

Unexpected morphological diversity in ancient dogs compared to modern relatives

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2 modern relatives

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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
- 55 dogs, suggesting a low degree of intentional human selection in early periods. The manufactor 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**

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

traits to satisfy functional needs (e.g. for work, hunting, or running) or for strictly aesthetic reasons led 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
- 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
- vsed. Different morphotypes appear identifiable in Western Europe as early as the Metal Ages (i.e.
- from the second millennium cal. BC), and this phenomenon intensified during the Middle Ages and
 modern times [11,12]. Few studies have explored morphological variability in earlier periods, yet
- modern times [11,12]. Few studies have explored morphological variability in earlier periods, yet
 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
- surrounding the place and timing of domestication [10,15–17] and the difficulty to distinguish wolves
- 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

explored to some degree. Genetic data providing information on coat color [5], mitochondrial

- haplogroup [6], or their ability to digest starch [10,35] have been published. Osteometric data are
- abundant, however, these consist of linear measurements which only provide information on the
- stature and gracility of the animals (e.g. [22–24,28,36]) and do not allow to explore the morphological
- 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
- significant and strong relationships between the mandible and the masticatory muscles have been
- demonstrated in modern dogs [37,38], mandible form may be used to make functional inferences on archaeological specimens.
- 115

With the present study, we aimed at describing the overall morphological variability in the mandible of 116 117 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 and Romania (figure 1A). Given that mandibles are rarely complete in the archaeological record, 123 124 making it more challenging to have a complete representation of an extensive sample from ancient remains, we used ten different protocols corresponding to the most common fragmentation patterns in 125 126 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 evolved separately over the last 3,600-5,000 years (the estimated time of first introduction to 131 Australia, mostly likely as a result of transport by Asian seafarers [39]), we predicted that their form 132 133 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**

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

- 145 We quantified the shape of 525 dog and eight wolf mandibles from 27 archaeological sites dated to
- 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,
- 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
- dolichocephalic ('long-headed') based on the cephalic index, i.e. the relative proportion of skull
 breadth to skull length [43]. We also quantified the shape of the mandibles of eight captive wolves and
- 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

quantified morphological variation using 3D geometric morphometrics. Ten different landmarking
 protocols (figure 1B,C; electronic supplementary material Tables S2 and S3) were considered to take

protocols (figure 1B,C; electronic supplementary material Tables S2 and S3) were considered to take 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

Variate Analyses CVA, etc.) were carried out in R v4.0.0 (2020-04-24) using the packages Morpho

and geomorph (see electronic supplementary material, supplementary text). We tested for differences

in the means or the variability in centroid size, differences in shape, or allometry-free shape, and 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

descriptive statistics for the ten fragments are shown in table 1 and illustrated in figures 2 and 3, as

well as in electronic supplementary material, figures S3 to S11 and S13. The results of the parallel

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

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

the masseteric fossa. Low values of second principal component (PC2; 13.5% of total variability)

- 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
- 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
- values and lower PC2 values and separate out towards the bottom right of the scatterplot. Most
- ancient dogs overlap at the center of the scatterplot with modern normocephalic breeds, modern
- 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. By contrast, the mandible shape of some modern breeds (figure 2B, branch b: mastiff, figure 2B, 218 219 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 from all ancient dogs except one (over 127). These observations are confirmed when the sample size 224 is increased by conducting the same analyses with fragment B (n=226; electronic supplementary 225 226 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.
- Ancient dogs significantly differ from modern dogs in mean mandible shape (p < 0.001 for all
- fragments, table 1). The discriminant analyses (Canonical Variate Analyses, CVA) performed on all fragments result in an excellent classification rate (over 87%, table 1), reinforcing the observation that ancient and modern dogs differ in shape, and that the differences involve different anatomical features located on all regions of the mandible. Ancient dogs had a more robust (body of the mandible being taller under the carnassial) and curved mandibles, with a straighter coronoid process, a more developed angular process, and a shallower masseteric fossa (figures 3 and S13).

