

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Journal of Archaeological Science: Reports

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

A multidisciplinary study of Iberian Chalcolithic dogs

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<https://doi.org/10.1016/j.jasrep.2022.103338>

Received 20 August 2021; Received in revised form 27 November 2021; Accepted 3 January 2022

Available online 17 February 2022

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ARTICLE INFO

Keywords:

Canis lupus familiaris
Chalcolithic period
Iberia
Palaeogenomics
Osteometry
Odontometry
Oral pathology

ABSTRACT

Domesticated dogs have been present in the Iberian Peninsula long before other domesticated species, back to the late Palaeolithic period. Their origin is still uncertain, but dogs were already well established during the Chalcolithic period (ca. 5000–4000 BP). This study employed a multidisciplinary approach comprising osteometric, radiographic and palaeogenomic analyses to characterize Chalcolithic Iberian *Canis* remains. Two Chalcolithic archaeological sites – Leceia, Oeiras, in Portugal, and El Casetón de la Era, Villalba de los Alcores, Valladolid, in Spain – were the main focus of this study. Osteometric and odontometric data from eleven other sites in Iberia were also included. Osteometric results show signs of phenotypic variability, likely the result of human-driven selective pressure. Dental radiographic and dental wear analyses allowed age at death estimation for four individuals (two juvenile and two adults). Three Chalcolithic Iberian dogs had their mitogenomes resequenced and the mitochondrial DNA analysis allowed to assign each individual to two of the major known haplogroups – A and C. Molecular sex inferred by the chromosomeX/chromosome1 coverage ratio allowed to identify one female and two males. This study unveils some aspects of the Iberian Chalcolithic dogs: these dogs already exhibited various morphotypes whose profiles might be associated to the performance of certain tasks, as well as mitogenomes of two distinct lineages that help tracking the evolutionary paths of Iberian dogs.

1. Introduction

The earliest evidence for dogs (*Canis lupus familiaris*, Linnaeus, 1758) in Iberia comes from the Upper Late Palaeolithic, Magdalenian level V or later, 19,000 or 12,500 years cal BP, in the form of a single humerus from the site of Erralla, Gipuzkoa, Spain (Altuna Etxabe and Mariezkurrena Gastearena, 1985; García-Moncó Piñeiro, 2005; Pionnier-Capitan, 2010; Vigne, 2005). The careful burial of dogs is well-documented at the archaeological sites of Cabeço da Arruda (Muge) and Poças de S. Bento's shell-middens, located in the Tagus and Sado estuaries in Southern Portugal, respectively, which date to the late Mesolithic (ca 7600 years cal BP). These remains are well preserved, probably as the result of extra care in their deposition and benefitting from burial treatment similar to what was provided for humans (Arias Cabal et al., 2015, 2016; Detry and Cardoso, 2010; Pires et al., 2019).

During the Neolithic, there was proliferation of the practice of dog deposition, in the form of complete or partial skeletons inside structures, occasionally associated with human burials (Albizuri Canadell et al., 2019; Altuna Etxabe, 1967; Altuna Etxabe and Mariezkurrena Gastearena, 2007; Cámara Serrano et al., 2010; Cava Almuzara, 1978; García-Moncó Piñeiro, 2008; Lizcano Prestel et al., 1992; Valera et al., 2010).

As for the Chalcolithic period (Copper age), ca. 5000–4000 years BP, some dog remains can be found in archaeological excavations throughout the Iberian Peninsula often as isolated or scattered remains, mixed with other faunas or materials (Carbajo Arana and Fernández Rodríguez, 2016; Costa, 2010; Davis and Mataloto, 2012; Liesau von Lettow-Vorbeck, 2011; Morales Muñoz and Liesau von Lettow-Vorbeck, 1994; Pires et al., 2001; Sanchis Serra and Sarrión Montañana, 2004; von den Driesch et al., 1976). Dogs' presence in human symbolic

activities must have been relevant and widespread during this period. In some cases, these remains appear to have been buried immediately after placement, due to their high level of completeness and their layout in correct anatomical orientation. Its association with human funerary contexts is also documented in different areas of the Iberian Peninsula. All these findings have been the subject of analysis over the last years to understand its relevance within the past human social dynamics (Blasco Bosqued et al., 2009; Cámara Serrano et al., 2012; Catagnano, 2016; Daza-Perea, 2011; Daza-Perea, 2015; Daza-Perea, 2017; Daza-Perea, 2019; Delibes de Castro et al., 2019; Delicado et al., 2017; García-Moncó Piñeiro, 2005; Liesau von Lettow-Vorbeck, 2012; Liesau von Lettow-Vorbeck et al., 2017; Liesau von Lettow-Vorbeck et al., 2008; Liesau von Lettow-Vorbeck et al., 2013; Liesau von Lettow-Vorbeck et al., 2014; Lomba Maurandi et al., 2009; Lomba Maurandi and Haber Uriarte, 2016; Moreno García, 2003; Valera, 2008; Valera et al., 2020).

Besides these buried dogs with an apparent special meaning, other dog remains belonging to specimens that participated in daily activities (e.g. human protection and hunting activities), as well as stray or village dogs, a term used to describe dogs that roam near human settlements as defined by Cafazzo et al. (2010), may have been a constant presence, mainly in sites where the social economy provided food surplus (Lah-tinen et al., 2021). Recent isotopic studies show diet similarities between dogs and humans at Perdígões site (Portugal) dated to the Chalcolithic, confirming this cohabitation (Valera, 2020b; Žalaitė et al., 2018).

Previous analyses of the Chalcolithic Iberian dog's morphology show that the coefficient of variation (CV) for traits such as M₁ tooth length (5,5%) and distal humerus breadth (9,9%) were below or approximately 10% (Pires et al., 2017) which following Simpson et al. (1960) is compatible with the observed in natural populations (i.e., not subject to strong artificial selection). Anatomical structures, such as teeth, might be slower (e.g. than long bones) in reflecting signs of intense selection for size differentiation (Albarella, 2002). A progressive diversification of dogs – a wide range of body sizes – was mainly observed during the Roman Age (Pires et al., 2017). This variability was speculated as the result of human-driven selection, aiming to manage various tasks such as property guarding, tracking, hunting and companionship, among other activities (Horard-Herbin et al., 2014).

The Chalcolithic period is described as a wide chrono-cultural period, apparently uniform, but can be divided in two distinct phases: pre-Bell Beaker and Bell Beaker Chalcolithic. The presence of the bell beakers in the interior of the Peninsula is detected by the 4550/4450 cal BP period and although it has spread roughly to the entire territory, there are some areas where the presence of such elements was not documented. That was not the case for Lisbon (Portugal) nor the Valladolid (Spain) regions where the presence of these beakers is well

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documented. In the Portuguese territory a large number of occurrences are described for the Estremadura coast and the Alentejo regions (Cardoso, 2014/2015). Given the radiocarbon dates available it is accepted that the first expansion of such culture occurred by 4650 cal BP (Cardoso, 2014) via a maritime route, from the Tagus and Sado estuaries towards the north, until Bretagne. The expansion of the Bell Beaker phenomenon from Iberia to other places is not associated with human migrations (and interbreeding) in its initial phase, and it has been considered mainly a cultural diffusion (Olalde et al., 2018). This period is characterized by sporadic contacts between Iberians and populations from other regions, such as North Africa with the detection of exotic materials (Cardoso, 2003; Domínguez-Bella et al., 2004; Schuhmacher et al., 2009), as well as the establishment of more complex societies, with intensity variations at a regional level. Peninsular societies from the VI and V millennia BP are characterized by their economic and social complexity in which a series of differences related to territorial and social aspects emerged (Blanco-González et al., 2018). Thus, we would expect an increase in dog diversity during this period, evidenced by a wider range of morphotypes and divergent genetic lineages.

Environmental circumstances, injuries, or diseases can modify the phenotype during an individual's lifetime, while *post-mortem* taphonomic processes can degrade the bone remains with a negative impact for the inference of phenotypic characteristics of ancient animals. If archaeological bones and teeth are preserved in conditions that allow for recovery of endogenous DNA content, i.e. DNA specific to the individual, it is possible to investigate the genomic composition of past specimens and improve our knowledge about past populations and the demographic events underlying their origins. Previous palaeogenetic analyses of Iberian Chalcolithic canid remains, based on a short fragment of the mitogenome (Pires et al., 2019), revealed the presence of sequences segregating within dog clades A and C. This is just a small part of the total diversity exhibited by this molecular marker at the time, as four major clades, A, B, C and D, were detected elsewhere in Eurasia (Botigué et al., 2017; Frantz et al., 2016; Ollivier et al., 2018; Thalmann et al., 2013). In fact, later during the Roman period, we can document the presence of another maternal lineage, the D clade (with Near Eastern origin according to Ollivier et al. (2018), in Iberian dogs (Pires et al., 2017), in addition to the genetic variability described above (A and C clades).

Dog remains from two Iberian archaeological sites dated to the Chalcolithic will be analyzed here and compared to other contemporary dogs in order to better understand the impact of the emergence of more complex human societies in the Iberian dog population, employing a multidisciplinary approach comprising osteometry, radiography and palaeogenomics to characterize those Iberian Canis remains. Firstly, the domestic/wild status of canid remains will be determined by the use of osteometrical analysis and only after samples will be further characterized phenotypically and at the mitogenome level. These data will be framed within the osteometrical and genetic information available for Iberian dogs (e.g. Juan Cabanilles and Martínez Valle, 1988; Martínez Valle, 1993; Daza-Perea, 2011, 2017; Delicado et al., 2017; Detry and Cardoso, 2010; Moreno García, 2003; Daza-Perea, 2015; Daza-Perea, 2019; Daza-Perea et al., 2019; Delibes de Castro et al., 2019; Pires et al., 2019; Sanchis Serra and Sarrión Montañana, 2004).

This kind of integrated studies are very powerful in revealing dogs morphotypes present in ancient times and their possible use based on body size and health conditions, as well as providing information about their matrilineal genetic diversity over time. Ultimately, these observations can be associated with human practices such as animal protection, breeding, selection and migrations. All these events have left marks on the genome of these animals which can be now traced or revealed.

2. Materials and Methods

2.1. Archaeological sites and materials

In this study, we analysed dog remains from the Iberian Peninsula

with a particular focus on two Chalcolithic (ca. 5000–4000 BP) archaeological sites: Leceia, Portugal, and El Casetón de La Era, Spain. From the El Casetón de la Era (Spain) archaeological site, we sampled two cranial elements. The *Canis* remains from this site were incomplete and were found isolated, possibly indicating different individuals. A similar scenario was observed in the Leceia site (Portugal), where all the elements were disconnected and poorly preserved, possibly indicating that for both sites, there was no burial or particular care in the disposal of these animals. This contrasts with other contemporaneous sites that show several dog deposits in ritual context such as the Camino de las Yeseras (Madrid, Spain) (Daza-Perea, 2011; Daza-Perea, 2015; Daza-Perea, 2017; Daza-Perea, 2019; Daza-Perea, 2016; Liesau von Lettow-Vorbeck et al., 2008; Liesau von Lettow-Vorbeck et al., 2014) or the Perdigoes (Alentejo, Portugal) sites (Valera, 2008; Valera, 2018; Valera et al., 2020).

From these sites we collected osteometric data – long bones' total length, from one sample from Leceia, odontometric – length and breadth of the M₁ tooth from four samples from Leceia, and obtained genomic data for one sample from Leceia and two samples from El Casetón de la Era. We also analysed dental eruption patterns and searched for signs of abnormalities. The samples and the respective analyses conducted are specified in [Supplementary Table S1](#) (details on the analysis for each sample).

Leceia (Oeiras, Portugal) is considered one of the most important Chalcolithic sites in the Iberian Peninsula. Located in the Estremadura region, near the coastline and the Tagus river estuary (Fig. 1), this region had a favourable climate for human settlements during Prehistory. The human occupation began in the late Neolithic, ca. 5460 to 4850 years cal BP, and continued in the early and late Chalcolithic, 4820 to 4350 years cal BP and ca. 4550/4450 to 4150 cal years BP, respectively (Cardoso, 2008; Cardoso and Soares, 1996). Since 1983, over 20 annual field seasons were carried out allowing the recovery of 122 carnivore remains, of which 81 were identified as belonging to dogs. Some of the latter displayed traces of human consumption or skin removal (Pires et al., 2001). Chalcolithic Leceia consisted of a fortified settlement with stable structures that harboured a large human community whose economy was largely based on agro-pastoral activities, rather than on hunting (Cardoso and Detry, 2002). Within this environment of abundant food resources, dogs were tolerated and probably participated in various human activities (mutualistic relationship). A minimum number of individuals of 10 was calculated for the Chalcolithic Leceia (Pires et al., 2001).

Out of 13 dog remains, one retrieved enough endogenous DNA for subsequent analysis (sample LYEP11, Fig. 2A) and was directly radiocarbon dated to 4517–4295 years cal BP which corresponds to the final period of the Bell Beaker Chalcolithic. Also, four samples from this site were subjected to odontometric analysis (LYEP10, LYEP20, LC88/L./INTE./DE/GG1/C3 and LC), one to osteometric analysis (Leceia 1998 – Ditch FN3 C2) and two to dental X-ray analysis (LYEP16 and LYEP20).

El Casetón de la Era (Villalba de los Alcores, Valladolid, Spain) is an archaeological site located in the North of Spain (Fig. 1), within the basin of the middle Douro river. It was discovered in 1997 using aerial photography and found to have been occupied during two distinct phases in Prehistory: the Chalcolithic, for approximately three quarters of the 3th Millennium BC; and the Bronze Age ca. 1600 to 1335 BCE (Delibes de Castro et al., 2018). In contrast to Leceia, El Casetón de la Era is composed of several concentric and circular ditches. Among the 27 carnivore remains that were excavated at this site, 16 were identified as dogs. From this site, a minimum number of 5 individuals was calculated. Bone marks related to human consumption were not observed, indicating that dogs were not used as a food source (Carbajo Arana and Fernández Rodríguez, 2016).

Two dog remains were selected for genomic analysis: specimen LYEP51 and specimen LYEP53 (Fig. 2B and C, respectively). Direct dating of other remains (GrA-42531: 4800–4420 cal BP (fauna) and GrA-42529: 4530–4290 cal BP (fauna) (Carbajo Arana, 2020)) from the same

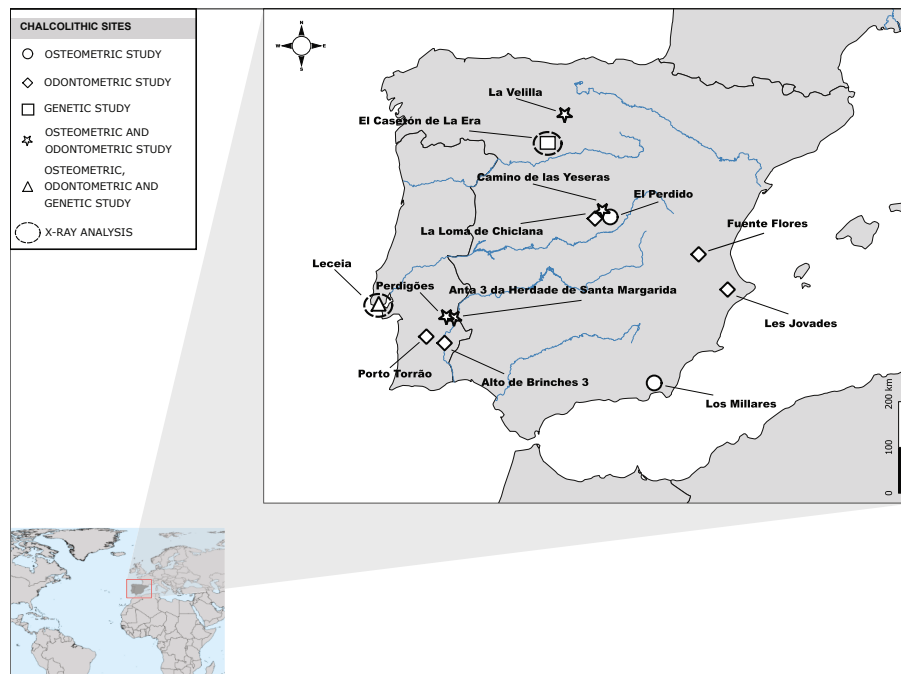


Fig. 1. Geographical location of 13 Chalcolithic archaeological sites in the Iberian Peninsula. Leceia and El Casetón de la Era, the main focus of this study, provided samples which were subject to osteometric, odontometric, genomic and X-ray analyses (see [Supplementary Table S1](#), for details on the data and references).

stratigraphic unit from where the LYEP51 sample was recovered, provided a chronology of the 5th millennia BP (calibrated) (4800–4290 cal BP). Regarding sample LYEP53, three radiocarbon dates from other remains (GrA-42532: 4580–4400 cal BP (fauna), GrA-34319: 4820–4440 cal BP (charcoal) and GrA-42527: 4530–4290 cal BP (fauna) ([Carbajo Arana, 2020](#); [Delibes de Castro et al., 2016](#))) of the same stratigraphic unit indicate a date of the 5th millennia BP (4820–4290 cal BP). These dates suggest that these specimens belong to a pre-Bell Beaker Chalcolithic context. Given the absence of mandibular teeth, only three samples from this site (maxillae) were subjected to the dental X-ray analysis (LYEP51, LYEP53 and LYEP54). We are uncertain if samples LYEP51 and LYEP54 belong to the same individual (they derive from the same stratigraphic unit and were considered as parts of the same individual in accounting the MNI), but, in this study, they were analysed as separate remains (and treated as individual samples).

