Journal of Archaeological Science: Reports 57 (2024) 104660

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

Dogs from the past: Exploring morphology in mandibles from Iberian archaeological sites using 3D geometric morphometrics

Raquel Blázquez-Orta [a,b], Laura Rodríguez [c,d], Mónica Major González [e], Verónica Estaca-Gómez [f], Ignacio De Gaspar [a,g], Robert S. Feranec [h], José Miguel Carretero [d], Juan Luis Arsuaga [b,i], Nuria García [a,b,i,*]

[a] Grupo UCM Ecosistemas Cuaternarios, Universidad Complutense de Madrid, 28040, Madrid, Spain
[b] Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, 28040, Madrid, Spain
[c] Área de Antropología, Departamento de Biodiversidad y Gestión Ambiental, Edificio Facultad de Ciencias Biológicas y Ambientales, Universidad de León, Spain
[d] Laboratorio de Evolución Humana, Departamento de Ciencias Históricas y Geografía, Universidad de Burgos, Edificio I+D+i, 09001, Burgos, Spain
[e] Áqaba arqueólogos, s.l., 28007, Madrid, Spain
[f] Departamento de Prehistoria, Historia Antigua y Arqueología, Facultad de Geografía e Historia, Universidad Complutense de Madrid, 28040 Madrid, Spain
[g] Sección Departamental de Anatomía y Embriología, Facultad de Veterinaria, Universidad Complutense de Madrid, 28040, Madrid, Spain
[h] Research and Collections, New York State Museum, Albany, NY, United States
[i] Centro Mixto UCM-ISCIII de Evolución y Comportamiento Humanos, 28029, Madrid, Spain

ARTICLE INFO

Keywords:
Morphology
Size
Canis lupus familiaris
Vulpes vulpes
Chalcolithic
Bronze Age
Iberian Peninsula

ABSTRACT

We describe the shape variability of nine dog hemimandibles recovered from two Holocene archaeological sites on the Iberian Peninsula. In this study we mainly focus on the Chalcolithic age dog remains recovered from Barrio del Castillo (Torrejón de Ardoz, Madrid), but also, make comparisons to dog specimens from El Portalón (Sierra de Atapuerca, Burgos) Bronze Age. We used geometric morphometrics (3D) to describe mandibular morphology and compared these specimens with a modern sample of Iberian wolves, dogs, and red foxes. As complete mandibles are rarely found in the archaeological record, we also analysed the variability of the shape on fragments of mandibles. Here, we examine if there is morphological variability or a continuity in size between Chalcolithic and Bronze Age dogs. A scenario of very similar dogs, with a continuity in the size, is expected in the inner regions of the peninsula in contrasts with the coastal sites (influenced by a higher commercial activity). Our results suggest a continuity in the size and morphology of M_1. These dogs still conserved diagnostic wolf traits in relation to the carnassial zone. Additionally, we observe that the region behind the M_1 in Chalcolithic and Bronze Age dogs is slightly different when we analysed the fragmentary mandibles.

1. Introduction

1.1. The origin of dogs

Due to genetic and morphological similarities, dogs and wolves are recognized as belonging to the same species, *Canis lupus* (Clutton-Brock, 1995; Vilà et al., 1997). In this context, the identification of *Canis lupus* in an archaeological site takes on a distinct significance depending on whether the specimen is attributed to a wolf or a dog, as it may have implications for domestication. Given these significant similarities and the importance of accurate classification, we will use distinct names: *Canis lupus familiaris* for dogs (Gentry et al., 2004) and *Canis lupus signatus* for Iberian wolves. The dog, (*Canis lupus familiaris*), was domesticated in the Upper Paleolithic from its agriotype, the grey wolf (*Canis lupus*). This idea has a consensus among palaeontologists (Kurtén, 1968; Olsen, 1985; Morey, 1992, 1994; Clutton-Brock, 1995), and various DNA analyses (Leonard et al., 2002; Savolainen et al., 2002; Thalmann et al., 2013; Vilà et al., 1997; vonHoldt et al., 2010) have confirmed it. While the ancestor of domestic dogs is no longer in question, the debate on the timing and region of the origin of wolf domestication is still open.

---

* Corresponding author.
E-mail addresses: rborta@ucm.es (R. Blázquez-Orta), lrodg@unileon.es (L. Rodríguez), info@arqueologosaqaba.com (M. Major González), vestaca@ucm.es (V. Estaca-Gómez), idegaspar@vet.ucm.es (I. De Gaspar), robert.feranec@nysed.gov (R.S. Feranec), jmcarre@ubu.es (J. Miguel Carretero), jlarfer@gmail.com (J. Luis Arsuaga), nugarcia@ucm.es (N. García).

https://doi.org/10.1016/j.jasrep.2024.104660
Received 20 March 2024; Received in revised form 24 June 2024; Accepted 24 June 2024

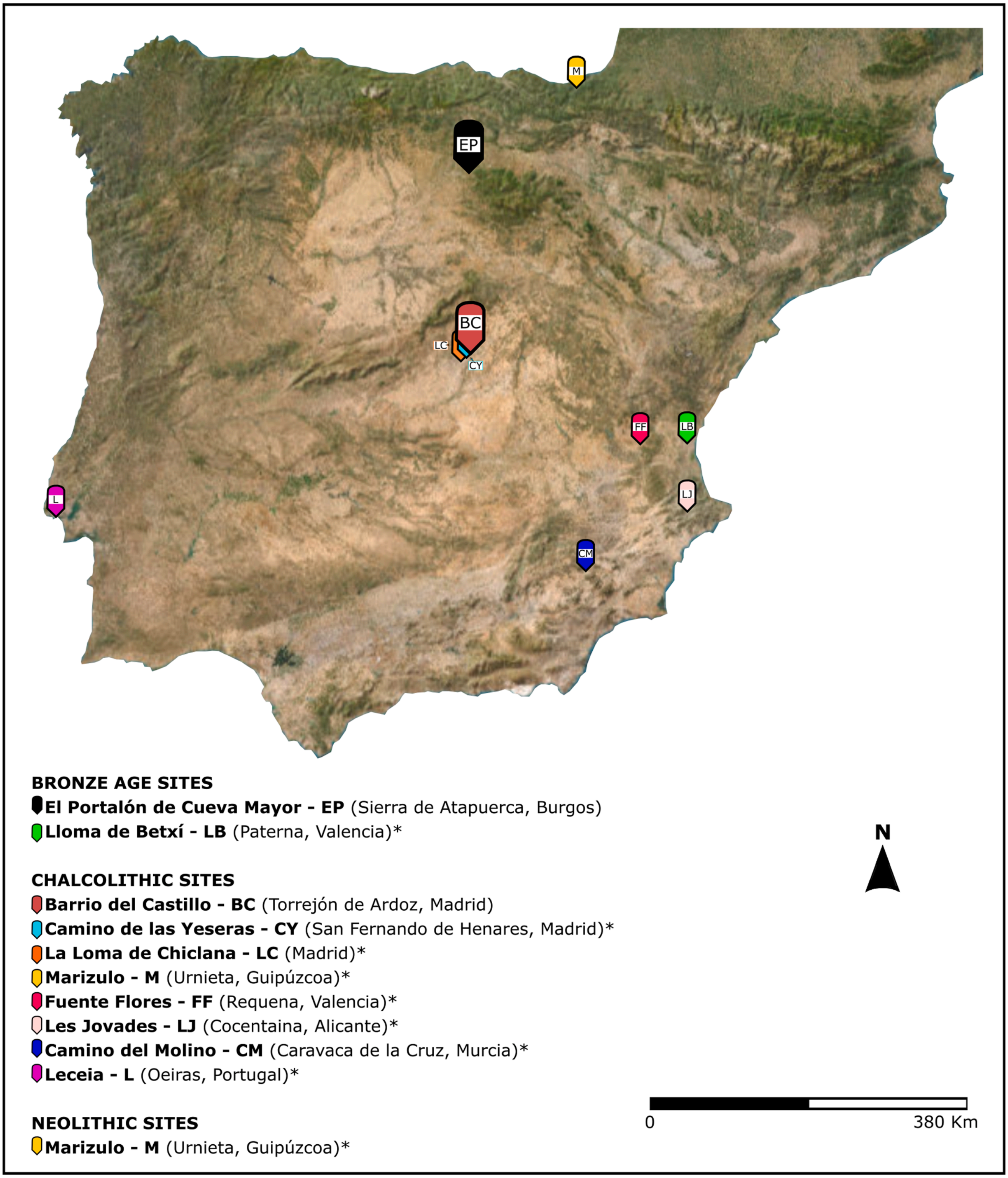

Fig. 1. Iberian Peninsula map showing sites of several cultural periods (Bronze Age, Chalcolithic and Neolithic). Barrio del Castillo (BC) and El Portalón (EP) are the main sites of this study. The sites marked with an asterisk in the legend are Iberian sites (with dog remains mentioned in the Fig. 7 and Tables 4-5) taken from bibliography (Altuna, 1967, 1980; Sanchis and Sarrión, 2004; Daza-Perea, 2015; Catagnano, 2016; Detry and Cardoso, 2010; Blaschikoff et al., 2022). Modified from ArcGis app (https://www.arcgis.com/apps/mapviewer/index.html).

Additional questions also remain regarding the reasons that gave rise to the domestication of wolves—a carnivore species that competes with humans for prey. Domestication may have arisen to obtain a benefit from humans, or because of a natural ecological association between wolves and people, without any benefit to people (Morey and Jeger, 2015). Several scenarios have been debated about the possible onset of domestication (Coppinger and Coppinger, 2001; Crockford, 2006; Hare et al., 2012; Morey and Jeger, 2015; Dugatkin, 2018). The main controversy about the time and geographical origin of wolf domestication is related to fossil specimens identified as “dog-like wolves”: some authors

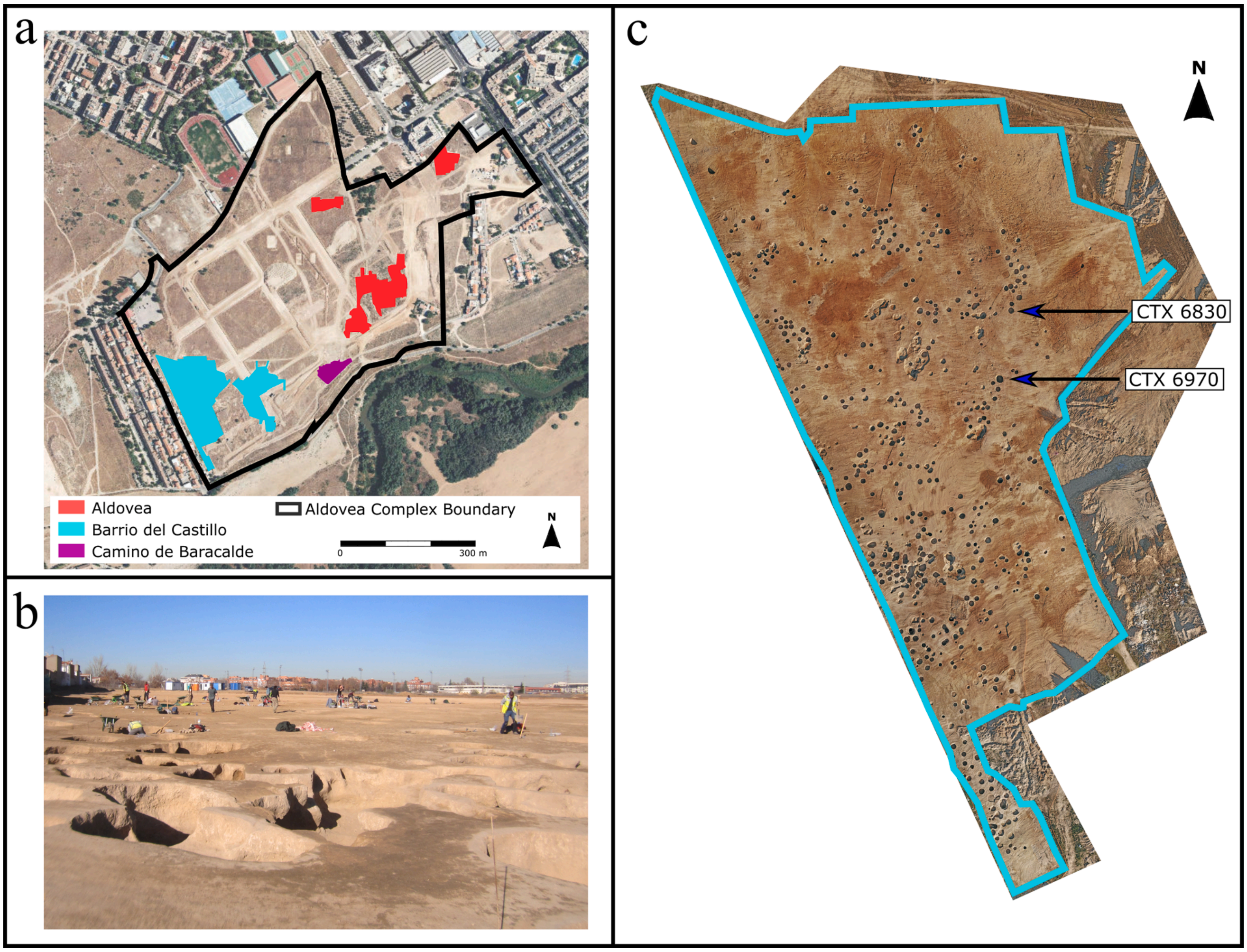

Fig. 2. Location of the Barrio del Castillo (BC) site. a) Aldovea Complex. The BC site is colored in blue. b) General view of the pits of the BC. c) View from above the BC site. The contexts 6830 and 6970 are marked with an arrow. Images: áqaba, s.l.

consider these forms as predecessors of dogs (accepting an early origin, even exceeding 30 ka) while others do not (Germonpré et al., 2009, 2012; Ovodov et al., 2011; Morey and Jeger, 2015). What seems to be widely accepted is that the most ancient archaeological remains of clearly domesticated dogs were found widespread in Europe, the Near East, and the Far East, with chronologies ranging from ~ 15,000 to ~ 8,000 cal. BP (Olsen, 1985; Dayan, 1994; Clutton-Brock, 1995; Savolainen, 2007; Frantz et al., 2016).

Studies on dog origins, conclude that most Paleolithic dogs (Magdalenian and Mesolithic) analysed in Western European sites share the same mitochondrial haplogroup C (Hervella et al., 2022), with some exceptions carrying haplogroup A (Pires et al., 2019). The scenario proposed from these studies suggest a continuity from ancient Magdalenian hunter-gatherer's populations towards more recent settled human populations (Epipaleolithic and Mesolithic).

