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Thomas Cucchi, Barbara Stopp, Renate Schafberg, Joséphine Lesur,  
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1 **Taxonomic and phylogenetic signals in Bovini cheek teeth: towards new biosystematic**  
2 **markers to explore the history of wild and domestic cattle**

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5 Thomas Cucchi<sup>1,\*,#</sup>, Barbara Stopp<sup>2,#</sup>, Renate Schafberg<sup>3</sup>, Joséphine Lesur<sup>1</sup>, Alexandre  
6 Hassanin<sup>4</sup>, Jörg Schibler<sup>2</sup>,

7

8 <sup>1</sup> CNRS, Muséum national d'Histoire naturelle, Sorbonne Universités, UMR 7209,  
9 Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements, 75005 Paris,  
10 France

11 <sup>2</sup> IPAS - Integrative Prehistory and Archaeological Science, University of Basel, 4051 Basel,  
12 Switzerland

13 <sup>3</sup> Martin-Luther-University Halle-Wittenberg, Museum of Domesticated Animals “Julius  
14 Kühn”, 06108 Halle, Germany

15 <sup>4</sup> CNRS, Muséum national d'Histoire naturelle, Sorbonne Universités, UMR 7205, Institut de  
16 Systématique, Évolution, Biodiversité, 75005 Paris, France

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18 # joint first

19 \* Corresponding author: [thomas.cucchi@mnhn.fr](mailto:thomas.cucchi@mnhn.fr)

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35 **Abstract**

36 Domestic cattle have contributed both to the rise of civilizations and the global loss of  
37 biodiversity, but the timing and mechanism of their domestication history remain to be fully  
38 understood. Palaeogenetics, which can now explore the target of human selection in the  
39 genome, have revolutionized our understanding of cattle domestication. However, biometric  
40 approaches of bone remains are still required as a prerequisite for targeted paleogenetic  
41 studies to document the taxonomic diversity of wild progenitors and the emergence of  
42 domestic morphotypes. But so far, biometric markers of cattle domestication have proven  
43 limited in their capacity to disentangle human intentionality from other biotic and abiotic  
44 factors.

45         Using a two-dimensional geometric morphometric approach (GMM), we assessed the  
46 taxonomic and phylogenetic signals of the enamel folding pattern of occlusal surfaces  
47 (EFPOS) in the maxillary and mandibular molars of wild and domestic species of the tribe  
48 Bovini, including ancient cattle breeds and archaeological aurochs and domestic cattle. The  
49 phylogenetic signal was assessed using a mitochondrial genome phylogeny across 11 wild  
50 taxa of the tribe Bovini. We found that EFPOS could accurately identify both the wild and  
51 domestic species of the Bovini taxa as well as shape differentiation among aurochs and  
52 modern and archaeological cattle. The phylogenetic differentiation among aurochs and both  
53 taurine and zebu cattle is strong, but the overall phylogenetic signal among the tribe Bovini is  
54 blurred by genetic introgression between wild and domestic *Bos* species in south-east Asia.

55         These results strongly suggest that the GMM analysis of dental traits are relevant  
56 markers that can be used before the implementation of targeted paleogenomic analyses as a  
57 mean to document the diversity and distribution of wild progenitors of domestic forms,  
58 identify the emergence of the earliest regional morphotype and their trajectory towards  
59 modern breeds.

60

61 **Key words:** Bovini, domestication, zooarchaeology, geometric morphometrics, teeth,  
62 phylogenetic signal, taxonomy

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## 67 **1. Introduction**

68 The domestication of aurochs in several parts of Eurasia had a dramatic effect on human  
69 history. Their domestic forms became the symbols of prestige, leadership and wealth, while  
70 their strength intensified agricultural production, driving the rise of cities and civilisations  
71 (Fagan 2015). Nowadays, they provide nearly 30% of the world's meat and over 87% of the  
72 world's milk (Scherf, 2000). They are also one of the main sources of unsustainability in our  
73 food production system, since 26% of the ice-free land on our planet is used for grazing  
74 livestock and a third of cropland is used for livestock feed production  
75 ([www.fao.org/nr/sustainability/sustainability-and-livestock](http://www.fao.org/nr/sustainability/sustainability-and-livestock)). Aurochs domestication also  
76 played a major role in the evolution of the tribe Bovini (Figure 1). Two domestic forms  
77 stemmed from aurochs: common cattle (*Bos primigenius taurus*) and zebu cattle (*Bos*  
78 *primigenius indicus*), one from the yak: the domestic yak (*Bos mutus grunniens*), one from the  
79 gaur: the gayal (*Bos gaurus frontalis*), and one from the Asian water buffalo: the river buffalo  
80 (*Bubalus arnee bubalis*) (Hassanin, 2014). Currently, due to habitat loss, these wild ancestors,  
81 if not extinct or endangered, have been reduced to small pockets of populations in confined  
82 areas (Figure 1). The worldwide dispersal of common and zebu cattle induced adaptations to  
83 highly diverse environments, such as lowlands and highlands or humid and arid conditions,  
84 driving the emergence of different phenotypes (e.g. Felius et al., 2011). This variety of  
85 characteristics evolved over thousands of years, but the emergence and development of well-  
86 defined, genetically isolated breeds was mainly established from the Industrial Revolution  
87 onwards (Ajmone-Marsan et al., 2010).

88 So far, the domestication of aurochs is the most documented history from  
89 archaeological and genetic evidence. The earliest evidence (10,500 BP) of the human control  
90 of aurochs based on male body size reduction comes from the northern Fertile Crescent  
91 (Helmer et al. 2005, Peters et al 2005). Since common or taurine cattle have a potential  
92 progenitor in the form of European aurochs, it is still debated how much local European  
93 aurochs have contributed to the genetic make-up of modern cattle (e.g. Cymbron et al., 2005;  
94 Beja-Pereira et al., 2006; Tresset et al., 2009; Schibler et al., 2014; Scheu et al., 2015;  
95 Upadhyay et al., 2017). The second domestication centre led to the origin of zebu cattle, also  
96 referred to as humped cattle. A general consensus stemming from archaeological (Meadow,  
97 1996) and genetic evidence (e.g. Bradley and Magee, 2006) considers the Indus Valley as the  
98 most likely centre of domestication for this animal. However, other regions in the Indian  
99 subcontinent are also considered potential domestication centres (Chen et al., 2010). The third  
100 domestication centre for aurochs has been claimed as Africa (Pérez-Pardal et al., 2010), but