2.2. Osteometric and odontometric methods

The osteometric data were directly collected by our team using both conventional and digital callipers (estimated error ± 0.1 mm), using a guide to the measurement of the animal bones from archaeological sites – the criteria defined by [von den Driesch \(1976\)](#). Details on these measurements can be consulted in [Supplementary Table S1](#), along with others obtained by different authors that were included in the analysis for comparison purposes and to provide an overview of the dog population of the Iberian Peninsula focused on the Chalcolithic period.

In total, 59 osteometric and odontometric measurements, in addition to two shoulder height estimations ([Supplementary Table S1](#)), were analysed in the present study which was focused on a total of 33 individuals provided from 12 (out of 13) archaeological sites indicated in the map ([Fig. 1](#)). The odontometric data includes breadth and length measurements from 25 first mandibular molar teeth (M_1) (four of them from the Leceia site) used to determine the characteristics of this dental element among different individuals. Regarding the osteometric data, long bones' total length measurements (humerus, femur, ulna, tibia or radius) from individual dogs from 7 archaeological sites (one sample from the Leceia site is included), allowed the estimation of the

shoulders' height for 11 individuals (as mentioned before, two published data, included as estimations). Unfortunately, neither complete long bones nor measurements from M_1 were recovered from samples from El Casetón de la Era.

We also included measurements from 62 extant Iberian wolf specimens (*Canis lupus signatus*, ([Cabrera Latorre, 1907](#)) (Portuguese specimens from reference collections at the Museu Nacional de História Natural e da Ciência, Lisbon, Portugal and the Laboratório de Arqueociências – Direcção Geral do Património Cultural, Lisbon, Portugal) such as length and breadth of their first mandibular molar tooth. The same measurements were collected from 13 skulls of the extant dogs' collection from Laboratório de Anatomia – Universidade Lusófona de Humanidades e Tecnologias (Lisbon, Portugal). These data were provided by [Detry and Cardoso \(2010\)](#) and [Pires et al. \(2019\)](#), and are useful to establish the domestic vs wild status of a specimen ([Davis and Gonçalves, 2017](#)).

The methodology revised by [Harcourt \(1974\)](#) was used to calculate the shoulder heights of the specimens, which consists in multiplying the total length of the long bones by a series of factors (depending on the specific bone). For comparison purposes, we added shoulder height data from 15 dogs from seven extant Iberian dog breeds available from the *Fédération Cynologique Internationale* (FCI).

The descriptive statistical analyses of osteometric data included estimating the coefficient of variation using the program PAST (version 4.05, cite https://palaeo-electronica.org/2001_1/past/past.pdf). The Coefficient of Variation (CV) ((standard deviation/average) x 100), for the M_1 length and breadth, as well as, for the shoulder height measurements were calculated for the Chalcolithic dogs and the extant wolf and dog assemblages. Differences regarding extant wolves and dogs' M_1 data were tested with Mann-Whitney *U* statistics using the *IBM SPSS statistics 23.0* software.

2.3. Age estimation and dental pathology assessment methods

Age at death was estimated by radiographic dental analysis. This methodology also allowed the screening for dental and periodontal pathologies. Age estimation by radiography was based on the observation

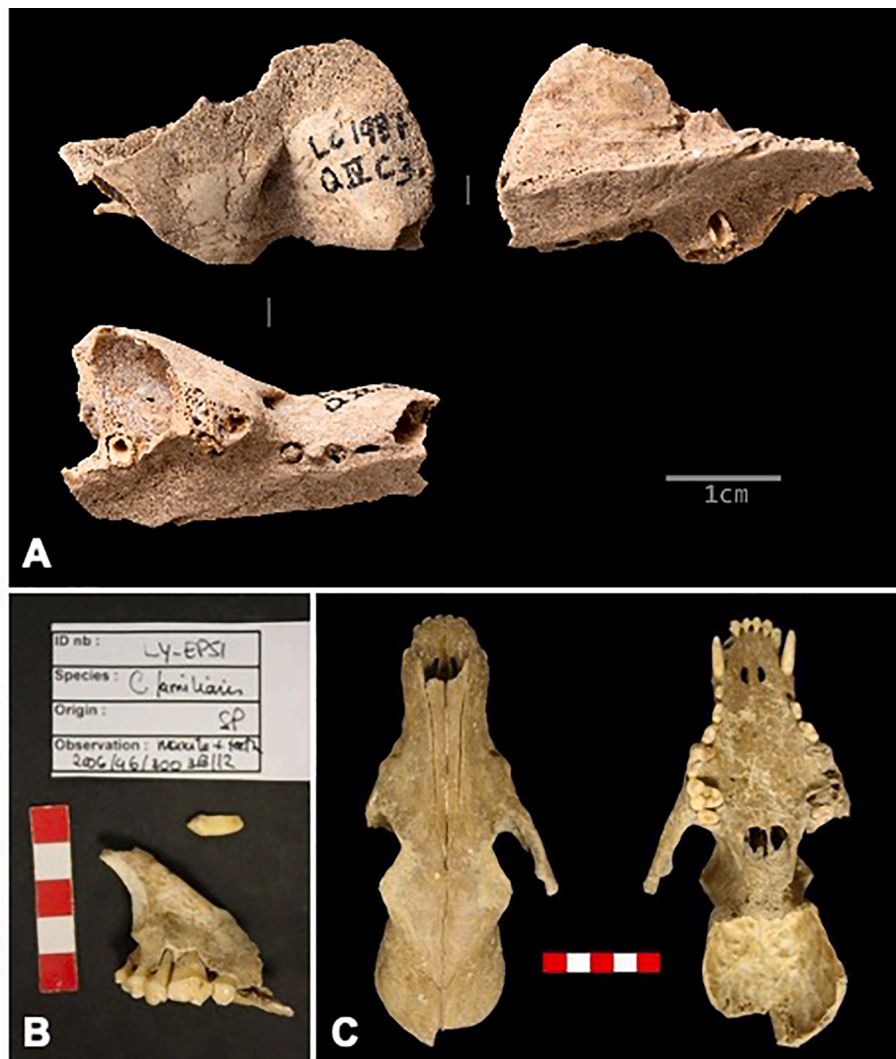


Fig. 2. Dog remains selected for genomic analysis. A: sample LYEP11, fragment of the right maxillary bone with no teeth, from Leceia, B: sample LYEP51, fragment of the right maxillary bone with PM⁴, M¹, M² and loose incisor I², from El Casetón de la Era. C: sample LYEP53, cranium with I¹, I², C¹, PM¹, PM², PM³, PM⁴, M¹, M², I¹, I², I³, I⁴, C¹, C², PM¹, PM², PM³ and M¹, from El Casetón de la Era.

of endodontic anatomy, namely, the morphology of the dental apex and the assessment of the pulp canal closure ratio (PCCR) (Nomokonova et al., 2020). This age estimation method was an alternative to the destructive and invasive observation of *cementum annuli* (Knowlton and Whittemore, 2001) and has been validated for maxillary and mandibular canine teeth, as well as for the mandibular M₁ tooth. Radiographic images of samples from Leceia (LYEP16 and LYEP20) were obtained using a dental X-ray generator (RXDC-eXTend, MyRay, Italy) and a direct digital intraoral sensor (ZenX2, MyRay, Italy) at the Faculty of Veterinary Medicine of the Lusófona University (Portugal). For samples from El Casetón de Era (LYEP51, LYEP53 and LYEP54) we used the dental generator X-Mind and sensor Sopix 2 (Acteon Satelec), and the conventional generator APR-VET (Sedecal) with the digital system FCR Capsula (Fujifilm) at the University of León (Spain).

Estimation of the age at death for the El Casetón de la Era dog remains (LYEP51, LYEP53 and LYEP54) had been already performed by Carbaño Arana and Fernández Rodríguez (2016) from the observed dental eruption pattern, in addition to the analysis of the epiphyseal fusion.

2.4. Palaeogenomic analysis

For three samples, one from Leceia (LYEP11) and two from El Casetón de la Era (LYEP51 and LYEP53), high-throughput sequencing (HTS) data was generated to obtain complete mitogenomes and for sex determination.

2.4.1. DNA extraction and preparation of genomic libraries

Sub-sampling and ancient DNA extractions were performed in facilities dedicated exclusively to palaeogenomic analysis at the Centre for Palaeogenetics of Stockholm University, Sweden. About 50 to 100 mg of bone or tooth powder were used for DNA extraction using a guanidinium/silica-based method (Yang et al., 1998). Double-stranded genomic libraries were prepared according to Meyer and Kircher (2010), and samples were single-indexed with specific 7-base pair (bp) barcode tags. Libraries were quantified and qualified using an Agilent 2100 Bioanalyzer and a Qubit Fluorometer. Shotgun resequencing was carried out on an Illumina HiSeq × Ten platform (High Output mode, paired-end 2 × 150 bp) at Science for Life Laboratory Sequencing Centre (SciLifeLab) in Stockholm, Sweden (see more details in [Supplementary Materials](#)).

2.4.2. Sequencing data processing

Paired-end data were filtered using cutadapt v1.18 (Martin, 2011), for removal of adapter sequences, trim bases with quality lower than 30 and discard reads with lengths <30 bp. Reads were then merged using AdapterRemoval v2.2.2 (Lindgreen, 2012). BWA v0.7.17 (Li and Durbin, 2009) with the sub-command aln and samse was used to align merged reads to the dog reference mitochondrial and nuclear genomes (CanFam3.1; NCBI Reference Sequence NC_002008.4 and GenBank assembly accession GCA_000002285.2, respectively). Reads with MapQ above 20 were then mapped to a composite reference genome, consisting of human, pig, cow, chicken, goat and sheep genomes following recommendations in Greig et al. (2015). All the reads that did not map properly (reads confidently mapping to the composite genome) were realigned to the dog mitochondrial and nuclear reference genomes. From this set of reads, the ones with a MapQ 20 or greater were kept and AddOrReplaceReadGroups and MarkDuplicates tools from PICARD v2.18.14 (Broad Institute 2018, <https://broadinstitute.github.io/picard/>) were used to add read groups and to remove duplicate reads, respectively. GATK v3.8.10 RealignerTargetCreator and IndelRealigner were used in order to realign reads in the region surrounding potential variant sites to accurately call variants. Post-mortem DNA damage patterns were assessed using MapDamage v2.0 (Jónsson et al., 2013), revealing extensive 5' C > T and 3' G > A deaminations (see Supplementary Fig. S1). Quality control of alignment sequencing data and coverage statistics were calculated using Qualimap v2.2.1 (Okonechnikov et al., 2016). ANGSD v0.930 (Korneliussen et al., 2014) was used to obtain the consensus mitochondrial sequence by depth of sample reads supporting a given variant, which was set to a minimum quality score of 20 and a minimum coverage of three reads. A flow chart of the mitogenome ancient analyses is shown in Supplementary Fig. S2. See supplementary information for details on sequencing data processing.

2.5. Bayesian phylogenetic analyses (BEAST)

The mitogenome sequences generated in this study (N = 64) and those shared from other authors (N = 15), as well as publicly available dog and wolf mitogenomes (N = 126) from several geographic locations and periods (see details in Supplementary Material Section 4.1 “Canis mitogenomic shared sequences” and Tables S2 and S3) were aligned, using the software MUSCLE v3.8.31 (Edgar, 2004), to the reference dog sequence NC_002008.4 (Kim et al., 1998) for a comprehensive phylogenetic analysis of dog maternal lineages. The coyote (accession number NC_008093.1) was used as an outgroup.

We analysed the phylogenetic relationships using the Bayesian inference implemented in BEAST v.1.10.4 (Suchard et al., 2018), restricting the analysis to sequences with at least 90% of informative sites (N = 205 and see Supplementary Table S2). Also, due to difficult-to-align regions, we used a trimmed sequence of 16,137 bp. We assessed the best-fit model of nucleotide evolution on jModelTest v.2.1.9 (Darriba et al., 2012; Guindon and Gascuel, 2003) and selected the GTR + I + G (King and Jukes, 1969; Palumbi, 1989; Tavaré, 1986; Yang, 1996) substitution model under the Akaike Information Criteria, without partitioning the alignment. We assumed a strict molecular clock and a Bayesian skyride model (Gill et al., 2013; Minin et al., 2008) to describe the coalescent process in the phylogenetic tree. This model is the most appropriate for sequences from different temporal intervals (Minin et al., 2008). Mean calibrated radiocarbon ages or stratigraphically assigned ages were used as priors for ancient samples (Supplementary Table S4). Uncertainty of age was not considered because it has a negligible or minimal impact on the resulting estimates in BEAST (Molak et al., 2015).

Time to the Most Recent Common Ancestor (TMRCA) for both dogs and wolves was taken from uniform distributions between 12,500–55,000 years BP and between 55,700–150,000 years BP, respectively. The canid mitochondrial mutation rate was taken from an exponential distribution with mean 1.0E-7 per bp per year, similar to the

value used by Duleba et al. (2015).

Three independent Markov Chain Monte Carlo (MCMC) chains were run. We analyzed the results of each MCMC chain, each with 20 million iterations, sampled at every 1000 iterations using Tracer v.1.7.1 (Rambaut et al., 2018) to check stability and convergence of the MCMC chains, and sufficient sampling by inspection of effective sample size (ESS) values for all parameters (exceed 200) and access the appropriate burn-in. The three individual runs were combined using Logcombiner v.1.10.4 in the BEAST software package (10% burn-in) and Maximum Clade Credibility (MCC) trees were summarized using TreeAnnotator v.1.10.4 (within BEAST (Suchard et al., 2018)) and visualized in FigTree v.1.4.4 (Rambaut, 2018). Henceforth, node age will refer to the median of the node height posterior distribution and HPDI to the highest posterior density interval.

2.6. Temporal median-joining network

We also investigated the phylogenetic relationships between dog mitochondrial haplotypes by constructing a median-joining network (Bandelt et al., 1999) in PopART v.1.7.1 (<http://popart.otago.ac.nz>). Due to difficult-to-align regions, we used a trimmed sequence of 16,137 bp in length (N = 133; 29 ancient and 104 historic/extant). Indels, gaps and missing positions were excluded from this analysis, which resulted in 519 polymorphic positions to be analysed. Temporal comparisons were made between ancient (Palaeolithic to Chalcolithic periods) and extant samples (see Supplementary Tables S2 and S3, for details of samples used).

2.7. Sex determination

Molecular sex inference of three ancient dog samples (LYEP11, LYEP51 and LYEP53) was done using the method described by Bro-Jørgensen et al. (2021) that compares the proportion of DNA reads mapped to the X chromosome and chromosome 1 (chrX/chr1 ratio). Chromosome 1 was chosen because of its similar size to the X chromosome (122.68 Mb and 123.87 Mb, respectively). Females are expected to have a similar number of reads when comparing the two copies of X chromosome with the two copies of autosomal chromosome 1 (ratio ca. 1.0). Males are expected to present half of the reads for the X chromosome, when compared with their chromosome 1 pair (ratio ca. 0.5). Whole genomes from Portuguese native dog breeds, two males and two females (DOGPT32 – Castro Laboreiro Watchdog, male; DOGPT34 – Castro Laboreiro Watchdog, female; DOGPT36 – Portuguese Warren Hound, female and DOGPT37 – Portuguese Warren Hound, male) of known sex, were used as controls. Historic wolves could not be sexed since only mitogenomic data were available.

3. Results

We describe several elements that were analysed using zooarchaeological and genomic methods from two archaeological sites from Spain and Portugal and integrate these data with other already published from Iberian *Canis* remains dated to the Chalcolithic period.

