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1 The effect of captivity on craniomandibular and calcaneal ontogenetic trajectories in wild boar

2 Short running title: Captivity and ontogenetic trajectories

3

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28 **Abstract**

29 Deciphering the plastic (i.e. non-heritable) changes induced by human control over wild animals in the  
30 archaeological record is challenging. Previous studies detected morphological markers associated with  
31 captivity in the cranium, mandible, and calcaneus of adult wild boar (*Sus scrofa*) but the developmental  
32 trajectories leading up to these changes during ontogeny remain unknown. To assess the impact of  
33 growth in a captive environment on morphological structures during postnatal ontogeny, we used an  
34 experimental approach focusing on the same three structures and taxon. We investigated the form and  
35 size differences of captive-reared and wild-caught wild boar during growth using three-dimensional  
36 (3D) landmark-based geometric morphometrics. Our results provide evidence of an influence of  
37 captivity on the morphology of craniomandibular structures, as wild specimens are smaller than captive  
38 individuals at similar ages. The food resources inherent to anthropogenic environments may explain  
39 some of the observed differences between captive-reared and wild specimens. The calcaneus presents  
40 a different contrasted pattern of plasticity as captive and wild individuals differ in terms of form but  
41 not in terms of size. The physically more constrained nature of the calcaneus and the direct influence  
42 of mobility reduction on this bone may explain these discrepancies. These results provide new  
43 methodological perspectives for bioarchaeological approaches as they imply that the plastic mark of  
44 captivity can be observed in juvenile specimens in the same way it has been previously described in  
45 adults.

46

47 **Keywords:** ontogeny, growth, domestication, geometric morphometrics, phenotypic plasticity

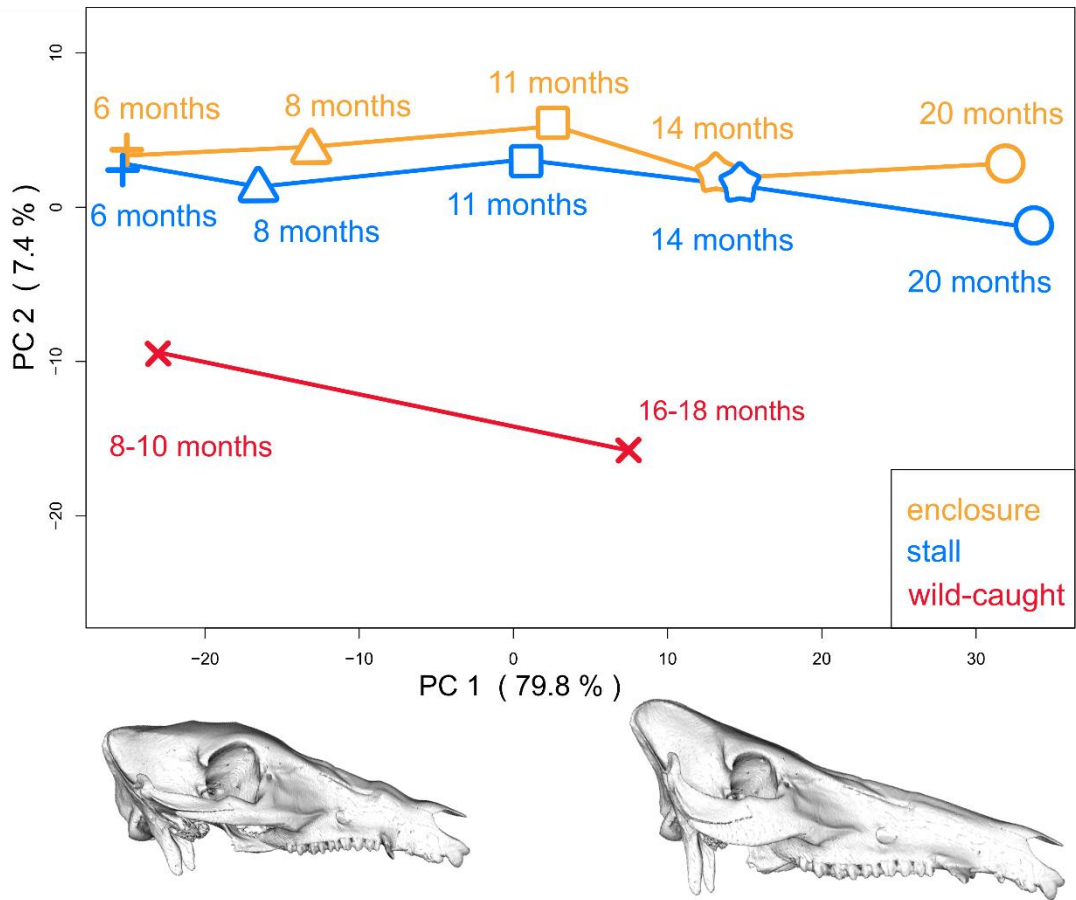
48

49 **Research Highlights**

50 We showed the influence of captivity, an early step of domestication, on the morphology of  
51 craniomandibular and postcranial structures during development. It underlines the plastic nature of  
52 bony structures and their ability to change in a short time period.

53

54 **Graphical Abstract**



55

## 56 **Introduction**

57 Animal domestication is an ongoing process (Vigne, 2011; Zeder, 2012) associated with substantial  
58 phenotypic changes that form part of the so-called domestication syndrome (Lord, Larson, Coppinger,  
59 & Karlsson, 2020; Sánchez-Villagra, Geiger, & Schneider, 2016; Zeder, 2012). Exploring the  
60 developmental mechanisms associated with the emergence of domestic phenotypes is crucial to  
61 document the roots of animal domestication over the last 15,000 years (Zeder, 2018).  
62 Zooarchaeologists previously considered that morphological changes observed in the archaeological  
63 record, such as bone shape and size modifications, were subsequent to the integration of animals into  
64 human society (Clutton-Brock, 1992) through adaptations to the new constraints of the anthropogenic  
65 environment (Price, 1999). Therefore, morphological markers have been deemed irrelevant to  
66 document the early processes of domestication (e.g. population control through captivity; Vigne,  
67 Carrère, Briois, & Guilaine, 2011), as they would only be detectable when genetic isolation and  
68 breeding selection are already in place (Frantz et al., 2015; Marshall, Dobney, Denham, & Capriles,  
69 2014). Yet, a series of recent experimental studies with wild boar (*Sus scrofa*) have demonstrated that  
70 early domestication steps, such as the control of wild animals, can be detected and quantified. These  
71 studies further showed that a lifetime in captivity induces changes in the functional demands (e.g.  
72 locomotor, foraging or feeding behaviours), modifying the shape of craniomandibular (Neaux, Blanc,  
73 Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli, Schafberg, et al., 2021) and  
74 postcranial (Harbers, Neaux, et al., 2020; Harbers, Zanolli, et al., 2020) bony structures. More  
75 importantly, these studies showed that captivity leaves an anatomical imprint on the musculoskeletal  
76 system beyond the phenotypic variation range observed in animals in their natural habitat. These results  
77 have been confirmed by studies on reindeer (*Rangifer tarandus*) comparing wild and captive  
78 populations (Pelletier, Kotiaho, Niinimäki, & Salmi, 2020, 2021).

79 While previous studies detected morphological markers associated with captivity in the cranium,  
80 mandible (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli,  
81 Schafberg, et al., 2021), and calcaneus (Harbers, Neaux, et al., 2020), and humerus (Harbers, Zanolli,  
82 et al., 2020) of adult specimens, the tempo of these changes during postnatal ontogeny remains  
83 unknown. Substantial differences in terms of shape and size between wild and captive animals have  
84 already been identified in mammals during growth but with contradictory results (O'Regan &  
85 Kitchener, 2005). While some studies found greater cranial dimensions in captive lion cubs (*Panthera*  
86 *leo*; Smuts, Anderson, & Austin, 1978) and captive-bred chinchillas (*Chinchilla lanigera*; Crossley &  
87 del Mar Miguélez, 2001), others showed a decrease in cranial dimensions in captive Indian  
88 rhinoceroses (*Rhinoceros unicornis*; Groves, 1982) and equids (*Equus* spp.; Groves, 1966). The  
89 morphological ontogenetic changes associated with captivity therefore remain to be understood.

90 To assess the impact of growth in a captive environment on morphological structures during postnatal  
91 ontogeny, we used an experimental approach focusing on the same bones and taxon on which  
92 morphological markers associated with captivity were detected, i.e. the cranium, mandible (Neaux,  
93 Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli, Schafberg, et al., 2021),  
94 and calcaneus (Harbers, Neaux, et al., 2020) of wild boar. We collected weaned wild boar piglets from  
95 a genetically homogenous population and raised them in a captive anthropogenic environment from  
96 the age of 6 months. We scanned them *in vivo* at five different age classes and compared them with  
97 wild-caught wild boar populations.

98 To determine the influence of captivity on the growth and development of the wild boar skeleton, we  
99 compared ontogenetic changes in form (i.e. size and shape) and size between captive-reared and wild-  
100 caught specimens. We predicted that form and size differences should not differ significantly at an  
101 early age but should rather start diverging in later age classes, when the effect of captivity on  
102 morphological structures becomes more prominent. Next, we investigated differences in ontogenetic



103 allometry, i.e. the relationship between shape and size over the course of ontogeny at different ages  
104 (Alberch, Gould, Oster, & Wake, 1979; Klingenberg, 2016), as allometry has been shown to affect  
105 postnatal ontogenetic trajectories in domesticated clades when compared to their wild counterparts  
106 (Sánchez-Villagra et al., 2017; Wilson, 2018). We hypothesized that differences in ontogenetic  
107 allometry should be significant between captive-reared and wild-caught wild boar, indicative of a  
108 plastic effect of captivity upon developmental trajectories.

