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## 4500 years of morphological diversification in Western Europe wild boars (*Sus scrofa*) and the consequences of the Neolithic transition

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1 **4500 years of morphological diversification in Western Europe wild boars (*Sus scrofa*)**  
2 **and the consequences of the Neolithic transition**

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20

21 **ABSTRACT**

22 Evolutionary biologists have recently solicited archaeologists to help document and understand  
23 the morphological evolution of animals in response to human activities and, more generally, to  
24 help reconstruct the history and significance of the anthropogenic impact on worldwide  
25 ecosystems. Artificial selection associated with domestication is the best-known example of a  
26 major anthropogenic morphological evolution preserved in the archaeological record. However,  
27 the impact of the domestication process and dispersal on the morphological evolution of  
28 animals has been far less explored. To fill this gap, we focused on 4500 years of evolution in  
29 Western Europe *Sus scrofa*, covering the Neolithic transition – a major anthropogenic  
30 ecological disturbance involving landscape modification and the translocation of domestic  
31 mammals. Using geometric morphometrics on key phenotypic markers preserved in the  
32 archaeological record, associated with isotopic studies, we explored how, and in response to  
33 which cultural drivers the Neolithic niche construction has influenced the morphological  
34 evolution of Western European wild boars (*Sus scrofa scrofa*). The decoupling of size and shape  
35 components from bone morphological variation has facilitated the identification of several  
36 processes of phenotypic diversification of *Sus s. scrofa* in response to human behaviour during  
37 the Neolithic transition in Western Europe.

38

## 39 INTRODUCTION

40 Over the last few centuries, the human niche construction (Odling-Smee et al., 2003) has  
41 become "the world's greatest evolutionary force" (Palumbi, 2001), generating a change in the  
42 ecological and evolutionary dynamics of species on a global scale (Hendry et al., 2017). The  
43 human engineering of ecosystems with habitat fragmentation (Cheptou et al., 2017),  
44 urbanisation (Alberti et al., 2017; McDonnell and Hahs, 2015) and the disruption of natural  
45 dynamics (Colautti et al., 2017) has induced rapid microevolutionary changes through strong  
46 directional selection, resulting in rapid diversification (Hendry et al., 2017, 2008, 2007). With  
47 the emergence of agriculture and, more generally speaking, the Neolithic transition, the human  
48 niche construction caused a major ecological disturbance, with the opening and fragmentation  
49 of the landscape, the emergence and spread of domesticated animals and plants from several  
50 independent centres across Eurasia, the protection of livestock from predators and competitors,  
51 and the dispersal of invasive species and pathogens (Ellis et al., 2021; Sullivan et al., 2017). To  
52 date, the influence of the Neolithic niche construction has been mainly explored through  
53 human-induced species distribution (Boivin et al., 2016; Cucchi et al., 2020; Vigne, 1999), and  
54 over the temporal depth of the direct human influence over species during the process of animal  
55 domestication (Ameen et al., 2019; Brassard et al., 2022; Clutton-Brock, 1992; Cucchi et al.,  
56 2021; Fages et al., 2019; Frantz et al., 2020; Larson and Fuller, 2014; Zeder, 2015). Yet, its  
57 consequences on non-domestic species evolution remain to be fully documented and  
58 understood (Erlandson et al., 2016; Sarrazin and Lecomte, 2016).

59 To contribute to this research avenue, this study explores the influence of the Neolithic  
60 transition in Western Europe on the phenotypic diversification of an indigenous species: the  
61 wild boar (*Sus scrofa*). Emerging in the Near East around 9500 BCE, the Neolithic dispersal  
62 reached central-western Europe by 5850 BCE through demic and cultural diffusion via the  
63 Danube River and the northern Mediterranean coasts, with the adaptation of technoeconomic  
64 strategies to different ecological conditions along the way (Manen et al., 2019, 2018). *Sus s.*  
65 *scrofa* was present in North Western Europe since the Middle Pleistocene, and was evidenced  
66 in MIS 7 by 250 ka BCE (Auguste, 2009). These animals were common and widespread from  
67 France to Belarus from the early Holocene onwards, varying in body size according to  
68 Bergman's rule, with northern individuals from north-eastern Germany being larger than  
69 southern ones from Spain and Italy (Albarella et al., 2009a). Despite the recent intensification  
70 or reintroduction and introgression with domestic pigs on the genetic make-up of wild boar  
71 populations in Europe (Goedbloed et al., 2013), their deep genetic structure across Europe  
72 remains mainly determined by the post glacial dispersal from southern refuges located in Spain,  
73 Italy for Western Europe, and the Balkans for Central Europe (de Jong et al., 2023;  
74 Niedziałkowska et al., 2021), with a loss of genetic diversity towards the northern range of the  
75 species (Vilaça et al., 2014).

76 The earliest anthropogenic influence over the genetic diversity of European *Sus scrofa* has been  
77 documented by paleogenetics with the introduction of domestic pigs of Near East ancestry by  
78 Neolithic stock-herders along the two dispersal waves mentioned previously (Larson et al.,  
79 2007). These pigs stemmed from the long domestication process of Near Eastern *Sus scrofa*  
80 populations between 9500 and 8000 BCE (Price and Hongo, 2019), from intensive hunting to

81 first evidence of body size reduction compared to their wild relatives by 8000 BCE (Price and  
82 Evin, 2019). These small pigs, entered Europe by 6500 BCE, arriving in Central Western  
83 Europe around 5400 BCE (Evin et al., 2015; Larson et al., 2007; Ottoni et al., 2013). By 5000  
84 BCE, the Near Eastern lineage no longer existed in the European pig genome, which, after this  
85 date, had 96% of its genetic variants coming from European wild boars. The extent of this  
86 genomic replacement is considered to have stemmed from introgressive hybridization  
87 facilitated by the small population size of Near Eastern pigs and a lack of barrier between them  
88 and the local wild boar populations (Frantz et al., 2019).

89 The introduction of domestic pigs into Europe by successive waves of newcomers from the  
90 Near East induced the co-occurrence of several lineages of *Sus scrofa* during part of the Neolithic  
91 period : the indigenous wild boar populations in their natural habitat, the domestic pig  
92 populations of Near Eastern origin reared by Neolithic people and their feralized populations.  
93 Indeed, thanks to paleogenetics, we know that hybridization and gene flow between wild,  
94 domestic and feral *Sus scrofa* populations, occurred all along the Neolithic (Frantz et al., 2019).  
95 This gene flow can be highlighted by traditional pig husbandry still undertaken in Papua New  
96 Guinea, where interbreeding is part of the rearing practices, with sows being left to fray with  
97 wild male boars (Dwyer, 1996), or in Mediterranean Europe (Albarella et al., 2011;  
98 Hadjikoumis, 2012; Halstead and Isaakidou, 2011). This does not exclude likely presence of  
99 commensal wild boars for which there is no genetic evidence. This co-habitation of several  
100 lineages of *Sus scrofa* produced new hybrid communities, with different ranges of interactions  
101 between suids and humans societies in Neolithic Europe (Albarella et al., 2011; Balasse et al.,  
102 2019), where boundaries between wild and domestic populations were not as tight as those  
103 currently engraved in the industrial and zootechnical views on animal domestication (Bogaard  
104 et al., 2021; Stépanoff and Vigne, 2018).

