uln | 0.88 | 0.07 | 0.16 | 0.91 | 0.28 | 0.49 | 0.96 | 0.11 | 0.55 | 0.97 | 0.09 | 0.15 | 0.95 | 0.48 | 0.59 |
| | Fem-Tib | 0.85 | 0.25 | 0.36 | 0.88 | 0.27 | 0.49 | 0.92 | 0.14 | 0.55 | 0.97 | 0.09 | 0.15 | 0.79 | 0.54 | 0.59 |
| | Fem-Fib | 0.78 | 0.87 | 0.87 | 0.87 | 0.95 | 0.95 | 0.87 | 0.29 | 0.55 | 0.95 | 0.26 | 0.30 | 0.84 | 0.55 | 0.59 |
| | Tib-Fib | 0.72 | 0.12 | 0.26 | 0.68 | 0.30 | 0.49 | 0.80 | 0.73 | 0.92 | 0.98 | 0.08 | 0.15 | 0.95 | 0.01 | 0.11 |
| Serial homology | Hum-Fem | 0.93 | 0.01 | 0.02 | 0.95 | 0.02 | 0.15 | 0.91 | 0.59 | 0.80 | 0.97 | 0.30 | 0.30 | 0.93 | 0.21 | 0.59 |
| | Rad-Tib | 0.90 | 0.27 | 0.36 | 0.70 | 0.77 | 0.95 | 0.94 | 0.23 | 0.55 | 0.98 | 0.03 | 0.10 | 0.93 | 0.51 | 0.59 |
| | Rad-Fib | 0.73 | 0.26 | 0.36 | 0.66 | 0.85 | 0.95 | 0.76 | 0.81 | 0.55 | 0.95 | 0.05 | 0.15 | 0.87 | 0.64 | 0.64 |
| | Uln-Tib | 0.84 | 0.36 | 0.41 | 0.92 | 0.29 | 0.49 | 0.94 | 0.05 | 0.55 | 0.97 | 0.09 | 0.15 | 0.91 | 0.05 | 0.25 |
| | Uln-Fib | 0.76 | 0.34 | 0.41 | 0.93 | 0.90 | 0.95 | 0.89 | 0.99 | 0.99 | 0.97 | 0.27 | 0.30 | 0.90 | 0.14 | 0.54 |
| Functional equivalence | Hum-Tib | 0.90 | 0.17 | 0.33 | 0.93 | 0.01 | 0.15 | 0.86 | 0.21 | 0.55 | 0.99 | 0.01 | 0.10 | 0.96 | 0.26 | 0.59 |
| | Hum-Fib | 0.77 | 0.65 | 0.69 | 0.80 | 0.63 | 0.85 | 0.90 | 0.81 | 0.93 | 0.95 | 0.11 | 0.16 | 0.91 | 0.48 | 0.59 |
| Non-homologous or functionally equivalent | Rad-Fem | 0.89 | 0.01 | 0.05 | 0.89 | 0.07 | 0.33 | 0.89 | 0.40 | 0.59 | 0.96 | 0.29 | 0.30 | 0.80 | 0.36 | 0.59 |
| | Uln-Fem | 0.94 | 0.01 | 0.04 | 0.93 | 0.19 | 0.49 | 0.89 | 0.86 | 0.93 | 0.98 | 0.02 | 0.10 | 0.97 | 0.37 | 0.59 |

928

929 **Supporting Information**

930 **Figure S1:** Summary of the anatomical areas of the rhino long bone. Bones figured here belong to *C.*
931 *simum*. **A: Humerus. Abbreviations** – B.g.: Bicipital groove; C.: Capitulum; D.t.: Deltoid tuberosity;
932 E.c.: Epicondylar crest; G.t.: Greater tubercle; G.t.c.: Greater tubercle convexity; H.: Head; I.t.:
933 Intermediate tubercle; L.e.: Lateral epicondyle; L.l.b.: Lateral lip border; L.t.: Lesser tubercle; L.t.c.:
934 Lesser tubercle convexity; M.e.: Medial epicondyle; M.i.i.: M. infraspinatus insertion; M.l.b.: Medial
935 lip border; M.t.m.t.: M. teres major tuberosity; N.: Neck; O.f.: Olecranon fossa; T.: Trochlea; T.g.:
936 Trochlear groove. **B: Radius. Abbreviations** – A.s.s.: Articular surface for the scaphoid; A.s.sl.:
937 Articular surface for the semilunar; C.p.: Coronoid process; D.a.s.u.: Distal articular surface for the
938 ulna; I.c.: Interosseous crest; I.s.: Interosseous space; L.g.c.: Lateral glenoid cavity; L.i.r.: Lateral
939 insertion relief; L.s.a.s.: Lateral synovial articular surface; M.g.c.: Medial glenoid cavity; M.s.a.s.:
940 Medial synovial articular surface; P.a.s.u.: Proximal articular surface for the ulna; P.p.: Palmar
941 process; R.s.p.: Radial styloid process; R.t.: Radial tuberosity. **C: Ulna. Abbreviations** – A.p.: Anconeal
942 process; A.s.h.: Articular surface for the humerus; A.s.p.: Articular surface for the pisiform; A.s.sl.:
943 Articular surface for the semilunar; A.s.t.: Articular surface for the triquetrum; D.a.s.r.: Distal articular
944 surface for the radius; I.c.: Interosseous crest; I.s.: Interosseous space; M.t.o.: Medial tuberosity of
945 the olecranon; O.t.: Olecranon tuberosity; P.b.: palmar border; U.s.p.: Ulnar styloid process. **D:**
946 **Femur. Abbreviations** – F.c.: Fovea capitis; G.t.: Greater trochanter; G.t.c.: Greater trochanter
947 convexity; G.t.t.: Greater trochanter top; H.: Head; I.s.: Intercondylar space; L.c.: Lateral condyle; L.e.:
948 Lateral epicondyle; L.t.r.: Lateral trochlear ridge; L.t.: Lesser trochanter; M.c.: Medial condyle; M.e.:
949 Medial epicondyle; M.t.r.: Medial trochlear ridge; N.: Neck; S.f.: supracondylar fossa; T.: Trochlea;
950 T.f.: Trochanteric fossa; T.g.: Trochlear groove; T.t.: Third trochanter. **E: Tibia. Abbreviations** – A.s.t.:
951 Articular surface for the talus; C.a.: Caudal apophysis; Ce.i.a.: Central intercondylar area; Cr.i.a.:
952 Cranial intercondylar area; D.a.s.f.: Distal articular surface for the fibula; E.g.: Extensor groove; I.c.:
953 Interosseous crest; L.a.s.: Lateral articular surface; L.c.: Lateral condyle; L.g.: Lateral groove; L.i.t.:
954 Lateral intercondylar tubercle; M.a.s.: Medial articular surface; M.c.: Medial condyle; M.g.: Medial
955 groove; M.i.t.: Medial intercondylar tubercle; M.m.: Medial malleolus; P.a.s.f.: Proximal articular
956 surface for the fibula; P.n.: Popliteal notch; S.s.m.p.: Sliding surface for the m. popliteus; T.c.: Tibial
957 crest; T.g.: Tuberosity groove; T.t.: Tibial tuberosity. **F: Fibula. Abbreviations** – A.s.t.: Articular surface
958 for the talus; Ca.l.: Caudo-lateral line; Ca.t.l.m.: Caudal tubercle of the lateral malleolus; Cr.l.: Cranio-
959 lateral line; Cr.t.l.m.: Cranial tubercle of the lateral malleolus; D.a.s.t.: Distal articular surface for the
960 tibia; D.g.m.: Distal groove of the malleolus; H.: Head; I.c.: Interosseous crest; L.g.: Lateral groove;
961 P.a.s.t.: Proximal articular surface for the tibia.

962



964 **Data S2:** Designation and location of the anatomical landmarks placed on each bone.

965

| Bone | Anatomical LM | Curve sliding semi-LM | Surface sliding semi-LM | Total |
|----------------|----------------------|------------------------------|--------------------------------|--------------|
| Humerus | 35 | 639 | 559 | 1233 |
| Radius | 23 | 393 | 493 | 909 |
| Ulna | 21 | 343 | 540 | 904 |
| Femur | 27 | 612 | 518 | 1157 |
| Tibia | 24 | 384 | 540 | 948 |
| Fibula | 12 | 269 | 454 | 735 |

966

967 **Table S2A:** Total number of anatomical landmarks (LM), curve sliding and surface sliding semi-
968 landmarks for each bone.