## 109 **Methods**

### 110 **Experimental design**

111 Captive wild boar groups (Appendix S1) consist of wild boar from the DOMEXP project: a  
112 multidisciplinary experiment aiming to assess the effect of captivity on the musculoskeletal system  
113 (<http://anr-domexp.cnrs.fr/>). They include the same specimens that were studied as adults by Neaux et  
114 al. (2021; 2021) and Harbers et al. (2020; 2020). We relied on a control population of wild boar living  
115 in a 100,000 m<sup>2</sup> fenced forest in Urciers (France). These specimens came from a wild boar farm, where  
116 human interactions are intentionally kept to a minimum in order to ensure that the behaviour of the  
117 wild boar remains as natural as possible. They are free to forage for food in the woods. From this  
118 population, we sampled 24 piglets that were divided into two groups of 12 specimens of equal sex ratio  
119 (6 males and 6 females). These groups were raised from the age of 6 months at the zoological reserve  
120 of La Haute-Touche (France) in two different contexts of mobility reduction: a 3,000 m<sup>2</sup> wooded pen  
121 ('enclosure' group) and an indoor stall of 100 m<sup>2</sup> ('stall' group). These space restrictions respectively  
122 represent a reduction of 97% and 99.9% of the range of the control population and do not allow the  
123 captive specimens to roam as freely as animals from natural populations of wild boar (Palencia et al.,  
124 2019; Russo, Massei, & Genov, 1997). We supplied individuals from both groups with processed dry  
125 food pellets including 15.5% of raw proteins adapted for domestic pig diet. These specimens were  
126 repeatedly scanned *in vivo* at the age of 6, 8, 11, 14, and 20 months, using a Computed Tomography

127 (CT) scanner with a spatial resolution of between 100 and 500  $\mu\text{m}$  at the Chirurgie et Imagerie pour la  
128 Recherche et l'Enseignement (CIRE) platform of the Institut National de Recherche pour l'Agriculture,  
129 l'Alimentation et l'Environnement (INRAE). This experiment received ethics approval from the French  
130 Ministère de l'Enseignement Supérieur, de la Recherche et de l'Innovation (APAFIS#5353-  
131 201605111133847).

### 132 **Comparative wild-caught wild boar samples**

133 For comparison with the two captive groups, we collected free-ranging specimens ('wild-caught'  
134 group). This group included 6 individuals from the control free-ranging population of Urciers (100,000  
135  $\text{m}^2$ ) mentioned previously. Also included in the 'wild-caught' groups are 15 free-ranging wild boar that  
136 were sampled in the forests of Chambord and Compiègne (approximated at 54,400,000  $\text{m}^2$  and  
137 150,000,000  $\text{m}^2$  respectively; Harbers, Neaux, et al., 2020), belonging to similar geographic and  
138 climatic environment (i.e. temperate central France), to reduce the confounding effects of geographic  
139 and climate-induced morphological variation known to exist in *Sus scrofa* (Albarella, Dobney, &  
140 Rowley-Conwy, 2009; Groves, 2021; Iannucci, Sardella, Strani, & Mecozzi, 2020). Like most wild  
141 boar in western Europe, these free-ranging specimens likely had an omnivorous diet consisting mostly  
142 of plants (e.g. acorns, roots, and crops) supplemented with animal matter (e.g. insect and earthworms)  
143 as a primary source of protein (Schley & Roper, 2003). These specimens were wild-caught either  
144 between 8 and 10 months or between 16 and 18 months of age. We based age estimation on the  
145 mandibular tooth eruption and wear stages in occlusal view comparing our specimens with the charts  
146 developed by Grant (1982) and Horard-Herbin (1997). The selection of wild-caught specimens has  
147 been performed to match at best the age variation of captive specimens. Due to the inherent difficulty  
148 of collecting juvenile wild-caught specimens, the individuals from our study do not cover fully this  
149 variation, leading possibly to slight over-interpretation of results.

150

## 151 **Data acquisition and analyses**

152 We used homologous landmarks and semilandmarks placed on three-dimensional (3D) surfaces to  
153 describe the morphology. Digitisation and landmark definition were performed following published  
154 protocols (Appendix S2; Harbers, Neaux, et al., 2020; Neaux, Blanc, Ortiz, Locatelli, Laurens, et al.,  
155 2021; Neaux et al., 2020). We performed all the analyses in the R environment (R Core Team, 2019).  
156 Coordinates were aligned using a generalised Procrustes superimposition (Rohlf & Slice, 1990),  
157 implemented in the `procSym` function of the package ‘Morpho’ (Schlager & Jefferis, 2020).

158 We chose to work on form, i.e. the combination of size and shape (Dryden & Mardia, 1998), rather  
159 than shape as form is a more comprehensive description of an object than shape alone in the context of  
160 ontogenetic studies (Mitteroecker, Gunz, Windhager, & Schaefer, 2013). We constructed the form  
161 space by augmenting the Procrustes coordinates by the logarithm ( $\log$ ) of centroid size (CS;  
162 Mitteroecker, Gunz, Bernhard, Schaefer, & Bookstein, 2004). The exploratory approach of the major  
163 directions of variation in this form space relies on a principal component analysis (PCA) on form  
164 variables performed on the mean form of each age class of each of the three groups. We visualized the  
165 deformations between negative and positive scores on the first two principal components as well as the  
166 deformations between age classes for each of the three groups using heatmaps through the `meshDist`  
167 function of ‘Morpho’. The lack of congruence in age class among wild-caught groups and the two  
168 captive groups prevented us from directly comparing the ontogenetic trajectories (Adams & Collyer,  
169 2009). We therefore tested the difference in form between captive-reared and wild-caught groups using  
170 a factorial MANOVA through the `procD.lm` function of ‘the package ‘geomorph’ (Adams, Collyer, &  
171 Kaliontzopoulou, 2019). We also tested the difference in CS and in body mass (Appendix S3) between  
172 captive-reared and wild-caught groups with a pairwise test and visualized it graphically with a bivariate  
173 plot. Body masses were measured on a scale before each scan *in vivo* for the captive-reared specimens  
174 and on uneviscerated specimens for the wild-caught ones.

175 To estimate and compare ontogenetic allometries between the three groups, we used a multivariate  
176 regression (Drake & Klingenberg, 2008) between shape (Procrustes coordinates) and size, computed  
177 as log CS (Collyer, Sekora, & Adams, 2015). We displayed graphically the difference in ontogenetic  
178 trajectories among our three mobility groups using a biplot of regression shape scores against log CS  
179 and tested it with a MANCOVA through the `procD.lm` function.

180

## 181 **Results**

### 182 **Form**

183 The factorial MANOVA (Table 1) showed that the ‘8-10 month wild-caught’ cranium, mandible, and  
184 calcaneus forms are not significantly different from the 6-month and 8-month old captive forms (i.e.  
185 stall and enclosure). Those structures are different from those of all the older captive groups. The ‘16-  
186 18 month wild-caught’ group is not significantly different from the 11-month and 14-month captive  
187 groups for any of the studied structures. The mandible and calcaneus of this age class do not differ  
188 from those of the 8-month ‘enclosure’ nor from the 8-month ‘stall’ groups for the mandible. They are  
189 different from those of all the other captive groups (see Appendix S4 for the Factorial MANOVA  
190 between all groups).

191 For the PCA (Fig. 1), PC1 for the cranium, mandible, and calcaneus show respectively 79.8%, 86.1%,  
192 and 75.5% of the total variance. For the three studied structures, PC1 displays mostly changes  
193 associated with growth as the younger specimens have the lower PC scores and the older ones have the  
194 higher scores. The cranium form changes associated with positive scores involve (1) an  
195 anteroposteriorly longer and more concave rostrum, (2) more robust zygomatic arches, and (3) smaller  
196 orbits relative to the overall cranium size (Fig 1.a). For the mandible, the associated form changes  
197 towards positive scores include (1) a reduction of the gonial angle, (2) a longer corpus and mandibular

198 symphysis, and (3) a mediolateral reduction of the space between the two mandibular rami in dorsal  
199 view (Fig 1.b). For the calcaneus, the changes towards positive scores consisted in (1) a shift of the  
200 sustentaculum tali and of the calcaneal sulcus towards the distal extremity, (2) a more dorsoplantarily  
201 curved calcaneus, and (3) a more elongated epiphysis that is orientated toward the plantar side (Fig  
202 1.c). PC2 bear less variation in form for the cranium, mandible, and calcaneus (respectively 7.4%,  
203 5.1%, and 9.1% of the total variance) but clearly distinguishes captive and wild-caught specimens.  
204 Cranial form changes along PC2 from wild-caught (low values) to captive individuals (high values)  
205 involved (1) a narrower cranium in dorsal view, specifically in the zygomatic region, (2) a less vertical  
206 occipital region, and (3) an anteroposteriorly shorter nasal and maxillary region (Fig 1.a). The mandible  
207 form changes along PC2 are characterized by (1) a mediolateral narrowing, (2) a higher ramus, and (3)  
208 a ventrally orientated ramus (Fig 1.b). The calcaneus form changes along PC2 mainly express (1) a  
209 downward shift of the sustentaculum tali and (2) an epiphysis more orientated toward the plantar side  
210 (Fig. 1.c). From 6 months to 20 months, the main changes for captive specimens are localised on the  
211 zygomatic arches and on the occipital region for the cranium (Fig. 1.d), on the ramus and on the  
212 symphysis for the mandible (Fig. 1.e), and on the epiphysis, the sustentaculum tali, and the cuboid facet  
213 for the calcaneus (Fig. 1.f). From 8-10 months to 16-18 months, the changes for wild-caught specimens  
214 are localised on the same areas but are less prominent.

## 215 **Size**

216 The size of the '8-10 month wild-caught' group is not significantly different from the 6-month and 8-  
217 month captive groups for the cranium, mandible, and calcaneus (Fig. 2; Table 2). It is different from  
218 all the older captive groups. The '16-18 month wild-caught' group is not significantly different from  
219 the 11- and 14-month captive groups for the cranium, the 8-, 11- and 14-month captive groups for the  
220 mandible, and all the captive groups from 8 to 20 months for the calcaneus. The body mass of the '8-  
221 10 month wild-caught' is not significantly different from the 6-, 8- and 11-month captive groups and

222 the '16-18 month wild-caught' group is not significantly different from the 11- and 14-month captive  
223 groups and the '20 months – enclosure' group. All the other groups are statistically different.