During the upper Paleolithic, dogs are already present in the Iberian Peninsula. A canid humerus, identified as a dog, was recovered in the archaeological excavations directed by J. Altuna in the Erralla cave (Gipuzkoa, Basque Country) (Altuna and Mariezkurrena, 1985; Altuna, 1994). A radiometric and genetic study conducted by Hervella et al. (2022) on this remain, confirms not only this determination, but also that a domestic dog lived ~ 17,000 years ago (17,410–17,096 cal BP) in the Basque Country. The Erralla specimen represents one of the earliest domesticated dogs in Europe, dated to the Magdalenian period, at the end of the LGM.

1.2. *Dogs' variability in the Iberian Peninsula*

Mesolithic dogs widely extend over the Iberian Peninsula, although in Central Iberia the fossil record is especially poor, resulting in fewer studies (Catagnano, 2016; Sanchis and Sarrión, 2004; Castaños Ugarte, 2004) compared to the better knowledge of dog morphotypes from eastern Iberian sites. During the Neolithic, Bronze Age, and Iron Ages there is a greater homogeneity of dog sizes as compared to the Chalcolithic and Roman periods where dogs are highly diverse in size (Catagnano, 2016). Several studies (Sanchis and Sarrión, 2004; Ruiz García-Vaso et al., 2013, 2014) carried out analyses on shoulder height and showed two size categories for dogs: small (<45 cm) and medium (~45–55 cm). Catagnano (2016) carried out a revision of sites with dog remains located in the Cantabrian margin and extended along the Mediterranean coast, although the morphometric study was focused on five Catalonian sites, and one located in Murcia. Albizuri et al. (2019) described Neolithic small-sized Iberian dogs from the Catalonian coast. A scapula of a small dog was recovered in the Neolithic level of Marizulo site (Guipúzcoa) (Altuna, 1967, 1980, 1994). Sanchis and Sarrión (2004) described a homogeneous population of small-medium size dogs from the Neolithic to the Bronze Age in Valencia. This homogeneity is also reported in other chronologies from Iberian sites (Castaños Ugarte, 2004; Catagnano, 2016; Gil Cano et al., 2011; Ruiz García-Vaso et al., 2013, 2014; Daza-Perea, 2015, 2019). However, it is in Roman times where a great variation in size is observed (Colominas, 2016; Pires et al., 2018). Other studies carried out by Pires et al. (2019) and Blaschikoff

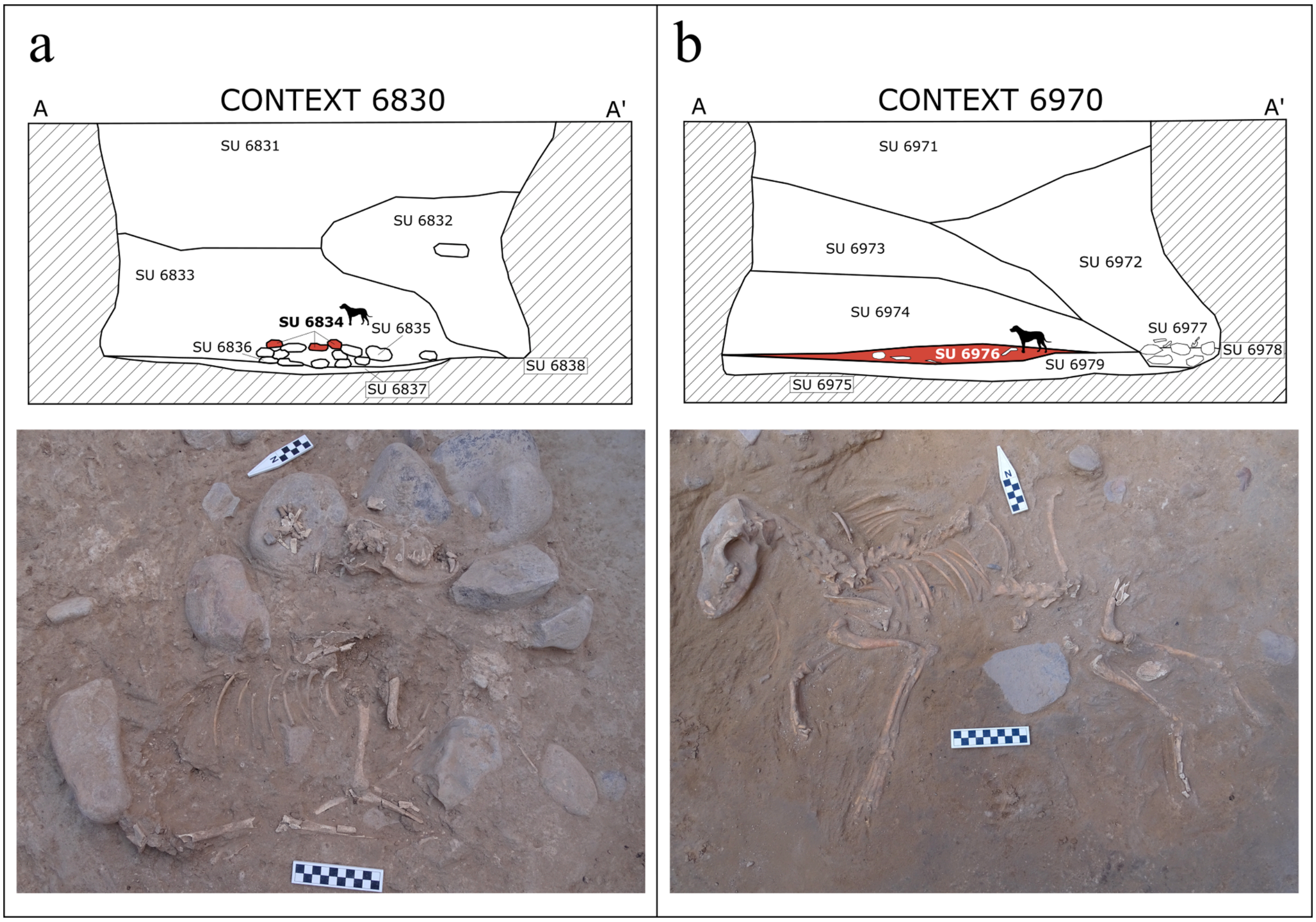

Fig. 3. Profiles and pictures of the Barrio del Castillo site. a) Context 6830. b) Context 6970. The mandibles of this study were recovered from Stratigraphic Units (SU) 6834 and 6976 (colored in red in the profiles). Images: áqaba, s.l.

et al. (2022) were focused on genetic analysis and performed a few measurements of the carnassial and long bones (radius, ulna, femur, and humerus, for shoulder heigh estimation) without identifying any differences in morphological patterns. Blaschikoff et al. (2022) showed that Iberian (Portugal and Valladolid) Chalcolithic dogs already exhibited various morphotypes, a medium size (mesomorphic type), and a larger size. There is a little variation since Neolithic to the Bronze Age and a larger variation from the Roman Period to present (Castaños Ugarte, 2004; Sanchis and Sarrión, 2004; Gil Cano et al., 2011; Ruiz García-Vaso et al., 2013, 2014; Daza-Perea, 2015, 2019; Colominas, 2016; Pires et al., 2018; Albizuri et al., 2019; Blaschikoff et al., 2022).

In addition to temporal differences, we hypothesize that there may be regional differences in the sizes of dogs; we would expect a greater size variation in coastal sites, which may be influenced by maritime exchange, compared to inland populations (where this diversity might remain constant). Maritime trade may have played a crucial role in animal diversity (Anderung et al., 2005; Meiri et al., 2017; Galindo-Pellicena et al., 2020). This is reflected in studies from sites in the eastern Mediterranean (Harding et al., 2023a) and the Levant (Chahoud et al., 2023; Harding et al., 2023b), where livestock from coastal areas show a greater morphological variability compared to inland areas, possibly due to higher maritime connectivity.

With this in mind, our aim in this article, is to increase the knowledge of the morphological variability of Iberian Chalcolithic dogs with a focus on the Central Iberian fossil record. For this purpose, we have focused on the Barrio del Castillo (Torrejón de Ardoz, Madrid) site that contains four mandibles of Chalcolithic age. Furthermore, to understand evolutionary changes or patterns in "ancient breeds" through time, we have compared the Barrio del Castillo Chalcolithic dogs with the El Portalón Bronze Age dogs, both occurring in central Iberia. Also, we address whether the genetic continuity observed by Hervella et al. (2022) is also reflected in the dogs' mandibular morphology, or, if the morphological variability among modern European dogs was already established before the Bronze Age, as proposed by Brassard et al. (2022).

2. Sites

2.1. *Barrio del Castillo (BC)*

The Aldovea Complex is an archaeological site located south of Torrejón de Ardoz (Madrid, Spain) (Fig. 1). It is divided into three different sections: Barrio del Castillo (BC), Camino de Baracalde and Aldovea (Fig. 2). BC where about 800 pits have been identified is at the southwest of the Aldovea Complex. Remains of pottery, lithic tools, and fauna, attributed to three cultural periods (Chalcolithic, Protocogotes and Cogotas), have been recovered (Major González et al., 2019). The BC faunal assemblage is under study: it consists of equids, bovines, ovicaprines, suids and dogs. A total of 1688 dog remains were recovered from these cultural periods (Chalcolithic, Protocogotes and Cogotas) (Estaca-Gómez, 2022).

Here, we analysed four hemimandibles of dogs recovered from the Chalcolithic period, specifically from contexts 6830 and 6970 (Fig. 3). Both are pits that have an oval layout and flat base. Context 6830 is a pit-like structure filled by several anthropogenic strata covering two canids deposited at the structure's base and separated by a quartzite stones/pebbles bed. In stratigraphic unit 6834 a complete canid was recovered in anatomical articulation. It was located on a quartzite bed and oriented SE/NW, placed on its left side. Context 6970 is a pit-like structure (SU

Table 1
Sample (modern and fossil remains) used in this study. The table shows the institutions and sites of each specimen, and the cultural period and dating of fossils. *These samples belong to dog remains analyzed for radiocarbon dating, but as they are not mandibles, they are not included it in the morphometric analyses. **This specimen lacks most of the region analyzed in the morphological study, so only the variable 'canine size' is included in the study.

Sample	Species	Institutions (modern) and site (fossils)	n	Specimens (fossils)	Cultural period [radiocarbonical datation (year cal. BP)]	Dating
Modern	*C.l. signatus*	LEH, Riaño, MACV, MVZ, MNCN	22			
	C.l. familiaris	Veterinary University	9			
	V. vulpes	MNCN	10			
Fossils	*C.l. familiaris*	El Portalón de Cueva Mayor (Sierra de Atapuerca, Burgos)	5	CMI-Y6-24–4	Late Bronze Age (level 3/4)	
				CMI-A6-48–4, CMI-A8-51–1, CMI-C4-63–2	Middle Bronze Age (level 3/4) [dates from 3330 ± 60 to 3560 ± 40 years BP; 1750–1490 to 2010–1760 years cal. BP]	Carretero et al. (2008)
				CMI-D2-87	Early Bronze Age (level 5) [dates from 3630 ± 40 to 3760 ± 40 years BP; 2290 to 1890 years cal. BP]	Carretero et al. (2008)
		El Portalón		ATP'18.1257*	Bronze Age [3660 ± 15]	This study (UC Irvine's KCCAMS)
		El Portalón		ATP'10.406*	Chalcolithic-Bronze Age [4195 ± 15]	This study (UC Irvine's KCCAMS)
		Barrio del Castillo (Torrejón de Ardoz)	4	BC'19.6976Q, BC'19.6976L_4, BC'19.6976 M, BC'19.6834_FP	Chalcolithic (context 6970) Chalcolithic (context 6830) [4570 ± 15 years BP]	This study (UC Irvine's KCCAMS)
		El Portalón		ATP'17.2450*	Neolithic [6215 ± 20]	This study (UC Irvine's KCCAMS)
		El Portalón	1	ATP'15.UE507.392**	Neolithic	

6975) filled by four anthropic levels (SSUU 6971, 6972, 6973 and 6974 that seal a faunal deposit (SU 6976 and SU 6977) located partly on a quartzite bed (SU 6978) and on fill (SU 6979). Stratigraphic unit 6976 is an anthropogenic stratum where several animals (suids, ovicaprines and canids) were placed, some of them in anatomical articulation.

2.2. *El Portalón de Cueva Mayor (EP)*

El Portalón is situated in the Sierra de Atapuerca, approximately 15 Km east of the city of Burgos in northern Spain (Fig. 1). EP is a Holocene archaeo-palaeontological site and constitutes one of the entrances to the Cueva Mayor-Cueva del Silo karst system (Carretero et al., 2008; Ortega et al., 2008; Pérez-Romero et al., 2015, 2016). The stratigraphic sequence of EP has a radiometrically dated chronology ranging from 30 ka to 1000 years BP (Carretero et al., 2008) and it is divided in a lower sedimentary unit (Upper Pleistocene) and an upper unit (Holocene). The Holocene unit contains numerous deposits that document different occupations including the Mesolithic, Neolithic, Chalcolithic, Bronze Age, Iron Age, Roman, and Medieval periods (Carretero et al., 2008; Pérez-Romero et al., 2016). Some deposits recovered in the upper unit consist of fauna remains, pottery, lithic and bone industry (Carretero et al., 2008; Pérez-Romero et al., 2015, 2016, 2017; Galindo-Pellicena et al., 2017; Francés-Negro et al., 2019). The EP fauna includes ovicaprines, bovines, equids and suids (Galindo-Pellicena et al., 2017). A total of 130 dog specimens (NISP) have been identified in EP from Neolithic to Bronze Age (Galindo-Pellicena et al., 2022). From EP, we analysed five *Canis* hemimandibles, recovered from the Middle Bronze Age and Early Bronze Age (Table 1).

3. Material and methods

3.1. *Material*

3.1.1. *Fossil sample*

The total fossil sample is comprised of nine hemimandibles from the EP and BC sites (Table 1). We chose the most complete and best-

Fig. 4. Hemimandibles of *Canis lupus familiaris* from Barrio del Castillo (a-d) and El Portalón (e) sites. a) BC'19.6976Q. b) BC'19.6976 M. c) BC'19.6976l. d) BC'19.6834_FP. e) ATP'15.UE507.392. Scale = 5 cm.

preserved mandibles for this study, and we dismissed the juvenile specimens. One of the requirements for this sampling was that the mandibles had to have the carnassial due to it is a relevant element to compare between these types of canids. Five remains from EP were recovered from Bronze Age levels, and they are deposited in the Regional Museum of Burgos. These mandibles were described in a previous study (Blázquez-Orta et al., 2022, fig. 2). Four Chalcolithic remains from BC (Fig. 4) were recovered. The 6976Q and 6976l fossils are left complete hemimandibles that preserve the complete dental series (except P_1 in 6976l). The 6976 M specimen is a fragment of the left hemimandible from the alveolus of the P_3 that preserve the dental series P_4-M_2. The 6834_FP remain is a fragment of the right hemimandible from P_4 that preserve the dental series P_4-M_2. We also analysed the canine of an additional mandible (ATP15.UE507.392) from the Neolithic level of EP which although is incomplete it provided enough information to compare to the Bronze Age and Chalcolithic dogs.

