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Journal of Archaeological Science: Reports

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

The domestic dog that lived ~17,000 years ago in the Lower Magdalenian of Erralla site (Basque Country): A radiometric and genetic analysis

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ARTICLE INFO

Keywords:

Domestication
Wolf
Dog
Chronology
Lower Magdalenian
Ancient DNA
Basque Country

ABSTRACT

Dogs are known to be the first species domesticated by humans, although the geographic and temporal origin of this process is still under debate in different fields of knowledge. In the present study, we examined a humerus from a canid recovered in the Lower Magdalenian level of the site of Erralla (Zestoa, Gipuzkoa, Basque Country, Spain), combining morphology, radiocarbon dating and genetics. Our results confirm the identification of this specimen as *Canis lupus familiaris*, discarding miss-identification with a dhole (*Cuon alpinus*) through genetic analyses of *cytochrome b* gene and mtDNA haplogroup. The direct AMS ¹⁴C dating (17,410–17,096 cal. BP) indicated that the Erralla specimen represents one of the earliest domesticated dogs in Europe, in the Lower Cantabrian Magdalenian period. We discuss our results in the light of the debate of the origin of dogs, conducting a critical review of the datings of sites of Eurasia that have provided remains of Paleolithic and Mesolithic dogs, including the so-called “dog-like wolves”.

1. Introduction

The dog (*Canis lupus familiaris*), the most anciently domesticated animal from its agriotype, the gray wolf (*Canis lupus*), appeared in the Upper Paleolithic. Nevertheless, when and where it was domesticated are still unsolved questions. The most ancient archaeological remains of clearly domesticated dogs were found in distant edges of Eurasia. They lived in Europe during the Magdalenian (Abri le Morin, France, 15,114–14,237 cal. BP) and the Epigravettian (Grotta Paglicci, Italy, 14,372–13,759 cal. BP), in the Near East during the Kebaran and Natufian cultures (Kebara, Israel, c. 12,500–12,000 BP) and in the Far East during the Peiligang culture (Jiahu, China, 9,000–7,800 cal. BP) (Boudadi-Maligne et al., 2012; Boschini et al., 2020; Tchernov and Valla, 1997; Gakuhari et al., 2015, respectively) (Fig. 1, N° 2, 3 and 4).

In addition, the dog was not only the first domesticated animal, but also the closest one to human beings. Burials of humans with dogs date from as early as 12,290–12,050 cal. BC (14,240–14,000 cal. BP), during the Late Magdalenian, in Bonn-Oberkassel (Germany, Europe) (Janssens

et al., 2018); c. 11,500–11,000 BP, during the late Natufian, in Eynan/Mallaha and Hayonim Terrace (Israel, Near East) (Tchernov and Valla, 1997); and 7,414–7,273 cal. BP during the Jōmon culture, in Kamikuroiwa (Far East, Japan) (Gakuhari et al., 2015). These data, in the context of paleopathological and symbolic studies, suggest that dogs and humans had a unique bond (Tchernov and Valla, 1997; Janssens et al., 2016) (Fig. 1, N° 5, 6 and 7).

Since the 1990s, geneticists have attempted to answer questions about dog domestication raised by archaeological findings (Vilà et al., 1997). Regarding the geographical origin of dog domestication, multiple sites have been proposed. Studies of mtDNA haplogroup diversity in contemporary dogs and wolves point to China (Savolainen et al., 2002; Pang et al., 2009; Wang et al., 2016), nuclear DNA markers point to Central Asia (Shannon et al., 2015) and whole genome sequencing points to the Near East (Freedman et al., 2014).

With respect to the temporal frame, nowadays dates between 17,000 and 10,000 years ago are the most recent dates proposed for the dog lineage divergence time, both with mtDNA (Savolainen et al., 2002) and

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<https://doi.org/10.1016/j.jasrep.2022.103706>

Received 19 July 2022; Received in revised form 21 October 2022; Accepted 21 October 2022

Available online 11 November 2022

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high-quality genomes of contemporary dogs (Freedman et al., 2014). Nevertheless, an uncertainty in these dates could bring them back to 40,000–30,000 years ago (Savolainen et al., 2002; Freedman et al., 2014). In fact, we should also take into account that the genetic divergence of wolves' and dogs' lineages does not have to concur with that of domestication. Proposed dates as recent as 17,000–10,000 would coincide in time with the first dog archaeological evidence, which seems unlikely.

Paleogenetics contradicts some of these conclusions from current canid population studies. According to Thalmann et al. (2013), the origins of most dog lineages can be traced back to ancient European wolves, suggesting a European origin for wolf domestication. However, some authors suggested a dual origin in Europe and Asia (Frantz et al. 2016; Bergström et al., 2022). Furthermore, with the contribution of ancient canids' DNA, the mutation rate of wolves was recalibrated, proposing that the divergence between dogs and wolves took place sometime between 40,000 and 27,000 years ago (Skoglund et al., 2015; Botigué et al., 2017). These paleogenetic findings support that wolf-dog lineages' divergence age differs from the age of the first domestication event.

Apparently in agreement with such dates proposed by paleogeneticists (40,000–27,000 years BP), some remains of very ancient canids (40,000–15,000 years BP), called “dog-like wolves”, have been described and identified by means of classic morphometry. Some studies suggest that these may be protodogs. The “dog-like wolves” from Western Europe come from the following sites: Goyet (Belgium), 31,890 ± 240/-220 BP, Aurignacian (Germonpré et al., 2009; Germonpré et al., 2012); Předmostí (Czech Republic), c. 27,000–26,000 BP, Gravettian (Germonpré et al., 2012; Prassack et al., 2020; Galeta et al., 2020); and the site of Chauvet cave (France), c. 26,000 BP, where no remains other than dog-like footprints were found (García, 2005) (Fig. 1, N° 8, 9 and 10). Some other “dog-like wolves” from Siberia are: Razboinichya (Altai, South Siberia, Russia), 33,000 cal. BP (Ovodov et al., 2011) and Ulakhan Sular (Yakutia, Northeast Siberia, Russia), 13,925 ± 70 BP (17,200 cal. BP approx.) (Germonpré et al., 2017). Those from East European plains are: Kostenki-8 (Russia) c. 25,000–22,000 BP, Gravettian (Germonpré et al., 2015a); Eliseevichi-I (Russia), c. 17,000–13,000 BP, Epigravettian (Sablín and Khlopachev, 2002); and Mezherich and Mezin (Ukraine), c. 15,000–14,500 BP, Epigravettian (Germonpré et al., 2009) (Fig. 1, N° 11, 12, 13 and 14).

Confronting these classic morphometry studies, some new

approaches conclude that “dog-like wolves” are clustered within the variability of the wolf, which must have been greater in the past (Boudadi-Maligne and Escarguel, 2014; Drake et al., 2015; Janssens et al., 2019). Some authors have proposed that those ancient canids may have been just a morphotype or ecotype of wolves in the Upper Paleolithic (Germonpré et al., 2015b; Prassack et al., 2021). Thus, they could not be confidently placed within the Paleolithic dogs (Janssens et al., 2021a, 2021b). This means that to date, the Magdalenian remains from Abri le Morin (France) and Bonn-Oberkassel (Germany) were the oldest dog remains identified as domesticated dogs (Boudadi-Maligne et al., 2012; Janssens et al., 2018).