#### 224 **Ontogenetic allometry**

225 We found overall ontogenetic allometry across all three structures in the three groups of mobility,  
226 which explains greater variation in calcaneus (26%) than in cranium (21%), and mandible (16%; Fig.  
227 3). The ontogenetic allometric trajectories depicted graphically are parallel between enclosure and stall  
228 captive groups across the three structures. They differ from the wild-caught group with a more positive  
229 allometry, although the interaction term was only significant for the calcaneus, indicative of a  
230 difference in allometric growth among the three groups for this structure.

#### 231 **Discussion**

232 For the cranium, mandible, and calcaneus, we found that the form and size of the '8-10 month wild-  
233 caught' wild boar are similar to those of younger captive specimens aged between 6 and 8 months, but  
234 are significantly different from the 11-month-old animals and older ones. This may suggest that the  
235 growth in captivity of a wild ungulate impacts the development of the three studied structures (O'Regan  
236 & Kitchener, 2005). Differences also exist later for the cranium and mandible, when the effect of the  
237 reduction of mobility on morphological structures becomes more prominent. Indeed, the form and size  
238 of the '16-18 month wild-caught' group are similar to the 11- and 14month-old captive specimens but  
239 statistically different from the 20-month-old ones. The same results are observed when comparing body  
240 mass between wild-caught and captive specimens. These results are strengthened by the fact that the  
241 wild-caught control specimens, belonging to the same initial herd as the captive ones, follow the same  
242 trend as the other wild-caught wild boar (see Fig. 1.a and 1.b). Unfortunately, 6-month-old wild-caught  
243 wild boar were not available. Yet, since the '8-10 month wild-caught' group is similar to the 6-month-  
244 old captive specimens, we could speculate that 6-month-old wild-caught wild boar would be similar to

245 younger specimens. This suggests that captive growth in wild boar induces a morphological divergence  
246 driven by an acceleration of changes in the size and form of the skull. This developmental delay in  
247 wild-caught wild boar compared to captive ones is characterised by a retention of more juvenile traits  
248 observed in younger wild specimens as evidenced by the MANOVA. This implies an increase in the  
249 developmental rate of captive wild boar when compared to that of wild-caught specimens. These  
250 findings are in line with previous studies on postnatal growth assessing that, for a given age, captive  
251 specimens are often significantly larger than wild-caught individuals. Comparing skeletal  
252 measurements, Zihlman et al. (2007) found that the tempo of growth in wild chimpanzees (*Pan*  
253 *troglydtes*) contrasts sharply with the rate demonstrated for captive individuals that can mature as  
254 much as 3 years earlier. Cheverud et al. (1992) also found a significant increase of the growth rate in  
255 toque macaques (*Macaca sinica*) raised in the laboratory when compared to wild specimens. Finally,  
256 captive-raised lion cubs were reported as being nearly twice the size of wild cubs of the same age  
257 (Schaller, 1973). The more consistently available food is probably the main cause of these differences  
258 (Turner, Cramer, Nisbett, & Gray, 2016). Indeed, one of the consequences of the spatial control of wild  
259 animals by humans is the presence of more constantly available food resources. As it is the case in the  
260 context of our experimental study, animals in captivity are regularly provisioned and do not need to  
261 spend energy searching for food, hence removing intra-group feeding competition. In addition,  
262 intrasexual competition is removed in stall specimens and drastically reduced for the pen specimens.  
263 Differences in cranial size during the postnatal development were previously described between  
264 domestic pigs and wild boar, especially in the neurocranial region, surrounding and protecting cerebral  
265 structures (Evin et al., 2017). Our study stresses that this increase of the size of neurocranial structures  
266 is not necessarily a product of the long selective breeding leading to the morphology observed in  
267 domestic pigs. Indeed, we observe a similar increase as a plastic response to captivity, considered as  
268 one of the earliest domestication steps (Vigne, 2011), most likely due to an unrestricted access to food

269 leading to a faster growth (Kimura & Hamada, 1996). Furthermore, these findings are consistent with  
270 recent studies suggesting that the commonly assumed reduction of brain size associated with  
271 domestication should be questioned (Lord, Larson, Coppinger, et al., 2020; Lord, Larson, & Karlsson,  
272 2020). Indeed, both early domestication steps, in the context of our study, and long term selective  
273 processes (Evin et al., 2017) result in a size increase and not a reduction of the structures surrounding  
274 the brain. Yet, although described previously (Finarelli, 2006; 2011), the presence of a clear positive  
275 relationship between brain size and cranial structures size is still unclear (Logan, & Palmstrom, 2015),  
276 highlighting the need for future studies directly addressing the evolution of endocranial shape and size  
277 in relation to domestication.

278 The calcaneus presents a different pattern when the specimens are older, i.e. when the effect of captivity  
279 becomes prominent as the '16-18 month wild-caught' group is similar to the 11-, 14-, and 20-month-  
280 old captive specimens in size. This result is supported by the fact that the wild-caught control specimens  
281 follow the same trend as the captive ones (see Fig. 1.c). The more physically constrained nature of the  
282 calcaneus, articulating with both the talus and the cuboid bones, may partly explain this difference. In  
283 this sense, Hanot et al (2017) described a strong and significant morphological integration between the  
284 calcaneus and talus in horses (*Equus caballus*). In comparison, lower level of integration were found  
285 between the cranium and mandible of wild boar, specifically for captive individuals (Neaux, Blanc,  
286 Ortiz, Locatelli, Schafberg, et al., 2021). This comparatively loose integration in the skull may allow  
287 more size variation, and a greater and more rapid growth of these structures in captive individuals.  
288 Further covariation studies of the tarsus of less specialized taxa than horses, such as wild boar, will  
289 help untangle the role of morphological integration in the observed differences between the  
290 craniomandibular and postcranial structures.

291 The calcaneus is subjected to high tensile, bending and compressive forces (Su, Skedros, Bachus, &  
292 Bloebaum, 1999) and has often being described has a key proxy to assess terrestrial mammal locomotor



293 behaviours (Bassarova, Janis, & Archer, 2009; Ginot, Hautier, Marivaux, & Vianey-Liaud, 2016;  
294 Panciroli, Janis, Stockdale, & Martín-Serra, 2017). In this respect, the phenotypic plasticity in shape  
295 (but not the size) of the calcaneus has been shown to capture the direct influence of the anthropogenic  
296 control of wild boar locomotor behaviour (Harbers, Neaux, et al., 2020). Conversely, the  
297 morphological modifications associated with the mandible in captive animals are not the direct  
298 consequence of mobility reduction but may rather be related to functional demands resulting from the  
299 anthropogenic environment (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021). They include the  
300 increase of feeding activity (Turner et al., 2016), the reduction of foraging behaviour (Mason & Mendl,  
301 1997), and the appearance of stereotypy (Rhodes et al., 2005), i.e. repeated sequences of movements  
302 with no obvious purpose, particularly common in captive animals (Fraser & Broom, 1990). In this  
303 sense, in PC2 of the PCA on the form space for the calcaneus, from negative to positive values, there  
304 is a clear gradient from wild-caught, to enclosure, to stall specimens (Fig. 1.c), while for the cranium  
305 (Fig. 1.a) and mandible (Fig. 1.b) captive individuals (i.e. enclosure and stall) are similar. This result  
306 is consistent with the hypothesis that the calcaneus captures mainly locomotor behaviour as the habitats  
307 of the wild-caught group is the larger ( $\geq 100,000 \text{ m}^2$ ), followed by the enclosure group ( $3,000 \text{ m}^2$ ) and  
308 finally the stall group ( $100 \text{ m}^2$ ). The PC2 for the cranium and mandible form space primarily records  
309 changes between the captive specimens (i.e. enclosure and stall) under anthropogenic control on the  
310 one hand and the wild-caught group on the other. This result is in line with the hypothesis that  
311 craniomandibular changes are not directly associated with a reduced mobility but rather with functional  
312 requirements resulting from the anthropogenic environment (e.g. feeding activity, foraging behaviour,  
313 stereotypy). The difference in the way captivity affects the calcaneus (direct influence) and the cranium  
314 and mandible (indirect influence) may explain this distinction and should be further explored.

315 The slope of the ontogenetic allometry for the cranium and mandible is not significantly different  
316 between captive-reared and wild-caught specimens. This result is in line with previous findings that

317 ontogenetic allometry generally does not evolve on short evolutionary time scales and that  
318 modifications of ontogenetic trajectories are usually achieved by heterochronic shifts along a shared  
319 slope rather than directional changes (Voje, Hansen, Egset, Bolstad, & Pélabon, 2014; Wilson, 2018).  
320 Moreover, previous results (Sánchez-Villagra et al., 2017;. Wilson, 2018) found no significant  
321 differences in the ontogenetic slopes between domestic pigs and wild boar contrary to dogs (*Canis*  
322 *lupus familiaris*) and wolves (*C. lupus*), and llamas (*Lama glama*) and guanacos (*L. guanicoe*). This is  
323 congruent with our results on wild boar captivity, as the control of mobility is considered one of the  
324 first steps of the domestication process leading to the morphology observed in modern pigs (Vigne,  
325 2011). The differences in the direction of the slope for the calcaneus shows that some level of  
326 directional change can nevertheless occur on a short-time scale. The distinctions between the skull and  
327 the calcaneus may once again arise from how mobility reduction influences these structures, i.e.  
328 respectively indirectly and directly.

## 329 **Conclusions**

330 Our results provide evidence that captivity influences the morphology of craniomandibular and  
331 postcranial structures of wild boar, as wild specimens are significantly smaller than captive individuals  
332 of a similar age. Consistently available food resources and the reduction of stress associated with the  
333 search for food and intra-group feeding competition may explain the distinction between captive-reared  
334 and wild specimens. The calcaneus presents a different pattern as captive and wild individuals differ  
335 in terms of form but not in terms of size. Furthermore, it is the only structure presenting differences in  
336 ontogenetic allometry. The more physically constrained nature of the calcaneus and the direct influence  
337 of mobility reduction on this bone may explain these specificities. These results provide new  
338 methodological perspectives for bioarchaeological approaches as they imply that the plastic mark of  
339 captivity can be observed in juvenile specimens as well as in adults (Cucchi et al., 2021; Harbers,  
340 Neaux, et al., 2020; Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli,

341 Schafberg, et al., 2021). Further studies need to explore the morphological integration during growth  
342 in captive conditions for both craniomandibular and postcranial structures in order to decipher the role  
343 of developmental and functional correlates between structures in generating the differences observed  
344 in our study.