3.1.2. *Modern sample*

As a comparative sample, a total of 41 hemimandibles of Iberian modern wolves (*Canis lupus signatus*), dogs (*Canis lupus familiaris*) and red foxes (*Vulpes vulpes*) were selected for this study (Table 1). Following Brassard et al. (2022) the largest, smallest, most brachycephalic or dolichocephalic extant dogs have no equivalent in the archaeological sample. Most of the currently existing dog breeds did not emerge until the 19th century (Dunner and Cañón, 2014). Also, considering that the first domestic forms were wolf-like (Germonpré et al., 2009, 2015) the sample of dogs studied here was selected due to their similarity (in size and shape) to their agriotype, the wolf (*Canis lupus*), and excluding those morphologies that correspond to breeds that are the product of human modification (Dunner and Cañón, 2014; Parker et al., 2017). The principal idea to add foxes in this analysis is to compare the morphology of *Vulpes* and *Canis*, once size was eliminated. Occasionally, fragmentary remains of small and slender canids are incorrectly attributed to foxes in archaeological contexts. A deep canid comparative analyses including *Vulpes* can help prevent misidentifications and increase our knowledge on canid morphology.

This sample comes from different museums and institutions: Museo Nacional de Ciencias Naturales (MNCN, Madrid), Museo de Anatomía Comparada de Vertebrados (MACV, Complutense University of Madrid-UCM), a natural reserve from Riaño, Laboratorio de Evolución Humana (LEH) from University of Burgos (UBU), the osteology collection of the Anatomy and Embriology Department from University of Veterinary (UCM) and Museum of Vertebrate Zoology (MVZ, Berkeley).

3.2. *Methods*

3.2.1. *Carnassial (M_1) and canine (C): Measurements and statistical analysis*

We measured the length and width of the M_1 (using a digital calliper to the nearest 0,01 mm) of the sample (Table 1). Also, we added M_1 measurements obtained from literature of 62 modern wolves (Detry and Cardoso, 2010) and 36 Neolithic to Bronze Age specimens from Iberian sites (Fig. 1) (Altuna, 1967, 1980; Sanchis and Sarrión, 2004; Daza-Perea, 2015; Catagnano, 2016; Blaschikoff et al., 2022). To compare the size of M_1 we performed basic statistics (mean, minimum, maximum, standard deviation, and coefficient of variation). Statistical analyses were carried out with SPSS (v. 26). A Kolmogorov-Smirnov test was performed to contrast the normality of M_1 (length and width). As Normality fails for M_1 variables, we have carried out a Kruskal-Wallis test (a non-parametric test) to determine whether there are significant differences between the studied groups.

We also analysed the canine size of the Neolithic mandible (ATP15. UE507.392) from EP and we compare it with the Bronze Age and Chalcolithic dogs. We took two measurements: anteroposterior (ØAPTC) and transverse diameter of the canine (ØTC). From these measurements

Table 2

Position of 35 landmarks (ldm) and 28 curve semilandmarks (Curve sldm) on complete mandibles. The type of each landmark is defined following Bookstein (1991).

Number	Type	Description	Type
1	ldm	Infradentale	I
2–3	ldm	Alveoli of the canine (oral-aboral points)	I
4	ldm	Alveolus of the first premolar (P_1) (oral point)	I
5, 6–7	ldm	Alveoli of the second premolar (P_2) (oral point, aboral points in labial-lingual side)	I
8–9, 10–11	ldm	Alveoli of the third premolar (P_3) (oral, aboral points in labial-lingual points)	I
12–13	ldm	Alveoli of the fourth premolar (P_4) (oral points in labial-lingual side)	I
14–15	ldm	Alveoli of the carnassial (M_1) (oral points in labial-lingual side)	I
16	ldm	Point of apex of paraconid (M_1)	I
17	ldm	Valley between paraconid and protoconid (M_1)	II
18	ldm	Point of apex of protoconid (M_1)	I
19	ldm	Point of apex of metaconid (M_1)	I
20	ldm	Valley between protoconid and talonid (M_1)	II
21	ldm	Point in hipoconid	I
22	Ldm	Point in entoconid	I
23–24	ldm	Alveoli of the M_1 (aboral points in labial-lingual side)	I
25–26	ldm	Alveoli of the second molar (M_2) (aboral points in labial-lingual side)	I
27	ldm	Alveolus of the third molar (M_3) (aboral point)	I
28	ldm	Coronoid process	I
29	ldm	Point in the mandibular notch	I
30	ldm	Midpoint of the angular process	II
31	ldm	Ventral point of the fossa masseterica	I
32	ldm	Point of the mandibular foramen	I
33	ldm	Mental foramen (aboral point)	II
34–35	ldm	Medial point in the condylar process (labial-lingual points)	II
36–38	Curve sldm	Labial border of M_1 (oral-aboral)	III
39–41	Curve sldm	Lingual border of M_1 (oral-aboral)	III
42–45	Curve sldm	Curvature of the ascendent ramus between points 27 and 28	III
46–49	Curve sldm	Curvature of the ascendent ramus between points 28 and 29	III
50–53	Curve sldm	Curvature of the ascendent ramus between points 29 and 30	III
54–63	Curve sldm	Curvature of the body mandible (aboral-oral)	III

Table 3

Position of 13 landmarks (ldm) and 10 curve semilandmarks (Curve sldm) on fragmentary remains of mandibles. The type of each landmark is defined following Bookstein (1991).

Number	Type	Description	Type
1–2	ldm	Alveoli of the fourth premolar (P_4) (oral points in labial-lingual side)	I
3–4	ldm	Alveoli of the carnassial (M_1) (oral points in labial-lingual side)	I
5–6	ldm	Alveoli of the carnassial (M_1) (aboral points in labial-lingual side)	I
7–8	ldm	Alveoli of the second molar (M_2) (aboral points in labial-lingual side)	I
9	ldm	Alveolus of the third molar (M_3) (aboral point)	I
10	ldm	Ventral point of the fossa masseterica	I
11	ldm	Point of the mandibular foramen	I
12	ldm	Point at the base of the mandibular ramus, right under aboral point of M_3	II
13	ldm	Point at the base of the mandibular ramus, right under oral point of P_4	II
14–16	Curve sldm	Labial border of M_1 (oral-aboral)	III
17–19	Curve sldm	Lingual border of M_1 (oral-aboral)	III
20–23	Curve sldm	Ventral border curve of the body mandible (oral-aboral)	III

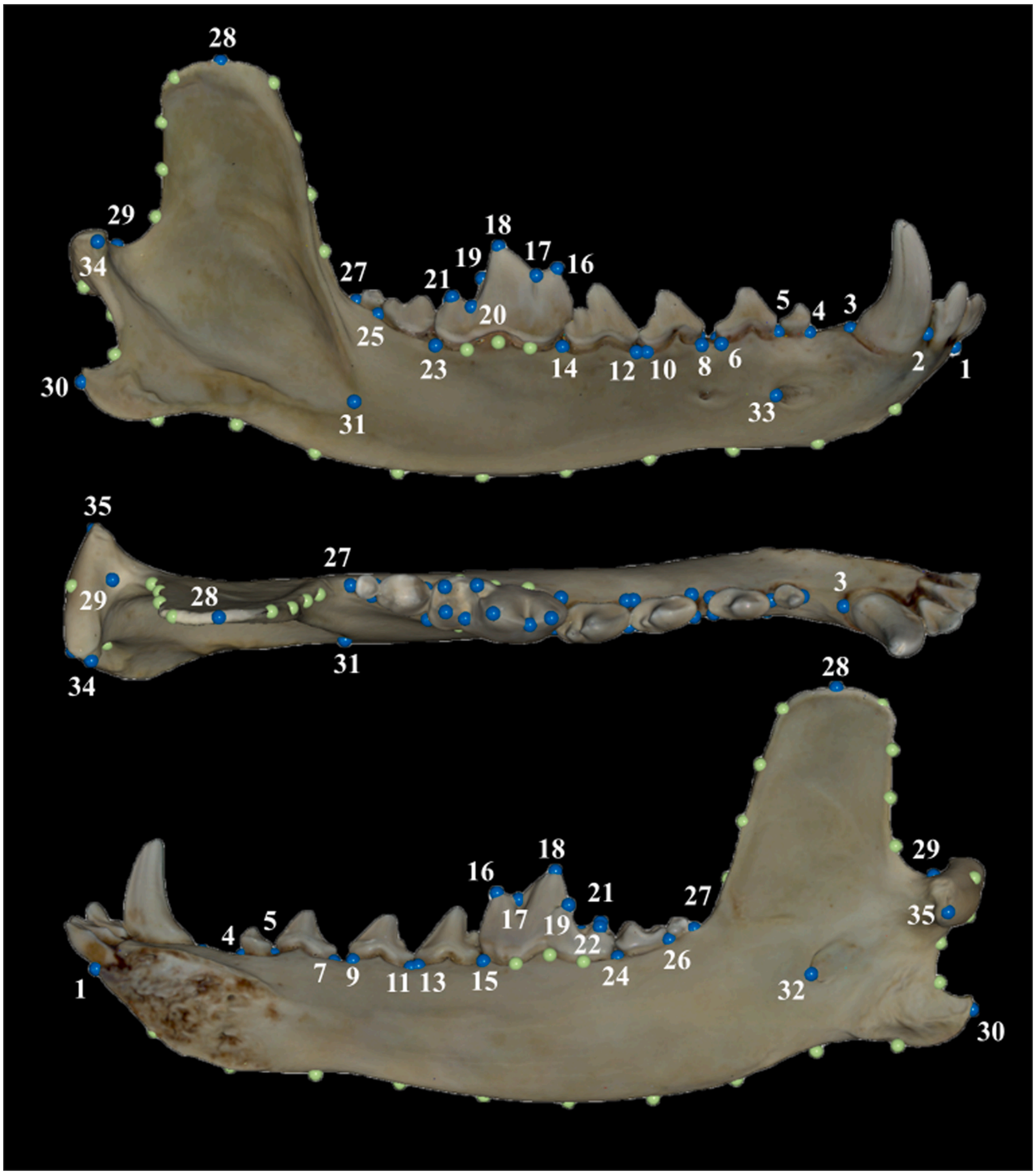

Fig. 5. Template of digitization (used for complete remains) on the hemimandible of *Canis l. signatus*. Landmarks (blue) and sliding curve semilandmarks (green) used to define the mandibular morphology of each specimen. Labial, occlusal, and lingual views. See Table 2 for landmark and semilandmark positions.

we calculate the mean ($\overline{X}$) and standard deviation. Also, we estimated the size of a dog from BC to compare it with dogs from other sites in the Iberian Peninsula. We estimated the shoulder height (height of the dog just behind the withers) using a tibia of specimen 6976Q following the factors in Harcourt (1974).

3.2.2. Geometric morphometrics: 3D scanning, landmarking protocol and statistical analysis

To extract relevant information of mandibles we use 3D Geometric Morphometrics (**GM**). This method allows us to visualize differences among complex shapes, locating the morphological variation though landmarks spatially (Zelditch et al., 2004). We created high-resolution 3D digital models of the fossil mandible specimens with a surface scanner. It is a structured light scanner (EinScan SP of Shining 3D) for digitally capturing all the information of the mandible such as texture, external surface, and colour. The result was a 3D digital model for each specimen. These 3D objects (PLY file) were exported to Viewbox software (free v.4.1.0.12; https://www.dhal.com), where we digitized landmarks and curve semilandmarks on different regions of the mandibles (Table 2, Table 3 and Fig. 5, Fig. 6). Landmarks are homologous anatomical points (Zelditch et al., 2004) that facilitate a better shape analysis. Bookstein (1991) defined three types of landmarks: type I (juxtaposition of tissues, for example points of contact between bones), type II (points of maxima curvature) and type III (extremal points or semilandmarks).

As part of our protocol, we employed semilandmarks to quantify curves on the mandibles. Points that represent those curves are not homologous; consequently, we applied a sliding process on semilandmarks through Viewbox software (free v.4.1.0.12). This sliding method is designed to reduce differences in shape between each specimen and the average shape of the sample (Gunz and Mitteroecker, 2013). The method used for this procedure was bending energy, which is defined as the amount of shape deformation of each specimen with respect to the reference configuration (Gunz and Mitteroecker, 2013; Gunz et al., 2005; Torres-Tamayo et al., 2018). Using bending energy procedure, the semilandmarks slide at the same time and they are influenced by the anatomical landmarks (Gunz and Mitteroecker, 2013).

We carried out an analysis on complete mandibles to obtain

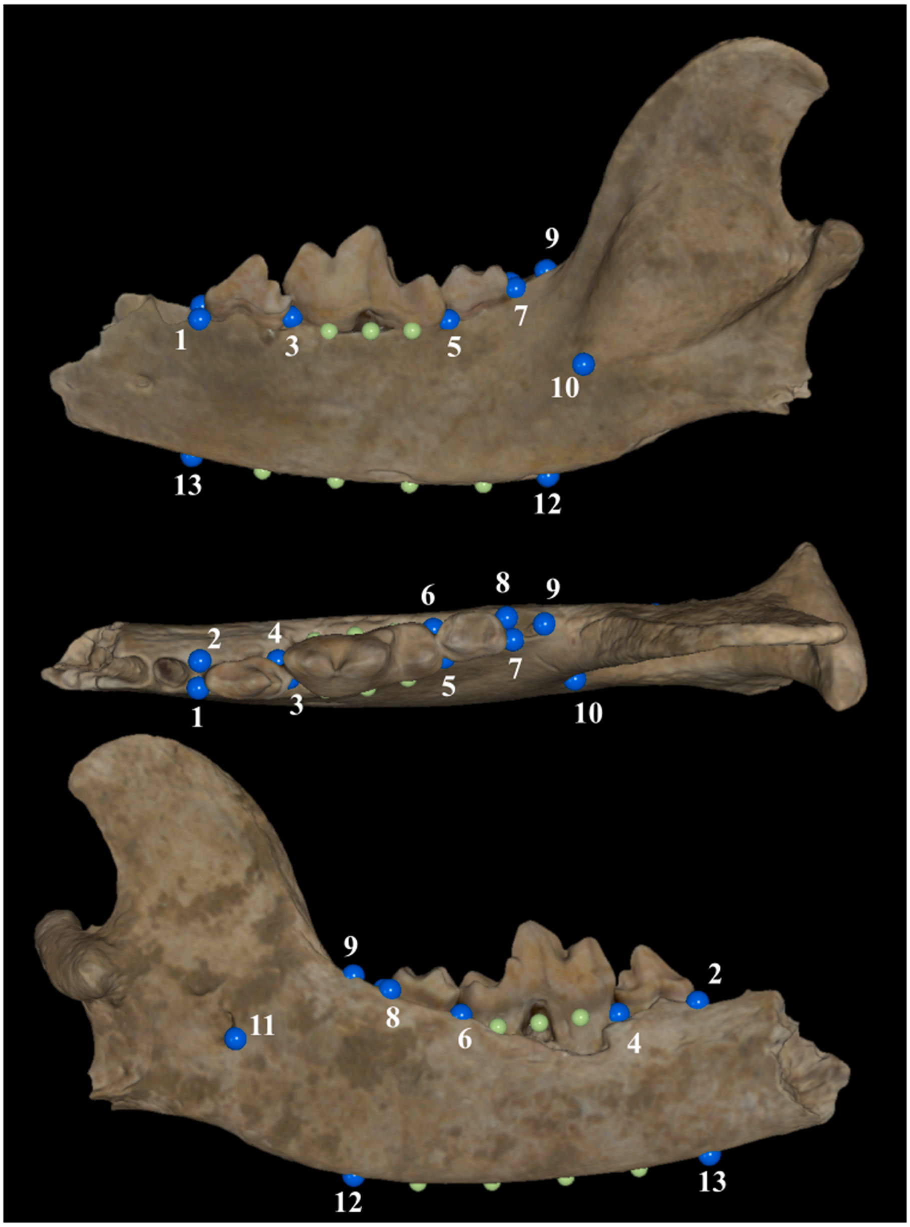

Fig. 6. Template of digitization (used for fragmentary remains) on the hemimandible *C.l. familiaris* (6976 M). Landmarks (blue) and sliding curve semilandmarks (green) used to define the mandibular morphology of each specimen. Labial, occlusal, and lingual views. See Table 3 for landmark and semilandmark positions.

information to discriminate between dogs, wolves, and foxes. A total of 63 landmarks and semilandmarks (Table 2, Fig. 5) were digitized on the mandibles to quantify the shape variation: 35 landmarks and 28 semilandmarks along 6 curves. These landmarks were adapted from Brassard et al. (2020) including landmarks placed on the cusps of the carnassial and on the curve of ascendant ramus. Additionally, as some of the specimens of the EP and BC are fragmentary and incomplete, we focused our research on informative regions of mandible derived from this previous study. For incomplete specimens, we digitized a total of 23 landmarks and semilandmarks (Table 3, Fig. 6): 13 landmarks, 10 semilandmarks along 3 curves.