969

| LM | Designation |
|-----------|--|
| 1 | Most distal point of the lateral border of the bicipital groove |
| 2 | Most proximal point of the lateral border of the bicipital groove |
| 3 | Most proximal point of the intermediate tubercle |
| 4 | Most proximal point of the medial border of the bicipital groove |
| 5 | Most distal point of the medial border of the bicipital groove |
| 6 | Most distal point of the intermediate tubercle |
| 7 | Most medial point of the top of the lesser tubercle |
| 8 | Most cranial point of the lesser tubercle convexity |
| 9 | Most medio-caudal point of the lesser tubercle convexity |
| 10 | Most medial point of the humeral head surface |
| 11 | Most caudo-distal point of the humeral head surface |
| 12 | Contact point between the tricipital line and the caudal border of the articular head surface |
| 13 | Most lateral point of the humeral head surface |
| 14 | Most caudal point of the greater tubercle convexity |
| 15 | Most proximal point of the greater tubercle convexity |
| 16 | Most cranial point of the greater tubercle convexity crest |
| 17 | Most proximal point of the m. infraspinatus lateral insertion |
| 18 | Most distal point of the m. infraspinatus lateral insertion |
| 19 | Most proximal point of the deltoid tuberosity |
| 20 | Most distal point of the deltoid tuberosity |
| 21 | Most proximal point of the epicondylar crest tuberosity |
| 22 | Most distal point of the epicondylar crest tuberosity |
| 23 | Most lateral point of the lateral epicondyle |
| 24 | Most distal point of the lateral epicondyle |
| 25 | Most proximo-lateral point of the capitulum |
| 26 | Most cranio-proximal point of contact between the trochlea and the capitulum |
| 27 | Most cranial point of the trochlea groove |
| 28 | Most cranio-medial point of the dorsal side of the trochlea |
| 29 | Most distal contact point between the trochlea border and the medial development of the trochlea lip |
| 30 | Most cranio-medial point of the ventral side of the trochlea |
| 31 | Most cranio-lateral point of the ventral side of the trochlea |
| 32 | Most caudo-distal point of contact between the capitulum and the trochlea |
| 33 | Most medial point of the medial epicondyle |
| 34 | Most caudal point of the medial epicondyle |
| 35 | Most lateral point of the medial epicondyle |

970

971 **Table S2B:** Designation of the anatomical landmarks on the humerus.

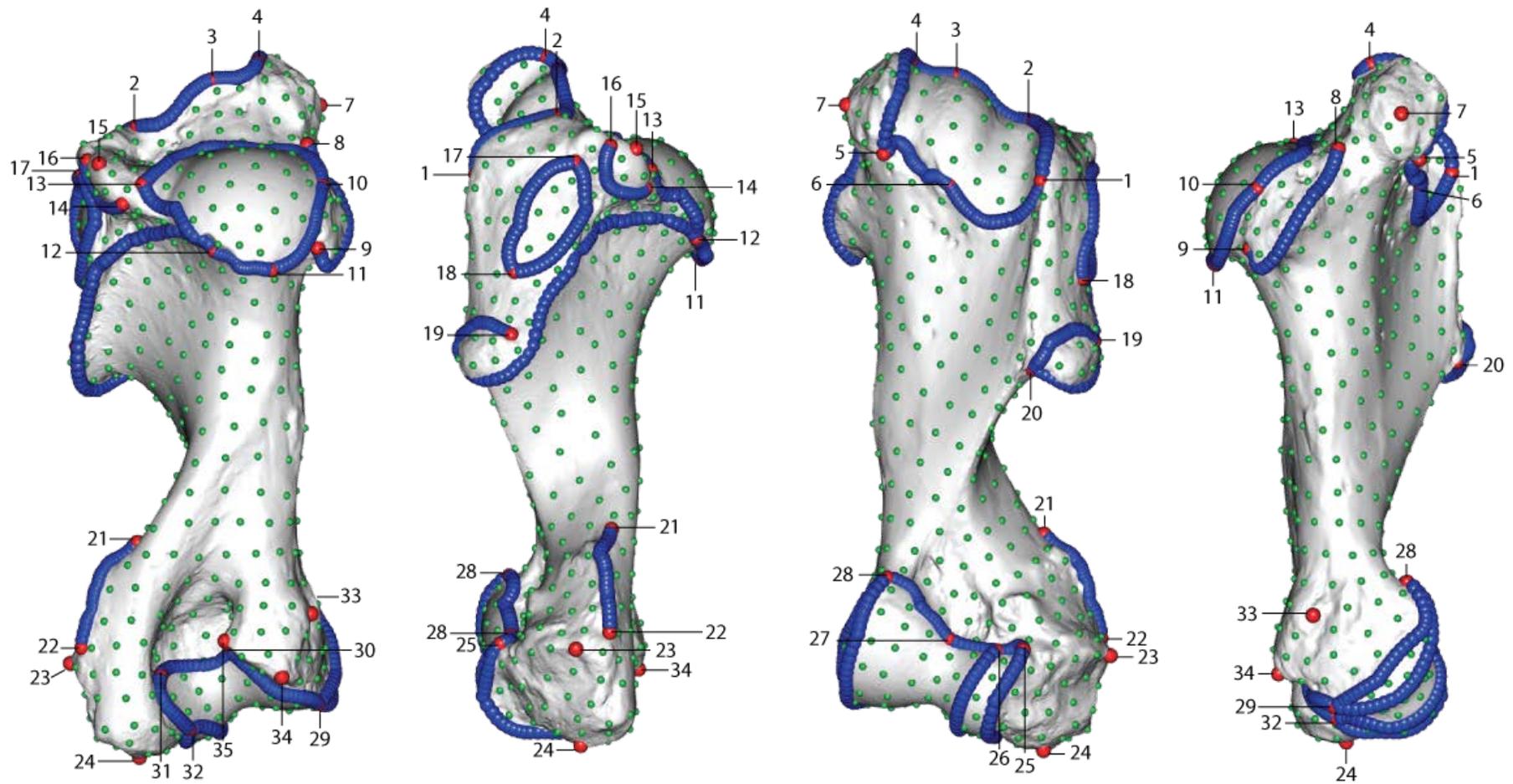


Figure S2C: Location of the anatomical landmarks (red spheres), curve sliding (blue spheres) and surface sliding (green spheres) semi-landmarks placed on the humerus. From left to right: caudal, lateral, cranial and medial views. Numbers refer to anatomical landmarks designation detailed in Table S1B.

| LM | Designation |
|-----------|---|
| 1 | Most caudo-lateral point of the lateral glenoid cavity |
| 2 | Most cranio-lateral point of the lateral glenoid cavity |
| 3 | Tip of the coronoid process |
| 4 | Most cranial point of the medial glenoid cavity |
| 5 | Most caudo-medial point of the medial glenoid cavity |
| 6 | Tip of the palmar process of the glenoid cavity ridge |
| 7 | Most cranial point of the lateral insertion relief |
| 8 | Most lateral point of the lateral insertion relief |
| 9 | Most caudo-distal point of the proximo-lateral articular facet for the ulna |
| 10 | Most caudo-distal point of the proximo-medial articular facet for the ulna |
| 11 | Most proximal point of the interosseous crest (= most distal point of the interosseous space) |
| 12 | Most distal point of the interosseous crest (crossing the distal epiphysis line) |
| 13 | Most cranio-lateral point of the disto-lateral articulation surface for ulna |
| 14 | Most proximo-lateral point of the disto-lateral articulation surface for ulna |
| 15 | Most caudo-lateral point of the disto-lateral articulation surface for ulna |
| 16 | Most medial point of the transversal crest |
| 17 | Tip of the radial styloid process |
| 18 | Maximum of curvature of the cranial ridge of the articular facet for the scaphoid |
| 19 | Most cranio-lateral point of the articular facet for the scaphoid |
| 20 | Most lateral point of the articular facet for the semilunar |
| 21 | Most caudo-lateral point of the articular facet for the semilunar |
| 22 | Most caudo-lateral point of the articular facet for the scaphoid |
| 23 | Most cranio-proximal point of the medial facet of distal radius |

Table S2D: Designation of the anatomical landmarks on the radius.