105 Considering the new ecological and evolutionary forces introduced into Europe by the Neolithic  
106 transition, we wanted to explore the extent of its influence on the morphological diversification  
107 of *Sus s. scrofa* in Western Europe, over 4500 years or archaeological record. The remains are  
108 dated from the Middle Mesolithic, by 7500 BCE, i.e. before the spread of farmers and their  
109 domestic pigs, until the Late Neolithic 3000 BCE, when the new social and economic  
110 organization of the Bronze Age emerged. During this timeframe, we attempt to (1) understand  
111 whether the Neolithic transition influenced the phenotypic evolution of the autochthonous wild  
112 boars, (2) define the phenotypic diversity of the several lineages of *Sus scrofa* present in Europe  
113 at that period and (3) determine to what extent Neolithic societies of Europe have intentionally  
114 altered the phenotypic traits of domestic *Sus scrofa*. To track these intraspecific changes in bone  
115 morphology, we had to comprehensively capture enough organismal complexity using high  
116 resolution phenotypic data with three dimensional coordinate points analyzed via geometric  
117 morphometrics (Bardua et al., 2019; Goswami et al., 2019) and morphometric mapping  
118 (Bondioli et al., 2010a; Morimoto et al., 2011). To track the morphological evolution across the  
119 archaeological record, we relied on three skeleton bones (calcaneus, humerus and mandible)  
120 chosen for their good preservation in the archaeological record, following an experimental  
121 research program on the effects of captivity over skeletal development in European wild boars  
122 (<http://anr-domexp.cnrs.fr/>). This experimental research showed that functional changes due to  
123 mobility reduction and changes due to directional selection induced different morphological

124 trajectories from the wild norm of variation, in both the calcaneus form (Harbers et al., 2020a)  
125 and the humerus shaft microanatomy (Harbers et al., 2020b). Likewise, the change in feeding  
126 behaviour with captivity induced functional responses in the skull and mandible, different from  
127 morphological changes induced by the last 200 years of selective breeding (Neaux et al., 2022,  
128 2021, 2020). All this evidence supports the use of these phenotypic markers to disentangle,  
129 functional changes due to a cultural control of the individual's environment (Hecker, 1982),  
130 from selective breeding at a population scale, during the Neolithic transition. Such approach  
131 has already proven useful to identify the local domestication of the feral populations of wild  
132 boars by PPNB Neolithic people of Cyprus (Cucchi et al., 2021).

133 For this study, *Sus scrofa* from Mesolithic contexts will provide the baseline (T0) for the  
134 variation norm of *Sus scrofa* prior to the Neolithic transition in Europe. The *Sus scrofa* bones  
135 from Neolithic contexts were not divided beforehand into a wild or domestic category using a  
136 bone size criterion, as is usually done in zooarchaeological and paleogenetic studies, for three  
137 main reasons. First, as previously said, the wild and domestic boundaries might not be a relevant  
138 concept to approach these interactions during the Neolithic. Then, these preliminary categories  
139 based on bone size differences are too subjective and might introduce interpretation biases.  
140 Third, size changes are not easily related to any clear biotic or abiotic factors. We have therefore  
141 chosen to assess the extent of Neolithic anthropogenic influence over *Sus scrofa* morphological  
142 diversity by confronting the archaeological specimen to a gradient of phenotypic variation  
143 representing (1) the reaction norms of *Sus scrofa* populations (Mesolithic and current) living in  
144 their natural habitat or (2) in contexts of controlled locomotion and feeding behaviours and (3)  
145 the phenotypic divergence induced by selective breeding over the last centuries. The relatedness  
146 of the Neolithic specimens to this anthropogenic gradient of phenotypic diversification in *Sus*  
147 *scrofa* was assessed using predictive and machine learning approaches. We also investigated  
148 the relationship between Neolithic suids and humans using stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen  
149 ( $\delta^{15}\text{N}$ ) isotope ratios in bone collagen, as a greater proximity to humans may have induced  
150 changes in the feeding environment and diet of suids (Balasse et al., 2019, 2016; Brusgaard et  
151 al., 2022; Cucchi et al., 2016; Maring and Riede, 2019).

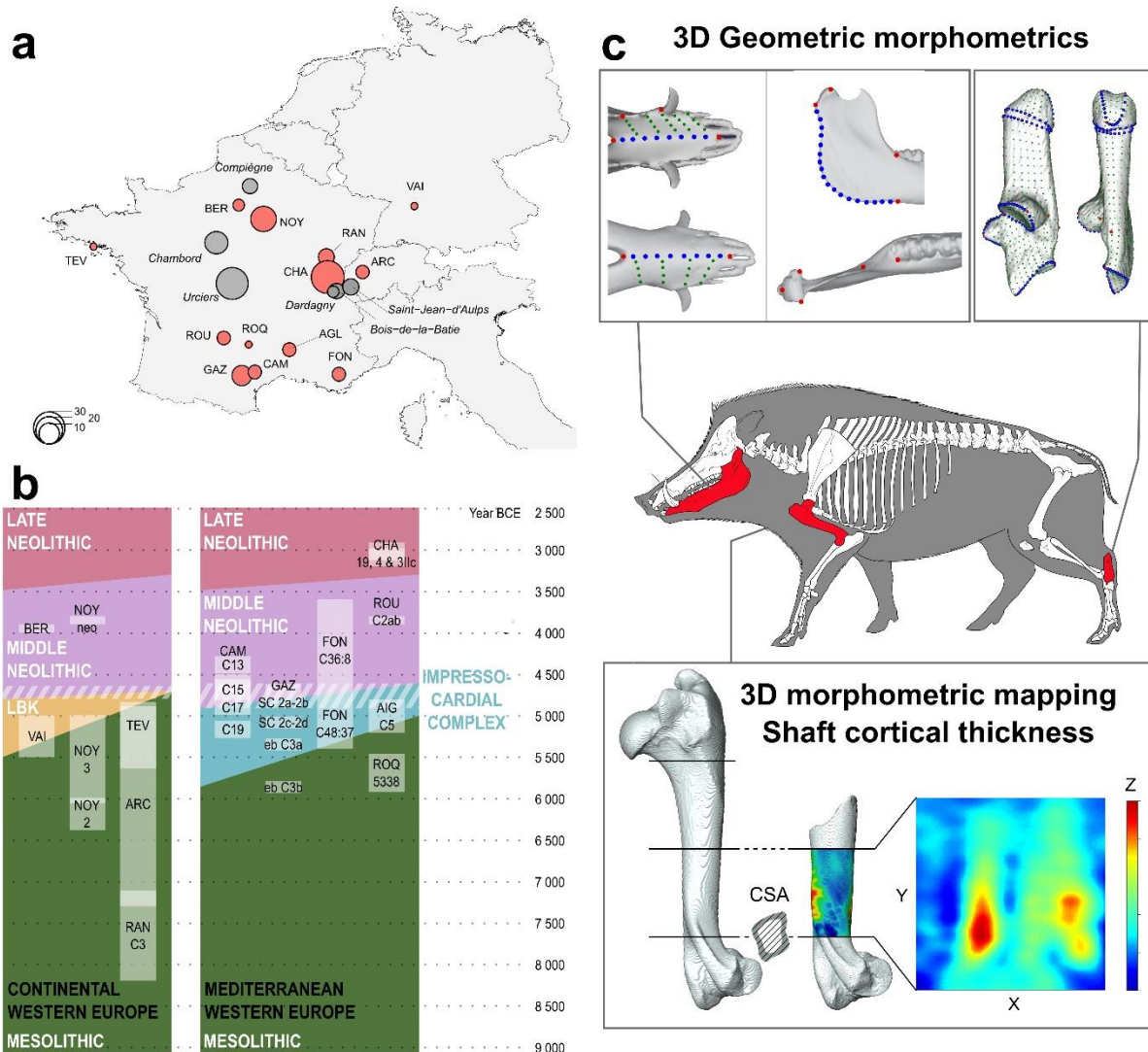
152

## 153 MATERIAL

154 From 101 archaeological *Sus scrofa* bones collected, we could analyze 73: calcanei (41), humeri  
155 (19) and mandibles (13) from adults and sub-adults (Supplementary Table S1). We analysed  
156 calcanea with epiphysis known to fuse around 2 years in wild boars (Bridault et al., 2000). The  
157 humeri all had a complete distal shaft with a fused distal epiphysis, occurring in wild boar by  
158 19–23 months (Bull and Payne, 1982). The mandibles belonged to specimens between 12 and  
159 60 months old, according to both the tooth eruption (Legge, 2013) and wear stages (Horard-  
160 Herbin, 1997) of the premolars and molars.

