



# The use of tooth marks for new research into identifying and understanding the first domestic dogs in Palaeolithic populations

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## ARTICLE INFO

### Keywords:

Dog-wolves  
Domestication  
Gravettian  
Tooth marks  
Geometric morphometrics  
Computational learning

## ABSTRACT

The domestication of wolves is a topic of great interest. To date, the most accepted hypotheses associate this phenomenon to the end of the Upper Palaeolithic, while many propose an earlier date closer towards the Aurignacian. The latter proposal hinges on extensive research using palaeontological, morphometric, biomolecular-isotopic, genetic data and microwear contributing valuable information to the current debates. Nevertheless, few confront the theoretical reasoning behind this process, analysing the sociocultural implications that link humans with canids. Under this premise the current overview considers the motivation behind this process while proposing new lines of investigation that may help confront these questions across the indirect methods using new technologies applied study of tooth marks of the sites.

## 1. Introduction

The domestication of wolves is a phenomenon that has always generated great expectations and interest in both the general public and researchers (Benecke, 1987; Dark, 2003; Vigne, 2006; Germonpré et al., 2009; Shipman, 2015; Janssens et al., 2018).

Mainly the debate on the domestication of wolves has focused attention on the when and where. The most accepted hypotheses generally situate this event in the Magdalenian, approximately from 16 to 12 Ka BP (Larson et al., 2012; Morey, 2014; Boudadi-Maligne and Escarguel, 2014; Ledoux and Boudadi-Maligne, 2015; Skoglund et al., 2015; Shipman, 2015), although some researches have suggested the presence of dogs in the Aurignacian or the Gravettian (Germonpré et al., 2009; Germonpré et al., 2012; Germonpré et al., 2015a; Germonpré et al., 2015b; Germonpré et al., 2017a; Germonpré et al., 2017b; Germonpré et al., 2018; Ovodov et al., 2011).

Abundant documentation exists for domestic dogs in the euroasiatic archaeological register towards the end of the Upper Palaeolithic (Table 1), while important Magdalenian sites is known in Northern Iberia such Erralla (Vigne, 2006); France, Switzerland and Germany

(Pionnier-Capitan et al., 2011), burials in Bonn-Oberkassel, Germany (Street, 2013; Morey, 2014; Janssens et al., 2018); the Middle East (Tchernov and Valla, 1997) and the Zhokov Island of Siberia (Pitulko and Kasparov, 2017). Likewise, numerous Mesolithic sites also present data of interest for non-Palaeolithic contexts (Morey and Waint, 1992; Larson et al., 2012). Under this premise, most research tends to agree on the dog as being the first species to have been domesticated by humans in chronologies earlier than the Neolithic.

In recent years, the latest advances in archaeometry have facilitated the creation of new hypotheses about the domestication of canids. From this perspective, new morphometric analyses of Upper Pleistocene canid skulls from Goyet Cave (Belgium), Razboinichya (Russia) and Předmostí (Czech Republic) have revealed morphological variations in the snout indicative of early dog species (Sablin and Khlopachev, 2002; Germonpré et al., 2009; Ovodov et al., 2011). This evidence fits with the criteria that some authors have used to differentiate between wolves and dogs. From this perspective, dogs have been shown to be smaller in size, and less robust with respect to the wolf. Additionally, dogs present a shorter and wider muzzle, a reduction in tooth size, teeth are closer together, orbital angles are different, while dogs also present a broader,

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<https://doi.org/10.1016/j.jasrep.2021.103252>

Received 22 July 2021; Received in revised form 17 October 2021; Accepted 1 November 2021

Available online 12 November 2021

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**Table 1**

Main Upper Pleistocene sites with canid fossils identified as dogs. Valibrated dates are prefixed with cal. More detail for the selected sites see source (Prassack et al., 2020; Pionnier-Capitan et al., 2011; Germonpré et al., 2009).

Locality	Country	Age (BP)	References
Goyet Cave	Belgium	cal. 35,700	Germonpré et al. (2009)
Rzboynichya	Siberia	cal. 33,000	Ovodov et al. (2011); Druzhkova et al. (2013)
Hohle Fels	Germany	29,800–35,700	Conard and Bolus (2008)
Předmostí	Czech Republic	cal. 28,500	Germonpré et al. (2017a)
Trou des Nutsos	Belgium	cal. 21,810	Dupont (1873)
Mezin	Ukraine	cal. 20,000–8000	Benecke (1987); Pidoplichko (1998); Janssens et al. (2018)
Erralla	Spain	cal. 19,000	Vigne (2006)
Ulakhan Sular	Siberia, Russia	cal. 16,900	Germonpré et al. (2017b)
Eliseevich I	Russia	cal. 16,945–16,190	Sablin and Khlopachev (2002)
Knierpette	Germany	cal. 16,700–13,800	Musil (1974), Musil (2000)
Hauterive-Champréveyres	Switzerland	cal. 15,000–14,000	Morel and Müller (1997)
Montespan	France	cal. 15,500–13,500	Pionnier-Capitan et al. (2011)
Le Closeau	France	cal. 15138–13,813	Pionnier-Capitan et al. (2011)
Tell Mureybet	Syria	cal. 15,500–11,000	Helmer (1991)
Abri du Morin	France	cal. 14,700	Boudadi-Maligne et al. (2012)
Bonn-Oberkassel	Germany	cal. 14,708–13,874	Nobis (1979), Street et al. (2015), Janssens et al. (2018)
Mezhrich	Ukraine	14,500	Germonpré et al. (2009)
Kesslerloch Cave	Switzerland	cal. 14,100	Napierala and Uerpmann (2012)
Pont d'Ambon	France	cal. 12,952–12,451	Célérier et al. (1999); Pionnier-Capitan et al. (2011)
Ushki-1	Russia	cal. 12,355–11,955	(Goebel et al. (2003)
S. Thibaud de Couz	France	cal. 12,027–11,311	Chaix (2000)
Ein Mallaha	Palestine	12,000	Davis and Valla (1978)
Senckenburg	Germany	12,000–9,000	Degerbøl (1961)
Saint Thibault	France	cal. 11,600	Chaix (2000)
Danger Cave	Utah, USA	11,000	Grayson et al. (1988)
Koster Site	Illinois, USA	cal. 9900	Perri et al. (2019)
Stilwell II Site	Illinois, USA	cal. 9900	Perri et al. (2019)
Zhokov Island	Siberia, Russia	cal. 9000	Pitulko and Kasparov (2017)

