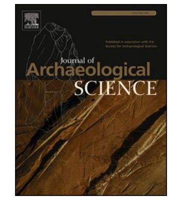
Journal of Archaeological Science 163 (2024) 105934

Contents lists available at ScienceDirect

Journal of Archaeological Science

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



Identification of age at death in red deer (*Cervus elaphus*) through the upper dentition: Eruption pattern, wear stage and crown heights

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ARTICLE INFO

Keywords:
Mortality profiles
Zooarchaeology
Age at death
Red deer
Dental wear
Dental eruption
Crown measurement

ABSTRACT

The present research aims to determine the age at which red deer (*Cervus elaphus*) specimens died by examining their upper dentition. We analyzed eighty free-ranging individuals from southern Spain to establish a reference database for age calculation. The age of these individuals was identified by the mandibular teeth inferred from their known death years and the maxillary teeth were evaluated relative to them. As a result, we have provided three non-destructive methods: a description of the eruption sequence and dental replacement, a referential code for occlusal wear stages, and a regression analysis considering the height of the cusps in both upper and lower dentition. These methods offer the possibility of estimating the age at which the animals died and categorizing them into specific age groups. To evaluate the practicality of this method, we applied it to the Middle Paleolithic archaeological site of Abric Romaní. All the proposed methods allow us to approximate the age at death of red deer individuals. The most accurate results, whenever feasible, are obtained by combining these different methods. This study facilitates the inclusion of upper dentition fossils that have traditionally been omitted from the analysis in archaeological sites, allowing a better adjustment of the quantitative methods used to calculate the number of skeletal elements and the number of individuals. This, in turn, enables a more accurate construction of the anatomical and mortality profiles.

1. Introduction

Identifying the age at death of the animals in archaeological sites is a crucial subject to understanding the origin of fossil accumulations (Frison, 1984; Klein, 1982; Klein et al., 1981; Kurtén, 1953), allowing to answer several questions about the behaviour of past hominin groups (Klein, 1978; Stiner, 1990). First, it informs about the type of prey selected based on age (Brugal and David, 1993; Gaudzinski and Roebroeks, 2000). Secondly, depending on the specimen, it can provide information about the time of year when the animal was killed, the functionality or use of the site, and the seasonality of human occupations (Lubinski and O'brien, 2001). Thirdly, this information makes it possible to construct mortality profiles that permit the proposal of the probable hunting tactics and techniques developed by human groups and other carnivorans in the environment (Bunn and Gurtov, 2014; Bunn and Pickering, 2010a, 2010b; Marín et al., 2017; Rodríguez-Hidalgo et al., 2017).

Methods for determining the age at death have conventionally focused mainly on animal dentition. In ungulates, the original tooth structure undergoes continuous wear and degradation from the moment of eruption due to mastication, which cannot be replaced or repaired (Pérez-Barbería et al., 2015). This degree of wear can be quantified and described in present-day species, enabling the creation of reference data for identifying the age of animals based on the characteristics of their dentition (Brown and Chapman, 1991a, 1991b; Frison and Reher, 1970; Rolett and Chiu, 1994). These methods are categorized as destructive and non-destructive. The destructive method is cementochronology, which involves counting the layers of cyclically deposited cement. These layers alternate between relatively narrow and relatively wide, reflecting a growth periodicity that generally corresponds to an annual cycle,

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https://doi.org/10.1016/j.jas.2023.105934
Received 26 September 2023; Received in revised form 22 December 2023; Accepted 27 December 2023
Available online 30 December 2023
0305-4403/

that permits to estimate of the age at death and the season when the animal was killed (Burke and Castanet, 1995; Livraghi et al., 2022; Pike-Tay, 1991). Non-destructive methods focus on measuring the height of the tooth crown (Fernandez and Legendre, 2003; Klein et al., 1981; Levine, 1982) and analyzing the wear of the occlusal surface (Brown and Chapman, 1991b; Payne, 1973, 1987). However, tooth wear can be affected by factors such as the type of diet, population pressure or the sex of the animals (Azorit et al., 2003; Pérez-Barbería et al., 2015). These methods are based on comparing the assessed wear stages of teeth with reference collections that include animals whose ages at death are known.

Within European ecosystems, especially in Mediterranean Europe, the red deer (*Cervus elaphus*) is and has been one of the most common ungulates throughout the Holocene and Pleistocene fossil record (Daujeard and Moncel, 2010; Marín et al., 2017; Pike-Tay, 1991; Steele, 2004; Stiner, 2006; Valensi and Psathi, 2004). Unlike other species, such as the horse (Burke, 2002; Fernandez, 2009; Fernandez and Legendre, 2003) or rhinoceros (Garutt, 1992; Louguet-Lefebvre, 2005), traditionally, the age of red deer has been calculated exclusively using the lower dentition. This method mainly involves observing the eruption pattern of mandibular teeth, assessing their wear degree, considering the height of the crown, examining the pattern of wear on the occlusal surface, and utilizing cementochronology (Azorit, 2011; Brown and Chapman, 1991b; Lowe, 1967; Riglet, 1977). However, this approach excludes a significant portion of the archaeological assemblage, specifically the upper dentition, which could also be used to estimate ages, construct mortality profiles, and more accurately establish abundance indices in archaeological assemblages.

This work aims to provide a reference database to calculate the age at death of red deer fossils based on their upper molar dentition, developed by analyzing the osteological collection of the Department of Biology of the University of Jaén (Spain). We present various non-destructive methods based on eruption pattern, wear stage and the measurement of crown height of the upper dentition of red deer, which offer the possibility of estimating the age of death of the animal and categorizing it into specific age groups. To evaluate the practicality of these methods, they were applied to the red deer material from the Middle Paleolithic site of Abric Romaní.

2. Materials

Red deer (*Cervus elaphus*) remains from the osteological collection of the research group PAIDI-RNM-175 at the University of Jaen (Spain) were used. These specimens were free-ranging individuals from controlled hunting game reserves in southern Spain, mainly in the Sierra Morena mountains. The collection includes numerous individuals with ages calculated by the mandibular dentition, spanning a wide age range. Their diet primarily consisted of grasses, peaking in spring. Browsing on woody plants was an important food resource at the end of winter and summer, while fruit consumption was more significant in autumn and winter (Azorit et al., 2012). This collection has previously been used, for example, in research related to dental eruption of the lower molariform teeth (Azorit et al., 2002), age determination and the use of cementochronology for inferences on body size, and growth and life history evolution in both fossil and extant deer (Azorit et al., 2004, 2022; Kolb et al., 2015). It has also been used in studies examining wear patterns related to diet (Berlioz et al., 2017). In this work, we specifically utilized the material available in the maxillary bones and upper molariform series.

Red deer in the wild can live up to 20 years (Fichant, 2003). However, individuals exceeding 16 years are scarce (Clutton-Brock et al., 1982). According to Steele and Weaver (2012), the potential ecological longevity (PEL) of *Cervus elaphus* is 192 months (equivalent to 16 years). Therefore, PEL will be adapted to 16 years because is the most used (Domínguez-Rodrigo et al., 2015). Following the model developed by Azorit (2011), we have ordered the individuals into seven Dental Age Groups (DAG) (Table 1). Azorit (2011) identified the age of individuals using the mandibular teeth, which involves a combination of methods including eruption pattern, wear stages of occlusal surfaces, and cementochronology. This age determination serves as a reference for associating the mandibles of known age with their corresponding maxillae. As a result, the individuals' age was calculated and ascribed to one of the seven known age groups (Table 1).

There are 80 individuals of known ages: 59 females, 19 males and two indeterminate-sex individuals. Up to about five years, there were roughly equal numbers of males and females, but the oldest animals of known sex were almost exclusively female (Table 1). This is because adult males were preferentially hunted, fewer on the landscape, and hunters tended to retain the complete skulls of older males. Most individuals are in DAG V and VI, with 22 and 21 individuals each, followed by DAG IV and III, each with 13 individuals, DAG VII with 6, DAG II with four, and DAG I with one individual. In total, 226 upper teeth and 182 lower teeth were analyzed. Lower teeth were previously described in Azorit (2011). Steele, (2002) indicated that combining right and left teeth does not significantly affect age at death analysis. Therefore, we opted to use only the left dentition for this study. Additionally, Klein et al. (1981) pointed out that bilaterally asymmetrical wear is virtually non-existent. The proportion of analyzed teeth for the upper and lower dentition was similar for the first molar (75/68), the second molar (75/67) and the Dp4 (17/15). On the contrary, the third molar (59/32) had a higher proportion of upper teeth analyzed than lower teeth.