161 These bones were collected from 13 archaeological sites in France, Switzerland and Germany  
162 (Figure 1). Within the *Sus scrofa* specimens, 28 came from five hunter-gatherer contexts dated  
163 from the Middle and Late Mesolithic between 8700 and 5000 BCE, and 45 specimens from  
164 eight Neolithic settlements between 5500 and 3000 BCE (Supplementary Table S1 and Text

165 S2). The latter includes 30 specimens of *Sus scrofa* (25 calcanei and 5 humeri) from the  
166 Neolithic site of Chalain, on which stable isotope analysis was performed and compared with  
167 the stable isotope analyses on large wild and domestic herbivores found at the same site,  
168 including 14 deer (*Cervus elaphus*), 5 aurochs (*Bos primigenius*) and 9 cattle (*Bos taurus*)  
169 (Supplementary Table S2). All Mesolithic specimens were considered as hunted wild boars,  
170 representative of the phenotypic variation of wild boars before the Neolithic transition. To  
171 assess the amount of anthropogenic diversification in Neolithic *Sus scrofa*, we used a  
172 comparative approach from a collection of *Sus scrofa* covering the phenotypic continuum from  
173 wild boars hunted in their natural habitat to highly selected domestic breeds, whose  
174 environment and reproduction was fully controlled by humans (SI3). The hunted wild boars  
175 included a sample of 28 Mesolithic specimens from Western Europe contexts (Figure 1) and a  
176 sample of 32 specimens from current populations hunted in France and Switzerland. We have  
177 also included 24 captive wild boars from an experiment undertaken at a zoological reserve of  
178 the Natural History Museum of Paris (see details of the experiment in (Harbers et al., 2020a)).  
179 They were collected from a control population of wild boars (sampled by 8 specimens) and  
180 raised in captivity from the age of 6 months to 2 years. These 24 specimens were randomly split  
181 into two groups with the same male to female sex ratio. One group was raised in a 3000 m<sup>2</sup> pen  
182 and the second in a 100 m<sup>2</sup> stall where males and females were separated. Modern pig samples  
183 included 23 specimens from traditional European landraces including 5 free-ranging Corsican  
184 landrace pigs and 9 specimens of industrial breeds. A sample of five hybrids (crossed between  
185 wild boars and pigs of different breeds) is also included.



186  
 187 **Figure 1:** **a.** Geographical location of the modern wild boars (grey filled circles) and  
 188 archaeological *Sus crofa* (red filled circles) samples in western Europe: Ranchot (RAN),  
 189 Arconciel (ARC), Gazel (GAZ), Chalain (CHA), Fontbrégoua (FON), Roquemissou (ROQ),  
 190 Grotte de l'Aigle (AIG), Camprafaud (CAM), Roucadour (ROU) Tévéc (TEV), Noyen (NOY),  
 191 Vaihingen (VAI) and Bercy (BER). **b.** Chronological and cultural contexts of the *Sus scrofa*  
 192 archaeological samples. **c.** Position of the phenotypic markers selected for the study of the *Sus*  
 193 *scrofa* skeleton with their respective protocol of morphometric digitization: 3D surface and  
 194 curve landmarks and semilandmarks respectively of mandible's symphysis and ramus (see  
 195 Neaux et al. 2020 for methodological details), 3D surface semilandmarks of the calcaneus (see  
 196 Harbers et al. 2020a for methodological details) and the 3D morphometric mapping and Cross  
 197 Section Area (CSA) of the humeral shaft (See Harbers et al. 2020b for methodological details).  
 198 The topography of the shaft cortical thickness is rendered by a standardized morphometric map  
 199 with chromatic scale from thinnest (dark blue) to thickest (red). Red areas represent area of  
 200 muscular insertions (see Harbers et al. 2020b for further methodological details).

201  
 202 **METHODS**

203 *Geometric Morphometrics*

204 The morphometric study associate the 3D surface semilandmarks geometric morphometrics  
205 (3D GM) of the calcaneus and mandible (Bardua et al., 2019; Mitteroecker et al., 2013) and the  
206 3D morphometric mapping of the humerus shaft cortical thickness (Bondioli et al., 2010a,  
207 2010b). The 3D models of the calcaneus were reconstructed from medical CT scans and  
208 photogrammetry after segmentation in Avizo v.8.0 or reconstruction using Agisoft Photoscan  
209 1.2.6.2834. Mandible 3D models were reconstructed from medical CT and laser scanning using  
210 an ARTEC Space Spider. All three acquisitions methods were compared using a common 3D  
211 GM framework without statistical biases (Waltenberger et al., 2021). The humeri were scanned  
212 using a medical CT and reconstructed to generate the external (periosteum) and internal  
213 (endosteum) 3D surfaces of the bone used to compute cortical thickness.

214  
215 3D GM analyses were performed on 3D models using landmark and semilandmark protocols  
216 on curves and surfaces previously detailed for the calcaneus (Harbers et al., 2020a) and the  
217 mandible (Neaux et al., 2020). For the mandibles, the protocol was adapted to the symphysis  
218 and ramus, which are the most common anatomical parts of the mandibles in the archaeological  
219 record. The acquisition and standardisation protocol for 3D morphometric mapping of the  
220 humeral shaft cortical thickness follows (Harbers et al., 2020b). We adjusted the protocol to  
221 ensure its applicability to archaeological humeri missing the proximal end of the diaphysis by  
222 mapping only the distal half of the shaft (3–50%). Despite this reduction, all the entheses  
223 distinguishing free-ranging wild boars, captive wild boars and pigs are observable (Figure 1,  
224 Harbers et al., 2020b). We used the cross-sectional area (CSA) at the distal end of the diaphysis  
225 (Figure 1c) as a proxy of the humerus size. The Pearson correlation coefficient showed that this  
226 variable was almost perfectly correlated ( $\rho = 0.965$ ) with the bone volume. Since the latter is  
227 also strongly correlated to body mass (Campione and Evans, 2020; Harbers et al., 2020b), we  
228 used the cross-sectional area as a body mass proxy of archaeological *Sus scrofa*.

229  
230 Size variation differences between the nine subgroups of wild boars and domestic pigs, in the  
231 humeral CSA and calcaneus and mandible centroid sizes, were tested using a factorial ANOVA  
232 and visualised with boxplots. To assess the structuration of size variation and identify the  
233 occurrence of several populations within Neolithic *Sus scrofa*, we performed model-based  
234 Gaussian mixture analyses using density estimation on size variables.