smaller, and more compressed, tympanic bullae (Schmitt and Wallace, 2014; Janssens et al., 2016).

Moreover, recent methodological approaches including biomolecular (Savolainen et al., 2002; Vila et al., 1997), genetic (Valadez, 2000; Germonpré et al., 2009; Germonpré et al., 2015a; Germonpré et al., 2017a; Germonpré et al., 2017b; Thalmann et al., 2013), dental microwear (Prassack et al., 2020) and isotopic studies (Germonpré et al., 2009; Germonpré et al., 2015b), have also been able to provide new perspectives for the study of dog domestication in fossils as old as 36 to 26 Ka BP.

Nevertheless, despite the most recent data, a strong school of thought still exists defending a much later domestication of canids towards post-glacial chronologies (Pionnier-Capitan et al., 2011; Crockford and Kuzmin, 2012; Pitulko and Kasparov, 2017). From this perspective, some authors question the reliability of interpretations presented by Germonpré et al. (2009), Germonpré et al. (2015a), Germonpré et al. (2015b), Germonpré et al. (2017a), Germonpré et al. (2017b) and Ovodov et al. (2011). Drake et al. (2015), for example, use

morphometric analyses to argue the skeletal remains from Goyet and Eliseevichi to be wolves, rather than dogs. Similarly, Perri (2016) argue against the reliability of morphological analyses, claiming the natural variability of wolf anatomy to be too wide to capture with these types of analyses. From this more sceptical perspective, Wilczyński et al. (2020) suggest early evidence of pavlovian dogs to be in fact wolves, while the abundant remains of canids in these sites is likely to be product of anthropogenic factors produced by specialised hunter-gatherer groups in the Palaeolithic. More generically, Welken et al. (2021) shows how from a biometric perspective the remains of canids, including wolves, are not diagnostic to differentiate the different types of canids and Loog et al. (2019) shows morphological differences between late Pleistocene and early Holocene wolf populations.

Consequently, a lack of consensus exists regarding the chronology of canid domestication. Product of these chronological debates, a similar question argued by specialists is the location where dog domestication began. From this perspective, many authors argue Europe to be an important focal point (Germonpré et al., 2009; Thalmann et al., 2013), while others turn towards an Asian origin (Olsen, 1985; Valadez 2000, Valadez 2002; Savolainen et al., 2002; Pang et al., 2009; Brown et al., 2011; Ding et al., 2012; Skoglund et al., 2015). Others do not exclude the possibility of both being independent and simultaneous (Botigué et al., 2017). Finally, Bergström et al. (2020) suggests that at least five major ancestry lineages had diversified of the end of Upper Pleistocene, demonstrating a deep genetic and long history of dogs during the Paleolithic.

Needless to say, many important questions remain unstudied. The first, and somewhat hardest to explain, lies in how this process occurred. The initial phases of wolf domestication are unlikely to have produced any significant genetic or morphological changes to the wolf, with a primary phase consisting of domesticated wolves that eventually evolved into what we now know as the dog. Under this premise, the very first domestic canids are likely to be very similar to the wolf.

Given the limitations of identifying the first stages of domestication from the first dogs, as well as the lack of consensus regarding either research from morphological or genetic changes, while several authors have also proposed new methods for the study the origin of dog domestication. Prassack et al. (2020) suggest the dental microwear is a behavioural marker that could appear before any morphological or genetic changes occur. From this perspective, microwear could be used to identify the transition from wolves to domesticated dogs in the archaeological record.

Also Bocherens et al. (2015) suggest a new vision. Theoretically, the process of domesticating a carnivore such as a wolf would begin with an “imprint” stage, whereby a wolf pup, while still blind, is captured and raised by a human. From such an early stage, the pup is able to create a bond with the human throughout its entire life, producing said “imprint”. Once this stage has begun, and while the process is maintained for future pup generations, the process of domestication begins. Needless to say, from a practical perspective this is hard to prove, requiring research to not only understand the palaeodiets of canids appearing in archaeological sites, but also providing an isotopic comparison with canids from surrounding palaeontological sites as well. Following this approach, Bocherens et al. (2015) were able to observe differences in the diet of humans and wolves compared to dogs and other carnivores. This would be the most empirical means of comparing both wild and supposedly neighbouring domesticated canids to establish an anthropogenic link.