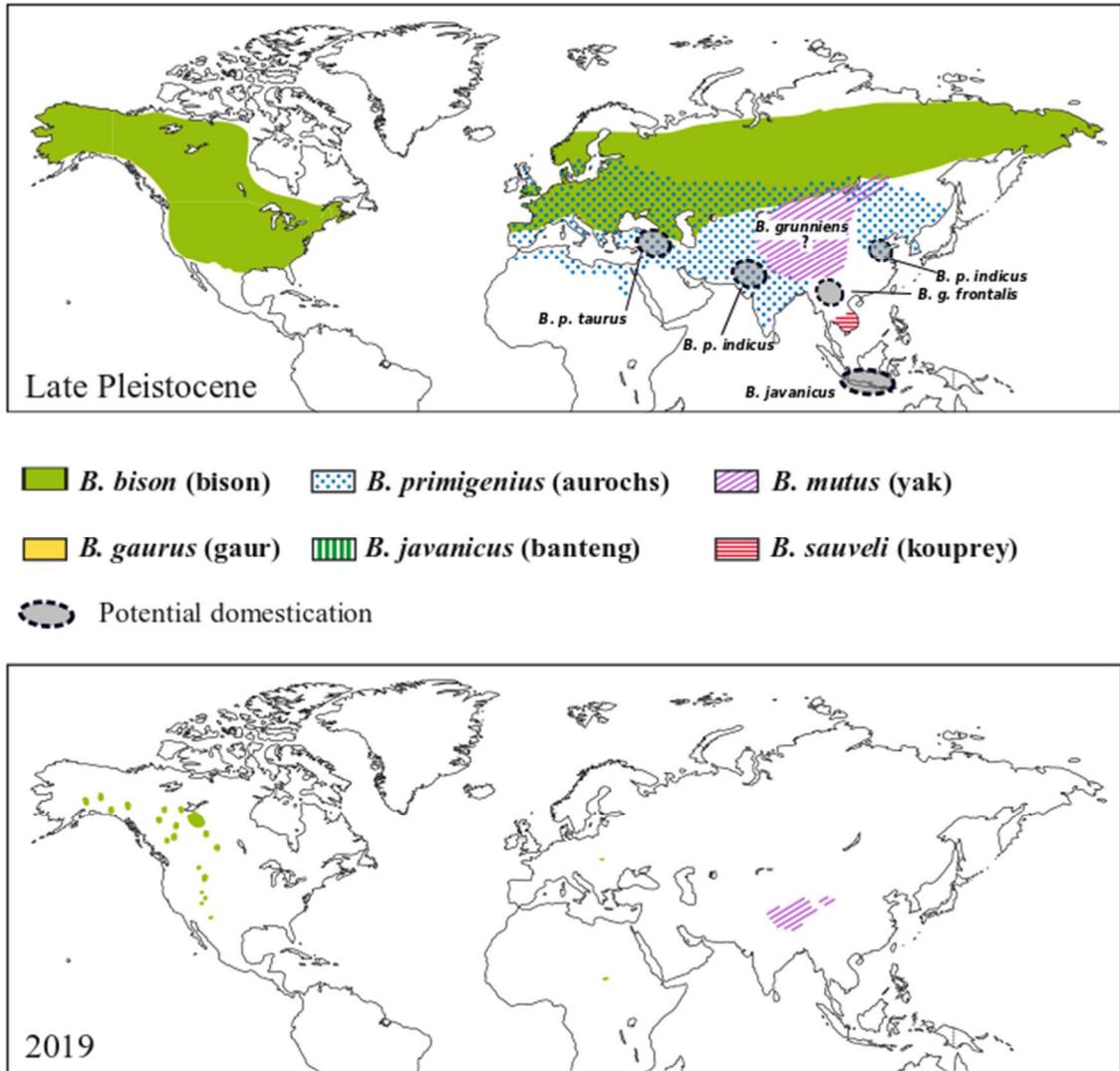
101 genetic evidence suggests that the first domestic cattle here were actually taurine cattle from  
102 the Middle East, with an admixture from local African aurochs (Pitt et al., 2019). In mainland  
103 and island south-east Asia, the domestication history of the yak in the Tibetan Plateau or the  
104 Asian water buffalo, the gaur and the banteng, mainly relies on genetic and genomic  
105 investigations from current wild and domestic populations (Bradley 2006). Although genetic  
106 and paleogenetic studies have provided huge insights into the broad origin and trajectories of  
107 taurine and zebu cattle, a refined understanding of the timing and mechanisms of their  
108 emergence remains to be undertaken in south-western Asia (Arbuckle et al. 2016). In south-  
109 east Asia, studies on the domestication process of wild cattle through archaeological evidence  
110 is progressing, with the first ancient mtDNA sequences just being published (Siripan et al.  
111 2019).

112 Along with genetic markers, documenting the domestication pathway of wild cattle could  
113 greatly benefit from more powerful morphometric tools to document, from the fossil record,  
114 the distribution range of wild cattle species and sub-species before the domestication process  
115 was initiated, and identify intraspecific morphological changes induced by the domestication  
116 process. The morphological markers used to identify cattle domestication from aurochs and  
117 subsequent livestock diffusion have so far relied on body-size reduction (Peters et al. 2005;  
118 Helmer et al., 2005; 2015, Arbuckle, 2014). This body-size reduction, used as domestication  
119 syndrome (Hemmer, 1990), is a pleiotropic consequence of the selection for behaviours  
120 facilitating adaption to the human environment (Trut, 2009; Wilkins et al., 2014). However,  
121 difficulty in disentangling human intentionality from other potential biotic and abiotic factors  
122 (Maurer et al., 1992) makes it a poor phenotypic marker of early domestication (Helmer et al.  
123 2005; Vigne, 2011; Zeder, 2015).

124 The geometric morphometrics (GMM) revolution in the study of biological forms (Zelditch et  
125 al. 2012) have provided an important breakthrough to track phenotypic responses associated  
126 with both the process of domestication and its geographical origins in the archaeological  
127 record (Cucchi et al., 2011; Larson, Dobney & Cucchi 2011; Evin, Dobney & Cucchi et al.  
128 2017). Mainly applied on suid teeth, GMM studies have contributed to reach new insights into  
129 pig domestication and dispersal in Island South East Asia (Larson et al. 2007; Cucchi et al.  
130 2009), China (Cucchi et al., 2011, 2016) and Europe (Otoni et al., 2013; Evin et al., 2015;  
131 Balasse et al., 2019), as well as into the emergence of landrace breeds in Gaul (Duval et al.,  
132 2015; 2018) and Bronze-Age Switzerland (Bopp-Ito et al., 2018). The GMM approach of the  
133 enamel folding pattern of the occlusal surfaces (EFPOS hereafter) has been used to  
134 distinguish Bovidae from South Africa (Brophy et al., 2014), explore diversity in Gallic-

135 Roman domestic cattle (Nuviala, Laffont & Montuire 2014) and assess taxonomic and  
136 phylogenetic signals in *Equus* mandibular teeth among extant wild, domestic and hybrid taxa  
137 (Cucchi et al., 2017).

138 In this study we would like to further assess the biosystematic resolution of EFPOS variation  
139 in Bovini. The first objective is to test whether EFPOS can reach an accurate taxonomic  
140 identification at the genus and species levels to document the diversity in wild cattle before  
141 the emergence of agriculture. The second is to test whether genetic isolation can lead to  
142 observable intraspecific phenotypic divergence. And finally, we tested the extant of  
143 phylogenetic signal in EFPOS variation to assess its potential in tracking genetic relationship.  
144 To provide a proof of concept useful across the wide geographic range where these questions  
145 apply, we have chosen to test these biosystematic signals from three molars ( $M^2$ ,  $M^3$  and  $M_3$ )  
146 commonly found in archaeological deposits and over two subtribes of Bovini: the Bubalina  
147 (*Bubalus* and *Syncerus*) and the Bovina (*Bos* and *Bison*) (Hassanin et al., 2013), which covers  
148 most of the current diversity in wild and domestic cattle. We assessed which molar would  
149 perform best in identifying the genus and species of the *Bovini* tribe and populations within  
150 *Bos p. taurus*, taking into account the age and different parameters of the EFPOS  
151 quantification. We assessed the phylogenetic signal using a mtDNA genome phylogeny from  
152 modern specimens contrasted with the interspecific morphospace of each molar.



153

154 Figure 1: Former range (Late Pleistocene) and current geographic distribution of wild species  
 155 of *Bovina* after Hassanin 2015 with localisation of their potential domestication centres after  
 156 Irving-Pease et al. 2018.

157

## 158 2. Materials and methods

159 Specimens analysed include three extant species of the subtribe Bubalina: the Asian water  
 160 buffalo (*Bubalus arnee*), the lowland anoa (*Bubalus depressicornis*) and the African buffalo  
 161 (*Syncerus caffer*); two extant species of Bison: the American bison (*Bison bison*), and the  
 162 European bison (*Bison bonasus*); four wild species of the genus *Bos*: the yak (*Bos mutus*), the  
 163 gaur (*Bos gaurus*), the banteng (*Bos javanicus*) and the extinct aurochs (*Bos primigenius*); and  
 164 two domestic species: common cattle (*Bos primigenius taurus*) and zebu cattle (*Bos*  
 165 *primigenius indicus*). The modern breeds of common cattle used in this study (Hollaender,  
 166 Jersey, Shorthorn and Wilstermarsch) are from the Museum of Domesticated Animals “Julius

167 Kühn” in Halle, which collected the specimens in the late 19<sup>th</sup> and early 20<sup>th</sup> century. These  
 168 specimens belong to the so-called ancient breeds or little developed country breeds.  
 169 Wilstermarsch and Hollaender belong to the Pied Lowland/Northwestern Lowland subunit,  
 170 whereas Shorthorn and Jersey belong to the British/Celtic/North European subunit (Felius et  
 171 al., 2011). Jersey and Hollaender are two milk breeds, while Wilstermarsch and Shorthorn are  
 172 dual-purpose/meat breeds. These different selective purposes are observable from their skull  
 173 morphotypes: milk breeds have longer and narrower skulls, whereas meat animals have  
 174 shorter and more compact ones (Duerst, 1931; Haring, 1949). We also included two  
 175 archaeological samples of domestic cattle (*Bos p. taurus*), one from the late Iron Age site of  
 176 Basel-Gasfabrik (BS, Switzerland, c. 150-80 BC) and one from the Bronze Age site of  
 177 Savognin-Padnal (GR, Switzerland, c. 1950-1050 BC).