236 (c) Modularity of the mandible

- The results of the modularity tests indicate significant modular structure in shape and allometry-free shape for all groups (p < 0.001, table 2). The CR coefficient is much lower in ancient dogs compared to modern dogs both when considering the shape (Z-score=11.3, p < 0.001) or the allometry-free shape (Z-score=10.5, p < 0.001), suggesting that mandible is more modular (i.e. less integrated) in ancient dogs (the anterior and posterior part of the mandibles covary less). The preliminary results obtained for the ancient and modern wolves and modern dingoes further suggest that modularity in 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 modern small dogs such as the pomeranian or dachshund, to larger sizes compatible with modern 249 250 large dogs such as the husky, golden retriever or German shepherd. However, the mandible size of 251 ancient doos was always much smaller than that of wolves and on average corresponds to that of modern beagles. Mandible shape varied from shapes similar to those of ancient or modern wolves or 252 253 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 doos, as well as 260 the relative short morphological distance between some dingoes and ancient dogs or between some ancient dogs and wolves or modern dogs of average morphologies suggests minimal intentional 261 262 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 discovered. This separation is not influenced by taphonomic or pathological processes (e.g. exostosis 266 267 associated with dental disease). Indeed, only the most complete mandibles were included in analyses with fragment A. Additionally, the parallel analyses performed with only anatomical landmarks 268 269 (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 explore this variability. 290

291

The anatomical differences between modern and ancient dogs may partly be explained by a change in the genetic composition of dog populations through time. Mitochondrial haplogroups C and D were dominant in Europe before the Bronze Age (63% and 20%, respectively), whereas they represent only 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

297 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
- 304 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
- 306 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.
- 308 309

310 Our analyses further show that the relationship between the anterior and posterior parts of the

- 311 mandible was less strong in ancient dogs compared to modern dogs (or captive wolves and
- 312 commensal dingoes, but the low sample size did not allow to draw conclusions for these animals).
- 313 The strong integration in the mandible of modern dogs, despite intense artificial selection, is
- 314 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
- 316 in canids [2]. This is consistent with previous studies evidencing similar patterns of developmental
- 317 integration in the skull of domestic/wild pairs of mammals [2,40,41]. The lower integration in ancient 318 dogs may be due to the fact that they were more submitted to natural (environmental) constraints
- 319 allowing some parts of the mandible to be more variable compared to modern dogs. In particular, the
- 320 mandibular ramus (providing attachment for masticatory muscles) is more likely to adapt quickly to
- 321 natural constraints and functional demands, related to, for example, diet, than the mandibular corpus
- 322 (bearing the teeth, which are much more conservative). The overall variability in diet in ancient dogs
- 323 likely being higher, this may have selected for more variability in the shape of the mandibular ramus.
- 324 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.
- 327 The observed differences in mean shape and integration of the mandible between modern and 328 ancient dogs and the fact that we did not find any extreme shapes in prehistoric dogs support the 329 hypothesis that the first farmers did not exert strong selection on dogs for aesthetic or utilitarian 330 reasons that might have constrained the anatomy (and modularity) of the mandible. Dogs were most 331 likely free-ranging and closer to a commensal lifestyle, as observed in some extant tribes of hunter-332 gatherers where humans share their diet with dogs [49]. This is further suggested by isotopic data for 333 some Neolithic dogs [29]. Additional feral dogs likely subjected to constraints closer to ancient dogs 334 (i.e. less intentional human selection and more natural constraints) are needed to investigate this
- 335 possibility further.
- 336 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 337 338 were eaten or buried complete, or in accordance with the mode of subsistence relying on hunting or 339 herding) to explore what drove diversity within the archaeological sample. This would allow more 340 profound insights into how the changes in human societies were accompanied by changes in the 341 morphology of dogs through time and space. Paleogenetic data might, for example, allow to test 342 whether the acquisition of the ability to digest starch was accompanied by changes in mandible form. 343 Additional contextual data would further enable a better understanding of when the morphological 344 diversification started: as soon as hunter-gatherers settled, with the farming transition, or later with the 345 complexification of Neolithic societies?

347 **5.** Conclusions

348 In summary, our comparison of mandible form between European dogs from the Mesolithic to the end of the Romanian Chalcolithic and modern breeds highlighted an unexpected diversity in dogs before 349 350 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-
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511 Figures and tables

- 512 **Figure 1.** Origin and fragmentation patterns of the archaeological mandibles. (A) Map showing
- selected sites dated from the Mesolithic to the end of the Romanian Chalcolithic in Western Europe
- 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,
- sliding semi-landmarks of surfaces are in green. 'module 1' and 'module 2' represent the two modules
 used in the modularity tests performed on the complete mandibles. Definitions of the anatomical
- 521 landmarks are provided in table S2.