While these techniques may appear to present promising results, debating authors have found that genetic, palaeontological and morphological evidence in the fossil record are not conclusive. From a different perspective, techniques presented by Bocherens et al. (2015) and Prassack et al. (2020) may be able to facilitate a consensus. Nevertheless, each of these techniques require the actual presence of canid remains in a site in order to carry out these types of analyses. This is evidently an issue when considering how canid remains are scarce,

and in some cases inexistent or heavily altered and fractured impeding any type of direct analysis.

As a means of confronting these limitations, and providing a new perspective for the present debate, the present study reflects on recent methodological advances that may prove valuable for identifying the presence of domesticated canids in archaeological sites. Through the combination of geometric morphometrics and computational learning algorithms, the present study defines a means of separating between taphonomic traces produced by wolves and those produced by different types of domestic dog. These methods can be considered an indirect means of identifying the presence of domesticated animals, without the need for physically identifying canid remains at the site. From this perspective, these methods are dependent on the remains of these carnivores food, rather on the carnivores themselves.

It is common knowledge that canids are important agents to intervene in archaeological assemblages, as seen through the multiple number of sites presenting tooth marked and extensively gnawed bones attributable to canid activity. Moreover, these types of alteration have been observed in sites of all chronologies (Lyon, 1970; Binford, 1978; Walters, 1984; Payne and Munson, 1985; Spenneman, 1990; Hudson, 1993; Ioannidou, 2003; Smith, 2006; Estaca-Gómez and Linares-Matás, 2019). Tooth marks are some of the most frequent evidences of carnivore activity to appear in the archaeological and palaeontological record. Furthermore, they can be characterised into multiple different types, including tooth scores, pits and punctures (Binford, 1981; Blumenshine, 1995). Recent efforts have shown how the use of advanced statistical and computational tools may be able to differentiate between different carnivores via the morphology of their tooth marks (Aramendi et al., 2017; Courtenay et al., 2019; Courtenay et al., 2020a; Courtenay et al., 2020b; Courtenay et al., 2021a; Courtenay et al., 2021b; Yravedra et al., 2019).

Based on the aforementioned corpus of research in this field, the present study develops the state of the art that can help differentiate the tooth marks produced by wolves and dogs; utilising machine learning algorithms and geometric morphometrics for the identification of wolf and domestic dog bite damage. From this perspective, this study presents a new and different perspective that may help in the identification of dog domestication process.

In addition, this study faces a question that is not very well developed in the current bibliography, namely considering the circumstances that motivated the domestication of the dog, as complement to the when and where.

## 2. Materials & methods

### 2.1. Sample

A total of 160 carnivore tooth pits were included and compared in this study. 80 of these marks come from different wolves' population from Spain (Courtenay et al., 2020b; Courtenay et al., 2021a; Courtenay et al., 2021b – *under review*), and 80 tooth pits were produced by six different dog breeds: 10 by Irish Setter, 10 by boxer, 15 by Rottweiler, 15 by labrador retriever, 15 by mastiff and 15 by a breedless dog. All these tooth pits marks were collected on the shafts of appendicular long bones (femurs, tibiae, humeri and radii). All bones used in these experiments were covered with meat prior to any carnivore activity. Additionally, all bones after carnivore intervention showed good preservation conditions.

For the case of Wolf samples, the present study included tooth marks produced by a mixture of captive and wild wolves (Courtenay et al., 2020a; Courtenay et al., 2020b; Courtenay et al., 2021a; Courtenay et al., 2021b). Wolf samples were obtained from both captive and wild wolves. Tooth mark samples originated from wild wolf packs residing in the province of Zamora (Villardeciervos and Flechas samples), north-western Spain, sharing borders with Portugal and located north of the River Duero (Castilla y León). This sample has been previously included

in Courtenay et al. (2021a) and Courtenay et al. (2021b). The Tooth mark samples from captive wolves were obtained from two separate parks, including Cabárceno (Obregón, Cantabria) and Hosquillo (Cuenca, Castilla la Mancha). The characteristics of the Cabárceno samples have been previously included in Yravedra et al. (2014), Yravedra et al. (2019), Aramendi et al. (2017), Courtenay et al. (2019), Courtenay et al. (2020a), Courtenay et al. (2020b) and Courtenay et al. (2021a) and Courtenay et al. (2021b), while the Hosquillo samples have been included in Moclán et al. (2019), Courtenay et al. (2020a), Courtenay et al. (2020b) and Courtenay et al. (2021a) and Courtenay et al. (2021b). Both samples were produced by groups of adult individuals, 7 individuals for Cabárceno and 5 for Hosquillo. The Cabárceno sample contains exclusively horse and cow appendicular bones while the Hosquillo samples also included appendicular bones of deer, Iberian ibex, roe deer and wild boar.

The Dog samples presented within the present study include tooth pits produced by an Irish Setter, Rottweiler, Boxer, Labrador Retriever and Mastiff. An additional mixed-breed dog was also included within the present study. The long bones modified by the setter, mastiff, Labrador retriever and boxer included cow bones, while the bones modified by the Rottweiler and the mixed-breed included long bones of pigs and goats. The variability produced by the size of the animal from which bone samples came from were considered not to be a conditioning factor in tooth mark morphology, as specified and observed by Courtenay et al. (2020b), Courtenay et al. (2021a) and Courtenay et al. (2021b).