In this study, we reconsidered a canid humerus recovered in the archaeological excavations directed by J. Altuna in the Erralla cave (Gipuzkoa, Basque Country) (Altuna et al., 1985) (Fig. 2). The cave is located in the Northeastern region of the Basque Country, 10 km in a straight line from the Cantabrian Sea and 460 m above the sea level. Its maximum length is 20 m and has two entrances, one at each end. The excavations affected 30 m² from the 90 m² of the cave. The site presents a solid stratigraphy, with well-defined and characterized levels (from oldest to most recent: level VII to level I). Level VII is directly over the bedrock of the cave, and, together with level VI, it is completely sterile. Level V, where the canid humerus was found, belongs to the Lower Cantabrian Magdalenian and is covered by level IV, which, despite its archaeological sterility, provided the remains of seven mountain goats (*Capra pyrenaica*), which were in anatomical position, indicating that they died in the cave, probably due to a lightning strike. Levels III and II belong to the Late Magdalenian, and level I is constituted by the current topsoil. Thus, the importance of the canid from this level V lies in the fact that the level is perfectly isolated, with no elements from the other levels. That is, it was found between two sterile levels, showing the absence of contamination with other cultural levels.

Level V provided a rich lithic and bone industry, typical of the Lower Magdalenian, as well as ornamental objects and other decorated items (e.g., assegai points, characteristic of the Cantabrian region in this period) (Baldeón, 1985). This level was laid during a very cold phase (Dryas I), as has been shown by pollen, sedimentological and archaeozoological analyses (Altuna et al., 1985). Moreover, the animal-based diet of humans of Erralla in this period indicates a predominance of *Capra pyrenaica* (84%) over *Cervus elaphus* (7.0%) (Altuna and Maritzkurrena, 1985).

In addition, the canid humerus was found in the lower part of level V.

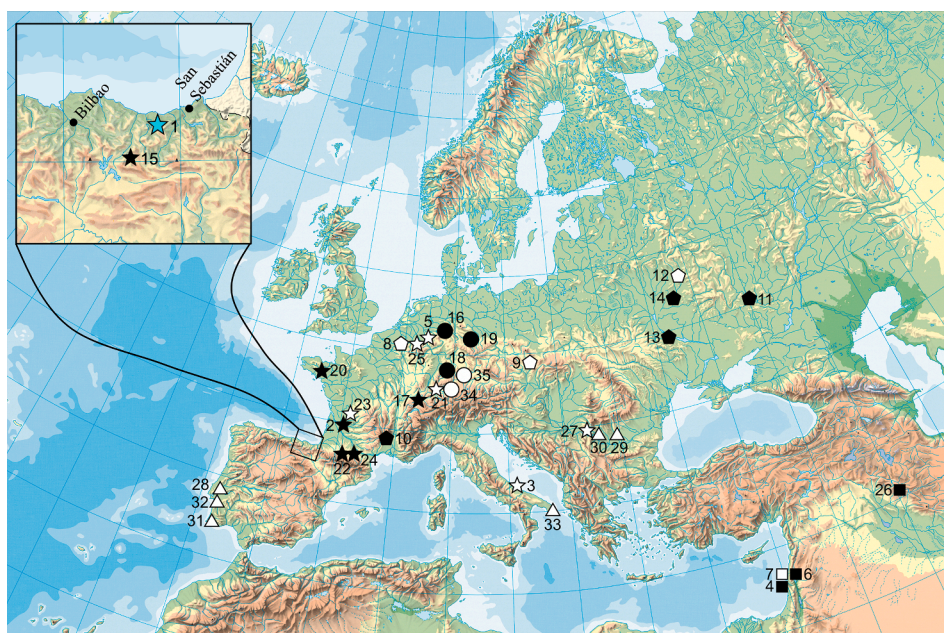


Fig. 1. Archaeological sites from West Eurasia cited in this article. Stars: Magdalenian, Epigravettian and Epipaleolithic dogs. Circles: Putative Magdalenian dogs. Triangles: Mesolithic dogs. Squares: Levantine Preneolithic dogs. Pentagons: Dog-like wolves. White: Canids whose genetic information is available. Blue: Erralla dog. 1, Erralla; 2, Abri le Morin; 3, Grotta Paglicci; 4, Kebara; 5, Bonn-Oberkassel; 6, Eynan/Mallaha; 7, Hayonim Terrace; 8, Goyet; 9, Předmostí; 10, Chauvet; 11, Kostenki-8; 12, Eliseevichi-I; 13, Mezherich; 14, Mezin; 15, Anton Koba; 16, Kniegrotte; 17, Hauterive-Champréveyres; 18, Teufelsbrücke; 19, Ölnitz; 20, Le Closeau; 21, Kesslerloch; 22, Grotte-abri du Moulin; 23, Pont d'Ambon; 24, Montespan; 25, Kartstein; 26, Palegawra; 27, Cuina Turcului; 28, Muge; 29, Icoana; 30, Ostrovul Corbului; 31, Vale Boi; 32, Poças S. Bento; 33, Romanelli; 34, Gnirshöhle; 35, Hohle Fels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 2. Erralla humerus. a) Anterior view. b) Posterior view. c) Medial view. d) Lateral view.

Specifically, the site was excavated in fine stratigraphical units, known as beds. Level V had eight beds, comprising from bed 17 (in its upper part, bordering with level IV) to bed 24 (in its lower part, bordering with level VI). The canid humerus was found in bed 22.

Three datings of Level V were performed by Teledyne Isotopes (New Jersey) on different sets of bones scattered throughout the entire level (Altuna et al., 1984; Altuna, 1985). The values provided were $15,740 \pm 240$, $16,200 \pm 240$ and $16,270 \pm 240$ BP (uncalibrated dates), which are in line with the Lower Magdalenian datings of other sites in the Basque Country and the Cantabrian region (Mariezkurrena, 1979, Mariezkurrena, 1990).

In 1985, Altuna and Mariezkurrena classified this bone as *Canis* sp. (Fig. 2), and compared it with 22 prehistoric wolf humeri from the Basque Country and Europe, as well as with present-time wolf humeri. It was considerably smaller than every other humerus. They also compared it with another canid that existed in that time in the Basque Country: *Cuon alpinus* (dhole); although the measurements were very similar, the morphology of the piece was closer to the dog than to the dhole. In 1994, Altuna, after showing the piece to prestigious archaeozoologists of that time, such as G. Nobis, R. Musil, A. Gautier, F. Poplin and M. Teichert, among others, considered that it was a dog (Altuna, 1994). However, this determination was not absolutely certain. Later, Vigne (2005) examined this canid bone, classifying it as a dog based on its morphology. Moreover, reviewing Altuna's paper (1985), Vigne calculated the calibrated values of the three datings of level V in Erralla, and proposed an approximate upper date of 17,500–17,000 cal. BC (c. 19,000 cal. BP). These dates have been incorrectly reproduced in some papers, maybe because they were considered too old for a domesticated dog (Pionnier-Capitan et al., 2011; Boudadi-Maligne et al., 2012; Janssens et al., 2018, among others).

In the present study, we examined the humerus of the canid from the Lower Magdalenian level of the site of Erralla, and we conducted a critical review of the European sites that have provided remains of Paleolithic and Mesolithic dogs. In the Basque Country, no other remains have been classified as domestic *Canis* in Magdalenian levels to date. There are some remains from the Azilian², such as the dog from the site of Anton Koba (Oñati, Gipuzkoa) (Armendariz, 1997; Altuna and Mariezkurrena, 2013) (Fig. 1, N° 15). Other remains of *C. l. familiaris* attributed to Mesolithic levels in sites of the Basque Country have been certainly determined, although their belonging to those levels is uncertain (Altuna, 1994). This is the reason why they are not included in the present work. Moreover, this is the first study to include a direct AMS ¹⁴C dating of this humerus and a genetic analysis for species identification, interpreting these results in the context of the existing data about the domestication of the wolf in Europe.

2. Materials and methods

2.1. Radiocarbon dating

A sample of 115 mg of bone powder from the Erralla humerus was sent to the Ångström Laboratory at Uppsala University (Sweden) for AMS ¹⁴C dating. The sample was stirred at 10 °C in 0.8 M HCl for 30 min to remove apatite. Then, distilled water maintained at pH 3 was added to the insoluble fraction, which was heated while stirring (6–8 h, 90 °C).

