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1 **Morphological and dietary adaptations to different socio-economic systems**
2 **in Chalcolithic dogs**

3

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19 **Author Contributions:** Colline Brassard, Marie Balasse, Stéphanie Bréhard and Anthony Herrel designed
20 research. Marie Balasse and Denis Fiorillo performed stable isotope data acquisition and analyses in the
21 context of a project (CROC) lead by Morgane Ollivier. Marie Balasse performed analyses and
22 interpretations of the stable isotopic data. Colline Brassard performed geometric morphometric (GMM) data
23 acquisition and analyses. Colline Brassard, Stéphanie Bréhard Anthony Herrel interpreted the GMM data.
24 Adrian Bălăşescu, Stéphanie Bréhard and Valentin Radu provided archaeological samples of dogs for
25 GMM analyses and detailed information regarding the archaeological contexts from which they were
26 recovered. Colline Brassard, Marie Balasse, Stéphanie Bréhard and Anthony Herrel wrote the manuscript,
27 with the scientific and editing input from Adrian Bălăşescu and Valentin Radu. All authors reviewed the
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30 **Abstract**

31 Dogs have cohabited with humans since the Upper Paleolithic and their lifestyle and diet during
32 late prehistory probably already depended on the role they played in past societies. Here, we
33 used a combination of stable isotope analyses and three-dimensional geometric morphometrics
34 to test for differences in, and associations between, diet and mandibular morphology based on
35 150 dogs of three sites of the Chalcolithic Gumelnița culture in Romania (4,550-3,900 cal. **BCE**)
36 characterized by different socio-economic systems. At Hârșova-tell and Bordușani-Popină, where
37 the subsistence economy is mainly based on herding, dogs have a variable diet that is rich in
38 domestic animals (sheep, cattle, pig) and may contain fish. In contrast, at Vitănești-Măgurice,
39 where hunting predominates, the diet of dogs is more specialized towards large game (red deer,
40 aurochs, wild horse), reflecting the composition of human food refuse. Moreover, dogs have more
41 robust (**but not larger**) mandibles at this site with shapes suggesting a greater importance of the
42 temporal muscle important for the capture of large prey and the breaking of large bones. The
43 strong covariation between mandible shape and stable isotope signatures suggests functional
44 adaptations to diet. Overall, our results support the idea that prehistoric dogs adapted to human
45 lifestyles.

46 **Keywords:** Chalcolithic, dog, mandible, isotopes, geometric morphometrics

47 **Highlights**

- 48 • Dog remains from Romanian Chalcolithic sites allowed analyses of diet and jaw shape
- 49 • Dog diet and jaw shape reflect the human subsistence economy
- 50 • Where hunting prevails, dogs show low $\delta^{15}\text{N}$ values corresponding to large game
- 51 • When hunting predominates, dogs have **more robust but similar sized** mandibles
- 52 • Covariations between diet and jaw shape show functional adaptations to diet

53 Introduction

54 In Europe, dogs have been integrated within human groups at least since the Magdalenian
55 period, circa 17,000 years ago (Boudadi-Maligne et al., 2020; Hervella et al., 2022; Janssens et
56 al., 2018). From the Mesolithic onwards, they played a diversity of roles, as they were subjected
57 to social or symbolic practices, were used as food supply (Grandal-d'Anglade et al., 2019;
58 Horard-Herbin et al., 2014; Larsson, 1994), and were also probably allies in hunting activities and
59 served for the protection of camps or villages. Accordingly, they were in the foreground of
60 changes in subsistence strategies or cultural practices which may have influenced their access to
61 food as well as their lifestyle (e.g. Arendt et al., 2016; Grandal-d'Anglade et al., 2019; Ollivier et
62 al., 2016). This may have left imprints on dog skeletal remains involving both the stable isotopic
63 signature reflecting diet (Grandal-d'Anglade et al., 2019; Laffoon et al., 2015; Schulting and
64 Richards, 2002) and jaw shape which is determined in part by muscle forces and prey properties
65 (Brassard et al., 2020c; Neaux et al., 2022; Nogueira et al., 2009).

66 Several previous studies have used three-dimensional (3D) geometric morphometrics to explore
67 the morphological diversity of ancient canids in North America or Russia (Ameen et al., 2017;
68 Drake et al., 2015, 2017; Ledoux and Boudadi-Maligne, 2015; Losey et al., 2022a). Yet, only a
69 few have focused on European Neolithic dogs (Brassard et al., 2022). We previously
70 demonstrate that, in Europe, dogs exhibit an important range of morphological variability in
71 mandible shape and size as early as the Neolithic and Chalcolithic (Brassard et al., 2022). The
72 lower jaw of modern and ancient dogs was found to differ in functionally important areas, possibly
73 reflecting differences in diet, competition, or the implication of ancient dogs in hunting or defense.
74 However, whether and how this diversity in mandible shape is related to specific environmental or
75 anthropogenic factors remains largely unexplored. In southern Romania, a great number of dog
76 remains – especially mandibles – were found in settlements from the Late Chalcolithic Gumelnița
77 culture, dated from *circa* 4,550-3,900 cal. BCE (Bălășescu, 2014; Bălășescu et al., 2005b, 2005a;
78 Lazăr et al., 2016). The chrono-cultural context and subsistence economy of human communities
79 at these sites are well-documented, offering the opportunity to better understand the
80 morphological variability in dogs in Eastern Europe at that time. In particular, the Gumelnița
81 culture is characterized by an important diversity in animal exploitation systems in comparison
82 with preceding Chalcolithic cultures (Bréhard and Bălășescu, 2012). While subsistence
83 economies rely on cattle and sheep/goat husbandry during the Early Chalcolithic, large game
84 played a major role in some communities of the Gumelnița, and a great variability is observed
85 among both the preferentially hunted and reared mammals (i.e., cattle, sheep/goat or pig)
86 species. These differences among Gumelnița communities possibly impacted the diet and role of
87 dogs as well as their morphology. Given that the mandible must resist the forces generated

88 during biting, the consumption and/or hunting of different food items likely imposes different
89 selective pressures on mandible shape that may reflect these different contexts (Karamani et al.,
90 2022; Neaux et al., 2022).

91 In this study we focused on three geographically and chronologically close sites: Hârşova-tell,
92 Borduşani-Popină and Vităneşti-Măgurice (Fig. 1). Despite the fact that these sites all relate to
93 the Gumelniţa culture and are partly contemporary, significant differences in their socio-economic
94 systems have been described previously. Whereas the animal exploitation system mostly relies
95 on husbandry at Borduşani-Popină and Hârşova-tell (although a substantial part of the
96 subsistence was also derived from aquatic resources, *i.e. fish and bivalves*), wild taxa
97 predominate the mammal assemblage (up to 61%) at Vităneşti-Măgurice (Bălăşescu et al.,
98 2005a, 2005b; Bréhard and Bălăşescu, 2012) (Fig. 1, SI 1). The greater importance of hunting
99 activities at Vităneşti-Măgurice, which focused on large game such as red deer, aurochs, wild
100 boar, and wild horse (Fig. 1, SI 1) may have had repercussions on dogs. Indeed, the dogs from
101 Vităneşti-Măgurice were likely more involved in hunting activities, and the proportion of large
102 game in their diet may have been more important. *The lower proportion of dog remains* in the
103 mammal assemblage of Vităneşti-Măgurice compared to Borduşani-Popină and Hârşova-tell (Fig.
104 1; SI 1) supports the assumption that dogs had different roles/tasks. At all sites dog carcasses
105 were, however, skinned, dismembered, and used for consumption as attested by numerous cuts
106 and localized burn marks observed on the bones (Lazăr et al., 2016) (SI 2). In addition,
107 preliminary stable isotope analyses performed on dog bone collagen (Balasse et al., 2017, 2016)
108 suggest differences in diet as attested by the lower stable nitrogen isotope values for the dogs
109 from Vităneşti-Măgurice.