235  
236 The differences in humeral cortical thickness topography and calcaneus shape variation  
237 between the nine subgroups of wild boars and domestic pigs were tested with factorial  
238 MANOVAs. Patterns of morphological differentiation (in a morphospace) among wild boars  
239 and pig samples were visualised using canonical variate analyses (CVA). CVA morphospaces  
240 were performed after principal component analysis (PCA) computed on Procrustes coordinates  
241 in Mesolithic and modern *Sus scrofa*, retaining 95% of variance for data dimensionality  
242 reduction to prevent artificial group discrimination (Mitteroecker and Bookstein, 2011).  
243 Neolithic *Sus scrofa* are projected into this canonical morphospace, using a generic function  
244 (predict) which will get fitted values according to the multiple linear model computed for the  
245 Mesolithic and modern data. To assess the interaction mode (hunting, control or reproductive  
246 isolation) with human Neolithic societies for each Neolithic *Sus scrofa*, we used a k-nearest



247 neighbor (kNN) classification in the two first canonical axes of the morphospace via a training  
248 model of three groups representing each of these interaction modes: (1) modern and Mesolithic  
249 wild-caught wild boars, (2) modern captive wild boars, and (3) modern pigs including industrial  
250 breeds and landraces. The value of “k” was chosen as the square root of the number of  
251 specimen’s “n” in the comparative material following (Lall and Sharma, 1996) ; therefore, k =  
252 9 for the humerus dataset (n = 86), k = 10 for the calcaneus dataset (n = 95) and k = 7 for the  
253 mandible dataset (n = 43). To check for the reliability of the kNN classification we assessed its  
254 congruence with the prediction obtained by fitting their values with the multiple linear  
255 discriminant model (CVA) performed for the three groups described previously.

256

257 To visualise calcaneus and mandible shape deformations along the canonical axes, we  
258 calculated the theoretical minimum and maximum shapes for each axis, then associated them,  
259 using a heatmap, on the landmarks corresponding to the distance between the minimum and  
260 maximum values along the first two canonical axes. To visualise variations in humerus cortical  
261 thickness topography along the canonical axes, we calculated the theoretical minimum and  
262 maximum morphometric map for each axis.

263

264 All the statistics were performed using R (R Core Team, 2017). ANOVA and PCA were  
265 performed using the R package "stat" (R Core Team, 2017). Model based Gaussian mixture  
266 analyses of size univariates were performed with “Mclust 5” (Scrucca et al., 2016). LDA  
267 prediction using the package “MASS” (Venables et al., 2002) and visualisations were performed  
268 using “geomorph” (Adams and Otárola-Castillo, 2013) and “rgl” (Adler and Murdoch, 2017).  
269 The kNN algorithm was performed using the package ‘class’(Torgo, 2011).

## 270 *Stable Isotope study*

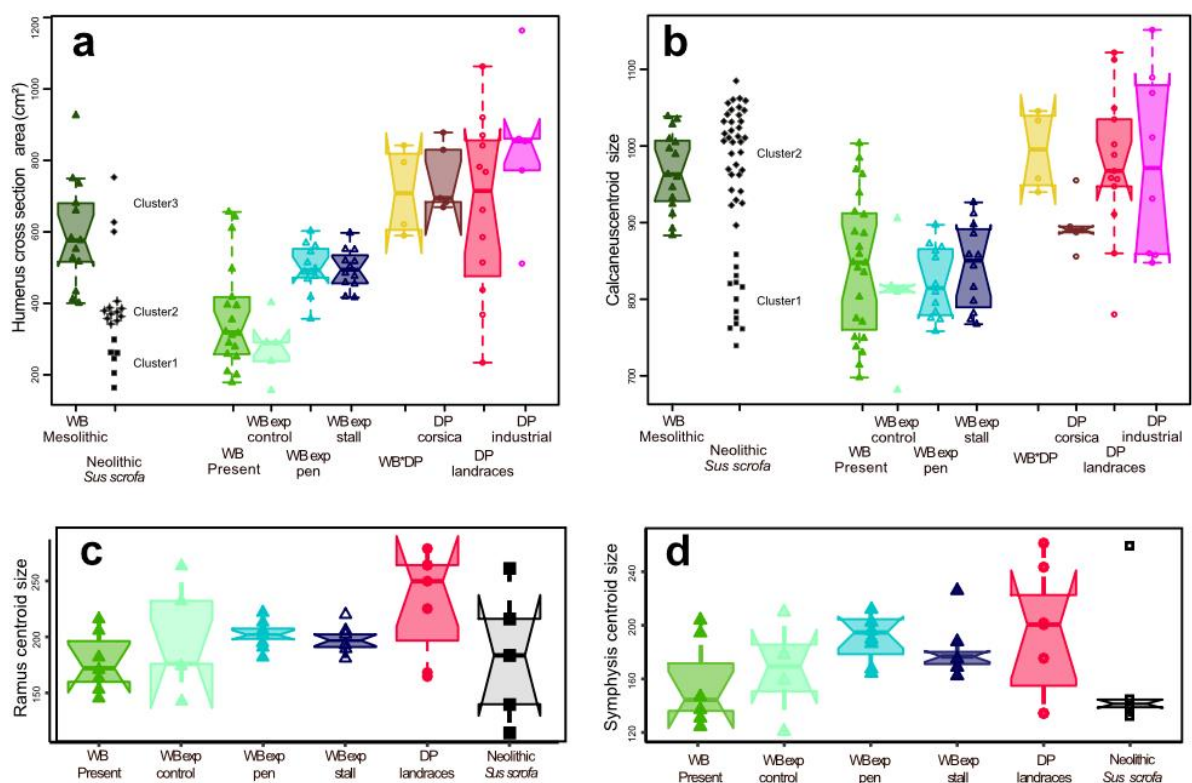
271 A piece of bone was cut from the diaphysis of the *Sus scrofa* calcaneus or humerus. Bone  
272 surfaces were cleaned by abrasion and reduced to powder. A fraction comprised between 355  
273 and 710 µm was used for collagen extraction. The extraction used approximately 150 to 250  
274 mg of powder and followed the procedure described in (Bocherens et al., 1991). Coupled  
275 measurements of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  were conducted on 300 to 400 µg of collagen on an elemental  
276 analyser Thermo Flash 2000 interfaced with a Thermo DeltaV Advantage IRMS. The analytical  
277 precision, estimated from the repeated analysis (N = 8 to 12 within each run) of our laboratory  
278 standard (alanine normalised to the IAEA-600 caffeine international standard), was 0.1‰ for  
279  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Over the course of these analyses, the alanine standard gave mean values  
280 of 0.58‰ for  $\delta^{15}\text{N}$  (expected value: 0.60‰), -22.08‰ for  $\delta^{13}\text{C}$  (expected value: -22.17‰),  
281 40,4 % for C content (expected value: 40.4%) and 15.6% for N content (expected value: 15.7%).  
282 The aurochs, deer and cattle bone collagen were extracted within the framework of a previous  
283 study, following the same procedure. The  $\delta^{13}\text{C}$  were published (Drucker and Bocherens, 2009)  
284 but the  $\delta^{15}\text{N}$  values remain unpublished.

## 285 **RESULTS**

286 *Bone size variation in modern and ancient Sus scrofa*

287 All four phenotypic markers displayed a common pattern of size variation (Figure 2), with  
 288 overall significant differences among the samples of wild, captive and domestic *Sus scrofa* for  
 289 the humerus cross section (ANOVA= F:10.81, p<0.0001), the centroid sizes of calcaneus  
 290 (ANOVA= F:9.302, p<0.0001), the mandible symphysis (ANOVA= F:2.635, p=0.0463) and the  
 291 ramus (ANOVA= F:3.428, p=0.0251). All four markers displayed (1) an important size decrease  
 292 between Mesolithic and extant wild boar populations of Western Europe (-16% for the  
 293 calcaneus) and (2) an increase in bone size (+15 % for the calcaneus) in traditional and industrial  
 294 pig breeds compared to modern hunted or captive wild boars, or even Mesolithic wild boars.  
 295 Captivity in wild boars does not induce any significant size changes in calcaneum and mandible  
 296 but it does show an increase in the CSA of the humerus compared to free ranging wild boars  
 297 (Figure 2), suggesting that captivity induce an increase in wild boar body mass but not of their  
 298 body size.