² Azilian: Postmagdalenian culture of the Epipaleolithic and Mesolithic periods in the Franco-Cantabrian region. It is named after Mas d'Azil cave (Pyrenees, France).

The soluble part, referred to as fraction D, contained most of the organic parts (the “collagen”) of the original bone. The fraction to be ^{14}C -dated was combusted to CO_2 , which was graphitised through a Fe-catalyst reaction prior to the accelerator determination. In the present investigation, fraction D was dated.

2.2. Sampling and DNA extraction

A small surface of the Erralla humerus (on the distal metaphysis) was previously decontaminated by mechanical abrasion with a dental file, in order to eliminate possible contaminating exogenous DNA. Then, 135 mg of bone powder were taken using a dentist drill.

DNA was obtained from the bone powder in a single extraction process using the silica-based method (Dabney et al. 2013), following the modifications proposed by Svensson et al. (2021), who used silica spin-column containing a volume extender from a High Pre-Viral Nucleic Acid Large Volume kit (Roche) (Yang et al., 1998; Glocke and Meyer, 2017). The total volume of DNA extract was 75 ml (eluted in buffer EB, QIAGEN) and two extraction blanks were processed as controls.

The amplification of each mitochondrial DNA fragment (D-loop and *cytochrome b* gene) was undertaken in independent PCRs. In case of positive amplification and absence of contamination, the amplifications were purified by ExoSAP-IT (USB Corporation), with subsequent sequencing in an ABI310 automatic sequencer using chemistry based on Big-Dye 1.1 (Life Technology). The obtained results were edited with BioEdit software (<https://www.mbio.ncsu.edu/BioEdit/bioedit.html>) and the sequences were aligned manually.

The DNA extraction and amplification were performed in the ancient DNA laboratory of the University of the Basque Country (Spain). Processing of the samples involved the application of a series of strict criteria detailed in Pääbo et al. (2004) and Gilbert et al. (2005) in order to authenticate the results. To prevent ancient DNA contamination, the extraction and preparation of the PCR were undertaken in a positive-pressure sterile chamber, physically separated from the laboratory where post-PCR processes were carried out. All the work surfaces were regularly cleaned with sodium hypochlorite and irradiated with UV light (254 nm). Suitable disposable clothing was worn (lab coverall, mask, gloves and cap). Contamination controls were applied in both the extraction and amplification processes.

2.3. Genetic analysis

The sequence of *cytochrome b* (*cytb*) gene is commonly used to identify the allocation of a species (Irwin et al., 1991; Kuwayama and Ozawa, 2000; Ludt et al., 2004). In our case, it was used to differentiate *Canis* from *Cuon*, which is another close genus of canids, as well as to ascertain the identification of the species within the genus *Canis*. To this end, a sequence of ~200 bp was analysed through the sequencing of two overlapping fragments of ~120 bp of the *cytb* gene, following the conditions described in Hervella et al. (2012).

Since the *cytb* sequence of *Canis lupus familiaris* (domestic dog) presents a small number of polymorphisms with respect to that of *Canis lupus* (wolf) (Linacre and Tobe, 2009), we verified the species that the Erralla humerus belongs to, through the sequencing of a fragment of 181 bp from the *D-loop* region of its mtDNA, between nucleotide positions 15495 and 15676, following the proposal from Pires et al. (2006, 2017, 2019), among other authors. Both analyses, i.e., the sequencing of the fragments from *cytb* and from the *D-loop*, were carried out in triplicate. The obtained *D-loop* sequence also allowed determining the mitochondrial haplogroup of the canid (Fregel et al., 2015).

A Median-Joining Network was constructed using the sequences (nps. 15,495–15,900) from the present study and other published data from Paleolithic and Mesolithic dogs in Europe (Pionnier-Capitan, 2010) using the Network 4.6.0.0 software (<https://www.fluxus-engineering.com>).

3. Results

3.1. Chronology: Radiocarbon dating of the humerus from the Erralla site

The direct AMS ^{14}C dating of the Erralla humerus (Ua-56946) was $14,221 \pm 48$ BP; 17,410–17,096 cal. BP (95.4%) (Table 1 and Fig. 3). The dating of the canid from the Erralla cave corresponds to the Magdalenian period; this is in line with the stratigraphic context in which it was found, which was archaeologically defined as a Lower Cantabrian Magdalenian level. The direct dating of the humerus reduces the temporal range attributed to it by the archaeological level, which was established based on the dating of remains of animals scattered throughout the entire level (Altuna, 1985) (see Introduction).

3.2. Morphometric analysis of the humerus from the Erralla site

The humerus recovered from the Erralla site presented extraordinary conservation, although the upper end, which corresponds to the humeral head, is missing (Fig. 2). A 3D reconstruction of the humerus was carried out, in order to preserve the valuable bone and provide a digital reproduction of it that enables its morphometric analysis (Supplementary data 1). The main measurements of the Erralla humerus are: minimum diaphysis width (14 mm), distal breadth (Bd) (34.5 mm) and distal thickness (23.5 mm) (Altuna and Mariezkurrena, 1985). We highlight distal breadth, since it is the osteometric methodology internationally used in macromammals (Driesch, 1976) (Fig. 4).

Fig. 4 shows that the distal breadth (Bd) of the Erralla humerus (34.5 mm) is outside of the range of variation of both Magdalenian and Mesolithic wolves of the Basque Country (42.4 ± 1.26 mm) and Würm wolves of Europe (42.1 ± 2.24 mm); however, it is within the variability range of a sample of Mesolithic dogs of Northern Europe (32 ± 4.63 mm).

Regarding the morphometric differentiation between *Canis* and *Cuon*, it is almost imperceptible at the level of the humerus. Although a more developed medial epicondyle in the medio-distal direction for the *Cuon* has been described (Pionnier-Capitan, M. et al., 2011), in the case of the Erralla humerus, no distinction was observed in relation to these morphological feature.

3.3. Species identification

The mtDNA recovered from the sample of Erralla was quantified through SYBRGreen RT-qPCR, using the primers for the *cytb* gene (Hervella et al., 2012), obtaining an average of 1,689 copies/ μl of extract, which is a higher value than 1000 copies/ μl , as indicated by the aDNA authentication criteria (Pääbo et al., 2004; Gilbert et al., 2005). Then, different amplifications were conducted following the protocol described in Hervella et al. (2012), in order to obtain the sequence of a fragment of ~200 bp of the *cytochrome b* gene. Negative controls and extraction blanks were systematically used to monitor possible contaminations. Neither PCRs blanks nor negative controls gave positive results. Sequences from three independent PCRs from the same DNA extract of Erralla were obtained. The three sequences showed the same polymorphisms. The sequence obtained (Supplementary data 2) was then included in the BLAST (NCBI) and Uniprot databases (Boutet et al., 2016). This sequence was identified as *Canis lupus familiaris* (99.6% probability) and not *Cuon alpinus* (dhole) (67.5%). The result implies that the Erralla humerus cannot be a dhole.

In order to confirm the identification of the species and obtain

Table 1
AMS ^{14}C direct dating of the Erralla humerus.