3.1. Zooarchaeology

3.1.1. Cranial characterization

Preserved complete skulls are rare in the Iberian Peninsula prehistoric archaeological record which limits our knowledge on dog cranial morphotypes from this period. Teeth, however, are often recovered and have traditionally been used to identify domestic specimens from its ariotype (Janssens et al., 2019).

The domestication of wolves resulted in specimens with divergent phenotypes – in particular smaller animals which exhibit smaller bones and teeth. Odontometry and osteometry are useful to distinguish dogs, as specimens of smaller size, from their wolf relatives (Janssens et al.,

2019; Pires et al., 2019). The Iberian *Canis* archaeological remains' M₁ length and breadth measurements are within the range of the extant dog data and are smaller than those found in extant Iberian wolves. The Mann-Whitney *U* test indicates statistically significant differences for the length ($U = 7.00$; $p < 0.001$; effect size = -0.64) and breadth measurements ($U = 23.00$; $p < 0.001$; effect size = 0.62) between extant Iberian wolves and dogs (Supplementary Fig. S3 A and B). Therefore, we were able to identify the archaeological *Canis* remains as dogs. Unfortunately, from El Casetón de la Era no mandibular first molars were recovered.

Coefficient values for the size variation observed in the length and breadth of the M₁ tooth for the Chalcolithic assemblage of Chalcolithic dogs and extant Iberian wolves are below 10% (see Supplementary Table S5). CV values for both parameters exceed 10% in the case of the extant dogs.

In Fig. 3A, we present first mandibular molar measurements of 25 Iberian dog remains dated to the Chalcolithic combined with data from 62 extant Iberian wolves (from Portugal) and 13 extant dogs from a reference collection from Lusófona University.

We observe variability for dogs' M₁ tooth size. The Chalcolithic *Canis* specimens analysed (N = 25) have mandibular first molars whose size varies from 15.7 to 22.2 mm, and from 6.4 to 9 mm for their length and breadth, respectively. The mandibular first molars of Leceia's dogs (N = 4 teeth) exhibited a high variability – large spread of data in the graph (Fig. 3A – red triangles).

3.1.2. Postcranial characterization: shoulder height

It was possible to estimate the shoulder height for 11 dog remains dated to the Chalcolithic period (Fig. 3B). We estimated shoulders' height measurements ranging from 41 to 58.4 cm. Two Chalcolithic specimens recovered from La Velilla and Anta 3 Santa Margarida sites show particularly large shoulder heights of 56.2 cm and 58.4 cm, respectively. This wide size variation may reflect the presence of different dog morphotypes which has been interpreted as the result of human driven selection for dogs for multiple purposes.

Shoulder heights data from seven extant native Iberian dog breeds recognized by the *Federation Cynologique Internationale* (FCI, <http://www.fci.be/en/Nomenclature/>), including females and males from each breed are represented in Fig. 3B (see also Supplementary Fig. S4). The average values for males and females correspond to the location of their silhouettes in Fig. 3B. The plot of the 11 Chalcolithic specimens from seven sites across Iberia shows the variability among these dogs whose sizes are close to those of extant Spanish Water Dog or Portuguese Warren hound of medium size (eumetric dogs) and range up to those of the Estrela Mountain dog (a mastiff type dog, hypermetric dog). The mentioned breeds were traditionally selected and are used nowadays as hunting companions and for livestock (mainly sheep/goat) guarding.

The coefficient value for shoulder height size variation is above 10%, compatible with high phenotypic variability. Morphological variation was already established among Chalcolithic dogs, probably as a consequence of human-directed selection pressure.

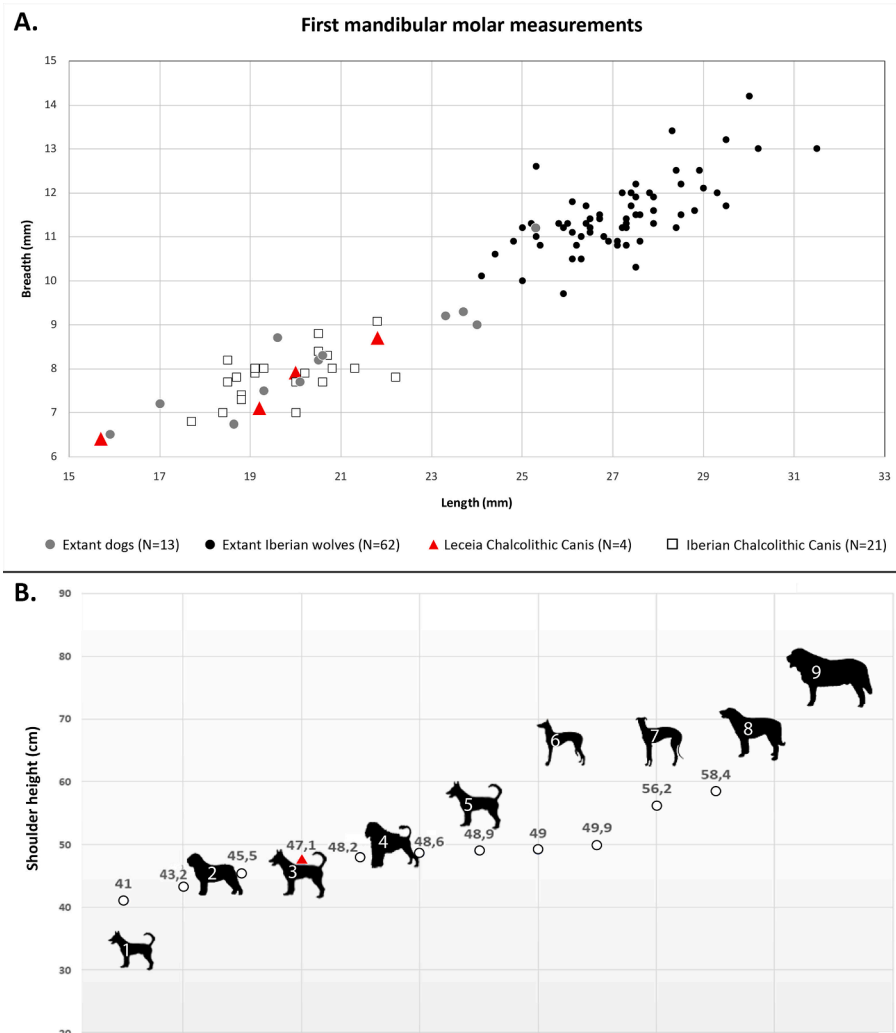


Fig. 3. A. Dot plot graph of the length versus breadth of the mandibular first molar (M₁) (in mm) from several dog archaeological remains dated to the Chalcolithic period – Leceia remains are represented by triangles – and from extant Iberian wolves from Portugal. B. Individual shoulders' heights for 11 Chalcolithic samples estimated from the [Harcourt \(1974\)](#) index and based on long bone total length measurements (humerus, femur, ulna, tibia or radius). Dots correspond to the following samples (from left to right): El Perdido (Dog 2); Millares; Camino de las Yeseras (A21 Dog 1); El Perdido (Dog 1); Camino de las Yeseras (A61); El Perdido (Dog 3); Camino de las Yeseras (A121); Perdigões; La Velilla (Dog 1); Anta-3 de Santa Margarida (Supplementary Table S1). The single dog remain from the Leceia Chalcolithic site (LC 98 FOSSO FN3) with a complete humerus preserved is shown as a red triangle. See Supplementary Table S1 for data provenance. Shoulder heights for seven extant Iberian dog breeds (note: Portuguese warren hound breed comprises three types of sized dogs) represented by dark silhouettes are shown: 1- Portuguese warren hound-small sized dogs, 2- Spanish Water Dog, 3- Portuguese warren hound-medium sized dogs, 4- Portuguese Water Dog, 5- Portuguese warren hound-large sized dogs, 6- Ibizan Podenco, 7- Spanish Greyhound, 8- Estrela Mountain Dog, and 9- Spanish Mastiff. Each silhouette displays the average shoulder height value for male and female dogs (from *in vivo* specimens), which data can be found in Supplementary Fig. S4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Age classes estimation of the studied samples based on morphology of the dental apex and the pulp canal closure ratio (PCCR) according to Nomokonova and collaborators (nd, not determined due to lack of reference information for these specific teeth).

Sample	Tooth	Dental apex	PCCR	Age class estimated by PCCR (months)
LYEP16	Maxillary PM ⁴ , distal root	Closed	0.823	nd
LYEP20	Mandibular M ₁ , mesial root	Closed	0.876	24–59
	Mandibular M ₁ , distal root	Closed	0.895	24–59
LYEP51	Incisor I ²	Closed	0.878	nd
	Maxillary PM ⁴ , distal root	Closed	0.806	nd
LYEP53	Maxillary canine	Closed	0.631	6–23
LYEP54	Maxillary canine	Closed	0.832	24–59

3.1.3. Age estimation based on teeth

The radiographic study allowed us to ascribe samples to different age classes, according to their teeth eruption pattern and the distinct pulp canal closure ratios (PCCR) (Table 1); furthermore, it allowed the comparison of methods for age estimation.

Among the five studied samples (Table 1), we inferred two (LYEP20 and LYEP54) to be adults, aged between 24 and 59 months, according to Nomokonova and colleagues (2020). LYEP20 could be the oldest specimen of the collection, because of its narrow pulp canal diameters with highest PCCR measured at mandibular M₁. X-ray analysis of sample LYEP53 indicates that the individual was a juvenile, because of the relatively higher pulp canal diameter (PCCR = 0.631) in comparison to the other samples. Age estimation based on the PCCR was not possible for LYEP16 and LYEP51 samples, because, to the best of the authors' knowledge, there is no available data of PCCR in both maxillary PM⁴ and incisor teeth.

The samples from El Casetón de La Era (LYEP51, LYEP53 and LYEP54) consist of upper teeth. All the teeth were permanent, which means the animals were older than five months. According to Carbajo Arana and Fernández Rodríguez (2016), the analysis of wear-stage for these teeth confirmed that these belonged to adult animals. Tooth wear was not intense in samples LYEP51 and LYEP53, and no dentine was exposed, so we can confirm that these were 6–23 months (young adults) at their age of death.

3.1.4. Evaluation of dental pathology

The observation of radiographic images also allowed us to characterize dental and periodontal alterations. The teeth not inserted in the alveolar bone, such as the maxillary canine fragment of LYEP54 (El Casetón de la Era) (Fig. 4A) and incisor I² of LYEP51 (El Casetón de la Era) (Fig. 4B) were excluded from the analysis of periodontal disease. Sample LYEP53 (El Casetón de la Era), considered as a juvenile or young adult dog, did not reveal signs of dental and periodontal pathology (Fig. 4C). Regarding sample LYEP16 (Leceia), no periodontitis radiographic signals, including alveolar bone lysis or widening of periodontal space, or periapical lesions are observed, both in maxillary PM⁴ and M⁴ teeth (Fig. 4D). In sample LYEP20 (Leceia), incisors, canine, PM₃, M₂ and M₃ teeth are missing and M₁ is avulsed from the alveolus by artefact. No periodontitis radiographic signals or periapical lesions are observed in LYEP20 PM₂ and PM₄ teeth. LYEP20 PM₁ tooth seemed to have not erupted (agenesia). Mandibular canal reveals an increased radiopacity compatible with mineral deposition (Fig. 4E).

In sample LYEP51 (El Casetón de la Era), periodontal spaces of mesiovestibular (MVR) and distal (DR) root are wider (*), maybe artifactually or associated with periodontitis (Fig. 4B). Regarding sample LYEP54 (El Casetón de la Era), the maxillary canine presents an artificial complicated crown fracture (#), an artifactual missing of the apical portion of the root and radiographic signs of dentine resorption (maybe artifactual/post mortem) (Fig. 4A).

3.2. Iberian Canis mitogenomes

We present newly generated mitogenomes for three Chalcolithic Iberian dogs from Leceia (LYEP11) and El Casetón de la Era

archaeological sites (LYEP51 and LYEP53). These Chalcolithic Iberian dog samples had a minimum of threefold read depth over 99% of the mitochondrial genome: the average sequencing depth for the mitogenomes were 50x, 16x and 20x for LYEP11, LYEP51 and LYEP53 samples, respectively (see Supplementary Table S6 for statistical results). Map-Damage analysis demonstrated that these samples have damage patterns typical of ancient DNA (Supplementary Fig. S1). To our knowledge these are the first Iberian dog mitogenomic data obtained for this time period – Chalcolithic, ca. 5000–4000 years ago. In addition, we combine these data with newly generated mitogenomes for 54 extant dogs (47 from Iberia – Portugal, and seven from North Africa – Morocco), three extant and three historic (dated to 1944–1975) Iberian wolves, one historic Iberian dog (Portuguese sample LYEP9, dated to the 1970s, see Supplementary file for sample details).

3.2.1. Haplogroup assignment

The analyses of 205 complete mitogenomes covering the present and prehistoric periods, reveals diversity, i.e. presence of various dog mitogenome clades which reflect different evolutionary trajectories. In Iberia, there are 21 internationally recognized dog breeds, including local varieties within breeds (FCI – <http://www.fci.be/en/Nomenclature/>). In our study, the mitogenomes from extant Portuguese dogs are distributed among the major dog clades A, B, C and D. North African dog breeds, such as Aidi and Sloughi, are also represented in these analyses, and segregate within clades A and D. Although breed formation and intensive selective breeding is a recent phenomenon - the origin of most of these breeds date back to 200 years ago (Lindblad-Toh et al., 2005; The American Kennel Club, 2006), the described population structure results from a temporally dynamic process and the analysis of ancient DNA time series can retrace some details of that process, namely population continuities or discontinuities.

Among the three prehistoric Iberian specimens dated to the Chalcolithic (LYEP11, LYEP51 and LYEP53), one segregates with clade A – sample LYEP11, and two with clade C – samples LYEP51 and LYEP53 (see Fig. 5 for the summarized BEAST tree and Fig. S5 A and B for more details). This confirms the findings of Pires and colleagues (2019) for haplogroup assignment of these specimens based on a short fragment of the D-loop (mtDNA hypervariable region 181 bp). The presence of clade A in the Chalcolithic period has been already reported for two samples from Iran – AL2571 (dated to ca. 5074 years BP) and Croatia – ALP001 (dated to ca. 4500 years BP) (Bergström et al., 2020). The Chalcolithic specimen LYEP11 from Leceia shares a common ancestor (ca. 9.7 ka years BP and 95% HPDI of 8252–11745 years BP) with sample THRZ02, a specimen from the Neolithic Israel, reported in Bergström and colleagues (2020) as well as with specimens from extant Iberian dog breeds, such as Portuguese Warren hound, Estrela Mountain dog and Azores Cattle dog. The C-type samples from El Casetón de la Era (Valladolid) – LYEP51 and LYEP53, are genetically closely related to the Irish Newgrange dog specimen lineage (NGD) which is dated to the Late Neolithic (ca. 5000 years BP from Frantz and colleagues (2016)) and to a Spanish dog (OL4029), dated to the Late Neolithic (ca. 5458 years BP from Bergström and colleagues (2020)). Together they share a common ancestor (ca. 19.5 ka years BP and 95% HPDI of 17,112–22,405 years BP) with four other contemporaneous European ancient specimens –

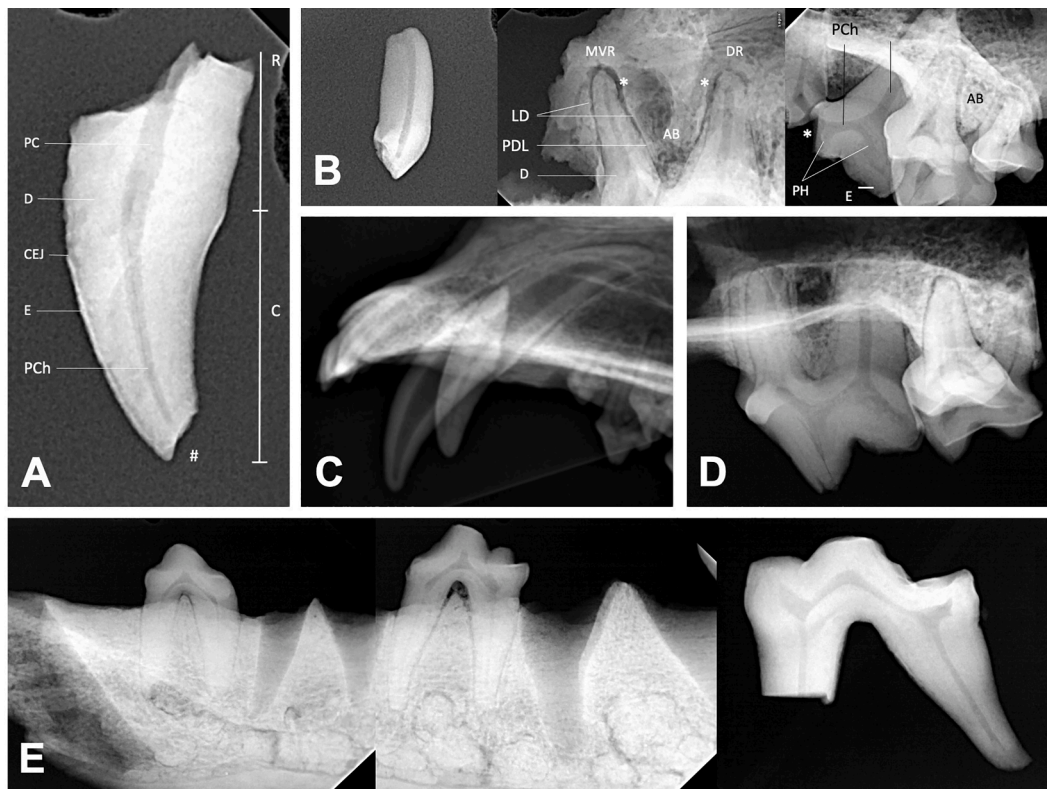


Fig. 4. Dental radiographic images of samples LYEP54 (A), LYEP51 (B), LYEP53 (C), LYEP16 (D) and LYEP20 (E) (for teeth description see Table 1), showing anatomical landmarks of tooth and periodontium. Legend: C – crown, R – root, E – enamel, D – dentine, CEJ – cemento-enamel junction, PDL – periodontal ligament space, LD – lamina dura, AB – alveolar bone, PC – pulp canal, PCh – pulp chamber, PH – pulp horn, MVR – PM⁴ mesiovestibular root, DR – PM⁴ distal root, artificially wide periodontal space (*), and crown fracture (#). Note: samples LYEP54 (A) and LYEP51 (B) may belong to the same individual as samples provided from the same stratigraphic unit.