110 To test whether dogs exhibit differences in diet and morphology between Gumelniţa sites
111 characterized by either predominant hunting (Vităneşti-Măgurice) or husbandry (Hârşova-tell and
112 Borduşani-Popină), we used two complementary approaches, stable isotope analyses and
113 geometric morphometrics. *Many studies have explored ancient dogs diet through stable isotope*
114 *analyses in a variety of contexts (e.g. Drake et al., 2017; Grandal-d'Anglade et al., 2019; Laffoon*
115 *et al., 2015; Losey et al., 2022b; Schulting and Richards, 2002). Additionally, as mentioned*
116 *above, 3D geometric morphometrics has been proven to be helpful to describe morphological*
117 *variability in ancient canids/dogs* (Brassard et al., 2022; Drake et al., 2017, 2015; Losey et al.,
118 2022a). *However, stable isotope analyses and GMM are rarely combined in dogs (Drake et al.,*
119 *2017; Losey et al., 2022b). Although* the combination of these approaches can bring new and
120 complementary insights into the adaptation of species to their environment (Balasse et al., 2016;
121 Barberena et al., 2020; Cucchi et al., 2016), in particular by testing the covariation between
122 mandibular morphology and the stable isotope signature. Stable carbon and nitrogen isotope

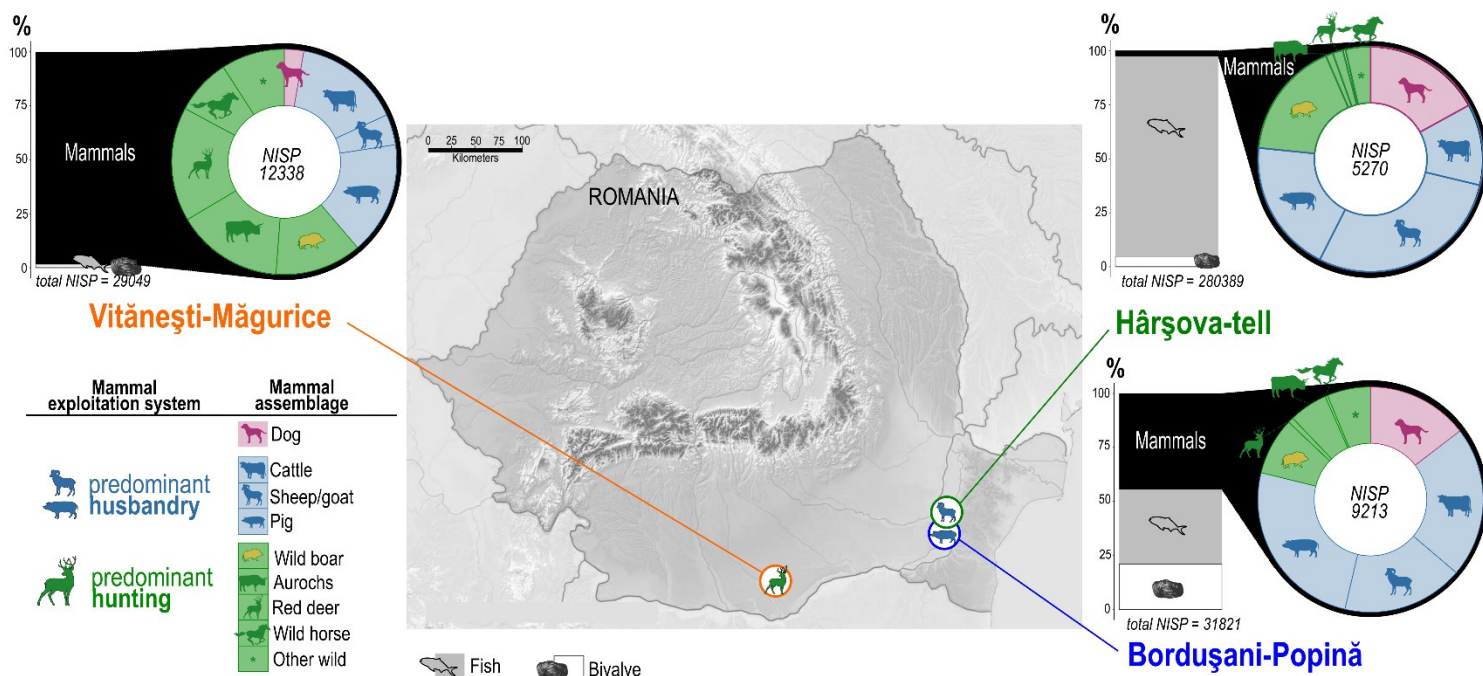
123 ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in bone collagen can be used to test the contribution of different dietary
124 sources, provided that these are isotopically distinct. Previous studies on the faunal remains from
125 Vitănești-Măgurice, Bordușani-Popină and Hârșova-tell showed differences between the $\delta^{13}\text{C}$
126 and $\delta^{15}\text{N}$ values measured in three large animal categories present in the subsistence economy:
127 domestic mammals, wild terrestrial mammals, and fish (Balasse et al., 2017, 2016). At all sites,
128 fish had generally lower $\delta^{13}\text{C}$ values compared to terrestrial fauna and the highest $\delta^{15}\text{N}$ values in
129 the entire food network (in case of piscivorous fish). Moreover, domestic herbivores (cattle and
130 sheep) yielded higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than wild herbivores (aurochs, red deer, roe deer,
131 wild boar and wild horse). Consequently, the respective contribution of these three main items in
132 the diet of dogs can be investigated using their bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

133 In parallel, geometric morphometrics is commonly used to describe bone shape allowing to
134 quantify morphological diversity (e.g. Brassard et al., 2022; Drake et al., 2017, 2015; Losey et al.,
135 2022a). In this study we focused our analyses on the shape of the lower jaw (i.e., the mandible).
136 Not only is it well preserved in archaeological faunal assemblages, but **in modern dogs it has**
137 **been proven to be** informative on the overall shape of the head (Brassard et al., 2020b) and
138 masticatory function through its relation with muscle size and position, and bite force (Brassard et
139 al., 2020a,c). The shape of the mandible is not only determined by genetics but it is also shaped
140 by environmental and anthropogenic constraints (phenotypic plasticity), as previously
141 demonstrated in other taxa (e.g. Anderson et al., 2014; Neaux et al., 2022). By performing
142 geometric morphometrics analyses on all mandibles for which stable isotopic data are available,
143 we can quantitatively test for a link between morphology and diet. This may in turn provide
144 information on the adaptation of contemporary dogs to different living conditions according to the
145 socio-economic system.

146 **Material and methods**

147 *Archaeological sites under study*

148 Hârșova-tell (Constanța County) and Bordușani-Popină (Ialomița County) are located
149 approximately 20 km apart, on the Danube River Plain in South-Eastern Romania. The
150 Bordușani-Popină village was established on the large islands of Balta Ialomiței and Hârșova-tell
151 on the eastern side of the river. Vitănești-Măgurice (Teleorman County) is located **around 250 km**
152 further west, in the Teleorman river floodplain in the middle South of the country.



154 **Fig. 1.** Location of the three Romanian archaeological sites of the Late Chalcolithic Gumelnița
 155 culture considered in this study, with bar and pie charts representing the relative proportion of
 156 mammals and aquatic resources (i.e. fish and bivalves) in the faunal assemblages at each site
 157 (“total NISP”), and of the main taxa identified among the mammal assemblages (see SI 1 for raw
 158 data). The color of each site is used as a color code in the following figures. Different symbols
 159 indicate the main mammal exploitation system. Other wild: roe deer, wild carnivores, and beaver.
 160 NISP: number of identified specimens.

161 *Cultural attribution and dating*

162 In this study, we only considered the animal remains which are related to the Gumelnița
 163 occupation of these settlements. Dogs from these sites are sub-contemporary, since the
 164 Gumelnița occupation is radiocarbon dated to circa 4,500-4,250 cal. BCE at Bordușani-Popină
 165 (Bréhard et al., 2014; Gillis et al., 2013), circa 4,350-4,050 cal. BCE at Hârșova-tell (Bréhard and
 166 Bălășescu, 2012), and circa 4480-4000 cal. BCE at Vitănești-Măgurice (see SI 3).