Lab number	$\delta^{13}\text{C}\text{‰}$ V-PDB	^{14}C age BP	95.4% probability cal. BC	95.4% probability cal. BP
Ua-56946	-17.8	$14,221 \pm 48$	15,460–15,146	17,410–17,096

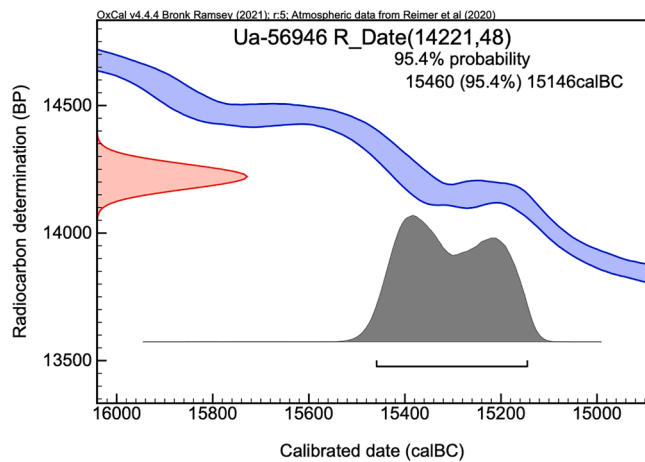


Fig. 3. Calibration probability distribution of the radiometric datings conducted on bone collagen of the Erralla humerus (Reimer et al., 2013), OxCal Software v4.4.4 Bronk Ramsey (2021) using IntCal20 curve.

information of the mitochondrial haplogroup that the Erralla dog belongs to, a region of 181 bp of the mitochondrial D-loop was sequenced (Supplementary data 3). For mtDNA data, the obtained sequences were compared by alignment to the reference sequence (Kim et al., 1998) (GenBank accession entry: NC_002008), and the polymorphism was numbered according to Pereira et al. (2004).

The sequence from the D-loop fragment was obtained by means of six PCRs (three for each fragment), detecting the same mutations in all of them. There was no ambiguity in the identification of polymorphisms, which were T15611C, T15639G (transversion) and T15650C. These polymorphisms correspond to the haplogroup C from *C. l. familiaris*, following the information provided by Fregel et al. (2015). These authors proposed a nomenclature of the phylogeny of the mitogenome of *C. l. familiaris*, considering the data of the mitogenomes of ancient and modern wolf and dog. The analysis of the D-loop reasserts the Erralla humerus assignment to *C. l. familiaris*.

3.4. ^{14}C datings of Magdalenian and Epipaleolithic sites where dog remains have been recovered

A review of ^{14}C datings of Magdalenian, Epigravettian and Epipaleolithic European sites (Fig. 1) was carried out in order to

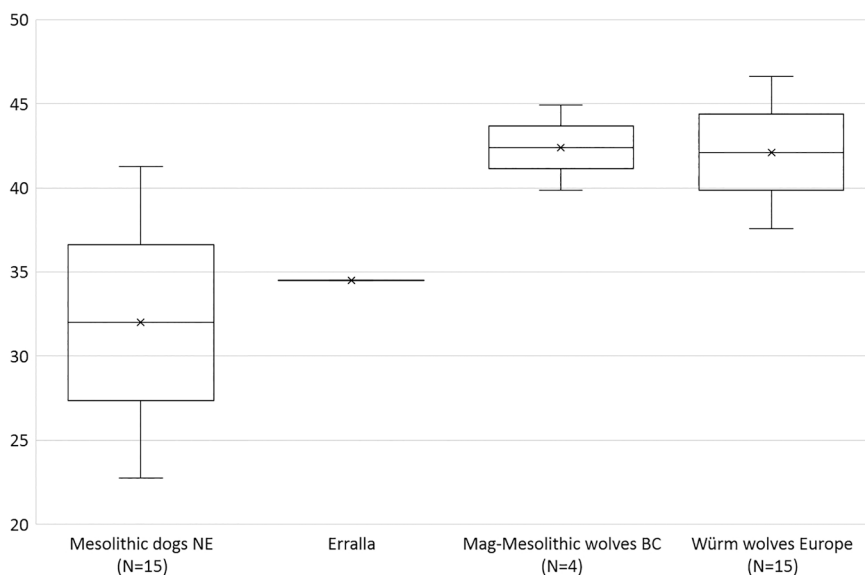


Fig. 4. Individual distal breadth of the Erralla humerus compared with that observed in Late Paleolithic and Mesolithic dogs and wolves. Measures given in mm. Mesolithic dogs from North Europe (Mesolithic dog NE), Magdalenian and Mesolithic wolves from the Basque Country (Mag-Mesolithic wolves BC), and Würm wolves from Europe (France and Belgium) (Chaix, 2000; Pionnier-Capitan et al., 2011; Germonpré et al., 2021). Box and whisker plots represent the mean \pm 1 (box) and 1.5 (whisker) standard deviations.

contextualise the dating obtained in the Erralla humerus and those from other ancient dogs (Table 2). We also incorporated calibrated values that were calculated in the present study, with the aim of enabling the comparison of the datings among sites, since we observed that some authors provide uncalibrated datings, others show BP calibrated datings and other authors present BC calibrated datings. Furthermore, the calibrated datings were not always done using the same calibration curve, and thus they were not truly comparable (Reimer et al., 2013, 2020). The values calibrated in this study, using the OxCal4.4 software with the IntCal20 curve (Reimer et al., 2020), are highlighted with (*) in Table 2. In addition, to calculate cal. BP from cal. BC dates, the corresponding + 1950 years were added (**).

Among the 15 sites of Europe with canid remains mentioned in this review, six have a direct ^{14}C dating on dog bone, eight on other remains of the level in which the canids appeared and only one of the sites (Montespan) lacks ^{14}C datings due to the insufficient amount of collagen (Pionnier-Capitan et al., 2011) (Table 2). Most of the *Canis* were confirmed morphologically as *Canis lupus familiaris*; however, three sites have bones that were only attributed to *Canis lupus familiaris*, but have not been confirmed as such. In the other sites, the *Canis lupus familiaris* was genetically or morphologically differentiated from *Cuon* genus. Nevertheless, in Grotta Paglicci, only two bones out of twelve (a tibia from level 5a and a metatarsal, directly dated, from level 4c) were morphologically and/or genetically differentiated from *Cuon*. In addition, some remains have a complex history of dating, re-dating, calibration, etc. This information is shown in Table 2, where the included references provide the details of each site.

Table 2 presents the direct dating of the Erralla dog humerus conducted in this study (Ua-56946), along with the previously published datings of level V, where this canid appeared (Altuna, 1985). In the Basque Country, there are different remains of dogs that have been morphologically confirmed, although their attribution to Azilian levels is uncertain (Altuna, 1994). Anton Koba (Oñati, Gipuzkoa) is the only site, to date, with a certain attribution to an Azilian level dated between $11,800 \pm 330$ and $11,700 \pm 180$ BP (Armendariz, 1997; Altuna and Mariezkurrena, 2013) (Table 2 and Fig. 1). This bone has not been genetically analysed yet, due to the restrictions imposed by the Cultural Heritage Department of the Basque Government, referred to the minimum weight of each bone remain (5 g) and the representation of the species in particular in the archaeological level.

The Magdalenian site of Abri le Morin (France) and the Epigravettian level 4c of Grotta Paglicci have the oldest direct datings to date, after that of Erralla, which are close to the Magdalenian sites of Kesslerloch

Table 2

¹⁴C datings of the Magdalenian, Epigravettian and Epipaleolithic levels of sites in Europe that contain remains attributed to dog.

