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# 1 Unexpected morphological diversity in ancient dogs compared to 2 modern relatives

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30 Herrel and Stéphanie Bréhard designed research. Colline Brassard collected the images of mandibles  
31 for GMM analyses and performed the GMM data acquisition. Colline Brassard, Raphaël Cornette,  
32 Anthony Herrel and Stéphanie Bréhard analyzed and interpreted the GMM data. Adrian Bălăşescu,  
33 Rose-Marie Arbogast, Vianney Forest, Céline Bemilli, Adina Boroneanţ, Fabien Convertini, Muriel  
34 Gandelin, Valentin Radu, Anne Tresset and Stéphanie Bréhard provided archaeological samples of  
35 *Canis* sp. for geometric morphometric analyses and detailed information regarding the archaeological  
36 contexts from which they were recovered. Claude Guintard, Tracey L. Kreplins, Elodie Monchâtre-  
37 Leroy and Patricia L. Fleming provided modern samples of dogs for G.M.M. analysis. Colline  
38 Brassard, Anthony Herrel and Stéphanie Bréhard wrote the manuscript, with the scientific and editing  
39 input from Adrian Bălăşescu, Adina Boroneanţ Fabien Convertini, Raphaël Cornette, Andréa Filippo,  
40 Patricia A. Fleming, Vianney Forest, Claude Guintard and Valentin Radu. All authors reviewed the  
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43 **Abstract**

44 Dogs are among the most variable species today, but little is known about the morphological  
45 variability in the early phases of their history. The Neolithic transition to farming may have resulted in  
46 an early morphological diversification as a result of changes in the anthropic environment or  
47 intentional selection on specific morphologies. Here, we describe the variability and modularity in  
48 mandible form by comparing 525 dog mandibles from European archaeological sites ranging from  
49 8,100 to 3,000 cal. BC to a reference sample of modern dogs, wolves, and dingoes. We use three-  
50 dimensional geometric morphometrics to quantify the form of complete and fragmented mandibles.  
51 We demonstrate that an important morphological variability already existed before the Bronze Age in  
52 Europe, yet the largest, smallest, most brachycephalic or dolichocephalic extant dogs have no  
53 equivalent in the archaeological sample, resulting in a lower variation compared to modern relatives.  
54 The covariation between the anterior and posterior parts of the mandible is lower in archaeological  
55 dogs, suggesting a low degree of intentional human selection in early periods. The mandible of  
56 modern and ancient dogs differs in functionally important areas, possibly reflecting differences in diet,  
57 competition, or the implication of ancient dogs in hunting or defense.

58 **Keywords:** Neolithic, Chalcolithic, dog, mandible, shape

59 **1. Background**

60 Although they descend from the same ancestor (the grey wolf; [1]), extant dogs are among the most  
61 variable species on the planet, both in terms of size and proportions [2]. This tremendous variability is  
62 the result of rapid phenotypic changes in response to strong intentional selection by humans over the  
63 last 200 years (defined herein as 'modern' times). This selection on specific physical or behavioral  
64 traits to satisfy functional needs (e.g. for work, hunting, or running) or for strictly aesthetic reasons led  
65 to the creation of breeds (defined by standards established since the nineteenth century) and to the  
66 diversity of forms observed today [3].

67 Whilst numerous studies have explored the genetic basis of the phenotypic variability in extant dogs  
68 (e.g. [4–10]), very little is known about **their** morphological variability **in the past in** Europe.  
69 Considering that the notion of breed refers to a very recent event, the terms "type" or "morphotype"  
70 (characterized by different cranial proportions) are more relevant to describe head shape in ancient  
71 dogs. A division into dolichocephalic (elongated and narrow skull, akin to greyhounds), brachycephalic  
72 (broad and short skull, akin to mastiffs or bulldogs), and intermediate mesocephalic types is thus often  
73 used. Different morphotypes appear identifiable in Western Europe as early as the Metal Ages (i.e.  
74 from the second millennium cal. BC), and this phenomenon intensified during the Middle Ages and  
75 modern times [11,12]. Few studies have explored morphological variability in earlier periods, yet  
76 different sizes of dogs are described as early as the late Upper Paleolithic in Western Europe [13,14].  
77 However, the early phases of domestication are particularly complex to consider given the uncertainty  
78 surrounding the place and timing of domestication [10,15–17] and the difficulty to distinguish wolves  
79 from early dogs due to the scarcity and the fragmented nature of these early canid remains [18]. The  
80 strong morphological similarity between early dogs and wolves [19–21], and possible hybridization  
81 between them [1,3] render this even more complex.

82 The **period from the Mesolithic onwards (i.e. from the tenth millennium cal. BC)** is of great interest to  
83 explore the morphological diversity of dogs in Europe. First, **because from this period onwards dogs**  
84 **show a marked phenotypic divergence from their ancestors and size seems to clearly distinguish**  
85 **them** [13,22–24]. **Second**, dog remains **become** recurring in European sites ([9,24–28]), their  
86 frequency increasing during the fifth millennium cal. BC throughout Europe (e.g. [22,24,29–33]).  
87 Third, genetic data show that modern dogs originate from at least five ancestral dog lineages which  
88 diversified by *circa* 9,000 years BC [10], several of them being responsible for early and successive  
89 gene flow which made up the genetic history of ancient dogs in Europe [6,10]. In parallel, the  
90 increasing sedentarization and subsequent transition to farming during the Neolithic in Western  
91 Eurasia (i.e. from the middle tenth millennium cal. BC) may have involved intentional selection of  
92 certain phenotypes (in terms of size or proportions) associated with specific tasks (hunting, guarding).  
93 In Europe, from the Mesolithic onwards, dogs were widely eaten, and their bones were occasionally  
94 used for the manufacturing of ornaments. Dogs were also the subject of other social or symbolic  
95 considerations as attested by the burial of complete bodies, sometimes in close association with  
96 human deposits. It is difficult to demonstrate their role in hunting or for the protection of camps or  
97 villages, but their scarce presence in prehistoric settlements, where they were neither eaten nor  
98 buried, could be an indication. In that respect, the vast diversity in the roles played by dogs at that  
99 time [11,22,25,29,30,34] may have been accompanied by an early morphological diversification, long  
100 before the Metal Ages.