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355

356 **Conflict of Interest Statement**

357 The authors declare no conflicts of interest.

358

359 **Data Availability Statement**

360 All analytical codes and data are freely available at: <https://zenodo.org/record/5547335> (Neaux,  
361 Harbers, Blanc, Ortiz, Locatelli, et al., 2021)

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- 554

555 Table 1. MANOVA  $p$ -values of the form coordinates between captive (stall and enclosure) and wild-  
 556 caught groups of wild boar (*Sus scrofa*) computed for the cranium, mandible, and calcaneus. Significant  
 557 values ( $p < 0.05$ ) are in bold. m.: months.

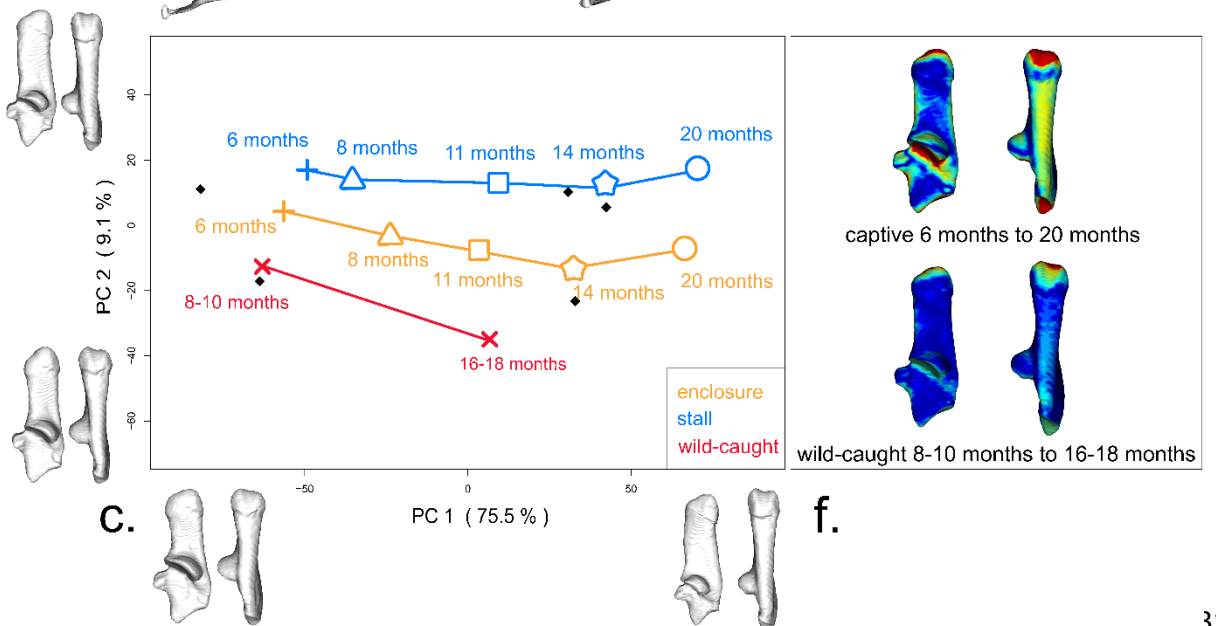
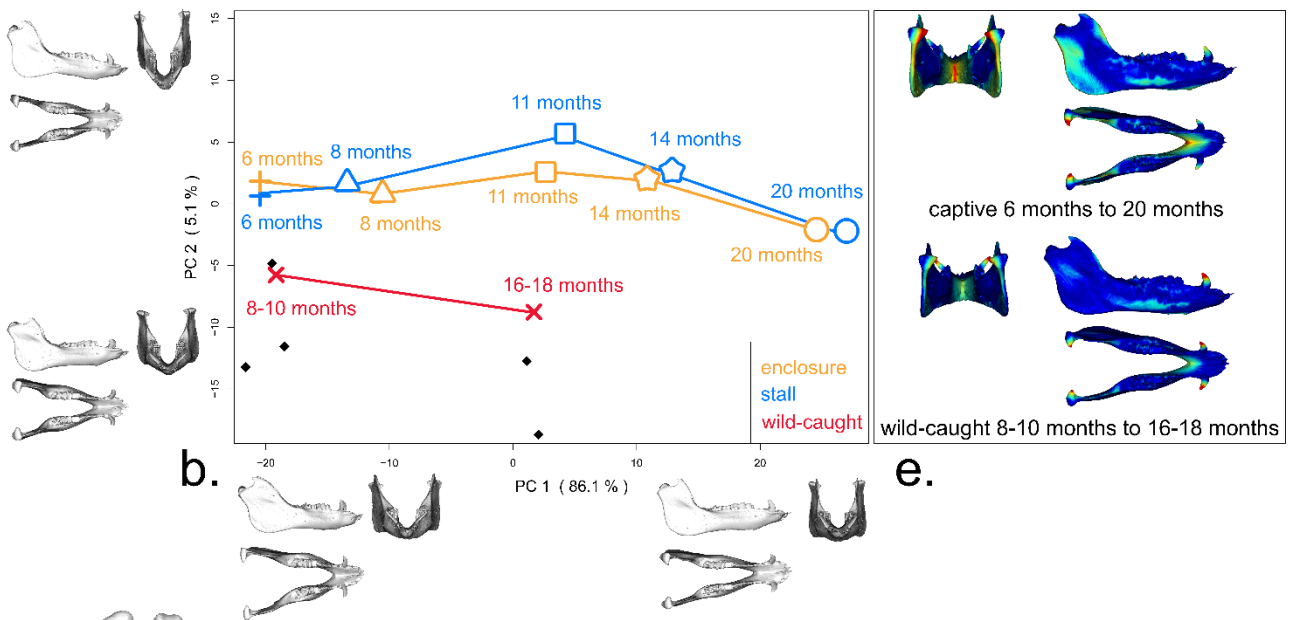
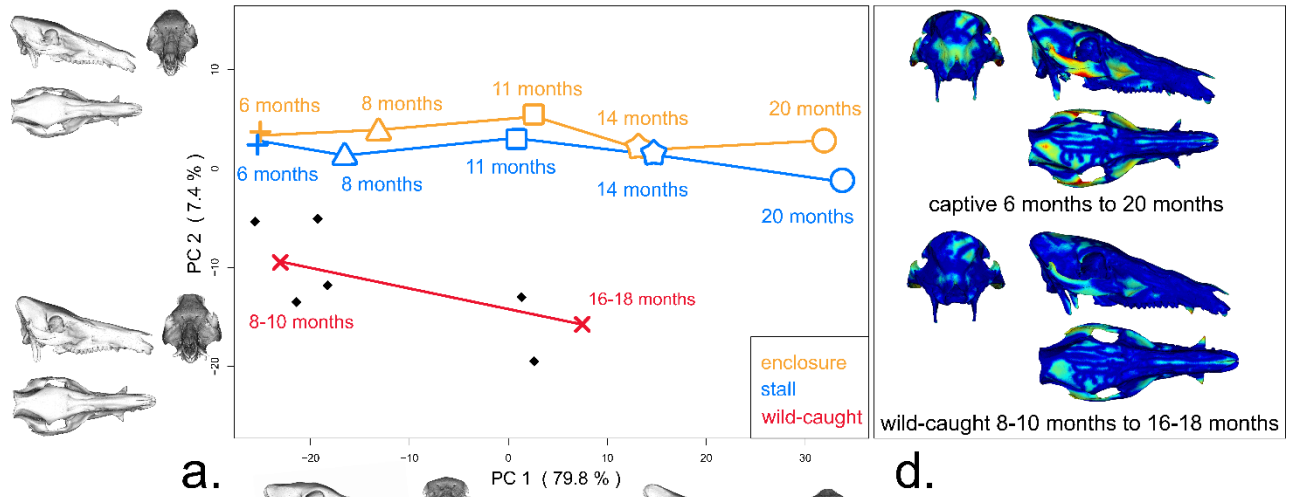
	Cranium		Mandible		Calcaneus	
	8-10 m.	16-18m.	8-10 m.	16-18 m.	8-10 m.	16-18 m.
	wild-caught	wild-caught	wild-caught	wild-caught	wild-caught	wild-caught
6 m. – enclosure	0.21	< <b>0.01</b>	0.55	< <b>0.01</b>	0.49	< <b>0.01</b>
6 m. – stall	0.27	< <b>0.01</b>	0.74	< <b>0.01</b>	0.35	<b>0.01</b>
8 m. – enclosure	0.11	<b>0.02</b>	0.27	0.09	0.13	0.09
8 m. – stall	0.22	<b>0.01</b>	0.38	0.05	0.22	<b>0.03</b>
11 m. – enclosure	< <b>0.01</b>	0.12	<b>0.01</b>	0.42	<b>0.01</b>	0.35
11 m. – stall	<b>0.01</b>	0.13	<b>0.01</b>	0.30	< <b>0.01</b>	0.20
14 m. – enclosure	< <b>0.01</b>	0.17	< <b>0.01</b>	0.21	< <b>0.01</b>	0.25
14 m. – stall	< <b>0.01</b>	0.15	< <b>0.01</b>	0.12	< <b>0.01</b>	0.09
20 m. – enclosure	< <b>0.01</b>	<b>0.01</b>	< <b>0.01</b>	<b>0.01</b>	< <b>0.01</b>	<b>0.02</b>
20 m. – stall	< <b>0.01</b>	<b>0.01</b>	< <b>0.01</b>	<b>0.01</b>	< <b>0.01</b>	<b>0.01</b>

558

559 Table 2. ANOVA  $p$ -values of the centroid size (CS) between captive (stall and enclosure) and wild-  
560 caught groups of wild boar (*Sus scrofa*) computed for the cranium, mandible, and calcaneus and  
561 ANOVA  $p$ -values of body mass. Significant values ( $p < 0.05$ ) are in bold. . m.: months.