Site	Level	Code	Dated sample	¹⁴ C Uncal. BP	Cal. BC	Cal. BP
Grotta Paglicci [Early Epigravettian] (Fig. 1, N° 3)	17b	GrN-14874	–	16,890 ± 160 ⁽⁸⁾	18,881–18,058 ^(*)	20,831–20,008 ^(**) 20,789–19,979 ⁽⁸⁾
	10	F-68	–	15,320 ± 250 ⁽⁸⁾	17,192–16,231 ^(*)	19,142–18,181 ^(**) 19,112–17,988 ⁽⁸⁾
8		F-66	–	15,460 ± 220 ⁽⁸⁾	17,242–16,307 ^(*)	19,192–18,257 ^(**) 19,245–18,220 ⁽⁸⁾
Erralla [Lower Magdalenian] (Fig. 1, N° 1)	5	Ua-56946	Dog humerus	14,221 ± 48⁽¹⁾	15,460–15,146⁽¹⁾	17,410–17,096⁽¹⁾
	5	I-12868	Animal remains (several)	16,270 ± 240 ⁽²⁾	18,334–17,121 ^(*)	20,284–19,071 ^(**)
	5	I-12551	Animal remains (several)	16,200 ± 240 ⁽²⁾	18,231–17,030 ^(*)	20,181–18,980 ^(**)
	5	I-12540	Animal remains (several)	15,740 ± 240 ⁽²⁾	17,643–16,400 ^(*)	19,593–18,350 ^(**)
Grotta Paglicci [Final Epigravettian] (Fig. 1, N° 3)	7	F-65	–	14,820 ± 210 ⁽⁸⁾	16,696–15,518 ^(*)	18,646–17,468 ^(**) 18,541–17,551 ⁽⁸⁾
	5bc	F-96	–	13,590 ± 200 ⁽⁸⁾	15,074–13,906 ^(*)	17,024–15,856 ^(**) 17,021–15,841 ⁽⁸⁾
	5c	Fi2147 Fi2148	Wolf humerus	12,570 ± 60 ⁽⁹⁾	13,225–12,556 ^(*)	15,175–14,506 ^(**) 15,200–14,450 ⁽⁹⁾
	4c	OxA-26316	Dog third metatarsal	12,175 ± 55⁽⁹⁾	12,361–11,910^(*)	14,311–13,860^(**) 14,372–13,759⁽⁹⁾
	Rw	Fi2146	Canid mandible	11,300 ± 800⁽⁹⁾	13,859–9,256^(*)	15,809–11,206^(**) 15,800–11,200⁽⁹⁾
Kniegrotte [Upper Magdalenian] (Fig. 1, N° 16)	8 Low	OxA-4852	Horse lumbar vertebra	13,520 ± 130 ⁽¹⁵⁾	14,799–13,942 ^(*)	16,749–15,892 ^(**)
	8 Upp	OxA-4832	Reindeer scapula	13,310 ± 110 ⁽¹⁵⁾	14,376–13,737 ^(*)	16,356–15,687 ^(**)
	8 Upp	OxA-4846	Horse femur	13,190 ± 130 ⁽¹⁵⁾	14,298–13,496 ^(*)	16,248–15,446 ^(**)
	8 Mid	OxA-4850	<i>Alopex lagopus</i> tibia	13,160 ± 140 ⁽¹⁵⁾	14,261–13,404 ^(*)	16,211–15,354 ^(**)
	8 Mid	OxA-4848	Horse metatarsal	13,150 ± 130 ⁽¹⁵⁾	14,222–13,412 ^(*)	16,172–15,362 ^(**)
	8 Upp	OxA-4845	Reindeer tibia	13,120 ± 130 ⁽¹⁵⁾	14,171–13,371 ^(*)	16,121–15,321 ^(**)
	8 Mid	OxA-4849	<i>Saiga tatarica</i>	13,130 ± 120 ⁽¹⁵⁾	14,160–13,401 ^(*)	16,110–15,351 ^(**)
	Hauterive-Champrévevres [Magdalenian] (Fig. 1, N° 17)	UZ-2285		Charcoal	13,050 ± 160 ^(15, 21)	14,162–13,229 ^(*)
UZ-2283			Charcoal	12,950 ± 110 ⁽¹⁵⁾	13,858–13,223 ^(*)	15,808–15,173 ^(**)
UZ-2286			Charcoal	12,870 ± 140 ⁽¹⁵⁾	13,842–13,035 ^(*)	15,792–14,985 ^(**)
UZ-2282			Charcoal	12,830 ± 160 ⁽¹⁵⁾	13,891–12,667 ^(*)	15,841–14,617 ^(**)
UZ-2171			Charcoal	12,730 ± 140 ⁽¹⁵⁾	13,700–12,546 ^(*)	15,650–14,496 ^(**)
UZ-2175			Charcoal	12,630 ± 130 ⁽¹⁵⁾	13,472–12,365 ^(*)	15,422–14,315 ^(**)
UZ-2172			Charcoal	12,620 ± 150 ⁽¹⁵⁾	13,531–12,320 ^(*)	15,481–14,270 ^(**)
UZ-2177			Charcoal	12,600 ± 150 ⁽¹⁵⁾	13,465–12,266 ^(*)	15,415–14,216 ^(**)
UZ-2173			Charcoal	12,540 ± 140 ⁽¹⁵⁾	13,319–12,238 ^(*)	15,269–14,188 ^(**)
UZ-2174			Charcoal	12,510 ± 130 ^(15, 21)	13,251–12,230 ^(*)	15,201–14,180 ^(**)
UZ-2287			Charcoal	12,500 ± 150 ⁽¹⁵⁾	13,274–12,176 ^(*)	15,224–14,126 ^(**)
Teufelsbrücke [Magdalenian] (Fig. 1, N° 18)		2	OxA-5723	<i>Capra ibex</i> calcaneum	13,080 ± 140 ⁽¹⁵⁾	14,141–13,311 ^(*)
	2	OxA-5724	Artiodactyl radiocubitus	12,940 ± 140 ⁽¹⁵⁾	13,945–13,141 ^(*)	15,895–15,091 ^(**)
	1	OxA-5725	<i>Capra ibex</i> tibia	12,900 ± 130 ⁽¹⁵⁾	13,853–13,111 ^(*)	15,803–15,061 ^(**)
	2	OxA-5722	Horse phalanx 2	12,860 ± 130 ⁽¹⁵⁾	13,801–13,051 ^(*)	15,751–15,001 ^(**)
	3	OxA-5726	Reindeer humerus	12,640 ± 130 ⁽¹⁵⁾	13,515–12,374 ^(*)	15,465–14,324 ^(**)
	3	OxA-5727	Horse mandible	10,040 ± 120 ⁽¹⁵⁾	10,019–9,277 ^(*)	11,969–11,227 ^(**)
Ölknitz [Magdalenian] (Fig. 1, N° 19)	OxA-5713		Horse 1st phalanx	12,740 ± 120 ⁽¹⁵⁾	13,665–12,655 ^(*)	15,615–14,605 ^(**)
	OxA-5714		Reindeer maxilla	12,620 ± 120 ⁽¹⁵⁾	13,408–12,366 ^(*)	15,358–14,316 ^(**)
	OxA-5709		Horse metacarpus	12,270 ± 120 ⁽¹⁵⁾	12,965–11,916 ^(*)	14,915–13,866 ^(**)
	OxA-5712		Reindeer radius	12,270 ± 110 ⁽¹⁵⁾	12,930–11,924 ^(*)	14,880–13,874 ^(**)
	OxA-5710		Horse 3rd metatarsus	12,080 ± 110 ⁽¹⁵⁾	12,361–11,662 ^(*)	14,311–13,612 ^(**)
	OxA-5711		Horse metacarpus	12,050 ± 110 ⁽¹⁵⁾	12,250–11,65 ^(*)	14,200–13,607 ^(**)
Abri le Morin [Upper Magdalenian] (Fig. 1, N° 2)	A-I	OxA-23627	Dog upper I3	12,540 ± 55⁽¹⁰⁾	13,182–12,508^(*)	15,132–14,458^(**) 15,114–14,237⁽¹⁰⁾
	A-III	OxA-23628	Dog carnassial	12,450 ± 55⁽¹⁰⁾	13,012–12,347^(*)	14,962–14,297^(**) 15,005–14,155⁽¹⁰⁾
Le Closeau [Azilian] (Fig. 1, N° 20)	GrA-18860		Horse long bone	12,510 ± 80 ^(7, 18)	13,157–12,363 ^(*)	15,107–14,313 ^(**) 15,138–14,513 ⁽¹⁸⁾
	GrA-18815		Bovid Phalanx	12,480 ± 70 ^(7, 18)	13,084–12,342 ^(*)	15,034–14,292 ^(**) 15,090–14,473 ⁽¹⁸⁾
	AA-41881		Wild boar	12,423 ± 67 ^(7, 18)	13,001–12,266 ^(*)	14,951–14,216 ^(**) 14,999–14,319 ⁽¹⁸⁾
	GrA-11665		Cervid femur	12,360 ± 60 ^(7, 18)	12,896–12,167 ^(*)	14,846–14,117 ^(**) 14,894–14,218 ⁽¹⁸⁾
	GrA-18816		Wild boar	12,350 ± 70 ^(7, 18)	12,897–12,148 ^(*)	14,847–14,098 ^(**) 14,884–14,189 ⁽¹⁸⁾
	GrA-11664		Horse tibia	12,350 ± 60 ^(7, 18)	12,892–12,153 ^(*)	14,842–14,103 ^(**) 14,877–14,194 ⁽¹⁸⁾
	GrA-18819		Cervid right radius	12,340 ± 70 ^(7, 18)	12,894–12,138 ^(*)	14,844–14,088 ^(**) 14,867–14,163 ⁽¹⁸⁾
	AA-41882		Lion right Metacarpal V	12,248 ± 66 ^(7, 18)	12,859–12,080 ^(*)	14,809–14,030 ^(**) 14,596–14,055 ⁽¹⁸⁾
	OxA-5680		Unidentified bone	12,090 ± 90 ^(7, 18)	12,255–11,817 ^(*)	14,205–13,767 ^(**) 14,367–13,855 ⁽¹⁸⁾
	OxA-6338		Unidentified bone	12,050 ± 100 ^(7, 18)	12,221–11,662 ^(*)	