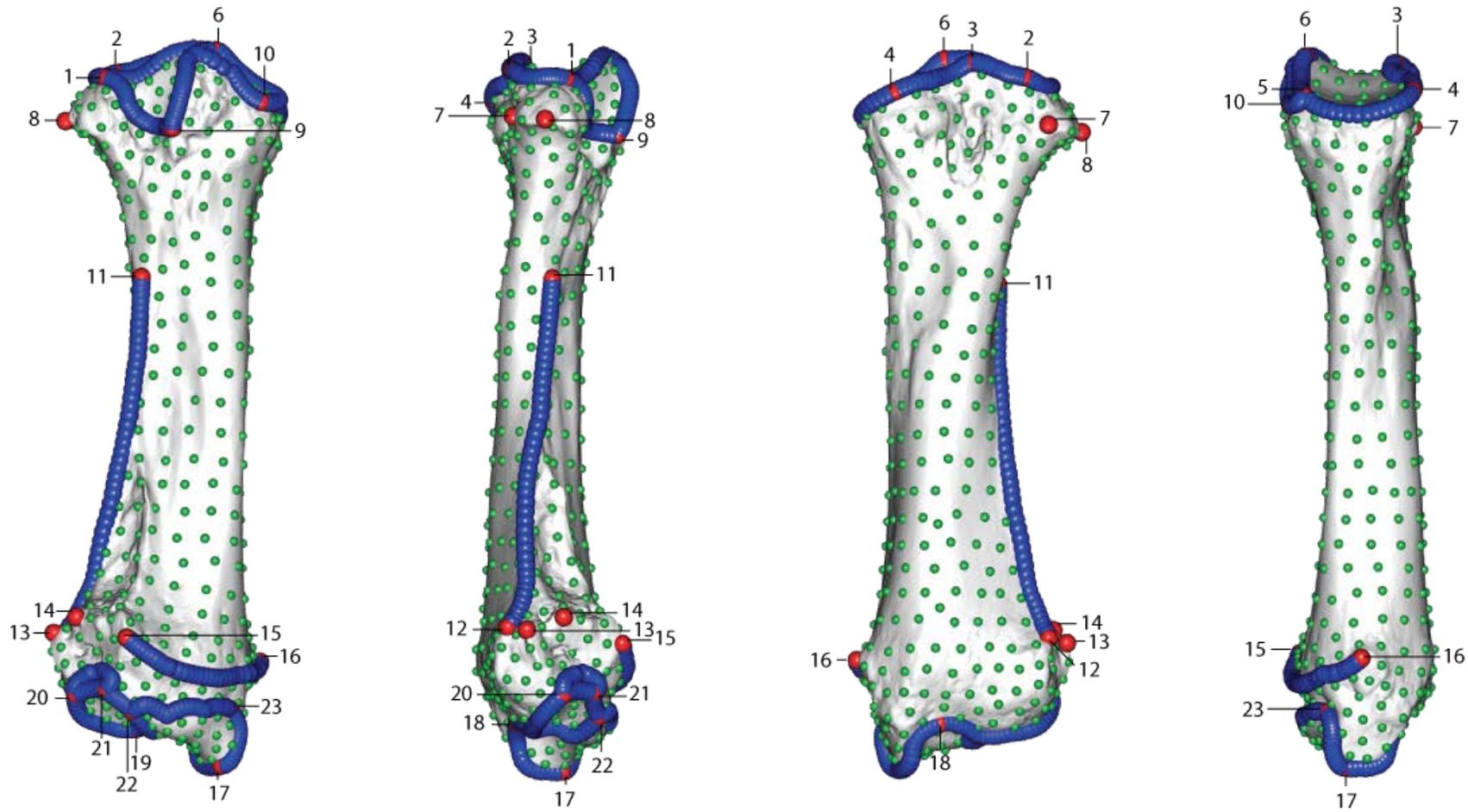


Figure S2E: Location of the anatomical landmarks (red spheres), curve sliding (blue spheres) and surface sliding (green spheres) semi-landmarks placed on the radius. From left to right: caudal, lateral, cranial and medial views. Numbers refer to anatomical landmarks designation detailed in Table S1D.

| LM | Designation |
|-----------|---|
| 1 | Most proximo-cranial point of the olecranon tuberosity cranial border |
| 2 | Most lateral point of the olecranon tuberosity |
| 3 | Most caudo-distal point of the olecranon tuberosity |
| 4 | Most medial point of the olecranon tuberosity |
| 5 | Most proximal point of the olecranon tuberosity |
| 6 | Cranial tip of the anconeal process |
| 7 | Most distal point of the lateral part of the trochlear notch articular surface |
| 8 | Maximum concavity point of the distal border of the trochlear notch articular surface |
| 9 | Most distal point of the medial part of the trochlear notch articular surface |
| 10 | Most distal point of the proximo-medial articular facet for the radius |
| 11 | Most distal point of the proximo-lateral articular facet for the radius |
| 12 | Most distal point of the proximal synostosis surface for the radius (= most proximal point of the interosseous space) |
| 13 | Most medio-caudal point of the distal radio-ulnar synostosis surface |
| 14 | Most disto-medial point of the articular surface with the semilunar bone |
| 15 | Most cranio-lateral point of the articular surface with the semilunar bone |
| 16 | Most disto-lateral point of the articular surface with the semilunar bone |
| 17 | Most cranio-lateral point of the distal radio-ulnar synostosis surface |
| 18 | Most lateral point of the distal epiphysis |
| 19 | Caudo-distal tip of ulnar styloid process |
| 20 | Most proximal contact point between the articular surfaces for the pisiform and the triquetrum |
| 21 | Most distal contact point between the caudal border of the ulna and the articular surface with the pisiform |

Table S2F: Designation of the anatomical landmarks on the ulna.

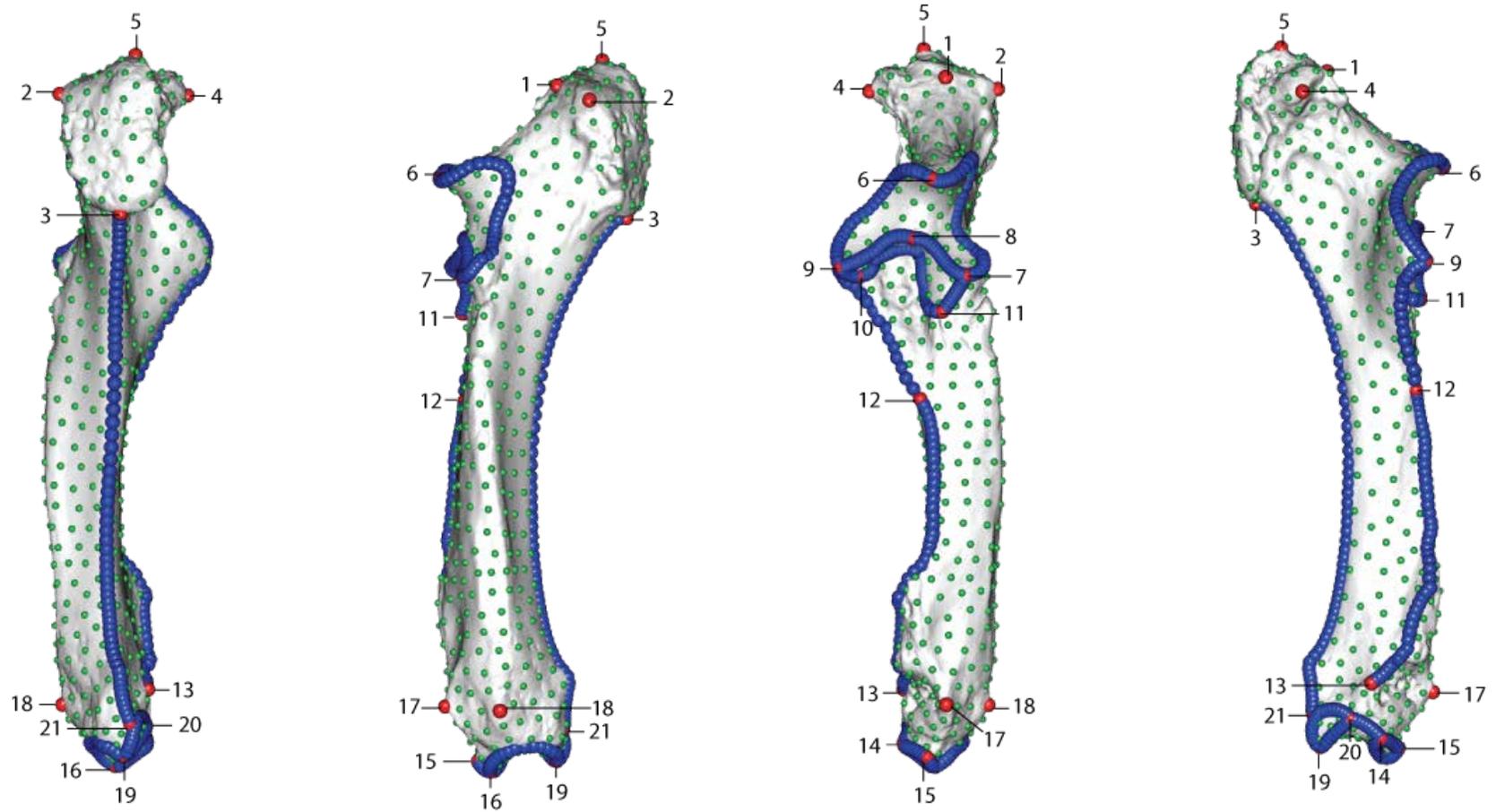


Figure S2G: Location of the anatomical landmarks (red spheres), curve sliding (blue spheres) and surface sliding (green spheres) semi-landmarks placed on the ulna. From left to right: caudal, lateral, cranial and medial views. Numbers refer to anatomical landmarks designation detailed in Table S1F.

| LM | Designation |
|-----------|--|
| 1 | Most proximo-cranial point of the greater trochanter |
| 2 | Most proximo-caudal point of the greater trochanter |
| 3 | Most medial point of the greater trochanter convexity |
| 4 | Most distal point of the intertrochanteric crest |
| 5 | Most disto-caudal point of the greater trochanter |
| 6 | Most cranio-lateral point of the convexity of the greater trochanter |
| 7 | Most proximal contact point between the intertrochanteric line and the medial line of the cranial face |
| 8 | Most lateral point of the border of the head |
| 9 | Most proximal point of the lesser trochanter |
| 10 | Most distal point of the lesser trochanter |
| 11 | Most proximal point of the gluteal tuberosity on the third trochanter |
| 12 | Most distal point of the gluteal tuberosity on the third trochanter |
| 13 | Most medial point of the medial epicondyle |
| 14 | Contact point between the intercondylar line and the medial condyle |
| 15 | Contact point between the intercondylar line and the lateral condyle |
| 16 | Most lateral point of the lateral epicondyle |
| 17 | Most proximal point of the lateral lip of the trochlea |
| 18 | Most proximal point of the trochlear groove |
| 19 | Most proximal point of the medial lip of the trochlea |
| 20 | Most distal point of the medial lip of the trochlea |
| 21 | Distal maximum of curvature of the trochlear groove |
| 22 | Most distal point of the lateral lip of the trochlea |
| 23 | Most medial point of the fossa extensoria |
| 24 | Most lateral point of the fossa extensoria |
| 25 | Most cranial point of the fossa extensoria |
| 26 | Most proximo-medial point of the lateral condyle articular surface |
| 27 | Most proximo-lateral point of the medial condyle articular surface |

Table S2H: Designation of the anatomical landmarks on the femur.