167 *Socio-economic systems*

168 Important differences in the socio-economic systems exist between the three sites during the
 169 Gumelnița occupation. When considering mammals, the subsistence economy mostly relies on
 170 husbandry at Bordușani-Popină and Hârșova-tell with 79% and 77% of the identified mammal
 171 remains being domestic (Fig. 1, SI 1). At Bordușani-Popină, domestic pigs predominate the
 172 number of remains, followed by domestic cattle, sheep/goats, and dogs (see synthesis in

173 (Bréhard and Bălăşescu, 2012)) (SI 1). At Hârşova-tell, domestic sheep/goats dominate during
174 the Gumelniţa occupation, followed by domestic pigs, dogs, and cattle. In contrast, at Vităneşti-
175 Măgurice, hunting was very important during the Gumelniţa: wild taxa, mostly red deer, aurochs,
176 wild boar, and wild horses, represent 61% of the mammal remains (Fig. 1, SI 1). Moreover,
177 aquatic resources were collected in large quantities during the Gumelniţa at Hârşova-tell and
178 Borduşani-Popină. Based on the **total** number of identified specimens (**total** NISP), fish represent
179 93% and 34% of the **total** archaeozoological remains, respectively, bivalves represent 5% and
180 21%, and mammals 2% and **45%** (Bălăşescu et al., 2005b) (Fig. 1). At Vităneşti-Măgurice, these
181 resources probably played a less important role as fish remains represent less than 1%, bivalves
182 1%, and mammals 98% of the remains. The very low **relative** proportion of fish at this site should,
183 however, be taken with caution as sediments have not been sieved **during excavations at this**
184 **site, contrary to Hârşova-tell and Borduşani-Popină.**

185 The **relative** proportion of dog **remains** is very high in the faunal assemblages of Borduşani-
186 Popină and Hârşova-tell during the Gumelniţa occupation (15% and 17% of mammal remains,
187 respectively), compared to Vităneşti-Măgurice (3%; Fig. 1, SI 1). At the three sites, dog bones are
188 fragmented and were found mixed with bones from other taxa in areas of household refuse.
189 Numerous cuts and localized burn marks were observed on dog bones, attesting that carcasses
190 were skinned and dismembered, and that the meat was eaten (Lazăr et al., 2016) (SI 2).

191 **Clear evidence of bone gnawing by dogs (or other carnivores) and pigs has been described at**
192 **the three sites (the number of bones gnawed ranges from 8% to 18% of the total mammal**
193 **remains, Bălăşescu unpublished), proving that dogs had access to carcasses at the three**
194 **settlements.**

195 *Material*

196 The study material used for the shape analysis is composed of 77, 46, and 27 dog (*Canis*
197 *familiaris*) mandibles from Borduşani-Popină, Hârşova-tell, and Vităneşti-Măgurice respectively
198 (see details about the sample in SI 4). **For preliminary comparison of mandible sizes, we also**
199 **considered mandibles of modern (n=8) and ancient wolves (n=7, including 3 from Vităneşti-**
200 **Măgurice) that were previously studied in Brassard et al. (2022).** Dogs were **primarily**
201 distinguished from wolves based on their **mandibular** size (see Brassard et al., 2022; see SI 6).
202 To limit the effect of ontogeny, only **dentally mature** specimens with the first molar completely
203 erupted were considered for geometric morphometric analyses. Among those, a subsample of 19
204 dogs from Borduşani-Popină, 17 dogs from Hârşova-tell, and 26 dogs as well as two foxes
205 (*Vulpes vulpes*) and three wolves (*Canis lupus*) from Vităneşti-Măgurice were selected for stable
206 isotope analysis. These newly acquired data complement previously published data from five dog

207 mandibles from each site (Balasse et al., 2016). Right and left mandibles were included to
208 increase the sample. At each site, we checked that they belong to different individuals (**Minimum**
209 **Number of Individuals**) by visually examining the global morphology, and by comparing the 3D
210 models and stable isotope signatures.

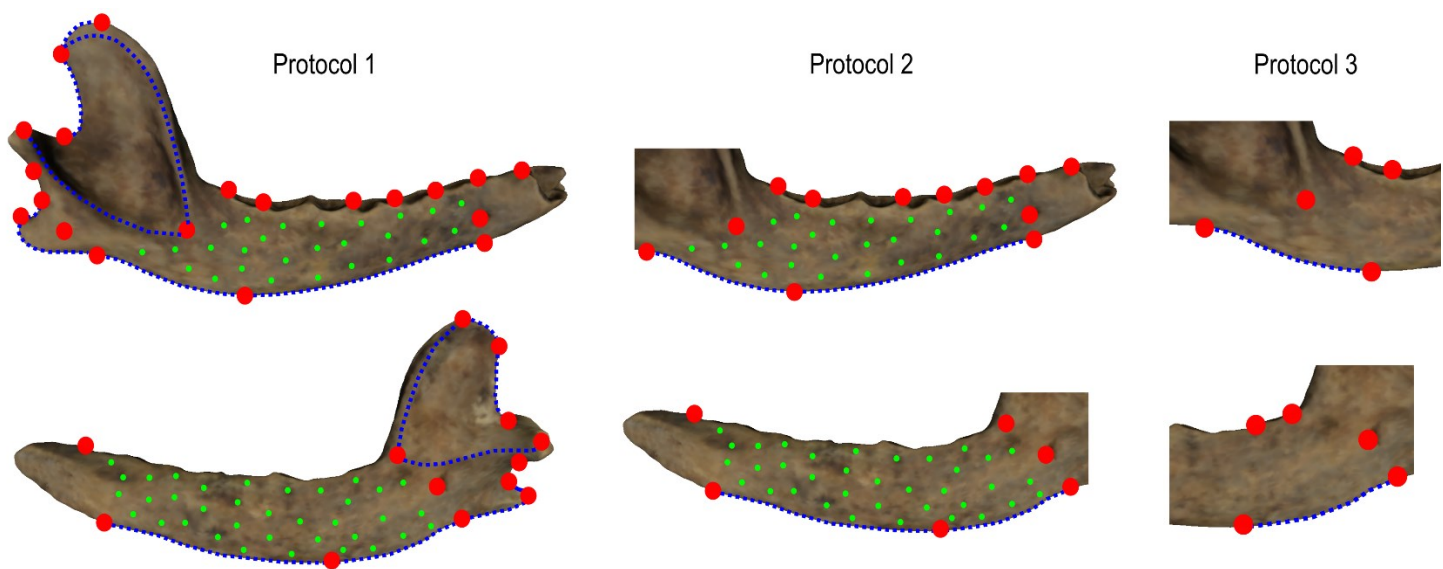
211 *Bone collagen extraction and stable isotope analysis*

212 Bone was sampled by sawing. After bone external surfaces and the spongiosa were removed by
213 drilling, the bone was mechanically reduced to powder and only the 355-710 micrometer fraction
214 was used for collagen extraction. Collagen was extracted from about 200-300 mg of this powder
215 following the procedure described by Bocherens et al. (1991), except for the final solubilization
216 step which was performed at 70°C. Coupled measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were
217 conducted on approximately 350 micrograms of collagen on an elemental analyzer (Thermo
218 Flash 2000) interfaced to a Thermo DeltaV Advantage IRMS. The analytical precision, determined
219 by six to 12 analyses of our laboratory standard (alanine) within each run, varied from 0.05‰ to
220 0.14‰ for $\delta^{13}\text{C}$ and from 0.10‰ to 0.16‰ for $\delta^{15}\text{N}$, and from 0.20% to 0.35% for C content and
221 from 0.07% to 0.13% for N content. Over the course of the analyses the alanine standard gave
222 mean values of $+0.75 \pm 0.13\text{‰}$ for $\delta^{15}\text{N}$ (N =40, expected value = $+0.59\text{‰}$), $-21.57 \pm 0.17\text{‰}$ for
223 $\delta^{13}\text{C}$ (n=30, expected value = -22.16‰), $15.60 \pm 0.19\%$ for N content (N = 24, expected value =
224 15.72%) and $40.36 \pm 0.59\%$ for C content (expected value = 40.44%). **The stable isotope ratios**
225 **were corrected accordingly using the Marbre LM average values for each analysis session.** We
226 compared the $\delta^{15}\text{N}$ values of dogs between the three sites using a Wilcoxon-Mann Whitney rank
227 test. At each site, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values measured in dogs were further compared to those
228 previously measured in the associated fauna to provide broad guidance on the composition of the
229 diet in dogs. Yet, this does not allow to account for the relative weight of the different isotopic
230 items. Data from Borduşani-Popină and Hârşova-tell were considered together as the $\delta^{15}\text{N}$ and
231 $\delta^{13}\text{C}$ values measured in the different species at both sites do not differ significantly (Balasse et
232 al., 2017).

233 *3D modelling of mandibles and geometric morphometric analyses*

234 Three-dimensional numeric models of the mandibles were obtained using photogrammetry. One
235 hundred photographs were taken from different angles while turning around the bone. The photos
236 were aligned using 'Agisoft PhotoScan' (©2014 Agisoft LLC, St Petersburg, Russia). Where
237 needed, the models were repaired (windows corresponding to extractions for DNA samples were
238 filled in), cleaned, simplified, and mirrored (all mandibles were transformed into a 'right' mandible)
239 using © 'Geomagic Wrap' 2013.0.1.1206 and 'MeshLab' v 2020.03 (Cignoni et al., 2008).