299 Size variation in Neolithic *Sus scrofa* calcaneus covers the whole size range from the smallest  
 300 wild boars to some of the largest industrial pig breeds. Regarding the body mass proxy (humeral  
 301 shaft cross section area), Neolithic *Sus scrofa* are within the range of Mesolithic and modern  
 302 wild boars. According to model-based density estimations, calcaneus size variation is clustered  
 303 into two groups: a small one, similar in size to current wild boars, and a large one, similar in  
 304 size to current pigs and Mesolithic wild boars. Current pigs, from landraces to industrial breeds  
 305 have a larger CSA than extant and Mesolithic wild boars. Density estimations found three  
 306 components of variation in the humeral CSA of Neolithic *Sus scrofa*: (1) a small one, similar to  
 307 small extant wild boars, (2) a medium one, similar to large extant wild boars, and (3) a large  
 308 one, similar to current-day pigs or Mesolithic wild boars.



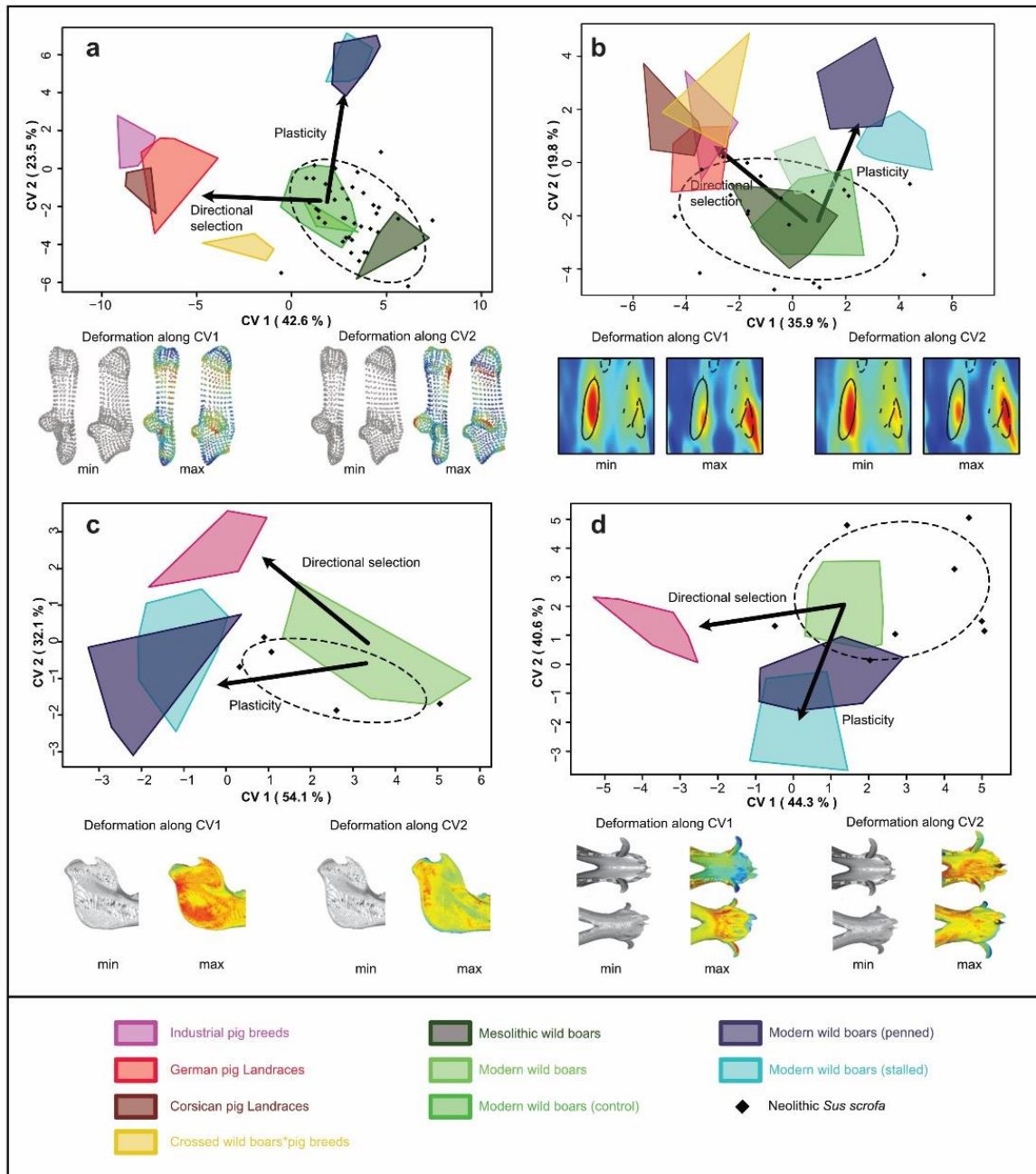
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310 **Figure 2:** Size variation in modern and archaeological *Sus scrofa* of Western Europe: (a)  
311 humerus shaft cross-section area (CSA), centroid size of (b) calcaneus (c) mandible's ramus,  
312 (d) mandible's symphysis. Modern samples are presented with notched boxplots. Model-based  
313 Gaussian mixture of size variation in archaeological *Sus scrofa* were performed for humerus  
314 shaft CSA (a) and calcaneus centroid size (b) with model-based clustering results displayed by  
315 different symbols and named accordingly. Abbreviations: WB=wild boars, WB  
316 exp=experimental wild boars, DP=domestic pigs.

### 317 *External and structural bone variation in modern and ancient Sus scrofa*

318 The variation in bone shape and humeral cortical thickness in Mesolithic and modern wild and  
319 domestic *Sus scrofa* displayed congruent patterns of diversification in the CVA morphospace,  
320 albeit with slight discrepancies (Figure 3). This variation is mainly influenced by human-driven  
321 selection between modern wild boars and modern pig breeds (CV1), while a plastic response to  
322 the human-driven control of mobility in wild boars is aligned with the second canonical axis  
323 (CV2), showing the prevalence of artificial selection over anthropogenic behavioural control in  
324 the phenotypic diversification of this species. It is worth noting that hybrids between wild boars  
325 and pigs (which were only available for the calcaneus and humerus) show a different  
326 diversification pattern: closer to hunted wild boars for the calcaneal shape variation (Figure 3a)  
327 and closer to landrace and industrial pig breeds for the topography humeral shaft cortical  
328 thickness, showing the greater influence of heredity in the former (Figure 3b). Finally, one can  
329 also note that Mesolithic and extant wild boars display similar humeral cortical topography  
330 (Figure 3b) but clear phenotypic divergence in their calcaneal shape variation (Figure 3a). For  
331 the mandibular-ramus (Figure 3c) and symphysis (Figure 3d), the divergence due to selection  
332 and plasticity is found along both the CV1 and CV2, but also resembles the pattern observed  
333 for post-cranial bones (even though the morphospace is rotated).

334 When projecting the variation of Neolithic *Sus scrofa* over the pattern of phenotypic  
335 diversification described previously, we observed that it was centred, albeit greater, within the  
336 phenotypic variation of Mesolithic and modern wild boars in their natural habitat; however,  
337 patterns differed according to the markers considered. Variability in humeral cortical  
338 topography stretches towards the directional selection trajectory of pig breeds and overlaps with  
339 the variation of landraces pigs (Figure 3b). On the other hand, the calcaneus shape variation  
340 spreads towards captive wild boars without overlapping (Figure 3a), the mandible-ramus  
341 displays a variation intermediate between hunted and captive wild boars (Figure 3c), while the  
342 symphysis reaches the range of captive wild boars (Figure 3d).