101 The morphological and genetic diversity of dogs during this time period in Western Eurasia has been  
102 explored to some degree. Genetic data providing information on coat color [5], mitochondrial  
103 haplogroup [6], or their ability to digest starch [10,35] have been published. Osteometric data are  
104 abundant, however, these consist of linear measurements which only provide information on the  
105 stature and gracility of the animals (e.g. [22–24,28,36]) and do not allow to explore the morphological  
106 variability of canids beyond size. Thus, to date, there is no large-scale study describing the  
107 morphological variability of European prehistoric dogs. Given the considerable number of mandibles

108 in archaeological assemblages, and the fact that mandibular shape has been proven to be a good  
109 indicator of cranial shape and thus of the overall head morphotype in modern dogs [37], this bone is a  
110 promising object to explore morphological variability in the head of ancient dogs (yet not  
111 systematically correlated to the morphology of the complete body in modern dogs). Additionally, as  
112 significant and strong relationships between the mandible and the masticatory muscles have been  
113 demonstrated in modern dogs [37,38], mandible form may be used to make functional inferences on  
114 archaeological specimens.

115  
116 With the present study, we aimed at **describing** the **overall** morphological variability in the mandible of  
117 a very large sample of European prehistoric dogs (defined herein as 'ancient' dogs) **and compare**  
118 **them to a sample of modern dogs**. We **included dogs from** the period ranging from the Mesolithic to  
119 the end of the Romanian Chalcolithic (*circa* 8,100 to 3,000 cal. BC) to avoid the possible  
120 misidentification of wolves, dogs, or their hybrids in the early phases of the domestication process.  
121 Three-dimensional geometric morphometric methods were used to describe mandible form in a  
122 sample of 525 archaeological mandibles of dogs and eight wolves from 27 sites in Western Europe  
123 and Romania (figure 1A). **Given that mandibles are rarely complete in the archaeological record,**  
124 **making it more challenging to have a complete representation of an extensive sample from ancient**  
125 **remains, we used ten different protocols corresponding to the most common fragmentation patterns in**  
126 **our sample (figure 1C, supplementary text Fig. S1).** For each fragment, the variability of ancient dogs  
127 was compared to variability evident in a sample of 66 modern dogs of various breeds, dingoes, and  
128 captive wolves. We used multivariate statistical tools to quantify the variability in both size and shape.  
129 Given the diversity in status of these prehistoric dogs we expected some variability in ancient dogs,  
130 yet less so than in modern dogs submitted to intensive intentional human selection. As dingoes have  
131 evolved separately over the last 3,600–5,000 years (the estimated time of first introduction to  
132 Australia, mostly likely as a result of transport by Asian seafarers [39]), we predicted that their form  
133 would be intermediate between that of the ancient and modern dogs. **Assuming that prehistoric dogs**  
134 **were subjected primarily to natural constraints while the anatomy of modern dogs is limited by strong**  
135 **developmental constraints [2,40,41], we expect the mandible of ancient dogs to be more plastic (i.e. to**  
136 **show morphological traits in response to their environment and allowing them to survive in new**  
137 **conditions [42]). We thus tested the relationship (i.e. covariation, integration) between the anterior**  
138 **(supporting the teeth and thus more conservative) and posterior part (supporting the masticatory**  
139 **muscles and thus more akin to represent functional variability showing adaptation to environmental**  
140 **constraints) of the mandible (figure 1B) and expect it to be lower (i.e. more modular, less integrated)**  
141 **in ancient dogs compared to modern relatives.**

## 142 **2. Methods**

143 A full description of the materials and methods used is provided in the electronic supplementary  
144 material, supplementary text.

145 We quantified the shape of 525 dog and eight wolf mandibles from 27 archaeological sites dated to  
146 between the Mesolithic and the end of the Romanian Chalcolithic across Western Europe and  
147 Romania (figure 1A; electronic supplementary material, Table S1). The distinction between dogs and  
148 wolves was made following a size criterion [13,14,22,35] (see supplementary text and figure S2). The  
149 modern sample was constituted of 66 dogs of various breeds (see electronic supplementary material,  
150 Dataset S1), most being represented by only one or two specimens with the exception of beagles (N  
151 = 20). Modern dogs were classified into brachycephalic ('short-headed'), mesocephalic, or  
152 dolichocephalic ('long-headed') based on the cephalic index, **i.e. the relative proportion of skull**  
153 **breadth to skull length** [43]. We also quantified the shape of the mandibles of eight captive wolves and  
154 eight wild Australian dingoes. Only specimens with the first molar completely erupted (**i.e. non-juvenile**  
155 **specimens**) were considered for analyses.

156 We used photogrammetry to obtain three-dimensional (3D) models of the mandibles. Next, we  
157 quantified morphological variation using 3D geometric morphometrics. Ten different landmarking  
158 protocols (figure 1B,C; electronic supplementary material Tables S2 and S3) were considered to take  
159 into account a maximum number of mandibles and mandible fragments, based on the fragmentation  
160 patterns most represented in the archaeological sample [44] (see electronic supplementary material,  
161 figure S1).