178 Due to a nomenclature problem (e.g. Gentry et al., 2004; Roskov et al., 2018), we made no  
 179 distinction between the wild and domestic forms of yak (*Bos mutus*), gaur (*Bos gaurus*),  
 180 banteng (*Bos javanicus*) or Asian water buffalo (*Bubalus arnee*) for this analysis.

181

Status	Species	M <sup>3</sup>	M <sup>2</sup>	M <sub>3</sub>
<b>modern wild taxa</b>	<i>Bison bison</i>	7	10	13
	<i>Bison bonasus</i>	14	9	10
	<i>Bos gaurus</i>	13	14	6
	<i>Bos mutus</i>	2	3	-
	<i>Bos javanicus</i>	15	12	3
	<i>Bubalus arnee</i>	12	11	4
	<i>Bubalus depressicornis</i>	2	4	5
	<i>Syncerus caffer</i>	21	28	11
<b>modern domestic taxa</b>	<i>Bos primigenius indicus</i> (zebu cattle)	5	5	6
	<i>Bos primigenius taurus</i> (common cattle)			
	Hollaender	13	12	10
	Jersey	8	7	8
	Shorthorn	8	10	10
	Wilstermarsch	5	5	5
<b>archaeological samples</b>	<i>Bos primigenius primigenius</i>	21	21	18
	<i>Bos primigenius taurus</i>			
	Basel-Gasfabrik (late Iron Age)	17	15	9
	Savognin-Padnal (Bronze Age)	15	12	7

<b>total sample size</b>	<b>178</b>	<b>178</b>	<b>125</b>
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182 Tab. 1: Sample size for the modern and archaeological *Bovini* used in this study. Maxillary  
183 molars: M<sup>3</sup>, M<sup>2</sup>; mandibular molar: M<sub>3</sub>.

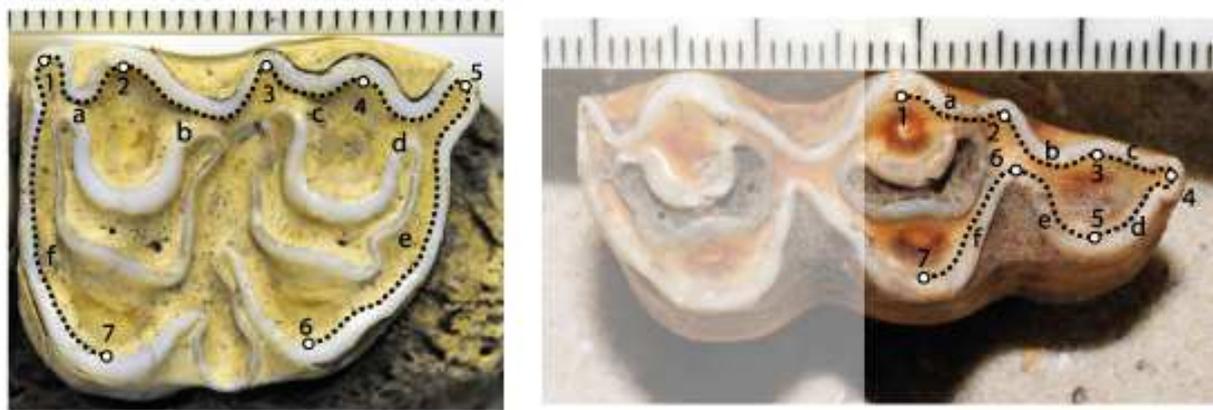
184

185 Our morphometric study focused on the maxillary second and third molars (M<sup>2</sup>, M<sup>3</sup>) and the  
186 mandibular third molar (M<sub>3</sub>) (fig. 2a, 2b). Both maxillary and mandibular third molars  
187 provide important advantages when dealing with archaeological material since they are easily  
188 distinguishable from the other teeth. Understanding the effect of attrition through ageing over  
189 the variation of the EFPOS was pivotal for this study. This effect has been proven null or  
190 negligible on the EFPOS of horses' cheek teeth (Seetah et al., 2014), and CT analysis on the  
191 third maxillary and mandibular molars of African bovids (Brophy et al., 2014) also indicate a  
192 negligible effect. To investigate whether this observation is also valid for bovine teeth, we  
193 only considered teeth with full abrasion for this study. To obtain a relative age determination  
194 for the modern and archaeological specimens, we used the wear stage recording systems  
195 accessible from the IPAS website  
196 (<https://duw.unibas.ch/de/ipna/forschung/archaeobiologie/archaeozoologie/methodik/>). With  
197 this system, each tooth is given a numerical score which corresponds to its eruption and  
198 attrition stages, combining the age systems of Barone 1986, Becker/Johansson 1981, Ducos  
199 1968, Habermehl 1975 and Grigson 1982.

200

### 201 *2.1 Geometric morphometric approach to Bovini molar's EFPOS*

202 Following previous studies on equines (Cucchi et al., 2017), we quantified the EFPOS of  
203 bovine molars with a 2D GMM approach combining landmarks of type 3 on the main enamel  
204 folds and semilandmarks on enamel curves between each landmark. For all three molars, we  
205 collected 7 landmarks (1–7) on the maximum curvature of the enamel folds at the junction  
206 between dentine and enamel, (fig. 2AB). The semilandmarks were then sampled equidistantly  
207 on the curves drawn between each landmark, at the junction between dentine and enamel (tab.  
208 2).



209  
 210 Fig. 2: A: Landmarks (1–7) and semilandmarks (a–f) used for the maxillary M<sup>2</sup> and M<sup>3</sup> (here  
 211 a M<sup>3</sup> of an archaeological *Bos p. taurus* from the Basel-Gasfabrik sample). B: Landmarks (1–  
 212 7) and semilandmarks (a –f) used for the M<sub>3</sub> (here a M<sub>3</sub> of an archaeological *Bos p. taurus*  
 213 from the Basel-Gasfabrik sample). Scale in mm.

214  
 215 We performed a Generalised Procrustes Superimposition (GPS) on all the 2D Cartesian point  
 216 coordinates of the EFPOS outline configurations to remove the effects of position, size and  
 217 orientation. The semilandmarks were slided using the Bending Energy method (Bookstein  
 218 1996). The GPS produces Procrustes coordinates which can be used as EFPOS' shape  
 219 parameter. GPS also computes the centroid size of the EFPOS as the square root of the sum of  
 220 the squared distances from the landmarks and semilandmarks to the centroid of the enamel  
 221 outline (Bookstein, 1996; Zelditch et al., 2012).

222

	a	b	c	d	e	f	Total
M <sup>3</sup>	23	28	20	22	38	44	175
M <sup>2</sup>	19	26	20	21	34	34	154
M <sub>3</sub>	21	22	16	15	17	22	113

223 Tab. 2: Number of semilandmarks (SLM) for each tooth and each curve (a–f). For the position  
 224 of the curves see fig. 1a/b.

225  
 226 The points and curves digitization were computed from the images using tpsDig V2.17 and  
 227 the GPS with tpsRelw v1.53 (Rohlf, 2016).