The 3D coordinates (X, Y and Z) obtained were exported to MorphoJ software (version 1.06d; Klingenberg, 2011) where we performed a Procrustes superimposition to homogenize the data (Rohlf and Slice, 1990; Rohlf and Marcus, 1993; Zelditch et al., 2004). We conducted a Principal Components Analysis (**PCA**) to compare shape variation (Zelditch et al., 2004) between mandibles and identify differences within the studied sample, which includes wolves, dogs and foxes. Furthermore, we conducted two analysis that includes information on centroid size (CS). The size in geometric morphometrics (CS) is defined as the square root of the summed squared deviations of the coordinates from their centroid (Zelditch et al., 2004; Mitteroecker and Gunz, 2009). First, we carried out a boxplot that shows the variation of the CS on complete mandibles. Second, we assess a regression analysis to know if the shape of each PC is correlated with size, as often larger organisms tend to have a different shape than smaller ones (Zelditch et al., 2004).

4. Results

4.1. *Carnassial (M_1) and canine (C). Metrical analysis*

The comparative analyses on M_1 (Table 4) revealed an important difference in size between the modern Iberian wolves (with a larger size of M_1) and the other analyzed groups (modern and fossil dogs). M_1 in modern Iberian wolves ($\overline{X}$ L M_1 = 27.20 mm and $\overline{X}$ W M_1 = 11.36 mm) have larger measurements than modern ($\overline{X}$ L M_1 = 23.07 mm and $\overline{X}$ W

Table 4
Basic statistics (n, Mean, Min, Max, St. dev, CV) on length and width of M_1. Modern wolves show a less dispersion of L M_1 regarding modern dogs and fossils, except EP dogs. The rows labelled "Modern wolves" refer to all modern wolves used in Fig. 7 (modern wolves from Table 1 and modern wolves from Detry and Cardoso, 2010), the rows labelled "Fossil (dogs from literature)" refer to all fossil dogs used in Fig. 7 marked with an asterisk (Altuna, 1967, 1980; Sanchis and Sarrión, 2004; Daza-Perea, 2015; Catagnano, 2016; Blaschikoff et al., 2022). Abbreviations: L M_1 (length of M_1), W M_1 (width of M_1), n (number of specimens), Min (minimum), Max (maximum), St. dev (standard deviation), CV (coefficient of variation).

Basic statistics (mm)						
L M_1	**n**	**Mean**	**Min**	**Max**	**St. dev**	**CV (%)**
Modern wolves	84	27.20	24.10	31.50	1.40	5.15
Modern dogs	9	23.07	20.67	25.29	1.39	6.04
Fossils (dogs from literature)	38	19.88	15.70	23.00	1.40	7.04
El Portalón	4	20.97	19.71	22.05	0.97	4.65
Barrio del Castillo	4	20.39	18.81	21.43	1.13	5.55
W M_1	**n**	**Mean**	**Min**	**Max**	**St. dev**	**CV (%)**
Modern wolves	84	11.36	9.70	14.20	0.79	6.94
Modern dogs	9	8.99	8.35	9.40	0.33	3.67
Fossils (dogs from literature)	36	7.80	6.40	8.70	0.53	6.78
El Portalón	4	7.25	6.78	7.50	0.32	4.42
Barrio del Castillo	4	7.62	6.87	8.09	0.54	7.05

$M_1 = 8.99$ mm) and fossil dogs ($\overline{X}$ L$M_1 = 19.88$ mm and $\overline{X}$ W $M_1 = 7.80$) (Fig. 7 and Table 4). Considering the coefficient of variation (CV), modern Iberian wolves show a lower dispersion of the length of the M_1 (L M_1) comparing modern dogs and fossils, except EP dogs. Also, modern dogs and EP dogs have a less dispersion of M_1 width (Table 4). EP dogs show less dispersion of M_1 size and fossils in general have a wider distribution. The results of the Kruskal-Wallis test for M_1 length (L M_1) are $H(4) = 101.7947$, $p < 0.001$ and for M_1 width (W M_1) are $H(4) = 100.4759$, $p < 0.001$. There are statistical differences ($p < 0.05$) among modern wolves and the modern and fossil dogs, but there are not statistic differences between modern and fossil dogs (Table 5).

The canine is considered a good size (and weight) estimator in canids (Dayan et al., 1992; Valkenburgh and Ruff, 1987). The dimensions of the Neolithic canine (ATP'15.UE507.392) are ØAPTC = 8,8 mm and ØTC = 7.09 mm. These values fall within the BC Chalcolithic sample ($\overline{X}$ ØAPTC = 8.52 ± 0.84 mm; $\overline{X}$ ØTC = 6.06 ± 0.05 mm) and the EP Bronze Age sample ($\overline{X}$ ØAPTC = 8.79 ± 0.79 mm; $\overline{X}$ ØTC = 6.45 ± 0.61 mm). These data support that the Neolithic, Chalcolithic and Bronze Age dogs have a similar size. Finally, following the size criterion of Sanchis and Sarrión (2004) and Catagnano (2016), the specimen 6976Q has a small-medium size (shoulder height estimated at 47,62 cm).

Table 5
Kruskal-Wallis test (p-values) on length and width of M_1. This test revealed a larger size of M_1 between modern wolves and the other analyzed groups (modern and fossil dogs). The rows labelled "Modern wolves" refer to all modern wolves used in Fig. 7 (modern wolves from Table 1 and modern wolves from Detry and Cardoso, 2010), the rows labelled "Fossil (dogs from literature)" refer to all fossil dogs used in Fig. 7 marked with an asterisk (Altuna, 1967, 1980; Sanchis and Sarrión, 2004; Daza-Perea, 2015; Catagnano, 2016; Blaschikoff et al., 2022).

Kruskal-Wallis test (p-values)		
L M_1	$H(4, n = 139) = 101{,}7947$; $p < 0.0001$	
	Modern wolves	**Modern dogs**
Modern wolves		0.00746
Modern dogs	0.00746	
Fossils (dogs from literature)	0.00000	0.66352
El Portalón (EP)	0.02094	1.00000
Barrio del Castillo (BC)	0.00827	1.00000
W M_1	$H(4, n = 137) = 100{,}4759$; $p < 0.0001$	
	Modern wolves	**Modern dogs**
Modern wolves		0.00725
Modern dogs	0.00725	
Fossils (dogs from literature)	0.00000	1.00000
El Portalón (EP)	0.00024	1.00000
Barrio del Castillo (BC)	0.00233	1.00000

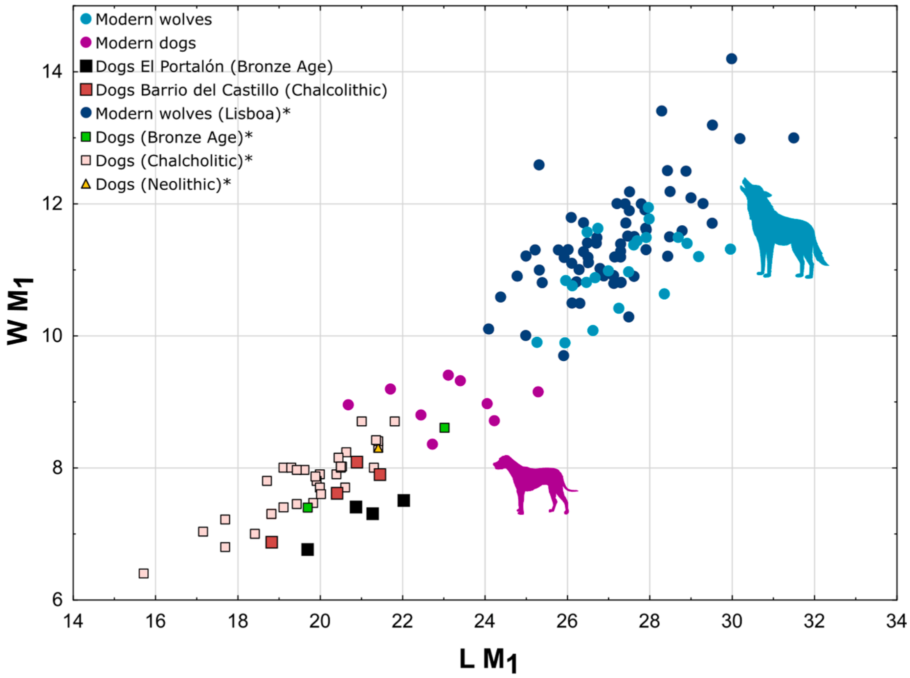

Fig. 7. Biplot LM_1 *vs.* WM_1. M_1 in modern wolves has larger measurements than modern and fossil dogs. The specimens marked with asterisk are taken from bibliography (Altuna, 1967, 1980; Sanchis and Sarrión, 2004; Daza-Perea, 2015; Catagnano, 2016; Detry and Cardoso, 2010; Blaschikoff et al., 2022).

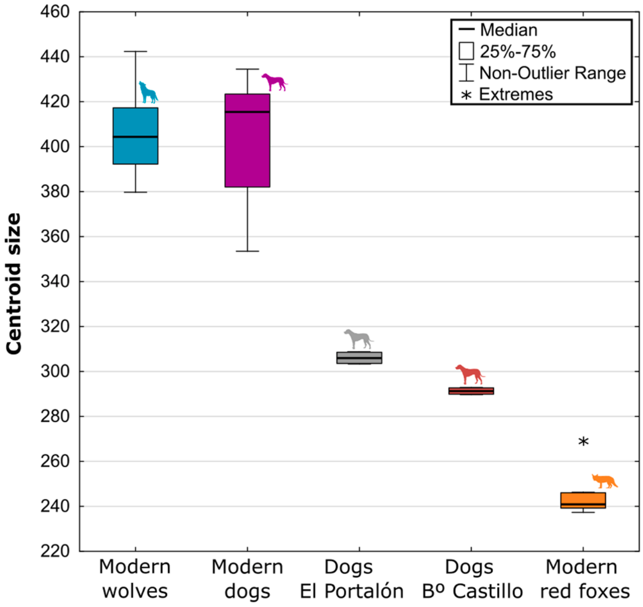

Fig. 8. Boxplot of the complete mandible centroid size of each taxon. Modern wolves and dogs are larger than fossils from EP and BC. Also, the fossils dogs are larger than modern foxes.

4.2. *Geometric morphometrics*

4.2.1. *Centroid size (CS) analyses*

The boxplot (Fig. 8) shows that modern wolves and dogs are larger than fossils from EP and BC. Also, the fossil dogs are larger than modern foxes. In both complete mandibles and fragmentary mandibles remains, PC1 is significantly related to size, so the shape change in PC1 is mainly explained by size (Fig. 9). We can observe than larger specimens (modern wolves and dogs) are related with positive scores and the smaller specimens (foxes) are related with negative scores of PC1. The intermediate sizes (dogs from EP and BC) are distributed in positive and negative scores of the PC1. In PC1 of complete mandibles, 75.69 % is explained by size, with a probability of 0,0001. However, in PC1 of fragmentary mandible remains, 65.38 % is explained for size, with a probability of 0,0001.

4.2.2. *Shape variation on complete mandibles*

The PCA (Fig. 10) shows that axes 1 and 2 (PC1 and PC2) accounted for 56.72 % of the total of variance (Table 6). PC1 (37.61 % of the variation) represents a shape change since narrowing mandibles (negative scores) to stretched mandibles (positive scores) in the ascending ramus and mandibular body. The shape changes associated with the ascending ramus include an anterior and posterior stretching– a lengthwise stretching in which the coronoid point moved upward, and angular process point moved downward (labial view). Also, a lengthwise stretching of the condylar process (occlusal view) is apparent. The shape deformation in the mandibular body was dorsoventral (labial view) and lateral (occlusal view) stretching of the whole mandible in positive scores on PC1. The most significant shape deformation along PC2 (19.11 % of the variation) axis was variation in landmarks belonging to the carnassial (M_1), which were enlarged (labial and occlusal view) in modern wolves and fossils. Also, there is a noticeable shape difference in coronoid process and curve points relative to ascending ramus which were shifted anteriorly in positive scores (modern wolves and fossils) and posteriorly in negative scores (modern dogs and foxes). In PC3 (7.09 % of the variation) (Table 6) there is not a separation between the analyzed groups, and for that reason we do not include it in this study.

In the morphospace defined by PC1 and PC2 (Fig. 10), a broader distribution of modern dogs can be observed compared to modern wolves and foxes. This distribution is attributed to their heterogeneity in relation to wild species. PC1 has an allometric component in which shape changes are correlated with CS (Fig. 9a). Specimens with higher values of CS (larger mandibles) present mandibles with a higher and wider mandibular body and ascending ramus, whereas specimens with lower values of CS (smaller mandibles) present mandibles with a lower and narrower mandibular body and ascending ramus (Fig. 9a and Fig. 10). PC2 is not correlated with size. We have summarised the shape changes observed in the PCA (Fig. 10) in Table 7.