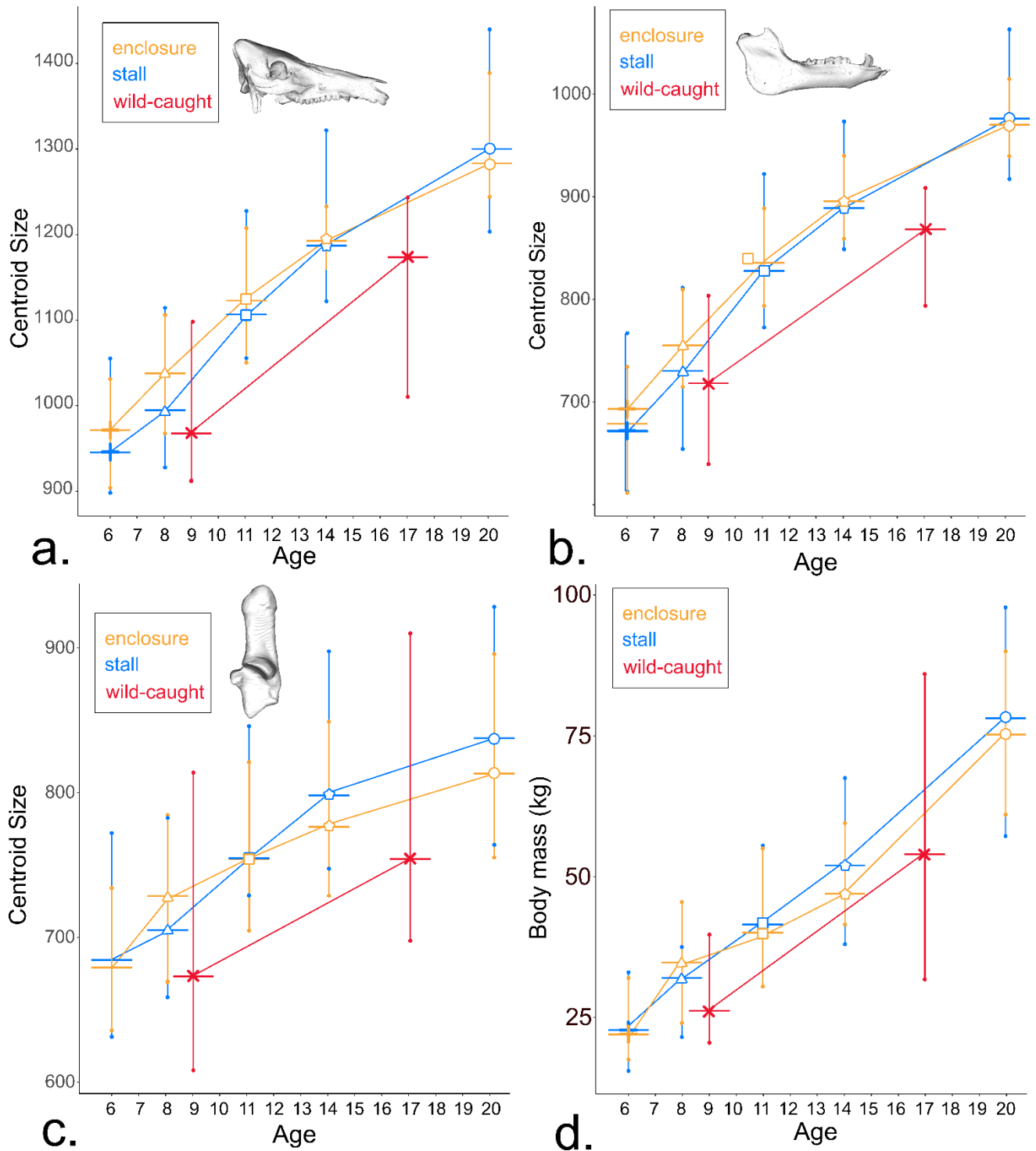
	CS Cranium		CS Mandible		CS Calcaneus		Body mass	
	8 to 10 m. wild- caught	16 to 18 m. wild- caught	8 to 10 m. wild- caught	16 to 18 m. wild- caught	8 to 10 m. wild- caught	16 to 18 m. wild- caught	8 to 10 m. wild- caught	16 to 18 m. wild- caught
6 m. – enclosure	0.75	< <b>0.01</b>	0.54	< <b>0.01</b>	0.93	< <b>0.01</b>	0.50	< <b>0.01</b>
6 m. – stall	0.67	< <b>0.01</b>	0.58	<b>0.01</b>	0.78	<b>0.01</b>	0.45	< <b>0.01</b>
8 m. – enclosure	0.37	<b>0.03</b>	0.39	0.09	0.18	0.12	0.81	<b>0.01</b>
8 m. – stall	0.60	<b>0.00</b>	0.61	0.05	0.32	0.06	0.64	< <b>0.02</b>
11 m. – enclosure	<b>0.01</b>	0.42	< <b>0.01</b>	0.79	<b>0.01</b>	0.62	0.20	0.12
11 m. – stall	<b>0.02</b>	0.37	<b>0.02</b>	0.81	< <b>0.01</b>	0.95	0.16	0.22
14 m. – enclosure	< <b>0.01</b>	0.71	< <b>0.01</b>	0.49	< <b>0.01</b>	0.63	< <b>0.02</b>	0.60
14 m. – stall	< <b>0.01</b>	0.60	< <b>0.01</b>	0.33	< <b>0.01</b>	0.28	<b>0.01</b>	0.99
20 m. – enclosure	< <b>0.01</b>	<b>0.04</b>	< <b>0.01</b>	<b>0.02</b>	< <b>0.01</b>	0.12	< <b>0.01</b>	0.06
20 m. – stall	< <b>0.01</b>	<b>0.02</b>	< <b>0.01</b>	<b>0.01</b>	< <b>0.01</b>	0.08	< <b>0.01</b>	<b>0.03</b>

562



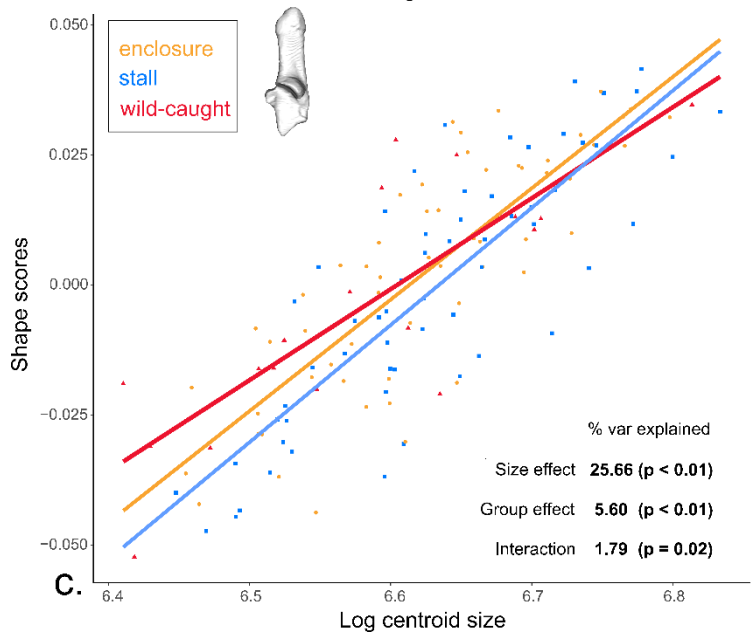
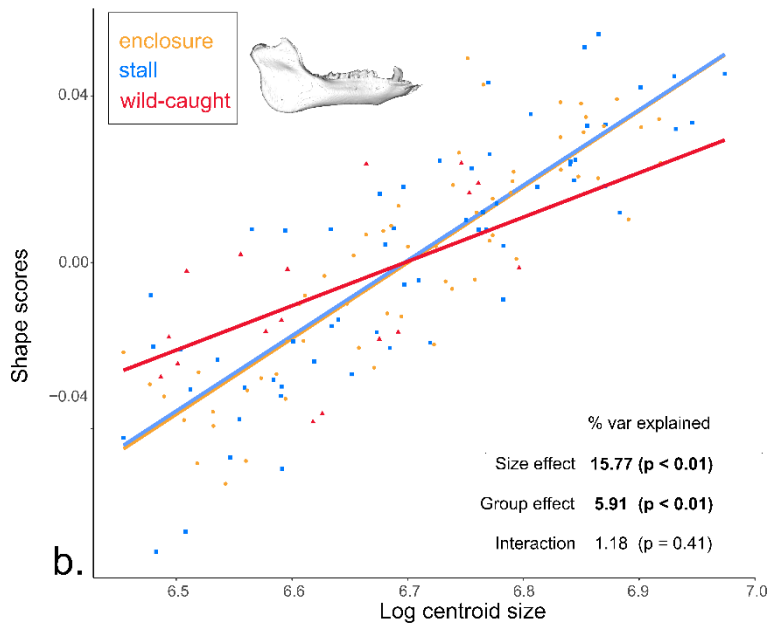
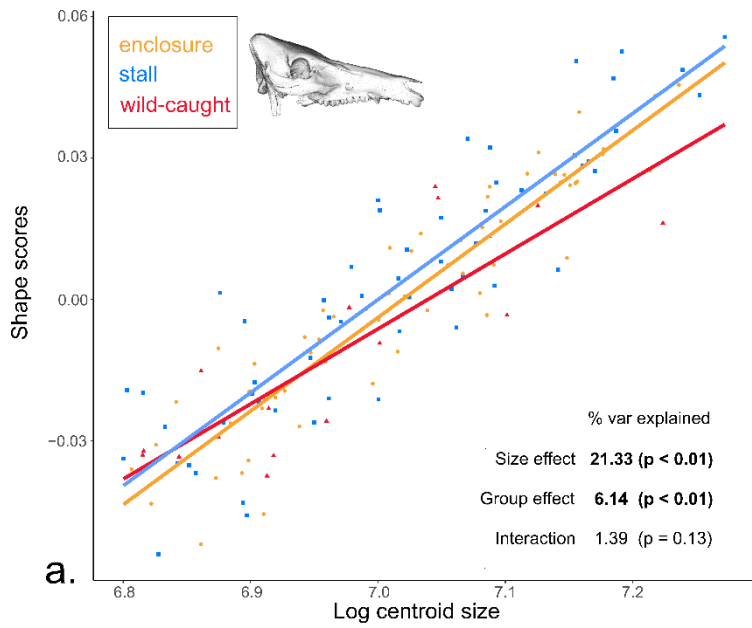