3. Methods

For the analysis of red deer (*Cervus elaphus*) upper teeth, we employed the same non-destructive methods as those developed for the lower dentition, including the evaluation of eruption pattern, tooth wear patterns and crown height measurements.

3.1. Eruption pattern

The eruption pattern of lower mandibular teeth for this collection was published by Azorit et al. (2002). Age determination was possible because of the precise knowledge of the individual's death dates, with the birth period in the eastern Sierra Morena occurring between June and July (Azorit, 1999). This allowed us to establish and correlate the tooth eruption, loss, and replacement patterns in both maxillary and mandibular teeth. We use the symbols proposed by Azorit et al. (2002), although it is important to note that in this case, we did not consider the terminology provided for the lower M3 since they refer to the wear of the third cusp of this tooth:

***: The tooth is still beneath the gingiva, but there is an open hole in the mandible that allows the dental crown to be partially visible.

**: The tooth is emerging through the gingiva, but only half or less of the crown is visible.

*: The tooth has almost completely emerged but not fully. The absence of an asterisk represents that the teeth have fully erupted.

(): The moment of initial tooth wear.

[]: The moment of final tooth wear.

3.2. Tooth wear pattern

The descriptions of tooth wear patterns were graphically illustrated following the proposal of Payne (1973, 1987) and subsequently adapted for *Cervus elaphus* by Mariezkurrena (1983), Brown and Chapman (1991c) and Azorit (2011). The analysis of occlusal surface wear was carried out by visual examination. High-quality photos of each maxilla and mandible were taken from occlusal views for later evaluation and categorization of their wear stages. These photos focused on the measured teeth, the Dp4, M1, M2 and M3. Each maxillary tooth was individually described with its corresponding wear stage and compared with its equivalent mandibular tooth. Each drawing was coded with the

Table 1
Number of red deer individuals and count of analyzed teeth in maxillae and mandibles organized by their Dental Age Group (DAG) and Potential Ecological longevity (PEL).

Dental Age Group	Time (PEL)	Number of Individuals			Number of analyzed teeth							
		Males	Females	Indet.	Maxilla				Mandible			
					Dp4	M1	M2	M3	Dp4	M1	M2	M3
I	0–5 months			1	1	1			1	1		
II	5 months-1.5 years	2	1	1	4	3	2		4	3	3	
III	1.5–2.5 years	6	7		12	13	13		10	11	10	
IV	2.5–4.5 years	5	8			13	13	12		11	11	11
V	4.5–6.5 years	3	19			21	21	21		20	20	9
VI	6.5–12 years	2	19			20	21	21		18	19	10
VII	12 > years	1	5			4	5	5		4	4	1
Total		19	59	2	17	75	75	59	15	68	67	32

To test the usefulness of this methodology, we opted to apply it to the Middle Paleolithic archaeological site of Abric Romaní. A total of 24 fossils of red deer from a total of 7 different levels (Levels H, I, K, L, M, P and Q) have been measured and described.

specimen number and each specimen was assigned to its corresponding DAG as described in Table 1.

3.3. Crown height measurements

The minimum crown height of the four cusps of the three permanent molars and the deciduous fourth premolar were measured from the occlusal surface to the junction of the enamel with the root dentine, whenever visible, following the indications proposed by Klein and Cruz-Uribe, (1984) for mandibular teeth (Fig. 1). No teeth were extracted from their alveoli for measurement. Only visible junctions were measured, resulting in 66 measurements out of 68 possible in the upper Dp4, 47 out of 60 in the lower Dp4, 271 out of 300 in the upper M1, 245 out of 272 in the lower M1, 199 out of 300 in the upper M2, 165 out of 268 in the lower M2, 63 out of 236 in the upper M3 and 40 out of 128 in the lower M3. These measurements were taken with an accuracy of 2 mm and recorded to two decimal places using a Stainless electronic calliper.

Klein et al. (1981) indicate that choosing a simple and easily definable measurement is convenient by using the minimum distance from the occlusal surface to the line separating the crown enamel from the root dentine, measured on the buccal surface. For multilobed teeth (Dp4 and molars), they arbitrarily opt for measuring at the most anterior lobe. They indicate that, for consistency in upper teeth, the measurement should be taken at the anterior cusp of the lingual face. This implies that, while the standard measurement for lower molars is taken at the Protoconid, it should be at the Paracone for upper molars. However, in our study, we have decided to measure all molar cusps and explore the

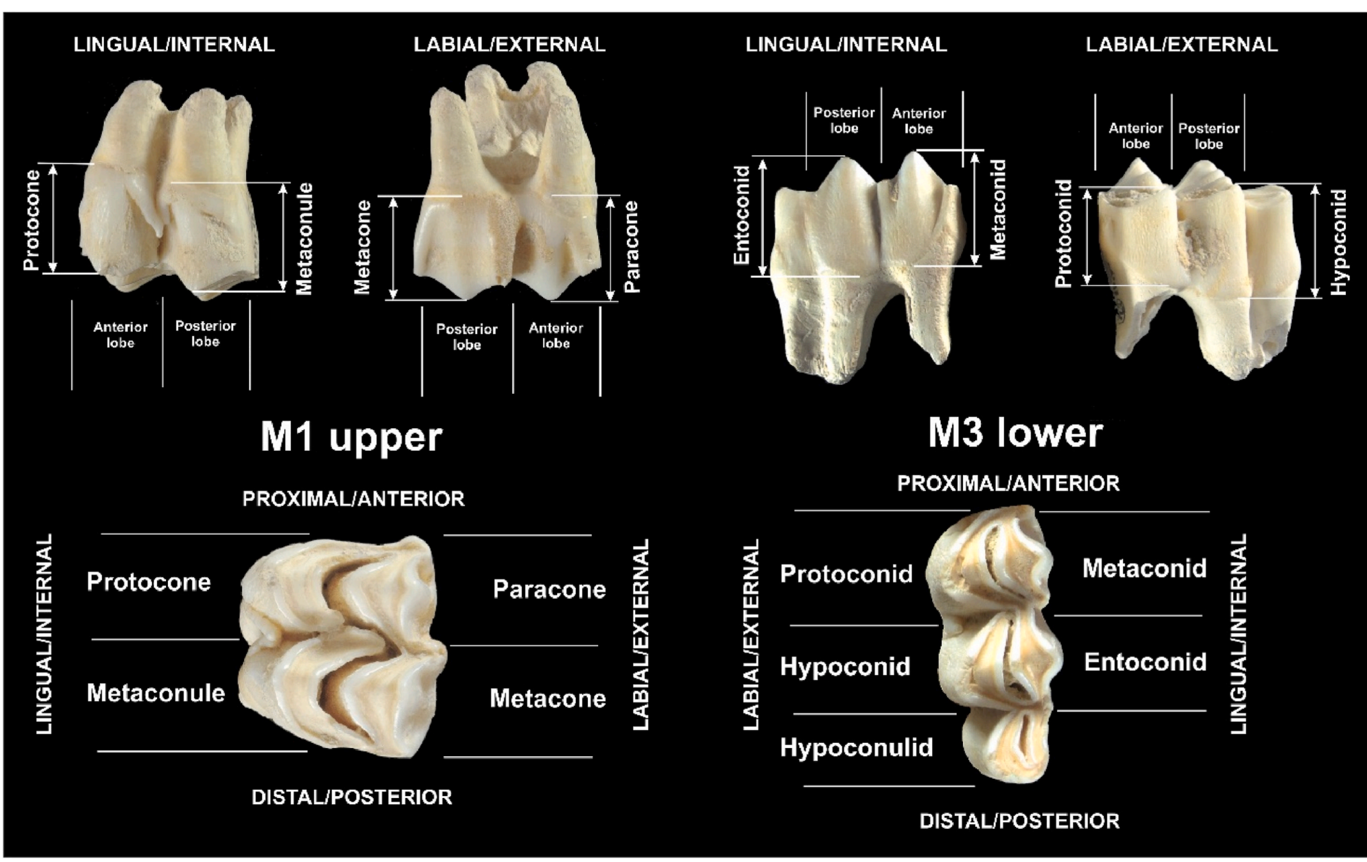

Fig. 1. Red deer left M^1 and left M_3 with their portions and the indications of crown height measurements of each lobe. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

correlation between wear and age of the corresponding cusps in both mandibular and maxillary teeth.