4.2.3. *Shape variation in fragmentary remains of mandibles*

The PCA (Fig. 11a) shows that axes 1 and 2 (PC1 and PC2) accounted for 59.21 % of the total of variance (Table 6). PC1 (41.19 % of the variation) represents a shape change since a dorsoventral (labial view) narrowing (negative scores) to dorsoventral (labial view) stretching in the mandibular body (positive scores). PC2 (18.02 % of the variation) represents a shape change related to a buccal-lingual narrowing (occlusal view) of the mandible between P_4.M_3, and a smaller M_1 alveolus (negative scores) to a buccal-lingual stretching (occlusal view) of the mandible between P_4-M_3, and an enlarged M_1 alveolus (positive scores). The deformation along PC3 (8.94 % of the variation) axis is related to changes in position of landmarks 10 and 11 (Fig. 11b). In positive scores, the landmark 10 (labial view) is moved ventral and to anterior/cranial. The landmark 11 (lingual view) is moved ventral and to caudal/posterior.

In the morphospace defined by PC1 and PC2 (Fig. 11a), a broader distribution of modern dogs can be observed compared to modern wolves and foxes. This distribution in the morphospace is mainly explained by size, i.e. shape changes are correlated with CS (Fig. 9b). Specimens with higher values of CS (larger mandibles) are mandibles with a dorsoventral stretching in the mandibular body, whereas specimens with lower values of CS (smaller mandibles) are mandibles with a dorsoventral narrowing in the mandibular body (Fig. 9b). In the morphospace defined by PC2 and PC3 an overlap between different groups can be observed (Fig. 11b). PC2 and PC3 are not significantly correlated with size. We have summarised the shape changes observed in the PCA (Fig. 11) in Table 8.

5. Discussion

During the Neolithic, a reduction in body size occurs in several animals, including cattle, pigs, goats, and sheep (Altuna, 1980; Zeder, 2006a, 2006b, 2008; Galindo-Pellicena et al., 2019, 2020). However, dogs are a particular case. Some studies suggest that during the Neolithic, Bronze Age, and Iron Ages dogs display a small range of sizes, in contrast to the Chalcolithic and Roman periods where dogs show a larger size range (Catagnano, 2016). The small-medium size range seems to be the most common size in Iberian dogs through the Neolithic-Bronze Age (Sanchis and Sarrión, 2004) and seems to be related to hunting, herding, and vigilance function (Catagnano, 2016; Ruiz García-Vaso et al., 2013). Our results, spanning from the Neolithic to the Bronze Age provide a better understanding of dog populations from within that period. M_1 (Table 4, Fig. 7) and CS (Fig. 8) analyses support identification of the remains from BC and EP as dogs. The estimation of shoulder height of one dog from BC suggests a small-medium size, a similar result as is seen in other Chalcolithic Iberian sites including Fuente Flores, Les Jovades (Sanchis and Sarrión, 2004), Camino del Molino (Catagnano, 2016, Daza-Perea, 2019), Camino de las Yeseras (Daza-Perea, 2019), and Leceia (Blaschikoff et al., 2022). CS analyses indicate the mandibles of BC and EP have a similar size (Fig. 8). At the same time, similar canine size is observed in the fossil sample between the EP (Neolithic and Bronze Age) and BC (Chalcolithic) dogs. This implies a continuity in dog's size from the Neolithic to the Bronze Age in the Inner Plateau.

Several studies have been conducted on dogs of these ages (Neolithic-Bronze Age) at other European sites (e.g., De Grossi Mazzorin and Tagliacozzo, 1997, 2000; Catagnano, 2016; Daza-Perea, 2019;

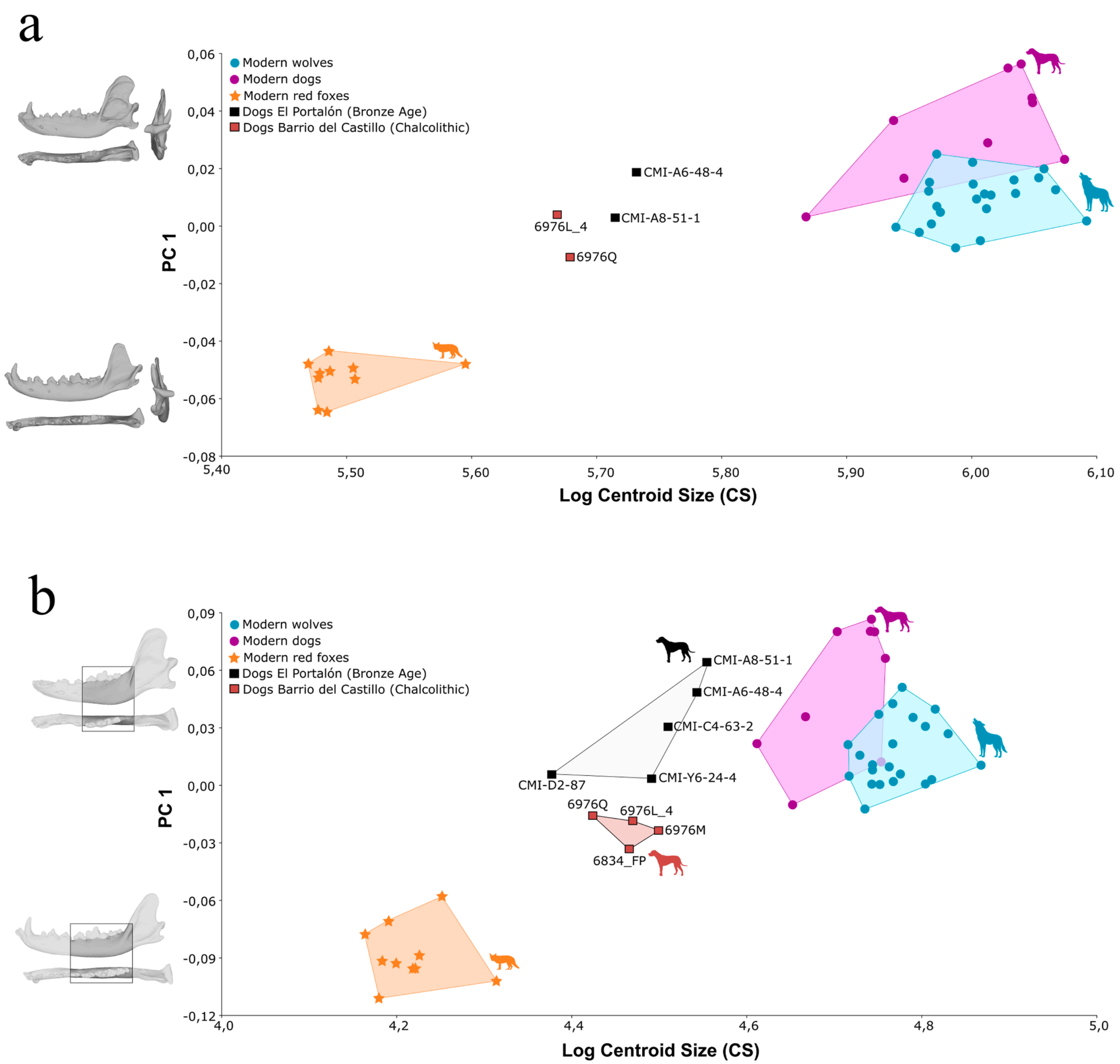

Fig. 9. Graphic of dispersion shows the correlation between the logarithm of Centroid Size (CS) and the PC1 in complete mandibles (a) and fragmentary mandibles remains (b). PC1 is significantly correlated with CS, so the shape change in PC1 is mainly explained by size. Larger specimens (modern wolves and dogs) are correlated with positive scores and the smaller specimens (foxes) are correlated with negative scores of PC1.

Brassard et al., 2022). De Grossi Mazzorin and Tagliacozzo (1997) found strong variability in the absolute size of 29 mandibles analysed from nine Italian Bronze Age sites and classified them in two size categories (small and small-medium). De Grossi Mazzorin and Tagliacozzo (2000) analysed skulls and mandibles of dogs from several Italian sites ranging in age from the Neolithic to the Roman period. These authors suggested the presence of several types of dogs, as noted by having mandibles of similar length, but with different morphologies. Comparing the results of the mandibles with the cranial analyses, they concluded that dogs of these periods would have a variable size range from small to medium and large.

Since dogs and wolves are the same species (*Canis lupus*) they are generally morphologically very similar, necessitating understanding the slight differences between them. While foxes and wolves showed consistent morphological patterns that characterize each species, the modern dog mandible sample presented here are very heterogeneous (Figs. 10 and 11). This shape variability observed in dogs is similarly detected in other studies (Brassard et al., 2020, 2022; Drake and Klingenberg, 2010; Drake et al., 2017). Despite the gracility of some dog remains, the morphological differences observed between *Canis* and *Vulpes* is clear and represents a useful tool to discriminate between both genera, even with incomplete mandibles. The GM technique can discriminate *Vulpes* and *Canis* from modern samples and is therefore useful to discriminate ancient dogs and foxes in archaeological contexts. The variability of the shape in the foxes is lower than in domestic dogs (Figs. 10 and 11). This is consistent with the results of other authors

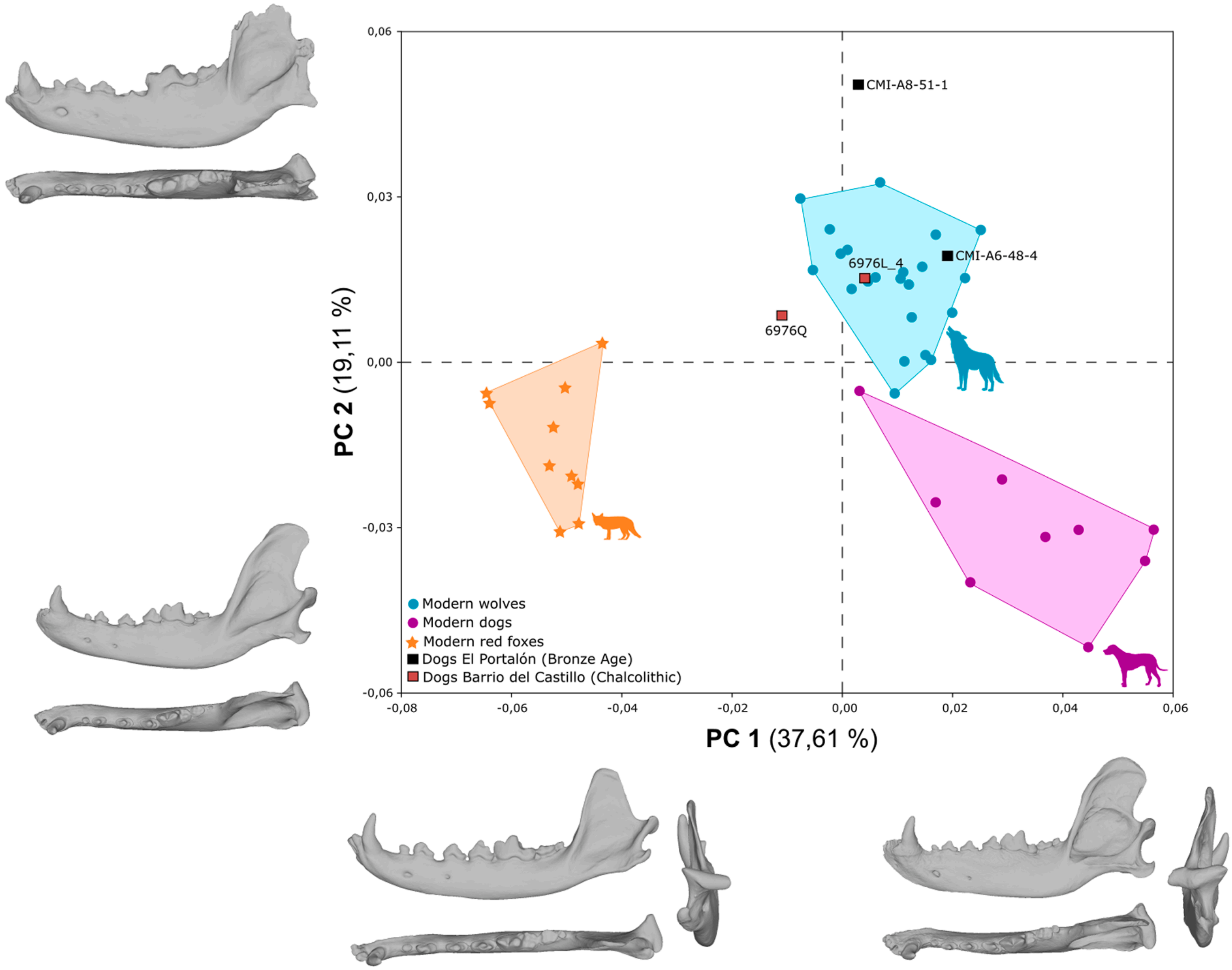

Fig. 10. PC1 *vs.* PC2. 3D models show shape variation of negative and positive extremes along PC1 (lateral, occlusal, and caudal views) and PC2 (lateral and occlusal views). PC1 represents a shape change since narrowing mandibles (negative scores) to stretched mandibles (positive scores) in the ascending ramus and mandibular body. PC2 represents the main shape change from a smaller M_1 (negative scores) to enlarged M_1 (positive scores).

Table 6
Eigenvalues, variance, and cumulative percentages by each of the Principal Components (PC) of the Principal Component Analysis (PCA) on complete mandibles and fragmentary remains of mandibles.

Complete mandibles			
CP	**Eigenvalues**	**% Variance**	**Cumulative %**
1	0,00099845	37,61	37,61
2	0,00050785	19,11	56,72
3	0,00022348	7,09	63,81
Fragmentary remains of mandibles			
CP	**Eigenvalues**	**% Variance**	**Cumulative %**
1	0,00269637	41,19	41,19
2	0,00118061	18,02	59,21
3	0,00061200	8,94	68,15

(Brassard et al., 2021; Drake and Klingenberg, 2010). It is expected that wild species show a greater homogeneity than domesticated ones.

In previous studies, it was shown that the EP dogs preserved traits typical of wolf such as in the morphology of M_1 (especially in the protoconid area) as well as in the mandibular region (Blázquez-Orta et al., 2022). In the present study, the results indicate that BC (Chalcolithic) and EP (Bronze Age) dogs have similar shape (Fig. 10) and similar CS (Fig. 8). All the Holocene dogs and modern wolves are similar in M_1 shape. Except for one fossil from BC (6976Q), the other specimens are characterised by robustness in the mandibular body and ascending ramus, as observed in modern wolves and dogs (Fig. 10). In fact, this shape is shared by all *Canis*.

In Fig. 11 the EP dogs seem to be more dispersed than the BC dogs, which may be interpreted as EP dogs are more variable. The morphology (shape correlated with CS) of EP mandibles resembles modern wolves and dogs (PC1), i.e., the EP specimens are characterised by a dorsoventral stretching of the mandibular body (region of mandible just behind the M_1), a pattern not observed in the BC dogs. When we focus the analysis on this specific region behind the carnassial (without considering the infradentale and ascending ramus areas) the Chalcolithic dogs are separated from the Bronze Age remains. There is not a big separation in the CS analysis between these remains (Fig. 9a), so these results suggest an increase of diversity in the morphology of the dog mandibles through time (Chalcolithic-Bronze Age).