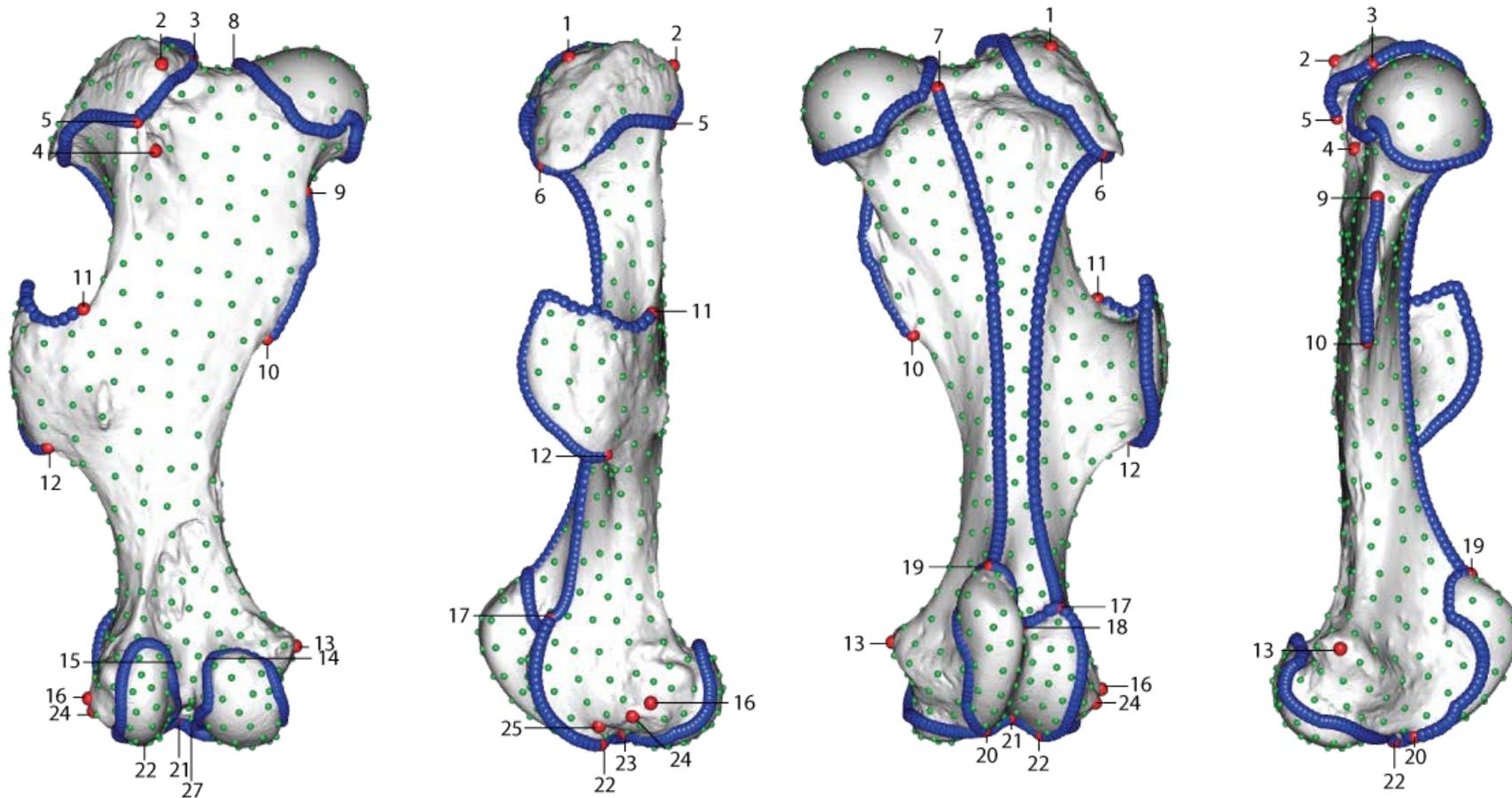


Figure S21: Location of the anatomical landmarks (red spheres), curve sliding (blue spheres) and surface sliding (green spheres) semi-landmarks placed on the femur. From left to right: caudal, lateral, cranial and medial views. Numbers refer to anatomical landmarks designation detailed in Table S1H. Landmark n°26 situated in the intercondylar space cannot be seen.

| LM | Designation |
|-----------|--|
| 1 | Most proximal point of the lateral tubercle of the intercondylar eminence |
| 2 | Most proximo-cranial point of the lateral tubercle of the intercondylar eminence |
| 3 | Most cranial point of the articular surface of the lateral condyle |
| 4 | Most caudal point of the articular surface of the lateral condyle |
| 5 | Most caudal point of the lateral tubercle of the intercondylar eminence |
| 6 | Most caudo-proximal point of the medial tubercle of the intercondylar eminence |
| 7 | Most proximal point of the medial tubercle of the intercondylar eminence |
| 8 | Most cranial point of the articular surface of the medial condyle |
| 9 | Most caudal point of the articular surface of the medial condyle |
| 10 | Most proximal point of the proximal tibio-fibular synostosis surface |
| 11 | Most distal point of the proximal tibio-fibular synostosis surface |
| 12 | Most proximal point of the lateral part of the tibial tuberosity |
| 13 | Most distal point of the lateral part of the tibial tuberosity |
| 14 | Most distal point of the tibial tuberosity groove |
| 15 | Most proximal point of the medial part of the tibial tuberosity |
| 16 | Most caudal point of the medial condyle |
| 17 | Most proximal point of the distal tibio-fibular synostosis surface |
| 18 | Most caudo-lateral point of the distal articular surface |
| 19 | Most cranio-lateral point of the distal articular surface |
| 20 | Most cranio-distal point of the intermediate ridge of the distal articular surface |
| 21 | Most distal point of the contact between the medial malleolus and the distal articular surface |
| 22 | Most distal point of the medial part of the distal articular surface |
| 23 | Most caudo-distal point of the intermediate ridge of the distal articular surface |
| 24 | Most medial point of the medial malleolus |

Table S2J: Designation of the anatomical landmarks on the tibia.