To estimate the age at the death of red deer, we followed the method proposed by Fernandez and Legendre (2003), using a third-order polynomial regression to correlate the age of the individuals with the crown height of both upper and lower teeth. The equation used is as follows: $age = \sum_{k=0}^{3} a_k * (crown\ height)^k$, were a_k represents the regression coefficient, crown height is measured in millimetres, and age is expressed in years.

4. Results

4.1. Eruption pattern

The sequence of dental eruption and the overall wear trends for mandibular and maxillary teeth are indicated in Table 2 and illustrated in Fig. 2. All the deciduous dentition in both mandibles and maxillae is present from birth. The first permanent tooth to erupt is the first molar, becoming visible above the gum line around three months of age. Both upper and lower M2 teeth typically erupt at 12 months. The eruption and initial wear of the permanent premolar and the third molar occurs approximately during the first 2.5 years of life.

4.2. Wear stage of the occlusal surface

The analysis of the maxilla and the mandible of red deer allows us to establish a relationship between the wear patterns of upper and lower teeth. The first and most notable result is that wear on lower teeth is generally advanced compared to upper teeth. This discrepancy in wear stages between upper and lower teeth is consistently observed across all age classes (Figs. 3–6).

Fig. 3 shows the relationship between wear stages for young individuals' teeth. DAG I is characterized by the beginning of the wear of the proximal lobe of upper and lower Dp4. Towards the end of DAG I, which occurs around five months, the lower and upper M1 begin to function, with initial wear on the anterior cusp. During this stage, the infundibulum in the anterior and posterior of M1 are not yet visible.

Differences between upper and lower wear become more apparent in DAG II. The cusps of the upper Dp4 are in active wear, even though there is no connection between the protocone and metaconule. In contrast, the lower Dp4 exhibits wear on all cusps of the lobes, but the degree of connection between them varies significantly. The upper M1 only displays wear on the anterior cusps (protocone-paracone) and none on the posterior (metaconule-metacone). In contrast, all cusps on the lower M1 exhibit wear, but there is no connection between them. The upper M1 remains unworn, and the lower M2 shows incipient wear only in individual R1086. This suggests that lower M2 become functional around 10 or 12 months, coinciding with the onset of wear on the anterior cusp.

DAG III begins with the union in wear between the protocone and metaconule of the upper Dp4 and continuous wear of the occlusal

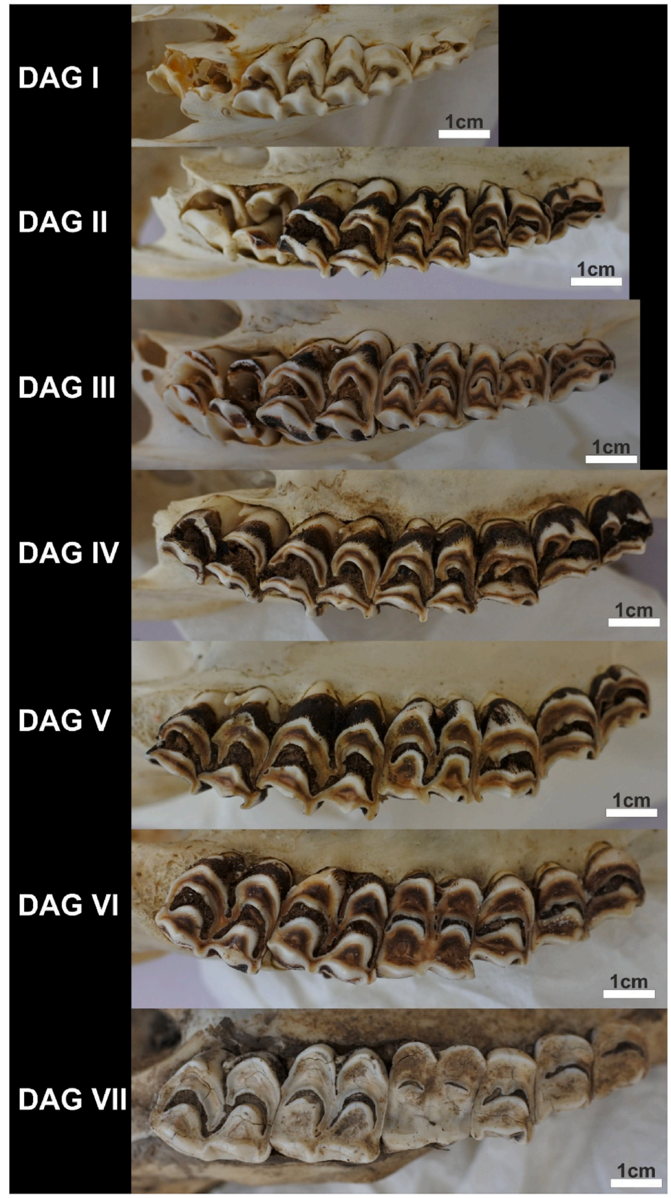

Fig. 2. Occlusal views showing the sequence of eruption and wear of upper left teeth in red deer. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Sequence of eruption and replacement of upper and lower dentition in red deer.

Age groups		DAG	PEL	Mandible Eruption sequence	Maxillar Eruption sequence
Juvenile	Young juvenile	I	0–5 months	$Dp_2+Dp_3+Dp_4+M_1$***	$Dp^2+Dp^3+Dp^4+M^1$***
				Initial wear ( )	Initial wear ( )
	Subadult Juvenile	II	5 months-1.5 years	$Dp_2+Dp_3+Dp_4+M_1$*$+M_2$**	$Dp^2+Dp^3+Dp^4+M^1$*$+M^2$**
		III	1.5–2.5 years	$[Dp_2+Dp_3+Dp_4]+M_1+M_2$	$[Dp^2+Dp^3+Dp^4]+M^1+M^2$
				Final wear [ ]	Final wear [ ]
Prime Adult	Early prime	IV	2.5–4.5 years	$(P_2+P_3+P_4) + M_1+M_2+(M_3)$	$(P^2+P^3+P^4) + M^1+M^2+(M^3)$
				Initial wear ( )	Initial wear ( )
		V	4.5–6.5 years	$P_2+P_3+P_4+M_1+M_2+M_3$	$P^2+P^3+P^4+M^1+M^2+M^3$
	Late prime	VI	6.5–12 Years	$P_2+P_3+P_4+M_1+M_2+M_3$	$P^2+P^3+P^4+M^1+M^2+M^3$
Old	Old	VII	12 >years	$P_2+P_3+P_4+[M_1]+M_2+M_3$	$P^2+P^3+P^4+[M_1]+ M^2+M^3$
				Final wear [ ]	Final wear [ ]