(continued on next page)

Table 2 (continued)

Site	Level	Code	Dated sample	¹⁴ C Uncal. BP	Cal. BC	Cal. BP
Anton Koba [Azilian] (Fig. 1, N° 15)	8	I-16236	Animal remains (several)	11,800 ± 330 ⁽³⁾	12,927–11,145 ^(*)	14,171–13,612 ^(**)
	8	I-17479	Animal remains (several)	11,700 ± 180 ⁽³⁾	12,071–11,241 ^(*)	14,327–13,813 ⁽¹⁸⁾
Kesslerloch [Magdalenian] (Fig. 1, N° 21)		KIA-33350	Dog right maxilla	12,225 ± 45⁽¹⁷⁾	12,369–12,090^(*) 12,360 + -210 ⁽¹⁷⁾	14,319–14,040^(**) 14,286–13,975 ⁽⁶⁾
Bonn-Oberkassel [Magdalenian] (Fig. 1, N° 5)		OxA-29869	Ulna sin. dog	12,390 ± 55⁽¹⁴⁾	12,916–12,232^(*) 12,900–12,150 ⁽¹⁶⁾	14,866–14,182^(**)
		OxA-4793		12,270 ± 100⁽¹⁹⁾	12,901–11,936^(*) 12,850–11,900 ⁽¹⁶⁾	14,856–13,886^(**) 14,809–14,140 ⁽²¹⁾
		KIA-4162	Humerus dext. dog	12,210 ± 60⁽¹⁹⁾	12,837–11,928^(*) 12,390–11,910 ⁽¹⁶⁾	14,787–13,878^(**) 14,337–13,861 ⁽²¹⁾
		KIA-4161	Maxila dext. dog	12,110 ± 45⁽¹⁹⁾	12,140–11,860^(*) 12,180–11,840 ⁽¹⁶⁾	14,090–13,810^(**) 14,122–13,799 ⁽²¹⁾
		KIA-4163	Ulna dext. dog	11,620 ± 60⁽¹⁹⁾	11,647–11,395^(*)	13,597–13,345^(**) 13,569–13,319 ⁽²¹⁾
Grotte-abri du Moulin (Troubat) [Azilian] ⁽²²⁾ (Fig. 1, N° 22)	6 base	Ly 5275	Charcoal	10,770 ± 100 ⁽⁵⁾	10,976–10,543 ^(*) 10,928–10,489 ⁽¹³⁾	12,926–12,493 ^(**) 12,878–12,439 ⁽¹³⁾
	6	Ly-9968	Deer bone	10,225 ± 45 ⁽¹³⁾	10,471–9795 ^(*) 10,165–9,816 ⁽¹³⁾	12,421–11,745 ^(**) 12,115–11,766 ⁽¹³⁾
Pont d'Ambon [Laborian] ⁽¹¹⁾ (Fig. 1, N° 23)		GifA-99102	Dog cubitus	10,730 ± 100⁽¹²⁾	10,941–10,536^(*)	12,891–12,486^(**) 12,952–12,451 ⁽¹⁸⁾
Kartstein [Epipaleolithic] (Fig. 1, N° 25)	2	KN-4023	<i>Lagopus</i>	10,090 ± 100 ⁽⁴⁾	10,021–9,316 ^(*) 9,578 ± 314 ⁽²⁰⁾	11,971–11,266 ^(**)
	2	KN-4072	<i>Rangifer</i>	9,550 ± 90 ⁽⁴⁾	9,228–8,642 ^(*) 8,724 ± 178 ⁽²⁰⁾	11,178–10,592 ^(**)
	2	KN-4073	<i>Rangifer</i>	9,530 ± 90 ⁽⁴⁾	9,217–8,635 ^(*) 8,683 ± 183 ⁽²⁰⁾	11,167–10,585 ^(**)

In **bold**: direct datings on dog bone remains. In *italics*: sites and levels where *Canis* remains were attributed to *C. l. familiaris*. Superscript brackets indicate the bibliographic reference: (1) this article; (2) Altuna, 1985; (3) Armendariz 1997; (4) Baales et al., 1996; (5) Barbaza, 1996; (6) Baumann et al., 2021; (7) Bodu et al., 2006; (8) Boschini et al., 2018; (9) Boschini et al., 2020; (10) Boudadi-Maligne et al., 2012; (11) Boudadi-Maligne et al., 2018; (12) Célérier et al., 1999; (13) Fat Cheung, 2015; (14) Higham et al., 2015; (15) Housley et al., 1997; (16) Janssens et al., 2018; (17) Napiarela and Uerpmann, 2012; (18) Pionnier-Capitan et al., 2011; (19) Street, 2002; (20) Street et al., 1994; (21) Street et al., 2015; (22) Boudadi-Maligne et al., 2020. (*) Calibrations calculated in this article with the IntCal 20 curve. (**) Dates in cal. BP calculated in this article.

and Bonn-Oberkassel. The site of Kesslerloch (Switzerland) provides a direct dating, whose BC calibration was performed by Napiarela and Uerpmann (2012), although a different calibration (in cal. BP) was reported in the genetic study of the dog (Baumann et al., 2021) (Table 2). The Bonn-Oberkassel dog (Germany) has been dated by different authors (Street, 2002; Higham et al., 2015). A review of this site by Janssens et al. (2018) provides a weighted mean dating of 12,290–12,050 cal. BC. Finally, the sixth direct dated dog is that of the Epipaleolithic site of Pont d'Ambon. Other Magdalenian and Epipaleolithic sites have only indirect datings coming both from different animals and charcoal remains.

The analysis of the direct dating of the Erralla dog, in the context of the dogs from the Upper Paleolithic and the Epipaleolithic, indicates that it is the oldest published to date. It belongs to the Lower Cantabrian Magdalenian, and it was found in an archaeological level dominated by the cold climate of the Lower Dryas I (Oldest Dryas), whereas the other mentioned dogs are from the Upper Magdalenian, the Final Epigravettian or the Epipaleolithic, and they belong to the interstadial Bølling/Allerød and Dryas III (Younger Dryas).