Just like with the complete mandibles, the analysis of the mandible

Table 7
Summary table of mandibular features observed in each group/fossil.

	Shape of ascending ramus and mandibular body (PC1)		**M$_1$ (PC2)**		**Position ascending ramus (PC2)**	
	Negative values	**Positive values**	**Negative values**	**Positive values**	**Negative values**	**Positive values**
Modern wolves		Stretched mandibles		Enlarged		Anteriorly shifted
Modern dogs		Stretched mandibles	Smaller		Posteriorly shifted	
Modern foxes	Narrowing mandibles		Smaller		Posteriorly shifted	
CMI-A6-48.4 (EP)		Stretched mandible		Enlarged		Anteriorly shifted
CMI-A8-51.1 (EP)		Stretched mandible		Enlarged		Anteriorly shifted
6976L_4 (BC)		Stretched mandible		Enlarged		Anteriorly shifted
6976Q (BC)	Narrowing mandible			Enlarged		Anteriorly shifted

fragments shows changes in M$_1$ area (PC2, Fig. 11), and shows the relevance of M$_1$ to discriminate between dogs and wolves (Clutton-Brock, 1962; Daza-Perea, 2019) as also shown in the analyses of M$_1$ size (Tables 4-5 and Fig. 7). This suggests that during the Chalcolithic and Bronze Age, dogs' mandibles resembled wolves in the M$_1$ region. All Chalcolithic dogs and three mandibles from the Bronze Age share a similar position of the ventral point of the masseteric fossa and the mandibular foramen with the modern dogs (PC3, Fig. 11b). Modern wolves show an important development of the masseteric muscle which is related with bite strength. This trait is more diverse in dogs and difficult to explain with the present sample.

It would be interesting to investigate whether the distribution of specimens in any PC is related to sex. If a clear separation between males and females is observed in the morphospace, and fossils are clustered on one side or the other, it could suggest that humans from those cultural periods had specific preferences regarding the sex of the dogs they selected or selecting those animals with a particular physical characteristic, possibly seeking temperament or behavioural traits associated with a particular sex.

The results of the present study reflect slight morphological variability between BC and EP dogs. From the Chalcolithic to the Late Bronze Age, dogs still preserve wolf-like traits. The analyses of both (complete and fragmentary mandibles) show a similar M$_1$ shape as observed in modern wolves (Figs. 10 and 11). However, there is a morphologic difference in the region just behind the M$_1$ between Chalcolithic and Bronze Age dogs that is observed in the fragmentary mandible analyses (Fig. 11a). Brassard et al. (2022) also observed variability in the European dogs, however, the sample used in that study covered a long-time span, from the Mesolithic to the end of the Chalcolithic, and included numerous breeds produced by humans in recent times (Dunner and Cañón, 2014; Parker et al., 2017), making the pattern change through time difficult to interpret. Their results demonstrated that the mandibles of ancient dogs, even by this time, showed great variability of size and shape, although when compared to modern relatives, this variation in the archaeological record is lower. To obtain more powerful conclusions, an increase of the present sample and especially to extent the chronological range of dog specimens to the Neolithic, will be valuable.

Our data support the idea that inland populations of dogs show very low diversity in contrast with observations from coastal sites (at least in size). It would be interesting for future research, to test the hypothesis that coastal populations have greater morphological diversity than inland populations. Human settlements in coastal zones are influenced by a higher commercial activity than populations from the Inner Peninsula resulting in exchange networks. Sites located along the Mediterranean coast including, Camino del Molino (Murcia), and Monachil and Purullena (both Granada), include a wider variation in size of dogs (Catagnano, 2016; Sanchis and Sarrión, 2004). This may be due to different European human mobilizations (Gónzalez-Fortes et al., 2019; Olalde et al., 2019; Bergström et al., 2020; Blaschikoff et al., 2022). An active Mediterranean communication network has dispersed animals coming from different European and African origins (Anderung et al., 2005; Meiri et al., 2017; Galindo-Pellicena et al., 2020), thus, the Iberian coastal populations reflect this diversity of dogs which is not observed in inner territories, at least during the Neolithic and Bronze Age. A higher morphological variability in coastal sites related to Mediterranean connectivity is also proposed for other domesticated animals (Harding et al., 2023a).

The continuity of size contrasts with the slight variation observed in morphology and could be explained by ethological issues. The type of food, climate or even the environment may determine differences between canids (Brugal and Boudadi-Maligne, 2011; Flower and Schreve, 2014; Brassard et al., 2023). Daza-Perea (2019) pointed out that a mandibular morphological variation already existed in dogs since the late IV millennium in the Iberian regions. She proposed that humans would have begun to select individuals to replicate useful characteristics and behaviours in these cultural periods. This would have led to the appearance of small and subtle anatomical changes that are directly related to the evidence of diversity in the shape of the mandible. The experiment with foxes conducted by the geneticist Dmitri Belyaev (Dugatkin, 2018; Trut et al., 2004) could help to explain the process of wolf domestication where the calmest foxes and most prosocial toward humans were selected during generations. The foxes showed morphological differences like dogs such as shorter and rounder snouts.

6. Conclusion

The classification of canids is an uncertain topic, surrounded by controversy. Here, we gather data from 3D GM analyses of four complete hemimandibles and five fragments of mandibles of dogs (*Canis lupus familiaris*) from two Holocene archaeological sites including Barrio del Castillo (southern Plateau, Chalcolithic) and El Portalón (northern Plateau, Bronze Age). The results showed that the fossils of these periods had a smaller size than the modern dogs' sample. We observed a continuity of size from the Neolithic to the Bronze Age. When we observed the variability of the mandibular shape through GM, we detected that these dogs still displayed diagnostic wolf traits around the carnassial area. However, there is a slight morphologic difference in the region just behind the M$_1$ between Chalcolithic and Bronze Age dogs that is observed from analyses of fragmentary mandibles. The morphology of *Vulpes* and *Canis* is separated in the GM analyses, therefore this technique is very useful to discriminate ancient dogs and foxes in archaeological contexts. The results of this study increase our knowledge on the mandibular morphological variability of dogs (from Chalcolithic and Bronze Age in Central Iberian). The specimens analysed in the inner regions of the peninsula are consistent with a scenario of very similar dogs which keep a morphological pattern lasting for ~ 1240 years. This pattern of continuity that dogs maintain in central Iberia contrasts with the results observed from prior studies on coastal sites. Human settlements in coastal zones are influenced by a higher commercial activity than populations from Inner Peninsula, resulting in exchange networks. Thus, coastal population could incorporate other dog morphotypes that are found in sites from the Mediterranean coast (Murcia, Granada). The size variation in dogs from these coastal sites differs from our central Iberia data.

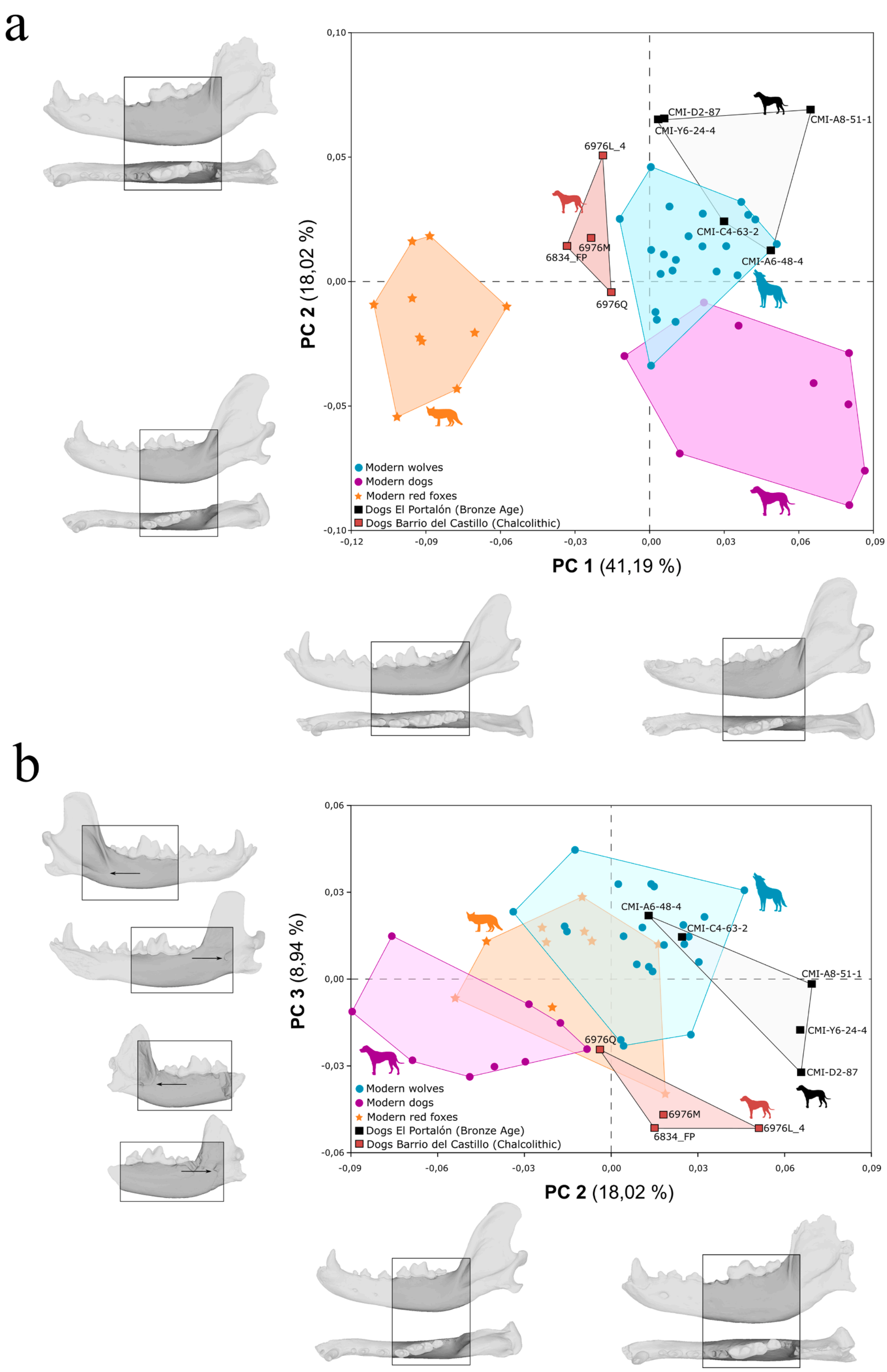

Fig. 11. PCA. a) PC1 *vs.* PC2. 3D models show shape variation of negative and positive extremes along PC1 (lateral and occlusal views) and PC2 (lateral and occlusal views). b) PC2 *vs.* PC3. 3D models show shape variation of negative and positive extremes along PC1 (lateral and occlusal views) and PC3 (labial and lingual views). PC1 represents a shape change since a dorsoventral (labial view) narrowing (negative scores) to dorsoventral (labial view) stretching in the mandibular body (positive scores). PC2 represents a shape change related to a buccal-lingual narrowing (occlusal view) of the mandible between P_4-M_3, and a smaller M_1 alveolus (negative scores) to a buccal-lingual stretching (occlusal view) of the mandible between P_4-M_3, and an enlarged M_1 alveolus (positive scores). In positive scores of PC3 the landmark 10 (labial view) is moved ventral and to anterior/cranial. The landmark 11 (lingual view) is moved ventral and to caudal/posterior.

Table 8
Summary table of mandibular features observed in each group/fossil.

	Mandibular body (PC1)		P_4-M_3 series (mandibular shape) (PC2)		M_1 alveolus (PC2)		Ventral point of the fossa masseterica (PC3)		Point of the mandibular foramen (PC3)	
	Negative values	Positive values	Negative values	Positive values	Negative values	Positive values	Negative values	Positive values	Negative values	Positive values
Modern wolves		Dorsoventral stretching		Buccal-lingual stretching		Enlarged		Moved ventral and cranial		Moved ventral and caudal
Modern dogs		Dorsoventral stretching	Buccal-lingual narrowing		Smaller		Moved dorsal and caudal		Moved dorsal and cranial	
Modern foxes	Dorsoventral narrowing		Buccal-lingual narrowing		Smaller			Moved ventral and cranial		Moved ventral and caudal
CMI-A6-48.4 (EP)		Dorsoventral stretching		Buccal-lingual stretching		Enlarged		Moved ventral and cranial		Moved ventral and caudal
CMI-A8-51.1 (EP)		Dorsoventral stretching		Buccal-lingual stretching		Enlarged	Moved dorsal and caudal		Moved dorsal and cranial	
CMI-C4-63–2 (EP)		Dorsoventral stretching		Buccal-lingual stretching		Enlarged		Moved ventral and cranial		Moved ventral and caudal
CMI-D2-87 (EP)		Dorsoventral stretching		Buccal-lingual stretching		Enlarged	Moved dorsal and caudal		Moved dorsal and cranial	
CMI-Y6-24–4 (EP)		Dorsoventral stretching		Buccal-lingual stretching		Enlarged	Moved dorsal and caudal		Moved dorsal and cranial	
6976L_4 (BC)	Dorsoventral narrowing			Buccal-lingual stretching		Enlarged	Moved dorsal and caudal		Moved dorsal and cranial	
6976Q (BC)	Dorsoventral narrowing		Buccal-lingual narrowing		Smaller		Moved dorsal and caudal		Moved dorsal and cranial	
6976 M (BC)	Dorsoventral narrowing			Buccal-lingual stretching		Enlarged	Moved dorsal and caudal		Moved dorsal and cranial	
6834_FP (BC)	Dorsoventral narrowing			Buccal-lingual stretching		Enlarged	Moved dorsal and caudal		Moved dorsal and cranial	

CRediT authorship contribution statement

Raquel Blázquez-Orta: Writing – original draft, Software, Methodology, Investigation. **Laura Rodríguez:** Writing – review & editing, Methodology. **Mónica Major González:** Resources, Project administration. **Verónica Estaca-Gómez:** Writing – review & editing. **Ignacio De Gaspar:** Writing – review & editing, Resources. **Robert S. Feranec:** Writing – review & editing, Resources. **José Miguel Carretero:** Resources, Project administration. **Juan Luis Arsuaga:** Resources, Project administration, Funding acquisition. **Nuria García:** Writing – review & editing, Validation, Supervision, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We thank the Museum of Burgos (with a special mention to M. Negro) for providing access to the fossils of El Portalón recovered in digs between 1972 and 1983. We also extend our gratitude to J. Yravedra for providing information regarding the material from Barrio del Castillo and assisting us to establish contacts for its study. Additionally, we are very grateful to L. Revuelta and J. A. de Pablo for kindly providing us access to the scanner at the Veterinary University (UCM) and technical support.