162 A suite of statistical analyses (landmark sliding, Procrustes superimposition, Student t-tests, ANOVAs,  
163 Procrustes ANOVAs, Principal Component Analyses PCA, discriminant analyses through Canonical  
164 Variate Analyses CVA, etc.) were carried out in R v4.0.0 (2020-04-24) using the packages Morpho  
165 and geomorph (see electronic supplementary material, supplementary text). We tested for differences  
166 in the means or the variability in centroid size, differences in shape, or allometry-free shape, and  
167 explored the covariation between the anterior and posterior parts of the mandible using modularity  
168 tests (figure 1B).

### 169 **3. Results**

170 In the following, we focus primarily on the results based on the complete mandibles. The results of  
171 descriptive statistics for the ten fragments are shown in table 1 and illustrated in figures 2 and 3, as  
172 well as in electronic supplementary material, figures S3 to S11 and S13. The results of the parallel  
173 analyses performed on a reduced number of landmarks are reported in the electronic supplementary  
174 material, table S3.

#### 175 **(a) Variability in mandible size**

176 Ancient dogs are significantly less variable in terms of mandible centroid size and tend to have  
177 smaller mandibles, on average, than modern dogs, having a mean mandible size comparable to  
178 modern beagles (figure 2C, table 1). The difference in size is significant for all mandible fragments  
179 analyzed (table 1). However, the range of sizes in ancient dogs was smaller than in the modern  
180 sample, with the largest brachycephalic modern dogs and the smallest toy dogs having no equivalent  
181 in the archaeological sample, which was expected. All modern wolves have mandibles larger than the  
182 largest one in ancient dogs, according to all fragments except the smallest (fragments G and I), for  
183 which there is some overlap between dogs and wolves (electronic supplementary material, figures  
184 S8C and S10C). Dingoes have mandibles of intermediate sizes, between those of dogs and wolves  
185 (figure 2C).

#### 186 **(b) Variability in mandible shape**

187 Ancient dogs have significantly less variability in mandible shape or allometry-free shape than modern  
188 dogs (table 1), demonstrating that the differences in morphological variability depend on more than  
189 just differences in size. The results are significant for all fragments except the smallest (fragments G  
190 and I). **In ancient dogs, a reduced part of the variability in shape is related to size compared to  
191 modern dogs (table 1).**

192 This greater variability in shape in modern dogs is observable on the first two axes of the principal  
193 component analysis (PCA) for most fragments and on the trees **depicting morphological similarity**  
194 (figure 2A-B, electronic supplementary material, figures S3 to S11). For the most complete mandibles  
195 (fragment A), low values of the first principal component (PC1; 21.9% of total variability) describe a  
196 relatively smaller jaw angle and smaller coronoid process, while high values describe a larger area for  
197 the masseteric fossa. Low values of second principal component (PC2; 13.5% of total variability)  
198 describe a shorter and more curved mandible with a greater ramus depth, while high values for PC2  
199 describe a flatter, shallower mandible. **The first principal component correlates** with centroid size

200 (PC1:  $R^2 = 0.25$ ,  $p < 0.001$ ; PC2:  $p = 0.16$ ; figure 2A): the dogs with the smallest mandibles (therefore  
201 the smallest dogs in terms of body size) are generally positioned to the left of the scatterplot and the  
202 biggest dogs tend to be positioned towards the right. Modern dogs contribute strongly to the variability  
203 described by the first two axes, and some modern breeds extend beyond the variability observed in  
204 ancient dogs, in particular large brachycephalic breeds (such as rottweilers, pitbulls, bulldogs,  
205 leonberger, boxer, mastiff), extremely dolichocephalic dogs (such as borzoi), and small toy dogs  
206 (papillon, chihuahua, dachshund). The most dolichocephalic modern dogs have higher PC2 values  
207 (appear towards the top of the scatterplot), while the most brachycephalic dogs have higher PC1  
208 values and lower PC2 values and separate out towards the bottom right of the scatterplot. Most  
209 ancient dogs overlap at the center of the scatterplot with modern normocephalic breeds, modern  
210 dingoes, and modern or ancient wolves. Interestingly, some ancient dogs occupy a unique part of the  
211 morphospace not occupied by modern canids on the negative part of PC1 (figure 2A).

212 The **trees** based on morphological distances (figure 2B) support the distinction between ancient and  
213 modern dogs and provide a more refined view on the positioning of ancient dogs compared to their  
214 modern counterparts. Modern and ancient dogs tend to be on separate branches and some branches  
215 (e.g. figure 2B, branches b and c) contain only ancient dogs. One branch clearly isolates the most  
216 brachycephalic modern dogs (figure 2B, branch a), distinct from the ancient dogs. Most  
217 dolichocephalic modern dogs (figure 2B, branch f) are similarly distinguished from most ancient dogs.  
218 By contrast, the mandible shape of some modern breeds (figure 2B, branch b: mastiff, figure 2B,  
219 branch d: husky, pomeranian, bichon teneriffe, sloughi) appears more similar to that of ancient dogs.  
220 The beagles ( $n=20$ ) are nearly all grouped on the same branch (figure 2B, branch e) in the middle of  
221 the ancient dogs. Modern dingoes group into three separate branches on this **tree**, mostly with  
222 modern and ancient wolves, but some are close to modern dogs and one is in the midst of ancient  
223 dogs. Most modern and ancient wolves isolate on a separate branch (figure 2B, branch g), distinct  
224 from all ancient dogs except one (over 127). These observations are confirmed when the sample size  
225 is increased by conducting the same analyses with fragment B ( $n=226$ ; electronic supplementary  
226 material, figure S3) and even other, smaller, fragments (figures S4 to S11). Not surprisingly, the  
227 analyses conducted on the smallest fragments G and I (figures S8 and S10) lead to a tree without  
228 clear structure.