343

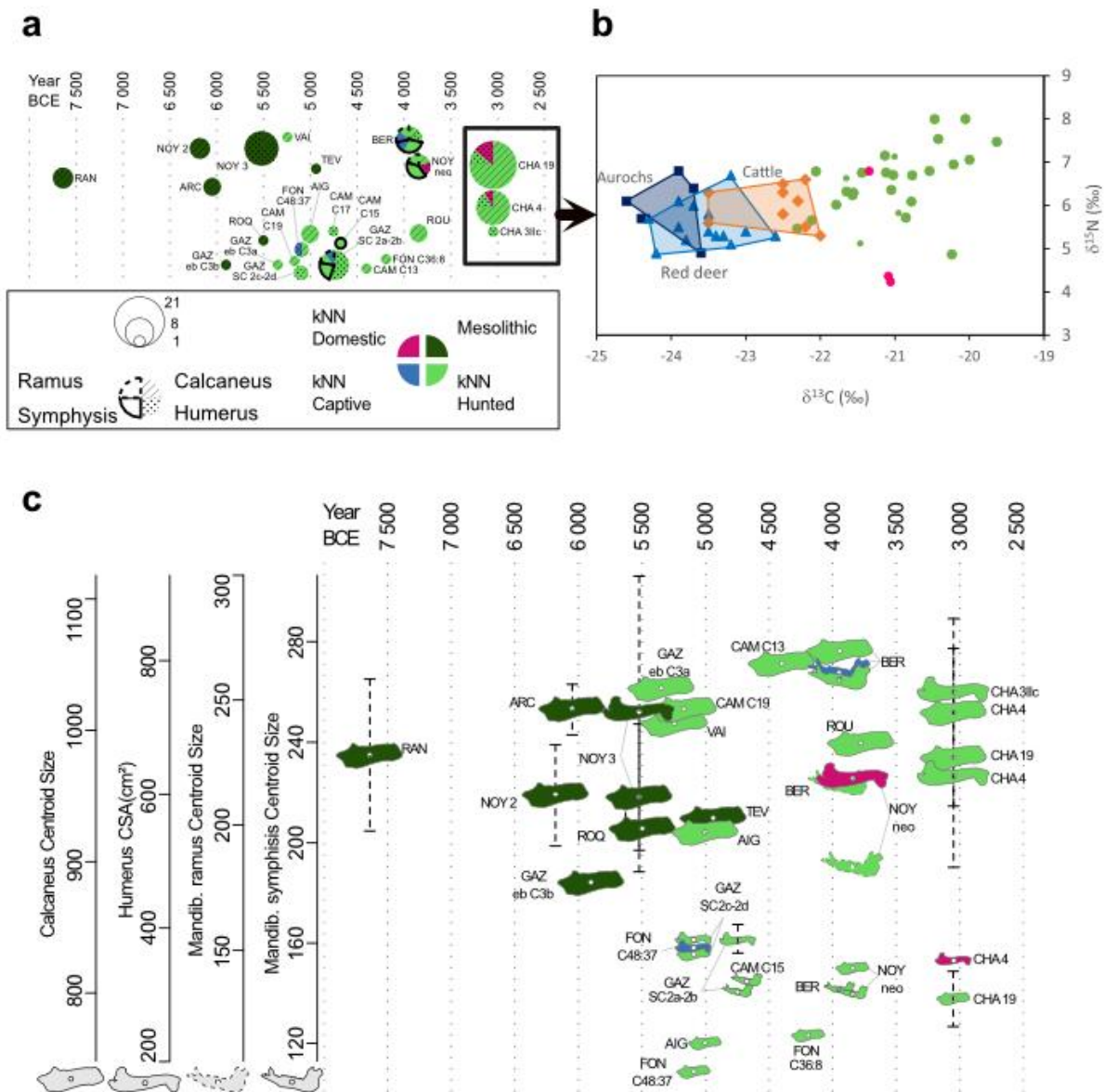
344 **Figure 3:** Phenotypic variation of Neolithic *Sus scrofa* compared to Mesolithic, modern  
 345 wild captive and domestic *Sus scrofa* from Western Europe. Morphospaces and shape  
 346 deformations from first and second CVA axes were computed from the shape variation of the  
 347 calcaneus (a), the morphometric mapping of the humeral shaft cortical thickness with the four  
 348 muscle attachment displayed (b), the mandible-ramus (c) and the mandible's symphysis (d).  
 349 *Neolithisation and phenotypic diversification in Sus scrofa*

350 CVA prediction and kNN Classification of the Neolithic *Sus scrofa* according to the hunted,  
 351 captive or domestic phenotypic comparative models computed separately for each  
 352 morphospace (Figure 4a, SI4) shows that 92% of the Neolithic *Sus scrofa* have a phenotypic  
 353 variation aligned with the variability of wild boar living in a natural habitat, suggesting that  
 354 they behaved like wild boar, in an environment without human ecological disturbance, apart

355 from harvesting. The projection of these morphometric inferences along the timeline from  
356 Mesolithic to Late Neolithic (Figure 4c) shows that by 5200 BCE, in Early Neolithic contexts  
357 of Southern France, and by 4000 BCE in Middle Neolithic France (Bercy) and Germany  
358 (Vaihingen), a new morphotype of small *Sus scrofa* can be observed. This small morphotype is  
359 on average 27% smaller than the large morphotype present since the Mesolithic and up to 29%  
360 smaller when compared with the large Neolithic *Sus scrofa* populations. Moreover, between  
361 the Mesolithic and the Late Neolithic, the large hunted *Sus scrofa* displays a 4% size increase.

362 CVA predictions and kNN algorithm identify only four Neolithic *Sus scrofa* with the  
363 phenotypic signature, for the humerus and mandible, of adult wild boars raised in captivity  
364 (Figure 4a). These captive specimens are observed around 5200 BCE in Early Neolithic  
365 contexts of Fontbrégoua, circa 4750 BCE at Gazel (context of transition between Early and  
366 Middle Neolithic) and later, by 4000 BCE, in the Middle Neolithic contexts of Bercy in  
367 Northern France.

368 Finally, the first phenotype that could be considered under anthropogenic reproductive selection  
369 was observed in the middle Neolithic site of Noyen-sur-Seine around 3800 BCE and in the late  
370 Neolithic site of Chalain around 3000 BCE. These five domesticated phenotypes were only  
371 detected via the morphometric mapping of the humeral cortical thickness, in both small and  
372 large morphotypes (Figure 4a).



373

374 **Figure 4:** a. Pie charts representing the classification of Neolithic specimens according to the  
 375 kNN algorithms in the canonical morphospace of each bone marker (humerus, calcaneus,  
 376 mandibular ramus and symphysis). The pie charts are spread horizontally along the  
 377 chronology of the archaeological contexts and vertically according to their latitudinal  
 378 positions. b. Diagram displaying the distribution of the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values obtained from  
 379 the bone collagen of *Sus scrofa* specimens from Chalain 3, 4 and 19. Also included are the  
 380 isotopic values for aurochs, red deer and cattle (Drucker and Bocherens, 2009). *Sus scrofa*  
 381 individuals are displayed according to their kNN identification and their model-based size  
 382 clustering (Small=small dot, Large=large dot) c. Phenotypic diversification of *Sus scrofa* from  
 383 Mesolithic to Late Neolithic displayed by size variation and kNN identification of each bone  
 384 (CSA=Cross Section Area). The large and small size of the bone pictograms correspond to  
 385 their size cluster identified by model-based Gaussian Density estimations.

386

387



388 *Results from stable isotope analysis at Chalain*

389 The collagen extraction yield averaged 136 mg/g (24–199 mg/g) and the collagen carbon and  
390 nitrogen contents averaged 42.3% (39.5–44.2%) and 15.2% (14.0–16.2%). The C:N atomic  
391 ratios varied from 3.24 to 3.31 in *Sus scrofa* and 3.17 to 3.25 in the remaining fauna (SI 2).  
392 These criteria testify to the high preservation of bone collagen at this site and support the  
393 suitability of all stable isotope data for interpretation.