HXH (Germany), CTC (Germany), C89 (Sweden) and C90 (Sweden) dated to the Early and Late Neolithic (ca. 7000, ca. 4700, ca. 4800 and ca. 4800 years BP, respectively) (Bergström et al., 2020; Botigué et al., 2017), and Portuguese dog breeds, such as, Estrela Mountain dog, Rafeiro Alentejano and Azores cattle dog, among others.

In our analyses no prehistoric Iberian dogs segregate within clade B or D (e.g Fig. 5 and Supplementary Fig. S6). However, the presence of these clades was detected in Prehistory in other places, namely Central Western Europe following an analysis of a fragment of mtDNA (Ollivier et al., 2018). Clade B has never been detected in Iberia before the present, whereas clade D has been detected in dog remains dated to the Roman period and after (Pires et al., 2017).

The mitogenomes of Iberian archaeological dogs, included in the temporal network (Supplementary Fig. S6), confirm the continuity of clade C across the Neolithic (sample OL4029) and Chalcolithic periods (samples LYEP51 and LYEP53), and the presence of clade A in the Chalcolithic (sample LYEP11 for the Chalcolithic; mitogenome information from previous periods from Iberia is still lacking). This confirms our previous data based on a short mtDNA fragment (Pires et al., 2019).

Regarding extant/historic Iberian wolves, all mitogenomes included in the analysis are grouped together in an exclusive Iberian clade (indicated by the symbol * in Fig. 5) close to dog haplogroup B. Together they share a common ancestor of ca. 14.2 ka years BP and 95% HPDI of 11,873–16,965 years BP. All the extant/historic Iberian wolf mitogenomes included in our analysis (N = 11; 5 from Portugal and 6 from Spain) share a common ancestor with an estimated date of ca. 13 ka years BP and 95% HPDI of 10,510–15,744 years BP. This early date is mainly due to a very divergent mitogenome (Spanish sample ID KU644670 from Koblmüller et al. (2016), which is the sample ewolf1 in

our dataset). These mitogenomes can be assigned to wolf Haplogroup 1 following Pilot et al. (2010). Unfortunately, no complete mitogenomes from ancient Iberian wolves have been recovered yet. We also observed a clear separation between extant/historic Iberian wolf (N = 11) and Portuguese dog breeds mitogenomes (N = 47).

3.2.2. Sex identification

Genomic data allowed for reliable sexing of three Iberian dog specimens dated to the Chalcolithic. Supplementary Fig. S8 shows the distribution of the chrX/chr1 ratios for each sample: samples LYEP11 and LYEP53 were males (ratio ca. 0.5) and LYEP51 a female (ratio ca. 1.0). For all samples we obtained a number of endogenous DNA sequence mapped reads above 5000, which according to Bro-Jørgensen et al. (2021) was considered to be sufficient to reliably determine the sex of a sample, based on DNA analysis.

Regarding the control samples – four extant dogs of known sex, their biological sex confirmation proves that this method of DNA mapped reads proportions chrX/chr1 ratios is reliable to infer the biological sex of ancient dog samples (see Supplementary Fig. S9). The sex of the extant wolves – samples LUP006829 (SMLM40 – female – ewolf5) and LUP006830 (SMLM 25 – male – ewolf6), for which we had nuclear data, was also confirmed.

Concerning molecular sexing, reference sequences from the dog Y chromosome could not be accessed directly through the CanFam3.1 annotated reference genome, since it was prepared from a female dog, which lacks the Y chromosome. However, through the strategy of the mapped reads' proportions chrX/chr1 ratios, we were able to infer the biological sex.

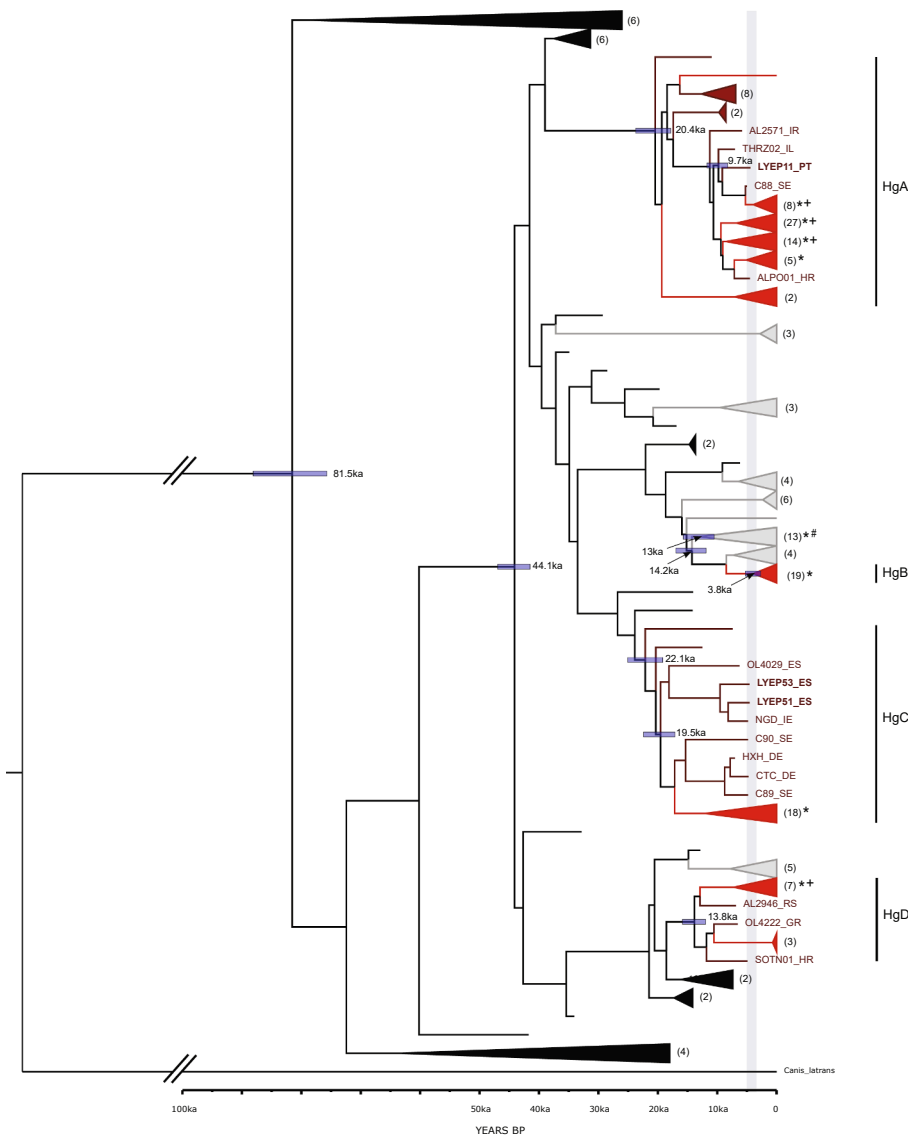


Fig. 5. Maximum Clade Credibility tree summarized from the Bayesian analysis of 205 ancient and extant/historic mitogenomes of *Canis lupus*. The tree includes newly generated mitogenomes from 54 extant dogs (47 from Iberia (Portugal) and seven from North Africa (Morocco)), three extant and three historic Iberian wolves, one historic Portuguese dog and three Chalcolithic Iberian dogs (LYEP11_PT (dated to 4517–4295 cal BP), LYEP51_ES (dated to 4800–4290 BP) and LYEP53_ES (dated to 4820–4290 BP), all in bold). The 15 ancient mitogenomes obtained from Bergström and collaborators (2020) together with another 126 publicly available data (see Supplementary Table S2) dated to several periods are also included. The coyote (*Canis latrans*) genome is added as the outgroup. Dates correspond to the node height posterior median and the solid light blue horizontal bars to their 95% HPDI. Light and dark red branches represent extant/historic and ancient dogs, respectively. Grey branches represent extant wolves, and black ones are ancient wolves and the coyote. The symbols * refer to mitogenomes from Iberia, + to North African dog breeds sequences and # to the 6 extant/historic Iberian wolves mitogenomes generated by this study. The vertical gray line highlights the time range considered for the Iberian Chalcolithic period (ca. 5–4 ka years BP). For clarity, the branch leading to the outgroup (coyote) was truncated. For simplicity, some clades in the tree have been collapsed according to haplogroup assignment. The number of samples within each collapsed node is indicated in parentheses. Samples' age older than 1000 years are given in ka (BP). For the whole tree, see Supplementary Materials (Fig. S5 A and B). Our Maximum Clade Credibility tree produced a very similar topology compared to the Maximum Likelihood tree (Supplementary Fig. S7). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Dog remains are not common in the archaeological record compared to remains from other domesticates. Dogs co-existed with humans mainly as companions/assistants or commensals and apparently were consumed only occasionally (Martín Rodríguez et al., 2014; Sanchis Serra and Sarrión Montañana, 2004). Most likely they played a significant role in common tasks depending on the particular habitat (e.g. hunting strategies assisted by dogs in pre-Neolithic times in Arabia, registered in art-rock (Guagnin et al., 2018) or represented in Roman iconography (Pires et al., 2017). Complete dog burials are sometimes observed, and on other occasions parts of dog skeletons were buried with care alongside humans (Albizuri Canadell et al., 2019; Davis and Valla, 1978; Detry and Cardoso, 2010; Liesau von Lettow-Vorbeck et al., 2017; Lomba Maurandi et al., 2009; Porfirio and Serra, 2014; Street et al., 2015). Their presence as a symbolic “item” in Prehistoric societies has been frequently documented, including in the Chalcolithic period (Blasco Bosqued et al., 2009; Cámara Serrano et al., 2012; Catagnano, 2016; Daza-Perea, 2011; Daza-Perea, 2015; Daza-Perea, 2017; Daza-Perea, 2019; Daza-Perea, 2016; Delibes de Castro et al., 2019; García-Moncó Piñeiro, 2005; Liesau von Lettow-Vorbeck, 2012; Liesau von Lettow-Vorbeck et al., 2017; Liesau von Lettow-Vorbeck et al., 2008; Liesau von Lettow-Vorbeck et al., 2013; Liesau von Lettow-Vorbeck

et al., 2014; Lomba Maurandi et al., 2009; Lomba Maurandi and Haber Uriarte, 2016; Valera, 2008; Valera et al., 2020).

In our study, archaeological materials from two deposits were analyzed more in depth: El Casetón de la Era (Spain) and Leceia (Portugal), and these remains apparently were not deposited with extra care. The former is a pre-Bell Beaker Chalcolithic site, and there is no evidence for the presence of exogenous materials (not from very distant regions, i.e. extra peninsular, nor from remote areas within the Iberian Peninsula). In Leceia, on the other hand, we find bell-beaker occupation levels, and the presence of clearly exogenous materials, such as ivory. However, since the beginning of the Chalcolithic (ca. 4750 cal BP) and coincident with the intensive edification of wall-defensive structures, the presence of exotic products is observed, revealing the diversity of contacts established by populations from Leceia (Cardoso, 1997; Cardoso, 2000).

Regarding the identification of *Canis* remains, the correlation between the length and breadth of the mandibular first molar shows that the Chalcolithic dogs are distinct (smaller) from wolves, supporting that our dataset belonged to dog specimens. Despite current re-evaluations of this method of differentiation between wolves and dogs (Janssens et al., 2019), if we consider these measurements together with the postcranial results using shoulder height estimations, whose values never overlap those of Iberian wolves (60–70 cm), there is support to classify our

archaeological samples as dogs. Dogs dated to the Chalcolithic presented medium-sized M_1 teeth (with a coefficient of variation value $< 10\%$), with a single dog from Leceia presenting the smallest M_1 tooth. Apparently, M_1 tooth length is slower in reflecting signs for intensive selection. Teeth tend to be more conservative than bones concerning size variations and more independent from sexual dimorphism, age and environmental changes (Albarella, 2002). Later, during the Roman period when differentiation of dog breeds is well documented, CV variation for M_1 length above 10% was detected (Pires et al., 2017). Considering the height at shoulder estimations we find, during the Chalcolithic, dogs of medium size – mesomorphic type, as well as taller animals. We detected two cases of dogs with high values for this parameter (La Velilla and Anta 3 de Santa Margarida sites), meaning that the emergence of dogs of varied sizes already existed in the Chalcolithic period, reflecting specific pressure (selection) for size differentiation. This size variation has already been reported and is particularly evident from two Chalcolithic large assemblages such as Camino del Molino (Catagnano, 2016; Gil Cano et al., 2011; Ruiz García-Vaso et al., 2014; Ruiz García-Vaso et al., 2013) and Camino de las Yeseras (Daza-Perea, 2011; Daza-Perea, 2015; Daza-Perea, 2017; Daza-Perea, 2019; Daza-Perea et al., 2019). It is worthwhile to point out that Gil Cano and colleagues (2011) report in the first analysis from Camino del Molino (dated to the Chalcolithic period, Spain) dogs whose shoulder height varies from 42 to 70 cm and from which two size classes can be distinguished – a medium size (shoulder heights ranging from 42 to 50 cm) and a bigger size (64–70 cm). A more recent study of the remains proposes a new classification of the dog remains into two groups, small and medium-sized, suggesting the possibility that the large specimens were actually wolves (Catagnano et al., 2015; Ruiz García-Vaso et al., 2014). Later, Catagnano (2016) reported a population of 29 dog specimens from the same site, whose shoulder heights ranged from 33 to 54.5 cm. In another study, the analysis of 25 dog specimens from five Iberian archaeological sites showed that the dogs' shoulder heights ranged between 39.5 and 56.4 cm (Daza-Perea, 2019). Regarding small size dogs, individuals shorter than 40 cm, were already detected in Iberia prior to the Chalcolithic, e.g. samples from Bóbila Madurell site, dated to the Neolithic, where an adult specimen with a shoulder height of 37.5 cm was found (Albizuri Canadell et al., 2019). After the Chalcolithic, in the Roman period, we observed an increased height variation among Iberian dogs (Colominas, 2016; Morales Muñoz et al., 2015; Pires et al., 2017). Within this period (Roman), Davis and Gonçalves (2017) observed a very small dog (23–24 cm) at São Miguel de Odrinhas (Portugal) and more recently from Augusta Emerita (Mérida, Badajoz) a 22,2 cm tall dog has been excavated (Bustamante, pers. com.). For this chronology, very small dogs in the zooarchaeological record have been reported that were possibly selected for aesthetic reasons (toy sized dogs or “lap dogs”) or had a genetic disease such as achondroplasty (Baxter, 2010). Human driven selection in dogs, associated with the development of certain skills to perform specific activities, such as guarding livestock, assistance in hunting or symbolic use, probably had an impact on their body sizes.