Funding

This work was supported by the project “Geología, geocronología y paleobiología de los yacimientos de la Sierra de Atapuerca VIII” (PID2021-122355NB-C31- FEDER/Ministerio de Ciencia e Innovación, Agencia Estatal); and by the UCM research group Ecosistemas Cuaternarios (931098). R.B-O is supported by a Fundación Atapuerca research fellowship financed by Cajaviva Fundación Caja Rural Burgos.

References

Albizuri, S., Nadal, J., Martín, P., Gibaja, J.F., Martín Cólliga, A., Esteve, X., Oms, X., Martí, M., Pou, R., López-Onaindia, D., Eulàlia Subirà, M., 2019. Dogs in funerary contexts during the Middle Neolithic in the northeastern Iberian Peninsula (5th-early 4th millennium BCE). J. Archaeol. Sci.: Rep. 24, 198–207. https://doi.org/10.1016/j.jasrep.2019.01.004.

Altuna, J., 1967. Fauna de mamíferos del yacimiento prehistórico de Marizulo (Urnieta), Guipúzcoa. *Munibe (Antropología-Arkeología)*, 19 (3-4), 271-298. San Sebastián.

Altuna, J., 1980. Historia de la domesticación animal en el País Vasco desde sus orígenes hasta la romanización. Munibe (Antropología-Arkeología) 32, 9–163.

Altuna, J., Mariezkurrena, K., 1985. Bases de subsistencia de los pobladores de Erralla: Macromamíferos. *Munibe (Antropología-Arkeología)*, 37, 87-111. San Sebastián.

Altuna, J., 1994. El perro en los yacimientos arqueológicos del norte de la Península Ibérica. En: Homenaje al Dr. Joaquín González Echegaray (Ed.: José A. Lasheras). *Museo y centro de investigación de Altamira. Monografías*, 17, 159-162.

Anderung, C., Bouwman, A., Persson, P., Carretero, J.M., Ortega, A.I., Elburg, R., Smith, C., Arsuaga, J.L., Ellegren, H., Götherström, A., 2005. Prehistoric contacts over the

Straits of Gibraltar indicated by genetic analysis of Iberian Bronze Age cattle. *PNAS*, 102 (24), 8431-8435. www.pnas.org/cgi/doi/10.1073/pnas.0503396102.

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., Lin, A.T., Storå, J., Sjögren, K.-G., Anthony, D., Antipina, E., Amiri, S., Bar-Oz, G., Bazaliiskii, V.I., Bulatović, J., Brown, D., Carmagnini, A., Davy, T., Fedorov, S., et al., 2020. Origins and genetic legacy of prehistoric dogs. Science 370 (6516), 557–564. https://doi.org/10.1126/science.aba9572.

Blaschikoff, L., Daza-Perea, A., Requicha, J., Detry, C., Rasteiro, R., Guimarães, S., Ureña, I., Serra, O., Schmidt, R., Valera, A., Almeida, N.J., Porfírio, E., Beatriz Santos, A., Delicado, C., Simões, F., Matos, J.A., Rosário Amorim, I., Petrucci-Fonseca, F., Davis, S.J.M., Muñoz-Mérida, A., Götherström, A., Fernández-Rodríguez, C., Cardoso, J.L., Ginja, C., Pires, A.E., 2022. A multidisciplinary study of Iberian Chalcolithic dogs. J. Archaeol. Sci: Rep. 42, 103338 https://doi.org/10.1016/j.jasrep.2022.103338.

Blázquez-Orta, R., Rodríguez, L., Galindo-Pellicena, M., García, N., 2022. Morphological study of mandibular Canis remains from the El Portalón (Sierra de Atapuerca) Holocene site. Implications for the origin of the domestic dog in prehistory. [Estudio morfológico de los restos mandibulares del género *Canis* en el yacimiento holoceno de El Portalón (Sierra de Atapuerca). Implicaciones en la aparición del perro en la prehistoria]. Spanish Journal of Palaeontology, 37(1), 53-68. Doi: 10.7203/sjp.24124.

Bookstein, F.L., 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press, Cambridge, 436.

Brassard, C., Merlin, M., Guintard, C., Monchâtre-Leroy, E., Barrat, J., Bausmayer, N., Bausmayer, S., Bausmayer, A., Beyer, M., Varlet, A., Houssin, C., Callou, C., Cornette, R., Herrel, A., 2020. Bite force and its relationship to jaw shape in domestic dogs. J. Exp. Biol. 223 (16) https://doi.org/10.1242/jeb.224352.

Brassard, C., Merlin, M., Monchâtre-Leroy, E., Guintard, C., Barrat, J., Garès, H., Larralle, A., Triquet, R., Houssin, C., Callou, C., Cornette, R., Herrel, A., 2021. Masticatory system integration in a commensal canid: interrelationships between bones, muscles and bite force in the red fox. J. Exp. Biol. 224 https://doi.org/10.1242/jeb.224394.

Brassard, C., Bălăşescu, A., Arbogast, R-M., Forest, V., Bemilli, C., Boroneant, A., Convertini, F., Gandelin, M., Radu, V., Fleming, P.A., Guintard, C., Kreplins, T.L., Callou, C., Filippo, A., Tresset, A.m Cornette, R., Herrel, A., Bréhard, S., 2022. Unexpected morphological diversity in ancient dogs compared to modern relatives. *Proceedings Royal Society B*, 289. Doi: 10.1098/rspb.2022.0147.

Brassard, C., Balasse, M., Bălăşescu, A., Radu, V., Ollivier, M., Fiorillo, D., Herrel, A., Bréhard, S., 2023. Morphological and dietary adaptations to different socio-economic systems in Chalcolithic dogs. J. Archaeol. Sci. 157 https://doi.org/10.1016/j.jas.2023.105820.

Brugal, J.-P., Boudadi-Maligne, M., 2011. Quaternary small to large canids in Europe: Taxonomic status and biochronological contribution. Quat. Int. 243, 171–182. https://doi.org/10.1016/j.quaint.2011.01.046.

Carretero, J. M., Ortega, A. I., Juez, L., Pérez-González, A., Arsuaga, J. L., Pérez-Martínez, R., Ortega, M. C., 2008. A Late Pleistocene-Early Holocene archaeological sequence of Portalón de Cueva Mayor (Sierra de Atapuerca, Burgos, Spain). *Munibe Antropología-Arkeologia, 59*, 67–80. http://cir.cenieh.es/handle/20.500.12136/2194.

Castaños Ugarte, P., 2004. Estudio arqueozoológico de los macromamíferos del neolítico de la cueva de Chaves (Huesca). Saldvie 4, 125–171.

Catagnano, V., 2016. Aproximación morfométrica y paleogenética al estudio de la variabilidad de *Canis l. familiaris* en la Península Ibérica desde el neolítico hasta época romana y su contextualización en el ámbito del mediterráneo occidental. (Tesis doctoral, Universitat Autònoma de Barcelona, Barcelona). Disponible en https://ddd.uab.cat/record/174983.

Chahoud, J., Vila, E., Albesso, M., 2023. Livestock management in the Northern Levant during the first millennium BCE. Quat. Int. 662–663, 63–81. https://doi.org/10.1016/j.quaint.2022.12.005.

Clutton-Brock, J., 1962. Near Eastern Canids and the affinities of the Natufian dogs. Z. Tierzuecht. Zuechtungsbiol. 76 (1–4), 326–333. https://doi.org/10.1111/j.1439-0388.1961.tb01213.x.

Clutton-Brock, J., 1995. Origins of the Dog: domestication and early history. In The domestic dog: its evolution, behaviour and interactions with people. 7 – 20, ed. J. Serpell. Cambridge University Press, NY.

Colominas, L., 2016. Morphometric variability of Roman dogs in Hispania Tarraconensis: The case study of the Vila de Madrid Necropolis. Int. J. Osteoarchaeol. 26, 897–905. https://doi.org/10.1002/oa.2507.

Coppinger, R., Coppinger, L., 2001. Dogs: A startling new understanding of canine origin, behavior & evolution. Scribner, New York, p. 352.

Crockford, S.J., 2006. Rhythms of Life: Thyroid Hormone and the Origin of Species. Trafford, Victoria, British Columbia, p. 272.

Dayan, T., 1994. Early domesticated dogs of the Near East. J. Archaeol. Sci. 21, 633–640. https://doi.org/10.1006/jasc.1994.1062.

Dayan, T., Simberloff, D., Tchernov, E., Yom-Tov, Y., 1992. Biol. J. Linn. Soc. 45, 315–331. https://doi.org/10.1111/j.1095-8312.1992.tb00647.x.

Daza-Perea, A., 2015. La fauna en el Calcolítico de la región de Madrid: los depósitos de canes. Másteres de la UAM, Facultad de Filosofía y Letras/11-12, Máster de Arqueología y Patrimonio. UAM Ediciones, Colección de Trabajos Fin de Máster para publicación digital. ISBN: 978-84-8344-452-8. https://libros.uam.es/?press=tfm&page=catalog&op=view&path%5B%5D=399&path%5B%5D=749&path%5B%5D=773-1.

Daza-Perea, A., 2019. *Estudio arqueozoológico del perro en la Prehistoria reciente de la Península Ibérica: caracterización de la especie y sus depósitos en contextos arqueológicos del Calcolítico y la Edad del Bronce (finales del IV-II milenio AC)*. (PhD, Universidad Autónoma de Madrid, Madrid). https://repositorio.uam.es/handle/10486/690366 (accessed 8 May 2023).

De Grossi Mazzorin, J., Tagliacozzo, A., 1997. Dog remains in Italy from the Neolithic to the Roman period. Anthropozoologica 25, 429–440.

De Grossi Mazzorin, J., Tagliacozzo, A., 2000. Morphological and osteological changes in the dog from the Neolithic to the Roman period in Italy. En S. J. Crockford (Ed.), ICAZ. Dogs Through Time: An Archaeological Perspective, *BAR International Series, 889*, 141–161.

Detry, C., Cardoso, J.L., 2010. On some remains of dog (*Canis familiaris*) from the Mesolithic shell-middens of Muge, Portugal. J. Archaeol. Sci. 37, 2762–2774. https://doi.org/10.1016/j.jas.2010.06.011.

Drake, A.G., Klingenberg, C.P., 2010. Large-scale diversification of skull shape in domestic dogs: Disparity and modularity. Am. Nat. 175 (3), 289–301. https://doi.org/10.1086/650372.

Drake, A.G., Coquerelle, M., Kosintsev, P.A., Bachura, O.P., Sablin, M., Gusev, A.V., Fleming, L.S., Losey, R.J., 2017. Three-dimensional geometric morphometric analysis of fossil canid mandibles and skulls. Sci. Rep. 7 (9508) https://doi.org/10.1038/s41598-017-10232-1.

Dugatkin, L.A., 2018. The silver fox domestication experiment. *Evolution: Education and Outreach*, 11, 16. doi: 10.1186/s12052-018-0090-x. Doi: 10.1186/s12052-018-0090-x.

Dunner, S., Cañón, J., 2014. Origen y diversidad de la especie canina. Canis et Felis 130, 18–26.

Estaca-Gómez, V., 2022. Informe arqueozoológico de los yacimientos de Barrio del Castillo y Aldovea (Torrejón de Ardoz, Madrid). (Archaeological report; Museo Arqueológico y Paleontológico Regional, Alcalá de Henares, Madrid).

Flower, L.O.H., Schreve, D.C., 2014. An investigation of palaeodietary variability in European Pleistocene canids. Quat. Sci. Rev. 96, 188–203. https://doi.org/10.1016/j.quascirev.2014.04.015.

Francés-Negro, M., Carrancho, A., Pérez-Romero, A., Arsuaga, J.L., Carretero, J.M., Iriarte, E., 2019. Storage or cooking pots? Inferring pottery use through archaeomagnetic assessment of palaeotemperatures. J. Archaeol. Sci. 110 https://doi.org/10.1016/j.jas.2019.104992.

Frantz, L.A.F., Mullin, V.E., Pionnier-Capitan, M., Lebrasseur, O., Ollivier, M., Perri, A., Linderholm, A., Mattiangeli, V., Teasdale, M.D., Dimopoulos, E.A., Tresset, A., Duffraisse, M., McCormick, F., Bartosiewicz, L., Gál, E., Nyerges, E.A., Sablin, M.V., Bréhard, S., Mashkour, M., Balasescu, A., Gillet, B., Hughes, S., Chassaing, O., Hitte, C., Vigne, J.-D., Dobney, K., Hänni, C., Bradley, D.G., Larson, G., 2016. Genomic and archaeological evidence suggest a dual origin of domestic dogs. Science 352 (6290), 1228–1231. https://doi.org/10.1126/science.aaf3161.

Galindo-Pellicena, M.A., Pérez-Romero, A., Francés-Negro, M., Álvarez, A., Iriarte, E., Arsuaga, J.L., Carretero, J.M., 2017. The equids from the Bronze Age levels of the El Portalón site (Atapuerca, Burgos, Spain). Quat. Int. 433, 124–141. https://doi.org/10.1016/j.quaint.2015.11.120.

Galindo-Pellicena, M.A., Arsuaga, J.L., Carretero, J.M., 2019. Pig management in the Chalcolithic and Bronze Age periods at the El Portalón site: Integration in the Iberia context. Quat. Int. 515, 138–149. https://doi.org/10.1016/j.quaint.2019.02.041.

Galindo-Pellicena, M.A., Arsuaga, J.L., Pérez-Romero, A., Iriarte, E., De Gaspar, I., Carretero, J.M., 2020. Metrical analysis of bovine remains from the Neolithic to the Bronze Age at the El Portalón site (Atapuerca, Burgos) in the Iberian context. Quat. Int. 566–567, 211–223. https://doi.org/10.1016/j.quaint.2020.06.001.

Galindo-Pellicena, M.A., Sala, N., De Gaspar, I., Iriarte, E., Blázquez-Orta, R., Arsuaga, J. L., Carretero, J.M., García, N., 2022. Long-term dog consumption during the Holocene at the Sierra de Atapuerca (Spain): Case study of the El Portalón de Cueva Mayor site. Archaeol., Anthrop. Sci. 14, 84. https://doi.org/10.1007/s12520-022-01522-5.

Gentry, A., Clutton-Brock, J., Groves, C.P., 2004. The naming of wild animal species and their domestic derivatives. J. Archaeol. Sci. 31, 645–651. https://doi.org/10.1016/j.jas.2003.10.006.

Germonpré, M., Sablin, M.V., Stevens, R.E., Hedges, R.E.M., Hofreiter, M., Stiller, M., Després, V.R., 2009. Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. J. Archaeol. Sci. 36, 473–490. https://doi.org/10.1016/j.jas.2008.09.033.

Germonpré, M., Lázničková-Galetová, M., Sablin, M.V., 2012. Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. J. Archaeol. Sci. 39, 184–202. https://doi.org/10.1016/j.jas.2011.09.022.

Germonpré, M., Lázničková-Galetová, M., Losey, R.J., Räikkönen, J., Sablin, M.V., 2015. Large canids at the Gravettian Předmostí site, the Czech Republic: The mandible. Quat. Int. 359–360, 261–279. https://doi.org/10.1016/j.quaint.2014.07.012.