240 Three-dimensional landmarks were placed on the 3D models using the ‘Landmark’ software,
241 version 3.0.0.6 (©IDAV 2002-2005) (Wiley et al., 2005). Three landmarking protocols were
242 considered based on the fragmentation of the material (Fig. 2, sample sizes for each protocol are
243 reported in Table 1; see SI 4 for a listing of the mandibles included in each protocol). The first
244 protocol is the most representative of the overall shape of the mandible, with a total of 388
245 landmarks (including 23 anatomical landmarks, 190 sliding semi-landmarks on curves, and 175
246 sliding semi-landmarks on the surface). Yet, whereas this protocol represents the sites of
247 Bordușani-Popină and Hârșova-tell well, the mandibles from Vitănești-Măgurice are mostly too
248 fragmented to be included in the analyses with this protocol (n=2). To provide better comparisons
249 with dogs from Vitănești-Măgurice, we used two other protocols adapted to fragmented
250 mandibles. The second protocol is the most representative of the shape of the mandibular body,
251 with a total of 121 landmarks (including 14 anatomical landmarks, 40 sliding semi-landmarks on
252 curves, and 67 sliding semi-landmarks on the surface). It allows to increase the sample size for
253 Vitănești-Măgurice (n=14), and thus to consider this site. The third protocol is a subsample of the
254 first protocol and only represents a very small part of the mandibular body at the junction with the
255 mandibular ramus (involving only six anatomical landmarks and 20 sliding semi-landmarks on
256 curves). This last protocol is less representative of the overall shape of the mandible, but allows
257 to incorporate more mandibles in the analyses (n=150), in particular mandibles from Vitănești-
258 Măgurice which are often fragmented (n=27, see sample details in Table 1).



260 **Fig. 2.** Landmarking protocols according to the different fragmentation patterns. Different types of
261 landmarks are represented by different colors: anatomical landmarks are in red, sliding semi-
262 landmarks on curves are in blue, sliding semi-landmarks on surfaces are in green. Sample sizes
263 for each protocol are reported in Table 1.

264 All statistical analyses were run in 'R' version 4.0.0 (2020-04-24) (R Core Team, 2021). The
265 sliding semi-landmarks were slid and transformed into spatially homologous landmarks using a
266 sliding semi-landmark procedure minimizing the overall bending energy, implemented in the
267 'Morpho' package (version 2.9) in R (Schlager, 2013). To decompose the mandible form into
268 centroid size (a proxy of the overall size of the object) and shape (which represents the
269 proportions based on the differences between the different landmarks), we performed a
270 Generalized Procrustes analyses (GPA) (Goodall, 1991) using the function 'procSym' (Dryden
271 and Mardia, 2016; Gunz et al., 2005; Klingenberg et al., 2002) from the package 'Morpho'. A well-
272 preserved mandible was warped to the consensus of the GPA using thin-plate spline deformation
273 for all further visualizations (Klingenberg, 2013).

274 To test for differences in mean mandible centroid size, we performed ANOVAs using the function
275 'aov'. To compare morphological disparity (i.e. variability) in mandible shape between sites we
276 performed a disparity test using the function 'morphol.disparity(coords ~ 1, groups= ~ site, iter =
277 999)' in the package 'geomorph' (Foote, 1993; Zelditch et al., 2012). This function estimates the
278 morphological disparity for each group (which is the Procrustes variance within each group
279 without covariates and using the overall mean of the sample, the value being adjusted by the
280 sample size for each group) and performs pairwise comparisons to identify differences among
281 groups. To test for differences in mean mandible shape, we performed Procrustes ANOVAs and
282 post-hoc tests, using the functions 'procD.lm(coords~site, iter=999)' and 'pairwise', respectively
283 (Adams and Collyer, 2017, 2016; Anderson and Braak, 2003; Anderson, 2001; Collyer et al.,
284 2015; Goodall, 1991). Differences between sites were visualized using Canonical Variate
285 Analysis (CVA), which maximizes among-group variances relative to within-group variances
286 (Campbell and Atchley, 1981; Klingenberg and Monteiro, 2005). CVA was performed on the
287 scores of the first Principal Components to reduce the number of variables (representing 97% of
288 the total variability in shape). To visualize shape deformations along the canonical axes, we
289 calculated the theoretical minimum and maximum shapes for each axis, and visualized the
290 deformation from the mean shape of the total sample towards these theoretical shapes (for
291 visualization purposes deformations were amplified by a factor 2) using functions 'restoreShapes'
292 and 'plotRefToTarget'. Considering that the effectiveness of the CVA to discriminate groups is
293 strongly dependent on the ratio between the number of variables and sample size (Mitteroecker
294 and Bookstein, 2011) we also performed k-Nearest Neighbour Classification (k-NN) with a leave-
295 one-out cross validation (using function 'knn.cv' from package 'class') (Ripley, 1996; Venables et
296 al., 2002). k-NN is a non-parametric method that classifies an individual according to the a priori
297 classification of its k neighbors (by Euclidean distance) using a majority vote. KNN is less
298 sensitive to number of variables with respect to the sample size than the CVA. The k was
299 determined using function knn.cv: we kept the k which led to the best cross-validation rate.

300 Considering that the leave-one out procedure leads to different results each time the analyses
301 are conducted, the results have to be considered as an approximate success rate.

302 We tested the relationship between isotopic signature ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and morphometric data
303 (mandible shape) for a subsample of mandibles for which we had both types of data (sample size
304 for each protocol is reported in Fig. 4). We explored the patterns of covariation between the two
305 datasets using a Two-Block Partial Least Square regression (2B-PLS), using the function 'pls2B'
306 (Rohlf and Corti, 2000). P-values were calculated based on 1000 permutations. Visualisation at
307 the minimum or maximum of the PLS axis was obtained using the functions 'plsCoVar', 'tps3d'
308 and 'deformGrid3D'.

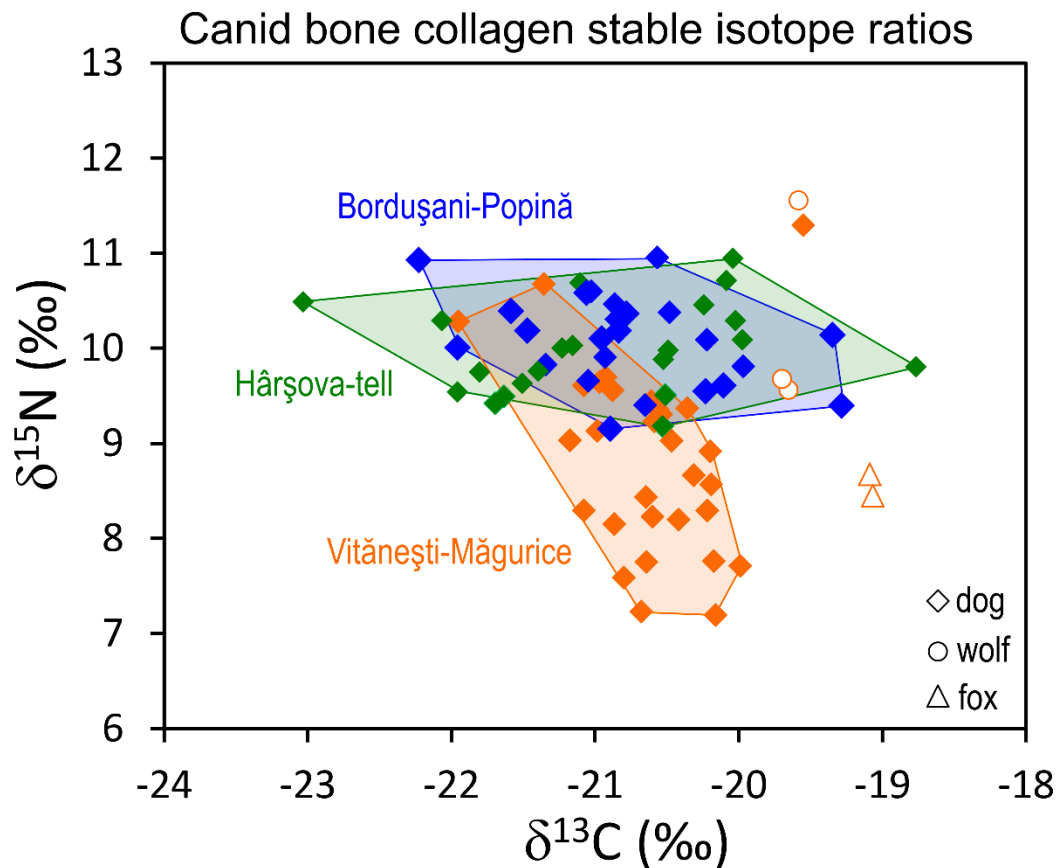
309 **Results**

310 *Bone collagen stable isotope analysis*

311 Of the 67 bone powders, only one from Hârşova-tell (Har3) was lost due to complete dissolution
312 during the initial demineralisation step with 1M HCl. One specimen from Vităneşti-Măgurice
313 (Vit12) also had an unusual sandy aspect after freeze-drying and low C and N contents (13.8%
314 and 5.0% respectively) and was excluded from the final dataset. Collagen extraction yielded an
315 average of 71 mg/g at Borduşani-Popină (27 to 123 mg/g), 99 mg/g at Hârşova-tell (64 to 124
316 mg/g), and 82 mg/g at Vităneşti-Măgurice (23 to 127 mg/g) (SI 4). Carbon contents vary from
317 31% to 44%, nitrogen contents from 12% to 16% and atomic C:N ratios from 3.12 to 3.28,
318 satisfying the criteria defined for reliable stable carbon and nitrogen isotope ratios (Ambrose,
319 1990; DeNiro, 1985; Guiry and Szpak, 2021).

