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# 8,000 years of morphometric evolution of sheep, goat, and pig in the Northwestern Mediterranean basin

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## Abstract

Understanding how domestic mammal species evolved through time provides insight into the artificial and natural selection processes that have shaped the diversity of domestic animals. The focus of this article is the morphometric evolution of sheep, goats, and suids in the Northwestern Mediterranean Basin over the last 8,000 years, employing a 2D geometric morphometrics protocol applied to the third lower molars.

Using a comprehensive dataset comprising 2,798 archaeological specimens from 176 sites in Southern France and Spanish Catalonia, along with 1,303 modern specimens, we aim to identify and contrast the environmental and anthropic factors influencing species evolution linked to past husbandry practices.

Each of these three taxa follows its own evolutionary trajectory, exhibiting variations over time and across different regions. Notably, reduction in the centroid size of sheep molars between the Neolithic and the early Iron Age could potentially be associated with an increased demand for meat and/or shifts in male-to-female ratios. A clear geographical structuring of caprines between the Neolithic and Antiquity is observed, likely influenced by a combination of factors including artificial selection, environmental changes, and socio-economic dynamics, as corroborated by previous studies. Moreover, a reduction in molar size

48 during the Middle Ages is observed across all three species, possibly linked to extensive  
49 agropastoral practices. Furthermore, divergent processes of breed improvement and  
50 standardization are identified in pigs and caprines.

51 This study highlights the complex nature of morphological variations in domestic species,  
52 emphasising the multifactorial influences involved. It underscores the importance of  
53 interdisciplinary approaches in understanding the factors contributing to morphological  
54 transformations over time.

55

56 **Keywords:** Geometric Morphometrics, *Ovis aries*, *Capra hircus*, *Sus scrofa*, Diachrony,  
57 Archaeozoology

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## 60 Introduction

61 In many post-Neolithic societies, human meat consumption relies primarily on the exploitation of  
62 domestic species. The evolution of domesticated species is a complex, continuous and still ongoing  
63 process, during which the relationships between humans and domesticates have evolved and is likely  
64 to be the result of multiple, intricate factors, including both human and natural selection (Price,  
65 1984, 1999, 2002; Zeder, 2012a). This has resulted in the many breeds we know today (Alhajeri et al.,  
66 2019; Drake, 2011; Selba et al., 2020).

67 The first farmed domestic mammals were cattle, sheep, goats and pigs, whose domestication started  
68 during the 10th millennium B.C. in the Near-East (Teletchea, 2019; Vigne, 2011; Zeder, 2008a, 2008b,  
69 2012b). Following their initial domestication, these domestic species spread westward with the first  
70 farmer Neolithic expansion, reaching the Northwestern Mediterranean basin ~8000 years ago, along  
71 with agricultural practices, ceramic production, sedentarism, increased storage activities, and  
72 significant population growth (Bocquet-Appel, 2008). Over the last 8 millennia, this region has  
73 witnessed significant socio-economic (e.g. Barberan 2013; Gascó 2004; Guizot 1843; Lopez Cachero  
74 2007; Vaginay et al. 2012), environmental (e.g. Araus et al. 1997; Azuara et al. 2015; Frigola et al.  
75 2007) and demographic changes (e.g. Armada et al., 2005; Lemerrier, 2004; Russell, 1962; Sanmartí,  
76 2004; Zémour et al., 2011). These transformations have undoubtedly influenced the evolution of the  
77 domesticated species and their relationship with humans, in an area that is outside of their original  
78 centres of domestication.

79 Among the first introduced domestic species, remains of pig (*Sus scrofa*), sheep (*Ovis aries*) and goat  
80 (*Capra hircus*) are abundant in the archaeological record. These species are of major economic  
81 importance and have been continually exploited in the region since the Neolithic. While meat is the  
82 primary product of the pig, sheep and goats are exploited for their milk, wool and skin (Gillis et al.,  
83 2019; Helmer and Vigne, 2004; Rast-Eicher and Jørgensen, 2013; Ryder, 1992; Shishlina et al., 2003;  
84 Vigne, 2005; Vigne and Helmer, 1999, 2007). Pigs have been the subject of numerous studies in the  
85 Northwestern Mediterranean basin and in Gaul, particularly for Roman period archaeological  
86 contexts, where morphological variation has been linked to economic and cultural shifts (Duval et al.,  
87 2015, 2018). However, outside of these well-documented periods, their long-term evolution remains  
88 poorly understood.

89 Sheep and goats are also two inseparable and iconic species of the Mediterranean landscapes. While  
90 biomolecular markers such as ancient DNA (Loreille et al., 1997) or palaeoproteins (ZooMS, Buckley et  
91 al., 2010; Buckley and Kansa, 2011) are now used for species identification, the two species are  
92 morphologically similar, making it often difficult to distinguish between them in archaeological  
93 contexts. Although discrete criteria (e.g. Halstead et al., 2002; Helmer, 2000; Zeder and Pilaar, 2010)  
94 and metrical analyses (Fernandez, 2001; Gillis et al., 2011; Salvagno and Albarella, 2017) have been  
95 historically used on teeth and bones, their reliability appears sometimes limited in archaeological  
96 contexts. Geometric morphometrics on the third lower molar have proven highly effective in  
97 distinguishing sheep from goats in both modern (Jeanjean et al., 2022) and archaeological (Jeanjean  
98 et al., 2023a) specimens. This approach has offered new perspectives for tracking the long-term  
99 evolution of the two species separately using as a marker of morphometric variation the third lower  
100 molar, a remain that is often found well preserved and in large number in archaeological  
101 assemblages from the Northwestern Mediterranean basin.

102  
103 The long-term morphometric evolution of domesticated species has been described for some regions  
104 and periods of time (e.g. Forest and Rodet-Belarbi 2002; Grau-Sologestoa 2015; Knockaert et al.  
105 2018; Nieto Espinet et al. 2021; Vuillien 2020), providing an improved understanding of  
106 zooarchaeological trends across different animals. This is particularly well-documented for cattle in  
107 specific chronologies and regions (e.g. Colominas et al., 2014; Duval et al., 2012; Frémondeau et al.,  
108 2017). However, those studies mainly rely on the comparison of chronocultural periods, and only few  
109 studies considered a continuous time scale. The aim of this study is to focus on the morphometric  
110 variation of caprines (sheep and goats) and suids in the Northwestern Mediterranean basin. This will

111 be achieved by applying geometric morphometrics to quantify the size and shape variation of the  
112 third lower molar during the last 8,000 years and originating from various archaeological,  
113 environmental and geographical contexts. Through this approach, we aim to improving our  
114 understanding of the morphological evolution of these domesticated species and shed light on the  
115 factors that have shaped the evolution of agrobiodiversity in the Northwestern Mediterranean basin  
116 from the Neolithic to nowadays specimens . Specifically, we 1) assess the identification of sheep and  
117 goat of 2,238 caprines remains and explore their relative proportions over time, 2) highlight the  
118 chronocultural attribution of morphological change in sheep, goats and pigs, 3) construct a  
119 diachronic trend for each species and 4) interpret those results in light of archaeological, biological  
120 and environmental data.  
121

---

## 122 Materials

### 123 Studied area

124 The study area is circumscribed by the Rhône River in the east and the Ebro River in the south. It  
125 encompasses the present-day regions of Occitanie in Southern France and Catalonia in Spain (Fig. 1).  
126 This area is characterised by different environmental landscapes, with the coastline to the South  
127 bordering the Mediterranean Sea, while the Pyrenees massif separates Spain from France (Fig. 1).  
128 Four regions are considered in this study ensuring sufficient specimens per category for the analyses  
129 (Fig. 1): Eastern and Western Languedoc, and the coastal and inland parts of Catalonia.

130 In southern France, the Languedoc region is separated by the Herault valley. Despite both region  
131 having a similar temperate climate based on Köppen classification (Beck et al., 2018, Fig. 1), these  
132 areas differ in topography and archaeological evidence. Age disparities range from the Neolithic  
133 (Lemerrier, 2004) to the Bronze Age, with different material cultures (Gasco, 2012; Gascó, 1988;  
134 Guilaine, 1990; Roudil, 1972) and funerary practices (Dedet and Schwaller, 2011). This differentiation  
135 continued into Antiquity, as the cities of Nîmes in the East and Narbonne and Béziers in the West  
136 each exerted influence on their surrounding landscapes (Assénat, 2010).

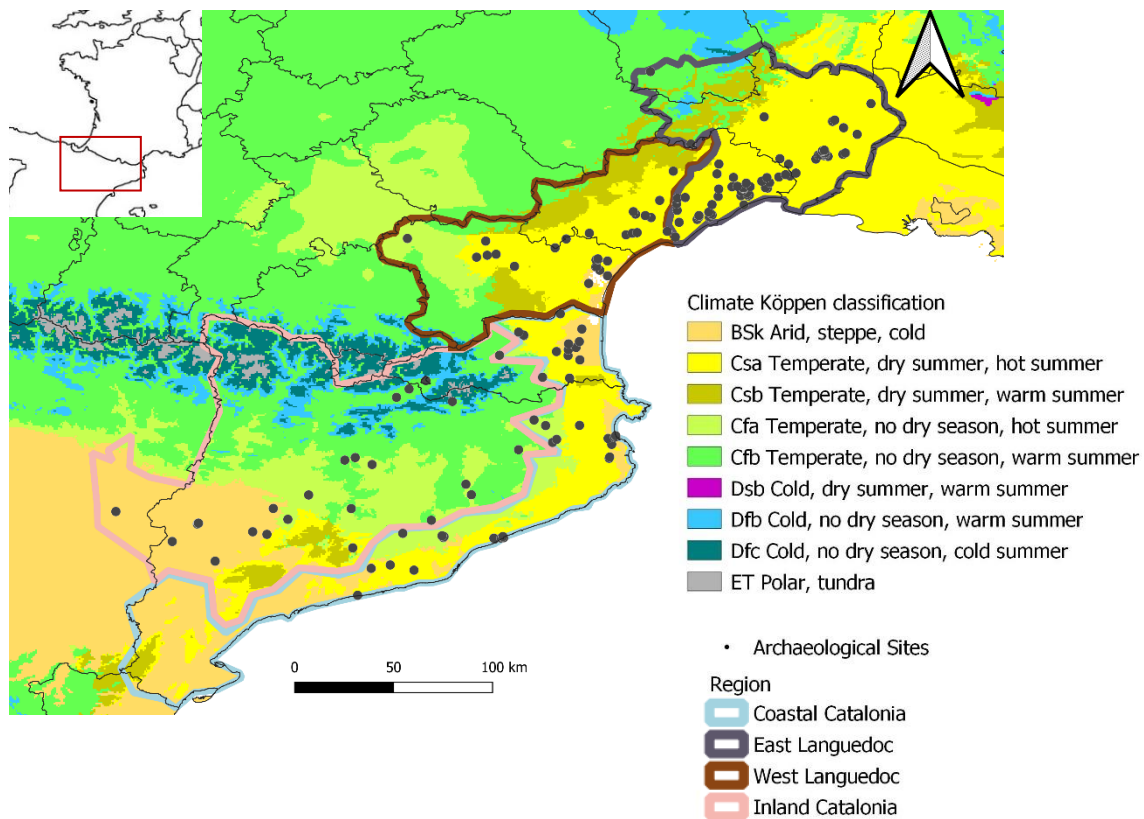
137 In Catalonia, the pre-littoral chain parallel to the coast, divides the region into coastal and more  
138 mountainous inland areas (Fig. 1). The coastal part of Catalonia experiences a temperate climate with  
139 hot and dry summers (Fig. 1), while the inland area is subject to a mixture of arid and temperate  
140 climates (Fig. 1), with a colder climate near the Pyrenees (Beck et al., 2018).