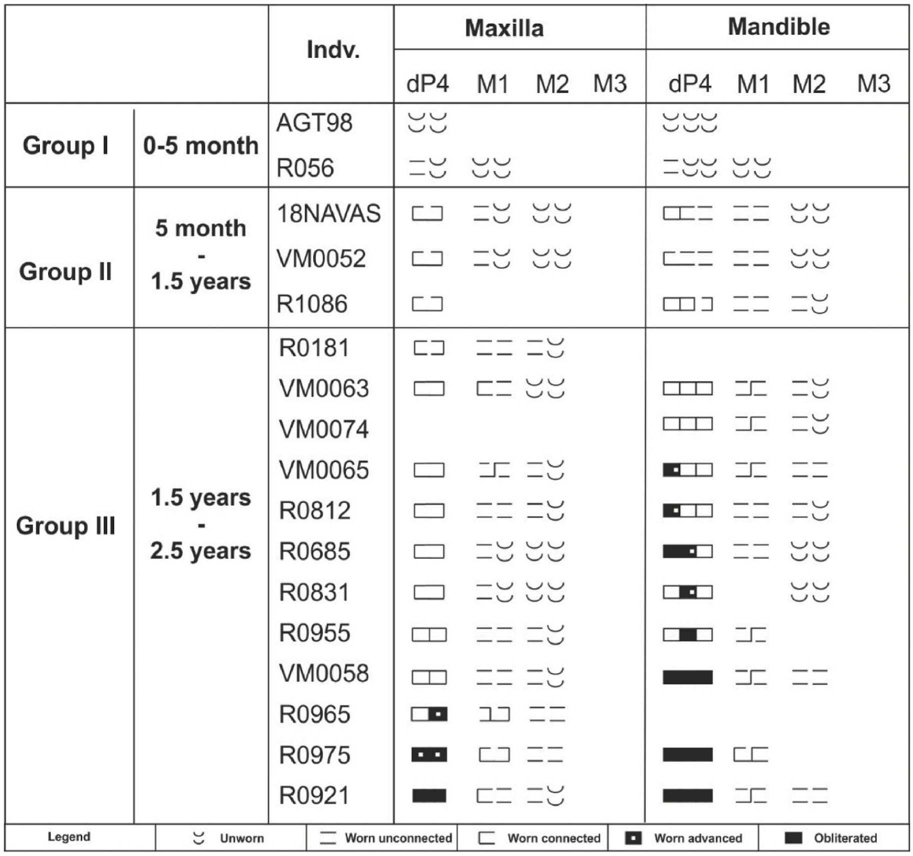

Fig. 3. Wear Stage symbols for mandibular and maxillary Dp4, M1, and M2 in red deer for DAG I, II, and III.

surface of the lower DP4. This stage concludes with the loss of the deciduous dentition (Fig. 3). Both upper and lower M1 teeth exhibit variability in wear patterns, but consistently worn surfaces are always more significant in lower dentition than in upper dentition. The upper and lower M2 start to wear, but variability remains high, similar to the M1. Notably, the cases of R0685 and R0831 are significant, as they exhibit advanced wear in dp4 while the M2 remains unworn. DAG III encompasses the final stages of wear for deciduous dentition.

Fig. 4 illustrates the relationship between upper and lower occlusal wear in early prime adults, organized into DAG IV and V. In DAG IV, there is considerable variability in the wear of upper and lower M1. The main differences between these teeth are related to the wear connections among the various cusps. Notably, while the upper M1 often exhibits an early connection on the anterior face between protocone and paracone (observed in 12 individuals), the lower M1 frequently displays a first connection between the labial and lingual faces (observed in seven individuals). The upper and lower M2 typically exhibit a similar wear stage, with all the cusps worn but not interconnected, as seen in seven individuals. In contrast, three individuals present a more advanced wear stage for lower M2, with the protoconid, metaconid, and lingual and labial surfaces in connection. DAG IV marks the eruption and initial functionality of M3. Notably, in none of the observed cases, does the posterior lobe of the upper M3 exhibit wear, while in the lower M3, the posterior lobe starts wearing. However, the hypoconulid remains unworn in all individuals (Fig. 4). In DAG IV, the lower and upper P2, P3, and P4 begin to be functional around 24 months of age.

As for DAG V, the disparities in wear between upper and lower dentition become more pronounced. Lower M1 started to have all the anterior and posterior lobe cusps in continuous wear, only two individuals not showing a connection of all cusps (Fig. 4). In contrast, for upper M1, eight individuals show no connection between protocone and metaconule, six individuals have protocone and metaconule connected in wear, and three individuals have less than two interconnected wear facets.

The upper and lower M2 in early prime adults of DAG V is characterized by the beginning of the connections of the cusp wear. As we observed with M1, the wear of the lower molars consistently exceeds that of the upper molars in all individuals. For instance, individual VM0062 has an upper M2 with all cusps showing wear but lacking connections. Conversely, the lower M2 displays wear on all cusps, with the protoconid and metaconid labial and lingual surfaces connected.

Within this age group, the M3 exhibits wear on all cusps of the occlusal surface. Similar to M2, the upper M3 shows only one individual with wear connection between two cusps (individual R0966). In contrast, in the lower M3, it is more common to find individuals at advanced wear stages, with two or more cusps connected through wear (Fig. 4).

Fig. 5 illustrates the wear patterns in late-prime adult specimens from DAG VI. The most significant difference is observed in the upper and lower M1. While the lower M1 starts to present a lobe or the complete occlusal surface in advanced wear with the loss of one of the two infundibula, the upper M1 presents the connection in wear between the lingual and labial faces showing two separated fossettes. The lower M2 shows homogeneous wear, with all cusps connected to each other. Conversely, in the upper M2, seven individuals exhibit an occlusal surface without connection of the protocone and metaconule, while eight individuals show this connection (Fig. 5). The lower M3 has a stage of homogeneous wear, with all the cusp slopes connected to the dentine. The upper M3 in none of the cases has the dentine connected between the lingual and vestibular face, and only in four individuals the protocone, metaconule, paracone and metacone are connected.

Fig. 6 shows the DAG of old individuals. As outlined in the methodology section, age groups are established based on the condition of the lower teeth. DAG VII begins when the lower M1 has lost both the

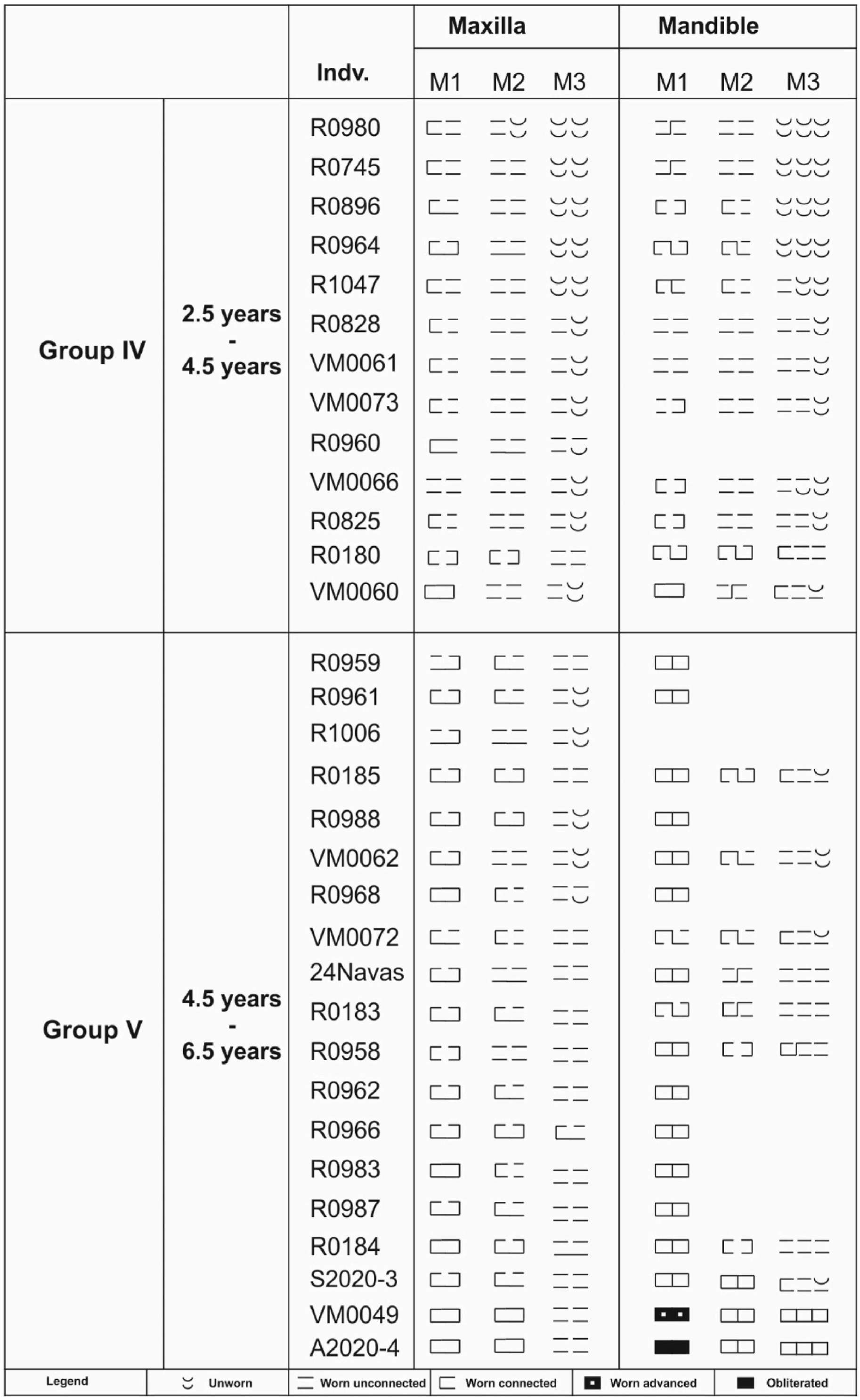

Fig. 4. Wear Stage symbols for mandibular and maxillary M1, M2, and M3 in red deer from DAG IV and V.