228  
 229 *2.2 Assessing taxonomic signals in bovine molars EFPOS size and shape while accounting for*  
 230 *age effect and allometry*

231  
 232 Differences in centroid size variation of the EFPOS among bovine taxa were tested for the

233 three molars using Analysis of Variance (ANOVA) with Bonferroni correction for pairwise  
234 comparisons (S11). EFPOS size differences between bovine species, while accounting for size  
235 varying with age, were tested for each molar with a single factor Analysis of Covariance  
236 (ANCOVA).

237 EFPOS shape differences between bovine species, while accounting for shape  
238 covarying with age and centroid size (allometry), were tested for each of the three molars with  
239 a single factor Multivariate Analysis of Covariance (MANCOVA). The MANCOVA assessed  
240 whether age and allometry effects differ significantly between the bovine species (interaction)  
241 and which of the three molars was the most affected by these two effects (R-squared).

242 We then assessed which of the three phenotypic markers ( $M^3$ ,  $M^2$ ,  $M_3$ ) would provide  
243 the greatest taxonomic resolution at the genus, species and population level, and which  
244 parameters of EFPOS quantification parameters (the shape, the size-free shape, the age-free  
245 shape or the form) would perform the best. The size- and age-free shape parameters are the  
246 residuals of the multivariate regression between the Procrustes coordinates as dependent  
247 variables and respectively the Log-centroid size and the age scores. The Procrustes from  
248 space were obtained by combining the Log-centroid size with the Procrustes coordinates  
249 (Mitteroecker and Gunz, 2009; Klingenberg 2015).

250 The taxonomic resolution (genus, species, and populations) for the three molars was assessed  
251 using Linear Discriminant Analysis (LDA). Its predicting approach calculated the percentage  
252 of cross validated correct classification (% CVC) of each specimen into its taxonomic group,  
253 following a 2 fold cross-validation over 10 000 iterations.

254 The genus factor comprised four groups: *Bos*, *Bison*, *Bubalus* and *Syncerus*. The species  
255 factor comprised the 11 specific groups of our dataset (tab. 1). The population factor was  
256 characterized by the 4 modern breeds and 2 archaeological populations (tab. 1). To avoid  
257 spurious results of the LDA induced by the high dimensionality of the shape parameters  
258 compared to the number of observation, we performed Principal Component Analysis (PCA)  
259 for each parameter and used only the PC scores explaining 99% of the total variance as  
260 variables in the LDA analysis. On average, 30 PC scores were enough to reach this threshold.

261

### 262 2.3 Assessing the phylogenetic signal in bovine molars EFPOS

263 To assess the phylogenetic signal of the three molars morphospace, we used the sequences of  
264 the complete mitochondrial genome of Bovini, extracted from the NCBI (National Center for  
265 Biotechnology Information) for the 11 following taxa (the accession numbers are indicated  
266 between brackets): domestic Asian buffalo – *Bubalus arnee bubalis* (JN632607), anoa –

267 *Bubalus depressicornis* (EF536351), African buffalo – *Syncerus caffer* (EF536353),  
268 American bison – *Bison bison* (JN632601), European bison – *Bison bonasus* (JN632602),  
269 domestic yak – *Bos mutus grunniens* (EF494179), domestic cattle – *Bos primigenius taurus*  
270 (V00654), zebu – *Bos primigenius indicus* (AY126697), gaur – *Bos gaurus* (JN632604),  
271 banteng – *Bos javanicus* (JN632606) and aurochs – *Bos primigenius primigenius*  
272 (GU985279).

273 The sequences were aligned on SeaView version 4 (Gouy et al., 2010). Our final alignment  
274 contained 16,284 characters. A Bayesian tree was constructed with MrBayes v3.2.1 (Ronquist  
275 et al., 2012) and the GTR+I+G model selected under jModelTest 2.1.7 (Darriba et al., 2012)  
276 using the Akaike information criterion. The posterior probabilities were calculated using four  
277 independent Markov chains run for 10,000,000 Metropolis-coupled MCMC generations, with  
278 tree sampling every 1000 generations and a burn-in of 25%.

279

280 To estimate the strength of the phylogenetic signal relative to a Brownian motion model of  
281 evolution, we used the *Kmult* method (Adams, 2014), a multivariate generalization of the *K*-  
282 statistic (Blomberg et al. 2003). Under a Brownian motion model of evolution the expected  
283 *Kmult* value is 1.0. Observed *Kmult* values were evaluated by comparing with the permuted  
284 *K*-value from randomized shape data relative to the tree topology of the molecular phylogeny.  
285 To visualise the association between the molecular phylogeny and the dental shape space we  
286 created a phylomorphospace, which fitted the shape changes from the bovini taxa onto the  
287 tree topology using a squared change parsimony approach (Klingenberg and Gidaszewski,  
288 2010).

289

290 Morphometric statistics were performed with R (RCoreTeam, 2016), and the libraries MASS  
291 (Venables & Ripley 2002) and geomorph (Adams and Otárola-Castillo, 2013).

292

### 293 **3. Results**

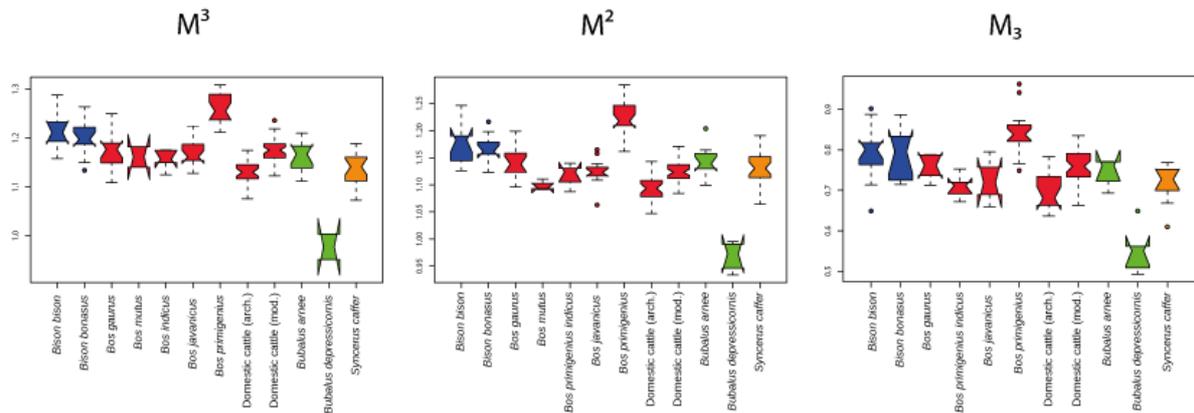
294

#### 295 *3.1 EFPOS size and shape differences among Bovini accounting for age and allometric effect*

296

297 The ANCOVA found significant overall differences in the size variation of the EFPOS among  
298 the Bovini species (modern and archeological *Bos p. taurus* have been separated) for each  
299 tooth (Figure 3, tab. 3, See SII for taxa pairwise comparisons for each molar). All three  
300 molars displayed the same pattern of size differentiation among taxa, although the

301 differentiations had a greater resolution for the maxillary molars. *Bos p. primigenius* is  
 302 significantly bigger than all the other species, while *Bubalus depressicornis* is the smallest.  
 303 After *Bos p. primigenius*, the bison's  $M^3$  and  $M^2$  were significantly larger than those of other  
 304 genera. We also observed that Iron Age common cattle were significantly smaller than  
 305 modern cattle breeds. In most cases there was an overlap in the size range of the remaining  
 306 taxa.  
 307



308  
 309 Fig. 3: Box plot of the  $M^3$ ,  $M^2$  and  $M_3$  centroid sizes (log) from the tribe Bovini, including  
 310 modern and archaeological domestic cattle (*Bos p. taurus*).  
 311

312 The size differences among Bovini species are reflected in the strong taxonomic signal in the  
 313 size variation of the EFPOS which is above 50% (R-squared) for all three molars, while an  
 314 age effect below 10% was only significant for the third maxillary and mandibular molars  
 315 (tab.3), common among the species (tab. 3: Age\*Taxa).  
 316