320 The distribution of stable isotope values in dogs from the three sites are shown in Fig. 3 and
321 reported in SI 4. Dogs $\delta^{13}\text{C}$ values overlap at the three sites, ranging from -23.0‰ to -18.8‰.
322 However, the dispersion in $\delta^{13}\text{C}$ values measured in dogs is considerably reduced at Vităneşti-
323 Măgurice (coefficient of variation $\delta = 0.46\%$; from -21.2‰ and -20‰), compared to Borduşani-
324 Popină ($\delta = 0.70\%$; -22.2‰ to -19.3‰) and Hârşova-tell ($\delta = 0.96\%$; -23‰ to -18.8‰). At
325 Borduşani-Popină and Hârşova-tell, dog $\delta^{15}\text{N}$ values vary within the same range (9.2‰ to
326 10.9‰). In contrast, the dogs from Vităneşti-Măgurice show a larger range (7.2‰ to 11.3‰) and
327 globally lower $\delta^{15}\text{N}$ values, with a majority of them (14/25 or 56%) below the lowest values
328 measured at Borduşani-Popină and Hârşova-tell (<9.2‰). When considering this new dataset
329 with previously published data for dogs at the three sites (Balasse et al., 2016), the $\delta^{15}\text{N}$ values
330 measured in the dogs from Vităneşti-Măgurice are significantly lower than those measured at
331 Borduşani-Popină and Hârşova-tell considered together (Wilcoxon-Mann Whitney rank T-test, $W =$
332 168.5, $p = 4.10 \cdot 10^{-8}$). The two foxes at Vităneşti-Măgurice have higher $\delta^{13}\text{C}$ values compared to dogs

333 (-19.1‰ each) and rather low $\delta^{15}\text{N}$ values (8.5‰ and 8.7‰), reflecting the significant contribution
 334 of fruits to their diet (Castañeda et al., 2020; Cavallini and Volpi, 1996). At Vitănești-Măgurice, the
 335 three wolves have $\delta^{15}\text{N}$ values of 9.6‰ to 11.6‰, among the highest within terrestrial vertebrates
 336 at this site. It is noteworthy that one dog from Vitănești-Măgurice (Vit38) differs from its
 337 counterparts at this site with higher values of $\delta^{13}\text{C}$ (-19.6‰) and $\delta^{15}\text{N}$ (11.3‰), more similar to
 338 those measured in one wolf, yet it is clearly a dog according to its mandibular size (Brassard et
 339 al., 2022).

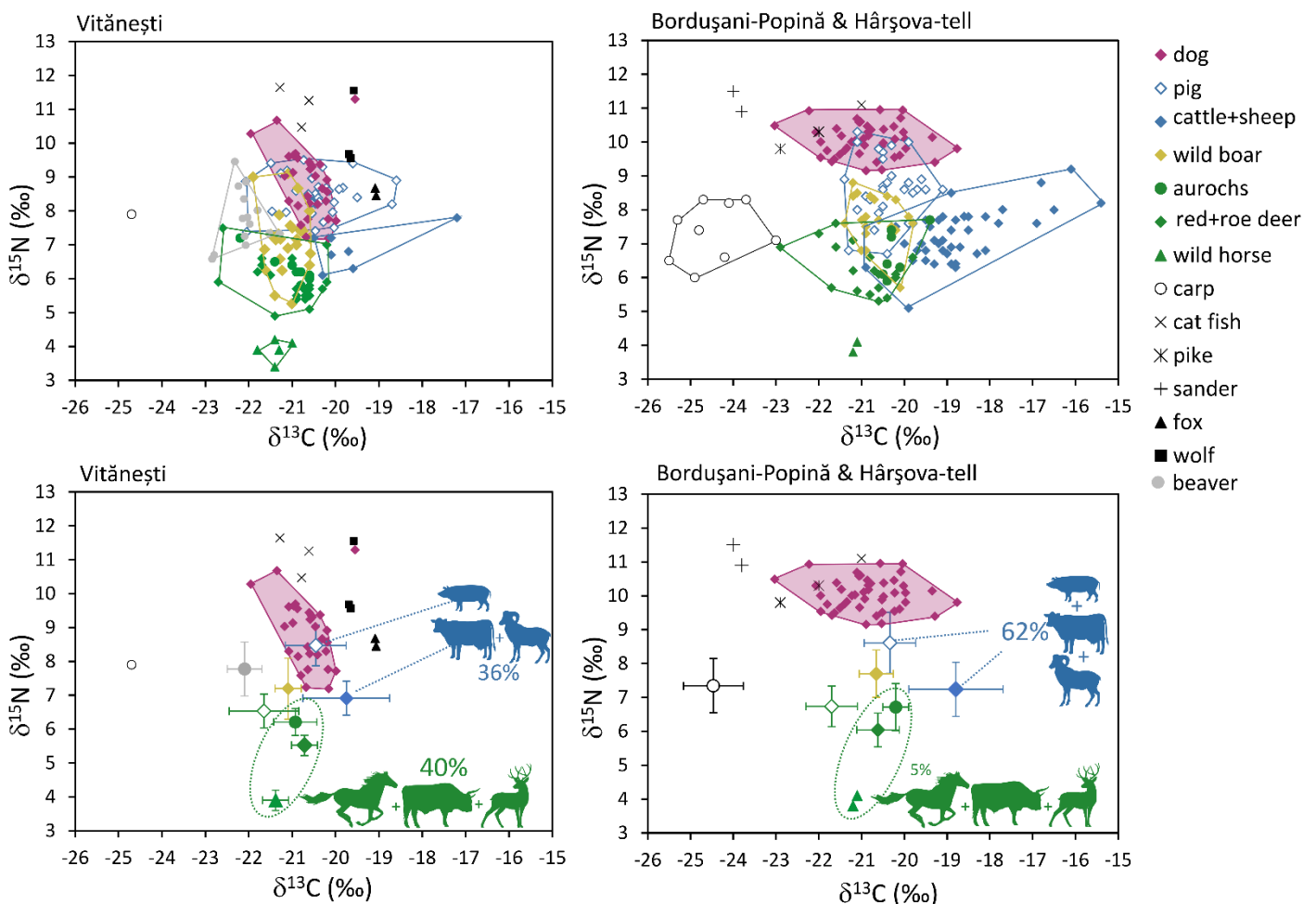


340

341 **Fig. 3.** Results from stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis in canid bone
 342 collagen from Bordușani-Popină ($n=24$), Hârșova-tell ($n=21$) and Vitănești-Măgurice (dogs = 31,
 343 wolves = 3 and foxes = 2). The dataset includes the data previously published in (Balasse et al.,
 344 2016).