229 Ancient dogs significantly differ from modern dogs in mean mandible shape ( $p < 0.001$  for all  
230 fragments, table 1). The discriminant analyses (Canonical Variate Analyses, CVA) performed on all  
231 fragments result in an excellent classification rate (over 87%, table 1), reinforcing the observation that  
232 ancient and modern dogs differ in shape, and that the differences involve different anatomical features  
233 located on all regions of the mandible. Ancient dogs had a more robust (body of the mandible being  
234 taller under the carnassial) and curved mandibles, with a straighter coronoid process, a more  
235 developed angular process, and a shallower masseteric fossa (figures 3 and S13).

### 236 **(c) Modularity of the mandible**

237 The results of the modularity tests indicate significant modular structure in shape and allometry-free  
238 shape for all groups ( $p < 0.001$ , table 2). The CR coefficient is much lower in ancient dogs compared  
239 to modern **dogs both when considering the shape ( $Z\text{-score}=11.3$ ,  $p < 0.001$ ) or the allometry-free**  
240 **shape ( $Z\text{-score}=10.5$ ,  $p < 0.001$ )**, suggesting that mandible is more modular (*i.e. less integrated*) in  
241 ancient dogs (the anterior and posterior part of the mandibles covary less). The preliminary results  
242 obtained for the ancient and modern wolves and modern dingoes further suggest that modularity in  
243 modern dogs is not different from that of wolves or dingoes.

244



245 **4. Discussion**

246 Our analyses clearly demonstrated that the morphological diversity in the head (the mandible being a  
247 proxy of overall head shape [37]) of European dogs was considerable well before the Bronze Age, yet  
248 lower than in modern dogs. In ancient dogs, mandible size varied from very small, similar to some  
249 modern small dogs such as the pomeranian or dachshund, to larger sizes compatible with modern  
250 large dogs such as the husky, golden retriever or German shepherd. However, the mandible size of  
251 ancient dogs was always much smaller than that of wolves and on average corresponds to that of  
252 modern beagles. Mandible shape varied from shapes similar to those of ancient or modern wolves or  
253 dingoes, to those of modern meso-dolichocephalic dogs (e.g. beagles, sloughi, bichon Tenerife,  
254 pomeranian, mastiff, shepherd dogs). As expected, no extreme forms were observed among the  
255 ancient dogs: the very brachycephalic (pitbull, amstaff, boxer, bulldog etc.) and very dolichocephalic  
256 (borzoi) modern dogs have no equivalent in ancient **times**. There was nevertheless substantial  
257 morphological variability in ancient dogs, indicating that dogs had diverse head shapes as early as the  
258 Neolithic in Europe. Yet, this diversification likely did not result from a drastic selection similar to the  
259 intentional breed selection over the past 150 years. The lower variability in ancient dogs, as well as  
260 the relative short morphological distance between some dingoes and ancient dogs or between some  
261 ancient dogs and wolves or modern dogs of average morphologies suggests minimal intentional  
262 human selection for specific morphotypes. In other words, if the first farmers selected for distinct  
263 morphotypes, they did not favor extreme morphologies.

264  
265 Interestingly, clear differences in the mean shapes between the ancient and modern samples were  
266 discovered. This separation is not influenced by taphonomic or pathological processes (e.g. exostosis  
267 associated with dental disease). Indeed, only the most complete mandibles were included in analyses  
268 with fragment A. Additionally, the parallel analyses performed with only anatomical landmarks  
269 (surface landmarks being more likely to be impacted by bone deformation) led to similar results (see  
270 electronic supplementary material, figure S12 and table S3). Neither it is influenced by ontogeny as  
271 the youngest specimens were removed from the analyses (see methods). Our modern sample covers  
272 a wide range of **shapes** (all morphological types including hypertypes are represented), however, is  
273 not exhaustive and lacks some landraces of dogs, such as those from Asia, or village dogs. Further  
274 analyses are thus needed before concluding that **the unique shapes observed in ancient dogs**  
275 definitively have no equivalent in modern dogs, and represent shapes that have disappeared.

276  
277 Our results are based on a large number of ancient mandibles (227), supported by fragments A and B  
278 (which are the most representative of the complete form of the mandible), and are generally confirmed  
279 when including data for smaller fragments (table 1). The two smallest fragments (G and I) lead to less  
280 conclusive results, likely because these fragments represent only a very small part of the mandible  
281 and are thus less representative of the complete mandible shape. This is supported by the distribution  
282 of the ancient dogs with complete mandibles in the PCA based on fragments I and G (electronic  
283 supplementary material, figures S8 and S10). Considering the composition of the archaeological  
284 sample (figure S1, table S1), the conclusions drawn are especially valid for the Middle Neolithic in  
285 Western Europe and the Late Chalcolithic in Romania. The earliest (Mesolithic and Early Neolithic)  
286 phases are poorly represented due to the scarcity of dog bones and their fragmentation (electronic  
287 supplementary material, figure S1, table S1). It thus cannot be excluded that during these early  
288 phases some other forms existed, possibly adding to the group of ancient dogs extending outside the  
289 variability of our modern sample. Further samples from these early periods would enable us to further  
290 explore this variability.