$M^3$	Df	SS	MS	R-Squared	F	Z	Pr (>F)	
Age	1	0.04363	0.043632	0.08556	43.5365	2.1454	0.001	**
Taxa	10	0.29316	0.029316	0.57487	29.2515	6.6617	0.001	**
Age*Taxa	9	0.00580	0.000644	0.01137	0.6427	-0.6191	0.753	ns
$M^2$	Df	SS	MS	R-Squared	F	Z	Pr (>F)	
Age	1	0.00148	0.001481	0.00312	1.9206	0.8700	0.168	ns
Taxa	10	0.33697	0.033697	0.71006	43.7088	7.3857	0.001	**
Age*Taxa	10	0.00968	0.000968	0.02040	1.2558	0.6748	0.266	ns
$M_3$	Df	SS	MS	R-Squared	F	Z	Pr (>F)	

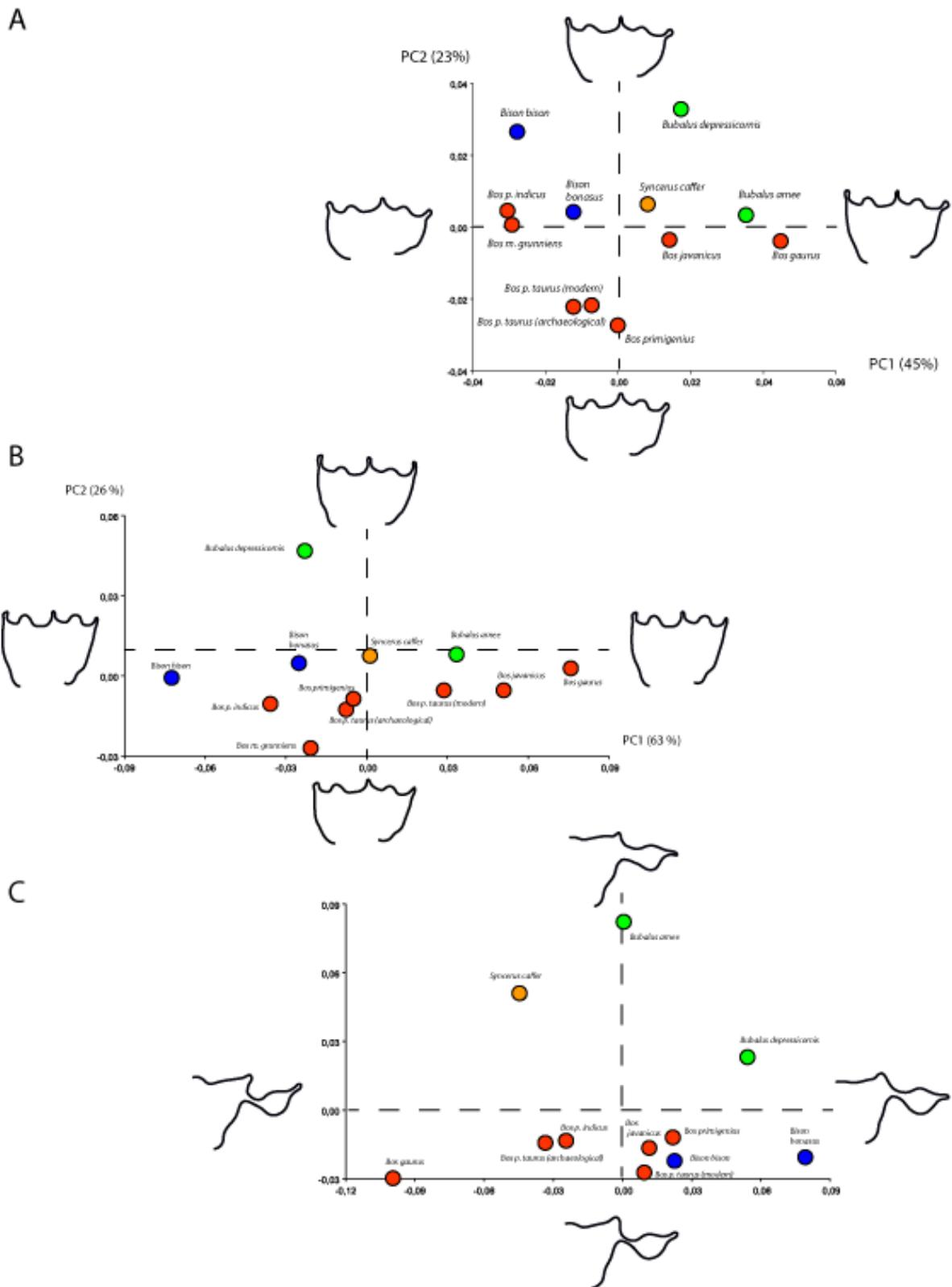
Age	1	0.03879	0.038795	0.05184	20.25	1.9168	0.001	**
Taxa	9	0.46190	0.051323	0.61718	26.79	6.6697	0.001	**
Age*Taxa	9	0.02931	0.003257	0.03917	1.70	1.1925	0.107	ns

317 Tab. 3: Results of the single factor ANCOVA test for age effect on the size variation of the  
318 M<sup>3</sup>, M<sup>2</sup> and M<sub>3</sub> (Age) and the size differences among Bovini taxa (Taxa) while accounting for  
319 size covarying with age (Age\*Taxa).

320

321 MANCOVA found significant overall EFPOS shape differences among the Bovini species for  
322 the three molars (tab. 4: "Taxa"). Patterns of shape variation differ according to the molars  
323 (figure 4), but most of the variation was triggered by the differentiation between the *Bubalina*  
324 and *Bovina* species. Within the *Bovina* species, the Bison species separate from the *Bos*  
325 species. Within the *Bos* species, *Bos p. indicus* separate from *Bos p. primigenius* and *Bos p.*  
326 *taurus*, and *Bos javanicus* and *Bos gaurus* separate significantly, except for the M<sub>3</sub>.

327



328

329 Figure 4: Patterns of shape variation among the Bovini species mean shape for M<sup>3</sup> (A), M<sup>2</sup> (B)

330 and M<sub>3</sub> (C). Shape deformation along the PCs axes are displayed using the shape of

331 specimens at the ends of the range of variability along PC1 and PC2.

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For both third molars, the age related attrition effect accounted for 10% and 12% of the EFPOS shape variation, while for the second maxillary molar the age effect reach 32% (tab. 4). It was reduced to around 18% by eliminating the youngest and oldest age groups. A common, and almost common, age effect among species for the third maxillary lower and mandibular molars for the  $M^2$  (tab.4) was found. We then obtained age-free shape variables using the residuals of the multivariate regression.

$M^3$	Df	SS	MS	R-Squared	F	Z	Pr (>F)	
Age effect	1	0.12673	0.126734	0.120641	29.579	6.4949	0.001	**
Taxa	10	0.16502	0.016502	0.157089	3.8515	6.2211	0.001	**
Age*Taxa	9	0.04322	0.004802	0.04141	1.1208	0.5946	0.276	ns
$M^2$	Df	SS	MS	R-Squared	F	Z	Pr (>F)	
Age effect	1	0.45424	0.45424	0.32858	117.1079	6.6222	0.001	**
Taxa	10	0.22299	0.02230	0.16130	5.7489	5.9444	0.001	**
Age*Taxa	10	0.06909	0.00691	0.04998	1.7813	2.0784	0.017	*
$M_3$	Df	SS	MS	R-Squared	F	Z	Pr (>F)	
Age effect	1	0.25647	0.256474	0.098254	17.5115	5.7224	0.001	**
Taxa	9	0.51961	0.057735	0.199060	3.9420	6.6318	0.001	**
Age*Taxa	9	0.16458	0.018287	0.063051	1.2486	1.1209	0.133	ns

341 Tab. 4: Results of the single factor MANCOVA test for age effect on the shape variation of  
 342 the  $M^3$ ,  $M^2$  and  $M_3$ , (Age effect) and the shape differences among Bovini species (Taxa) while  
 343 accounting for shape covarying with age (Age\*Taxa) , where “\*\*” denotes interaction.