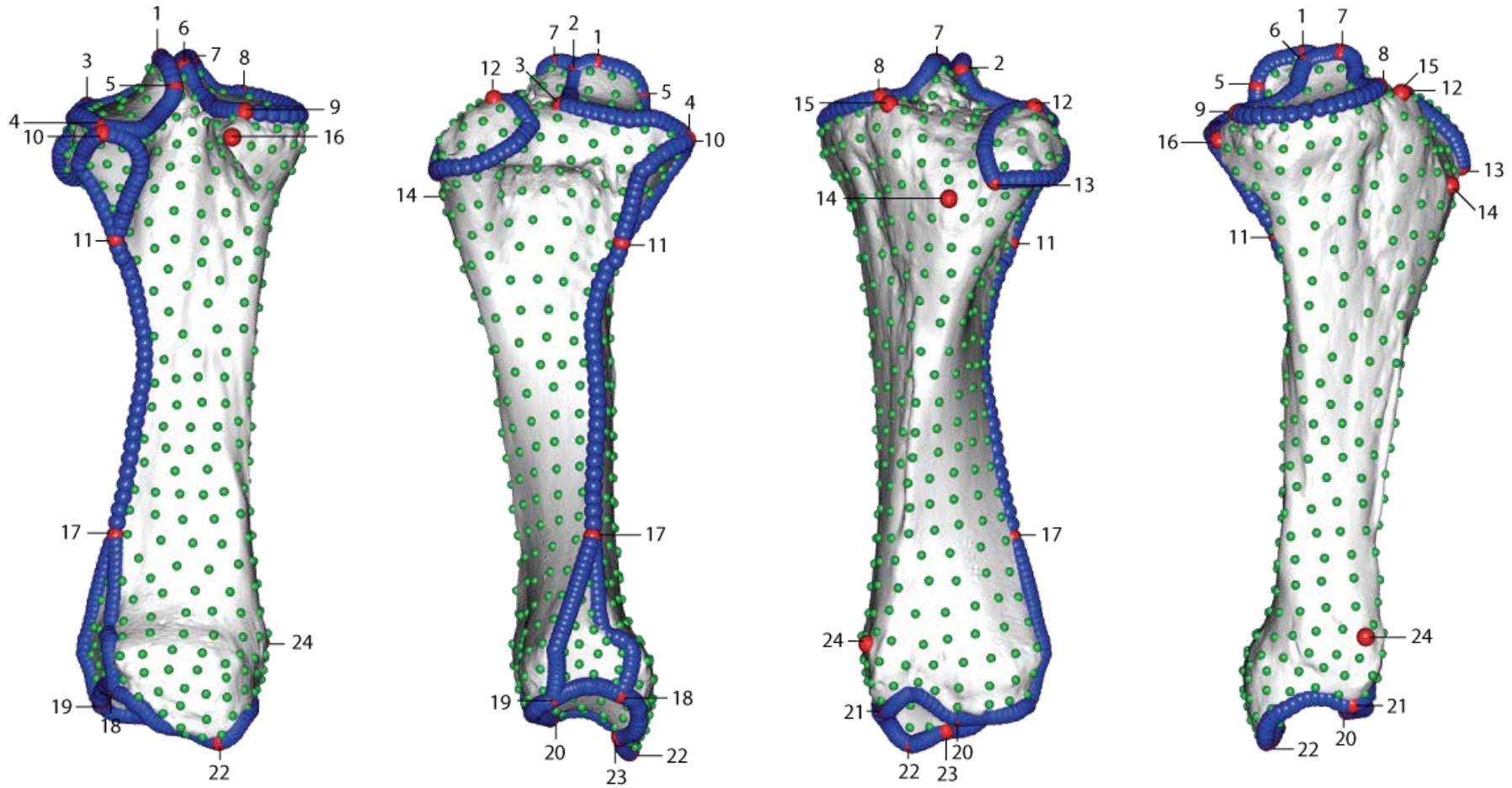
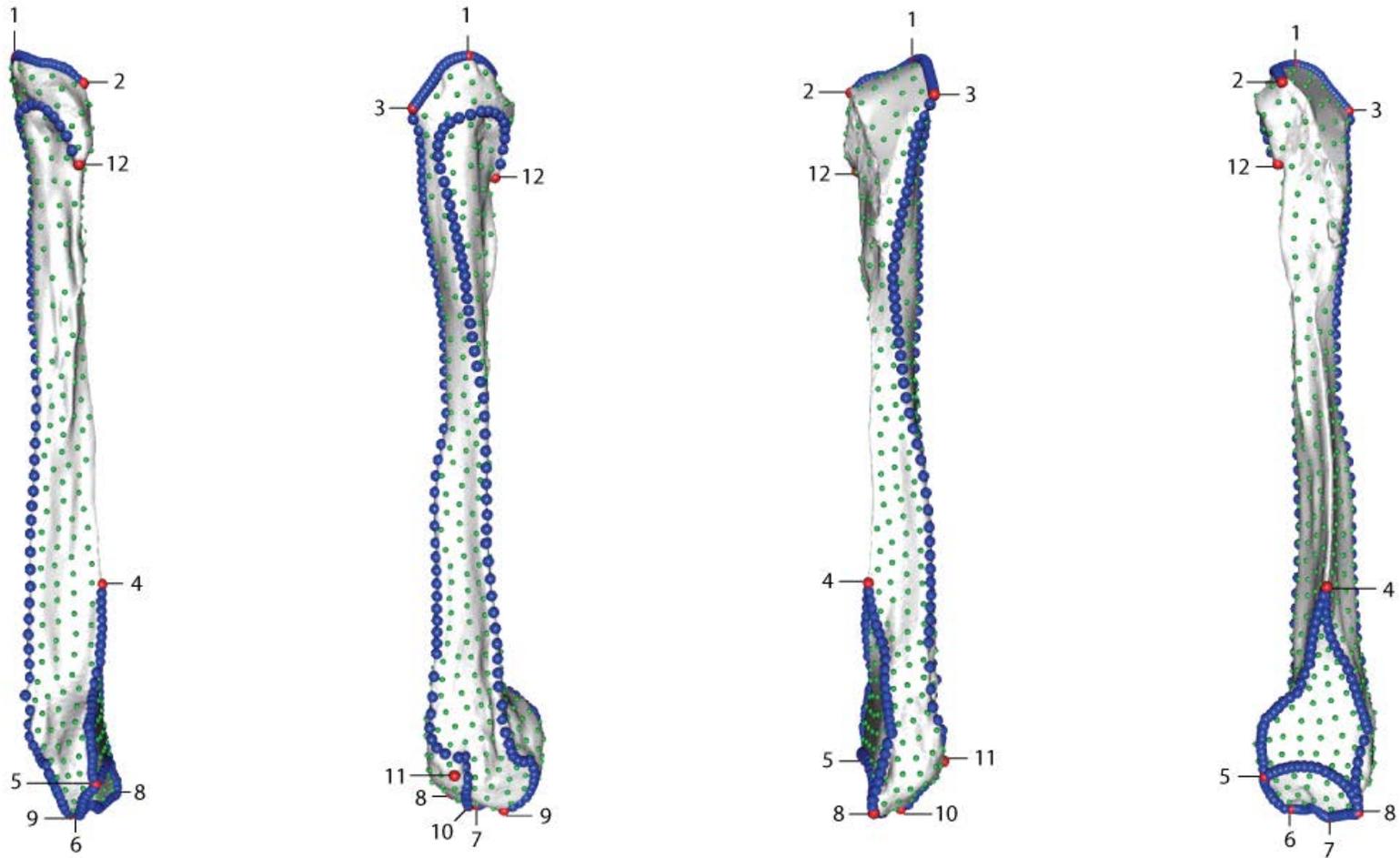


Figure S2K: Location of the anatomical landmarks (red spheres), curve sliding (blue spheres) and surface sliding (green spheres) semi-landmarks placed on the tibia. From left to right: caudal, lateral, cranial and medial views. Numbers refer to anatomical landmarks designation detailed in Table S1J.

| LM | Designation |
|-----------|--|
| 1 | Most proximal point of the proximal tibio-fibular synostosis surface |
| 2 | Most caudo-medial point of the proximal tibio-fibular synostosis surface |
| 3 | Most cranio-lateral point of the proximal tibio-fibular synostosis surface |
| 4 | Most proximal point of the distal tibio-fibular synostosis surface |
| 5 | Most caudal point of the distal articular facet |
| 6 | Most distal point of the caudal part of the distal articular facet |
| 7 | Most distal point of the cranial part of the distal articular facet |
| 8 | Most cranial point of the distal articular facet |
| 9 | Distal tip of the caudal ridge of the lateral malleolar sulcus |
| 10 | Distal tip of the cranial ridge of the lateral malleolar sulcus |
| 11 | Most lateral point of the cranial ridge of the lateral malleolar sulcus |
| 12 | Most disto-medial point of the proximal epiphysis = end of the latero-caudal crest |