394 The  $\delta^{13}\text{C}$  values measured in *Sus scrofa* vary between -22.3‰ and -19.6‰ (Figure 4b). These  
395 values are higher than those measured in aurochs (-24.6‰ to -23.6‰) and red deer (-24.3‰ to  
396 -22.6‰) and partly overlap with those measured in domestic cattle (-23.5‰ to -22.0‰) at the  
397 same site (Figure 4). In *Sus scrofa*, the  $\delta^{15}\text{N}$  values vary from 4.2‰ to 8.0‰ and are on average  
398 higher (6.4‰) than those measured in aurochs, red deer and cattle when considered together  
399 (mean = 5.8‰, from 4.9‰ to 6.8‰) (Supplementary Table S2 and Figure 4). The  $\delta^{13}\text{C}$  and  
400  $\delta^{15}\text{N}$  values of the four suids with a “wild caught” phenotype and a small size do not differ  
401 from the large size wild caught *Sus*. The three suids classified in the “domestic pig” phenotypic  
402 category have intermediate  $\delta^{13}\text{C}$  values (-21.3‰ to -21.1‰), two of which have the lowest  $\delta^{15}\text{N}$   
403 values of this dataset for *Sus scrofa* (4.2‰ and 4.4‰).

404 **DISCUSSION**

405 Using wild boars from the Mesolithic, as with the T0 for *Sus Scrofa* evolution during the  
406 Holocene, we first observed that current wild populations of *Sus scrofa* in the area under study  
407 have lost 16% of their body size compared to wild populations living in Western Europe some  
408 2500 years before the Neolithic transition. This supports our current understanding of a global  
409 body mass reduction of large mammals by the end of the Pleistocene (Smith et al., 2018).  
410 Considering that body size in wild boars follows Bergman’s rule (Albarella et al., 2009b), it has  
411 been argued that their body size reduction over the last 10 000 years was mainly due to  
412 adaptations to the global temperature increase during the Holocene [52,53]. However, human  
413 disturbance as the driver of the reduction in the body size of large mammals since the Late  
414 Pleistocene is also proposed (Pelletier and Coltman, 2018; Pigeon et al., 2017; Smith et al.,  
415 2018; Sullivan et al., 2017), with the unbalanced human harvesting of large prey as a key driver  
416 for body size reduction in large mammals (Darimont et al., 2015, 2009). Interestingly, we found  
417 a slight increase of wild boar body size during the Neolithic, in agreement with what has been  
418 found for wild boar populations during the Neolithic and Bronze Age in the Iberian Peninsula  
419 (Navarrete Belda and Saña Seguí, 2017). This suggests that the harvesting behaviour inducing  
420 size-selective harvesting of wild *Sus scrofa* populations occurred later, probably over the last  
421 two centuries, when harvesting pressure accelerated drastically (Coltman et al., 2003; Pigeon  
422 et al., 2017).

423 With the Neolithic transition in Western Europe by the 6<sup>th</sup> millennium BCE, we can observe  
424 the co-existence of a large and a small morphotype of *Sus scrofa*, with an almost 30% size  
425 difference during the whole Neolithic. The occurrence of small-sized *Sus scrofa* from the early  
426 Neolithic onward in Europe would be congruent with the well-documented arrival in Western  
427 Europe of small populations of *Sus scrofa* domesticated from a Near Eastern population (Evin  
428 et al., 2015; Krause-Kyora et al., 2013; Ottoni et al., 2013). The factors explaining this size

429 difference compared to endemic European wild boar have not been fully investigated yet, but  
430 they might be inherited from both the wild ancestral populations in the Near East, considered  
431 as a smaller sub-species (*Sus scrofa lybicus*) (Groves, 2007), with their body size reduction  
432 being the process of domestication by 8000 BCE in this area (Price and Evin, 2019). Both  
433 genetic legacies have left a strong phenotypic imprint on this population which then dispersed  
434 throughout Europe (Evin et al., 2015; Ottoni et al., 2013). Despite their size difference,  
435 however, both the large and small Neolithic *Sus scrofa* in our dataset displayed a shape  
436 variability within the norm of reaction of wild boars behaving in their natural habitat, without  
437 any mobility control.

438 The wild behaviour suggested by their bone morphology is not contradicted by their feeding  
439 behaviour, assessed through the stable isotopic study of the 30 large and small *Sus scrofa* from  
440 the Late Neolithic site of Chalain (Figure 4b). Here, the  $\delta^{13}\text{C}$  values measured in aurochs and  
441 red deer reflect a forested habitat, where the canopy effect results in lower  $\delta^{13}\text{C}$  values in plants  
442 (van der Merwe and Medina, 1991) and in the herbivores feeding on them (bone collagen  $\delta^{13}\text{C}$   
443 values in modern deer from deciduous forests average  $-23.8\text{‰}$  and are mostly  $\leq -22.6\text{‰}$ ;  
444 (Drucker et al., 2008), values corrected for the fossil fuel effect). The higher  $\delta^{13}\text{C}$  values  
445 measured in *Sus scrofa* may not be directly comparable to those measured in herbivores because  
446 their diet may have included a significant proportion of fruits (Ballari and Barrios-García, 2014;  
447 Schley and Roper, 2003). Fruits have higher  $\delta^{13}\text{C}$  values (by  $1\text{‰}$ ) compared to leaves in  
448 understory vegetation (Roberts et al., 2017), and this difference is inherited in frugivorous  
449 species compared to folivorous species ( $+1-1.5\text{‰}$  (Krigbaum et al., 2013). Taking this into  
450 account, the *Sus scrofa* found at Chalain would have occupied a wide range of habitats from  
451 forests to open environments, while their  $\delta^{15}\text{N}$  values suggest a low to moderate contribution  
452 of animal protein in their diet. Overall, these results are in agreement with the opportunistic  
453 omnivorous feeding behaviour and wide foraging habitat observed in modern wild boars  
454 (Ballari and Barrios-García, 2014), as well as in Mesolithic European wild boars which were  
455 alternatively found foraging in woodlands on a very low animal protein diet (in Denmark  
456 (Maring and Riede, 2019)), in a wider range of habitats with varying degree of openness (in the  
457 Netherlands; (Brusgaard et al., 2022)) or in an open environment and with a greater animal  
458 protein component (in Belgium; (Bocherens et al., 2007)).

459 Both morphometric and isotopic signatures suggest that the evolutionary interaction between  
460 both large and small Neolithic *Sus scrofa* populations and the Neolithic societies of Western  
461 Europe was mainly driven by harvesting (hunting). This hypothesis is supported by the recent  
462 integrated study of Late Mesolithic-Neolithic human-suid interaction in Rhine-Meuse, which  
463 found no evidence of small suid management during the Neolithic occupation (Brusgaard et al.,  
464 2022). However, previous studies from Eastern Europe in Late Neolithic Romania have  
465 considered small *Sus scrofa* as domestic livestock living in close proximity to the Neolithic  
466 settlements (Balasse et al., 2019, 2016; Evin et al., 2015), suggesting that suid interactions with  
467 Neolithic societies/villagers has differed at both ends of the Neolithic dispersal in Europe.  
468 Nevertheless, the co-occurrence of large and small wild morphotypes of *Sus scrofa* in Neolithic  
469 Western Europe raises several questions. Were these small *Sus scrofa* feral populations,  
470 stemming from the domestic *Sus scrofa* introduced by early Neolithic farmers, roaming free  
471 and independently from the care of Neolithic people and hunted throughout the period? If so,



472 can we consider that events of admixture and gene flow between the small and large populations  
473 were limited in time and space, preventing the morphological homogenisation of the two  
474 lineages? Were these small *Sus scrofa* under the care of Neolithic people and therefore  
475 “domestic” (Dwyer, 1996), albeit under an extensive management system as seen in the pre-  
476 industrial diversity of pig production in New Guinea (see synthesis and references in (Price and  
477 Hongo, 2019)) where they are considered as livestock but behave freely in a natural habitat,  
478 with occasional proximity to the settlement? In these extensive management systems, females  
479 are captured (along with the occasional male) and penned for several months for impregnating  
480 and then left free to roam in order to be harvested in the wild for pork (Dwyer, 1996). Their  
481 short period of captive life would not have left a strong enough imprint in their bone variation  
482 for our morphometric approach to detect. Whatever the answers, the emergence of this small,  
483 wild type of *Sus scrofa* has produced a new phenotypic and genetic diversity in the *Sus scrofa*  
484 populations of Western Europe.