564 Figure 1. Principal component analyses for the cranium (a) mandible (b), and calcaneus (c) of wild  
565 boar (*Sus scrofa*) in the PC1-PC2 form space. Symbols represent the mean form for each group. Black  
566 dots represent the “control’ specimens from the wild-caught group, i.e. the specimens belonging to the  
567 same initial population as the individuals from the stall and enclosure groups. Form changes are  
568 depicted in lateral, dorsal and frontal views for the cranium and the mandible, and in medial and plantar  
569 views for the calcaneus. Heatmap of the intensity of form variation between captive (i.e. enclosure and  
570 stall) groups (6 months and 20 months) and between wild-caught groups (8-10 months and 16-18  
571 months) for the cranium (d), mandible (e), and calcaneus (f). Blue indicates a low intensity of variation  
572 and red indicates a high intensity of variation. Form changes are depicted in lateral, dorsal and frontal  
573 views for the cranium and the mandible, and in medial and plantar views for the calcaneus



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575 Figure 2. Boxplots of centroid size (CS) for the cranium (a), mandible (b), and calcaneus (c) and of  
 576 body mass (d) of wild boar (*Sus scrofa*). The vertical lines represent all the values within 1.5 times of  
 577 the interquartile range accounting for 50% of the data, from the 25th percentile to the 75th percentile.  
 578 The horizontal lines are the median values.



580 Figure 3. Regression of log centroid size (CS) on shape scores for the cranium (a), mandible (b) and  
581 calcaneus (c) of wild boar (*Sus scrofa*) and effects of size, group, and interaction between size and  
582 group on the regression of log CS on shape scores. Significant values ( $p < 0.05$ ) are in bold.

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589 The effect of captivity on craniomandibular and calcaneal ontogenetic trajectories in wild boar

590 Short running title: Captivity and ontogenetic trajectories

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608

609 SUPPORTING INFORMATION

610 **Appendix S1: Groups and specimens used**

611 a. List of groups included in the study and number of specimens

Cranium	Cranium	Mandible	Calcaneus
Enclosure	12	12	12
Stall	12	12	12
8-10 months wild-caught	10	12	10
16-18 months wild-caught	8	6	8
TOTAL	42	42	42

612

b. List of specimens. M: male, F: female, nd: not determined individuals. Specimens are localised at the Muséum national d'Histoire naturelle (Paris, France)

Catalogue number	Sex <sup>1</sup>	Age class	Status	Location	Cranium	Mandible	Calcaneus
2017-557	F		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
H285	M		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-560	M		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-562	M		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-555	F		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-556	F		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-569	F		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
H319	F		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-554	F		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-571	M		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-574	M		stall	Réserve de la Haute-Touche	Yes	Yes	Yes

2017-575	M		stall	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-558	M		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-559	F		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-561	M		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-563	M		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-564	M		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-565	F		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-566	F		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-567	F		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-568	F		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-570	F		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-572	M		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
2017-573	M		enclosure	Réserve de la Haute-Touche	Yes	Yes	Yes
PRA_186	nd	8-10 months	wild-caught	Urciers	Yes	Yes	No
PRA_172	F	8-10 months	wild-caught	Urciers	Yes	Yes	Yes



PRA_174	F	8-10 months	wild-caught	Urciers	Yes	Yes	Yes
2017-582	M	8-10 months	wild-caught	Urciers	Yes	Yes	Yes
2017-584	M	8-10 months	wild-caught	Urciers	Yes	Yes	Yes
CHA_S_77	F	8-10 months	wild-caught	Chambord	Yes	Yes	Yes
CHA_S_509	F	8-10 months	wild-caught	Chambord	Yes	Yes	Yes
CHA_S_581	M	8-10 months	wild-caught	Chambord	Yes	Yes	Yes
CHA_S_664	F	8-10 months	wild-caught	Chambord	Yes	No	Yes
CHA_S_577	nd	8-10 months	wild-caught	Chambord	No	Yes	No
COMP_2013-1262	nd	8-10 months	wild-caught	Compiègne	Yes	Yes	No
COMP_2013-1247	F	8-10 months	wild-caught	Compiègne	No	Yes	Yes
COMP_2013-1269	F	8-10 months	wild-caught	Compiègne	No	Yes	Yes
2017-583	M	16-18 months	wild-caught	Urciers	Yes	Yes	Yes
2017-581	F	16-18 months	wild-caught	Chambord	Yes	Yes	Yes
2017-577	M	16-18 months	wild-caught	Chambord	Yes	Yes	Yes
2017-579	F	16-18 months	wild-caught	Chambord	Yes	Yes	Yes

2017-580	F	16-18 months	wild-caught	Chambord	Yes	Yes	Yes
2017-578	F	16-18 months	wild-caught	Chambord	Yes	No	Yes
COMP_2013-1264	F	16-18 months	wild-caught	Compiègne	Yes	Yes	Yes
COMP_2013-1270	M	16-18 months	wild-caught	Compiègne	Yes	No	Yes

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<sup>1</sup>Sexes and ages for wild-caught specimens were estimated based on osteological observations, using respectively the morphology of canine cross section (Mayer & Brisbin, 1988) and the mandibular tooth eruption and wear stages in occlusal view (Grant, 1982).

Grant, A., 1982. The use of tooth wear as a guide to the domestic ungulates. In: Wilson, B., Grigson, C., Payne, S. (Eds.), *Ageing and Sexing Animal Bones from Archaeological Sites*. UK, pp. 991–108.

Mayer, J.M., & Brisbin, I.L., 1988. Sex identification of *Sus scrofa* based on canine morphology. *Journal of Mammalogy* 69:408–4

## Appendix S2: Digitisation and definitions of landmarks

### a. Digitisation protocol

All specimens were scanned using a Computed Tomography (CT) scanner with a spatial resolution of between 100 and 500  $\mu\text{m}$ . The wild boar from Urciers were scanned as living specimens at the *Chirurgie et Imagerie pour la Recherche et l'Enseignement* (CIRE) platform of the *Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement* (INRAE). Other individuals were scanned as dry specimens using a CT scanner close to the collections they were housed in. We segmented the bones using the segmentation tools of the Avizo v8.0 software, and then converted the volumes into three-dimensional PLY surfaces format. We digitised the anatomical landmarks and semilandmarks using IDAV Landmark v3.0 software (Wiley et al., 2005). To remove variation related to their initial arbitrary position along the curves, the semilandmarks were slid along the tangent of the curves minimising bending energy (Gunz and Mitteroecker, 2013).

Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and surfaces. *Hystrix, the Italian Journal of Mammalogy*. 24, 103–109.

Wiley, D., Amenta, N., Alcantara, D., Ghosh, D., Kil, Y.J., Delson, E., Harcourt-Smith, W., Rohlf, F.J., St. John, K., Hamann, B., Motani, R., Frost, S., Rosenberger, A.L., Tallman, L., Disotell, T., O'Neill, R., 2005. Evolutionary Morphing. In: *Proceedings of IEEE Visualization 2005*. Presented at the VIS'05, IEEE, Minneapolis, MN, pp. 431–438.

b. Number of landmarks

	Homologous landmarks	Sliding semi- landmarks	Surface sliding semi- landmarks
Cranium	14	181	0
Mandible	70	28	0
Calcaneus	23	48	763

c. Definitions of cranial (1-70), mandibular (71-94), and calcaneus (95-108) homologous landmarks.

Landmark	Definition
1	Most anterior midline point of the nasals
2	Most anterior, dorsal midline point of the premaxillae
3, 4	Most anterior point of the nasal-premaxilla suture
5, 6	Most anterior, lateral point of the upper canine alveolus
7, 8	Suture at the meeting point of premaxilla, maxilla, and nasal
9, 10	Most anterior point of the infraorbital foramen
11, 12	Most posterior point of the infraorbital foramen
13, 14	Most anterior lateral point of the facial tuberosity
15, 16	Most ventral point of the zygomatic-maxilla suture
17, 18	Most anterior, lateral point of the orbit
19, 20	Most dorsal point of the lower lacrimal foramen
21, 22	Most posterior point of the supraorbital foramen
23, 24	Most dorsal point of the orbit
25, 26	Most ventral point of supraorbital process of the frontal bone
27, 28	Meeting point of the parietal-frontal suture and temporal line
29, 30	Most anterior, dorsal point of the zygomatic process of the squamosal bone
31, 32	Most posterior point of the zygomatic bone
33, 34	Most dorsal point of the zygomatic process of the squamosal bone
35, 36	Most anterior, lateral point of the nuchal crest
37, 38	Most anterior point of the palatine fissure
39, 40	Most posterior point of the palatine fissure