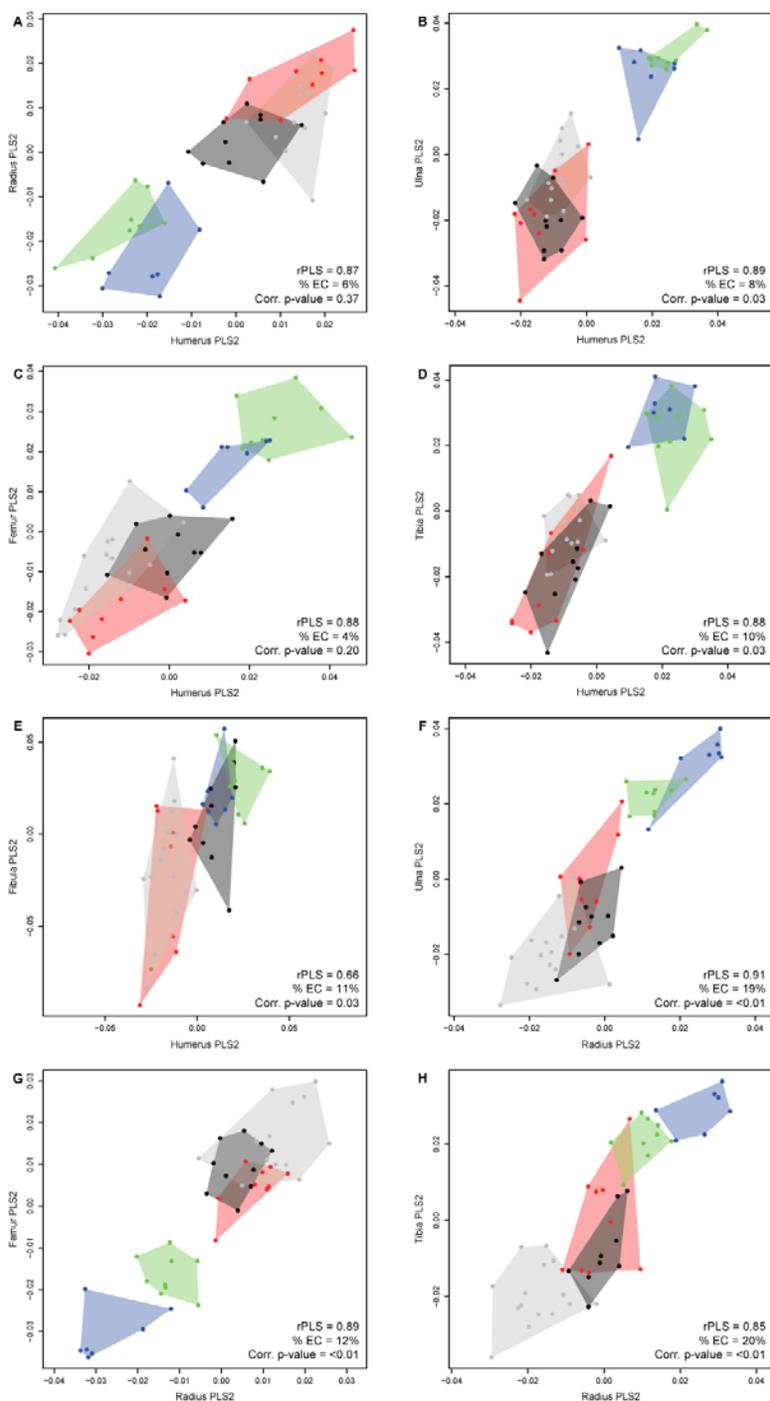
0 **Table S2L:** Designation of the anatomical landmarks on the fibula.

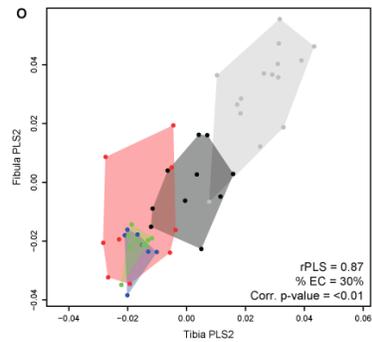
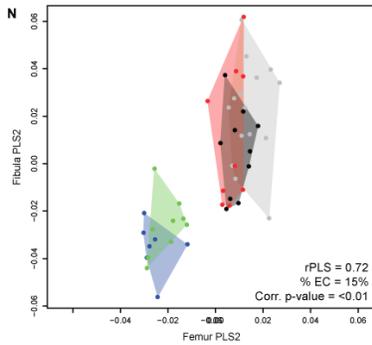
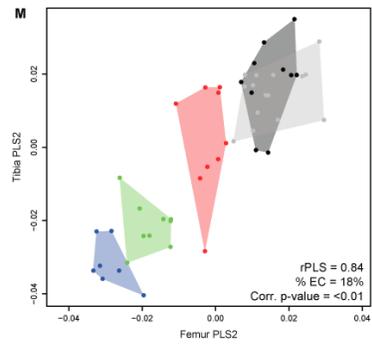
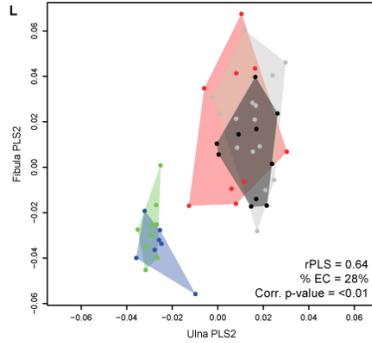
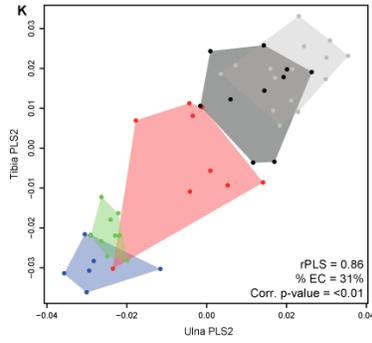
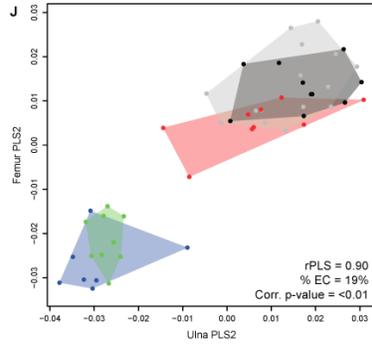
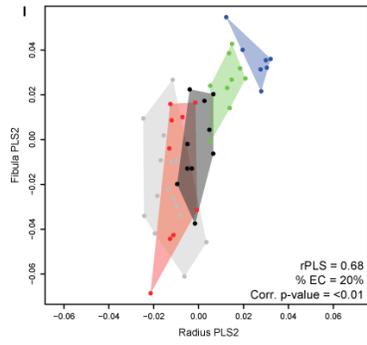


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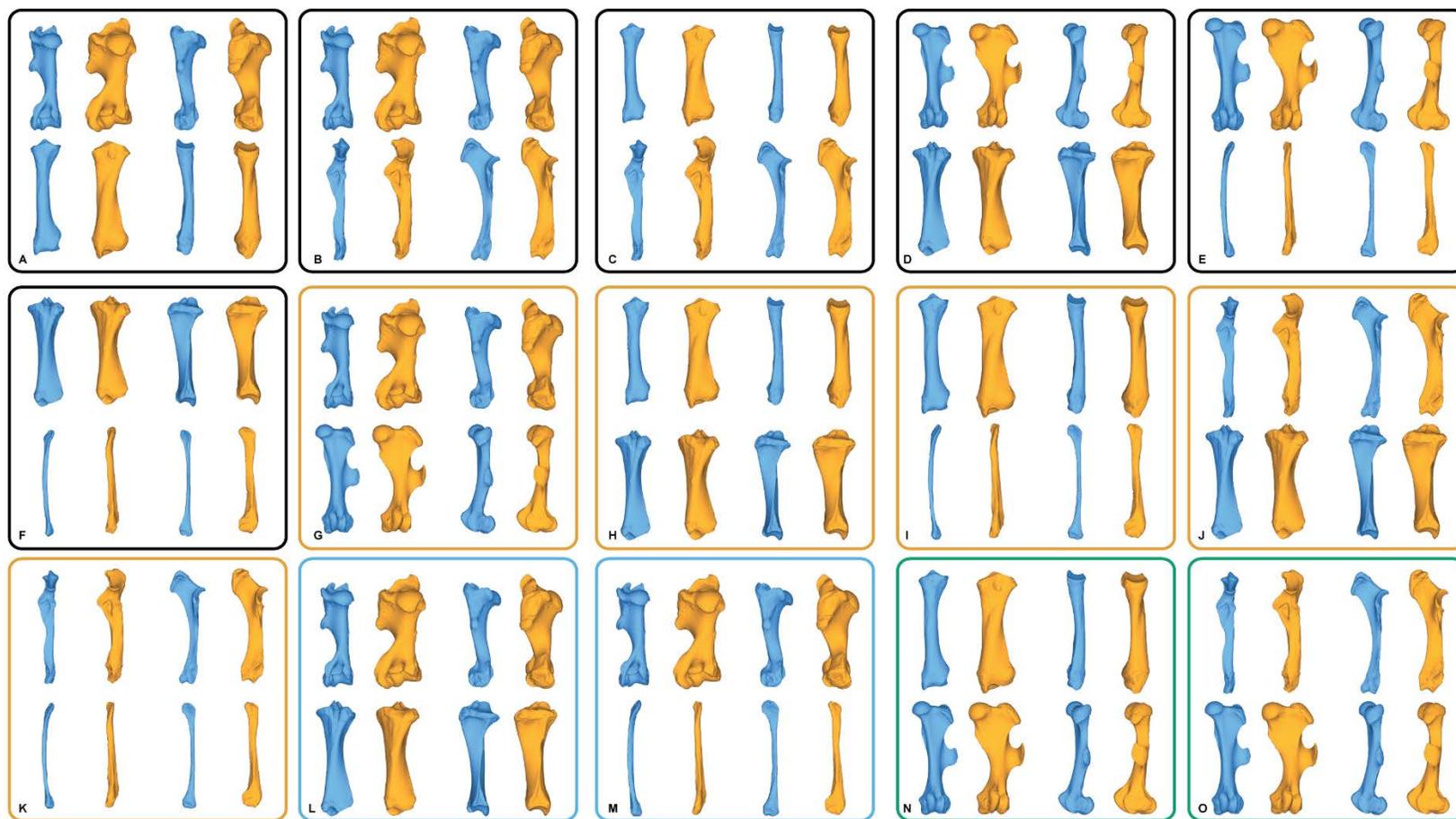
2 **Figure S2M:** Location of the anatomical landmarks (red spheres), curve sliding (blue spheres) and surface sliding (green spheres) semi-landmarks
 3 placed on the fibula. From left to right: caudal, lateral, cranial and medial views. Numbers refer to anatomical landmarks designation detailed in
 4 Table S1L.