After eruption of dogs' adult dentition and closure of the dental apex around 18 months of age, there is an increase in dentin thickness and a decrease in pulp canal width, through secondary dentin deposition by odontoblasts (Gorrel, 2004). In our study, the obtained dental X-rays allowed us to identify animals of different ages based on the analysis of the pulp canal closure ratios. Although the accuracy of this method decreases with age, alternative methods, such as the *cementum annuli* analysis, may not be so easy to apply as well due to its destructive character. Moreover, the association between tooth wear and increasing age is not easy to establish, either in archaeological wolves or dogs' specimens, because of different diets, body size variability and high frequency of missing teeth and tooth fractures (Nomokonova et al., 2020).

In our assemblage, no evidence of dental conditions, such as periodontitis, the most common oral pathology in extant mature adult dogs (Gorrel, 2004), was found, which could be explained by the fact that

there were no elderly dogs among our samples.

The analysis of mitogenomes is more powerful than that of short mitochondrial DNA fragments allowing for greater phylogenetic resolution and precision for estimating divergence times (Duchêne et al., 2011) as well as genetic diversity (Cairns and Wilton, 2016). However, it is important to note that the Iberian *Canis* phylogeny presented here reveal only the evolutionary history of the organelle mitochondria – i.e., maternally inherited, essentially a non-recombining single locus, and not necessarily the timing of the emergence of both species or a domestication event (see Fig. 5). These results need to be complemented by information on autosomes and the sex chromosomes, including paternal lineages, to quantify degrees of admixture between populations and infer evolutionary processes more accurately. Such comprehensive genomic analysis of the Iberian wolves and dogs' trajectories, can account for demographic processes including local recruitment of wolves into the domestic stock, introgressive hybridization or incomplete lineage sorting (e.g. Larson and Burger (2013)).

The frequency of mitochondrial dog clades varies across time and space. In particular, clades A and C were detected in Iberia in prehistoric times (Pires et al., 2019) and this study). For other parts of Europe, clade C haplotypes were more common in ancient dogs until the Neolithic (for example, CTC and HXH samples from Germany (Botigué et al., 2017), and the Newgrange dog specimens from Ireland (Frantz et al., 2016)) and clade A more rare. In the case of clade C, a continuity during the Neolithic within Europe has been described (Botigué et al., 2017). However, some authors mention a near complete turnover of dog ancestry during the Neolithic, in which the dominant clade C was substituted by clade D dogs coming from the East or Southeastern Europe (Ollivier et al., 2018). Bergström and colleagues (2020) also try to explain the genomic ancestry cline they observe across ancient European dogs, with a possible admixture between dogs associated with Mesolithic hunter-gatherers and those brought by incoming Neolithic farmers. During the Neolithic, clade A dogs remain detectable (in the region of present-day Israel), specifically a sample from the Levant Neolithic dating to ca. 7000 years BP (sample THRZ02 from Bergström and colleagues (2020)). A strong genetic structure among the earliest European dogs, stemming from different domestication processes, should be investigated. As mentioned previously, other dog clades, such as B and D, are rarely detected in Iberian dogs. So far, clade D was only detectable in ancient dogs dated to Roman times onwards (Pires et al., 2017) and clade B has never been detected in Iberian ancient dogs. However, both are present in extant autochthonous Iberian dog breeds (Pires et al., 2006; Pires et al., 2017; van Asch et al., 2005). Dogs' arrival date in Iberia and migration routes are under investigation. Other clades such as E, F or X have never been detected in Iberian ancient dogs or in local autochthonous dog breeds. Except for clade B, the results of this study are consistent with a scenario where extant Iberian dogs emerged from an already genetically diverse dog population.

The mitogenomic diversity of Iberian dogs during the Chalcolithic period may be associated with the complex history of human mobility and population admixture during the preceding period, the Neolithic. By analyzing ancient human genomic and dietary data, Valdiosera and colleagues (2018) documented a substantial change in the genomic composition of Iberians during the Neolithic with the arrival of the first farmers, but after the Neolithic a relative genetic continuity is detected in Iberia, in contrast to what happens in other parts of Europe with major genetic turnovers. Based on whole genomic data, González-Forbes and colleagues (2019) detected a signal for population admixture between Iberians and Africans of sub-Saharan origin, mainly in Spanish samples dated to the Middle Neolithic and Chalcolithic. These authors associate these observations with the presence of a western route for human migration from Africa into the Iberian Peninsula in prehistoric times. During the Chalcolithic period there was an intensification and extension of human interactions, intra and extra peninsular, particularly during the Bell Beaker period, in which the presence of exotic materials assumed a particular significance. In Iberia, the pattern of consumption

and circulation of ivory of African origin suggests several distribution routes – terrestrial via west Andalusia and the Guadiana basin, and maritime via the Atlantic (Valera, 2020a). The presence of ivory artefacts of African savannah elephants (*Loxodonta a. africana*), dated to the Early Chalcolithic, found at the Leceia archaeological site, is compatible with the maritime route via the Atlantic between Portugal and North Africa or even with more distant regions. e.g. sub-Saharan regions (Schuhmacher et al., 2009). The presence of the donkey (*Equus asinus* L.) in Leceia can be related to the ivory trade between North Africa and Iberia during the Chalcolithic (Cardoso et al., 2013). Olalde and colleagues (2019) also documented contacts (sporadic) with North Africa during the Chalcolithic period using human genome-wide data. More recently, Bergström and colleagues (2020) established a comprehensive comparison of ancient dog and human DNA from Europe, the Near East, and Siberia, and were able to show that in some cases there is a strong overlap between the evolutionary paths reflected by the human and dog genomes, meaning that some human populations took their dogs during migrations. In other cases, such overlap was not detected. Only a high-resolution ancient DNA transect focused on the genomic composition of the Mesolithic and Neolithic Iberian and North African dogs, would allow us to deeply understand the origins of the Chalcolithic ones.

The fixation of clade Hg1 in the extant Iberian wolf population (Pilot et al., 2010) with a single exception reported in Hg2 (Pires et al., 2017) is probably related to strong genetic drift due to geographical isolation, which according to Silva and colleagues (2020) who examined whole genome data from contemporary specimens, dates back to the end of the Pleistocene, well before the recent extinction of wolves in Central Europe due to anthropogenic causes. Ancient DNA analysis revealed a predominance of Hg2 in western Europe (Pilot et al., 2010). Nowadays, the Italian wolf population is unique as it retains specimens harbouring mitochondrial Hg2 (Ciucani et al., 2019).

Ancient Iberian wolves need to be better studied at the genomic level. There is a data lacuna that can be explained by their scarcity in the archaeological record, the antiquity of the recovered remains, and the inherent DNA degradation in historic/ancient specimens. This is particularly relevant for remains collected in the Iberian Peninsula since it has a temperate/arid climate, which negatively influences the preservation of DNA through time (Bollongino et al., 2008). Low endogenous DNA content (<1%) in our Iberian Chalcolithic samples and DNA damage, pose severe technical challenges. Our team previously attempted to analyze Iberian wolf samples dated to the Palaeolithic, but we could only recover partial D-loop sequences using a PCR-based approach (Pires et al., 2019).

Sex determination for ancient faunal remains is important to understand behavior and social structure of wild animals (e.g. Pečnerová et al. (2017)) as well as past animal/human relationships (e.g. Davis et al. (2012)). For the majority of the referred archaeological remains in this study, the absence of osteometric data or specific osteological elements for sex determination, prevented us from determining their sex. In dogs, sexual dimorphism is hard to identify from osteometric data due to the large diversity of dog morphotypes and extensive overlap between males and females. Although there are morphometric methodologies available, such as the “table test”, this method requires long bones like humeri in their complete form, a condition that is uncommon in materials from these chronologies. Based on nuclear genomic data we confirmed the sex of four control samples (extant dogs of known sex) and were able to infer the sex of three of our ancient samples, two males and one female. Bergström and colleagues (2020) have reported an overrepresentation of males in their ancient dog study. We cannot conclude the same due to our reduced sample size (N = 3 Chalcolithic dog samples).

Our multidisciplinary approach offers a general profile of the Iberian dogs during the Chalcolithic period. The shoulder’s height variability of the specimens analysed in this study, in conjunction with the genetic diversity indicate that Chalcolithic dogs could have been maintained, bred and selected for specific purposes, perhaps associated with

livestock husbandry practices and hunting. When nuclear data become available, the search for herding or guarding dog genetic signatures, described in extant breeds, should be investigated.

5. Conclusions

The understanding of ancient dogs can greatly benefit if a multidisciplinary approach is employed. In this paper, we were able to provide a characterization of some Iberian dogs dated to the Chalcolithic, paving the way to understand humans’ interests in their maintenance and breeding. Briefly, it was determined their: (i) shoulders’ height based on osteometric data and confirmed that morphological diversity was already present in such early times which can be associated to the use humans did of these dogs; (ii) age at death combining tooth wear, dental eruption pattern analysis as well as pulp canal closure ratios which allowed the conclusion that these animals died young; (iii) global dental health and it was clear that these individuals, due to their youth, did not suffer from periodontitis, as extant dogs severely do after adulthood; and lastly, (iv) through DNA analysis, maternal lineages’ diversity and biological sex which improve our knowledge about the Iberian dogs evolutionary path. Data as such, are relevant to interpret dogs’ presence and significance in archaeological contexts.

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.

Acknowledgements

We thank Raquel Godinho from the EcoGenomic research group (BIOPOLIS-CIBIO/InBIO) for sharing pre-processed data on Iberian wolves; Henrique Carvalho from the Portuguese Nature and Forests Conservation Institute (ICNF, <http://www.icnf.pt>) for providing access to Iberian wolf samples from the tissue bank – SMLM, *Sistema de Monitorização de Lobos Mortos* (tissue samples from necropsied animals); Greger Larson from the Palaeogenomics & Bio-Archaeology Research Network, School of Archaeology, Oxford, UK for support with sequencing of two Iberian wolf samples; José Manuel Gonzalo-Orden from Faculty of Veterinary (University of León, Spain) for X-ray analysis of El Casetón de la Era dog samples; Ângela Lopes for genomic DNA extraction from blood samples of extant Portuguese dog breeds specimens; and Bergström and colleagues for sharing the 15 ancient mitogenome fasta sequences processed by Audrey Lin.

The research leading to these results has received funding from FEDER Funds through the Operational Competitiveness Factors Program “COMPETE”, and by National Funds through the Foundation for Science and Technology (FCT Grant POCI-01-0145-FEDER-029545 – PTDC/HAR-ARQ/29545/2017), by the project UIDB/CVT/00772/2020 and associated laboratory AL4AnimalS, as well as from individual grants and contracts: DL57/2016/CP1440/CT0029 (A.E. Pires), DL57/2016/CP1375/CT0003 (I.R. Amorim), 2020.02754.CEECIND (C. Ginja), CEECINS/00127/2018 (J. Requicha), DL 57/2016/CP1443/CT0029 (C. Detry), 2020.06605.BD (A.B. Santos) and 2020.05503.BD (C. Delicado).

A considerable amount of the osteometric data included in this research were obtained during the development of the Master thesis and PhD of A. Daza-Perea at Universidad Autónoma de Madrid, thanks to the granting of materials and expertise from C. Liesau, P. Ríos, Argea Consultores S.L., and Trébede, Patrimonio y Cultura S.L. We must thank the support of the FPI PhD BES-2012-056461 grant, which was associated with the HAR2011-28731 Project, both financed by the Spanish Ministry of Economy and Competitiveness.

Author contributions

A. Daza-Perea, C. Detry, C. Fernández-Rodríguez, J.L. Cardoso, A. Valera, N. Almeida, E. Porfírio, Ana Beatriz Santos and C. Delicado contributed with measurements from own studies of archaeological materials, and archaeological information.

C. Fernández-Rodríguez, and J.L. Cardoso contributed with archaeological samples for DNA analysis.

A. Daza-Perea and C. Detry collected zooarchaeological and osteometric data and did the zooarchaeological analysis.

J. Requicha did some X-ray analyses and all the interpretation of the radiological data.

I. Ureña and S. Guimarães carried out the ancient DNA laboratory work, supervised by C. Ginja.

L. Blaschikoff did DNA extractions from extant samples and its preparation for whole genome sequencing, supervised by A.E. Pires.

A. Muñoz-Merida did the mitogenomes annotation and assisted in the genbank submission process.

L. Blaschikoff processed the genome sequence data.

L. Blaschikoff performed the bioinformatics analyses with contributions from R. Schmidt, supervised by O. Serra, R. Rasteiro, S. Guimarães, C. Ginja and A.E. Pires.

A. Daza-Perea, C. Detry and L. Blaschikoff performed graphical representations.

A. Daza-Perea and C. Detry performed the statistical analysis for biometric data.

F. Simões, J.A. Matos, I.R. Amorim, F. Petrucci-Fonseca contributed blood samples' storage conditions (curation of the blood samples' bank for extant wolves and dogs), wet lab kits and protocols for DNA extractions from blood samples from extant dog specimens.

S.J.M. Davis contributed comments to the zooarchaeological methodologies during the early stage of this research.

A. Götherström hosted and supervised the Palaeogenetics laboratory work developed for ancient samples.

L. Blaschikoff, A. Daza-Perea, C. Detry, A.E. Pires, J. Requicha wrote the paper with input and comment from all the authors.

R. Schmidt, I.R. Amorim and C. Ginja did the english revision of the manuscript.

A.E. Pires and C. Ginja raised funds, headed this investigation and managed project administration.

Data accessibility

Complete mitogenome of ancient and extant *Canis* have been deposited in GenBank, <https://www.ncbi.nlm.nih.gov/nucleotide/>, namely of 54 extant Iberian and African dog breeds (accession numbers MW916015-916068), one historic Iberian dog (accession number MW916080), three ancient Iberian dogs (accession numbers MW916081-MW916083), three extant Iberian wolves (accession numbers MW916087, MW916078 and MW916079) and three historic Iberian wolves (accession numbers MW916084-916086).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2022.103338>.

References

Albarella, U., 2002. Size matters: how and why biometry is still important in zooarchaeology. In: Brothwell, D.R. (Ed.), *Bones and the Man: Studies in honour of Don Brothwell*. Oxbow Books. https://eprints.whiterose.ac.uk/112979/1/Albarella_U_2002_Size_matters_how_and.pdf.

Albizuri Canadell, S., Nadal Lorenzo, J., Martín Rodríguez, P., Gibaja Bao, J.F., Martín Colliga, A., Esteve Gràcia, X., Oms Arias, F.X., Martí Rosell, M., Pou Calvet, R., López-Onaindia, D., Subirà i de Galdàcano, M. E., 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 Etxabe, J., 1967. Fauna de mamíferos del yacimiento prehistórico de Mazirulo (Urnieta) en Guipúzcoa. *Munibe* 19 (3/4), 271–297. <http://www.aranzadi.eus/fileadmin/docs/Munibe/1967271297.pdf>.

Altuna Etxabe, J., Mariezkurrena Gastearena, K., 1985. Bases de subsistencia de los pobladores de Erralla: macromamíferos. *Munibe* 37, 87–117. <http://www.aranzadi.eus/fileadmin/docs/Munibe/1985001206AA.pdf>.

Altuna Etxabe, J., Mariezkurrena Gastearena, K., 2007. Restos de Macromamíferos de SJAPL. In: Vegas Aramburu, J.I. (Ed.), *San Juan Ante Portam Latinam: una inhumación colectiva prehistórica en el valle medio del Ebro: memoria de las excavaciones arqueológicas, 1985, 1990 Y 1991*. Diputación Foral de Alava, Departamento de Cultura y Euskera, pp. 91–97.

Arias Cabal, P., Diniz, M., Araújo, A.C., Armendáriz Gutiérrez, Á., Teira Mayolini, L.C., 2015. At the edge of the marshes: new approaches to the Sado valley Mesolithic (Southern Portugal). In: Bicho, N., Detry, C., Douglas Price, T., Cunha, E. (Eds.), *Muge 150th: The 150th Anniversary of the Discovery of Mesolithic Shellmiddens*. Cambridge Scholars Publishing, pp. 301–319.