344  
 345 The MANCOVA found significant but very weak allometric effects in the  $M^3$  and  $M_3$  shape  
 346 variation, explaining less than 5% of the shape variation (tab. 5). Furthermore, this allometric  
 347 effect did not interact with the taxonomic signal, which suggests a common allometric effect  
 348 on molar shape that does not affect species differentiation. We obtained size-free shape  
 349 variables using the residuals of the multivariate regression.

350

$M^3$	Df	SS	MS	R-Squared	F	Z	Pr (>F)	
Allometry	1	0.02365	0.0236487	0.022512	4.9849	3.1304	0.003	**
Taxa	10	0.17921	0.0179213	0.170598	3.7776	6.1584	0.001	**
Allometry*taxa	10	0.06013	0.0060126	0.057235	1.2674	1.1413	0.128	ns

M <sup>2</sup>	Df	SS	MS	R-Squared	F	Z	Pr (>F)	
Allometry	1	0.00756	0.0075614	0.00547	1.2441	0.6824	0.256	ns
Taxa	10	0.28292	0.0282919	0.20465	4.6550	5.2857	0.001	**
Allometry*taxa	10	0.09522	0.0095223	0.06888	1.5668	1.6533	0.041	*
M <sub>3</sub>	Df	SS	MS	R-Squared	F	Z	Pr (>F)	
Allometry	1	0.11535	0.115347	0.044189	7.9699	4.0634	0.001	**
Taxa	9	0.60338	0.067042	0.231150	4.6323	7.3664	0.001	**
Allometry*taxa	9	0.24170	0.026855	0.092593	1.8556	2.9532	0.002	**

351 Table 5: Results of single factor MANCOVA test for the allometric effect over shape  
352 variation of the M<sup>3</sup>, M<sup>2</sup> and M<sub>3</sub> as well as shape differences between Bovini species (Taxa)  
353 while accounting for shape covarying with size (Log CS), where "\*" denotes interaction.

354

### 355 3.3 Taxonomic signals in Bovini cheek teeth shape and form

356

357 The taxonomic resolution from the genus to the population levels differed among the  
358 phenotypic markers and their morphometric variables, according to the percentage of CVC  
359 (tab. 6). Maxillary molars performed better than the mandibular ones in separating the taxa to  
360 the genus and species level, which is not surprising since only half of the M<sub>3</sub> could be  
361 quantified. The M<sup>2</sup> shape was the most efficient at discriminating the different genera in  
362 bovines with almost 90% correct classifications, closely followed by both third molars.  
363 Discrimination of species was still high for the M<sup>3</sup> and M<sup>2</sup> shapes with more than 75% of  
364 correct classifications for the M<sup>3</sup>, but was enhanced in all three molars when using the form  
365 variables with M<sup>2</sup>, reaching nearly 85% CVC. For population discrimination the CVC  
366 dropped below 50%, with the M<sub>3</sub> providing the best signal (48%). Finally, correcting for age  
367 or size effects did not significantly improve the discrimination of genus and species in  
368 bovines.

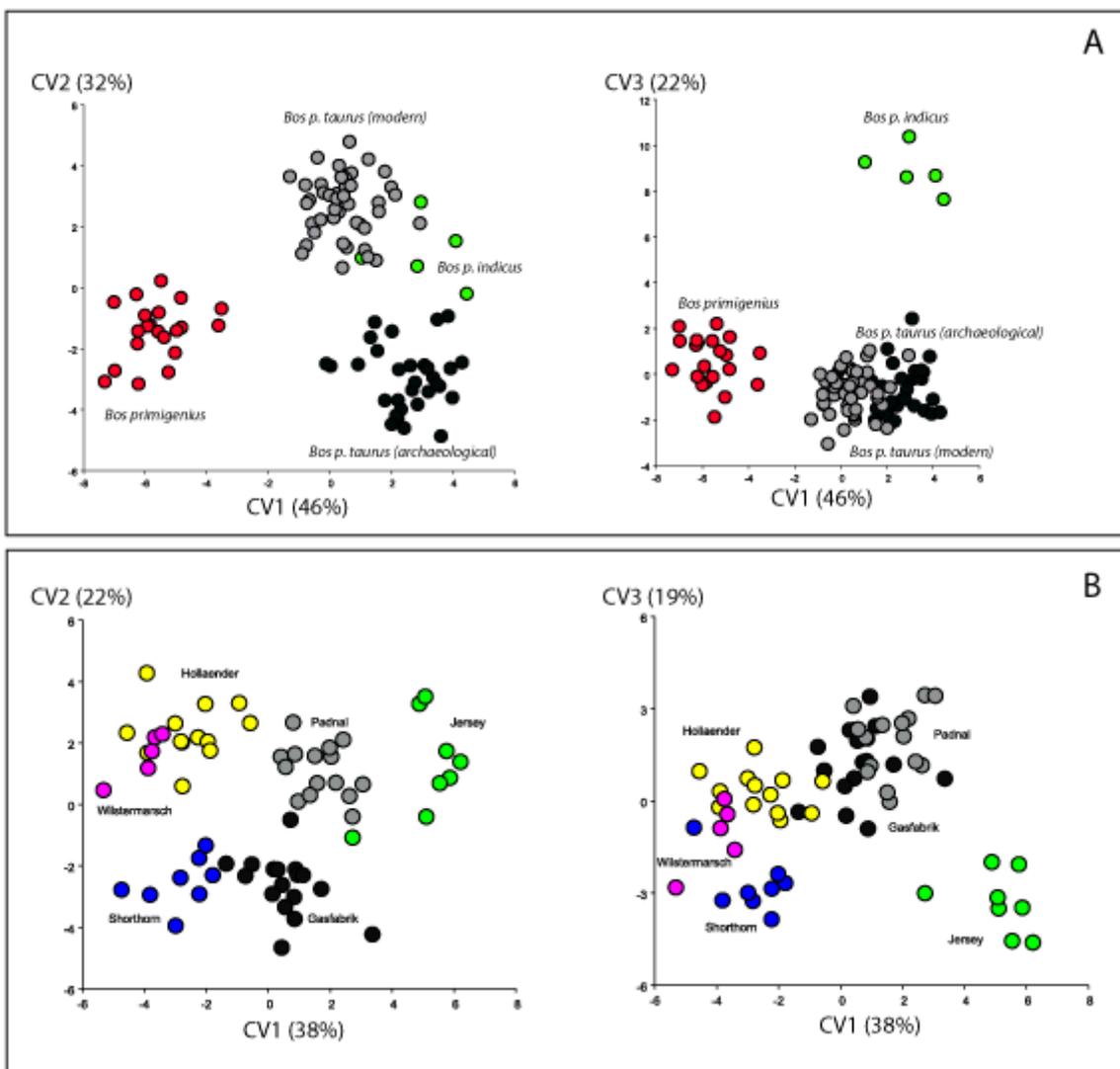
369

	Shape			Size-free shape		Age-free shape		Form		
	Genus	Species	Population*	Genus	Species	Genus	Species	Genus	Species	Population*
M <sup>3</sup>	88.03	<b>75.5</b>	44.12	89.06	<b>75.52</b>	87.5	73.43	<b>88.51</b>	82.82	38.24
M <sup>2</sup>	<b>89.95</b>	72.48	30.3	<b>89.42</b>	73.02	<b>89.95</b>	<b>74.61</b>	88.36	<b>84.65</b>	30.3
M <sub>3</sub>	84.18	66.18	<b>48.38</b>	84.89	53.96	84.89	53.24	87.77	66.91	<b>38.71</b>

370 Tab. 6: Percentage of correct classification after cross validation for M<sup>3</sup>, M<sup>2</sup>, and M<sub>3</sub> at  
371 different taxonomic levels: genus, species and population and according to four phenotypic  
372 parameters: Shape, Size-free shape, Age-free shape and Form. \*: analysis performed on extant  
373 populations of *Bos p. taurus* only.