291  
292 The anatomical differences between modern and ancient dogs may partly be explained by a change  
293 in the genetic composition of dog populations through time. Mitochondrial haplogroups C and D were  
294 dominant in Europe before the Bronze Age (63% and 20%, respectively), whereas they represent only  
295 around 11% and 3% of extant European dogs, respectively [15]. Haplogroups A and B currently  
296 overwhelmingly dominate (64% and 22%, respectively) in Europe. **This change results from complex**

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migrations, replacements and admixture through time and space. Considering the distinct geographic distribution of the different maternal lineages before the Neolithic period [6,15] each may be characterized by specific phenotypic traits, yet this remains unstudied to date. They may also reflect differences in the anthropic environment or the way of life of dogs. Given that the most discriminant traits are located in areas of functional importance (robustness and curvature of the mandibular body, size of the angular and coronoid processes, shallowness of the masseteric fossa), this may have resulted in differences in jaw function and bite force [45]. The differences in the curvature of the body of mandible under the carnassial suggests a greater importance of the role of the temporal muscle in ancient dogs (figure 3A and B). This may be related to diet of these dogs which were likely feeding on more tough and hard foods than most modern dogs, thus placing very different demands on mandibular function and form (e.g. [46,47]). Additionally, a greater bite force and/or implication of the temporalis muscle would have been useful in dogs used for defense or hunting.

Our analyses further show that the relationship between the anterior and posterior parts of the mandible was less strong in ancient dogs compared to modern dogs (or captive wolves and commensal dingoes, but the low sample size did not allow to draw conclusions for these animals). The strong integration in the mandible of modern dogs, despite intense artificial selection, is concordant with previous comparisons between modern dogs and wolves [40] or other wild canids such as the red fox [33], and may be explained by developmental factors constraining mandible shape in canids [2]. This is consistent with previous studies evidencing similar patterns of developmental integration in the skull of domestic/wild pairs of mammals [2,40,41]. The lower integration in ancient dogs may be due to the fact that they were more submitted to natural (environmental) constraints allowing some parts of the mandible to be more variable compared to modern dogs. In particular, the mandibular ramus (providing attachment for masticatory muscles) is more likely to adapt quickly to natural constraints and functional demands, related to, for example, diet, than the mandibular corpus (bearing the teeth, which are much more conservative). The overall variability in diet in ancient dogs likely being higher, this may have selected for more variability in the shape of the mandibular ramus. Such a difference in integration related to artificial selection was previously demonstrated in the long bones of modern horses and donkeys [48], and by comparing the mandible of dogs and commensal red foxes [33], but never, to our knowledge, in the mandible of other domestic/wild mammal pairs.

The observed differences in mean shape and integration of the mandible between modern and ancient dogs and the fact that we did not find any extreme shapes in prehistoric dogs support the hypothesis that the first farmers did not exert strong selection on dogs for aesthetic or utilitarian reasons that might have constrained the anatomy (and modularity) of the mandible. Dogs were most likely free-ranging and closer to a commensal lifestyle, as observed in some extant tribes of hunter-gatherers where humans share their diet with dogs [49]. This is further suggested by isotopic data for some Neolithic dogs [29]. Additional feral dogs likely subjected to constraints closer to ancient dogs (i.e. less intentional human selection and more natural constraints) are needed to investigate this possibility further.

Now that the global variability in dogs prior to the Bronze Age has been described overall, it would be of interest to confront morphological data with genetic, isotopic, or contextual data (i.e. whether dogs were eaten or buried complete, or in accordance with the mode of subsistence relying on hunting or herding) to explore what drove diversity within the archaeological sample. This would allow more profound insights into how the changes in human societies were accompanied by changes in the morphology of dogs through time and space. Paleogenetic data might, for example, allow to test whether the acquisition of the ability to digest starch was accompanied by changes in mandible form. Additional contextual data would further enable a better understanding of when the morphological diversification started: as soon as hunter-gatherers settled, with the farming transition, or later with the complexification of Neolithic societies?

346

## 347 **5. Conclusions**

348 In summary, our comparison of mandible form between European dogs from the Mesolithic to the end  
349 of the Romanian Chalcolithic and modern breeds highlighted an unexpected diversity in dogs before  
350 the Bronze age, suggesting that dogs showed significant morphological diversity in the head as early  
351 as the Neolithic. Additionally, ancient dogs have mandible shapes that differ, on average, from  
352 modern dogs, which may be partly related to the changes in the genetic composition of dog  
353 populations through time, but also suggests changes in lifestyle and access to food, considering that  
354 the anatomical differences are located in areas of functional importance. This, added to the fact that  
355 no extreme shapes were observed in ancient dogs and that the integration between the anterior and  
356 posterior parts of the mandibles is lower in ancient dogs, suggests that if the first farmers selected for  
357 distinct morphotypes, they did not favor extreme morphologies unlike the results of recent breed  
358 selection.

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## 377 **Data Availability**

378 All data used for the analyses (**3D models of the mandibles, R scripts and datasets**) are available in a  
379 **Dryad depository** [50]. [Reviewer url: [https://datadryad.org/stash/share/i4fl41GWJHMfvB-  
380 mu3LNg8srMOi\\_vgwvmzIfHSGL7g](https://datadryad.org/stash/share/i4fl41GWJHMfvB-mu3LNg8srMOi_vgwvmzIfHSGL7g)]