### 2.2. Methods

#### 2.2.1. Digital reconstructions

Digital reconstructions of pit marks were performed using Structured Light Surface Scanning (SLSS). The software used was the DAVID SLS-2 Structured Light Surface Scanner located in the C.A.I. centre of Archaeometry and Archaeological Analysis, Complutense University of Madrid. The equipment used includes a DAVID USB CMOS Monochrome 2-Megapixel camera, an ACER K11 LED projector, a 15 mm calibration marker board and a USB Flash Drive where the software is located. Both mechanism, camera and projector, were connected to a portable ASUS X550VX personal laptop (8 GB RAM, Intel® Core™ i5 6300HQ CPU (2.3 GHz), NVIDIA GTX 950 GPU) via USB and HDMI. Once calibrated, the scanning process provides a 3D model with a density of up to 1.2 million points of one simple piece, which can be exported in different formats (.obj, .ply, etc).

The landmark configuration for this study consists of a total of 30 landmarks; 5 fixed Type-II landmarks and 25 computational landmarks projected across the entirety of each tooth pit. Landmark collection was performed using the free Landmark Editor software (v.3.0.0.6.) by a single experienced analyst. Detailed explanations as well as an instructional video on how to place both landmarks and semi landmarks can be consulted in the Supplementary Appendix and main text of Courtenay et al. (2020a).

#### 2.2.2. Data analysis

Geometric morphometric landmark configurations were first standardized using a series of orientation, translation and scaling procedures. This transformation of landmark data is frequently referred to as Generalized Procrustes Analysis (GPA) (Rohlf, 1999; Slice, 2001). GPA is an effective means of extracting morphological data in a quantitative manner, allowing for the characterization of shape and form patterns across different configurations (Dryden and Mardia, 1998; Bookstein, 1991). Prior to any further hypothesis testing, allometric analyses were first considered to assess the impact tooth pit size may have on morphological variance. For this purpose, centroid sizes across each individual were calculated, while the logarithm of these sizes were used to calculate regressions on shape variables (Adams et al., 2013). If shape-size relationships proved of importance, final superimpositions were performed excluding the scaling step of the GPA procedure

(otherwise known as *form*).

Once landmark coordinates had been normalized, coordinate data was subject to dimensionality reduction in the form of Principal Component Analysis (PCA). PCA is a common visualization technique to assess patterns in morphological trends. Each of these graphs were coupled with the computation of Thin Plate Splines (Bookstein, 1989; Bookstein, 1991), so as to visualize and assess these variations across each PC score. The PC scores representing the highest morphological variability (<95%) were then extracted for further processing.

To assess the degree of statistical differences between samples, a Multivariate Analysis of Variance (MANOVA) was performed. The type of MANOVA calculation was conditioned by the underlying normality of PC information; if PC scores were found to be distributed normally, the “Hotelling-Lawley” formulae was used, while non-normally distributed PC scores used “Wilk’s Lambda” test statistic. PC score normality was assessed using the Shapiro-Wilk test.

Results of each statistical hypothesis test were additionally evaluated considering values of  $p < 0.003$  (i.e.  $p < 3\sigma$ ) to be a robust indicator of notable differences between samples (Benjamin and Berger, 2019; Colquhoun, 2019; Courtenay et al., 2021a; Courtenay et al., 2021b – under review). To support this,  $p$  values were also accompanied by a calculations of their False Positive Risk (FPR) (Colquhoun, 2019). FPR values are used to assess the probability that an observed  $p$ -value is a false positive, otherwise known as a Type I statistical error (Colquhoun, 2019). For FPR calculations a prior probability of 0.5 was adopted, assuming complete randomness (Colquhoun, 2019).

Finally, for the purpose of assessing the degree of sample differentiation, a supervised Support Vector Machine (SVM) was trained for classification purposes. SVMs map out input data into a high-dimensional feature space, as defined by a *kernel* function (Cortes and Vapnik, 1995). The present study employed the use of a radial kernel. Once projected into the transformed feature space, a hyperplane is constructed with maximized margins so as to separate between groups. For the purpose of the present study, SVMs were trained on PC scores using a  $k$ -fold cross validation ( $k = 10$ ) algorithm and a 70:30% train: test split ratio. A loop function was used to perform random searches for optimal *cost* and *gamma* hyperparameters over the course of 50 iterations (Yravedra et al., 2019). SVM evaluation was performed using traditional machine learning evaluation techniques. These include the calculation of accuracy, as well as the true positive as well as the true negative rates known as sensitivity and specificity. SVM evaluation also included the calculation of a Kappa ( $\kappa$ ) statistic, as well as an Area Under the receiver operator characteristic Curve (AUC).  $\kappa$  values of above 0.8 usually indicate above perfect model performance, while AUC can frequently be interpreted in a similar fashion. Finally, the Mean Squared Error (MSE) was calculated across the testset to evaluate the overall confidence of the algorithms. All statistics and classification tasks were performed in the R programming language (v.4.0).