anterior and posterior infundibulum. For the upper M1, the pattern of the occlusal wear delay remains consistent throughout the lifespan of the deer. For instance, in the cases of individuals A2020–4 and R0954, the lower M1 has the occlusal surface obliterated, while the upper M1 still retains the infundibulum. In the case of individual R0984, even when lower M1 has completely lost its occlusal surface, retaining only the roots, the upper M1 still preserves its occlusal surface. Complete wear of the occlusal surface is observed in the upper M2 of individuals in this age group. As for the lower M2, late prime individuals exhibit wear on all occlusal surfaces. The wear stage of the upper M3 varies within this group, ranging from individuals without connection between the protocone and metaconule to those with all cusps connected through wear. However, an animal with an upper M3 where the cusps are connected through wear can be considered old. Conversely, regarding the lower M3, there is no great diversity. All individuals in this group display complete wear on the occlusal surface, with the exception of individual A2020-4, which shows an advanced wear stage on the hypoconulid (Fig. 6).

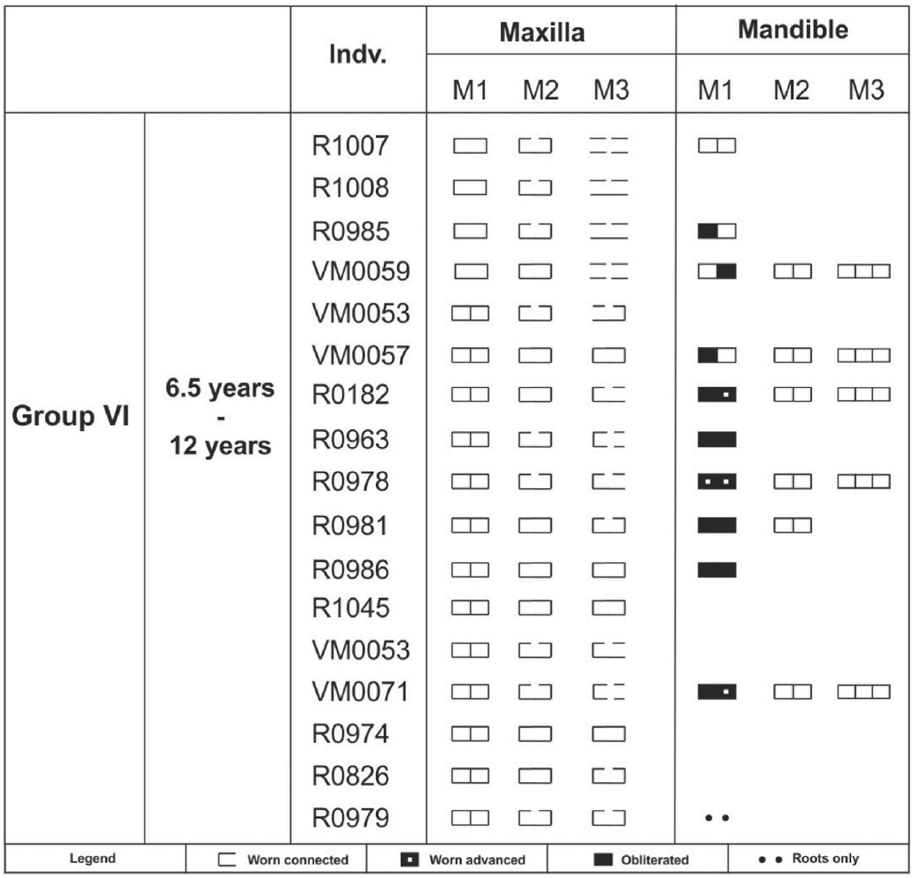

Fig. 5. Wear Stage symbols for mandibular and maxillary M1, M2 and M3 for red deer of DAG VI.

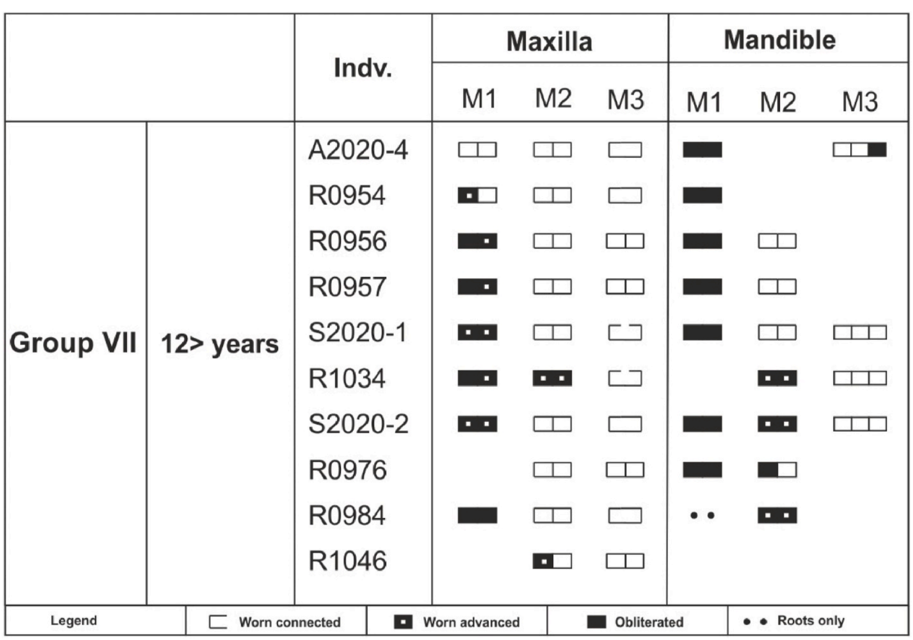

Fig. 6. Wear Stage symbols for mandibular and maxillary M1, M2, and M3 in red deer from DAG VII.

The differences in the wear of the occlusal surface of lower M1 and lower M2 between age groups III and V will be challenging to establish when the tooth is presented in isolation, outside of a dental sequence, as the difference between these two groups is produced by the transition from deciduous to complete permanent dentition. This assumption is especially true for identifying DAG IV, characterized by the appearance of P4 and M3 during its first wear phase. When comparing the degree of wear identified for each age group per tooth, both in our work and in research carried out by other specialists using current and archaeological materials, a general wear pattern tends to be seen first on the mesial slopes of the labial and lingual paired cusps, then on the distal cusps. On the other hand, this principle is highly variable, and examples can be found that vary enormously in animals of the same age in the wear of the same tooth (Mariezkurrena, 1983).

4.3. Crown height

The crown height measurements have been tested to assess the correlation between age and wear for each cusp of the upper and lower teeth. All the measurements taken are in Tables A1 and A2 of appendices. A strong negative relationship between the crown height of different cusps and the age of individuals has been found (Table 3), which is to be expected as the crown declines with age, except for the protoconid and hypoconid of lower M3, and the paraconid and metaconid of the lower Dp4. The lack of significant correlation in these cases may be attributed to the small sample size. Therefore, the most reliable correlations, which can provide the most accurate age estimation through measurement, are found with the metaconid in the lower dentition and the paracone in the upper dentition.