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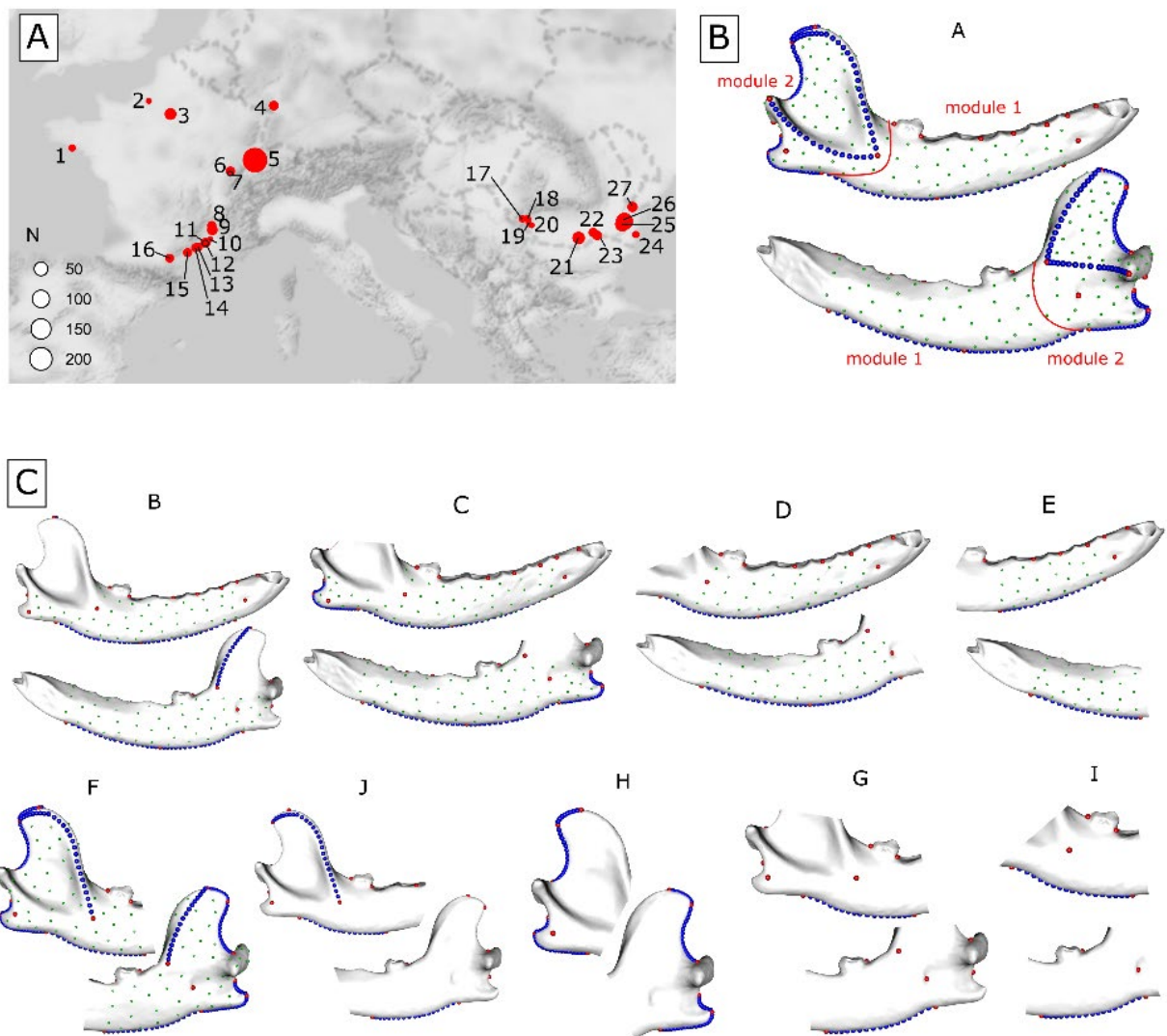
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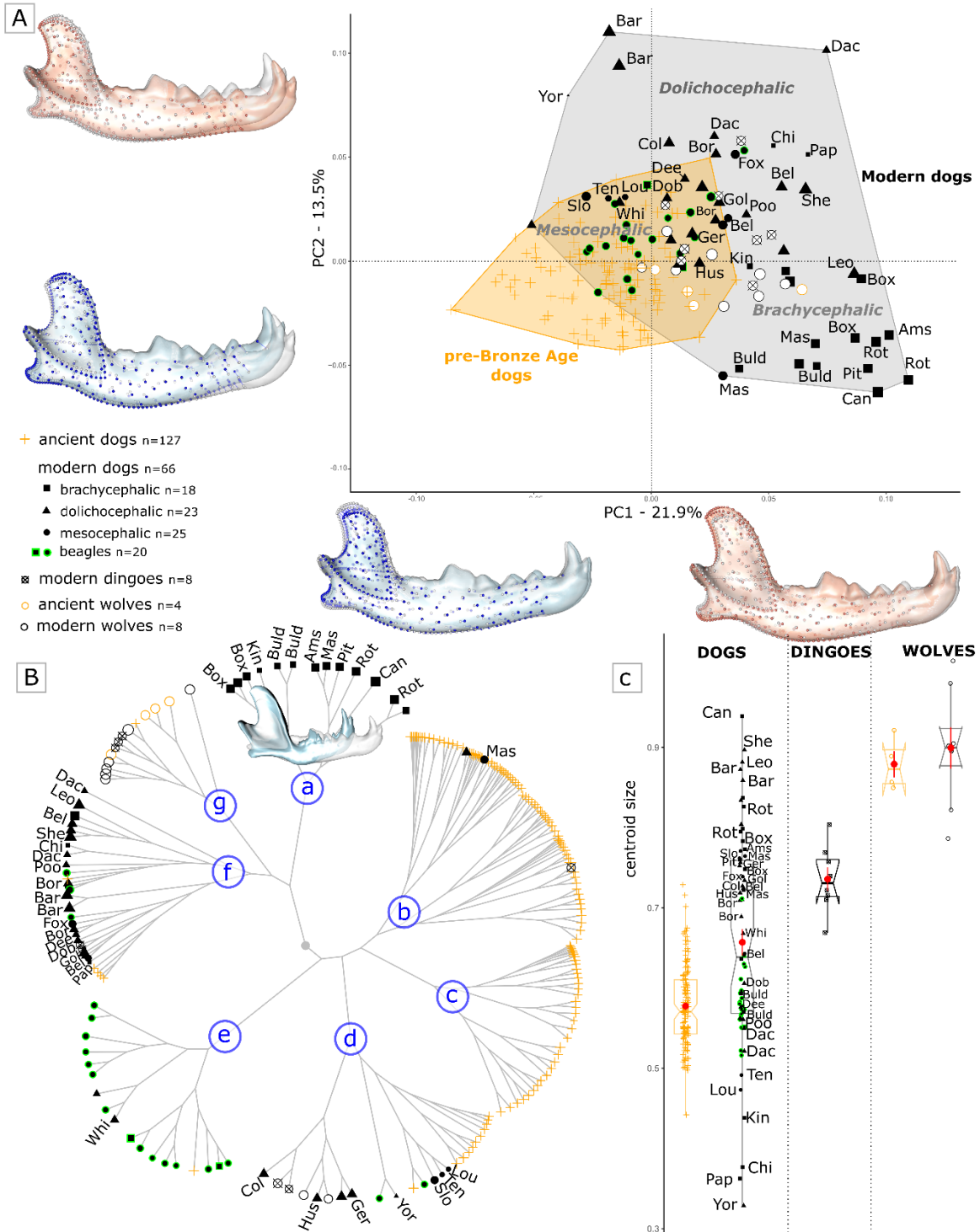
511 **Figures and tables**