141 The Roussillon region, due to its geographical proximity to Catalonia and its separation from  
142 Languedoc by the Corbières mountains (1230 m, Pech de Bugarach, Fig. 1), has traditionally been  
143 associated with northern Catalonia. For this reason, in this study, the Roussillon region is considered  
144 to be part of Catalonia, and thus divided into two parts as explained before.  
145

### 146 Archaeological sample

147 A total of 2,798 third lower molars of caprines (N=2,238) and suids (N=560) were selected from  
148 archaeozoological assemblages originating from 176 settlement sites. These sites, most of which  
149 have been extensively studied by archaeozoologists (SI Tab. 1), have a well-controlled stratigraphy  
150 spanning the last 8,000 years (Tab.1). Each specimen is characterised by its geographic region of  
151 origin (*i.e.* one of the four regions), and its temporal range, determined by the earliest (*terminus post*  
152 *quem*, TPQ) and latest (*terminus ante quem*, TAQ) dates of the most precise stratigraphic context  
153 from which it was excavated, targeting the stratigraphic unit wherever possible. To facilitate  
154 comparison of broad trends, each specimen was assigned to one of the six broad chronocultural  
155 periods: Neolithic, Bronze Age, Iron Age, Antiquity, Middle Ages and Modern/Contemporary Period  
156 (Tab. 1). This chronological classification, determined in collaboration with local specialists, spans  
157 significant socio-economic, cultural, and environmental changes representing major transitional  
158 periods from the advent of agriculture in the region to the present day (Blin et al., 2016). Despite the

159 broad time frames these categories cover, they serve as pivotal markers delineating significant socio-  
 160 cultural phases in the history of the region.  
 161  
 162



163  
 164 <Figure 1>: Map of the studied area, with the location of archaeological sites, depending on climate  
 165 using Köppen classification (Beck et al., 2018). Coloured outlines correspond to region delimitations  
 166 with eastern Languedoc in purple, western Languedoc in brown, inland Catalonia in pink and coastal  
 167 Catalonia in blue. Map created using the Free and Open Source Q GIS (QGIS Development Team,  
 168 2009). For a map detailed with archaeological site numbers, see SI Fig.1

169  
 170 For the purpose of the study each specimen is characterised by: its geographic origin (i.e. one of the  
 171 four regions), its dating represented by the TPQ and TAQ of the most precise stratigraphic context  
 172 from which it stems, and its attribution to one of the six large chronocultural attributions.  
 173

174 <Table 1>: Number of studied specimens through chronocultural attributions and by regions.  
 175 Numbers are separated by Caprines and Suids (C - S).

	Catalonia		Languedoc	
	Coastal	Inland	West	East
Neolithic (N ; 6 mil. -2 mil BCE)	41 - 7	38 - 0	39 - 4	273 - 9
Bronze Age (Br; 2 mil. - 8 <sup>th</sup> c. BCE)	17 - 8	6 - 0	28 - 7	10 - 3
Iron Age (Ir; 8 <sup>th</sup> c. - 2 <sup>nd</sup> c. BCE)	206 - 18	240 - 25	115 - 57	219 - 88
Antiquity (Ant ; 2 <sup>nd</sup> c. BCE - 5 <sup>th</sup> c.CE)	201 - 45	79 - 15	41 - 54	156 - 107
Middle Ages (MA; 5 <sup>th</sup> c.CE - 15 <sup>th</sup> c.CE)	50 - 1	81 - 13	45 - 17	323 - 79
Modern/Contemporary Period (MOD/CONT; 15 <sup>th</sup> c.CE to the present day)	6 - 0	6 - 0	1 - 0	17 - 3

## 177 Methods

### 178 Geometric morphometrics

#### 179 2D image acquisition

180 Third lower molars were studied using two-dimensional geometric morphometrics. All studied  
181 specimens had fully-erupted third lower molars. Standardised photographs were taken using a Nikon  
182 d90 LSR camera paired with a 60 mm macro lens (AF-S Micro NIKKOR) attached to a photographic  
183 arm (Manfrotto 244RC) following published protocols for suids (Evin et al., 2013) and caprines  
184 (Jeanjean et al., 2022). For caprines, the third lower molars were positioned perpendicular to the lens  
185 with the root equally visible on both lingual and labial sides (Jeanjean et al., 2022). For suids,  
186 the third lower molars were positioned with their occlusal surface flat to the camera lens (using a  
187 spirit level), and the same amount of root visible on both lingual and labial sides of the anterior cusps  
188 (Evin et al., 2013).

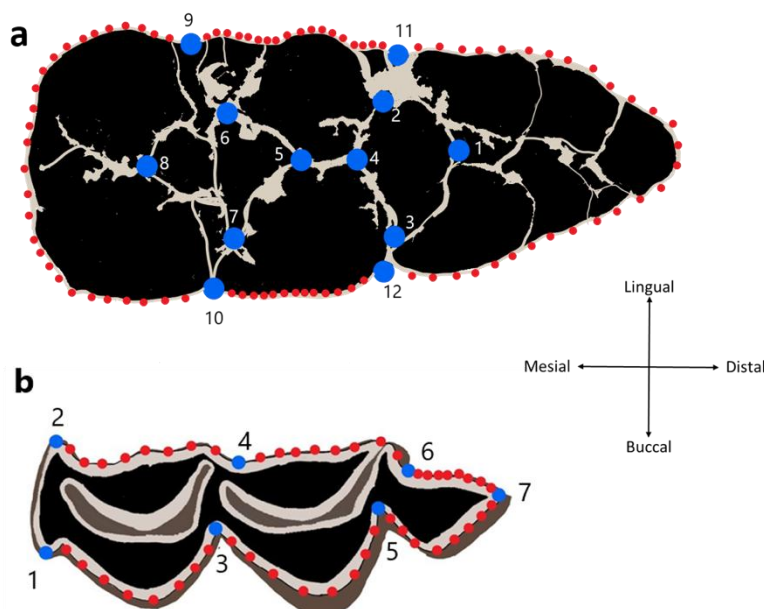
#### 189 GMM data acquisition

190 For caprines, the shape and size of the third lower molar were quantified using 7 landmarks and 48  
191 sliding semi-landmarks distributed along 6 curves (8 equidistant points each, Fig. 2, Jeanjean et al.,  
192 2022). The effectiveness of this protocol in distinguishing between archaeological sheep and goats  
193 has been previously established (Jeanjean et al., 2023a).

194 The size and shape of the suid third lower molar was assessed using the coordinates of 12 landmarks  
195 and 87 sliding semi-landmarks distributed along 4 curves (Fig. 2, Evin et al., 2013). In order to assess  
196 the potential presence of wild boar in the archaeological samples, data from 56 domestic pigs and 68  
197 extant wild boars from Western Europe were included.

198 All raw data and information on both archaeological and modern specimens are provided in SI Tab. 2  
199 and 3.

200



201

202 <Figure 2>: Geometric morphometric protocols for (a) suids and (b) caprines. Landmarks are shown in  
203 blue, sliding semi-landmarks in red.

204

205 Coordinates were superimposed using a Generalized Procrustes Analysis (GPA) with the sliding semi-  
206 landmarks allowed to slide by minimizing the sum of the Procrustes distances between each

207 individual and the mean shape (Perez et al., 2006; Sampson et al., 1996; Sheets et al., 2004). The  
208 Procrustes residuals were then subjected to Principal Component Analysis (PCA) (Goodall, 1995;  
209 Gower, 1975; Rohlf and Slice, 1990).

---

## 210 **Statistics**

### 211 **Identification of archaeological sheep and goat**

212 Archaeological sheep and goats were identified based on the proximity of their third lower molar  
213 shape with modern and archaeological reference collections. Our current reference collection,  
214 identical to that in Jeanjean et al. (2023b), includes 521 sheep and 222 goats. To this collection, we  
215 added 64 archaeological sheep and 45 archaeological goats whose identification was confirmed by  
216 ZooMS (SI Tab. 2 and 3 of Jeanjean et al. 2023b). The caprines identified by Zooms are from Catalonia  
217 and Languedoc and dated from the Neolithic to the Modern period. The identification of all the  
218 remaining archaeological specimens was therefore based on comparison with 585 sheep and 267  
219 goats (SI Tab. 2).

220 A predictive linear discriminant analysis approach was employed, based on the 20 first PCA  
221 components maximising the leave-one out cross-validation accuracy between the two species  
222 (Baylac and Friess, 2005). Because unbalanced sample sizes may bias classification accuracy  
223 (Kovarovic et al., 2011), a resampling procedure was applied, sampling over 100 permutations the  
224 largest group to match the size of the smallest (here the goat) group (Evin et al., 2013). The accuracy  
225 of the species identification was expressed as the median and 90% interval of the distribution of the  
226 100 cross-validation percentages.

227 The a posteriori percentages of identification of the archaeological specimens were summarized by  
228 the percentage of times a given specimen was identified to a specific group (Evin et al., 2015). All  
229 discriminant analyses were considered, and no cut-off threshold was set for posterior probabilities.  
230 Only linear discriminant analysis (LDAs) with a correct cross-validation percentage (CVP) above the  
231 3<sup>rd</sup> quartile of all CVP values were retained to select the most discriminant analyses.

### 232 **Differences between sheep and goat**

233 Following the identification of archaeological caprines, differences in the proportion of sheep and  
234 goats between periods and regions were assessed using a chi-squared test. To test for differences in  
235 the temporal trends in the evolution of sheep and goats, one-way ANOVA and MANOVA were  
236 conducted based on chronocultural attribution.

237

### 238 **Temporal variation**

239 Temporal variations were investigated for both size and shape. For each taxon, one-way ANOVA and  
240 MANOVA were employed to test for overall differences in size and shape over time, with size or  
241 shape serving as the dependent variable and time as a discrete factor, using chronocultural  
242 attributions.

243 Differences in size between periods were assessed using pairwise Wilcoxon tests, while pairwise  
244 shape differences between periods were assessed using MANOVA. Size and shape differences were  
245 paired with correct cross-validation percentages (CVP, mevoCVP function, Evin et al. 2015,  
246 Bonhomme and Evin, 2019) between periods. CVPs were computed from discriminant analyses,  
247 paired with leave-one-out correct cross-validation based on resampled groups of the same size,  
248 following the methodology of Evin et al. (2013). CVP complements p-values by quantifying how  
249 accurately groups can be re-identified, indicating the degree of morphological differentiation  
250 between periods. This approach provides a measure of group distinctiveness, beyond statistical  
251 significance alone (Amrhein et al., 2019).

### 252 **Regional structuring**



253 Because we studied four regions and 6 chrono-cultural periods, the number of groups render the  
254 visualisation difficult to read. Therefore, the regional pattern of variation was assessed for three  
255 larger time frames covering – from Neolithic to the Iron Age (6<sup>th</sup> mil - 2<sup>nd</sup> c. BCE), - Iron Age and  
256 Antiquity (8<sup>th</sup> c BCE - 5<sup>th</sup> c.CE), and - from Antiquity to Contemporary period (2<sup>nd</sup> c. BCE. – to the  
257 present day). As a consequence, some specimens were included in two subsequent analyses (but  
258 never duplicated in a single analysis). This allows the study of transitions between successive  
259 periods. For each time frame, size and shape differences between periods and regions were assessed  
260 using two-way ANOVA and MANOVA. Pairwise regional analyses were conducted only when both  
261 temporal and regional differences were present. As in previous analyses, pairwise shape differences  
262 were assessed using MANOVA, paired with cross-validation percentages. Statistical tests were only  
263 applied when the sample size of each group was larger than 5.