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41, 42	Most anterior point of the cheek-tooth row (excluding P1)
43, 44	Most posterior point of the cheek-tooth row
45	Most posterior point of the posterior nasal spine on the palatine bone
46, 47	Most ventral, lateral point of the pterygoid process of the sphenoid
48, 49	Most posterior point of the pterygoid hamulus
50, 51	Meeting point of the pterygoid process with the ridge of the lateral pterygoid plate
52, 53	Meeting point of the pterygoid hamulus with the ridge of the medial pterygoid plate
54	Most posterior point of the vomer in contact with the sphenoid
55, 56	Most ventral, lateral, posterior point of the sphenoid-squamosal suture
57, 58	Most ventral, medial, posterior point of the sphenoid-squamosal suture
59, 60	Most posterior, medial point of the petro-occipital fissure
61, 62	Most lateral point of the occipital condyle
63	Most anterior, ventral midline point of the premaxilla
64	Most posterior midline point of the nuchal crest
65, 66	Most posterior, lateral point of the nuchal crest
67, 68	Most lateral point of the foramen magnum
69	Most posterior, dorsal point of the foramen magnum
70	Most anterior point, ventral of the foramen magnum
71, 72	Most anterior, lateral point of the lower canine alveolus
73, 74	Most anterior point of the cheek-tooth row (excluding P1)
75, 76	Most lateral point at the maximum of curvature between the mandibular ramus and corpus
77, 78	Most lateral point at the maximum of curvature between the coronoid process and the mandibular ramus

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79, 80	Most dorsal point of the coronoid process
81, 82	Most lateral point of the mandibular condyle
83, 84	Most posterior point of the mandibular condyle
85, 86	Point at the maximum of curvature of the mandibular angle
87	Most ventral, posterior point of the mandibular symphysis
88	Most ventral, anterior point of the mandibular symphysis
89, 90	Most medial point of the mandibular condyle
91	Most dorsal, posterior point of the mandibular symphysis
92	Most dorsal, anterior point of the mandibular symphysis
93, 94	Most anterior point of the mandibular foramen
95	Distal end of the cuboid facet
96	Proximo-plantar end of the cuboid facet
97	End of the beak of the coracoid process
98	Maximum of curvature of the plantar bulge on the plantar margin
99	Dorso-proximal end of the calcaneal sulcus
100	Planto-lateral end of sustentaculum tali
101	Dorsal end of the sustentaculum tali
102	Medial end of sustentaculum tali
103	Plantar end of the epiphysis
104	Dorso-proximal end of the bulge of the proximal part (not on the epiphysis)
105	Proximal end of the lateral lobe of the epiphysis (secondary lobe)
106	Proximal end of the medial lobe of the epiphysis (main lobe)
107	Dorsal end of the epiphysis
108	Dorso-proximal end of the lateral part of the coracoid process

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d. Definitions of cranial (I to XIV), mandibular (XV to XXII), and calcaneus (XVI to XXIX)

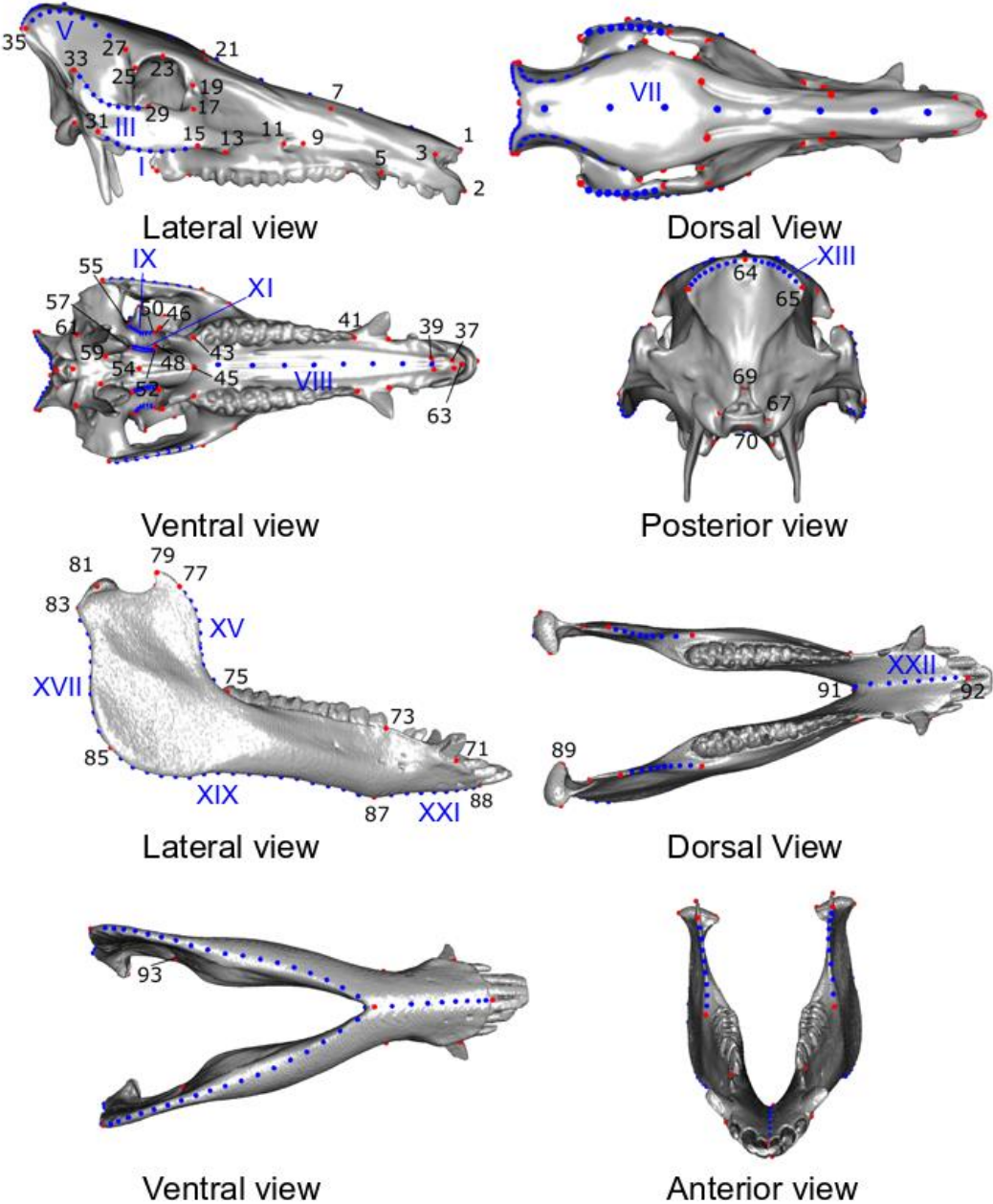
curves

Curve	Definition
I	from LM 13 to LM31
II	from LM 14 to LM32
III	from LM 29 to LM33
IV	from LM 30 to LM34
V	from LM 27 to LM35
VI	from LM 28 to LM36
VII	from LM 1 to LM64
VIII	from LM 45 to LM63
IX	from LM 50 to LM55
X	from LM 51 to LM56
XI	from LM 52 to LM57
XII	from LM 53 to LM58
XIII	from LM 64 to LM65
XIV	from LM 64 to LM66
XV	from LM 75 to LM77
XVI	from LM 76 to LM78
XVII	from LM 83 to LM85
XVIII	from LM 84 to LM86
XIX	from LM 85 to LM87
XX	from LM 86 to LM87
XXI	from LM 87 to LM88

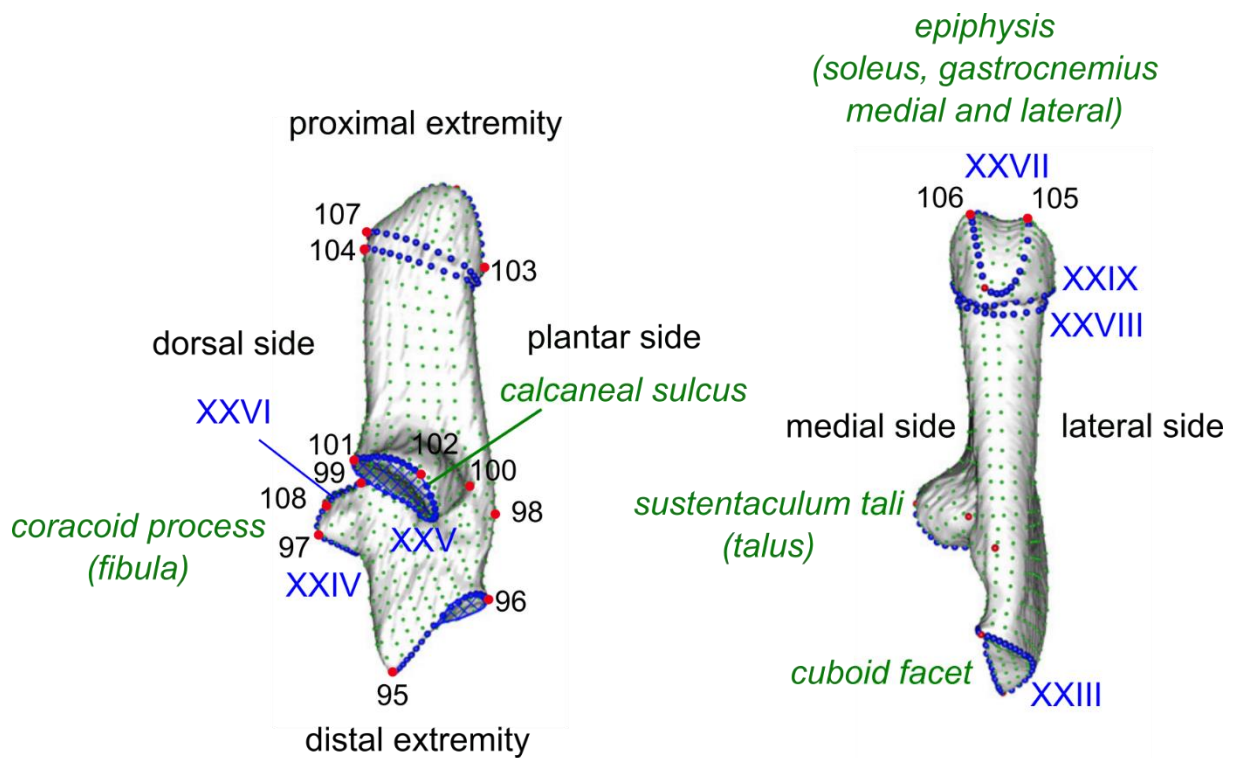


- XXII from LM 91 to LM92
  - XXIII Edge of the articular surface of the cuboid facet
  - XXIV Medial edge of the coracoid process
  - XXV Edge of the articular surface of the sustentaculum tali
  - XXVI Lateral edge of the coracoid process
  - XXVII Edge of the attachment surface of the tendon on the epiphysis
  - XXVIII Distal delineation of the junction zone between the epiphysis and the rest of the calcaneus
  - XXIX Proximal delineation of the junction zone between the epiphysis and the rest of the calcaneus
-

e. Wild boar (*Sus scrofa*) cranium and mandible showing the homologous landmarks (red dots and Arabic numerals) and semilandmarks (blue dots and Roman numerals) used in the study.



f. Wild boar (*Sus scrofa*) calcaneus showing the homologous landmarks (red dots and Arabic numerals) and semilandmarks (blue dots and Roman numerals) used in the study.