374

375 CVA shows significant divergence (MANOVA:  $Pillai=1.6655$ ,  $F=2.9535$ ,  $p<0.0001$ ) between  
 376 the ancestral wild shape of the Aurochs and the domestic phenotype of common and zebu  
 377 cattle, between common and zebu cattle and between modern and archaeological common  
 378 cattle, with zebu cattle showing the greatest divergence (Figure 5A). The CVC is too low to  
 379 accurately separate the different populations of modern cattle based on their molar shape  
 380 (Tab. 6). However, we found significant differentiation patterns (MANOVA:  $Pillai=2.423$ ,  
 381  $F=1.558$ ,  $p=0.001545$ ) among modern and archaeological common cattle (Figure 5B), where  
 382 Iron Age and Bronze Age cattle from Switzerland are within the variation range of modern  
 383 breeds. In this morphospace, Jersey ancient breeds is the most divergent phenotype. Also, Iron  
 384 Age and Bronze Age cattle displayed greater phenotypic similarities with Hollaender ancient  
 385 breeds (SI 2).



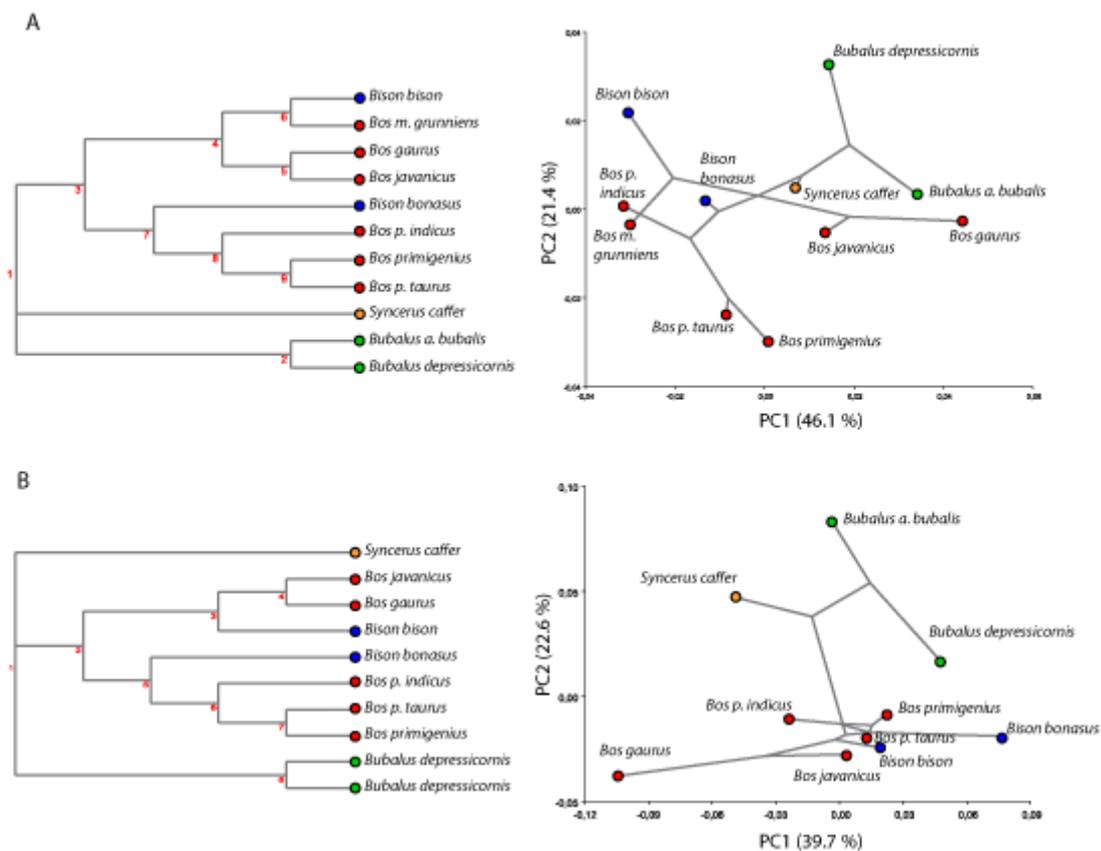
386  
 387 Fig. 5: Patterns of  $M^3$  shape differentiation within the first three canonical factors of the CVA  
 388 (A) among wild extinct aurochs (*Bos primigenius*) and modern and archaeological domestic  
 389 cattle (*Bos p. taurus*) and (B) among modern and archaeological common cattle.

390

391 3.4 Phylogenetic signal in Bovini molar shape.

392

393 The *Kmult* statistics found a low but significant phylogenetic signal in  $M^3$  (*Kmult* observed =  
394 0.206; P-value = 0.009) and  $M_3$  (*Kmult* observed = 0.2781; P-value = 0.003) but not in the  $M^2$   
395 (*Kmult* observed = 0.17; P-value = 0.18). Both third molars phylomorphospace captured the  
396 phylogenetic signal separating the Bovinae from the Bubalina and *Bos* from *Bison* species  
397 within the Bovina (fig. 6). The low phylogenetic signal in  $M^3$  is driven by the phenotypic  
398 relationships of the cattle of south-east Asia – the banteng (*Bos javanicus*) and the gaur (*Bos*  
399 *gaurus*) within the Bubalina, and greater dental shape similarity between the yak (*Bos mutus*)  
400 and the humped cattle (*Bos p. indicus*) than with the American bison (*Bison bison*), both being  
401 incongruent with the mitochondrial phylogeny (fig. 6A). For the  $M_3$  (figure 6B), the low  
402 phylogenetic signal is due to greater phenotypic similarities of *Bos p. primigenius* and the  
403 common cattle (*Bos p. taurus*) with the American bison (*Bison bison*), than with the European  
404 one (*Bison bonasus*), as well as a greater similarity between the bateng (*Bos javanicus*) and  
405 the common cattle (*Bos p. taurus*) than with the gaur (*Bos gaurus*).



406

407

408 Fig. 6: Bovini MtDNA genome phylogeny and dental shape Phylomorphospace of  $M^3$  (A) and

409 M<sub>3</sub> (B).

410

#### 411 **4. Discussion**

412

##### 413 *4.1. Identifying the diversity of the wild progenitors and the domestication process in Bos* 414 *species*

415 Our study has shown that both the EFPOS size and shape variations of the maxillary molars  
416 provided reliable taxonomic resolution at the genus and species levels. The resolution to  
417 species was not affected by the age effect, or only slightly for the M<sup>2</sup> shape, and could be  
418 increased when using the form parameter, bringing together the taxonomic resolution of both  
419 size and shape. These results are congruent with previous studies on South African Bovids  
420 (Brophy et al. 2014) and equids (Cucchi et al., 2017) in rejecting the general idea that  
421 hypsodont teeth from ruminants are not good taxonomic characters because of the attrition  
422 blurring process. As expected the second molar was the most affected by attrition, leading to  
423 potential spurious identification. Therefore, we suggest to implementing taxonomic studies on  
424 the M<sup>3</sup>.

425 Our study also showed that both maxillary and mandibular third molar shape  
426 variations had a significant phylogenetic signal among Bovini species, finding phenotypic  
427 relationships congruent with the most recent phylogeny (Hassanin, 2014; Hassanin, 2015).  
428 Both molars captured the genetic relationship between aurochs (*Bos p. primigenius*) and the  
429 two lines of domestic cattle (*Bos p. taurus / indicus*), between the two species of bison (*Bison*  
430 *bison* and *Bison bonasus*) and the yak (*Bos mutus*), and between gaur (*Bos gaurus*) and  
431 banteng (*Bos javanicus*). However, the strength of this signal was weakened by the  
432 phenotypic relationship between the south-east Asian cattle (*Bos gaurus* and *Bos javanicus*)  
433 and the *Bubalina*, as well as the one between *Bos mutus* and *Bos p. indicus* for the M<sup>3</sup> and the  
434 phenotypic proximity between *Bos javanicus* and *Bos p. taurus* for the M<sub>3</sub>. Since we could not  
435 make a distinction between the wild and domestic forms of yak (*Bos mutus*), gaur (*Bos*  
436 *gaurus*), and banteng (*Bos javanicus*) for this analysis, it is likely that this incongruence  
437 between genotype and phenotype is the consequence of genetic introgression among *Bos*  
438 species (Hassanin 2015, Wu et al. 2018).