## 264 Diachronic trends

265 Diachronic trends were visualised with time as a continuous factor, *i.e.* without considering the  
266 discrete chrono-cultural periods. To account for dating uncertainty in the TPQ/TAQ range, a  
267 resampling procedure was implemented. Each date was uniformly sampled 1000 times within the  
268 TPQ and TAQ interval. This allows the generation and visualisation of 1000 regression curves  
269 between the dates and the size of the specimen. This procedure was executed using the pataqu R  
270 package (Bonhomme and Evin, 2023). However, due to limited sample sizes, it was not always  
271 possible to visualise size variation in diachrony. In such cases, differences in size between periods  
272 were visualised using boxplots and tested using pairwise Wilcoxon tests paired with CVP.

273 Shape variation was first visualised using Principal Component Analysis (PCA), followed by Canonical  
274 Variate Analysis (CVA) for maximum discrimination between groups. Similarities between regional  
275 periods were visualised using a neighbour-joining network, computed on the Euclidean distance  
276 between each mean shape of regional periods, using the Vegdist function from the vegan R package  
277 (Oksanen et al., 2022). The use of mean shape helped mitigate issues associated with very small  
278 sample sizes, which can vary significantly from one period to another.

279  
280 All analyses were performed using the R language v4.3.1 (R Core Team, 2023) through the Rstudio  
281 interface v023.9.1.494 (Posit team, 2023). Morphometric analyses were performed using the R  
282 packages geomorph (Adams et al., 2022; Baken et al., 2021; Collyer and Adams, 2018, 2021) and  
283 Morpho (Schlager, 2017), and the visualisations were obtained with ggplot2 (Wickham, 2016).

---

## 284 Results

### 285 Sheep Goat Identification

286 The reference datasets of securely identified specimens (*i.e.* modern specimens and archaeological  
287 specimens identified by Zooms) allowed the correct identification of unknown specimens with a  
288 probability of 96.36% (95.82-96.77%).

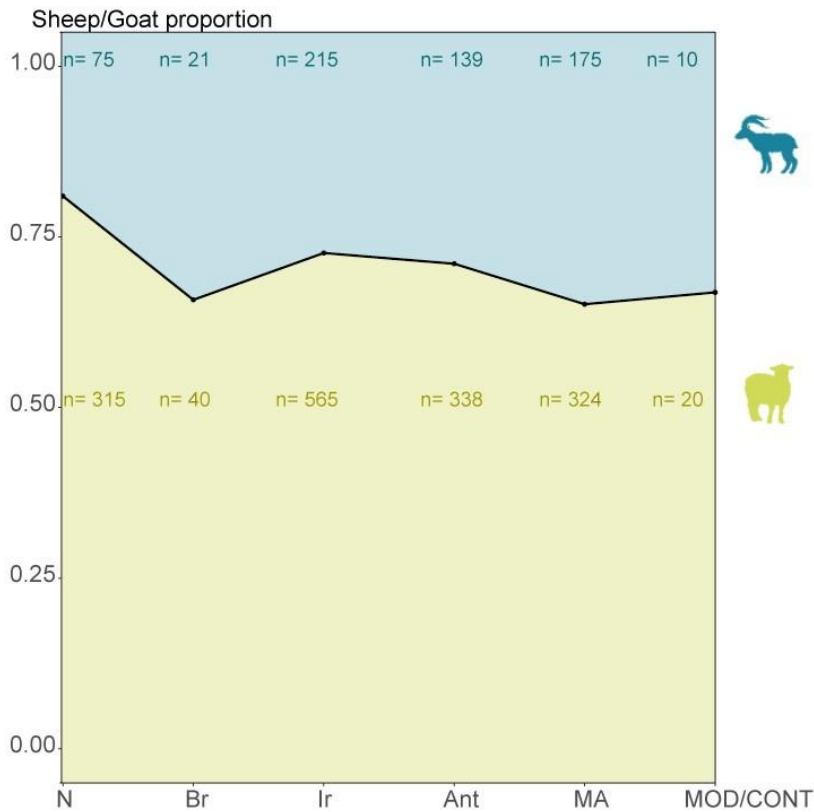
289 Among the 2,238 archaeological specimens studied, 109 were from the archaeological reference  
290 dataset and had already been identified by ZooMS (64 sheep, and 45 goat). On the 2,129 remaining  
291 teeth, 1,539 were identified as belonging to sheep and 590 to goats. Both species were present in all  
292 periods (SI Tab. 4) with a sheep/goat ratio varying from 80% to 65%, with an average of 5 sheep to 2  
293 goats (Fig 3, see SI Fig 2 and SI Tab 5 for detail by region). However, this ratio varies across periods  
294 ( $X^2=29,12$ ,  $p\text{-value}=2 \times 10^{-5}$ ), particularly with a proportional increase in goats during the Bronze Age  
295 compared to the Neolithic ( $X^2=1,00$ ,  $p\text{-value}=0.011$ , from 19% to 34%) followed by a stability in  
296 sheep/goat proportion.

297

298

299

300



301 <Figure 3 > Sheep and goat proportions through time. Time was visualized by periods. Sheep are in  
 302 green, goats in blue. Differences between proportions through time were tested with a  $\chi^2$ . N=  
 303 Neolithic, Br= Bronze Age, Ir=Iron Age, Ant= Antiquity, MA= Middle Ages, MOD-CONT= Modern and  
 304 Contemporary Periods.

### 305 Overall diachronic variation

306 The overall diachronic variation revealed that for the three taxa, the specimens differed through time  
 307 in their molar size and shape (Tab.2). However the distinction between periods is low (all CVP under  
 308 25%, Tab. 2) meaning that the differences are not strong enough to reliably classify specimens into  
 309 their correct periods based on morphology alone. Moreover, sheep and goats exhibit distinct  
 310 evolutionary patterns over time in both size (2-way ANOVA, interaction:  $F=8.07$ ,  $p\text{-value} = 1,15 \times 10^{-8}$ )  
 311 and shape (2-way MANOVA, interaction:  $F=1.93$ ,  $p\text{-value} = 2 \times 10^{-16}$ ).

312  
 313 <Table 2>: Differences in size and shape of the third lower molar through the 7 chronological periods  
 314 (including the six broad chronocultural periods for archaeological samples and the Reference  
 315 collection of modern specimens). Results of one-way ANOVA and MANOVA respectively for size and  
 316 shape are provided for sheep, goats and suids with mention of the F- statistic of the test, and of the p-  
 317 value. The p-values in bold are inferior to 0.05. The Cross-Validation Percentages (CVP) are calculated  
 318 between the 7 chronological periods.

	Size			Shape		
	F	p-value	CVP	F	p-value	CVP
Sheep	131	<b><math>&lt;2 \times 10^{-16}</math></b>	22.9% [15.68-30]	3.32	<b><math>2 \times 10^{-140}</math></b>	23.96% [17.82-32.14]
Goat	29.51	<b><math>3 \times 10^{-32}</math></b>	23.45% [14.21-31.57]	1.68	<b><math>2 \times 10^{-20}</math></b>	18.84% [12.79-27.14]
Suid	79.12	<b><math>1 \times 10^{-83}</math></b>	21.25% [8.33-37.5]	1.72	<b><math>3 \times 10^{-35}</math></b>	22.96% [8.33-37.5]

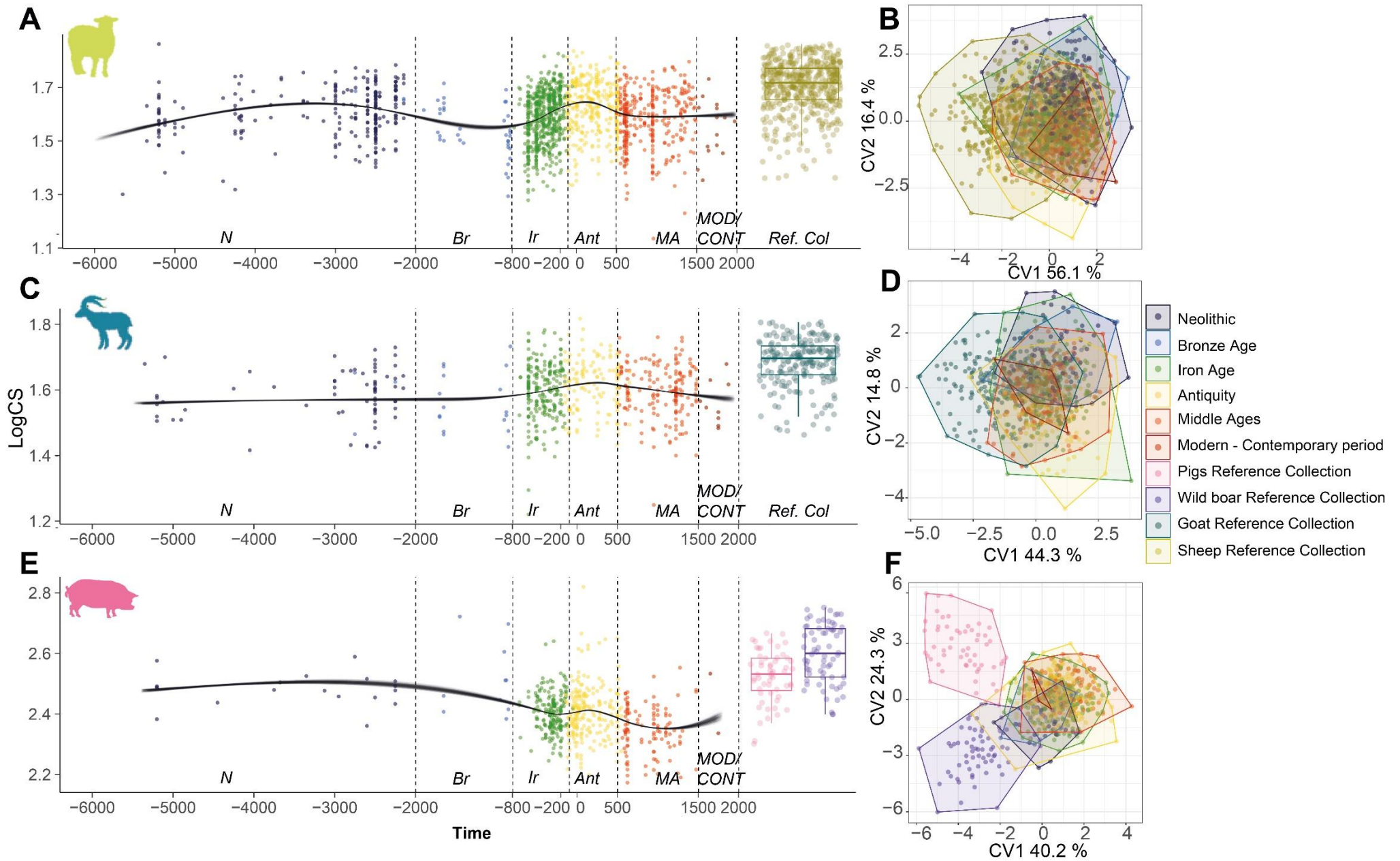
319  
 320 Sheep molar size increased from the beginning of the Early Neolithic, i.e. 6<sup>th</sup> millennium BCE, until  
 321 the beginning the Late Neolithic, i.e. end of the 4<sup>th</sup> millennium BCE (Fig. 4A). A significant increase  
 322 was recorded during the middle Iron Age, around the 6<sup>th</sup> c. BCE, continuing until the Roman

323 Principate beginning of the 2<sup>nd</sup> c. CE. At this time, the third lower molar of sheep reached its  
324 maximum size in the archaeological record. A subsequent decrease was observed until the beginning  
325 of the 9<sup>th</sup> c. CE, followed by a period of stagnation until the Modern and Contemporary Period, where  
326 data are sparse. However, the average size of archaeological third lower molars of sheep is smaller  
327 than that of the current ones, and they also exhibit shape differences (SI Tab. 6). The shape  
328 differences of the third lower molar are significant between successive periods, *i.e.* between  
329 Neolithic and Bronze Age, Bronze Age and Iron Age, Iron Age and Antiquity, and Antiquity and Middle  
330 Ages (SI Tab. 6).