485 Beyond the body-sized diversity of *Sus scrofa*, fostered by the translocation of domesticated  
486 pigs of Near Eastern ancestry, few anthropogenic morphological changes beyond the  
487 phenotypic variation of *Sus scrofa* living freely in its natural habitat can be observed during the  
488 Neolithic niche construction in Europe. The first phenotypic change observed during the Early  
489 and Middle Neolithic is a plastic response of tarsal and skull bones similar to the variation  
490 induced by a life in captivity (Harbers et al., 2020a; Neaux et al., 2021, 2020). The rare  
491 occurrence of this plastic response to captivity in the Neolithic *Sus scrofa* suggests that captivity  
492 was a rare practice in Neolithic Europe and that wild capture management (Dwyer and  
493 Minnegal, 2020), as described above, would have been the main interaction at that time.  
494 According to this management system, only a few females and occasionally castrated males  
495 were kept in captivity, which would explain why so few occurrences are observable in the  
496 archaeological record. The limitations of our study, aside from the finite number of individuals  
497 to cover such a long time period over such a large geographic area, are therefore double. First,  
498 our methodological approach relies on adult and sub-adult specimens, while husbandry  
499 practices could necessitate the culling of most males before the age of two. This means that the  
500 phenotypic variation of a large proportion of the population may not have been sampled in this  
501 study, reducing the possibility to capture phenotypic adaptations to Neolithic habitat  
502 transformations at a greater scale. Further age-free phenotypic markers, therefore, need to be  
503 developed. The second limitation is the reductionist character of a comparative approach  
504 relying on a modern referential, even with experimental conditions such as the one presented  
505 here. The complexity of the potential configuration encompassing the interaction between  
506 people and suids during the Neolithic can never be fully covered or deciphered.

507 Around 6000 years ago, by the Middle and especially the Late Neolithic, the 3D topography of  
508 the humeral shaft cortical thickness can pick rare but significant phenotypic changes along the  
509 selective trajectory towards modern pig breeds (Figure 3b). To understand the human intention  
510 behind these changes, one need to consider first that differences in cortical topography between  
511 hunted wild boars and current pig breeds are due to functional changes driven by selection for  
512 fast growth and muscle production, altering the gait of the animal (Harbers et al., 2020b). Then,  
513 that humeral shaft topography in wild boars is mainly influenced by body mass variation  
514 (Harbers et al., 2020b). Accordingly, the similarity in the shaft cortical topography of some

515 Middle and Late Neolithic *Sus scrofa* with current pig breeds suggests that they might have  
516 reached extreme body masses leading to a functional change in their humeral shaft anatomy.  
517 Was their diet controlled for extreme weight gain? Are we witnessing the early evidence of  
518 selection for fast body growth or greater fat production? It is impossible to answer this question  
519 yet; although, in the pre-industrial pig husbandry systems of New Guinea, there are  
520 ethnographic examples of captured wild boars fattened to the point that they cannot stand on  
521 their feet (Dwyer, 1996). The isotopic signature of Late Neolithic specimens of Chalain, where  
522 “domestic”, “wild” and “captive” phenotypes are present, did not provide any evidence that  
523 these “domestic” pigs had a diet richer in animal protein compared to the others (Figure 4b).  
524 However, if these special pigs had been fattened with a grain-rich diet, we would not have been  
525 able to observe it with these isotopic proxies, unless the grains were grown on manured fields  
526 (Price and Hongo, 2019).

## 527 **CONCLUSION**

528 This study has provided strong confirmation that the archaeological record can help track the  
529 impact of a millennia of human niche construction on the evolution of animals (Laland and  
530 O’Brien, 2011) and contribute to the documentation of their evolutionary trajectory (Sarrazin  
531 and Lecomte, 2016). We found that the Neolithic Niche Construction had inceptive but limited  
532 impact on the phenotypic evolution of *Sus scrofa* in Western Europe. In the 4500-year  
533 timeframe of our study we did not find any evidence of size-selective harvesting, though a  
534 strong size decline between Pre-Neolithic and modern wild boar populations was observed,  
535 suggesting that harvesting pressures on size in *Sus scrofa* populations did not happen during  
536 the Neolithic transition. The main impact was the translocation of allochthonous domestic  
537 populations of a smaller size, which increased the local phenotypic diversity of *Sus scrofa* in  
538 Western Europe. The feralisation of these alien populations did not seem to induce a novel  
539 selective pressure on local populations or a phenotypic homogenization among the local and  
540 feral populations. Nevertheless, the greater phenotypic diversity in Western Europe *Sus scrofa*  
541 produced by this introduction could have fostered the local domestication in Europe. A loose  
542 rearing model, which would have induced no observable traits for most of the Neolithic *Sus*  
543 *scrofa* in our dataset, might have been the most common husbandry practice for these animals  
544 during this period; nonetheless, rare evidence of phenotypic divergence from the variation seen  
545 in boars in a natural habitat was documented. The first is observed from the Early Neolithic  
546 onwards and is most likely due to major mobility constraints. Later in the Neolithic, phenotypic  
547 changes suggest new selective pressures on *Sus scrofa* populations cared for by Neolithic  
548 people, maybe as early evidence of selective breeding for fast growth or fat production. Further  
549 research is still required, therefore, including paleogenomic and metabolomic studies on  
550 relevant and well-dated samples from Mesolithic to modern times in order to document the  
551 rapid evolutionary pace of cultural processes.

552

## 553 **CONFLICT OF INTERESTS**

554 The authors declare that the research was conducted in the absence of any commercial or  
555 financial relationships that could be construed as a potential conflict of interest.

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566 *Author Accepted Manuscript arising from this submission.”*

567 **SUPPLEMENTARIES**

568 **Table S1.** Details for each archaeological *Sus scrofa* bones studied with information on their  
569 archaeological stratigraphic contexts, anatomical position, lateralisation, ageing and sexing.

570

571 **Text S2:** Description and references for the archaeological contexts from which the  
572 phenotypic markers of the study have been collected.

573 **Table S3:** Description of the modern corpus of *Sus scrofa* specimens used for the study.

574

575 **Figure S4:** Display of the phenotypic classification for each archaeological remain of *Sus*  
576 *scrofa* according to both LDA and kNN predictive approaches performed on the shape  
577 variables. Also included are the results of the model-based clustering approach performed on  
578 the size variables.

579

580 **Table S5.** Stable isotope extraction yields from *Sus scrofa* remains collected at the  
581 archaeological site of Chalain (France).

582

583 **DATA AVAILABILITY**

584 The morphometric dataset for this study can be found in the Dryad repository following this  
585 link:

586 <https://datadryad.org/stash/share/bIB4h5ellfpy2nafCVwhNm3Im1xOIRIX9ICR6Bu08DE>.

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