Arias Cabal, P., Diniz, M., Cubas Morera, M., Duarte, C., Iriarte Avilés, E., Teira Mayolini, L.C., 2016. Looking for the traces of the last hunter-gatherers: geophysical survey in the Mesolithic shell middens of the Sado valley (Southern Portugal). *Quat. Int.: J. Int. Union Quat. Res.* 435 (Part B), 61–70. <https://doi.org/10.1016/j.quaint.2016.02.016>.

Bandelt, H.J., Forster, P., Röhl, A., 1999. Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* 16 (1), 37–48. <https://doi.org/10.1093/oxfordjournals.molbev.a026036>.

Baxter, I.L., 2010. Small Roman dogs. *Alexandria Archive* 901, 1–9. https://www.academia.edu/29025805/Small_Roman_Dogs.

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>.

Blanco-González, A., Lillios, K.T., López-Sáez, J.A., Drake, B.L., 2018. Cultural, demographic and environmental dynamics of the Copper and Early Bronze Age in Iberia (3300–1500 BC): towards an interregional multiproxy comparison at the time of the 4.2 ky BP event. *J. World Prehistory* 31 (1), 1–79. <https://doi.org/10.1007/s10963-018-9113-3>.

Blasco Bosqued, C., Liesau von Lettow-Vorbeck, C., Ríos Mendoza, P., Blanco García, J.F., Aliaga Almela, R., Moreno García, E., Daza-Perea, A., 2009. Kupferzeitliche Siedlungsbestattungen mit Glockenbecher- und Prestigebeigaben aus dem Grabenwerk von El Camino de las Yeseras (San Fernando de Henares, Madrid). *Untersuchungen zur Typologie des Grabritus und zu dessen sozialer Symbolik*. *Madrid Mittelungen* 50, 40–70. <https://publications.dainst.org/journals/mm/article/view/2665>.

Bollongino, R., Tresset, A., Vigne, J.-D., 2008. Environment and excavation: pre-lab impacts on ancient DNA analyses. *C.R. Palevol* 7 (2), 91–98. <https://doi.org/10.1016/j.crpv.2008.02.002>.

Botigüé, L.R., Song, S., Scheu, A., Gopalan, S., Pendleton, A.L., Oetjens, M., Taravella, A.M., Seregély, T., Zeeb-Lanz, A., Arbogast, R.-M.-M., Bobo, D., Daly, K., Unterländer, M., Burger, J., Kidd, J.M., Veeramah, K.R., 2017. Ancient European dog genomes reveal continuity since the Early Neolithic. *Nat. Commun.* 8, 16082. <https://doi.org/10.1038/ncomms16082>.

Bro-Jørgensen, M.H., Keighley, X., Ahlgren, H., Scharff-Olsen, C.H., Rosing-Asvid, A., Dietz, R., Ferguson, S.H., Gotfredsen, A.B., Jordan, P., Glykou, A., Lidén, K., Olsen, M.T., 2021. Genomic sex identification of ancient pinnipeds using the dog genome. *J. Archaeol. Sci.* 127, 105321. <https://doi.org/10.1016/j.jas.2020.105321>.

Cabrera Latorre, A., 1907. *Los lobos de España*. *Boletín de La Real Sociedad Española de Historia Natural* 7, 193–197.

Cafazzo, S., Valsecchi, P., Bonanni, R., Natoli, E., 2010. Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behav. Ecol.* 21 (3), 443–455. <https://doi.org/10.1093/beheco/arg001>.

Cairns, K.M., Wilton, A.N., 2016. New insights on the history of canids in Oceania based on mitochondrial and nuclear data. *Genetica* 144 (5), 553–565. <https://doi.org/10.1007/s10709-016-9924-z>.

Cámara Serrano, J.A., Riquelme Cantal, J.A., Pérez Barea, C., Lizcano Prestel, R., Burgos Juárez, A., Torres Torres, F., 2010. Sacrificio de animales y ritual en el Polideportivo de Martos-La Alberquilla (Martos, Jaén). *Cuadernos de Prehistoria Y Arqueología de La Universidad de Granada* 20, 295–327. <https://revistaseug.ugr.es/index.php/cpag/article/view/135>.

Cámara Serrano, J.A., Sánchez Susí, R., Laffranchi, Z., Martín Flórez, S., Riquelme Cantal, J.A., Spanedda, L., García Cuevas, M.F., González Herrera, A., Jiménez Brobeil, S.A., Nicás Perales, J., 2012. La cronología y variedad de los sistemas funerarios en Marroquíes. Una aproximación desde las excavaciones del Sistema Tranviario de Jaén. *SAGVNTVM. Papeles Del Laboratorio de Arqueología de Valencia* 44, 47–66. <https://core.ac.uk/download/pdf/71010902.pdf>.

Carbajo Arana, M., 2020. La gestión de los recursos ganaderos y cinegéticos durante la Prehistoria reciente en el valle del Duero: El Casetón de la Era (Villalba de los Alcores, Valladolid). Doctoral dissertation. Universidad de Valladolid. Facultad de Filosofía y Letras. <https://core.ac.uk/download/pdf/288887064.pdf>.

Carbajo Arana, M., Fernández Rodríguez, C., 2016. Los carnívoros del recinto de fosos de El Casetón de la Era (Villalba de los Alcores, Valladolid). In: Pinto Coelho, I., Bento Torres, J., Serrão Gil, L., Ramos, T. (Eds.), *Entre ciência e cultura: da interdisciplinaridade à transversalidade da Arqueologia*, Actas das VIII Jornadas de Jovens em Investigação Arqueológica, celebradas em 2015 en la Universidade Nova de Lisboa. Centro de Estudos de Património. Departamento de História, Arqueologia

- e Património. Universidade do Algarve, pp. 277–282. https://www.academia.edu/44155411/Los_carn%C3%ADvoros_del_Recinto_de_Fosos_Calcol%C3%ADtico_de_El_Caset%C3%B3n_de_la_Era_Villalba_de_Los_Alcores_Valladolid.
- Cardoso, J.L., 2003. O uso do marfim, no território português, durante o Calcolítico: a propósito de um alfinete recolhido no povoado pré-histórico de Leceia (Oeiras). *Estudos Arqueológicos de Oeiras* 11, 85–96. <https://repositorioaberto.uab.pt/handle/10400.2/6102>.
- Cardoso, J.L., 2008. The chalcolithic fortified site of Leceia (Oeiras, Portugal). *Verdolay: Revista del Museo Arqueológico de Murcia* 11, 49–66. <https://repositorioaberto.uab.pt/handle/10400.2/3259>.
- Cardoso, J.L., 2014/2015. The Bell-beaker complex in Portugal: an overview. *O Arqueólogo Português, Série V* (4/5), pp. 275–308. <https://repositorioaberto.uab.pt/bitstream/10400.2/6468/1/2014-2015%20Artigo%20OAP%20Joao%20Cardoso.pdf>.
- Cardoso, J.L., 2014. Absolute chronology of the Beaker phenomenon North of the Tagus estuary: demographic and social implications. *Trabajos de Prehistoria* 71 (1), 56–75. <https://doi.org/10.3989/tp.2014.12124>.
- Cardoso, J.L., Detry, C., 2002. Estudo arqueozoológico dos restos de ungulados do povoado pré-histórico de Leceia (Oeiras). *Estudos Arqueológicos de Oeiras* 10, 131–182. <https://repositorio.ul.pt/handle/10451/28800>.
- Cardoso, J.L., Soares, A.M., 1996. Contribution d'une série de datations 14C, provenant du site de Leceia (Oeiras, Portugal), à la chronologie absolue du néolithique et du chalcolithique de l'Estremadura Portugaise. *Actes Du Colloque de Périgueux. Supplément à La Révue d'Archeometrie*, pp. 45–50. <https://repositorioaberto.uab.pt/bitstream/10400.2/3833/1/1996%2c%20contribution%20d%27une%20serie%20de%20datations%2014C%20du%20site%20de%20Leceia%2c%20Oeiras.pdf>.
- Cardoso, J.L., Vilstrup, J.T., Eisenmann, V., Orlando, L., 2013. First evidence of Equus asinus L. in the Chalcolithic disputes the Phoenicians as the first to introduce donkeys into the Iberian Peninsula. *J. Archaeol. Sci.* 40 (12), 4483–4490. <https://doi.org/10.1016/j.jas.2013.07.010>.
- 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. Doctoral dissertation. Universitat Autònoma de Barcelona. <https://ddd.uab.cat/reco rd/174983>.
- Catagnano, V., Ramírez Bellido, O., Gil Cano, F., Ruiz Garcia-Vaso, C., Vázquez Autón, J. M., Saña Seguí, M., 2015. I resti di canidi dalla necropoli in grotta di Camino del Molino (Caravaca de la Cruz Murcia, Spagna). *Atti dell'8° Convegno Nazionale Di Archeozologia* (1), 285–292. <https://doi.org/10.1285/i9788883051487p285>.
- Cava Almuzara, A.C., 1978. El depósito arqueológico de la cueva de Marizulo (Guipúzcoa). *Munibe* 30, 155–172. <http://www.aranzadi.eus/fileadmin/docs/Munibe/1978155172.pdf>.
- Ciucani, M.M., Palumbo, D., Galaverni, M., Serventi, P., Fabbri, E., Ravegnini, G., Angelini, S., Maini, E., Persico, D., Caniglia, R., Cilli, E., 2019. Old wild wolves: ancient DNA survey unveils population dynamics in Late Pleistocene and Holocene Italian remains. *PeerJ* 7, e6424. <https://doi.org/10.7717/peerj.6424>.
- Colominas, L., 2016. Morphometric variability of Roman dogs in Hispania tarraconensis: the case study of the Vila de Madrid necropolis. *Int. J. Osteoarchaeol.* 26 (5), 897–905. <https://doi.org/10.1002/oa.2507>.
- Costa, C., 2010. Os restos faunísticos de animais vertebrados do Sector I dos Perdígões (fossas e fossos 3 e 4). *Apontamentos de Arqueologia e Património* 6, 53–74. http://www.nia-era.org/publicacoes/doc_download/6-apontamentos-6.
- Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and high-performance computing Europe PMC Funders Group. *Nat. Methods* 9, 772. <https://doi.org/10.1038/nmeth.2109>. <https://www.nature.com/articles/nmeth.2109>.
- Davis, S.J.M., Gonçalves, A., 2017. Animal remains from the 4th-5th century AD well at São Miguel de Odrinhas, Sintra, Portugal: tiny sheep and a dwarf dog. *Revista Portuguesa de Arqueologia* 20 (1), 139–156. <https://repositorio.ul.pt/handle/10451/35170>.
- Davis, S.J.M., Mataloto, R., 2012. Animal remains from Chalcolithic São Pedro (Redondo, Alentejo): evidence for a crisis in the Mesolithic. *Revista Portuguesa de Arqueologia* 15 (1), 47–85. https://www.patrimoniocultural.gov.pt/media/uploads/revistaportuguesadearqueologia/rpa15/03_SJMDavis_RMataloto.pdf.
- Davis, S.J.M., Svensson, E.M., Albarella, U., Detry, C., Götherström, A., Pires, A.E., Ginja, C., 2012. Molecular and osteometric sexing of cattle metacarpals: a case study from 15th century AD Beja, Portugal. *J. Archaeol. Sci.* 39 (5), 1445–1454. <https://doi.org/10.1016/j.jas.2011.12.003>.
- Davis, S.J.M., Valla, F.R., 1978. Evidence for domestication of the dog 12,000 years ago in the Natufian of Israel. *Nature* 276 (5688), 608–610. <https://doi.org/10.1038/276608a0>.
- Daza-Perea, A., 2011. Los depósitos de perros en Camino de las Yeseras. In: *Blasco Bosqued, C., Liesau von Lettow-Vorbeck, C., Ríos Mendoza, P. (Eds.), Yacimientos calcolíticos con Campaniforme de la región de Madrid: nuevos estudios.* Universidad Autónoma de Madrid, pp. 211–222. https://www.researchgate.net/publication/283408324_Los_depositos_de_perros_en_Camino_de_las_Yeseras.
- Daza-Perea, A., 2015. La fauna en el Calcolítico de la región de Madrid: los depósitos de canes. *Servicio de Publicaciones de la Universidad Autónoma de Madrid.* <https://libros.uam.es/tfm/catalog/download/399/749/773?inline=1>.
- Daza-Perea, A., 2016. La fauna del depósito del área 40 de Camino de las Yeseras: otro ejemplo del uso simbólico del perro durante el Calcolítico. In: *Coelho, I.P., Torres, J. B., Gil, L.S., Ramos, T. (Eds.), Entre ciência e cultura: da interdisciplinaridade à transversalidade da arqueologia, Actas das VIII Jornadas de Jovens em Investigação Arqueológica, celebradas em 2015 en la Universidade Nova de Lisboa.* Centro de Estudos de Património. Departamento de História, Arqueologia e Património. Universidade do Algarve, pp. 297–301. https://www.researchgate.net/publication/n/326683949_La_fauna_del_deposito_del_area_40_de_Camino_de_las_Yeseras_otro_ejemplo_del_uso_simbolico_del_perro_durante_el_Calcolitico.
- Daza-Perea, A., 2017. Preliminary studies of late prehistoric dog (*Canis lupus f. familiaris* Linnaeus, 1758) remains from the Iberian Peninsula: osteometric and 2D geometric morphometric approaches. *Appendix 1. Pap. Inst. Archaeol.* 27 (1), 12. <https://doi.org/10.5334/pia-487>.
- 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 a.C). Doctoral dissertation. Universidad Autónoma de Madrid. <https://repositorio.uam.es/handle/10486/690366>.
- Daza-Perea, A., Liesau von Lettow-Vorbeck, C., de Chorro y de Villa-Ceballos, M. A., & Cabrera Taravillo, C., 2019. Anexo 3. Datos y medidas de los restos de perros de Camino de las Yeseras. In: *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 a.C).* Daza-Perea, A. Doctoral dissertation. https://repositorio.uam.es/bitstream/handle/10486/690366/daza_perea-arantzazu%20anexo1_vol.%20II.pdf?sequence=2&isAllowed=y.
- Delibes de Castro, G., Crespo Díez, M., Martín Vela, R., Rodríguez Marcos, J.A., 2018. A ditched enclosure in the Middle Douro Valley: El Casetón de La Era (Villalba de los Alcores, Valladolid). *Sastre Blanco, J.C., Rodríguez-Monterrubio, O., Fuentes Melgar, P. (Eds.), In: Archaeology in the River Duero Valley.* Cambridge Scholars Publishing, pp. 61–84. https://www.researchgate.net/publication/327622874_A_ditched_enclosure_in_the_Mid-Douro_Valley_El_Caseton_de_la_Era_Villalba_de_Los_Alcores_Valladolid.
- Delibes de Castro, G., Crespo Díez, M., Rodríguez Marcos, J.A., 2016. Anatomía de un recinto de fosos calcolítico del valle medio del Duero: el Casetón de la Era (Villalba de los Alcores, Valladolid). In: *Bonet Rosado, H., Martí Oliver, B. (Eds.), Del neolítico a l'edat del bronze en el Mediterrani occidental. Estudis en homenatge a Bernat Martí Oliver.* Diputació de Valencia, Museu de Prehistòria de València, pp. 387–401. http://www.mupreva.es/web_mupreva_dedalo/publicaciones/864/es.
- Delibes de Castro, G., Esparza Arroyo, Á., Velasco Vázquez, J., Zapatero Magdaleno, P., Fernández Rodríguez, C., Carballo Arana, M., Palomo Díez, S., Misiego Tejada, J., 2019. Dos tumbas individuales calcolíticas en las inmediaciones de los dolmenes de Osorno y Simancas: estudio bioantropológico, ofrenda de perros y “postvida” megalítica en el valle medio del Duero. *Anexo 1. Trabajos de Prehistoria* 76 (2), 236. <https://doi.org/10.3989/tp.2019.12235>.
- Delicado, C.S., Santos, A.B., Porfirio, E., Serra, M., Detry, C., 2017. Alto de Brinches 3 (Serpa): estudio da fauna recuperada nos contextos do 3º e 2º milénios a.n.e. *Cadernos Do GEEVH* 6 (1), 28–55. https://repositorio.ul.pt/bitstream/10451/30488/1/Alto_de_Brinches_3_Serpa_estudo_da_fauna.pdf.
- Detry, C., Cardoso, J.L., 2010. On some remains of dog (*Canis familiaris*) from the Mesolithic shell-middens of Juge, Portugal. *J. Archaeol. Sci.* 37 (11), 2762–2774. <https://doi.org/10.1016/j.jas.2010.06.011>.
- Domínguez-Bella, S., Calado, D., Cardoso, J.L., Clop, X., Tarrío, A., 2004. Raw materials in the Neolithic-Aeneolithic of the Iberian Peninsula. *Slovak Geol. Mag.* 10, 17–42. <https://repositorioaberto.uab.pt/bitstream/10400.2/3227/1/2004%2c%20Raw%20materials%20in%20the%20Neolithic-Aeneolithic%20of%20the%20Iberian%20Peninsula.pdf>. <https://repositorioaberto.uab.pt/handle/10400.2/3227>.
- Duchêne, S., Archer, F.I., Vilstrup, J., Caballero, S., Morin, P.A., 2011. Mitogenome phylogenetics: the impact of using single regions and partitioning schemes on topology, substitution rate and divergence time estimation. *PLoS ONE* 6 (11), e27138. <https://doi.org/10.1371/journal.pone.0027138>.
- Duleba, A., Skonieczna, K., Bogdanowicz, W., Malyarchuk, B., Grzybowski, T., 2015. Complete mitochondrial genome database and standardized classification system for *Canis lupus familiaris*. *Forensic Sci. Int. Genet.* 19, 123–129. <https://doi.org/10.1016/j.fsigen.2015.06.014>.
- Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32 (5), 1792–1797. <https://doi.org/10.1093/nar/gkh340>.
- Frantz, L.A.F., Mullin, V.E., Pionnier-Capitan, M., Lebrasseur, O., Olivier, M., Perri, A., Linderholm, A., Mattiangeli, V., Teasdale, M.D., Dimopoulos, E.A., Tresset, A., Duffraisse, M., McCormick, F., Bartosiewicz, L., Gál, E., Nyerges, É.A., Sablin, M.V., Bréhard, S., Mashkour, M., et al., 2016. Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science* 352 (6290), 1228–1231. <https://doi.org/10.1126/science.1231611>.
- García-Moncó Pineiro, C. (2005). El perro en la Prehistoria de la Península Ibérica. Estudio crítico de la documentación Arqueozoológica anterior al calcolítico en su contexto euroasiático. [Master's dissertation]. Universidad de Cantabria.
- García-Moncó Pineiro, C., 2008. De Brennan a Bogart. Un mayor papel protagonista en el perro entre las primeras sociedades productoras de la Península Ibérica. In: *IV Congreso Del Neolítico Peninsular: 27-30 de Noviembre de 2006.* 1, pp. 411–417. https://www.marqalicante.com/contenido/publicaciones/pub_58.pdf.
- 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 poblaban el sureste español durante el Calcolítico. *Primeros resultados. XVII Congreso Nacional Y VIII Iberoamericano de Historia de La Veterinaria.* <https://www.historiaveterinaria.org/update/restos-oseos-perro-calcolitico-1457370544.pdf>.
- Gill, M.S., Lemey, P., Faria, N.R., Rambaut, A., Shapiro, B., Suchard, M.A., 2013. Improving bayesian population dynamics Inference: a coalescent-based model for multiple loci. *Mol. Biol. Evol.* 30 (3), 713–724. <https://doi.org/10.1093/molbev/mss265>.