331 Despite a large overlap between archaeological and current sheep, some ancient shapes have no  
332 equivalent in our current dataset, and conversely, some current shapes have no equivalent in the  
333 past (SI Fig. 3). The current size of sheep teeth largely overlaps with those from the archaeological  
334 record (Fig. 4A).

335  
336 For goats, no size variation was observed from the beginning of the Neolithic until the middle Iron  
337 Age, around the middle of the 6<sup>th</sup> c. BCE (Fig. 4C). Following this period, the size increased until the  
338 beginning of the 2<sup>nd</sup> c. CE, before decreasing until 1,200 CE. Beyond this date, data are too scarce to  
339 identify any variation (Fig. 4C). Similar to sheep, goats from the current reference collection have, on  
340 average, larger teeth than the archaeological ones, and they differ in shape (except for Neolithic, SI  
341 Tab. 6). Shape differences of the third lower molar between periods are only recorded between  
342 Neolithic and Iron Age, Neolithic and Antiquity, and Antiquity differ from Bronze Age, Iron Age, and  
343 Middle Ages. However, all periods differ from the Reference collection (SI Tab. 6). The majority of  
344 archaeological goat morphologies from the various chronocultural attribution largely overlap, with  
345 only few exceptions (Fig. 4D). Some current goat morphologies are not present in the past, and *vice*  
346 *versa* (SI Fig. 3).

347  
348 For suids, no trend could be analysed prior to the Iron Age due to insufficient data (less than 25  
349 individuals until the Iron Age). However, from the Iron Age onwards, a slight increase in size is  
350 observed until the beginning of the 3<sup>rd</sup> c. CE, followed by a decrease until 1,000 CE (Fig. 4E). When  
351 compared to present-day wild boars and pigs, archaeological suids are, on average, smaller (except  
352 for Modern and Contemporary suids, SI Tab. 6). On the two first CVA axes, current wild boars and  
353 pigs do not overlap with archaeological suids, while all archaeological periods do overlap (Fig. 4F).  
354 Some morphologies of current pigs and wild boars are not identified in the past (SI Fig. 3). Shape  
355 differences are observed across successive periods from the Neolithic to the Middle Ages. All periods  
356 exhibit differences when compared to the current wild boar and domestic pig reference, with the  
357 only exception being the Modern and Contemporary Period suids, due to insufficient sample size (SI  
358 Tab. 6).



359 <Figure 4 > : Size (A, C, E) and shape (B, D, F) variation through time for sheep (A, B), goat (C, D) and suids (E, F). Shape differences are available in SI Tab. 5. Canonical  
 360 variation analysis (CVA) are done for all taxa, and grouped by chronologies. Differences between archaeological periods and Reference collection were tested using pairwise  
 361 Wilcoxon test (SI Tab. 6)

## 362 Geographical diachronic variation

363 To ensure a clear interpretation of the results concerning different regions, the timeframe was  
 364 divided into three overlapping larger time frames : Neolithic - Bronze Age - Iron Age (6<sup>th</sup> mil - 2<sup>nd</sup> c.  
 365 BCE); Iron Age – Antiquity (8<sup>th</sup> c BCE - 5<sup>th</sup> c.CE) and Antiquity - Middle Ages - Modern/Contemporary  
 366 (2<sup>nd</sup> c. BCE. – to the present day).

### 367 SHEEP

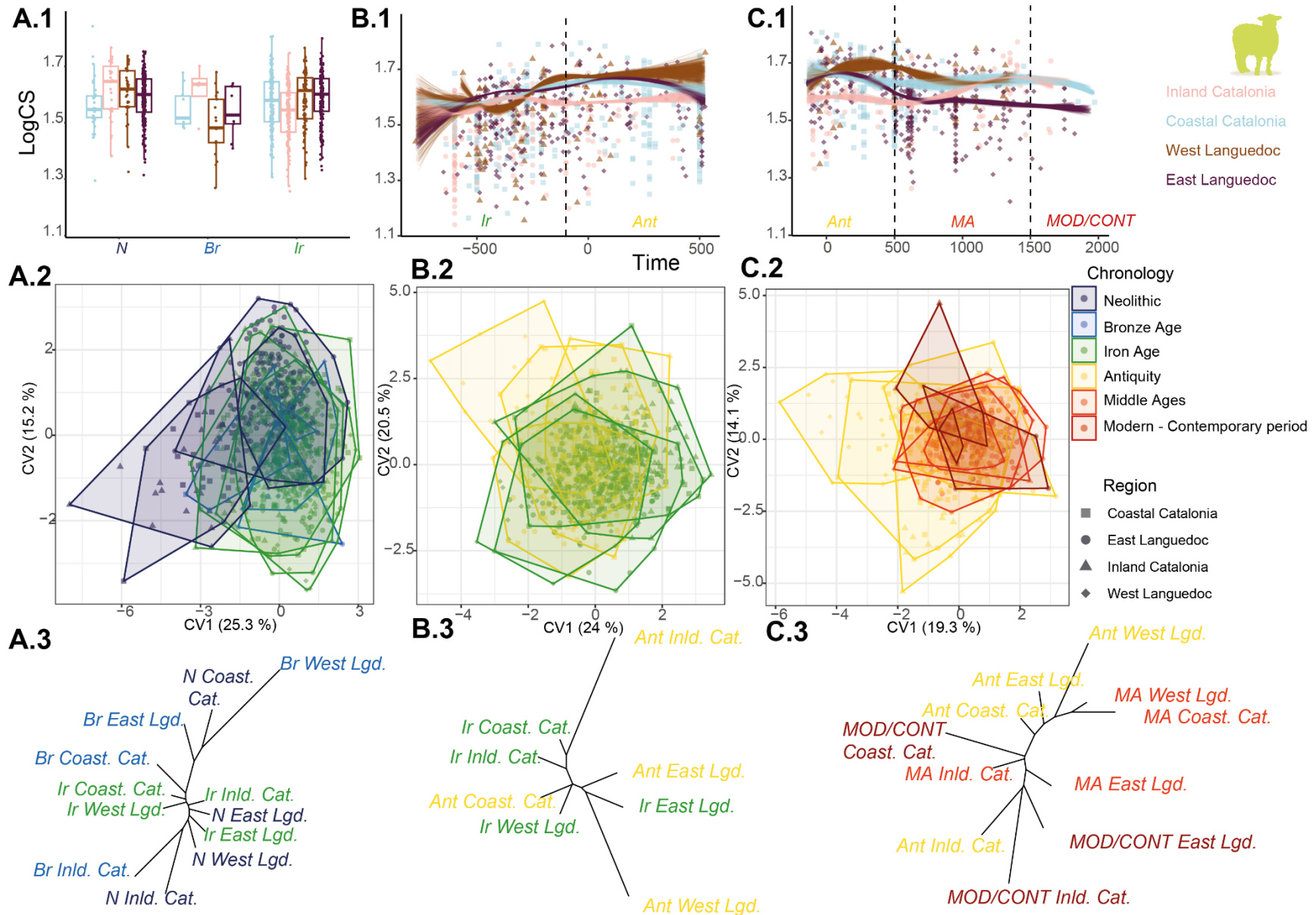
368 For the time frame from the Neolithic to the Iron Age, variations in the size and shape for the sheep  
 369 molars were observed between periods and regions, with a significant interaction between the two  
 370 factors (Tab. 3). Consequently, the four regions were analysed separately from the Neolithic to the  
 371 Iron Age.

372  
 373 <Table 3>: Third lower molar shape differences between chronocultural periods and region for sheep.  
 374 Time was divided into three chronological frames: Neolithic-Bronze Age-Iron Age, Iron Age- Antiquity  
 375 and Antiquity-Middle Ages-Modern/Contemporary Period. Results of two-way ANOVA and MANOVA  
 376 respectively for size and shape are provided for the three chronological frames with mention of the F-  
 377 statistic of the test, and of the p-value. Cross-Validation percentages (CVP) are calculated, only if p-  
 378 value is inferior to 0.05 (in bold).

Chronocultural attribution	Factors	Size			Shape		
		F	p-value	CVP	F	p-value	CVP
Neolithic - Bronze Age - Iron Age	Periods	10.73	<b>2.49x10<sup>-5</sup></b>	40.77% [30.79-46.67]	2.22	<b>4.90x10<sup>-18</sup></b>	42.27% [34.96-50.04]
	Regions	4.28	<b>0.01</b>	27.02% [22.62-28.91]	1.86	<b>5.97x10<sup>-16</sup></b>	35.32% [32.45-37.94]
	Periods * Regions	4.78	<b>8.32x10<sup>-5</sup></b>	10.19% [4.17-18.75]	1.40	<b>1.81x10<sup>-9</sup></b>	12.27% [4.06-22.92]
Iron Age - Antiquity	Periods	35.96	<b>2.92x10<sup>-9</sup></b>	56.49% [55.06-57.59]	1.91	<b>6.47x10<sup>-7</sup></b>	58.22% [56.37-60.28]
	Regions	13.80	<b>8.43x10<sup>-9</sup></b>	28.84% [19.22-31.36]	1.43	<b>4.88x10<sup>-6</sup></b>	32.41% [29.75-34.94]
	Periods * Regions	1.17	0.32		1.13	0.07	
Antiquity - Middle Ages - Modern/Contemporary	Periods	18.60	<b>1.38x10<sup>-8</sup></b>	39.13% [23.33-48.33]	1.36	<b>1.10x10<sup>-3</sup></b>	38.38% [28.25-48.42]
	Regions	6.30	<b>3.22x10<sup>-4</sup></b>	28.99% [22.23-31.64]	1.19	<b>0.02</b>	32% [27.71-35.94]
	Periods * Regions	5.83	<b>2.81x10<sup>-5</sup></b>	9.59% [2.27-18.3]	1.06	0.20	

379  
 380 Due to the small quantity of available data prior to the beginning of the Early Iron Age, particularly  
 381 for Catalonia, size variation was visualized using boxplots (Fig. 5A.1). A decrease in size of sheep third  
 382 lower molars was observed from the Neolithic to the Bronze Age in Western Languedoc, and similarly  
 383 from the Neolithic to the Iron Age in Inland Catalonia. Sheep molar size increased between Bronze  
 384 Age and Iron Age in Western Languedoc (Fig. 5.1, SI Tab. 7). During the Neolithic and Iron Age,  
 385 regional disparities emerged (Fig. 5A.1, SI Tab. 7).  
 386 A geographical structure for shape became significant between the Neolithic and the Iron Age, (Fig.  
 387 5A.2 and 5A.3). The morphologies of Neolithic third lower molar in Catalonia (both from Inland and  
 388 Coastal areas) differed from almost all other regions and chronologies (except with Bronze Age from  
 389 Coastal Catalonia; Figure 5A.2, SI Tab. 7). Conversely, the mean shape of teeth showed a closer  
 390 morphological similarity within Iron Age sheep across different regions than those from the Neolithic  
 391 and Bronze Age (Fig. 5A.3). Shape differences were significant both inter-regionally and inter-  
 392 periodically (SI Tab. 7).