5 **Figure S3:** Plots of the second PLS axes computed on raw shapes. A: humerus-radius; B: humerus-ulna; C:
6 humerus-femur; D: humerus-tibia; E: humerus-fibula; F: radius-ulna; G: radius-femur; H: radius-tibia; I:
7 radius-fibula; J: ulna-femur; K: ulna-tibia; L: ulna-fibula; M: femur-tibia; N: femur-fibula; O: tibia-fibula.
8 rPLS: value of the PLS coefficient; % EC: percentage of explained covariation; Corr. p-value: corrected p-
9 value using a Benjamini-Hochberg correction.





11 **Figure S4:** Shape deformations associated with the first PLS axes for the fifteen bone pairs. Blue: negative side of the axis. Orange: positive side of
 12 the axis. The colour code of the squares expresses the type of relation between bones as described in the Figure 1 (black: intra-limb relation;
 13 orange: serial homology; blue: functional analogy; green: non-homologous or analogous bones). A: humerus-radius; B: humerus-ulna; C: radius-
 14 ulna; D: femur-tibia; E: femur-fibula; F: tibia-fibula; G: humerus-femur; H: radius-tibia; I: radius-fibula; J: ulna-tibia; K: ulna-fibula; L: humerus-
 15 tibia; M: humerus-fibula; N: radius-femur; O: ulna-femur.

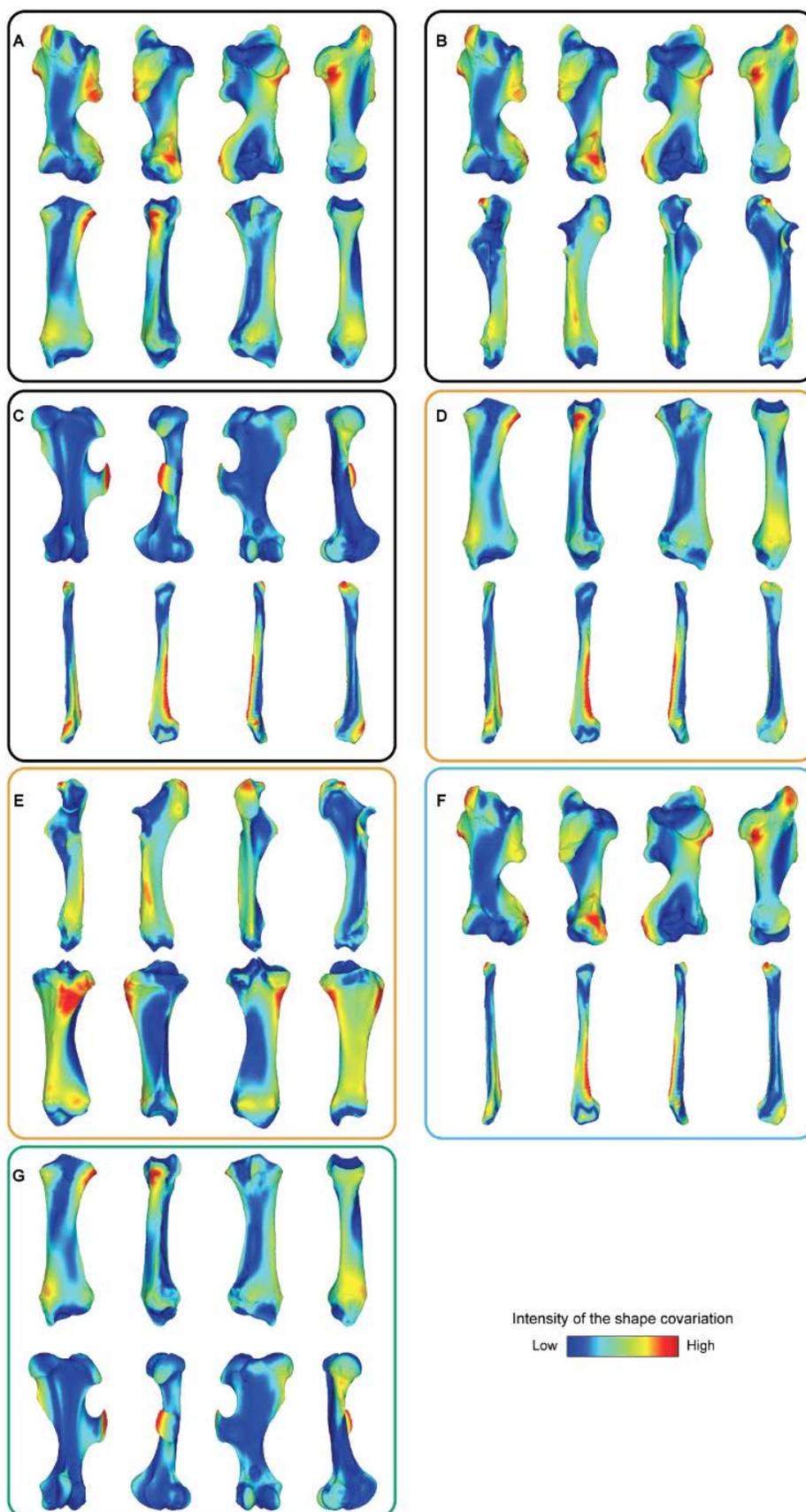


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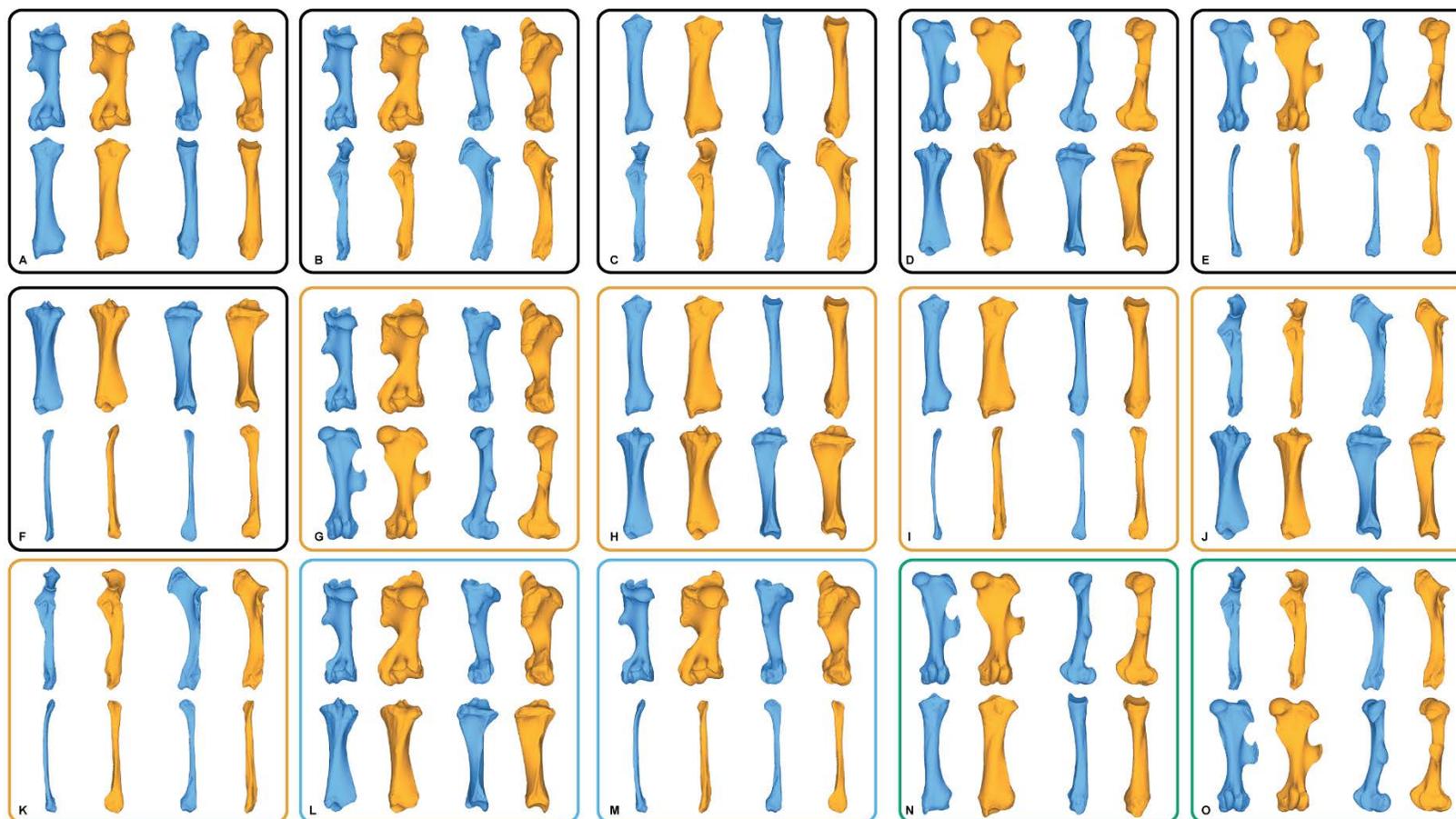
17 **Figure S5:** Colour maps of the location and intensity of the shape deformation associated to the first PLS
18 axes for 4 pairs of bones among the five species of rhinoceros. For each bone, the shape associated to
19 the positive part of the first PLS axis was coloured depending on its distance to the shape associated to
20 the negative part (blue indicates a low deformation intensity and red indicate a high deformation
21 intensity). The colour code of the squares expresses the type of relation between bones as described in
22 the Figure 1 (black: intra-limb relation; orange: serial homology; blue: functional analogy; green: non-
23 homologous or analogous bones). A: humerus-radius; B: humerus-ulna; C: femur-fibula; D: radius-fibula;
24 E: ulna-tibia; F: humerus-fibula; G: radius-femur (orientation from left to right in each case: cranial,
25 lateral, caudal and medial).