3.5. Archaeogenetics

3.5.1. Median-Joining Network: mtDNA sequences from Magdalenian and Mesolithic dogs

The mitochondrial DNA data of the European dogs from the Magdalenian (Erralla, Bonn-Oberkassel and Kesslerloch), Epigravettian (Grotta Paglicci), Epipaleolithic (Pont d'Ambon, Kartstein and Cuina Turcului) and Mesolithic, show that haplogroup C is the main haplogroup in these periods, although some Mesolithic dogs present other haplogroups, such as B in a dog of Italy and A in five dogs of Portugal

(Table 3).

To determine the relationship between the mitochondrial haplogroups of the Magdalenian, Epipaleolithic and Mesolithic European dogs, a Median-Joining Network (MJN) was performed (Table 3, Fig. 5). For this analysis, we considered the information of the nucleotides comprised between positions 15495 and 15900 of the mtDNA D-loop.

The Magdalenian, Epigravettian and Epipaleolithic dogs, including that from Erralla (highlighted in blue) (Fig. 5), present the diagnostic polymorphisms of mitochondrial haplogroup C, thus they share the same node along with five Mesolithic European dogs: a dog from the Cabeço da Arruda site (Muge, Portugal) and four from the Icoana site (Romania) (Table 3, Fig. 1, N° 3, 28 and 29). Haplogroup C includes two more haplotypes corresponding to two dogs from Romania [one from Cuina Turcului (Epipaleolithic) and another from Ostrovul Corbului (Mesolithic) (Fig. 1, N° 27 and 30)]. Mesolithic dogs present a greater mitochondrial haplogroup diversity, since, apart from haplogroup C, haplogroup A was found in five dogs of Portuguese sites (Fig. 1, N° 28, 31 and 32) and haplogroup B in a dog from Italy (Romanelli cave) (Fig. 1, N° 33).

4. Discussion

In the analysis of the canid bone found in the Lower Magdalenian level of the Erralla site (Basque Country, Spain), Altuna and Markezurrena (1985) concluded that the morphometric data excluded it from being a wolf, although its size, similar to that of a dhole, raised doubts about the identification of its species. Four sets of bone remains scattered throughout level V, where the canid humerus was found, provided values between 16,270 ± 240 and 15,740 ± 240 BP (20,223–18,536 cal. BP, calibration performed in the present study,

Table 3

Mitochondrial haplogroup of Magdalenian, Epigravettian, Epipaleolithic and Mesolithic dogs of Europe published to date.

Archaeological site	Country	Age cal. BP	Laboratory code	Accession number	Hg	Source
Erralla	Spain	17,410–17,096	Ua-56946	–	C	Present study
Bonn-Oberkassel	Germany	14,809–13,319	NA	KF661093	C	Thalmann et al., 2013
Grotta Paglicci (Apulia)	Italy	14,372–13,759	OxA-26316	MH376892	C	Boschin et al., 2020
Cuina Turcului	Romania	*13,229	ENS, France	dryad.8gp06	C	Pionnier-Capitan, 2010
Kesslerloch	Switzerland	14,286–13,975	MAMS-23874	KF661087	C	Thalmann et al., 2013
Pont d'Ambon	France	12,952–12,451	ENS, France	dryad.8gp06	C	Pionnier-Capitan, 2010
Kartstein	Germany	12,378–11,256	NA	KF661094	C	Thalmann et al., 2013
Romanelli Cave	Italy	11,393–11,198	NA	AY741668	B	Verginelli et al., 2005
Icoana	Romania	*9,197	ENS, France	dryad.8gp06	C	Pionnier-Capitan, 2010
Icoana	Romania	*9,197	ENS, France	dryad.8gp06	C	Pionnier-Capitan, 2010
Icoana	Romania	*9,197	ENS, France	dryad.8gp06	C	Pionnier-Capitan, 2010
Icoana	Romania	*9,197	ENS, France	dryad.8gp06	C	Pionnier-Capitan, 2010
Ostrovul Corbului	Romania	*8,921	ENS, France	dryad.8gp06	C	Pionnier-Capitan, 2010
Muge (Cabeço da Arruda)	Portugal	7,570	Beta-152956	KY014676	C	Pires et al., 2019
Poças S. Bento	Portugal	7,595	OxA-26094	KY014682	A	Pires et al., 2019
Muge (Cabeço Amoreira)	Portugal	7,735	OxA-24571	KY014677	A	Pires et al., 2019
Muge (Cabeço Amoreira)	Portugal	7,735	WK-36713	KY014683	A	Pires et al., 2019
Muge (Cabeço Amoreira)	Portugal	7,755	Beta-448544	KY014675	A	Pires et al., 2019
Vale Boi (Algarve)	Portugal	7,903	Beta-448544	KY014652	A	Pires et al., 2019

(*): approximate datings. The following is indicated: archaeological site, country, chronology (according to bibliography), laboratory code, accession number from Genbank, mitochondrial haplogroup (Hg) and source of the genetic study.

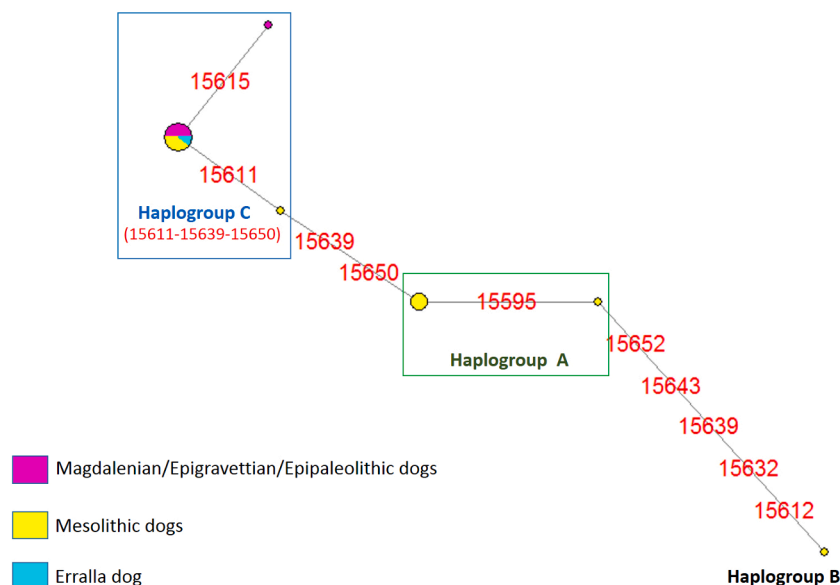


Fig. 5. Median-Joining Network of mtDNA haplotypes distribution of the Magdalenian/Epigravettian/Epipaleolithic (pink), Mesolithic dogs (yellow) and Erralla dog (blue). Data encompass mtDNA D-loop (nps. 15495 to 15900). Position 15639 is transversion. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2). This chronology was older than the datings of the oldest dogs identified until then [Bonn-Oberkassel (Nobis, 1984), Kniegrotte and Teufelsbrücke (Musil, 1984)]. In 1994, in an article about dogs in the archaeological sites of the Northern Iberian Peninsula, Altuna insisted on the certain determination of this canid (Altuna, 1994). Later, Vigne (2005) agreed with the identification of Altuna, indicating that the humerus belonged to an individual of the genus *Canis*. The comparison of the distal breadth of the Erralla humerus in the context of the Late Paleolithic and Mesolithic dogs and wolves (Fig. 4) is also in line with the previously mentioned evaluations.

The direct dating of the Erralla humerus through AMS ^{14}C (17,410–17,096 cal. BP) (Lab. Uppsala) (present study) is in agreement

with the datings of level V, where this dog bone was found (Table 2). The chronological discrepancy is due to the fact that the dating methodologies used when the site was studied (Altuna, 1985) were less developed than the current dating methodologies; furthermore, they required large amounts of bone taken from the entire level. The present study ends the uncertainty about the age of the Erralla dog, and validates it in its chronological context.