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395 <Figure 5>: Variation in size and shape of archaeological sheep's molar through time according to region. Time was divided in as follows: Neolithic - Bronze Age - Iron Age  
 396 (A), Iron Age- Antiquity (B) and Antiquity - Middle Ages - Modern/Contemporary Period (C). For each period, diachronic size variation (1), canonical variate analysis (2) and  
 397 dissimilarity networks (3) were plotted. Shape differences for each studied period are available in SI Tab. 7, 8 and 9. Due to too small sample size, sheep size between  
 398 Neolithic and Iron Age were visualized using boxplots, and size differences assessed with pairwise Wilcoxon tests. N= Neolithic, Br = Bronze Age, Ir= Iron Age, Ant = Antiquity,  
 399 MA = Middle Ages, MOD/CONT = Modern/Contemporary Period, Coast. Cat= Coastal Catalonia, Inld Cat = Inland Catalonia, West Lgd = West Languedoc, East Lgd = East  
 400 Languedoc.

401 During the Iron Age and Antiquity, sheep molars varied in both shape and size across time and  
402 regions. However, the evolution of both size and shape was not consistent over time across regions  
403 (Tab. 3).

404 During the Iron Age, the size of the third lower molar exhibited an increase in both regions, but with  
405 distinct trends. In West Languedoc, the size of sheep's third lower molar began to increase from the  
406 beginning of the 4<sup>th</sup> c. BCE, reaching its maximum around 150 BCE. Both Coastal Catalonia and East  
407 Languedoc followed a similar trend, with an increase until 200 CE, followed by a decline until 500 CE  
408 (Fig. 5B.1). In Inland Catalonia, sheep molars first reached their maximum size around 350 BCE,  
409 before decreasing until 100 BCE and subsequently stagnating. Thereafter, a stagnation is observed,  
410 but further trends are challenging to describe due to limited data. During Antiquity, sheep in Inland  
411 Catalonia had smaller molars compared to those in other regions (Fig. 5B.1). Despite the temporal  
412 differences in shape (SI Tab. 8), a clear overlap is observed among the periods (Fig. 4B.2). However, a  
413 regional structuring is visible, with a distinct Catalan shape on one hand and a Languedocian shape  
414 on the other (Fig. 5B.2 and 5B.3). Shape differences are significant between all regions, during both  
415 the Antiquity and the Iron Age (with the exception of East Languedoc and Coastal Catalonia during  
416 Iron Age and Antiquity, SI Tab. 8).

417  
418 From Antiquity to Modern/Contemporary Period, sheep molars varied in both shape and size across  
419 time and regions. However, the evolution of shape and size over time was not homogeneous across  
420 regions (Tab. 3).

421 After reaching their maximum size in Antiquity (with the exception of Inland Catalonia), the size of  
422 sheep third lower molars decreased until the end of the 10<sup>th</sup> c. CE in both Languedoc and Coastal  
423 Catalonia. A different trend is observed in Inland Catalonia, where after a period of stagnation until  
424 650 CE, sheep molar size increased until the end of the Middle Ages (Fig. 5C.1).

425 In terms of shape, there is no clear chronological or regional structuring, with differences observed  
426 among sheep from Antiquity and the Middle Ages in both Eastern Languedoc, and Inland Catalonia  
427 (Fig. 5C.2 and 5C.3, SI Tab. 9). Data from the Modern and Contemporary Period from different  
428 regions are relatively similar, with some shape differences compared to previous periods (Fig. 5C.2  
429 and 5C.3).

430

## 431 GOAT

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432 For goats, size variations are observed during specific periods, namely from the Iron Age to Antiquity  
433 and from the Antiquity-Middle Ages to the Modern/Contemporary Period. Additionally, size  
434 variations are region-dependent during the Iron Age and Antiquity (Tab.4).

435 In terms of shape, variations differ depending on periods from Neolithic to Antiquity. During the  
436 Neolithic, Bronze Age, and Iron Age, the shape of the goat third lower molar varies, but not uniformly  
437 across regions. Conversely, during the Iron Age - Antiquity period, the shape of the goat third lower  
438 molar showed a more uniform regional variation (Tab. 4).

439 Based on these results, regional size variation is investigated from the Iron Age to Antiquity, while  
440 the regional shape variation is studied from the Neolithic to the Iron Age.

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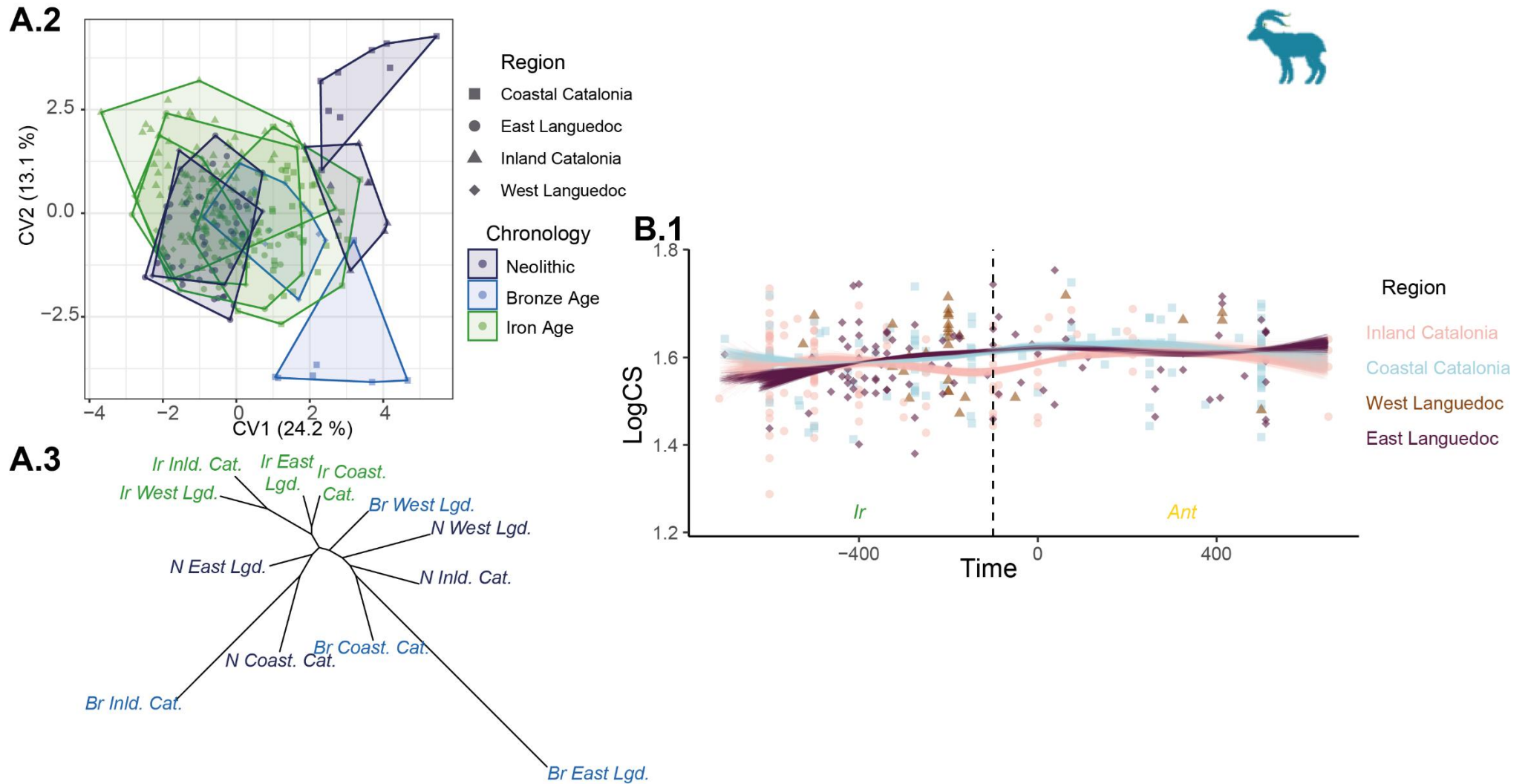
<Table 4>: Third lower molar shape differences through chronocultural periods and regions for goats. Time was divided into three time frames: Neolithic-Bronze Age-Iron Age, Iron Age- Antiquity and Antiquity-Middle Age-Modern/Contemporary Period. Results of two-way ANOVA and MANOVA respectively for size and shape are provided for the three chronological frames with mention of the F - statistic of the test, and of the p-value. Cross-Validation percentages (CVP) are calculated, only if p-value is inferior to 0.05 (in bold) and with more than 5 specimens.

Chronocultural attribution	Factors	Size			Shape		
		F	p-value	CVP	F	p-value	CVP
Neolithic - Bronze Age - Iron Age	Periods	1,760	0,174		<b>1,254</b>	0,029	38.43% [28.57-47.7]
	Regions	0,545	0,652		<b>1,407</b>	2,08E x10 <sup>-4</sup>	31.72% [25.61-37.23]
	Periods * Regions	1,426	0,204		<b>1,262</b>	3,45x10 <sup>-4</sup>	
Iron Age - Antiquity	Periods	3,455	0,064		<b>1,438</b>	0,012	57.88% [54.68-60.43]
	Regions	2,855	<b>0,037</b>	30.25% [24.92-35]	1,026	0,389	
	Periods * Regions	0,083	0,969		0,892	0,881	
Antiquity - Middle Ages - Modern/Contemporary	Periods	3,895	<b>0,021</b>	44.5% [26.67-56.67]	1,188	0,071	
	Regions	0,819	0,484		0,994	0,521	
	Periods * Regions	1,116	0,353		1,005	0,466	

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Similar to sheep, a geographical structuring pattern emerged for goat teeth during the Neolithic. The morphologies of Neolithic and Bronze Age teeth in Catalonia showed no overlap with those from other regions and chronologies in a discriminant analysis, with significant regional differences between Catalonia and Languedoc during the Neolithic (Fig. 6A.1, SI Tab. 7). Along this geographical structuring, a proximity between regions was observed during the Iron Age, a pattern not seen during the Bronze Age and Neolithic periods, with no significant difference between regions (Fig. 6A.2, SI Tab. 7). From the Iron Age to Antiquity, the size of the goat third lower molar in West Languedoc and Coastal Catalonia increased from 400 BCE to around 300 CE (Fig. 6B). In Inland Catalonia, the increase in size occurred later, starting around the beginning of our era and reaching a maximum size also around 300 CE. The size of the third lower molars then became uniform across these three regions and remained stable until the end of Antiquity. However, due to insufficient data from eastern Languedoc for this period, it was not possible to describe the trend (Fig. 6B).





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<Figure 6>: Variation in size and shape of the goat third lower molar through time according to region. Time was divided as follows: Neolithic/Bronze Age/Iron Age (A) and Iron Age/ Antiquity (B). Diachronic size variation (1), canonical variate analysis (2) and dissimilarity networks (3) were plotted if ANOVA/MANOVA interactions p-value were inferior to 0.05. Shape differences for each studied period are available in SI Tab. 7. N= Neolithic, Br = Bronze Age, Ir= Iron Age, Ant = Antiquity, MA = Middle Ages, MOD/CONT = Modern/Contemporary Period, Coast. Cat.= Coastal Catalonia, Inld Cat = Inland Catalonia, West Lgd = West Languedoc, East Lgd = East Languedoc.

468 **SUIDS**

469 For suids, the size variations between chronological periods were only observed between the  
 470 Neolithic, Bronze Age, Iron Age periods and between Antiquity and the Modern/Contemporary  
 471 periods (Tab. 5). Shape variations were observed during the Iron Age and Antiquity and the Antiquity-  
 472 Middle Ages-Modern/Contemporary periods (Tab. 5). Region influenced shape evolution only during  
 473 the Antiquity-Middle Ages-Modern/Contemporary periods, exhibiting consistent trends over time  
 474 (Tab. 5).

475 Since the diachronic differences have already been thoroughly examined (see section Overall  
 476 diachronic variation), the regional differences were not investigated further.