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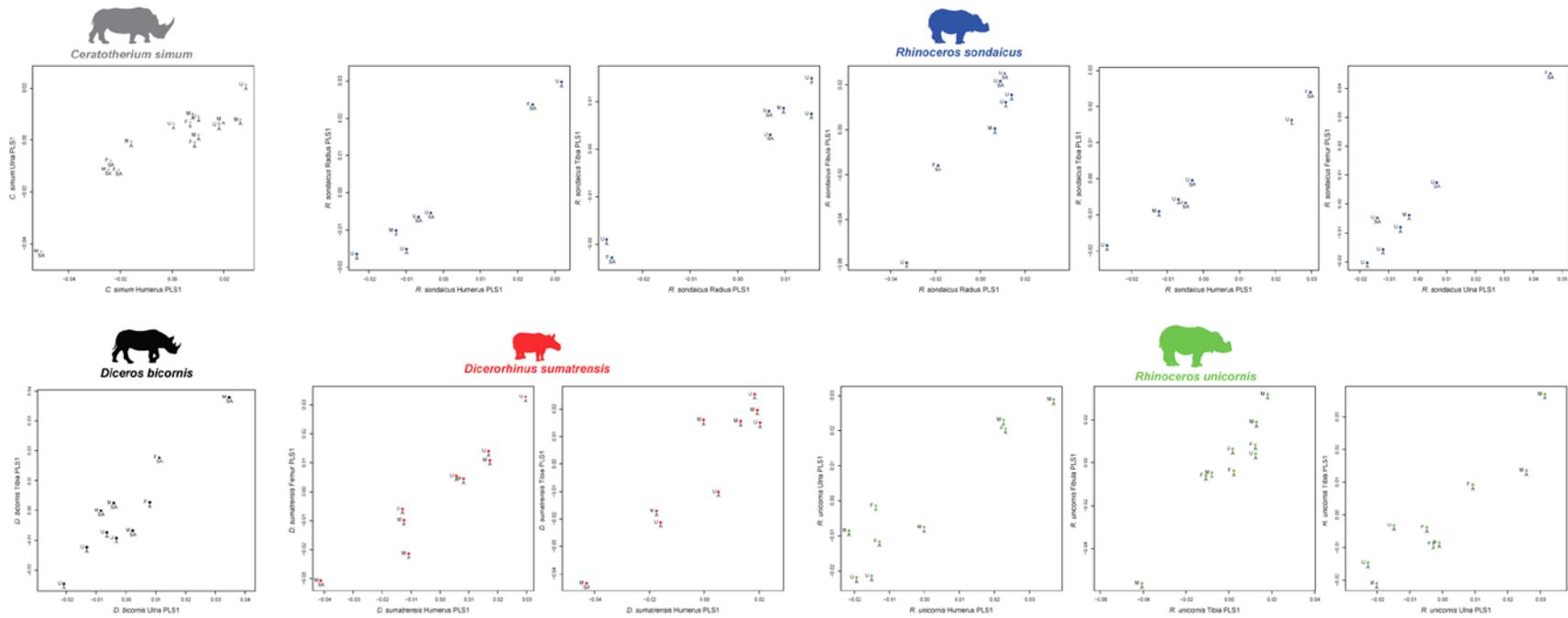


29 **Figure S6:** Shape deformations associated with the first PLS axes for the fifteen bone pairs. Blue: negative side of the axis. Orange: positive side of
 30 the axis. The colour code of the squares expresses the type of relation between bones as described in the Figure 1 (black: intra-limb relation;
 31 orange: serial homology; blue: functional analogy; green: non-homologous or analogous bones). A: humerus-radius; B: humerus-ulna; C: radius-
 32 ulna; D: femur-tibia; E: femur-fibula; F: tibia-fibula; G: humerus-femur; H: radius-tibia; I: radius-fibula; J: ulna-tibia; K: ulna-fibula; L: humerus-
 33 tibia; M: humerus-fibula; N: radius-femur; O: ulna-femur.



34

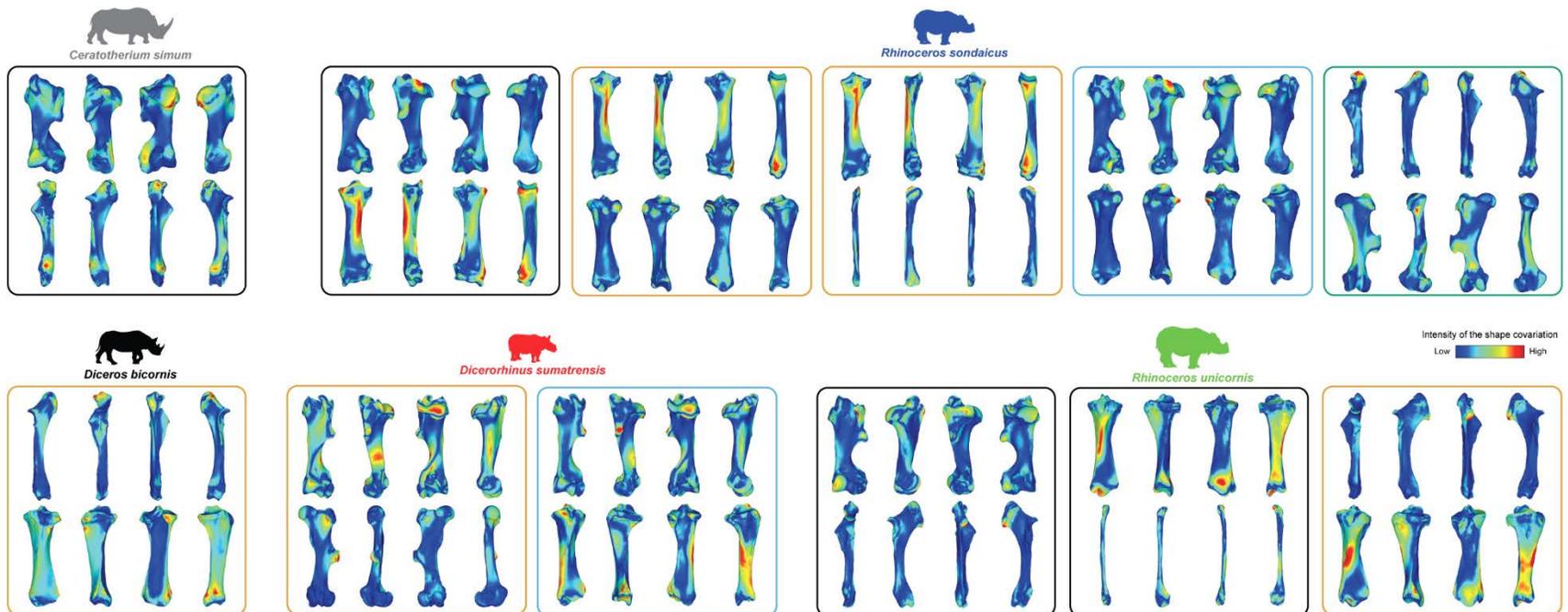
35 **Figure S7:** Plots of the first PLS axes computed at the intraspecific level for all the pairs displaying a significant p-value before the Benjamini-
 36 Hochberg correction. Abbreviations: A: adult; SA: subadult; M: male; F: female; U: sex unknown.



37

38

39 **Figure S8:** Colour maps of the location and intensity of the shape deformation associated to the first PLS axes for all the pairs displaying a
 40 significant p-value before the Benjamini-Hochberg correction. For each bone, the shape associated to the positive part of the first PLS axis was
 41 coloured depending on its distance to the shape associated to the negative part (blue indicates a low deformation intensity and red indicate a
 42 high deformation intensity). The colour code of the squares expresses the type of relation between bones as described in the Figure 1 (black:
 43 intra-limb relation; orange: serial homology; blue: functional analogy; green: non-homologous or analogous bones).



44