Gil Cano, F., Ruiz García-Vaso, C., Conde Gómez, D., Avilés Fernández, A., Haber Uriarte, M., Vázquez Autón, J.M., 2011. Análisis de restos óseos de cánidos encontrados en el yacimiento "Camino del Molino" (Caravaca de la Cruz, Murcia): una oportunidad excepcional para estudiar los perros que poblaron el sureste español durante el Calcolítico. Primeros resultados. XVII Congreso Nacional y VIII Iberoamericano de Historia de la Veterinaria (Valencia, 2011).

Gónzalez-Fortes, G., Tassi, F., Trucchi, E., Henneberger, K., Paijmans, J.L.A., Díez-del-Molino, D., Schroeder, H., Susca, R.R., Barroso-Ruíz, C., Bermudez, F.J., Barroso-Medina, C., Bettencourt, A.M.S., Sampaio, H.A., Grandal-d'Anglade, A., Salas, A., de Lombera-Hermida, A., Fabregas Valcarce, R., Vaquero, M., Alonso, S., Lozano, M., Rodríguez-Alvarez, X.P., Fernández-Rodríguez, C., Manica, A., Hofreiter, M., Barbujani, G., 2019. A western route of prehistoric human migration from Africa into the Iberian Peninsula. Proc. Royal Soc. B 286. https://doi.org/10.1098/rspb.2018.2288.

Gunz, P., Mitteroecker, P., Bookstein, F.L., 2005. Semilandmarks in three dimensions. In: Slice, D.E. (Ed.), Modern Morphometrics in Physical Anthropology. Kluwer

Academic/Plenum Publishers, New York, pp. 73–98. https://doi.org/10.1007/0-387-27614-9.

Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and surfaces. *Hystrix, the Italian J. Mammal. 24* (1), 103-109. Doi: 10.4404/hystrix-24.1-6292.

Harcourt, R.A., 1974. The dog in prehistoric and early Historic Britain. J. Archaeol. Sci. 1 (2), 151–175. https://doi.org/10.1016/0305-4403(74)90040-5.

Harding, S.A., Hadjikoumis, A., Vermeersch, S., Marom, N., 2023a. The contribution of Mediterranean connectivity to morphological variability in Iron Age sheep of the Eastern Mediterranean. bioRxiv. Doi: 10.1101/2022.12.24.521859.

Harding, S., Vermeersch, S., Ujma, C., Deonarain, G., Susnow, M., Shafir, R., Gilboa, A., Lehmann, G., Marom, N., 2023b. Hoofprints in the sand: A study on domestic sheep (*Ovis aries*) from Iron Age southern Phoenicia using traditional biometric methods. Quat. Int. 662–663, 82–93. https://doi.org/10.1016/j.quaint.2023.02.014.

Hare, B., Wobber, V., Wrangham, R., 2012. The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. Anim. Behav. 83 (3), 573–585. https://doi.org/10.1016/j.anbehav.2011.12.007.

Hervella, M., San-Juan-Nó, A., Aldasoro-Zabala, A., Mariezkurrena, K., Altuna, J., de-la-Rua, C., 2022. The domestic dog that lived ∼17,000 years ago in the Lower Magdalenian of Erralla site (Basque Country): A radiometric and genetic analysis. *J. Archaeol. Sci.: Rep.*, 46, 103706. Doi: 10.1016/j.jasrep.2022.103706.

Klingenberg, C.P., 2011. MorphoJ: an integrated software package for geometric morphometrics. Mol. Ecol. Resour. 11, 353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x.

Kurtén, B., 1968. Pleistocene mammals of Europe. Weidenfeld & Nicholson, London.

Leonard, J.A., Wayne, R.K., Wheeler, J., Valadez, R., Guillén, S., Vilà, C., 2002. Ancient DNA evidence for old world origin of new world dogs. Science 298, 1613–1616. https://doi.org/10.1126/science.1076980.

Major González, M., Señorán Martín, J.M., López-López, G., Martínez Granero, A.B., Izquierdo Zamora, A., 2019. Los yacimientos prehistóricos de Aldovea. Torrejón de Ardoz, Madrid. En Actas de la RAM: Reunión Arqueología Madrileña, 50-59.

Meiri, M., Stockhammer, P.W., Marom, N., Bar-Oz, G., Sapir-Hen, L., Morgenstern, P., Macheridis, S., Rosen, B., Huchon, D., Maran, J., Finkelstein, I., 2017. Eastern Mediterranean mobility in the bronze and early iron ages: Inferences from ancient DNA of pigs and cattle. Sci. Rep. 7 (701) https://doi.org/10.1038/s41598-017-00701-y.

Mitteroecker, P., Gunz, P., 2009. Advances in geometric morphometrics. Evol. Biol. 36, 235–247. https://doi.org/10.1007/s11692-009-9055-x.

Morey, D.F., 1992. Size, shape and development in the evolution of the domestic dog. J. Archaeol. Sci. 19, 181–204. https://doi.org/10.1016/0305-4403(92)90049-9.

Morey, D.F., 1994. The early evolution of the domestic dog. Am. Sci. 82 (4), 336–347. https://www.jstor.org/stable/29775234.

Morey, D.F., Jeger, R., 2015. Paleolithic dogs: Why sustained domestication then? J. Archaeol. Sci.: Rep. 3, 420–428. https://doi.org/10.1016/j.jasrep.2015.06.031.

Olalde, I., Mallick, S., Patterson, N., Rohland, N., Villalba-Mouco, V., Silva, M., Dulias, K., Edwards, C.J., Gandini, F., Pala, M., Soares, P., Ferrando-Bernal, M., Adamski, N., Broomandkhoshbacht, N., Cheronet, O., Culleton, B.J., Fernandes, D., Lawson, A.M., Mah, M., et al., 2019. The genomic history of the Iberian Peninsula over the past 8000 years. Science 363 (6432), 1230–1234. https://doi.org/10.1126/science.aav4040.

Olsen, S.J., 1985. Origins of the domestic dog. University of Arizona Press, Tucson.

Ortega, A. I., Juez, L., Carretero, J. M., Ortega, M. C., Arsuaga, J. L., Pérez-González, A., 2008. El Neolítico en la nueva secuencia estratigráfica del yacimiento del Portalón de Cueva Mayor (Sierra de Atapuerca, Burgos). In M. S. Hernández-Pérez, J. A. Soler-Díaz, J. A. López-Padilla (Eds.), IV Congreso del Neolítico Peninsular. *Museo Arqueológico de Alicante*, *1*, 221–229.

Ovodov, N.D., Crockford, S.J., Kuzmin, Y.V., Highman, T.F.G., Hodgins, G.W.L., Van der Plicht, J., 2011. A 33,000-year-old incipient dog from Altai Mountains of Siberia: Evidence of the earliest domestication disrupted by the last glacial maximum. PLoS One 6 (7), 1–7. https://doi.org/10.1371/journal.pone.0022821.

Parker, H.G., Dreger, D.L., Rimbault, M., Davis, B.W., Mullen, A.B., Carpintero-Ramirez, G., Ostrander, E.A., 2017. Genomic analyses reveal the influence og geographic origin, migration, and hybridization on modern dog breed development. Cell Rep. 19, 697–708. https://doi.org/10.1016/j.celrep.2017.03.079.

Pérez-Romero, A., Alday, A., Iriarte, E., Francés-Negro, M., Galindo-Pellicena, M.A., Álvarez, A., Juez, L., Arsuaga, J.L., Carretero, J.M., 2016. La cerámica de la Edad del Bronce en el yacimiento de El Portalón de Cueva Mayor (Sierra de Atapuerca, Burgos, España). Munibe Antropologia-Arkeologia 67, 105–126. https://doi.org/10.21630/maa.2016.67.06.

Pérez-Romero, A., Carretero, J. M., Alday, A., Galindo-Pellicena, M. A., Adán, G., Juez, L., Arsuaga, J. L., 2015. La gestión del utillaje óseo de la Edad del Bronce en el yacimiento de El Portalón de Cueva Mayor, Sierra de Atapuerca, Burgos. *Complutum*, *26*(1), 113–131. Doi: 10.5209/rev_CMPL.2015.v26.n1.49343.

Pérez-Romero, A., Iriarte, E., Galindo-Pellicena, M.A., García-González, R., Rodríguez, L., Castilla, M., Francés-Negro, M., Santos, E., Valdiosera, C., Arsuaga, J.L., Alday, A., Carretero, J.M., 2017. An unusual Pre-bell beaker copper age cave burial context from El Portalón de Cueva Mayor site (Sierra de Atapuerca, Burgos). Quat. Int. 433, 142–155. https://doi.org/10.1016/j.quaint.2015.06.063.

Pires, A.E., Detry, C., Fernandez-Rodriguez, C., Valenzuela-Lamas, S., Arruda, A.M., De Grossi Mazzorin, J., Ollivier, M., Hänni, C., Simões, F., Ginja, C., 2018. Roman dogs from the Iberian Peninsula and the Maghreb – A glimpse into their morphology and genetics. Quat. Int. 471, 132–146. https://doi.org/10.1016/j.quaint.2017.11.044.

Pires, A.E., Detry, C., Chikhi, L., Rasteiro, R., Amorim, I.R., Simões, F., Matos, J., Petrucci-Fonseca, F., Ollivier, M., Hänni, C., Cardodo, J.L., Arias, P., Diniz, M., Araújo, A.C., Bicho, N., Sousa, A.C., Moreno-García, M., Arruda, A.M., Fernández-Rodríguez, C., Porfírio, E., Arnaud, J.M., Valente, A., Gonçalves, D., Alves, L., Götherström, A., Davis, S.J.M., Ginja, C., 2019. The curious case of the Mesolithic Iberian dogs: An archaeogenetic study. J. Archaeol. Sci. 105, 116–129.

Rohlf, F.J., Marcus, L.F., 1993. A revolution in morphometrics. Trends Ecol. Evol. 8 (4), 129–132. https://doi.org/10.1016/0169-5347(93)90024-J.

Rohlf, F.J., Slice, D., 1990. Extensions of the Procrustes Method for the Optimal Superimposition of Landmarks. Syst. Zool. 39 (1), 40–59. https://doi.org/10.2307/2992207.

Ruiz García-Vaso, C., Vázquez Autón, J.M., Orenes Hernández, M., Gil Cano, F., 2013. Los perros que vivieron en la región de Murcia hace 4000 años: nuevos datos sobre tamaños, edad, alimentación y patologías. Comunicación XIX Congreso nacional de Historia de la Veterinaria y X Congreso Iberoamericano (Madrid, 18-20 de octubre de 2013).

Ruiz García-Vaso, C., Vázquez Autón, J.M., Lomba Maurandi, J., Avilés Fernández, A., Haber Uriarte, M., Orenes Hernández, M., Gil Cano, F., 2014. El yacimiento calcolítico "Camino del Molino" (Caracava de la Cruz, Murcia): Una oportunidad excepcional para estudiar los cánidos que poblaron el sureste español hace 4000 años. Primeros resultados. *Orígenes y raíces*, 6, 5-7.

Sanchis, A., Sarrión, I., 2004. Restos de cánidos (*Canis familiaris ssp.*) en yacimientos valencianos de la Edad del Bronce. *Archivo de Prehistoria Levantina*, 25, 161-198.

Savolainen, P., Zhang, Y., Luo, J., Lundeberg, J., Leitner, T., 2002. Genetic evidence for an East Asian origin of domestic dogs. Science 298, 1610–1613. https://doi.org/10.1126/science.1073906.

Savolainen, P., 2007. Domestication of dogs, in: Jensen, P. (Ed.), The behavioural biology of dogs. Cromwell Press, Trowbridge, pp. 21-37.

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V.J., Sawyer, S.K., Greenfield, D.L., Germonpré, M.B., Sablin, M.V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D.M., Acosta, A.A., Giemsch, L., Schimitz, R.W., Worthington, B., Buikstra, J.E., Druzhkova, A., Graphodatsky, A.S., Ovodov, N.D., Wahlberg, N., Freedman, A.H., Schweizer, R.M., Koepfli, K.P., Leonard, J.A., Meyer, M., Krause, J., Pääbo, S., Green, R.E., Wayne, R.K., 2013. Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. Science 342, 871–874. https://doi.org/10.1126/science.1243650.

Torres-Tamayo, N., García-Martínez, D., Lois Zlolniski, S., Torres-Sánchez, I., García-Río, F., Bastir, M., 2018. J. Anatomy 232, 227–237. https://doi.org/10.1111/joa.12743.

Trut, L.N., Plyusnina, I.Z., Oskina, I.N., 2004. An experiment on fox domestication and debatable issues of evolution of the dog. Russ. J. Genet. 40 (6), 644–655. https://doi.org/10.1023/B:RUGE.0000033312.92773.c1.

Valkenburgh van, B., Ruff, C.B., 1987. Canine tooth strength and killing behaviour in large carnivores. J. Zool. Lond. 212, 379–397. https://doi.org/10.1111/j.1469-7998.1987.tb02910.x.

Vilà, C., Savolainen, P., Maldonado, J.E., Amorim, I.R., Rice, J.E., Honeycutt, R.L., Crandall, K.A., Lundeberg, J., Wayne, R.K., 1997. Multiple and ancient origins of the domestic dog. Science 276, 1687–1689. https://doi.org/10.1126/science.276.5319.1687.

vonHoldt, B.M., Pollinger, J.P., Lohmueller, K.E., Han, E., Parker, H.G., Quignon, P., Degenhardt, J.D., Boyko, A.R., Earl, D.A., Auton, A., Reynolds, A., Bryc, K., Brisbin, A., Knowles, J.C., Mosher, D.S., Spady, T.C., Elkahloun, A., Geffen, E., Pilot, M., Jedrzejewski, W., Greco, C., Randi, E., Bannasch, D., Wilton, A., Shearman, J., Musiani, M., Cargill, M., Jones, P.G., Qian, Z., Huang, W., Ding, Z.-L., Zhang, Y., Bustamante, C.D., Ostrander, E.A., Novembre, J., Wayne, R.K., 2010. Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. Nature 464, 898–902. https://doi.org/10.1038/nature08837.

Zeder, M., 2006a. Central Questions in the Domestication of Plants and Animals. *Evolutionary Anthropology: Issues, News and Reviews*, 15, 105-117. Doi: 10.1002/evan.20101.

Zeder, M., 2006b. Archaeological approaches to documenting animal domestication, in: Zeder, MA., Bradley, DG., Emshwiller, E., Smith, BD (Eds.), Documenting domestication: new genetic and archaeological paradigms. University of California Press, pp. 171-180.

Zeder, M., 2008. Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. PNAS 105 (33), 11597–11604. https://doi.org/10.1073/pnas.0801317105.

Zelditch, M. L., Swiderski, D. L., Sheets, H. D., Fink, W. L., 2004. *Geometric Morphometrics for Biologists: A Primer*. Elsevier Academic Press.