477  
 478 <Table 5>: Third lower molar shape differences through time and regions for suids. Time was divided  
 479 in three chronological frames: Neolithic-Bronze Age-Iron Age, Iron Age- Antiquity and Antiquity-  
 480 Middle Ages-Modern/Contemporary Period. Results of two-way ANOVA and MANOVA respectively  
 481 for size and shape are provided for the three chronological frames with mention of the F statistic of  
 482 the test, and of the p-value. Cross-Validation percentages (CVP) are calculated, only if p-value is  
 483 inferior to 0.05 (in bold). Due to small sample size, only groups with more than 5 specimens are taken  
 484 into account for CVP calculation.

		Size			Shape		
		F	p-value	CVP	F	p-value	CVP
Neolithic - Bronze Age - Iron Age	Periods	15,861	<b>3,74x10<sup>-7</sup></b>	50.48% [46.3-55.56]	1,144	0,289	
	Regions	2,026	0,111		1,144	0,236	
	Periods * Regions	1,662	0,16		0,955	0,638	
Iron Age - Antiquity	Periods	0,005	0,941		1,476	<b>0,003</b>	58.01% [56.1-60.11]
	Regions	1,388	0,246		1,143	0,050	
	Periods * Regions	0,547	0,65		1,095	0,131	
Antiquity - Middle Ages - Modern/Contemporary	Periods	17,167	<b>8,17 x10<sup>-8</sup></b>	27.33% [0-66.67]	1,212	<b>0,046</b>	44.11% [22.22-66.67]
	Regions	1,094	0,352		1,220	<b>0,016</b>	30.56% [23.21-39.29]
	Periods * Regions	0,784	0,503		1,096	0,161	

485

486 **Discussion**

487 In this study, we focused on the third lower molar, which is considered as a good marker of  
 488 phenotypic variation in archaeozoology (Butler, 1939; Dahlberg, 1945).

489 In this field, morphometric variation through time is classically studied through an overall stature  
 490 analysis obtained via Log Size Index (e.g. Colominas et al., 2014; Duval et al., 2013; Espinet et al.,  
 491 2021; Grau-Sologestoa et al., 2021), a scaling technic based on classical biometric data. While this  
 492 approach allows simultaneous analysis of a large number of linear measurements, it does not provide  
 493 results as detailed as the ones provided by geometric morphometric methods.

494 The covariation between teeth and post-cranial elements is poorly understood but some studies  
 495 suggest bones and teeth record similar temporal trends, with minor discrepancies, as shown in pigs  
 496 (Albarella, 2002; Albarella and Payne, 2005). Teeth have also been found less affected by sex-linked  
 497 size differences than post-cranial elements (Albarella et al., 2006; Mayer et al., 1998; Price and  
 498 Arbuckle, 2015). Caution is needed when comparing classical biometric and geometric morphometric  
 499 datasets until further research clarifies their covariation. Nevertheless, due to the relative paucity of  
 500 other studies on teeth morphometry, our results are primarily compared with studies based on post-  
 501 cranial data.

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## 502 Neolithic-Bronze Age - Iron Age

503 Our study has highlighted a reduction in the size of the third lower molar of sheep between the end  
504 of the 4<sup>th</sup> millennium and the 6<sup>th</sup> c. BCE. This was previously documented in caprines with postcranial  
505 data in Catalonia (Franquesa Casacuberta et al., 2000), Northern (Ménier, 1984), and also in Southern  
506 France (Forest, 2018a, 2018b). This trend is also observed more broadly across Europe (Audoin-  
507 Rouzeau, 1991a) and coincides with a similar trend in cattle (Audoin-Rouzeau, 1991b; Bopp-Ito et al.,  
508 2018b; Davis, 2012; Ménier, 1984; Tresset et al., 2012; Valenzuela-Lamas and Albarella, 2017).  
509 Several hypotheses have been proposed to explain this phenomenon (Audoin-Rouzeau, 1991b; Duval  
510 and Clavel, 2018; Espinet et al., 2021; Manning et al., 2015; Valenzuela-Lamas and Albarella, 2017):

- 511 (1) **Climate:** According to Bergmann's rule that animals are typically larger in colder regions  
512 (Bergmann, 1847), one might expect a decrease in the size of domestic animals in warmer  
513 climatic conditions. Although a colder climate was recorded in the Mediterranean around  
514 6,000 years ago (particularly during the summer months, Mauri et al., 2015), our  
515 observations indicate a size decrease, suggesting that climate alone cannot explain this size  
516 decrease. If climate were the sole factor, we would expect to see a reduction across all the  
517 studied taxa. Yet, according to research by Manning (Manning et al., 2015) and our own  
518 observations, this rule does not apply uniformly to all domestic taxa, at least for the  
519 Neolithic. Nevertheless, interactions between climate, environment, and husbandry practices  
520 are complex, and this hypothesis needs to be further investigated.
- 521 (2) **Reproduction:** A change in reproductive strategies, possibly due to increased meat demand  
522 in Europe could also influence size (Manning et al., 2015). To increase yields and production,  
523 shorter birthing cycles may have been encouraged, resulting in younger animals giving birth.  
524 This could have led to smaller offspring and potentially have affect long-term size (ibid.).
- 525 (3) **Sex-ratio:** An increased proportion of females enhancing greater milk production (Manning  
526 et al., 2015) could also account for the size reduction (Galindo-Pellicena et al., 2020).  
527 However, evidence for this hypothesis is limited, even if similar cattle sex ratios have been  
528 observed between the Neolithic and Bronze Age at a Spanish archaeological site (Galindo-  
529 Pellicena et al., 2020).
- 530 (4) **Animals feeding:** Changes in diet could also explain the decrease in animal sizes between the  
531 Neolithic and the Iron Age. Data from the Neolithic indicate that sheep grazed in wooded  
532 areas (Navarrete et al., 2019; Sierra et al., 2021). In contrast, recent studies have evidenced  
533 that sheep were likely fed in more open areas during the Iron Age (Jiménez-Manchón et al.,  
534 2023b, 2023a; Lespes, 2020), and so were less-controlled populations.

535 These diverse hypotheses are not mutually exclusive; indeed, it is plausible that various factors may  
536 interact with one another, as it has already been argued (Audoin-Rouzeau, 1991b; Espinet et al.,  
537 2021; Valenzuela-Lamas and Albarella, 2017).

538  
539 Different trends between sheep and goats are observed as early as the Neolithic, with large size  
540 fluctuation for sheep but not for goats. This lack of variation in goats was noted by Gillis et al. (2019)  
541 in mortality profiles. While it was not clear whether goats were managed for specific purposes,  
542 young sheep were preferred for slaughter, likely related to milk management and preference for  
543 tender meat (Gillis et al., 2019). Combined with our findings, this suggests distinct selection and  
544 management practices for sheep and goats following their introduction to the region.

545  
546 During the Neolithic, sheep and goats exhibited also a regional structuring of morphologies, with the  
547 Catalan caprines being particularly different from the others. Several factors may explain this  
548 pattern.

549 One possibility is the inclusion of wild species, *e.g.* the mouflon (*Ovis orientalis musimon*, a feral form  
550 of sheep), the alpine (*Capra ibex*) or Iberian ibex (*Capra pyrenaica*) or the Barbary sheep  
551 (*Ammotragus lervia*), as their identification still presents a challenge (Fernandez, 2001) even when  
552 using biomolecular methods, such as ZooMS (*e.g.* Jeanjean et al., 2023a). However, previous studies

553 have shown that the proportion of hunted mammal remains was relatively low compared to  
554 domestic animals from the beginning of the Neolithic (Antolín et al., 2018; Castaños-Ugarte, 2004;  
555 Martín and Oms, 2021; Piqué et al., 2015), making the hunting hypothesis insufficient to explain the  
556 differences.

557 Another factor could be interactions between Catalonia and Languedoc, as since the Early Neolithic  
558 both human populations and animals moved at the regional level (McClure and Welker, 2017).  
559 However, the lack of similar regional patterns for suids suggests that while cultural differences may  
560 have shaped caprine morphology, they likely did not affect suid morphology as measured here.  
561 Therefore, the observed regional structuring in caprines during the Neolithic cannot be solely  
562 explained by limited exchanges between the two regions.

563 Finally, it is possible that certain morphologies were selectively favoured in one region over another,  
564 potentially paired with different management practices. This hypothesis could be further tested by  
565 comparing morphometric data with palaeogenetic studies to explore potential regional selection or  
566 different population origins.

567  
568 The limited suid data for this period prevents definitive conclusions, and comparisons should be  
569 approached cautiously. While in our study suid third molar size decreased between the end of the  
570 Neolithic and the end of the Iron Age, increase in pig size was observed in the Czech Republic (Kyselý,  
571 2016) and in European wild boar (Cucchi et al., 2023). In contrast, size stability has been recorded in  
572 Switzerland for the Bronze Age (Bopp-Ito et al., 2018a). Our results do not align with these  
573 observations. Given the limited data available for this period in the region, it remains challenging to  
574 establish general trends in the size of domestic pigs. Collaborative studies integrating the results  
575 obtained here with measurement data of the cranial and post-cranial skeleton will undoubtedly shed  
576 more light on our current observations (Mureau et al. in prep).

577  
578 Overall, for the pre- and proto-historic periods, despite the clear trends of size and shape change, it is  
579 still difficult to identify and contrast the various factors potentially involved in the morphometric  
580 evolution and structure of these taxa. Although a number of factors have been proposed  
581 (environmental, climatic, socio-cultural, husbandry practices, etc.), it seems more necessary than  
582 ever to take into account interdisciplinary analyses, which would shed light on the factors governing  
583 these evolutions.

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## 584 Iron Age - Antiquity

585 For all three taxa, we observed an increase in the size of the third molar from the Iron Age to  
586 Antiquity, with the maximum size of archaeological specimens recorded between the 2<sup>nd</sup> and the 3<sup>rd</sup>  
587 c. AD, as consistent with previous findings (Colominas et al., 2009, 2014; Duval et al., 2015, 2018;  
588 Espinet et al., 2021; Frémondeau et al., 2017; Valenzuela-Lamas and Albarella, 2017; Valenzuela et  
589 al., 2013, 2017). Several hypotheses have been proposed to explain this increase in size during the  
590 Iron Age and Antiquity (Audoin-Rouzeau, 1991b; Espinet et al., 2021; Lepetz, 1996; Valenzuela-Lamas  
591 and Albarella, 2017):

592 (1) **Trade and migration:** The increase in the size of domestic animals has often been associated  
593 with the processes that followed the Roman conquest, including trade and population  
594 transfers from different areas under Roman influence (Audoin-Rouzeau, 1995; Benecke,  
595 2001; Gaeng et al., 2019; Méniel, 1990; Yvinec, 1983). However, evidence of larger animals  
596 predating Roman conquest, as found here, suggests that Romanization is not the sole cause  
597 of this size increase (Espinete et al., 2021; Forest and Rodet-Belarbi, 2002; Frémondeau et al.,  
598 2017; Trentacoste et al., 2018).

599 (2) **Artificial selection:** A common hypothesis is that the increase in size resulted from artificial  
600 selection by breeders (Brunaux and Méniel, 1983; Forest and Rodet-Belarbi, 2002; Lepetz,  
601 1997; Méniel, 1996) to increase meat and wool production, leading to a gradual increase in  
602 animal body size over generations (Lepetz, 1996).

603 **Technical advances:** Improvements in agricultural practices and irrigation during Antiquity likely  
604 enhanced animal nutrition (Lepetz, 1996), facilitating the maintenance of larger animals during  
605 Antiquity (Audoin-Rouzeau, 1995; Espinet et al., 2021; Valenzuela-Lamas and Albarella, 2017). This  
606 could have allowed for the selection or crossbreeding of larger animals from other regions. Finally,  
607 enhanced connectivity between ecologically complementary regions could have facilitated long-  
608 distance transhumance movements within these areas, ensuring better year-round feeding for  
609 animals.