345 When $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of dogs are compared to those of the associated fauna (Fig. 4) we
 346 observe that, at the three sites, dogs occupy the highest place in the terrestrial food web: they
 347 show the highest $\delta^{15}\text{N}$ values, only being surpassed by the wolf at Vitănești-Măgurice. This place
 348 is shared with the pigs at Vitănești-Măgurice, and to a lower extent at Bordușani-Popină and
 349 Hârșova-tell. Most $\delta^{15}\text{N}$ values measured in Vitănești-Măgurice for wild and domestic herbivores
 350 do not differ significantly from those measured at Bordușani-Popină and Hârșova-tell (SI 5)

351 except for the red deer, which shows slightly lower values at Vitănești-Măgurice ($\delta^{15}\text{N} = 5.5 \pm 0.3$,
 352 versus 6.0 ± 0.5 at Bordușani-Popină and Hârșova-tell). More significantly, at the three sites,
 353 globally lower $\delta^{15}\text{N}$ values are measured in large wild herbivores (red deer, aurochs and wild
 354 horse) compared to domestic animals (cattle, sheep and pig) (Fig. 4). In particular, the wild horse
 355 yielded the lowest $\delta^{15}\text{N}$ values of the dataset (average: 3.9‰ and 4‰ respectively at Vitănești-
 356 Măgurice and Bordușani-Popină - Hârșova-tell). Moreover, at Bordușani-Popină and Hârșova-tell,
 357 the global faunal spectrum occupies a wide range of $\delta^{13}\text{C}$ values (-25.5‰ to -15.4‰), including
 358 two sources of primary importance in the human subsistence: aquatic resources (pelagic fish;
 359 carp in particular) contributing with the lowest $\delta^{13}\text{C}$ values and cattle and sheep with the highest
 360 $\delta^{13}\text{C}$ values (Fig. 4). The $\delta^{13}\text{C}$ values measured in dogs are intermediate.



362 **Fig. 4.** Comparison between the stable carbon ($\delta^{13}\text{C}$) and nitrogen isotope values ($\delta^{15}\text{N}$)
 363 measured in dog bone collagen with the values previously measured in other species from the
 364 same assemblages (Balasse et al., 2017, 2016). A: Projection of all data. B: Average value of
 365 stable isotopes data per group for all species except dogs, and the relative proportion of each

366 group in the mammal assemblages (in % of NISP; cf. Fig. 1). Detailed results for each specimen
 367 are reported in SI 4.

368 **Morphological differences between dogs from different sites**

369 For each of the protocols, no significant differences in size were evidenced between sites (Table
 370 1). Based on protocol 3 dog mandibles are much smaller and do not overlap those of modern and
 371 ancient wolves for all three sites (SI 6).

372 **Table 1.** Results of the analyses to compare mandible shape and size between sites. BOR:
 373 Bordușani-Popină; HAR: Hârșova-tell; VIT: Vitănești-Măgurice; P: p-value; R² coefficient of
 374 determination; CV: success rate of the cross-validation; n PC: number of principal components
 375 considered in analyses; PV: Procrustes variance. Significant differences are in bold.

		Protocol 1	Protocol 2	Protocol 3
Sample size		28 BOR, 14 HAR, 2 VIT	66 BOR, 35 HAR, 14 VIT	77 BOR, 46 HAR, 27 VIT
Morphological disparity			p>0.08	p(HAR-VIT) 0.034
		p(BOR-VIT) 0.040	p(BOR-VIT) 0.080	p(BOR-VIT) 0.031
		PV _{HAR} 0.0036	PV _{HAR} 0.0044	PV _{HAR} 0.0098
		PV _{BOR} 0.0034	PV _{BOR} 0.0044	PV _{BOR} 0.010
		PV _{VIT} 0.0059	PV _{VIT} 0.0062	PV _{VIT} 0.017
Difference in mean shape (Procrustes ANOVA)		P = 0.001, R ² = 0.12	P < 0.001, R ² = 0.063	P < 0.001, R ² = 0.12
		HAR-BOR 0.005	HAR-BOR 0.008	HAR-BOR 0.003
		HAR-VIT 0.005	HAR-VIT 0.10	HAR-VIT 0.009
		BOR-VIT 0.001	BOR-VIT 0.001	BOR-VIT 0.001
Difference in mean size (ANOVA)		P=0.3	P=0.14	P=0.8
KNN (set.seed(100))	k	8	8	6
	CV	82% BOR	74% BOR	75% BOR
		29% HAR	34% HAR	37% HAR
		100% VIT	14% VIT	19% VIT
CVA - PCA 97% of	n PC	PC 1 to 28	PC 1 to 25	PC 1 to 9

var

CV	100% BOR	89% BOR	81% BOR
	100% HAR	69% HAR	46% HAR
	100% VIT	86% VIT	44% VIT

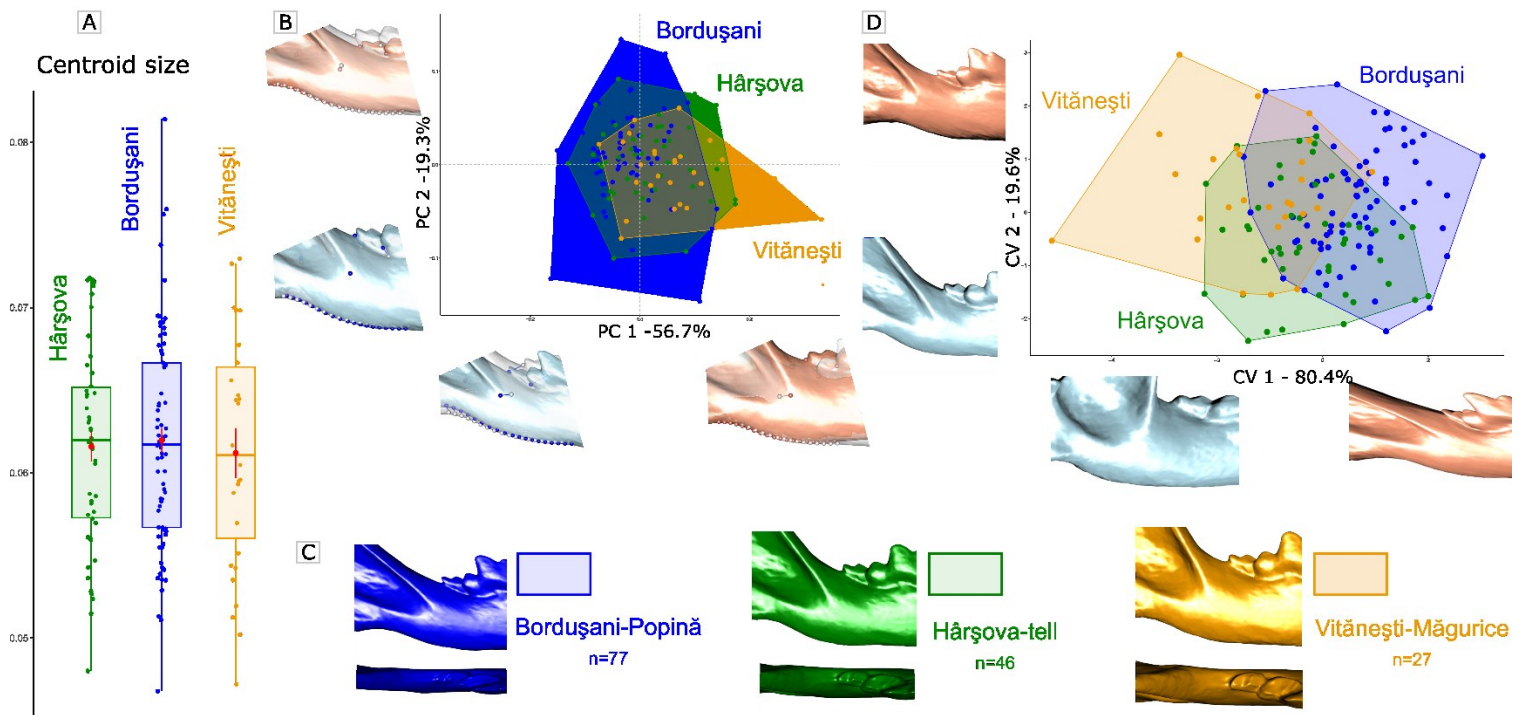
376

377 Analyses conducted with the smallest fragment (protocol 3) revealed, in spite of the small portion
378 of mandible that it represents, that dogs from Vitănești-Măgurice have slightly more variable
379 mandible shapes compared to dogs from the two other sites, and that the dogs of the three sites
380 significantly differ in the mean mandible shape. The most important shape differences are
381 between the dogs from Vitănești-Măgurice and those from Bordușani-Popină according to the
382 Procrustes ANOVAs (Table 1), which is observable on the scatterplot representing the two first
383 principal components. Some dogs from Vitănești-Măgurice have very high PC1 scores compared
384 to the other dogs of our sample, and as such they are in a part of the scatterplot not occupied by
385 dogs from Bordușani-Popină and Hârșova-tell (Fig. 5B). These dogs (which distinguish along
386 PC1 in Fig. 5B and along CV1 in Fig. 5C) are characterized by a **relatively** more robust mandible.
387 The rates of good classification in CVA and KNN are rather low (Table 1) due to strong overlap
388 between sites. This is not surprising considering the reduced nature of this fragment, which is
389 unlikely to reflect the total variation in mandible shape.