512 **Figure 1.** Origin and fragmentation patterns of the archaeological mandibles. (A) Map showing  
513 selected sites dated from the Mesolithic to the end of the Romanian Chalcolithic in Western Europe  
514 and Romania. Site key, chrono-cultural attribution and dating are presented in electronic  
515 supplementary material, dataset S1. B-C) Three dimensional landmarks considered in the geometric  
516 morphometric analyses for the most complete (B) or fragmented (C) mandibles, **matching the ten**  
517 **subsets of fragments (letters A to J)**, represented on lateral (top image) or medial (bottom image)  
518 views of the mandible. Anatomical landmarks are in red, sliding semi-landmarks of curves are in blue,  
519 sliding semi-landmarks of surfaces are in green. 'module 1' and 'module 2' represent the two modules  
520 used in the modularity tests performed on the complete mandibles. Definitions of the anatomical  
521 landmarks are provided in table S2.

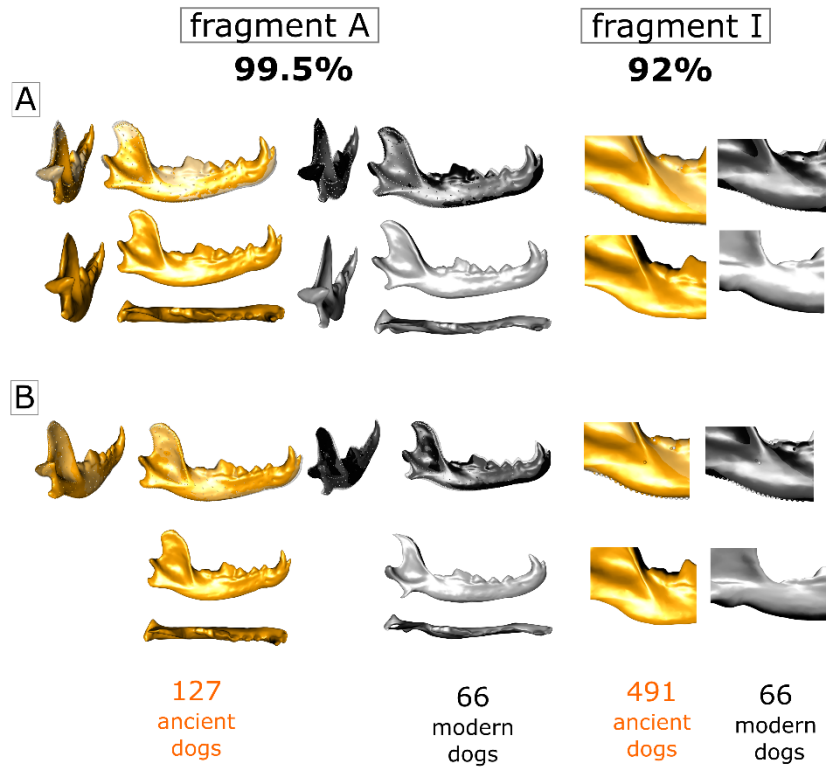




523 **Figure 2.** Visualization of the variability in mandible shape and size in ancient dogs with complete  
 524 mandibles (fragment A), with comparison with ancient wolves and modern *Canis*. (A) Principal  
 525 Component Analyses on modern and ancient specimens with fragment A (66 modern dogs, eight  
 526 modern dingoes, eight modern wolves, 127 ancient dogs and four ancient wolves). Icons size is  
 527 proportional to the log<sub>10</sub> of the centroid size. Deformations at the minimum and maximum of the PC  
 528 axes are represented in blue and pink, respectively. (B) Tree depicting the morphological similarity  
 529 between mandibles based on pairwise Euclidean distances. Icon size is proportional to the log<sub>10</sub> of the  
 530 centroid size. (C) Boxplot of the centroid sizes of modern and ancient canids. Ancient canids are  
 531 orange, modern canids are in black. The labels of modern dogs indicate the breed (key is presented  
 532 in electronic supplementary material, dataset S1). Groups (a), (b), (c), (d), (e), (f) and (g) are  
 533 mentioned in the text.



535 **Figure 3.** Visualization of the differences between modern (black/grey) and ancient (orange) dogs,  
 536 based on the results of the CVA performed on mandible shapes (A) or allometry-free shapes (B) for  
 537 fragments A and I. The sample size and percentage of cross-validation are indicated. On the upper line,  
 538 shapes at the minimum and maximum of CV scores are superposed to the mean shape of the  
 539 CVA and vectors of deformations between the two shapes are represented. On the lower line,  
 540 deformations from the mean shape to the minimum or maximum of the CV scores are magnified by 3.  
 541 See electronic supplementary material, figure S13 for visualizations with other fragments.