610 The size increase for sheep and goats occurred at different times across regions. Sheep reached their  
611 maximum size around 150 BCE in Western Languedoc and two centuries later in Eastern Languedoc.  
612 Goats grew in size earlier in Coastal Catalonia (400 BCE, peaking by 350 CE) and later in Inland  
613 Catalonia (around 300 CE). These regional differences within Catalonia have been previously  
614 highlighted (Espinete et al., 2021). Moreover, previous studies have also reported divergent size  
615 trends between Languedoc and Catalonia. The size increase of caprines in Languedoc occurred at  
616 least between the 2nd and 4th centuries CE (Forest, 2008; Jeanjean et al., 2023b), while in Catalonia,  
617 this maximum was reached between the 1st and 3rd centuries CE (Colominas et al., 2009; Espinete et  
618 al., 2021).

619 Despite the Roman Empire's influence over all of the Northwestern Mediterranean, sheep  
620 morphologies exhibited clear geographical structuring between Languedoc and Catalonia. This  
621 suggests that Roman influence did not lead to a homogenisation of domestic animal morphology,  
622 shedding new light on the various hypotheses proposed above, especially on the Romanization  
623 concept (Valenzuela-Lamas and Albarella, 2017). The presence of morphologically distinct animals in  
624 both regions reflects different agricultural and pastoral demands and practices, with each territory  
625 maintaining its own breeding specificity until at least the end of Antiquity (Duval et al., 2015; Espinete  
626 et al., 2021).

627 Notably, no significant morphological differences were found between Eastern and Western  
628 Languedoc, raising questions about limited impact of major cities like Nîmes and Narbonne on local  
629 breeding practices. This variation invites further research into the cities' roles in the evolution of  
630 livestock morphology, potentially leading to homogenised production.

631  
632 Furthermore, for goats, this is the only time period in our study where size variation is observed. An  
633 increase in size was also observed between the Bronze Age and the Roman period in Northern Italy  
634 (Trentacoste et al., 2021). This suggests different selection pressures between sheep and goats,  
635 which are sometimes raised together. It would seem, therefore, that goats are less subjected to  
636 selection than sheep, or that the hardiness of the latter is maintained over time (Jeanjean et al., in  
637 prep).

638  
639 Altogether our results suggest that a combination of environmental, socio-economic, and technical  
640 processes may have contributed to the increase of molar size of sheep, goat and suids in Antiquity, as  
641 has been previously proposed (Colominas et al., 2017; Espinete et al., 2021). Future genetic studies  
642 could potentially reveal new markers associated with the Roman conquest or the selection of certain  
643 morphologies.

---

## 644 Antiquity - Middle Ages - Modern/Contemporary Period

645 Following a peak in size in Antiquity, a decrease was observed during the Late Antiquity/Early Middle  
646 Ages transition across all three taxa. This trend has been recorded in several other geographic areas.  
647 For instance, a decrease in size for domestic animals is recorded in France from the 6<sup>th</sup> c. CE (Yvinec,  
648 1991), in Spain until the 10<sup>th</sup> c. for caprines, and until the 15<sup>th</sup> c. for suids (Grau-Sologestoa, 2015).  
649 This size reduction is also attested in Britain (Holmes, 2014; O'Connor, 2010; Rizzetto et al., 2017)  
650 and Germany (Stephan, 2008), while in Italy, no significant size changes were observed in sheep,  
651 goats or pigs from the end of Antiquity to the Late Middle Ages (Lepetz and Matteredne, 2003;  
652 Salvadori, 2010). The medieval size reduction has been associated with changes in agropastoral

653 management (Grau-Sologestoa, 2015) such as extensive farming (*e.g.* woodland grazing) and  
654 feralization of livestock (Albarella, 2006).

655 For pigs, this decrease in size was followed by an increase from the year 1,000 CE onwards. However,  
656 the sparse results in this study necessitate cautious interpretation. When comparing this trend with  
657 existing literature, we find an increase in pig size in Northern Spain (Grau-Sologestoa, 2015) and  
658 England (Albarella, 2006) during the medieval period. This increase in size was likely related to  
659 changes in pig feeding practices after the High Middle Ages, with pigs no longer being kept in the  
660 open air but in stalls, as suggested for England (Hamilton and Thomas, 2012; Hammond and  
661 O'Connor, 2013), and linked to a shift from extensive farming, sometimes in woodlands, to intensive  
662 farming in Northwestern Europe (White, 2011). This hypothesis could explain the similar patterns  
663 found in our results. Feeding practice modifications through time could be further investigated  
664 through the use of isotopic and micro-wear analyses.

665 Thus, the Middle Ages do not appear to have been a long period of decline in animal size, depending  
666 on the region, especially for sheep in Inland Catalonia, but rather a period of more fluctuation than  
667 previously thought (Audoin-Rouzeau, 1995). The increase observed here aligns with this hypothesis.  
668

669 While archaeological studies of Modern and Contemporary remains are relatively rare in the  
670 northwestern Mediterranean basin, the shape of specimens from this period appear distinct from  
671 our reference collection. Interestingly, for the three species, specimens from this period are not  
672 larger than those from previous phases.

673 The improvement of animal traits leading to modern breeds during the medieval period have been  
674 documented, especially in England (Albarella, 1997; Audoin-Rouzeau, 1997; Davis and Beckett, 1999;  
675 Grimm, 2010; Thomas et al., 2013). Modern and contemporary improvements have also been  
676 identified in cattle (Hutchins and Steadman, 1999) and sheep (O'Connor, 1995; Vann and Grimm,  
677 2010). Changes in the shape of metapodials have been recorded, with more robust bones observed  
678 in the 19<sup>th</sup>c. compared to previous centuries (Vann and Grimm, 2010). An increase in the size of  
679 English sheep has also been recorded in the post-medieval period (O'Connor, 1995). These  
680 morphological changes have been linked to the wool trade in the region (Stephenson, 1988). In this  
681 context, 'improvement' refers to an increase in the size of the sheep, which results in a greater  
682 quantity of wool (Vann and Grimm, 2010). However, our results did not reflect any significant  
683 morphological changes during the Modern and Contemporary Period.

684 Our results raise questions about the transition in the relatively short period between the Modern  
685 and Contemporary Period and the current diversity which, in conjunction with the emergence of the  
686 breed concept, seems to be a period of great morphological change. Usually, herd improvement in  
687 livestock can occur through three processes: selection of larger individuals within local herds,  
688 introduction of complete herds of larger breeds from other regions, or introduction of a large male  
689 from elsewhere (Vann and Grimm, 2010). However, given that data for this time period remain  
690 largely unexplored, we are unable to fully address these questions that are fundamental to  
691 understanding modern morphological diversity.

692 The morphological gap between archaeological remains and modern datasets raises questions about  
693 the utility of modern references for studying archaeological remains. While modern reference  
694 material has been shown to reliably identify archaeological specimens (*e.g.* Hanot et al., 2017;  
695 Jeanjean et al., 2023a), other studies have highlighted a significant morphological gap between  
696 archaeological and modern data (Brassard et al., 2022). To effectively apply the principle of actualism  
697 in archaeological studies, it is essential to better understand the morphological changes over time  
698 between recent archaeological data and contemporary reference datasets. While modern references  
699 are useful, we must consider their limitations in capturing long-term morphological evolution when  
700 analysing temporal variation.  
701  
702

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## Conclusion

703  
704 Our study has revealed a unique evolutionary trajectory for each of the three taxa studied, showing  
705 temporal and regional variations influenced by various factors. The results improve our  
706 understanding of the morphological evolution of these domestic species and shed light on the factors  
707 that have shaped agrobiodiversity and its evolution in the Northwestern Mediterranean basin over  
708 the last 8,000 years.

709 The complexity of size and shape variation among domestic species since their introduction to the  
710 region underlined has led to several hypotheses aiming to explain that variation, emphasizing the  
711 role of multifactorial influences. Interdisciplinary approaches, incorporating *e.g.* genetic, paleo-  
712 climatic, isotopic and microwear analyses with anthropogenic and environmental information are  
713 needed to gain a more comprehensive understanding of the factors driving change.

714 By tracing the morphological evolution of these three domestic species from their arrival in the  
715 region to their current breeds, this study marks a significant step towards the understanding of the  
716 evolution of domestic species.

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732  
733

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## CRedit (Contributor Roles Taxonomy)

734 Marine Jeanjean : Conceptualization, Data curation, Formal Analysis, Investigation, Methodology,  
735 Software, Validation, Visualization, Writing – original draft

736 Cyprien Mureau : Data curation, Resources, Writing—review and editing

737 Silvia Valenzuela-Lamas : Resources, Writing—review and editing

738 Ariadna Nieto-Espinet : Resources, Writing—review and editing

739 Sergio Jimenez-Manchon : Resources, Writing—review and editing

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742 Audrey Renaud : Resources,

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746 Vincent Bonhomme : Methodology, Software, Writing—review and editing  
747 Jérôme Ros : Writing—review and editing  
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749 Allowen Evin: Conceptualization, Formal Analysis, Funding acquisition, Methodology, Project  
750 administration, Resources, Software, Supervision, Validation, Writing—review and editing  
751