390 Analyses performed with the complete mandibular body (protocol 2; SI 6) also support the
391 existence of shape differences between sites, with dogs in Vitănești-Măgurice having **relatively**
392 more robust mandibles with a taller mandibular body. The rates of good classification are
393 approximately the same for the KNN classification than for analyses with the smallest fragment.
394 The description of the anatomical particularities of the dogs from Vitănești-Măgurice is supported
395 by the visualizations made with the complete mandibles (protocol 1): the two robust mandibles
396 from Vitănești-Măgurice, with a tall, large and backwardly inclined coronoid process, are clearly
397 distinguishable from those from the two other sites on the right part of the PCA and along CV2 (SI
398 7). Additionally, analyses conducted with the complete mandibles show significant differences in
399 the mean mandible shape between dogs from Hârșova-tell and Bordușani-Popină (n=14 and
400 n=28, respectively).

401 According to the first axis of the CVA based on protocol 1 (SI 7), dogs from Bordușani-Popină
402 have a taller mandibular body than in Hârșova-tell, with a ventral border of the mandibular body
403 being more regularly curved; the coronoid process is more vertical and smaller, and the angular
404 process is lower and larger. In dogs from Hârșova-tell, there is a pronounced curvature right

405 under the carnassial tooth and the body goes straight upwards. Moreover, the coronoid process
 406 is oriented more backwards and is taller. The anatomical differences between dogs from
 407 Hârșova-tell and Bordușani-Popină are confirmed by analyses performed with protocols 2 and 3
 408 (SI 6 and Fig. 5, respectively). For all protocols, the rates of good classification with the KNN
 409 method are similar and rather low, in particular for Hârșova-tell and Vitănești-Măgurice. This
 410 relatively low success rate suggests an important overlap between the three sites: only the most
 411 extreme shapes (mainly in Vitănești-Măgurice for protocol 2 and Bordușani-Popină for protocol 3)
 412 can be attributed with success to a site.



414 **Fig. 5.** Variability in mandible form in dogs from the Gumelnița culture and differences between
 415 the three sites, based on results from protocol 3. Dogs of the three sites (77 from Bordușani-
 416 Popină, 46 from Hârșova-tell and 27 from Vitănești-Măgurice) are indicated by different colors.
 417 (A) Boxplots of the centroid size. *See SI 6 for size comparison with modern and ancient wolves.*
 418 (B) Principal Component Analysis on mandible shape. The theoretical shapes at the minimum and
 419 maximum of the PC axes (in blue and pink, respectively) are superimposed on the mean shape
 420 (white) and the vectors of deformation are reported. (C) Mean shapes for each site. (D)
 421 Canonical Variate Analysis on mandible shape. Theoretical shapes at the minimum and maximum
 422 of the CV axes are represented in blue and pink, respectively (the deformations from the mean
 423 shape are amplified by a factor 2). Results for protocols 1 and 2 are reported in the
 424 supplementary material, SI 7 and 8, respectively.

425

426 **Relationship between stable isotope data and mandibular morphology**

427 Significant covariations between mandible shape and stable isotope ratios are observed (Fig. 6).

428 The results are statistically significant only for the protocols 2 and 3, which allow to conduct
429 analyses on a sufficiently high sample size (Fig. 6B,C). The covariations are mostly driven by

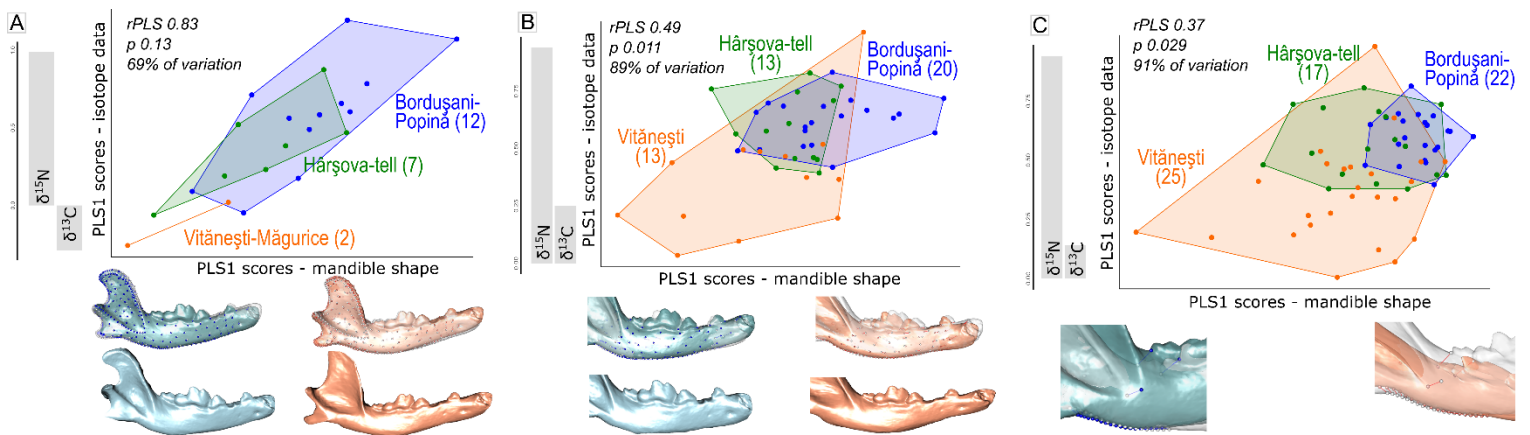
430 $\delta^{15}\text{N}$ values. Dogs with high $\delta^{15}\text{N}$ values (at the top right of the scatter plots), mostly from
431 Borduşani-Popină and to a lesser extent from Hârşova-tell, are associated with slender

432 mandibles with a smaller but more ventrally curved mandibular body. The bottom left of the
433 scatterplot, only represented by specimens from Vităneşti-Măgurice in protocols 2 and 3,

434 associates dogs with low $\delta^{15}\text{N}$ values and robust mandibles with a tall mandibular body (Fig.

435 6B,C). Dogs from Vităneşti-Măgurice are distributed throughout the scatterplot, whereas dogs

436 from the two other sites are only present towards the top right for protocols 2 and 3.



438 **Fig. 6.** Visualization of relationships between mandible shape and isotope data based on the 2-
439 Block Partial Least Square Analysis performed using protocols 1 (A), 2 (B), and 3 (C). Vectors of
440 isotope data ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and shapes at the minimum and maximum of the PLS axis are
441 represented. Top illustrations represent the deformations from the consensus to the extreme of
442 the axis with the vectors of deformation in lateral view. Illustrations represent the shape at the
443 extreme of the axis (amplified by a factor 2). The different sites are indicated by different colors.

444 **Discussion**

445 *Reconstructing the diet of dogs at Borduşani-Popină, Hârşova-tell and Vităneşti-Măgurice*

446 The results from the stable isotope analyses demonstrate that at all sites dogs are positioned at
447 the top of the food chain. However, we observed some differences between the dogs from
448 Vităneşti-Măgurice and those from the two other sites, which are partly due to the animal

449 subsistence economy based on the hunting of large game at Vitănești-Măgurice (Fig. 1, SI 1 for
450 details). Among the large game recovered, red deer (16% of the total remains and the best
451 represented wild herbivore at Vitănești-Măgurice, versus only 6/2% at Bordușani-Popină
452 /Hârșova-tell) and wild horses (8% of the mammal remains versus less than 1% at Bordușani-
453 Popină and Hârșova-tell) are well represented. Their lower $\delta^{15}\text{N}$ values compared to domestic
454 livestock, and the fact that they may potentially have contributed more to the diet of dogs, could
455 partly explain why the dogs have lower $\delta^{15}\text{N}$ values at Vitănești-Măgurice compared to
456 Bordușani-Popină and Hârșova-tell. Additionally, at Vitănești-Măgurice, higher $\delta^{15}\text{N}$ values were
457 measured in wolves compared to dogs, suggesting a difference in diet composition. Whereas this
458 may not necessarily be in terms of the nature of the prey it may imply differences in the relative
459 proportions of prey with a lower proportion of large herbivores (aurochs and horse) in the diet of
460 wolves. These species were targeted by the human community and therefore more readily
461 available to the dogs at this site. The larger variation in $\delta^{13}\text{C}$ values in dogs from Bordușani-
462 Popină and Hârșova-tell compared to Vitănești-Măgurice reflects the contribution of a diversity of
463 resources to the diet of dogs rather than being specialized in one specific source (aquatic
464 resources/protein from domestic stock). Yet, this also reflects greater interindividual variability in
465 dog feeding behavior at these two sites with a more significant contribution of fish in the dogs with
466 the lowest values (-22.2‰ and -23‰) and a higher contribution of domestic cattle or sheep
467 protein in the dogs showing the highest values (-19.3‰ to -19.8‰). It is possible that the dogs
468 from these sites had more autonomy (commensal lifestyle), resulting in a more varied diet. At
469 Vitănești-Măgurice, the reduced range in $\delta^{13}\text{C}$ values reflects again a higher specialization in the
470 consumption of protein from large game (Fig. 4). Interestingly, although dogs and pigs hold a
471 similar position at the top of the food chain at Vitănești-Măgurice, possibly due to the
472 consumption of human food waste by pigs (Balasse et al., 2016), the greater range in $\delta^{13}\text{C}$ values
473 in pigs and a trend towards higher values suggest that some of the pigs clearly fed on a higher
474 proportion of domestic animal protein compared to dogs, which were more specialized in large
475 game.