- González-Fortes, G., Tassi, F., Trucchi, E., Henneberger, K., Paijmans, J.L.A., Díez-del-Molino, D., Schroeder, H., Susca, R.R., Barroso-Ruiz, C., Bermudez, F.J., Barroso-Medina, C., Bettencourt, A.M.S., Sampaio, H.A., Grandal-d'Anglade, A., Salas, A., de Lombera-Hermida, A., Fábregas Valcarlos, 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. R. Soc. B: Biol. Sci.* 286 (1895), 20182288. <https://doi.org/10.1098/rspb.2018.2288>.
- Correl, C., 2004. Anatomy of the teeth and periodontium. In: Correl, C. (Ed.), *Veterinary Dentistry for the General Practitioner*. Philadelphia: W. B Saunders, pp. 30–33. <https://doi.org/10.1016/B978-0-7020-2747-5.50007-4>.
- Greig, K., Boocock, J., Prost, S., Horsburgh, K.A., Jacomb, C., Walter, R.S., Matisoo-Smith, E., 2015. Complete mitochondrial genomes of New Zealand's first dogs. *PLoS ONE* 10 (10), e0138536. <https://doi.org/10.1371/journal.pone.0138536>.
- Guagnin, M., Perri, A.R., Petraglia, M.D., 2018. Pre-Neolithic evidence for dog-assisted hunting strategies in Arabia. *J. Anthropol. Archaeol.* 49, 225–236. <https://doi.org/10.1016/j.jaa.2017.10.003>.
- Guindon, S., Gascuel, O., 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst. Biol.* 52 (5), 696–704. <https://doi.org/10.1080/10635150390235520>.
- 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](https://doi.org/10.1016/0305-4403(74)90040-5).
- Horard-Herbin, M.-P., Tresselt, A., Vigne, J.-D., 2014. Domestication and uses of the dog in Western Europe from the Paleolithic to the Iron Age. *Anim. Front.* 4 (3), 23–31. <https://doi.org/10.2527/af.2014-0018>.
- Janssens, L., Perri, A., Crombé, P., Van Dongen, S., Lawler, D., 2019. An evaluation of classical morphologic and morphometric parameters reported to distinguish wolves and dogs. *J. Archaeol. Sci.: Rep.* 23, 501–533. <https://doi.org/10.1016/j.jasrep.2018.10.012>.
- Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P.L.F., Orlando, L., 2013. mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. *Bioinformatics* 29 (13), 1682–1684. <https://doi.org/10.1093/bioinformatics/btt193>.
- Juan Cabanilles, J., Martínez Valle, R., 1988. Fuente Flores (Requena, Valencia). Nuevos datos sobre el poblamiento y la economía del neo-eneolítico valenciano. *Archivo de Prehistoria Levantina* 18, 181–231. <http://mupreva.org/pub/6400>.
- Kim, K.S., Lee, S.E., Jeong, H.W., Ha, J.H., 1998. The complete nucleotide sequence of the domestic dog (*Canis familiaris*) mitochondrial genome. *Mol. Phylogenet. Evol.* 10 (2), 210–220. <https://doi.org/10.1006/mpev.1998.0513>.
- King, J.L., Jukes, T.H., 1969. Non-Darwinian evolution. *Science* 164 (3881), 788–798. <https://doi.org/10.1126/science.164.3881.788>.
- Knowlton, F.F., Whittemore, S.L., 2001. Pulp cavity-tooth width ratios from known-age and wild-caught coyotes determined by radiography. *Wildl. Soc. Bull.* 29 (1), 239–244. <http://www.jstor.org/stable/3784003>.
- Kobl Müller, S., Vilà, C., Lorente-Galdos, B., Dabad, M., Ramirez, O., Marques-Bonet, T., Wayne, R.K., Leonard, J.A., 2016. Whole mitochondrial genomes illuminate ancient intercontinental dispersals of grey wolves (*Canis lupus*). *J. Biogeogr.* 43 (9), 1728–1738. <https://doi.org/10.1111/jbi.12765>.
- Kornelissen, T.S., Albrechtsen, A., Nielsen, R., 2014. ANGSD: analysis of next generation sequencing data. *BMC Bioinf.* 15, 356. <https://doi.org/10.1186/s12859-014-0356-4>.
- Lahtinen, M., Clinnick, D., Mannermaa, K., Salonen, J.S., Viranta, S., 2021. Excess protein enabled dog domestication during severe Ice Age winters. *Sci. Rep.* 11 (1), 7. <https://doi.org/10.1038/s41598-020-78214-4>.
- Larson, G., Burger, J., 2013. A population genetics view of animal domestication. *Trends Genet.* 29 (4), 197–205. <https://doi.org/10.1016/j.tig.2013.01.003>.
- Liesau von Lettow-Vorbeck, C., 2011. Los restos de mamíferos del ámbito doméstico y funerario. Patrimonio. In: Blasco Bosqued, C., Liesau von Lettow-Vorbeck, C., Ríos Mendoza, P. (Eds.), *Yacimientos calcólicos con campaniforme de la región de Madrid: Nuevos estudios*. Universidad Autónoma de Madrid, pp. 171–198. https://www.researchgate.net/publication/292809767_La_Arqueozoología_un_elemento_clave_en_la_concepcion_espacial_de_Camino_de_las_Yeseras_Los_restos_de_mamiferos_delambito_domestico_y_funerario.
- Liesau von Lettow-Vorbeck, C., 2012. Depósitos con ofrendas de animales en yacimientos Cogotas I: antecedentes y características. In: Rodríguez Marcos, J.A., Fernández Manzano, J. (Eds.), *Cogotas I. Una cultura de la Edad del Bronce en la Península Ibérica. Homenaje a M.^a Dolores Fernández-Posse*. Universidad de Valladolid, pp. 219–257. https://www.researchgate.net/publication/309312887_Depositos_co_n_ofrendas_animales_en_yacimientos_Cogotas_I_Antecedentes_y_Caracteristicas.
- Liesau von Lettow-Vorbeck, C., 2017. Fauna in living and funerary contexts of the 3rd Millennium BC in Central Iberia. In: Bartelheim, M., Bueno, P., Kunst, M. (Eds.), *Key Resources and Sociocultural Developments in the Iberian Chalcolithic*. Tübingen Publishing, pp. 107–128. https://www.researchgate.net/publication/321833662_Fauna_in_Living_and_Funerary_Contexts_of_the_3rd_Millennium_BC_in_Central_Iberia.
- Liesau von Lettow-Vorbeck, C., Blasco Bosqued, C., Ríos Mendoza, P., Vega Miguel, J., Mendiña García, R., Blanco García, J.F., Baena Preysler, J., Petri, A., Gómez Pérez, J.L., 2008. Un espacio compartido por vivos y muertos: El poblado calcólico de fosos de Camino de las Yeseras (San Fernando de Henares, Madrid). *Complutum* 19 (1), 97–120. <https://revistas.ucm.es/index.php/CMPL/article/view/30417>.
- Liesau von Lettow-Vorbeck, C., Daza-Perea, A., Blasco Bosqued, C., Llorente Rodríguez, L., Ríos Mendoza, P., Vega de Miguel, J., Mendiña García, R., de Chorro y de Villa-Ceballos, M. de L.A., Morales Muñoz, A., 2017. The child, the dog and the raven: a singular Bronze Age burial from Camino de las Yeseras (Madrid). In: Valente, M.J., Costa, C., Detry, C. (Eds.), *Faro – Portugal*. Universidade do Algarve, p. 20. <https://repositorio.ul.pt/bitstream/10451/36794/1/EZI2017-5RAPI-BookofAbstracts.pdf>.
- Liesau von Lettow-Vorbeck, C., Daza-Perea, A., Llorente Rodríguez, L., Morales Muñoz, A., 2013. More questions than answers: the singular animal deposits from Camino de las Yeseras (Chalcolithic, Madrid, Spain). *Anthropozoologica* 48 (2), 277–286. <https://doi.org/10.5252/az013n2a6>.
- Liesau von Lettow-Vorbeck, C., Vega de Miguel, J., Daza-Perea, A., Ríos Mendoza, P., Mendiña García, R., Blasco Bosqued, C., 2014. Manifestaciones simbólicas en el acceso Noreste del Recinto 4 de Foso en Camino de las Yeseras (San Fernando de Henares, Madrid). *Saldvie* 13–14, 53–69. https://www.researchgate.net/publication/308794930_Manifestaciones_simbolicas_en_el_acceso_Noreste_del_Recinto_4_de_Foso_en_Camino_de_las_Yeseras_San_Fernando_de_Henares_Madrid.
- Li, H., Durbin, R., 2009. Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics* 25 (14), 1754–1760. <https://doi.org/10.1093/bioinformatics/btp324>.
- Lindblad-Toh, K., Wade, C.M., Mikkelsen, T.S., Karlsson, E.K., Jaffe, D.B., Kamal, M., Clamp, M., Chang, J.L., Kulbokas 3rd, E.J., Zody, M.C., Mauceli, E., Xie, X., Breen, M., Wayne, R.K., Ostrander, E.A., Ponting, C.P., Galibert, F., Smith, D.R., DeJong, P.J., et al., 2005. Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature* 438, 803–819. <https://doi.org/10.1038/nature04338>.
- Lindgreen, S., 2012. AdapterRemoval: easy cleaning of next-generation sequencing reads. *BMC Research Notes* 5, 337. <https://doi.org/10.1186/1756-0500-5-337>.
- Lizcano Prestel, R., Cámara Serrano, J.A., Riquelme Cantal, J.A., Cañabate Guerrero, M. L., Sánchez Vizaño, A., Afonso Marrero, J.A., 1992. El Polideportivo de Martos. Producción económica y símbolos de cohesión en un asentamiento del Neolítico Final en las Campiñas del Alto Guadalquivir. *Cuadernos de Prehistoria de La Universidad de Granada* 16–17, 5–101. <https://revistaseugr.es/index.php/cpag/article/view/1259>.
- Lomba Maurandi, J., Haber Uriarte, M., 2016. El registro funerario calcólico en el extremo suroccidental de la Península Ibérica: los valles del Guadalentín y Segura (Murcia). In: Bonet Rosado, H., Martí Oliver, B. (Eds.), *Del neolítico a l'edat del bronze en el Mediterrani occidental. Estudis en Homenatge a Bernat Martí Oliver*. Diputació de València, Museu de Prehistòria de València, pp. 349–364. http://www.mupreva.es/web_mupreva_dedalo/publicaciones/864/es.
- Lomba Maurandi, J., López Martínez, M., Ramos Martínez, F., Avilés Fernández, A., 2009. El enterramiento múltiple, calcólico, de Camino del Molino (Caravaca, Murcia). Metodología y primeros resultados de un yacimiento excepcional. *Trab. Prehist.* 66 (2), 143–159. <https://doi.org/10.3989/tp.2009.09025>.
- Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet*. *J. 17* (1), 10. [https://doi.org/10.14806/ej.17.1.200](https://doi.org/10.14806/ej.17.1.10.14806/ej.17.1.200). <https://journal.embnnet.org/index.php/embnnetjournal/article/view/200>.
- Martín Rodríguez, P., Saladié Ballesté, P., Nadal Lorenzo, J., Vergès Bosch, J.M., 2014. Butchered and consumed: Small carnivores from the Holocene levels of El Mirador Cave (Sierra de Atapuerca, Burgos, Spain). *Quat. Int.* 353, 153–169. <https://doi.org/10.1016/j.quaint.2014.08.011>.
- Martínez Valle, R., 1993. La fauna de vertebrados. In: Bernabeu Aubán, J. (Ed.), *El III milenio a.C. en el País Valenciano. Los poblados de Jovades (Cocentaina, Alacant) y Arenal de la costa (Ontinyent, Valencia)*, 26. SAGVNTUM. *Papeles del Laboratorio de Arqueología de Valencia*, pp. 123–151. <https://ojs.uv.es/index.php/sagvntum/article/view/2688/2306>.
- Meyer, M., Kircher, M., 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harbor Prot.* (6) <https://doi.org/10.1101/pdb.prot5448>.
- Minin, V.N., Bloomquist, E.W., Suchard, M.A., 2008. Smooth skyride through a rough skyline: Bayesian coalescent-based inference of population dynamics. *Mol. Biol. Evol.* 25 (7), 1459–1471. <https://doi.org/10.1093/molbev/msn090>.
- Molak, M., Suchard, M.A., Ho, S.Y.W., Beilman, D.W., Shapiro, B., 2015. Empirical calibrated radiocarbon sampler: a tool for incorporating radiocarbon-date and calibration error into Bayesian phylogenetic analyses of ancient DNA. *Mol. Ecol. Resour.* 15 (1), 81–86. <https://doi.org/10.1111/1755-0998.12295>.
- Morales Muñoz, A., Liesau von Lettow-Vorbeck, C., 1994. Arqueozoología del Calcólico: ensayo crítico de síntesis. In: Blasco Bosqued, C. (Ed.), *El horizonte campaniforme de la Región de Madrid en el centenario de cienpoulos*. Departamento de Prehistoria y Arqueología. Universidad Autónoma de Madrid, pp. 227–277. https://www.researchgate.net/publication/288971300_Arqueozoología_del_Calcólico_en_Madrid_Ensayo_critico_de_sintesis.
- Morales Muñoz, A., López Arrabé, J., Casado Violat, S., Llorente Rodríguez, L., 2015. Caracterización morfométrica de los perros de la unidad estratigráfica 26 del pozo-depósito de la Tabacalera (*Canis familiaris*). In: Fernández Ochoa, C., Orejas Saco del Valle, A., García Díaz, P., Gil Sendino, F. (Eds.), *La Fábrica de Tabacos de Gijón. Arqueología e Historia de un espacio milenar*. Ayuntamiento de Gijón, pp. 238–245. https://www.academia.edu/23603090/Caracterizaci%C3%B3n_morfom%C3%A9trica_de_los_perros_de_la_unidad_estratigr%C3%A1fica_26_del_pozo-dep%C3%B3sito_de_la_Tabacalera_Canis_familiaris.
- Moreno García, M., 2003. Estudio dos restos faunísticos. In: Gonçalves, V.S. (Ed.), *STAM-3, a Anta 3 da Herdade de Santa Margarida (Reguengos de Monsaraz)*. Instituto Português de Arqueologia, pp. 432–439. <https://repositorio.ul.pt/bitstream/10451/40774/1/STAM-3HG.pdf>.
- Nomokonova, T., Losey, R.J., McLachlin, K., Bachura, O.P., Gusev, A.V., Kosintsev, P.A., Fedorova, N.V., Sablin, M.V., 2020. Age estimation of archaeological dogs using pulp cavity closure ratios. *Journal of Archaeological Science* 123, 105252. <https://doi.org/10.1016/j.jas.2020.105252>.
- Okonechnikov, K., Conesa, A., García-Alcalde, F., 2016. Qalimap 2: advanced multi-sample quality control for high-throughput sequencing data. *Bioinformatics* 32 (2), 292–294. <https://doi.org/10.1093/bioinformatics/btv566>.