543 **Table 1.** Results of the statistical analyses performed on all fragments to compare the variance or  
544 mean in mandible size, shape and allometry-free shape between modern ( $n = 66$ ) and ancient dogs  
545 (sample size and the proportion of the total archaeological sample for each fragment is reported in the  
546 table). The sample sizes of ancient wolves used for visualization in the Principal Component Analyses  
547 and trees depicting morphological similarity for each fragment are also reported. CVA: Canonical  
548 Variate Analysis; P:  $p$  value;  $R^2$  coefficient of correlation; PVa: Procrustes Variance of ancient dogs;  
549 PVm: Procrustes variance of modern dogs.

Fragment	Sample size		Mandible size		Mandible shape			Allometries		Mandible allometry-free shape		
	ancient dogs	ancient wolves	Variance	Mean	Disparity	Mean	CVA	ancient	modern	Disparity	Mean	CVA
A	127 – 24%	4	$P<0.001$	$P<0.001$	PVa 0.0039 PVm 0.0069 $P<0.001$	$R^2$ 0.12 $P<0.001$	99.5%	$R^2$ 0.027 $P<0.001$	$R^2$ 0.082 $P<0.001$	PVa 0.0038 PVm 0.0065 $P<0.001$	$R^2$ 0.093 $P<0.001$	83%
B	227– 43%	4	$P<0.001$	$P<0.001$	PVa 0.0038 PVm 0.0065 $P<0.001$	$R^2$ 0.091 $P<0.001$	99%	$R^2$ 0.028 $P<0.001$	$R^2$ 0.079 $P<0.001$	PVa 0.0037 PVm 0.0062 $P<0.001$	$R^2$ 0.077 $P<0.001$	94%
C	216– 41%	4	$P<0.001$	$P=0.006$	PVa 0.0034 PVm 0.0054 $P<0.001$	$R^2$ 0.080 $P<0.001$	98%	$R^2$ 0.029 $P<0.001$	$R^2$ 0.097 $P<0.001$	PVa 0.0033 PVm 0.0049 $P<0.001$	$R^2$ 0.074 $P<0.001$	95%
D	392– 75%	6	$P<0.001$	$P=0.004$	PVa 0.0051 PVm 0.0068 $P=0.004$	$R^2$ 0.047 $P<0.001$	99%	$R^2$ 0.033 $P<0.001$	$R^2$ 0.051 $P<0.001$	PVa 0.0049 PVm 0.0066 $P=0.003$	$R^2$ 0.043 $P<0.001$	98%
E	437– 83%	7	$P<0.001$	$P<0.001$	PVa 0.013 PVm 0.018 $P=0.009$	$R^2$ 0.050 $P<0.001$	99%	$R^2$ 0.14 $P<0.001$	$R^2$ 0.12 $P<0.001$	PVa 0.011 PVm 0.017 $P=0.003$	$R^2$ 0.023 $P<0.001$	96%
F	155 – 29%	5	$P<0.001$	$P<0.001$	PVa 0.0062 PVm 0.0076 $P=0.013$	$R^2$ 0.088 $P<0.001$	97%	$R^2$ 0.021 $P<0.001$	$R^2$ 0.082 $P<0.001$	PVa 0.0061 PVm 0.0075 $P=0.037$	$R^2$ 0.068 $P<0.001$	83%
G	386– 74%	6	$P<0.001$	$P=0.017$	$P=0.11$	$R^2$ 0.053 $P<0.001$	97%	$R^2$ 0.053 $P<0.001$	$R^2$ 0.062 $P<0.001$	PVa 0.0096 PVm 0.017 $P=0.029$	$R^2$ 0.053 $P<0.001$	96%
H	160 – 30%	5	$P<0.001$	$P<0.001$	PVa 0.0035 PVm 0.0053 $P<0.001$	$R^2$ 0.056 $P<0.001$	92%	$R^2$ 0.0099 $P<0.13$	$R^2$ 0.093 $P<0.001$	PVa 0.0035 PVm 0.0048 $P=0.002$	$R^2$ 0.041 $P<0.001$	83%
I	488– 93%	7	$P<0.001$	$P=0.21$	$P=0.9$	$R^2$ 0.021 $P<0.001$	93% 98% ancient 62% modern	$R^2$ 0.023 $P<0.001$	$R^2$ 0.051 $P<0.001$	PVa 0.010 PVm 0.013 $=0.032$	$R^2$ 0.025 $P<0.001$	93% 98% ancient 62% modern
J	215 – 41%	5	$P<0.001$	$P<0.001$	PVa 0.0044 PVm 0.0058 $P<0.001$	$R^2$ 0.11 $P<0.001$	97%	$R^2$ 0.027 $P<0.001$	$R^2$ 0.097 $P<0.001$	PVa 0.0043 PVm 0.0056 $P=0.009$	$R^2$ 0.075 $P<0.001$	91%
Total	525	8										

552 **Table 2.** Results of the modularity tests performed on the complete mandibles. n: sample size; CR:  
 553 CR coefficient **or covariation** ratio, quantifying the degree of modularity; *p* value: empirically calculated  
 554 *p* value from the resampling procedure; Effect size: the multivariate effect size associated with **the**  
 555 **covariance ratio**.

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	n	Shape			Allometry-free shape		
		CR	<i>p</i> value	Effect size	CR	<i>p</i> value	Effect size
Ancient dog	127	0.60	0.002	-15.2	0.60	0.002	-15.0
Modern dog	66	0.85	0.002	-12.8	0.85	0.002	-12.7
Ancient wolf	4	0.94	0.002	-11.7	0.93	0.002	-12.6
Modern wolf	8	0.88	0.002	-13.0	0.86	0.002	-14.6
Modern dingo	8	0.82	0.002	-14.2	0.83	0.002	-14.1

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