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## SI Data

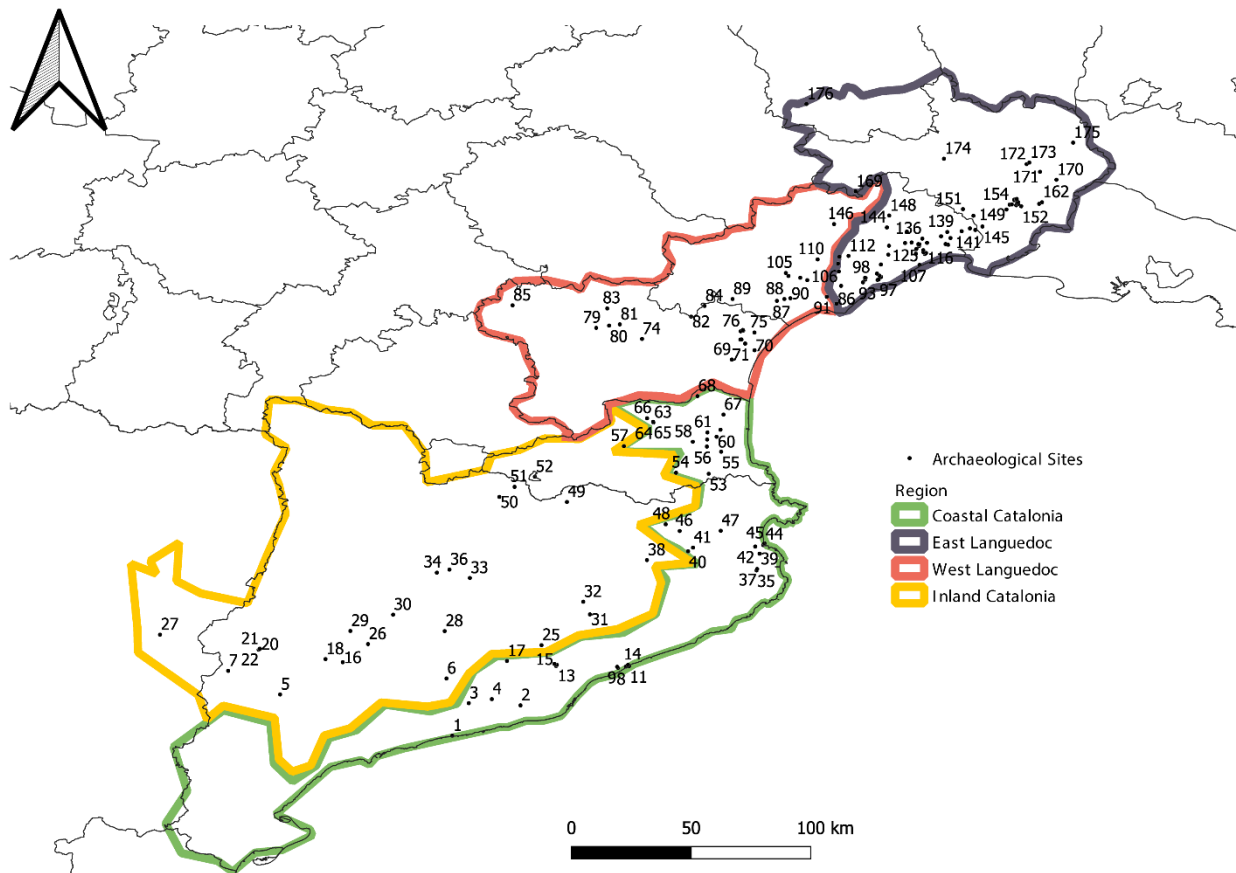
752  
753 SI Tab. 1 : List of studied archaeological sites. The number of teeth per chronology is specified as  
754 follows : Sheep + Goat + Suids. Abbreviations of the chronologies are available in Tab. 1.  
755  
756 SI Tab. 2: List of caprine third lower molars (both archaeological and modern referential) and their  
757 scaled coordinates. Regions and periods are available for all the specimens, while some TPQ TAQ are  
758 missing.  
759  
760 SI Tab. 3: List of suid third lower molars (both archaeological and modern referential) and their scaled  
761 coordinates. Regions and periods are available for all the specimens, while some TPQ TAQ are  
762 missing.  
763  
764 SI Tab. 4: Sheep, goat and suid sample sizes through time and region (Sheep-Goats-Suids). N=  
765 Neolithic, Br= Bronze Age, Ir=Iron Age, Ant= Antiquity, MA= Middle Ages, MOD-CONT= Modern and  
766 Contemporary Periods  
767  
768 SI Tab 5: Chi <sup>2</sup> test of sheep/goat proportions by time and region.  
769  
770 SI Tab. 6: Sheep, goat and suid size and shape differences between periods. Shape differences were  
771 tested using MANOVA, while size was tested using pairwise Wilcoxon tests. Tests are paired with  
772 Cross-Validation percentages only if p-values are significant. Statistical tests were done only for  
773 sample size ≥5, otherwise p-values are not displayed (grey box). N= Neolithic, Br = Bronze Age, Ir=  
774 Iron Age, Ant = Antiquity, MA = Middle Ages, MOD/Cont = Modern/Contemporary Period, Ref.Col =  
775 Reference Collection, pc= domestic pigs, wb= wild boar.  
776  
777 SI Tab. 7: Sheep and goat molar shape and size differences between Neolithic and Iron Age. Shape  
778 differences were tested using MANOVA. When necessary, size differences between regional periods  
779 were tested using pairwise Wilcoxon test. Tests are paired with Cross-Validation percentages only if  
780 p-values are significant. Statistical tests were done only for sample size ≥5, otherwise p-values are  
781 not displayed (grey box). N= Neolithic, Br = Bronze Age, Ir= Iron Age, Ant = Antiquity, Coast. Cat= =  
782 Coastal Catalonia, Inld Cat = Inland Catalonia, West Lgd = West Languedoc, East Lgd = East  
783 Languedoc.  
784  
785 SI Tab. 8: Differences in sheep molar shape between Iron Age and Antiquity. Shape differences were  
786 tested using MANOVA. Tests are paired with Cross-Validation percentages only if p-value are  
787 significant. Statistical tests were done only for sample size≥5, otherwise p-value are not displayed.  
788 Ant = Antiquity, MA = Middle Ages, MOD/Cont = Modern/Contemporary Period, Coast. Cat= =  
789 Coastal Catalonia, Inld Cat = Inland Catalonia, West Lgd = West Languedoc, East Lgd = East  
790 Languedoc.  
791  
792



793 SI Tab. 9: Differences in sheep and goat molar shape between Antiquity and Modern/Contemporary  
 794 Period. Shape differences were tested using MANOVA. Tests are paired with Cross-Validation  
 795 percentages only if p-value are significant. Statistical tests were done only for sample size  $\geq 5$ ,  
 796 otherwise p-value are not displayed. Ant = Antiquity, MA = Middle Ages, MOD/Cont =  
 797 Modern/Contemporary Period, Coast. Cat = Coastal Catalonia, Inld Cat = Inland Catalonia, West Lgd  
 798 = West Languedoc, East Lgd = East Languedoc.

799  
 800

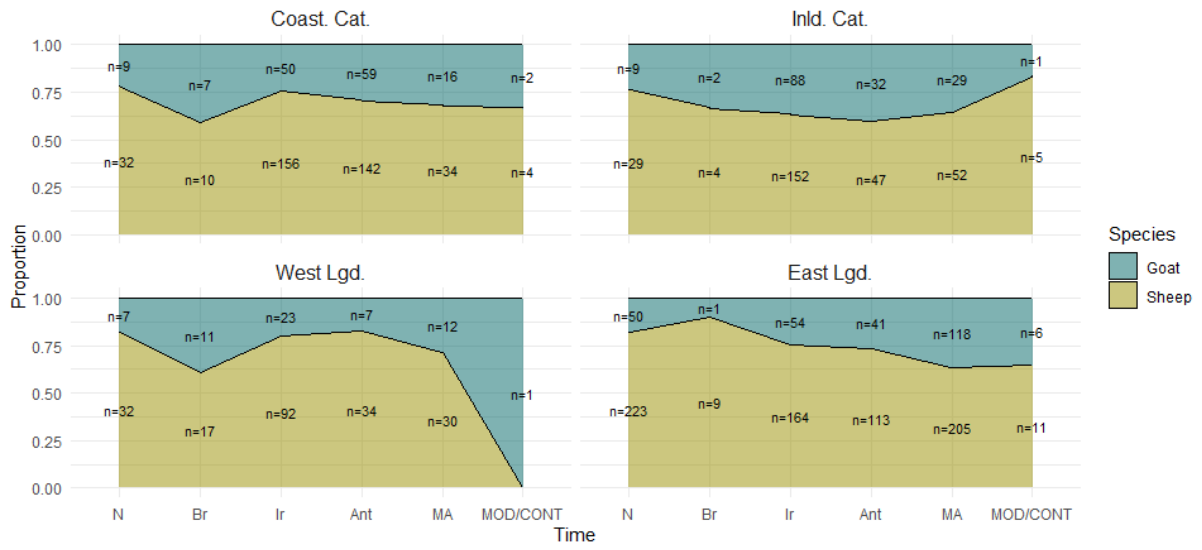
801 SI Figure 1: Map of the studied area, with the location of archaeological sites with ID number.  
 802 Coloured outlines correspond to the region delimitation with Inland Catalonia in yellow, coastal  
 803 Catalonia in green, western Languedoc in red and eastern Languedoc in purple. Map created using  
 804 the Free and Open Source Q GIS (QGIS Development Team, 2009).  
 805



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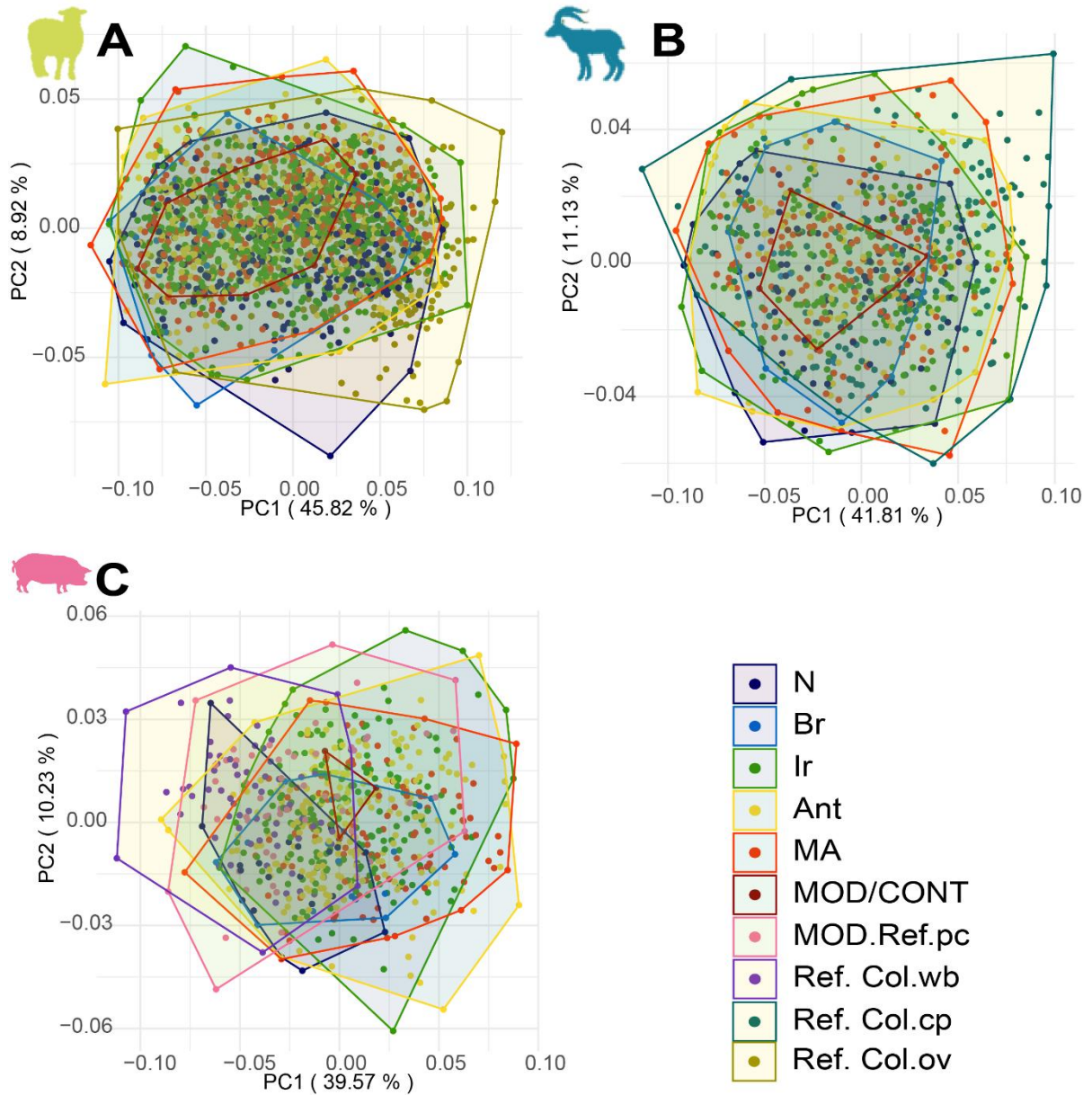
812 SI Figure 2: Sheep and goat proportions through time and region. Time is visualized by periods. Sheep  
 813 are in green, goats in blue. Differences between proportions through time were tested with a  $\chi^2$  (SI  
 814 Tab 5). N= Neolithic, Br= Bronze Age, Ir=Iron Age, Ant= Antiquity, MA= Middle Ages, MOD-CONT=  
 815 Modern and Contemporary Periods.

Proportion of sheep/goats by region over time



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819 SI Figure 3: Two first axes of the PCA showing variation between periods independently for sheep (A),  
 820 goats (B) and suids (C). N= Neolithic, Br = Bronze Age, Ir= Iron Age, Ant = Antiquity, MA = Middle  
 821 Ages, MOD/Cont = Modern/Contemporary Periods, Ref.Col = Reference Collection, pc= domestic  
 822 pigs, wb= wild boar.  
 823



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 825  
 826

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