### 3. Results

Both wolf and dog samples are described by notable allometric patterns ( $R^2 = 0.038$ ,  $F = 6.2$ ,  $p = 0.001$ ,  $FPR = 1.8\%$ ). Allometric residuals are additionally well distributed (Shapiro  $w = 0.99$ ,  $p = 0.25$ ,  $FPR = 48.5\%$ ), supporting the goodness-of-fit of the regression line, and thus the implications of these results.

Considering this, Geometric Morphometric analyses in form space produced a principal component analysis with a total of 90 highly inhomogeneous PC scores (Shapiro  $w = 0.89$ ,  $p = 2.4e-09$ ,  $FPR = 1.3e-05\%$ ). The first 5 of these PC scores representing up to 97% of total sample variability. PC1 (86.72% variance) is considerably described by changes in the oval nature of tooth pit morphologies, while the point of maximal depth also seems to shift (Fig. 1). PC2 (3.79% variance), on the other hand, shows a similar shift, with dog tooth pits appearing more rounded with the point of maximal depth closer towards the centre of the pit. MANOVA testing additionally highlight these changes in

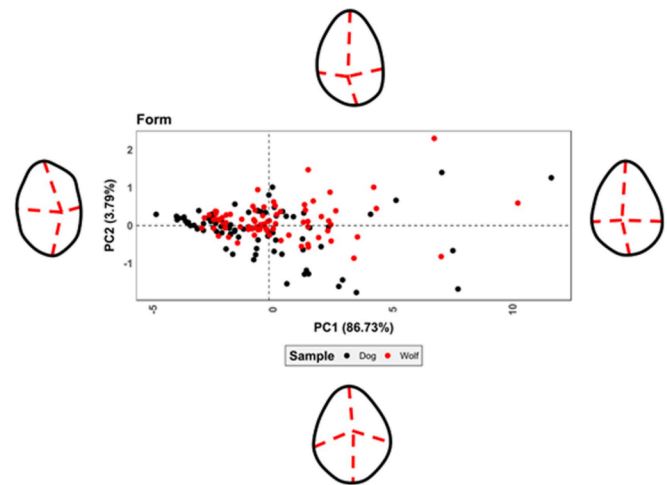


Fig. 1. Scatter plot presenting the principal component analyses in form space of the dog and wolf tooth pits. Variances in morphology are represented on either extremity of their corresponding PC score axis.

morphology to be of notable interest ( $p = 0.002$ ,  $FPR = 3.3\%$ ).

SVM results confirm observations by Yravedra et al. (2019) highlighting a clear separability between the two carnivore species based on tooth mark morphology. SVM accuracy was calculated at  $97.1 \pm 0.025\%$ , with high sensitivity (0.94) and specificity (1.00) values, indicating a very small number ( $n = 4$ ) of dog tooth marks to be mistaken with wolf tooth marks. Kappa values ( $\kappa = 0.94$ ) indicate an almost perfect agreement between the predicted labels and the true labels, while AUC (0.97) values are also far above the golden standard. Finally, the MSE was calculated at 4.2%, indicating SVMs to have an approximate 95.7% confidence when making each prediction.

### 4. Discussion

Multiple questions have been raised about the early domestication of wolves. The bibliography has highlighted the interest in knowing when domestication occurred and where it occurred. For this, multiple techniques have been developed that have tried to answer these questions. So far, the palaeontological, morphological, and genetic evidences, are the main source of information regarding these advances (Bergström et al., 2020; Boudadi-Maligne and Escarguel, 2014; Botigué et al., 2017; Crockford and Kuzmin, 2012; Germonpré et al., 2009; Germonpré et al., 2012; Drake et al., 2015; Ovodov et al., 2011; Pang et al., 2009; Thalmann et al., 2013). Nevertheless, the results shown are not conclusive and several authors reveal an independent and simultaneous origin in different regions (Botigué et al., 2017), with a variety of morphological data regarding palaeolithic dogs (Pionnier-Capitan et al., 2011), and five different possible lineages (Bergström et al., 2020).

For this reason, other authors have promoted alternative methods with the aim of contributing to the knowledge about the domestication of the dog (Germonpré et al., 2009; Bocherens et al., 2015; Prassack et al., 2020). Following in the wake of these new applications, we have proposed a new way of identifying dog domestication through the taphonomic analysis of tooth marks.

#### 4.1. New methodological used in the identification of early domestication of wolves.

From a methodological perspective, the present study has shown how tooth marks of dogs and wolves can be distinguished. Secondly, similar to previous efforts (Yravedra et al., 2019), the present study confirms that each of these breeds of dogs are separable from wolves, reaching >95% accuracy with above exceptional  $\kappa$  values (0.94).

While future analyses should take into consideration more breeds of



dog, as well as a wider array of different tooth mark types, the present study has shown how research of this type can present a promising new perspective for analysing prehistoric dog and wolf activity without requiring the physical presence of canid remains at the site.

In combination with methods proposed using palaeontological, morphological and biometric traits (Vigne 2006; Germonpré et al., 2009; Germonpré et al., 2012; Germonpré et al., 2017a; Germonpré et al., 2017b; Boudadi-Maligne and Escarguel, 2014; Drake et al., 2015; Ledoux and Boudadi-Maligne, 2015), alongside palaeogenetics (Savolainen et al., 2002; Pang et al., 2009; Brown et al., 2011; Crockford and Kuzmin, 2012; Ding et al., 2012; Larson et al., 2012; Thalmann et al., 2013; Skoglund et al., 2015; Botigué et al., 2017), isotopic data (Germonpré et al., 2009; Bocherens et al., 2015), and microwear analyses (Prassack et al., 2020), archaeologists are now presented with an ever-growing source of information that may aid in answering these questions.