It has been observed in seven individuals that with the lower M1, the crown height of the protoconid cannot be measured because the dentine-enamel junction line is not yet visible, it is possible to measure the crown height of the protocone in the upper M1. The reverse case, where the protocone cannot be measured while the protoconid can be measured, has not been identified.

Furthermore, polynomial regression of order 3, correlating the crown height of each cusp with age, indicates that the metaconid in lower molars and the paracone in upper molars have the most significant and straight negative correlation. This suggests that applying the equation derived from these two cusps should yield the most accurate measure of age at death (Table 3).

As a result of the age calculation using the polynomial regression order 3, we have proven a higher accuracy in the age calculation by measuring the first and second upper molar. This is probably due to the larger sample size of these teeth. The next tooth that best fits the age identified is the upper M3. The calculation of the age of Dp4 does not give results that can be adjusted with the actual age of the animals, nor the results given by the other methods offered in this work, so it has been decided not to use the equation resulting from the polynomial regression order 3 in the calculation of the age of Dp4.

4.4. Abric Romaní assemblage

The age of the individuals was first considered in terms of eruption and replacement sequence (Table 4). Then, the occlusal surface wear of each individual was described (Fig. 7) and was grouped into the corresponding DAG group (Table 4). To calculate age by measuring crown height, whenever possible, the height of the Paracone was used. If this was impossible, another crown height was used in this hierarchical order, firstly the Metacone, then the Protocone and finally the Metaconule.

5. Discussion

This study provides three methods to assess the age of death in red deer (*Cervus elaphus*) based on upper dentition. The results of the eruption and dental replacement, the wear pattern of the occlusal surface and the measurement of the height of the cusps of the upper and lower dentition of red deer have been offered.

After applying the methods to the Abric Romaní assemblage, it has been verified that these proposed techniques enable the classification of specimens into their corresponding DAG and into the young juvenile,

Table 3

Values for the polynomial regression of order 3 calculation by teeth and cusp. Regression coefficient value = a0, a1, a2, a3; Chi-squared distribution = Chiˆ2; Akaike information criterion = Akaike ICc; Rˆ2 = determination coefficient; F-test = F; p-value = p. For a given crown height (=H, in mm), the equation for age (in years) is: **Aga=a_0+a_1H + a_2H2+a_3H3.**

Tooth	Cusp	a_0	a_1	a_2	a_3	Chiˆ2	Akaike ICc	Rˆ2	F	p
Dp4 lower	Paraconid	8.653	10.7257	−22.398	9.30933	114.46	122.46	0.19497	0.88805	0.47742
	Metaconid	7.36667	22.5022	−39.52	15.8578	113.07	121.07	0.27263	1.3743	0.30174
	Entoconid	13.2933	−5.10756	−0.890659	0.664886	22.85	30.85	0.5398	3.91	0.043813
	Conid	8.0388	10.4351	−20.8568	8.06293	7.5662	15.566	0.86444	23.382	4.4747E-05
	Protoconid	15.5312	−12.2464	4.43081	−0.685604	18.846	26.846	0.65306	6.2745	0.011466
	Hypoconid	24.6093	−39.7121	28.6112	−7.16841	23.4	31.4	0.57196	4.4541	0.031165
Dp4 upper	Paracone	10.1795	13.1326	−25.8208	10.3154	32.132	40.132	0.5857	5.1837	0.017852
	Protocone	9.84253	5.39671	−11.7312	4.57529	9.6217	17.622	0.67179	7.5051	0.0052308
	Metacone	25.9951	−38.2355	27.8306	−7.00019	26.612	34.612	0.49705	3.2943	0.06628
	Metaconule	18.9006	−18.8061	10.5943	−2.36876	6.281	14.282	0.82538	15.755	0.00040626
M1 lower	Metaconid	16.6225	−1.40467	0.0333	−0.000124	268.54	276.54	0.78102	72.521	4.2714E-20
	Protoconid	15.7144	−1.51186	0.0563957	−0.000986741	359.08	367.08	0.66708	38.07	1.2249E-13
	Entoconid	17.2395	−1.69361	0.0740537	−0.00154197	248.41	256.41	0.78042	71.082	9.8262E-20
	Hypoconid	15.6276	−1.2672	0.0265823	−0.000142896	233.92	241.92	0.75907	57.762	5.2759E-17
M1 upper	Paracone	17.3893	−1.49019	0.02068	0.000562199	118.37	126.37	0.91377	243.74	**1.2212E-36**
	Protocone	14.6016	−1.26819	0.0214743	0.000286795	134.35	142.35	0.85216	122.96	1.622E-26
	Metacone	18.9075	−1.57512	0.0104759	0.00113258	131.39	139.39	0.9107	214.17	5.4724E-33
	Metaconule	16.0549	−1.596	0.0317926	0.00042805	175.31	183.31	0.85147	120.39	4.8429E-26
M2 lower	Metaconid	22.3091	−1.82377	0.0820634	−0.00225331	270.04	278.04	0.70838	33.197	4.7234E-11
	Protoconid	23.2963	−2.67908	0.151458	−0.00382365	301.29	309.29	0.65896	24.475	5.4761E-09
	Entoconid	22.0326	−2.26069	0.14965	−0.00454685	116.18	124.18	0.72752	15.13	4.7331E-05
	Hypoconid	25.9013	−4.12937	0.334773	−0.00962931	106.12	114.12	0.66538	9.9423	0.0007393
M2 upper	Paracone	21.1996	−1.32946	−0.000458464	0.000874566	154.6	162.6	0.88969	155.93	**1.0021E-27**
	Protocone	16.3067	−0.952731	−0.00240393	0.000594374	99.942	107.94	0.80936	59.439	3.6463E-15
	Metacone	24.4733	−2.1102	0.0678117	−0.00104085	107.05	115.05	0.88101	101.19	5.4732E-19
	Metaconule	19.1568	−1.44304	0.0197389	0.000312073	94.193	102.19	0.84536	71.069	7.2886E-16
M3 lower	Metaconid	34.0538	−5.46137	0.445215	−0.012867	44.285	52.285	0.81154	12.918	0.0013028
	Protoconid	7.35281	0.806754	−0.0643828	0.00028518	52.078	60.078	0.62132	3.8285	0.065272
	Entoconid	30.1853	−4.59423	0.379735	−0.0112856	91.195	99.195	0.6374	4.6877	0.035812
	Hypoconid	−26.2442	10.1124	−0.823281	0.0191714	21.993	29.993	0.84482	10.888	0.0076831
M3 upper	Paracone	27.5575	−2.91654	0.17187	−0.00464253	134.53	142.53	0.82481	56.496	**1.07887E-13**
	Protocone	32.3207	−5.10699	0.383695	−0.0104486	48.388	56.388	0.74961	18.96	6.1511E-06
	Metacone	44.576	−8.16247	0.652297	−0.0177936	70.948	78.948	0.78769	24.733	6.186E-07
	Metaconule	23.1558	−2.82035	0.213618	−0.00654787	43.686	51.686	0.76192	18.134	1.5337E-05

Table 4
Upper teeth specimens from the Abric Romaní rock shelter. It is including the dental series of, the side, measurement in mm of each cusp by all the measurement teeth, the age and the dental age group identified for each specimen.