439 The high taxonomic resolution up to the species level, the lack of significant impact of  
440 attrition in this resolution and the strength of the phylogenetic signal recorded in the M<sup>3</sup>  
441 clearly suggest that this molar should be preferred for biosystematic studies of Bovini dental  
442 series from fossil and archaeological contexts. Since the wild ancestors of domestic cattle are

443 either extinct (aurochs) or reduced to very small pockets of range distribution, this  
444 biosystematic power would prove extremely valuable to document the diversity and  
445 distribution of the wild progenitors of domestic forms, from the Pleistocene and early  
446 Holocene archaeological records. Applied to all the available dental series of Bovini in the old  
447 world, this marker would help illustrate the natural geographic distribution of aurochs variants  
448 and test the relevance of the three different sub-species proposed by zooarchaeologists  
449 (Clutton-Brock 1989). In south-east Asia, these studies would help map the distribution of the  
450 four wild species of *Bos* and understand their geographic diversity and sympatry.

451 The discrimination and the phylogenetic signal recorded in the M<sup>3</sup> between the wild  
452 and domestic European forms of Bovini (*Bison bonasus*, *Bos p. primigenius* and *Bos p.*  
453 *taurus*, *Bos p. indicus*) clearly suggest that GMM on M<sup>3</sup> could trace the phylogenetic histories  
454 of domestic cattle in the core area of the Fertile crescent. However, this approach alone could  
455 prove unable to identify the early process of domestication, when high gene flow between  
456 wild and domestic populations would prevent the expression of genetically induced  
457 phenotypic divergence (Irving-Pease et al. 2018, Vigne 2015). Unless corralling and  
458 reproductive control were strong enough to foster the adaptive phenotypic change induced by  
459 the anthropic environment (Zohary et al. 1998).

460 The biosystematic resolution of the M<sup>3</sup> could also prove useful to document the  
461 subsequent dispersal of domestic forms outside the distribution range of their wild ancestor.  
462 For example, the possibility of identifying the two domestic cattle (*Bos p. taurus* and *indicus*)  
463 and their relationships with their potential wild progenitor could help provide new clues on  
464 the development of herding in Africa, imported from the Near East during the 7<sup>th</sup> millennium  
465 BC (Linseele, 2013; Lesur et al., 2014). According to the latest understanding, the first  
466 domestic bovine in Africa are considered to be taurine cattle – zebu seem to occur later,  
467 during the 2<sup>nd</sup> millennium BC – but we still do not know where it entered the continent,  
468 although genetic data suggest it happened through the Horn of Africa (Hanotte et al., 2002;  
469 Gifford-Gonzalez and Hanotte, 2011).

470 The scarcity of evidence for zebu in archaeological contexts partly lies in the fact that  
471 only limited morphological criteria have been established to identify zebu from taurine  
472 specimens (Grigson, 1976; Grigson, 1980). However, these criteria are not especially useful  
473 for archaeological material because the study was based on cranial parts that are seldom  
474 preserved in ancient contexts. For the moment, only a few studies have suggested the ancient  
475 presence of zebu in Africa, and only from the 1<sup>st</sup> millennium BC (Chaix, 2011; Chaix, 2013).  
476 The GMM approach of EFPOS, therefore, provides a new method to address this issue.

477 However, the remaining difficulty lies in the fact that hybridization between the two species  
478 may have occurred very early in Africa (Hanotte et al., 2002; Lesur, 2017). The method now  
479 needs to integrate hybridised African specimens to check if we can also discriminate them.

480

#### 481 *4.2. Identifying the emergence of early cattle morphotype in archaeology*

482

483 Identifying the emergence of early domestic cattle breeds due to human selective pressure, for  
484 traits such as greater milk yield, is in the realm of palaeogenomic studies (Bradley & Magee  
485 2006, Irving- Pease et al. 2018) but not of morphometrics. Indeed, morphometric changes in  
486 skeleton bones cannot be directly related with a specific selective pressure (Zeder 2015), such  
487 as meat or milk yield. However, documenting the origin and pace of morphometric changes  
488 over a large dental series from the 4<sup>th</sup> millennium BC in the Near and Middle East and from  
489 the 3<sup>rd</sup> millennium BC in Europe until Antiquity, would allow us to pinpoint the timing of the  
490 emergence of regional morphotypes due to neutral genetic shifts fostered by geographic  
491 isolation, as has already been performed for pigs (Duval et al. 2014, 2018). Once these key  
492 locations and periods are identified, targeted paleogenomic analysis could then be more  
493 efficiently implemented to explore selective traits within these regional morphotypes.

494 Our study found clear M<sup>3</sup> shape divergence between aurochs, Bronze and Iron Age  
495 Switzerland cattle and modern cattle breeds, suggesting that regional morphotypes are clearly  
496 attested in this region from the Bronze Age. Furthermore, these archaeological cattle  
497 morphotypes show greater phenotypic similarity towards modern cattle breeds than to their  
498 aurochsen progenitor, suggesting that great selective breeding in cattle was already in place  
499 from the 2<sup>nd</sup> millennium BC in Europe. But was that selection directed towards adaptation to  
500 mountainous regions or towards greater meat or milk production? Only paleogenomic  
501 analyses would be able to provide a definite answer. The population signal in the molar shape  
502 variation of *Bos p. taurus* is too weak to make safe taxonomic identification. However,  
503 phenotypic proximities between the Bronze Age and Iron Age morphotypes with the  
504 Hollaender breed (Felius et al. 2011), suggest that these Bronze and Iron Age morphotypes  
505 may have been selected for milk production. Other potential explanations could be the genetic  
506 consequence of different regional connections between the two sites. Archaeological finds  
507 evidence that the Padnal people had connections with the north of Italy and with the north and  
508 east of Switzerland (Rageth, 1986). The Basel-Gasfabrik people, on the other hand, had more  
509 connections with the west and south of France as well as with the Mediterranean (Spichtig,  
510 2005). This hypothesis will have to be tested with a paleogenetic approach and a large

511 comparative molar shape analysis of the Bronze and Iron Age domestic cattle sampled from  
512 Switzerland and Italy.

513

## 514 **CONCLUSION**

515 Our understanding of the origin and trajectories of wild cattle domestication have been  
516 mainly driven by the advance in genetic studies of modern and ancient *Bos* species, but  
517 zooarchaeologists still need powerful biometric markers to document the timing and  
518 mechanisms of cattle domestication in the old world and implement targeted biomolecular  
519 studies.

520 Our GMM approach of the taxonomic and phylogenetic signals encapsulated in the  
521 variation of molar morphology of wild and domestic species of the tribe Bovini found that  $M^3$   
522 shape variation could accurately separate the genera and species of both wild and domestic  
523 modern specimens of the tribe Bovini with high statistical accuracy, as well as their  
524 phylogenetic relationships. But recent genetic introgression between wild and domestic *Bos*  
525 species in eastern Asia have partly blurred this phylogenetic signal. The taxonomic resolution  
526 at a population level does not reach such a reliable probabilistic classification. However,  
527 significant differentiation patterns among aurochs and modern and ancient cattle breeds  
528 clearly suggest that genetic divergence indirectly triggered by intentional breeding selection  
529 can be deciphered from the archaeological record.

530 This proof of concept strongly suggest that GMM analysis of  $M^3$  applied on *Bos*  
531 remains from Pleistocene and Holocene dental series and through Eurasia would be a useful  
532 pre requisite for targeted bio molecular studies for three main reasons: (1) to document the  
533 diversity and distribution of wild progenitors of domestic forms; (2) to identify where and  
534 when the first domestic phenotype emerged; and (3) to trace the emergence of the earliest  
535 regional morphotype and their trajectory towards modern breeds.

536

537

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548

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551 TC and BS designed the study, BS collected the morphometric and Age data, TC and BS  
552 analyzed and interpreted the data, TC and BS wrote the paper in collaboration with RS, AH,  
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554

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