476 *Morphological variability in relation to diet*

477 While the dogs from Vitănești-Măgurice had a diet more specialized in large game (especially
478 wild horse and red deer as demonstrated by their lower $\delta^{15}\text{N}$ values and lower variability in $\delta^{13}\text{C}$
479 values), they also had **relatively** more robust mandibles (**but of similar sizes**) resulting in strong
480 differences in the mean mandible shape compared to the two other sites (Fig. 5; Table 1). These
481 morphological differences may be explained, at least partly, by different functional constraints
482 imposed by the need to produce high bite forces at wide angles of jaw opening needed to crack
483 bones of large mammals (Brassard et al., 2021, 2020a, 2020c; Turnbull, 1970). The link between

484 anatomical traits and diet is supported by the significant and strong covariation between mandible
485 shape and isotopic signature. The visualization of shape deformation along the covariation axis
486 (Fig. 6) shows that dogs with lower $\delta^{15}\text{N}$ values present **relatively** more robust mandibles and with
487 anatomical features (taller mandibular body) that suggest a greater importance of the temporal
488 muscle (Turnbull, 1970). This muscle is particularly solicited to produce force at wide gape
489 angles. Hence, the more powerful jaws of the dogs from Vitănești-Măgurice could have provided
490 them with a selective advantage both during the hunting of large game and while breaking their
491 bony remains.

492 The higher $\delta^{15}\text{N}$ values observed in dogs from Hârșova-tell and Bordușani-Popină suggest that
493 they mostly fed on herded mammals (pig, sheep and cattle) of globally smaller size. Moreover,
494 the greater variability in the diet in dogs from Hârșova-tell and Bordușani-Popină is accompanied
495 by a reduced variability in mandible shape, likely because the consumption of fish does not exert
496 strong mechanical constraints on the jaw. The observed generalist morphologies at these sites
497 thus reflect the ability of these animals to cope with a diverse but not mechanically demanding
498 diet. In addition, the mandibular morphology of dogs at Vitănești-Măgurice tends to be more
499 variable than at Hârșova-tell and Bordușani-Popină, paralleling the greater variability in $\delta^{15}\text{N}$
500 values at this site. Along with the specialization towards large wild mammals (suggested by the
501 lower variability in $\delta^{13}\text{C}$), this may illustrate the variability in the proportion of wild horse/red
502 deer/aurochs in the diet of different dogs with dogs consuming more wild horse having the lowest
503 isotopic values and the **relatively** most robust mandibles. This may suggest that different dogs
504 were used to hunt different prey or that dogs had different roles or diets depending on their sex,
505 for example. It is also possible that the preferentially hunted species varied through the five
506 centuries of the Gumelnița occupation of the site; **however**, our dog sample size is too small to
507 test this hypothesis.

508 **Given that** dogs are **present in lower proportion** in human food refuse at Vitănești-Măgurice
509 **compared to the two other sites (Fig. 1), we propose that dogs may have accompanied humans**
510 **in hunting activities rather than being only a food resource.** The morphology of the dogs from
511 Vitănești-Măgurice could therefore be the result of either voluntary selection by humans for
512 certain morphologies of interest for hunting. Alternatively, involuntary selection by an adaptation
513 to the way of life and the resources available could have shaped the mandibles of these dogs
514 (the dogs could have fed on hunted prey as well as leftovers from carcass processing and human
515 food scraps of mostly wild large mammals). It is also possible that these dogs, if they were used
516 for hunting, were fed by humans with hunting leftovers to encourage them (e.g. Laporte, 2021;
517 Plata et al., 2019), favouring the **involuntary** selection of robust **jaws**. **Yet, the small size of the**
518 **dogs (by comparison to modern or ancient wolves, see SI 6) makes it unlikely that they had the**

519 physical ability to catch and kill such large prey (in line with the hypothesis of Losey et al.
520 (2022b). Yet, they may have helped humans in hunting by running or driving down the game (as
521 done by small modern hounds such as beagles), but strong bite force would not have been a
522 particularly favored trait while hunting. Accordingly, the more likely explanation for their relatively
523 more robust mandibular traits compared to the two other sites is that they fed on hunting leftovers
524 and that the hard-to-chew and large diet items placed high functional demands on their
525 masticatory apparatus, requiring relatively more strength when opening the jaw at a large gape
526 (Herrel et al., 2008).

527 *Morphological variability during the Chalcolithic period*

528 An important part of the variability in mandible shape in Hârşova-tell, Borduşani-Popină and
529 Vităneşti-Măgurice overlaps which may be related to the fact that the three populations share a
530 same ancestral genetic pool (Ollivier et al., 2018), or similar lifestyles (Figs 5B,D, S1B and
531 S2B,D). Yet, we also evidenced some unique shapes allowing to distinguish the three sites. The
532 most obvious differences separate Vităneşti-Măgurice from the two other sites, reflecting how
533 differences in the socio-economic system may have driven dog diversity in the past. However,
534 significant differences were also observed in the morphology of the dogs from Borduşani-Popină
535 and Hârşova-tell (which is particularly evident with complete mandibles, Fig. S1, Table 1). In
536 particular, in Borduşani-Popină, some dogs are characterized by a taller mandibular body, a
537 smaller and more triangular coronoid process and a lower angular process. These differences are
538 observed despite the fact that the two dog populations are sub-contemporary and geographically
539 very close, that the sites share similar characteristics regarding to the socio-economic system,
540 and that humans consume dogs in large proportions in both settlements. These local differences
541 are thus unlikely to be related to differences in the living conditions of dogs. Yet, **the differences**
542 **in mandible shape cannot be explained solely through genetic differences (plasticity renders**
543 **things more complicated to decipher), they may at least partly** reflect genetic drift or founder
544 effects suggesting that exchanges of dogs between Hârşova-tell and Borduşani-Popină remained
545 rare. This remains to be explored by paleogenetic approaches. **If confirmed, this would also**
546 **suggest that each settlement had its own population of dogs, and more widely that interbreeding**
547 **would likely be even rarer with far more distant foraging communities.**

548 **Conclusion**

549 Using a combination of isotopic and morphometric analyses, we identified differences in the diet
550 and morphology of three sub-contemporary dog populations, dated to the same Chalcolithic
551 culture and geographically close, but characterized by different socio-economic systems. At
552 Vităneşti-Măgurice, where the animal exploitation system is mainly based on hunting, dogs have

553 a **relatively** more robust mandibular morphology (**but of similar size**), while their diet is more
554 specialized in wild large mammals (red deer, aurochs, wild horse). This reflects adaptations to
555 constraints imposed by their diet and possibly their role in hunting. In contrast, the dogs from
556 Hârşova-tell and Borduşani-Popină have a diet that contains more domestic animals (sheep,
557 cattle, pig), but also involves the consumption of fish in some individuals. Importantly, mandible
558 shape reflects isotopic signatures in individual dogs suggesting that diet is an important driver of
559 the observed variation in mandible shape. Overall, dog mandibular morphology and diet appear
560 to reflect human practices. The differences observed between the three sites reflect differences in
561 the trophic level, and local adaptations to different diets depending on the living conditions. This
562 illustrates the adaptation of dogs to different socio-economic systems as hypothesized.

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574 Interdisciplinaires) project (CROC) supervised by Morgane Ollivier (University of Rennes).

575 **Data Availability**

576 Detailed information about the sample and additional details of the results mentioned in the main
577 text are provided in the electronic supplementary material. Three-dimensional models of the
578 mandibles are available in the Dryad Digital Repository:
579 <https://datadryad.org/stash/dataset/doi:10.5061/dryad.gqnk98sqd>. All data used for the
580 morphometric analyses (3D coordinates of landmarks, R scripts and datasets) are available in SI
581 **9.**

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