The main difference between the present study and other methods, however, is the way in which this data is inferred. The presence of gnawed bones are much more frequent in archaeological sites than finding the physical remains of the actual animal responsible for the accumulation. This is evident when considering the wide array of sites presenting modified accumulations product of canid activity (Lyon, 1970; Binford, 1978; Walters, 1984; Spenneman, 1990; Hudson, 1993; Stiner, 1994; Yravedra et al., 2018; Estaca-Gómez and Linares-Matás, 2019). Needless to say, the resolution of information that can be obtained directly from canid fossil remains is still a fundamental piece of evidence, which supports the importance of more interdisciplinary approaches in this type of research. Nevertheless, bones with tooth marks are more frequent in archaeological sites, while all Holocene sites presenting evidence of dog activity are accompanied by tooth marks.

This is the reason which the technique that we propose here is a good tool for the analysis of taphonomic evidence frequently recovered from archaeological sites. The analysis of tooth marks could help to identify the action of dogs, especially in places where fossil remains of canids are not directly found.

Nevertheless, and although the technique has presented good results, there are some questions that could be raised. The first of them is related to the morphological variety that exists among canids. It is possible that the great diversity of dog breeds, as well as the different subspecies of wolves, this technique may not be able to correctly classify dog tooth marks in the fossil record. The second question is to know what results the technique gives when applied to bones with tooth marks.

Regarding the first question, the different studies developing classification techniques for the study of the carnivores that produce tooth marks have shown optimistic results (Yravedra et al., 2019; Courtenay et al., 2020a; Courtenay et al., 2020b; Courtenay et al., 2021a). At the same time, when different types of canids such as the wild dog *Lycaon pictus* and the wolf have been compared, these differences have also been significant. Therefore, and after observing our results when comparing several dog breeds, it can be seen how the present technique is robust in the differentiation of different canids. Nevertheless, future research should increase the reference framework by expanding the experimental sampling to a greater variety of dog types.

Regarding its application to the fossil record, this activity is being planned in future works that will show if the technique is really decisive. In any case, when we have applied similar methods to the fossil record, high classification rates have been obtained in the identification of the carnivore that has modified the bones of some sites (Aramendi et al., 2017; Aramendi et al., 2019; Arriaza et al., 2021). If with this methodological application we can contribute to the discussion of how to identify the action of the dog in the fossil record, we believe that another key question is to know what elements motivated the domestication of the wolf to the dog.

#### 4.2. What motivation the domestication of wolf?

Regards to the motivation behind the domestication of dogs, a number of different theoretical points can be raised. The majority of efforts into the analysis of wolf domestication focus primarily on the biological and palaeontological aspects of wolves/dogs, and the question of Where? And When?, without focusing as much attention on the cultural factors behind this process (Bergström et al., 2020; Boudadi-Maligne and Escarguel, 2014; Botigué et al., 2017; Crockford and Kuzmin, 2012; Germonpré et al., 2009; Germonpré et al., 2012; Germonpré et al., 2015a; Germonpré et al., 2015b; Ding et al., 2012; Drake et al., 2015; Ovodov et al., 2011; Pang et al., 2009; Savolainen et al., 2002).

This consequently makes establishing the first evidence of canid domestication much harder, making most efforts into genetic and morphological analyses difficult if not impossible. Likewise, it cannot be forgotten that there may not have been a singular domestication episode (Botigué et al., 2017; Bergström et al., 2020). Human populations may have domesticated these animals parallel to one another, on both a spatial and chronological scale (Botigué et al., 2017).

In light of this, we believe that before research can truly be developed from a biological perspective, the cultural components of these phenomena must also be explored. Shipman (2015), Ovodov et al. (2011) and our personal observation with the Askari at Olduvai Gorge propose a number of possible advantages for canid domestication. Among them, these authors propose the relevance of patrolling dogs in camps as a form of protection from other carnivores at night. Activities of this sort are notable in contemporary semi-nomad societies, such as Maasai camps near the Ngorongoro crater (personal observations), and Nunamiut camps as noted by Binford (1978). Likewise dogs are also able to contribute in transportation tasks, such as pulling sleighs (Binford, 1978; Shipman, 2015; Turner, 2015), or transporting small cargo and equipment, which have also been documented extensively ethnographically (Honigsmann and Wendell, 1949; Harako, 1976; Binford 1978; Binford 1981). Dog participation in hunting activities such as locating, tracking, killing, herding is also notable across the ethnographic record (Harako, 1976), and is a likely candidate for explaining their popularity in ancient hunter-gatherer societies (Lupo, 2017).

Alongside these factors, it may be noteworthy to detail why the wolf was the first carnivore to have been domesticated by humans. Some suggest the strong link between humans and canids to be based on the favourable social behaviour of wolves, proving easy to integrate these animals into the socio-cultural circle of human families. Valadez (2000) and Valadez (2002), for example, proposes an early domestication of wolves, arguing wolf populations to have grown accustomed to having human settlements close and scavenging from their waste. Upon forming specialised dependencies, over time these animals may have grown closer facilitating human domestication. Wheat and Temrin (2020), from a behavioural perspective, argue wolves and dogs to be closely linked from socially. These authors observe young wolves to be similarly capable of understanding human cues and almost equally interested in “play” like behaviours typically expressed by domestic puppies.