- **Figure 2.** Visualization of the variability in mandible shape and size in ancient dogs with complete mandibles (fragment A), with comparison with ancient wolves and modern *Canis*. (A) Principal Component Analyses on modern and ancient specimens with fragment A (66 modern dogs, eight modern dingoes, eight modern wolves, 127 ancient dogs and four ancient wolves). Icons size is
- 527 proportional to the log₁₀ 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 log₁₀ 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
- 538 line, 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,
- 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
- 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; R² 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	Disparit y	Mean	CVA
A	127 – 24%	4	<i>P</i> <0.001	<i>P</i> <0.001	PVa 0.0039 PVm 0.0069 <i>P</i> <0.001	R ² 0.12 <i>P</i> <0.001	99.5%	R ² 0.027 <i>P</i> <0.001	R ² 0.082 <i>P</i> <0.001	PVa 0.0038 PVm 0.0065 <i>P</i> <0.001	R ² 0.093 <i>P</i> <0.001	83%
В	227– 43%	4	<i>P</i> <0.001	<i>P</i> <0.001	PVa 0.0038 PVm 0.0065 <i>P</i> <0.001	R ² 0.091 <i>P</i> <0.001	99%	R ² 0.028 <i>P</i> <0.001	R ² 0.079 <i>P</i> <0.001	PVa 0.0037 PVm 0.0062 <i>P</i> <0.001	R ² 0.077 <i>P</i> <0.001	94%
С	216– 41%	4	<i>P<</i> 0.001	<i>P</i> =0.006	PVa 0.0034 PVm 0.0054 <i>P</i> <0.001	R ² 0.080 <i>P</i> <0.001	98%	R ² 0.029 <i>P</i> <0.001	R ² 0.097 P<0.001	PVa 0.0033 PVm 0.0049 <i>P</i> <0.001	R ² 0.074 <i>P</i> <0.001	95%
D	392– 75%	6	<i>P</i> <0.001	<i>P</i> =0.004	PVa 0.0051 PVm 0.0068 <i>P</i> =0.004	R ² 0.047 <i>P</i> <0.001	99%	R ² 0.033 <i>P</i> <0.001	R ² 0.051 <i>P</i> <0.001	PVa 0.0049 PVm 0.0066 <i>P</i> =0.003	R ² 0.043 <i>P</i> <0.001	98%
E	437– 83%	7	<i>P</i> <0.001	<i>P</i> <0.001	PVa 0.013 PVm 0.018 <i>P</i> =0.009	R ² 0.050 <i>P</i> <0.001	99%	R ² 0.14 <i>P</i> <0.001	R ² 0.12 <i>P</i> <0.001	PVa 0.011 PVm 0.017 <i>P</i> =0.003	R ² 0.023 <i>P</i> <0.001	96%
F	155 – 29%	5	<i>P</i> <0.001	<i>P</i> <0.001	PVa 0.0062 PVm 0.0076 P=0.013	R ² 0.088 <i>P</i> <0.001	97%	R ² 0.021 P<0.001	R ² 0.082 P<0.001	PVa 0.0061 PVm 0.0075 <i>P</i> = 0.037	R ² 0.068 <i>P</i> <0.001	83%
G	386– 74%	6	<i>P</i> <0.001	<i>P</i> =0.017	<i>P</i> =0.11	R ² 0.053 <i>P</i> <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 <i>P</i> <0.001	96%
Н	160 – 30%	5	<i>P</i> <0.001	<i>P</i> <0.001	PVa 0.0035 PVm 0.0053 <i>P</i> <0.001	R ² 0.056 <i>P</i> <0.001	92%	R ² 0.0099 P<0.13	R ² 0.093 P<0.001	PVa 0.0035 PVm 0.0048 <i>P</i> =0.002	R ² 0.041 <i>P</i> <0.001	83%
Ι	488– 93%	7	<i>P</i> <0.001	<i>P</i> =0.21	<i>P</i> =0.9	R ² 0.021 <i>P</i> <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 <i>P</i> <0.001	93% 98% ancient 62% modern
J	215 – 41%	5	<i>P</i> <0.001	<i>P</i> <0.001	PVa 0.0044 PVm 0.0058 <i>P</i> <0.001	R ² 0.11 <i>P</i> <0.001	97%	R ² 0.027 P<0.001	R ² 0.097 P<0.001	PVa 0.0043 PVm 0.0056 <i>P</i> =0.009	R ² 0.075 <i>P</i> <0.001	91%
Total	525	8										

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

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