The genetic analysis conducted in the Erralla humerus indicates that the sequence of the *cytochrome b* gene (~200 bp) coincides with that of the genus *Canis* and not with that of the genus *Cuon*. The probability value was above 90% coincidence with the sequence of *Canis*, based on the information of the BLAST (NCBI) and Uniprot databases (Boutet

et al., 2016). In addition to the genetic information obtained from the fragment of *cytochrome b*, the analysis of the mutations of a fragment of 181 bp of the mtDNA D-loop (nps. 15495–15676) allowed assigning the Erralla humerus to the *Canis lupus familiaris* species with 99.6% probability and 98% identity (NCBI nucleotide database). Similarly, the mtDNA sequence recovered from the Erralla humerus corresponds to haplogroup C, which is the clade that includes the Magdalenian European dogs analysed to date (Table 3) (Thalmann et al., 2013; Frantz et al., 2016). Therefore, the mtDNA analysis indicates that the humerus of the Erralla site belongs to a dog (*C. l. familiaris*) of mitochondrial haplogroup C.

To date, only another three Upper Paleolithic (Magdalenian and Epigravettian) dogs from the sites of Kesslerloch (Switzerland), Bonn-Oberkassel (Germany) and Grotta Paglicci level 4c (Italy) have been identified by a double criterion, i.e., morphometric and genetic (Nobis, 1979; Napierala and Uerpmann, 2012; Thalmann et al., 2013; Boschini et al., 2020) (Table 2 and 3, Fig. 1), whereas other Magdalenian and Epigravettian dogs have been identified only by the morphometric criterion (Abri le Morin, Hauterive-Champrévevres, Le Closeau, Montespan and Grotta Paglicci level 5a: Bodu et al., 2006; Pionnier-Capitan et al., 2011; Boudadi-Maligne et al., 2012; Boschini et al., 2020) (Table 2, Fig. 1). Lastly, it is important to highlight that some Magdalenian canids have been attributed to *C. l. familiaris*, although they have not been certainly confirmed: Ölknitz, Teufelsbrücke and Kniegrotte (Musil 1985, 1980; 1974, respectively) (Table 2, Fig. 1). Our study about the Erralla bone allows including it within the scarce group of Magdalenian European dogs identified as *C. l. familiaris* through both criteria (morphometric and genetic). Thus, their belonging to other possible genera is discarded, as well as their inclusion within the morphometric variability of the wolf.

The dating of the Erralla humerus is the oldest among the datings of Paleolithic dogs found to date, both the Magdalenian dogs [Abri le Morin (15,114–14,237 cal. BP: Boudadi-Maligne et al., 2012), Kesslerloch (14,286–13,975 cal. BP: Napierala and Uerpmann, 2012; Baumann et al. 2021), Bonn-Oberkassel (mean age 14,240–14,000 cal. BP: Street, 2002; Street et al., 2015)] and the Epigravettian dog of Grotta Paglicci, level 4 (14,372–13,759 cal. BP: Boschini et al., 2020). Furthermore, the chronology of the Erralla dog is older or similar to that of some specimens of “dog-like wolves” (Elisevichi I, c. 17,000–13,000 BP; Mezin and Mezheric, c. 15,000–14,500; Ulakhan Sular, 17,200 cal. BP aprox.) (Sablin and Khlopachev, 2002; Germonpré et al., 2009; Germonpré et al., 2017) (Fig. 1). The coincidence in time of the Erralla dog with some “dog-like wolves” opens new discussion lines about the wolf domestication process, in which the so-called “dog-like wolves” may have been a predomestication phase that might have occurred in several places of Eurasia in different times. However, some authors claim that “dog-like wolves” cannot be the predecessors of dogs (Ovodov et al., 2011; Morey and Jeger, 2015), although this debate should be approached with further genetic evidence.

The chronology and data of the mtDNA of the Erralla dog indicate that there was at least one dog lineage in Western Europe that belonged to haplogroup C, already in the Lower Magdalenian. Most of the Magdalenian and Mesolithic dogs analysed to date share the same mitochondrial haplogroup (Table 3, Fig. 5), except for some Portuguese Mesolithic dogs that carry haplogroup A (Pires et al., 2019). These results suggest that there could have been a continuity in the population of dogs of Magdalenian hunter-gatherers in the Epipaleolithic and Mesolithic.

Moreover, the present study about the Erralla dog may contribute to the debate on the date of the wolf domestication origin, since there is no agreement between the results of paleogenetics and the conclusions inferred from genetic data of modern canids. Thus, some of the dates proposed for the divergence of the dog lineage from the wolf, such as that of 17,000–10,000 BP (Pang et al., 2009; Freedman et al., 2014, among other studies) differ from those in paleogenetic studies, which propose dates between 41,500 and 36,900 BP (Botigué et al., 2017). In

this respect, the existence of domestic specimens in the Lower Magdalenian, as is the case of the Erralla dog, proves that some inferences based in present-day genetic data offer dates that are too recent. Therefore, this shows the importance of having data of ancient DNA to calibrate mutation rates and make more accurate estimations about the age of the dog lineage (Skoglund et al., 2015).

The origin of clade C, which includes the Magdalenian dogs analysed to date, has been traced back to the period between 24,000 and 16,000 BP in Europe by a paleogenetic study (Thalmann et al., 2013), which coincides with the Last Glacial Maximum (LGM). Similarly, some genetic studies suggest that the population of the dog lineage increased around those dates (Duleba et al., 2015). Moreover, it has been proposed that the original population of European hunter-gatherer dogs would be mostly of haplogroup C (Frantz et al., 2016; Ollivier et al., 2018). Therefore, the Erralla dog, from ~ 17,000 years cal. BP, belonging to clade C, highlights the importance of LGM in the origins of wolf domestication. The population changes and the increase of density that took place in the glacial refugia. (Straus and González Morales, 2012; Maier, 2017) could have accelerated a domestication process, which may have begun earlier, through the enhancement of the interaction between humans and wild species during this stage of the climate crisis.

In conclusion, the data analysed to date indicate that, during the Magdalenian, the domestic dog was part of the groups of Western European hunter-gatherers. The dog from Erralla (17,410–17,096 cal. BP) is one of the oldest specimens identified as *Canis lupus familiaris*, and it shares the mitochondrial haplogroup C with the Magdalenian dogs analysed to date. These findings prove that this haplogroup existed in Europe at least since the Lower Magdalenian, during the Early Dryas, and lead us to consider a possible domestication of the wolf older than what has been proposed so far, at least in Western Europe.

CRediT authorship contribution statement

Montserrat Hervella: Conceptualization, Methodology, Formal analysis, Resources, Supervision, Writing - original draft. **Asier San-Juan-Nó:** Methodology, Formal analysis, Writing - original draft. **Aloña Aldasoro-Zabala:** Methodology, Formal analysis, Writing - review & editing. **Koro Mariezkurrena:** Conceptualization, Funding acquisition, Resources, Writing - original draft. **Jesús Altuna:** Conceptualization, Funding acquisition, Resources, Supervision, Writing - original draft. **Concepción de-la-Rua:** Conceptualization, Methodology, Funding acquisition, Formal analysis, Resources, Supervision, Writing - original draft, Writing - review & editing.

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

No data was used for the research described in the article.

Acknowledgments

This research was supported by a Basque Government Grant for the study of the Erralla canid (C.R.) and for Research Groups in the Basque University Education System (IT 1693-22). The award of a predoctoral fellowship to A.S.J.N. by the Spanish Government (FPU, Ministerio de Ciencia Innovación y Universidades) and a previous fellowship by the Basque Government contributed to this research. We are grateful to the Basque Government (Cultural Heritage Department) for granting us permission to study the canid specimen and to the Centro de Colecciones Patrimoniales de Gipuzkoa (Gordailu) for granting us access to the studied archaeozoological specimen. The authors would like to thank J.

Wesbuer for carrying out the 3D reconstruction of the Erralla humerus, and Dr. T. Fernandez-Crespo for her help in the calibration of the AMS ¹⁴C datings.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2022.103706>.

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