Nevertheless, despite the soundness of these hypotheses, issues still exist that should not be forgotten. Shipman (2015) and Ovodov et al. (2011) propose the domestication of wolves as hunting companions for taking down mammoths. Needless to say, proboscidean and megamammals are not the type of prey canids are generally known for hunting (Gittleman, 1985; Vézina, 1985). While wolves are seen as an outlier in the animal kingdom, presenting diverse prey selection with regards to prey size (Mech, 1970; Dale et al., 1995), these canids most frequently hunt small animals such as birds, small mammals, amphibians and reptiles, as well as medium sized mammals (ca. 150–200 kg). While documentation exists of wolves hunting bison and moose, these cases have been noted for weak individuals and many trapped in snow. Normally, prey selection for medium to small sized mammals consist of ibex, deer, roe deer and foal (Mattioli et al., 1995; Jędrzejewski et al., 2000). An animal the size of an elephant would therefore not be the

typical prey of a wolf. From this perspective, wolves would not seem the most obvious hunting companions for this type of prey. If anything, wolves may have been able to help with tracking tasks and more indirect activities.

Considering theories regarding wolves as sledge hounds, Pitulko et al. (2016) and Pitulko and Kasparov (2017) argue a lack of evidence before the Pleistocene-Holocene transition, with a single implement for possible sledge use found in Zhokhov. While early sledges are more likely to have been made from perishable materials that would not be present in the palaeolithic fossil record, Sinding et al. (2020) debate genetic adaptations for sledge use in dogs to only have occurred some 9.5 Ka years ago. This data thus indicates sledge use to be an element of more advanced domestication than earlier sites may suggest.

When considering the social behaviour of wolves as justification for their domestication, significant issues present themselves when considering other analogies within the animal kingdom. Hyenas, for example, are equally gregarious carnivores with complex social mannerisms that also frequently coexisted in proximity with human settlements for millions of years (Blumenshine, 1995; Stiner, 1994; Blasco, 1997; David, 2004). Similarly, other canids such as the African wild dog and dhole are also gregarious and were not domesticated. Under this premise, the domestication of wolves cannot be limited to a simple social factor among carnivore behavioural patterns. While this element may have facilitated the domestication process, the overall phenomenon should be considered much more complex with more evidence needed to support these claims (Bergström et al., 2020).

Considering each of these hypotheses, in continuation we propose a different thesis behind the motivation for wolf domestication. While these theories remain purely theoretical, future investigation may benefit from a new perspective that may be able to facilitate our interpretation of the fossil record and human evolution.

Regardless of whether wolf domestication occurred in one place or time than another, most data suggests the beginning of this phenomena to have occurred in a moment of low temperatures towards the end of the glacial periods across Eurasia (Pionnier-Capitan et al., 2011; Larson et al., 2012; Morey, 2014; Boudadi-Maligne and Escarguel, 2014; Ledoux and Boudadi-Maligne, 2015; Skoglund et al., 2015). Depending on the hypotheses, some authors would suggest this to have occurred either with or later than the Gravettian in Europe (Germonpré et al., 2009; Germonpré et al., 2012; Germonpré et al., 2015a; Germonpré et al., 2015b; Germonpré et al., 2017a; Germonpré et al., 2017b; Germonpré et al., 2018; Ovodov et al., 2011; Prassack et al., 2020).

Notwithstanding, both the Gravettian and Epigravettian cultures extend across Eurasia, including areas of Siberia where the famous *mammoth bone homes* are located. These large accumulations of mammoth bones, positioned to build structures and shelter, provided adequate refuge for human populations throughout the hostile palaeoclimatic conditions of North-East Asia (Van Huissteden et al., 2003). This, alongside the use of fire and animal hides, allowed *Homo sapiens* to travel across most of Eurasia effectively without being hindered by glacial winds and the cold (Kolstrup and Wijmstra, 1977; Soffer, 1993). *Homo sapiens* territories thus saw a drastic expansion that, for more than 10 Ka years, allowed settlements to reside in areas such as Beringia before the Maximum Glacial (Irving and Harington, 1973; Kitchen et al., 2008; Pitulko et al., 2004; Pitulko et al., 2016; Bourgeon et al., 2017), as opposed to the theories of Hoffecker et al. (1993) who believed these occupations to have occurred much later (post 12–11 Ka).

While the use of shelter helps answer multiple questions about where and how human populations lived in North-East Asia, little is known about how these groups obtained their food and supplies. Perhaps the domestication of the wolf to dog could have contributed to the subsistence of human groups looking for carcasses of prey buried in the snow.

These northern areas under glacial conditions presented a climate and ecosystem predominantly composed of tundra and boreal forests, conditions in which obtaining vegetative resources would have been difficult if not impossible with longer winters (Bonan et al., 1992; Foley

et al., 1994). As for hunting, the predominant fauna available consist in animals adapted to open cold environments, such as moose, horses, mammoth, woolly rhino, bison and saiga antelope (Soffer, 1993; Puzachenko et al., 2021). Each of these species are further characterised by their extensive movement across the continent.