- Olalde, I., Brace, S., Allentoft, M.E., Armit, I., Kristiansen, K., Booth, T., Rohland, N., Mallick, S., Szécsényi-Nagy, A., Mittnik, A., Altena, E., Lipson, M., Lazaridis, I., Harper, T.K., Patterson, N., Broomandkoshbacht, N., Diekmann, Y., Faltyskova, Z., Fernandes, D., et al., 2018. The Beaker phenomenon and the genomic transformation of northwest Europe. *Nature* 555, 190–196. <https://doi.org/10.1038/nature25738>.
- 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., Broomandkoshbacht, N., Cheronet, O., Cullen, 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>.
- Ollivier, M., Tresset, A., Frantz, L.A.F., Bréhard, S., Bălăşescu, A., Mashkour, M., Boroneant, A., Pionnier-Capitan, M., Lebrasseur, O., Arbogast, R.-M., Bartosiewicz, L., Debue, K., Rabinovich, R., Sablin, M.V., Larson, G., Hänni, C., Hitte, C., Vigne, J.-D., 2018. Dogs accompanied humans during the Neolithic expansion into Europe. *Biol. Lett.* 14 (10) <https://doi.org/10.1098/rsbl.2018.0286>.
- Palumbi, S.R., 1989. Rates of molecular evolution and the fraction of nucleotide positions free to vary. *J. Mol. Evol.* 29 (2). <https://link.springer.com/article/10.1007/BF02100116>.
- Pečnerová, P., Díez-Del-Molino, D., Dussex, N., Feuerborn, T., von Seth, J., van der Plicht, J., Nikolskiy, P., Tikhonov, A., Vartanyan, S., Dalén, L., 2017. Genome-based sexing provides clues about behavior and social structure in the Woolly Mammoth. *Current Biology* 27 (22), 3505–3510.e3. <https://doi.org/10.1016/j.cub.2017.09.064>.
- Pilot, M., Branicki, W., Jędrzejewska, W., Goszczyński, J., Jędrzejewska, B., Dykyy, I., Shkvyrya, M., Tsingarska, E., 2010. Phylogeographic history of grey wolves in Europe. *BMC Evol. Biol.* 10 (1) <https://doi.org/10.1186/1471-2148-10-104>.
- Pionnier-Capitan, M., 2010. La domestication du chien en Eurasie: étude de la diversité passée, approches ostéoarchéologiques, morphométriques et paléogénétiques. Doctoral dissertation. Ecole Normale Supérieure de Lyon. <http://www.theses.fr/2010ENSL0593>.
- Pires, A.E., Amorim, I.R., Borges, C., Simões, F., Teixeira, T., Quaresma, A., Petrucci-Fonseca, F., Matos, J., 2017. New insights into the genetic composition and phylogenetic relationship of wolves and dogs in the Iberian Peninsula. *Ecol. Evol.* 7 (12), 4404–4418. <https://doi.org/10.1002/ece3.2949>.
- Pires, A.E., Detry, C., Chikhi, L., Rasteiro, R., Amorim, I.R., Simões, F., Matos, J., Petrucci-Fonseca, F., Ollivier, M., Hänni, C., Cardoso, J.L., Arias, P., Diniz, M., Araújo, A.C., Bicho, N., Sousa, A.C., Moreno-García, M., Arruda, A.M., Fernández-Rodríguez, C., et al., 2019. The curious case of the Mesolithic Iberian dogs: an archaeogenetic study. *J. Archaeol. Sci.* 105, 116–129. <https://doi.org/10.1016/j.jas.2019.03.002>.
- Pires, A.E., Detry, C., Fernández-Rodríguez, C., Valenzuela-Lamas, S., Arruda, A.M., De Grossi Mazzorin, J., Ollivier, M., Hänni, C., Simões, F., Ginja, C., 2017. Roman dogs from the Iberian Peninsula and the Maghreb – a glimpse into their morphology and genetics. *Quat. Int.: J. Int. Quat. Res.* 471, 132–146. <https://doi.org/10.1016/j.quaint.2017.11.044>.
- Pires, A.E., Ouragh, L., Kalboussi, M., Matos, J., Petrucci-Fonseca, F., Bruford, M.W., 2006. Mitochondrial DNA sequence variation in Portuguese native dog breeds: diversity and phylogenetic affinities. *J. Heredity* 97 (4), 318–330. <https://doi.org/10.1093/jhered/esl006>.
- Pires, F., Cardoso, J.L., Petrucci-Fonseca, F., 2001. Estudo arqueozoológico dos carnívoros do povoado pré-histórico de Leceia (Oeiras). *Estudos Arqueológicos de Oeiras* 10, 183–247. <https://repositorioaberto.uab.pt/handle/10400.2/6061>.
- Porffiro, E., Serra, M., 2014. In death as in life. Ties between man and animals in the Recent Prehistory of lower Alentejo: two case studies from Alto de Brinches 3 and Torre Velha 3 (Serpa). In: Detry, C., Dias, R. (Eds.), *Proceedings of the First Zooarchaeology Conference in Portugal. Held at the Faculty of Letters, University of Lisbon, 8th–9th March 2012. British Archaeological Reports International Series. Archaeopress, Oxford*, pp. 47–56.
- Rambaut, A., 2018. FigTree 1.4.4 software, Institute of Evolutionary Biology. *Molecular Evolution, Phylogenetics and Epidemiology*. <http://tree.bio.ed.ac.uk/software/figtree/>.
- Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using tracer 1.7. *Syst. Biol.* 67 (5), 901–904. <https://doi.org/10.1093/sysbio/syy032>.
- Ruiz García-Vaso, C., Vázquez Autón, J.M., Lomba Maurandi, J., Aviles Fernández, A., Haber Unarte, M., Drenes Hernández, M., Gil Cano, F., 2014. El yacimiento calcolítico “Camino del Molino” (Caravaca de la Cruz, Murcia): una oportunidad excepcional para estudiar los cánidos que poblaron el sureste español hace 4000 años. Primeros resultados. *Orígenes Y Raíces. Revista de la Sociedad de Estudios Históricos Y Etnográficos de las Tierras Altas del Argos, Quipar Y Alhárabe* 6, 5–7. <https://historiadelaVeterinaria.es/wp-content/uploads/2018/09/art%3%adculo-revista-or%3%adgenes-y-ra%3%adces-2014.pdf>.
- 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. XIX Congreso nacional de Historia de la Veterinaria y X Congreso Iberoamericano (Madrid, 18-20 de octubre de 2013), pp. 1–4. <http://www.historiaveterinaria.org/update/texto-completocomunicacion-errores-calcolítico-francisco-gil-cano-1457373672.pdf>.
- Sanchis Serra, A., Sarrrión Montañana, I., 2004. Restos de cánidos (*Canis familiaris* spp.) en yacimientos valencianos de la Edad del Bronce. *Archivo de Prehistoria Levantina* 25, 161–198. http://mupreva.org/web_mupreva_dedalo/publicaciones/760/va.
- Schuhmacher, T.X., Cardoso, J.L., Banerjee, A., 2009. Sourcing African ivory in Chalcolithic Portugal. *Antiquity* 83 (322), 983–997. <https://doi.org/10.1017/s0003598x00099294>.
- Silva, P., Galaverni, M., Ortega-Del Vecchyo, D., Fan, Z., Caniglia, R., Fabbri, E., Randi, E., Wayne, R., Godinho, R., 2020. Genomic evidence for the Old divergence of Southern European wolf populations. *Proc. Biol. Sci./R. Soc.* 287 (1931) <https://doi.org/10.1098/rspb.2020.1206>.
- Simpson, G.G., Roe, A., Lewontin, R.C., 1960. *Quantitative zoology*. Harcourt Brace.
- Street, M., Napierala, H., Janssens, L., 2015. The late Palaeolithic dog from Bonn-Oberkassel in context. In: Giemisch, L., Schmitz, R.W. (Eds.), *The Late Glacial Burial from Oberkassel Revisited*. Verlag Phillip von Zabern, Darmstadt, pp. 253–274. https://www.researchgate.net/profile/Luc_Janssens3/publication/302987232_Street_M_Giemisch_L_Janssens_L_Napierala_H_Schmitz_R_W_New_analyses_of_the_Late_Palaeolithic_dog_from_Bonn-Oberkassel_German_Rhineland_Paper_presented_at_the_Hugo_Obermaier_Annual_Meeting_Brunswick_Low/links/5bf29659299bf1124fd57c3/Street-M-Giemisch-L-Janssens-L-Napierala-H-Schmitz-z-R-W-New-analyses-of-the-Late-Palaeolithic-dog-from-Bonn-Oberkassel-German-Rhineland-Paper-presented-at-the-Hugo-Obermaier-Annual-Meeting-Br.pdf.
- Suchard, M.A., Lemey, P., Baele, G., Ayres, D.L., Drummond, A.J., Rambaut, A., 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evol.* 4 (1), vey016. <https://doi.org/10.1093/ve/vey016>.
- Tavaré, S., 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. In: *Lectures on Mathematics in the Life Sciences*, p. 17.
- Thalman, O., Shapiro, B., Cui, P., Schuenemann, V.J., Sawyer, S.K., Greenfield, D.L., Gernon, M.B., Sablin, M.V., Lopez-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D.M., Acosta, A.A., Giemisch, L., Schmitz, R.W., Worthington, B., Buikstra, J.E., Druzhkova, A., et al., 2013. Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science* 342 (6160), 871–874. <https://doi.org/10.1126/science.1243650>.
- The American Kennel Club, 2006. *The Complete dog book*. Ballantine Books.
- Valdiosera, C., Günther, T., Vera-Rodríguez, J.C., Ureña, I., Iriarte, E., Rodríguez-Varela, R., Simões, L.G., Martínez-Sánchez, R.M., Svensson, E.M., Malmström, H., Rodríguez, L., Bermúdez de Castro, J.-M., Carbonell, E., Alday, A., Hernández Vera, J.A., Götherström, A., Carretero, J.-M., Arsuaga, J.L., Smith, C.I., Jakobsson, M., 2018. Four millennia of Iberian biomolecular prehistory illustrate the impact of prehistoric migrations at the far end of Eurasia. *PNAS* 115 (13), 3428–3433. <https://doi.org/10.1073/pnas.1717762115>.
- Valera, A.C., 2008. O recinto calcolítico dos Perdigoês: fossos e fossas do Sector I. *Apontamentos de Arqueologia e Património* 3, 19–27. http://www.nia-era.org/publicacoes/doc_download/3-apontamentos-3.
- Valera, A.C., 2018. Os Perdigoês Neolíticos. Gênes e desenvolvimento (de meados do 4º aos inícios do 3º milénio ac). Valera, A.C., (ed.); vol. 1. NIA/Era Arqueologia, http://www.nia-era.org/publicacoes/doc_download/124-perdigoes-monografica-1-o-s-perdigoes-neoliticos.
- Valera, A.C., 2020a. Interação e recursos exóticos na Pré-História Recente: a circulação e consumo de marfim em Portugal. Vilaça, R., Aguiar, R.S. (coordinators). In: (I) mobilidades na Pré-história. Pessoas, recursos, objetos, sítios e territórios. Imprensa da Universidade de Coimbra, pp. 135–181. <http://monographs.uc.pt/iuc/catalog/book/23>.
- Valera, A.C. (Ed.), 2020b. O sepulcro 4 dos Perdigoês. Um tholos da segunda metade do 3º milénio AC, vol. 2. Colección: Perdigoês monográfica.
- Valera, A.C., Basílio, A.C., Almeida, N., 2020. The fragment, the half, and the whole: approaching pottery and fauna depositions in Pit 50 of Perdigoês enclosure (first half of the 3rd millennium BC). *Estudos do Quaternário/Quaternary Studies* 20, 11–33. <https://doi.org/10.30893/eq.v0i20.189>. Colección: Perdigoês monográfica.
- Valera, A.C., Bottaini, C., Basílio, A.C., 2020. A deposição de uma alabarda em contexto campaniforme na área central do recinto dos Perdigoês (Reguengos de Monsaraz). *Apontamentos de Arqueologia e Património* 14, 41–48. <https://dspace.uevora.pt/rdpc/handle/10174/28256>.
- Valera, A.C., Nunes, T., Costa, C., 2010. Enterramentos de canídeos no Neolítico: a fossa 5 de Corça 1 (Brinches, Serpa). *Apontamentos de Arqueologia e Património* 5, 7–17. http://www.nia-era.org/publicacoes/doc_download/5-apontamentos-5.
- van Asch, B., Pereira, L., Pereira, F., Santa-Rita, P., Lima, M., Amorim, A., 2005. mtDNA diversity among four Portuguese autochthonous dog breeds: a fine-scale characterisation. *BMC Genet.* 6, 37. <https://doi.org/10.1186/1471-2156-6-37>.
- Vigne, J.-D., 2005. L'humérus de chien magdalénien de Erralla (Gipuzkoa, Espagne) et la domestication tardiglaciaire du loup en Europe: The Magdalénian dog humerus of Erralla (Gipuzkoa, Spain) and the Late Glacial wolf domestication in Europe. *Munibe* 57, 279–287. http://www.colle-online.com/rub_histoire/chien_magdalénien_de_erralla.pdf.
- von den Driesch, A., 1976. *A Guide to the Measurement of Animal Bones from Archaeological Sites: As Developed by the Institut Für Palaeoanatomie*.

- Domestikationsforschung und Geschichte Der Tiermedizin of the University of Munich. Harvard University Press.
- von den Driesch, A., Boessneck, J., 1976. Die Fauna von Castro do Zambujal (Fundmaterial der Grabungen von 1966 bis 1973 mit Ausnahme der Zwingerfunde). In: von den Driesch, A., Boessneck, J. (Eds.), Studien über frühe Tierknochenfunde von der Iberischen Halbinsel. Institut für Palaeoanatomie, Domestikationsforschung und Geschichte der Tiermedizin der Universität München. Deutsches Archäologisches Institut Abteilung Madrid, pp. 4–129.
- Yang, D.Y., Eng, B., Wayne, J.S., Dudar, J.C., Saunders, S.R., 1998. Technical note: Improved DNA extraction from ancient bones using silica-based spin columns. *Am. J. Phys. Anthropol.* 105 (4), 539–543. [https://doi.org/10.1002/\(SICI\)1096-8644\(199804\)105:4<539::AID-AJPA10>3.0.CO;2-1](https://doi.org/10.1002/(SICI)1096-8644(199804)105:4<539::AID-AJPA10>3.0.CO;2-1).
- Yang, Z., 1996. Among-site rate variation and its impact on phylogenetic analyses. *Trends Ecol. Evol.* 11 (9), 367–372. [https://doi.org/10.1016/0169-5347\(96\)10041-0](https://doi.org/10.1016/0169-5347(96)10041-0).
- Žalaitė, I., Maurer, A.F., Grimes, V., Silva, A.M., Ribeiro, S., Santos, J.F., Barrocas Dias, C., Valera, A.C., 2018. Diet and mobility of fauna from Late Neolithic-Chalcolithic site of Perdigões, Portugal. *J. Archaeolog. Sci.: Rep.* 19, 674–685. <https://doi.org/10.1016/j.jasrep.2018.03.033>.