Specimen	Dental series	Side	Tooth	Paracone	Metacone	Protocone	Metaconule	Age groups	DAG
AR91-H-H56-1	Pm2+Pm3+Pm4+ M1+M2+M3	left	M1	6,97	4,86	6,35	3,07	Late prime	VI
			M2	9,72	9,11	9,06	6,65		
			M3	10,82	10,47	9,52	9,38		
AR91-H-L59-3	M1	right	M	13,97	14,53	13,18	12,99	Early Prime	V
AR91-H-L59-5	M1	right	M1	7,62	8,94	7,53	7,93	Late Prime	VI
AR91-H-M45-1	M1+M2+(M3*)	right	M1	nm	8,21	nm	6,73	Early Prime	V
			M2	9,61	10,89	8,56	8,89		
			M3	19,28	21,18	nm	Nm		
AR91-I-I58	[M1]	right	M1	6,03	7,25	3,47	nm	Old	VII
AR92-I-K46-29	(Dp2+Dp3+Dp4)	right	Dp4	11,73	13,03	10,87	11,29	Young juvenile	I
AR92-I-L46-7	M1	right	M1	nm	8,54	7,50	6,63	Late Prime	VI
AR92-I-M46-4	(Dp2+Dp3+Dp4)	right	Dp4	12,87	14,22	12,78	13,36	Young juvenile	I
AR96-K-J47-21	M1+M2+(M3)	right	M1	nm	nm	10,47	11,06	Early Prime	V
			M2	nm	19,59	17,18	17,49		
			M3	21,76	21,71	20,76	20,05		
AR96-K-K49-4	M1	right	M1	nm	17,42	16,29	16,25	Early Prime	IV
AR97-K-M44-134	M1	left	M1	11,7	13,36	10,92	10,19	Early Prime	IV
AR97-K-M45-22	M2	left	M2	16,94	19,03	14,96	14,58	Early Prime	V
AR96-K-M45-71	M3	left	M3	21,01	20,34	18,73	18,94	Subadult juvenile	III
AR96-K-M52-5	[Dp4]	left	Dp4	4,07	4,89	4,98	5,11	Early Prime	V
AR96-K-N46-20	M2	right	M2	15,29	nm	12,98	nm	Early Prime	V
AR97-L-S50-2	M1	left	M1	nm	nm	8,34	8,98	Early Prime	IV
AR01-M-K50-20	(M2)	left	M2	23,94	nm	23,05	21,75	Subadult juvenile	III
AR01-M-M41-48	M1	left	M1	18,85	19,74	19,35	19,43	Subadult juvenile	III
AR00-M-S41-5	Dp3+Dp4+M1	right	Dp4	12,36	12,88	10,37	10,87	Subadult juvenile	II
			M1	19,61	20,25	18,56	18,35		
AR00-M-S43-23	M1+M2	right	M1	nm	20,72	17,56	17,6	Subadult juvenile	III
			M2	21,66	21,81	20,48	20,59		
AR13-Pinf-P49-2	(Dp2+Dp3+Dp4)	right	Dp4	10,92	nm	10,27	13,12	Subadult juvenile	II
AR13-Pinf-R50-1	M1	left	M1	17,11	18,59	13,37	15,43	Subadult juvenile/Early prime	III/IV
AR16-Qa-P58-120	M2	left	M2	nm	nm	20,37	20,84	Subadult juvenile/Early prime	III/IV
AR17-Qa-R62-38	M2	left	M2	nm	16,12	nm	13,65	Early Prime	V

subadult juvenile, early prime, late prime and old age groups, which allows the construction of well-adjusted mortality profiles as well as establishing an MNI more adjusted to the original assemblage. The description of occlusal surface wear is the most reliable method and has allowed for adjusting the age more precisely. Brown and Chapman (1991b) point out that age identification through red deer mandibular teeth cannot always be given for a particular developmental stage. However, it is feasible to construct a useable chronology of dental development.

It has been verified that applying the polynomial regression equation of order 3 to the crowns of molars in the same individual does not consistently yield uniform results. For instance, consider the case of individual AR91-H-H56-1: the occlusal surface wear suggests it corresponds to a late prime adult individual, and the Paracone measurement of M1, M2, and M3 fall within the range of this age group. However, the values provided by the predictive equation vary among the different teeth, forcing the age to be estimated using the three teeth. Another example is AR92-I-L47-7, which is an M1 with a type of wear identified within the DAG V and DAG VI. The application of the predictive measurement provides an age of 6.9 years, falling within the late prime age range. Therefore, the minimum age inferred from wear alone would be prime adult, but the equation has allowed for an adjustment up to late prime. These discrepancies may arise because the dp4 and M3 samples are smaller, potentially leading to reduced robustness in the quadratic equation. Instead, the age assignments for M1 and M2 using the quadratic equation align well with those assigned through tooth wear, facilitating the straightforward classification of individuals within their respective DAGs. In all cases, the different methods complement each other. If the wear due to breakage or concretion of the occlusal surface cannot be described in a tooth, crown measurements can assign the animal to an age group, and vice versa. Additionally, if a tooth has a fractured crown line, the description of wear type can aid in age assignment.

The individuals identified in this study through the age assignment using maxillae have been compared with the information regarding mandibles from corresponding levels at the Abric Romaní, which was previously published (Marín et al., 2017, 2019). The majority of dental remains come from mandibles found in levels I, K, and L. While calculating the age of maxillae allows us to align the MNI with the age of the individuals, it does not alter the initial calculation made based on mandibles (Table 5). On the contrary, for level H, all the deer dental remains correspond to maxillary teeth. Thus, accurate identification of the age of the individuals is essential to know the MNI for this level and establish the mortality profile. In three cases, combining age information from maxillae and mandibles has resulted in a more precise adjustment of the mortality profile. These instances are observed in level I, M and level P. In level I, was identified one individual of DAG VI, not identified in the mandibular dentition. In level M, three individuals from DAG III were identified, increasing the count by two individuals compared to the initial calculation based on the mandibular dentition. Similarly, in the case of level P, an individual from DAG II was identified using maxillary teeth, incorporating a new individual that was not initially identified using the mandibular teeth.

In the analysis conducted by Klein et al. (1981) regarding the measurement crown height in deer teeth, they decided not to include upper teeth in their analysis because they considered that the wear patterns of the crown in red deer and other similar species were highly similar between the lower teeth and their corresponding upper teeth. However, the upper teeth analysis results through several proxies have verified that wear on the upper and lower teeth does not occur similarly within the same individual. In all observed cases, the wear on the occlusal surface is consistently greater in the mandibular teeth compared to the maxillary teeth (Figs. 3–6). Contrary to the belief held by Klein et al., (1981), it has been verified that measuring crown height for upper teeth is not inherently more challenging than for lower teeth in the sample we have examined. On the contrary, the junction line between the root and