Combining our knowledge on the environmental conditions of Siberia and Beringia with the ecology of the different herbivores reveal drastically difficult living conditions, especially in terms of obtaining resources during the longer winter months, and with the more rigorous climatic conditions of the End Upper Pleistocene (Krolopp and Sümegi, 1995; Karabanov et al., 1998; Preusser et al., 2003; Daniels et al., 2021; Puzachenko et al., 2021). Moreover, when considering extreme sub-zero temperatures, moving long distances in a hunt for food is unfeasible, especially when considering the energy necessary to construct these *mammoth bone homes* and the added contempt of abandoning them. Under these extreme conditions, survival would only have been possible using advanced strategies to obtain food. From this perspective, the domestication of wolves becomes increasingly understandable.

As for the function of wolves in these societies, these carnivores would have been a great tool for facilitating the capture of meat without expending too much energy. Wolves hunt and track primarily based on smell, providing a useful tool to quickly locate animals in low visibility, or carrion buried in the snow (Fig. 2). Once located, *in situ* butchery activities could easily be carried out to scavenge upon carcasses, or transport elements back to base settlements. Neither should we reject the possibility that upon finding large megafaunal remains, the settlement was the one to relocate. Upon occupation of territories surrounding megafaunal remains for long periods of time, settlements with *mammoth bone homes* could eventually be constructed, providing shelter while searching for new sources of food.

Upon the success of strategies such as those proposed here, and in addition with the shelter provided by the mammoth bone beds, the use of fire, and the meat of animal carcass found buried in the snow with the help of dogs, *Homo sapiens* were able to adapt to living in the hostile glacial conditions of Northeastern Eurasian.

With the time, a way of life for these human populations would have been consolidated throughout Siberia. From here, more complex hunting strategies, such as the use of bow and arrows, alongside different behavioural attributes could have developed (Nývltová Fišáková, 2005; Maschenko et al., 2003; Zenin et al., 2003; Iakovleva and Djindjian,



Fig. 2. Dog searching food in the snow.

2005; Pitulko et al., 2016; Waters et al., 2011). With time, the role of canids would have held a great importance at the heart of these settlements, becoming every bit more integrated into human way of life. This would explain the variability of palaeolithic dogs described after the last glacial maximum (see Pionnier-Capitan et al., 2011), as well as the diversity of genetic lineages (Bergström et al., 2020).

Similarly, with posterior phases of domestication, training of these carnivores could allow for more flexible hunting strategies according to the time and year and conditions these populations found themselves in. As the rate of success increases, these populations would have spread into Beringia before the Maximum Glacial with greater chances of survival (Bourgeon et al., 2017; Pitulko et al., 2004; Pitulko et al., 2016).

Under this premise, the arrival of *Homo sapiens* to the Americas whether along the coast (Braje et al. 2017) or cross-continental (Bourgeon et al., 2017; Dixon, 2001; Erlandson et al., 2015), would have been possible preceding the Clovis culture with the help of his dogs.

## 5. Conclusion

The present study has raised multiple questions about analyses into the early domestication of wolves. These questions are of great importance when reflecting on the nature of the first populations to arrive in Beringia as well as the early populations in the Americas. Similarly, information of this type can provide valuable insights into subsistence and survival strategies of populations residing in the harsh climates of Northern Eurasia during the upper Palaeolithic.

While a number of techniques currently exist for research of this type, the present study also contemplates a new perspective and line of investigation that may be able to shed new light on these questions.

Recent years have seen important advances in morphological, palaeontological, biometric, genetic, isotopic and microwear analyses, nevertheless, these methods are highly dependent on the presence of canid remains in a site. Furthermore, even if canid remains are found, many analyses are hindered by poor preservation. The present study has shown how recent advances in geometric morphometrics and computational learning applied to the taphonomy of tooth marks may be able to overcome these issues, as they are not dependent on the physical presence of canid remains. In sum, therefore, we believe that a combination of all of these methods may shine new light on the early domestication of canids towards the end of the Palaeolithic era.

## CRedit authorship contribution statement

**José Yravedra:** Conceptualization, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization. **Darío Herranz-Rodrigo:** Methodology, Validation, Formal analysis, Data curation, Writing – review & editing, Visualization. **Cecilia Mendoza:** Methodology, Formal analysis, Investigation, Data curation. **Pablo Aragón-Poza:** Conceptualization, Investigation. **Lloyd A. Courtenay:** Methodology, Software, Validation, Supervision.

## 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

Lloyd Courtenay is supported by the FPI Predoctoral Grant (Ref. PRE2019-089411) associated to project RTI2018-099850-B-I00 and the University of Salamanca, support of the PGC2018-093612-B-I00 project provided by the Spanish Ministry of Science, Innovation and Universities (MICINN). D.H.R. is also supported by the Spanish Ministry of Science, Innovation and Universities, under the contract PEJ2019-005420-A as part of the I + D + I Garantía Juvenil. We thank

Santiago Borragán and the Parque de la Naturaleza de Cabárceno for allowing us to use bone samples modified by wolves. We want to thank Rubén Llorente Pérez for providing us with bone samples modified by some dogs. Finally, we appreciate the comments of Antonio Pineda and the other anonymous reviewers for their comments and suggestions.

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