**Appendix S3: Body mass measurements (kg)**

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	Captive wild boar				
	6 months	8 months	11 months	14 months	20 months
2017-557	18.5	32.5	51.0	60.5	83.0
H285	24.0	27.0	30.5	38.0	59.0
2017-560	21.5	28.5	55.5	56.5	77.0
2017-562	29.0	37.5	40.5	50.0	76.0
2017-555	15.5	21.5	31.0	49.5	77.0
2017-556	27.0	34.0	35.0	40.0	59.0
2017-569	26.0	36.5	38.5	45.0	57.2
H319	19.5	29.5	51.5	67.5	97.8
2017-554	21.5	31.5	42.5	54.0	77.0
2017-571	18.0	24.0	31.0	44.5	68.0
2017-574	33.0	37.5	50.0	67.0	95.5
2017-575	30.5	35.0	42.5	57.5	78.5
2017-558	19.0	30.5	40.0	55.5	80.5
2017-559	18.0	24.0	36.0	43.0	62.0
2017-561	26.0	39.5	47.0	59.5	83.0
2017-563	31.0	45.0	56.5	73.5	89.0
2017-564	22.0	31.2	30.5	44.5	61.0
2017-565	17.5	29.0	33.0	41.5	61.5
2017-566	21.0	32.0	38.0	46.0	66.5
2017-567	32.0	38.0	50.0	53.5	81.0
2017-568	27.0	38.5	48.5	50.5	77.0

2017-570	19.5	30.0	40.0	45.0	67.0
2017-572	32.0	45.5	55.0	73.0	90.0
2017-573	24.0	37.5	36.5	47.0	73.5

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wild-caught wild boar

	8-10 months	16-18 months
PRA_186	30.0	
PRA_172	23.0	
PRA_174	28.0	
2017-582	35.0	
2017-584	52.0	
CHA_S_77	20.9	
CHA_S_509	24.3	
CHA_S_581	20.5	
CHA_S_664	36.0	
CHA_S_577	25.0	
COMP_2013-1262	NA	
COMP_2013-1247	23.9	
COMP_2013-1269	39.7	
2017-583		53.0
2017-581		49.8
2017-577		35.3
2017-579		31.7
2017-580		68.5
2017-578		20.0

COMP_2013-1264	60.8
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COMP_2013-1270	86.0
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1 **Appendix S4: Pairwise analyses between all groups**

2 a. MANOVA p-values of the form coordinates between all groups computed for the cranium,  
 3 mandible, and calcaneus.

Cranium	8 to 10 months wild caught	16 to 18 months wild caught	6 months enclosure	6 months stall	8 months enclosure	8 months stall	11 months enclosure
16-18 months wild caught	0.00						
6 months enclosure	0.21	0.00					
6 months stall	0.27	0.00	0.98				
8 months enclosure	0.11	0.02	0.24	0.20			
8 months stall	0.22	0.01	0.34	0.46	0.88		
11 months enclosure	0.00	0.12	0.00	0.00	0.11	0.03	
11 months stall	0.01	0.13	0.00	0.00	0.13	0.06	0.70
14 months enclosure	0.00	0.17	0.00	0.00	0.01	0.00	0.26
14 months stall	0.00	0.15	0.00	0.00	0.00	0.00	0.15
20 months enclosure	0.00	0.01	0.00	0.00	0.00	0.00	0.00
20 months stall	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mandible	8 to 10 months wild caught	16 to 18 months wild caught	6 months enclosure	6 months stall	8 months enclosure	8 months stall	11 months enclosure
16-18 months wild caught	0.02						
6 months enclosure	0.55	0.01					
6 months stall	0.74	0.01	0.89				
8 months enclosure	0.27	0.09	0.18	0.22			

8 months stall	0.38	0.04	0.25	0.39	0.73		
11 months enclosure	0.00	0.42	0.00	0.00	0.07	0.03	
11 months stall	0.00	0.30	0.00	0.00	0.04	0.02	0.95
14 months enclosure	0.00	0.21	0.00	0.00	0.00	0.00	0.33
14 months stall	0.00	0.12	0.00	0.00	0.00	0.00	0.16
20 months enclosure	0.00	0.01	0.00	0.00	0.00	0.00	0.00
20 months stall	0.00	0.00	0.00	0.00	0.00	0.00	0.00

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	8 to 10	16 to 18	6 months	6 months	8 months	8 months	11
Calcaneus	months wild	months wild	6 months	6 months	8 months	8 months	11
	caught	caught	enclosure	stall	enclosure	stall	months
							enclosure

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16-18 months wild caught	0.01						
6 months enclosure	0.49	0.00					
6 months stall	0.35	0.01	0.89				
8 months enclosure	0.13	0.09	0.18	0.21			
8 months stall	0.22	0.03	0.31	0.68	0.74		
11 months enclosure	0.01	0.35	0.01	0.03	0.37	0.09	
11 months stall	0.00	0.20	0.00	0.02	0.13	0.07	0.56
14 months enclosure	0.00	0.25	0.00	0.00	0.02	0.01	0.29
14 months stall	0.00	0.09	0.00	0.00	0.00	0.00	0.08
20 months enclosure	0.00	0.02	0.00	0.00	0.00	0.00	0.01
20 months stall	0.00	0.01	0.00	0.00	0.00	0.00	0.01



5 b. ANOVA *p*-values of the centroid size (CS) between all groups computed for the cranium,  
 6 mandible, and calcaneus and of body mass (kg).

	8 to 10	16 to 18	6 months	6 months	8 months	8 months	11	
Cranium	months wild	months wild	6 months	6 months	8 months	8 months	11	months
	caught	caught	enclosure	stall	enclosure	stall	enclosure	stall
16-18 months wild								
caught	0.00							
6 months enclosure	0.75	0.00						
6 months stall	0.67	0.00	0.86					
8 months enclosure	0.37	0.03	0.22	0.14				
8 months stall	0.60	0.00	0.37	0.30	0.70			
11 months enclosure	0.01	0.42	0.01	0.00	0.09	0.04		
11 months stall	0.02	0.37	0.00	0.00	0.11	0.04	0.96	
14 months enclosure	0.00	0.71	0.00	0.00	0.01	0.00	0.20	
14 months stall	0.00	0.60	0.00	0.00	0.00	0.00	0.14	
20 months enclosure	0.00	0.04	0.00	0.00	0.00	0.00	0.00	
20 months stall	0.00	0.02	0.00	0.00	0.00	0.00	0.00	

	8 to 10	16 to 18	6 months	6 months	8 months	8 months	11	
Mandible	months wild	months wild	6 months	6 months	8 months	8 months	11	months
	caught	caught	enclosure	stall	enclosure	stall	enclosure	stall

16-18 months wild								
caught	0.02							
6 months enclosure	0.54	0.00						
6 months stall	0.58	0.01	0.94					
8 months enclosure	0.39	0.09	0.15	0.18				

8 months stall	0.61	0.05	0.25	0.29	0.74		
11 months enclosure	0.01	0.79	0.00	0.00	0.09	0.03	
11 months stall	0.02	0.81	0.00	0.00	0.08	0.03	0.99
14 months enclosure	0.00	0.49	0.00	0.00	0.00	0.00	0.25
14 months stall	0.00	0.33	0.00	0.00	0.00	0.00	0.15
20 months enclosure	0.00	0.02	0.00	0.00	0.00	0.00	0.00
20 months stall	0.00	0.01	0.00	0.00	0.00	0.00	0.00

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	8 to 10	16 to 18					11	
Calcaneus	months wild	months wild	6 months	6 months	8 months	8 months	months	mo
	caught	caught	enclosure	stall	enclosure	stall	enclosure	st

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16-18 months wild								
caught	0.01							
6 months enclosure	0.93	0.00						
6 months stall	0.78	0.01	0.74					
8 months enclosure	0.18	0.12	0.15	0.27				
8 months stall	0.32	0.06	0.29	0.50	0.70			
11 months enclosure	0.01	0.62	0.01	0.02	0.25	0.12		
11 months stall	0.00	0.95	0.00	0.00	0.10	0.03	0.65	
14 months enclosure	0.00	0.63	0.00	0.00	0.02	0.01	0.28	
14 months stall	0.00	0.28	0.00	0.00	0.00	0.00	0.09	
20 months enclosure	0.00	0.12	0.00	0.00	0.00	0.00	0.02	
20 months stall	0.00	0.08	0.00	0.00	0.00	0.00	0.01	

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	8 to 10	16 to 18					11	
Mass	months wild	months wild	6 months	6 months	8 months	8 months	months	mo
	caught	caught	enclosure	stall	enclosure	stall	enclosure	st

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16-18 months wild							
caught	0.01						
6 months enclosure	0.50	0.00					
6 months stall	0.45	0.00	0.91				
8 months enclosure	0.81	0.01	0.33	0.28			
8 months stall	0.64	0.02	0.19	0.18	0.80		
11 months enclosure	0.20	0.12	0.04	0.03	0.27	0.39	
11 months stall	0.16	0.22	0.02	0.01	0.19	0.26	0.82
14 months enclosure	0.02	0.60	0.00	0.00	0.02	0.05	0.26
14 months stall	0.01	1.00	0.00	0.00	0.00	0.01	0.09
20 months enclosure	0.00	0.06	0.00	0.00	0.00	0.00	0.00
20 months stall	0.00	0.01	0.00	0.00	0.00	0.00	0.00

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