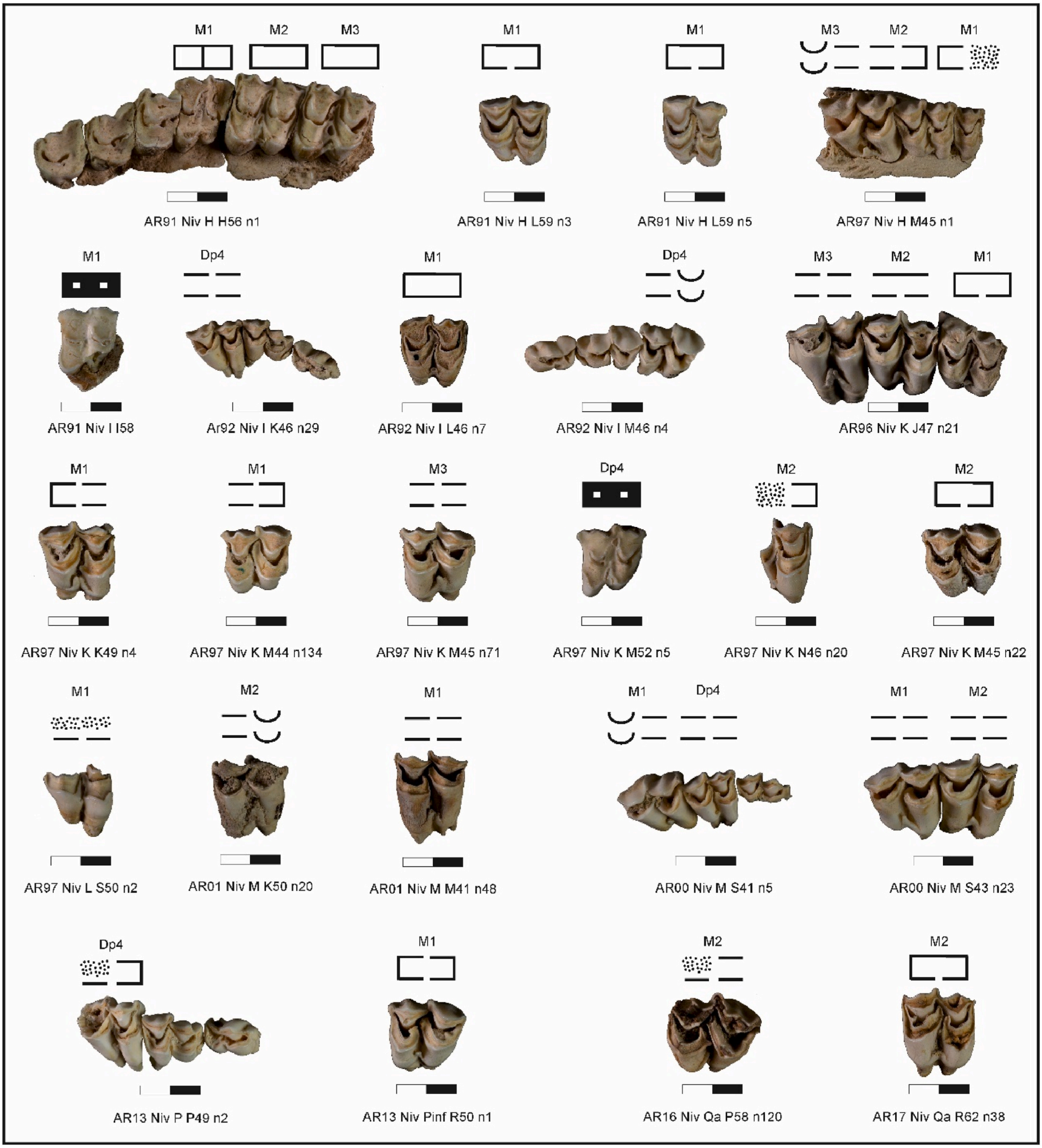

Fig. 7. Wear Stage symbols and dental remains of maxilla from the Abric Romaní rock shelter.

crown appears earlier in maxillary teeth than in mandibular teeth, facilitating the measurement process.

Finally, Klein et al. (1981) suggested that maxillary teeth are less frequent in archaeological assemblages due to poorer preservation or less frequent transportation. This assumption is, for the most part, applicable to many levels at Abric Romaní (Table 5). It is important to note that assemblages with a higher representation of maxillary teeth are also possible, as exemplified by level H at Abric Romaní, where all the red deer teeth belong to the maxilla. This particular assemblage highlights that the teeth of the mandible do not always have to be more abundant than those of the maxilla. Additionally, at levels M and P, incorporating the age of the maxilla has improved the accuracy of age adjustments for the jaws, leading to an increase in the Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) by one more individual, respectively. Archaeological examples exist where the proportion of dental remains in the maxilla is similar to or even higher

Table 5
Number of individuals identified using mandibular and maxillary teeth from levels at Abric Romaní, classified by their DAG.

Level	Element	DAG							
		I	II	III	IV	V	VI	VII	Total
H	Mandible								
	Maxilla				2	2			4
I	Mandible	3	2		1			1	7
	Maxilla	2					1	1	4
K	Mandible	2		2	2	2	1	2	11
	Maxilla			1	2	2			5
L	Mandible	2			1	2	1	1	7
	Maxilla				1				1
M	Mandible	1	1	1	1	1	2	1	8
	Maxilla		1	3					4
P	Mandible			1	1	1	1		4
	Maxilla		1	1					2

than that in the mandible. For instance, in the Covalejos cave (Cantabria, Spain), the total proportion of all isolated maxillary teeth (NR: 634) is very similar to isolated mandibular teeth (NR: 680). In the same site, at level C, the proportion is even higher in the maxilla (NR: 220) compared to the mandible (NR: 157) (Ugarte, 2021). This phenomenon is also observed in other European Middle Paleolithic sites, such as at level 5 of the Abri du Maras (Ardeche, France), where red deer remains are dominated mainly by maxillary teeth (Marín et al., 2020), in the rock shelter of Navalmaillo (Madrid, Spain), where the mandibular and maxillary remains of red deer present the same proportion (Moclán et al., 2021), as in the site of Valdegoba (Burgos, Spain) with 567 lower teeth and 548 upper teeth (Arceredillo and Fernández-Lomana, 2009) or San Bernardino cave (Alps, Italy) with a similar proportion of upper and lower teeth (13/13) (Terlato et al., 2021). Therefore, it becomes imperative to develop methods that allow us to accurately determine the age of these maxillary teeth, akin to the precision achieved with mandibular teeth. In other ungulate species such as the bison (Hill, 2008), horses (Fernandez and Legendre, 2003) and rhinoceroses (Garutt, 1992; Louguet-Lefebvre, 2005), both upper and lower teeth are used to determine the age of death. For this reason, providing a reliable reference for assigning the dental age of the maxilla in deer will enable the inclusion of a significant portion of material from archaeological assemblages in research.

6. Conclusions

The eruption and wear patterns of teeth, along with the measurement of crown height in the maxillary and mandibular dentition of red deer (*Cervus elaphus*), provide non-destructive and easily replicable methods for researchers to determine the age at death of animals. These methods will prove invaluable in refining the construction of MNE and MNI in archaeological sites. We have verified that occlusal surface wear is consistently more pronounced in mandibular than in maxillary teeth. Consequently, the wear patterns between these two dentitions cannot be considered equivalent, and it is incorrect to apply methods developed for the mandibular dentition to the maxillary dentition. This work will enable the inclusion of fossil specimens traditionally excluded from these analyses in examining mortality profiles at archaeological sites.

CRediT authorship contribution statement

Juan Marín: Conceptualization, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing, Supervision. **Palmira Saladié:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing - review & editing. **Concepción Azorit:** Data curation, Investigation, Writing - review & editing. **Antonio Rodríguez-Hidalgo:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing - review & editing.

Declaration of competing interest

None.

Acknowledgements

This research was conducted under the auspices of the following projects Grant PID2021-122355NB-C32, funded by MCIN/AEI/10.13039/501100011033 and by ERDF A way of making Europe, SGR 2021-01239 (AGAUR), and PID2022-1426610B–I00 (MICINN-FEDER). We also want to thank the RNM175 Research Group of the University of Jaén and the Andalusian Research Plan (PAIDI), Andalusian Regional Government. We thank the editor, Efthymia Nikita, and the reviewers, Teresa E. Steele and Camille Daujeard, for their comments and suggestions that improved the original version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2023.105934.

References

Arceredillo, D., Fernández-Lomana, J.C.D., 2009. Age of death and seasonality based on ungulate tooth remains from the upper Pleistocene site of Valdegoba (Burgos, Spain). J. Taphon. 7, 73–89.
Azorit, C., 1999. Estudio de la edad y su aplicación a la gestión cinegética del ciervo (Cervus elaphus hispanicus) en Sierra Morena. University of Jaén. Ph. D. dissertation.
Azorit, C., Analla, M., Carrasco, R., Calvo, J.A., Muñoz-Cobo, J., 2002. Teeth eruption pattern in red deer (Cervus elaphus hispanicus) in southern Spain. An. Biol. 24, 2002.
Azorit, C., Analla, M., Rosales, J.M.-C., Carrasco, R., 2003. Efecto del sexo, densidad y año de muerte, sobre el desgaste dental del ciervo (Cervus elaphus hispanicus Erxleben, 1777)(Mammalia, Cervidae) en Sierra Morena, España. Bol. Real Soc. Esp. Hist. Nat. Sección Biológica 98, 115–122.
Azorit, C., López-Montoya, A.J., Mateo-Calahorro, B.P., Analla, M., 2022. Seasonal investigation of fallow deer cellular cementum from Mediterranean ecosystems and its implications for reliable cementochronology applications. Quat. Int. 610, 133–143.
Azorit, C., Muñoz-Cobo, J., Hervés, J., Analla, M., 2004. Aging through growth marks in teeth of Spanish red deer. Wildl. Soc. Bull. 32, 702–710.
Azorit, C., Tellado, S., Oya, A., Moro, J., 2012. Seasonal and specific diet variations in sympatric red and fallow deer of southern Spain: a preliminary approach to feeding behaviour. Anim. Prod. Sci. 52, 720–727.
Azorit, C.A., 2011. Guía para la determinación de la edad del ciervo ibérico (Cervus elaphus hispanicus) a través de su dentición: revisión metodológica y técnicas de elección. An. Real Acad. Cienc. Vet. Andal. Orient. 24, 235–264.
Berlioz, E., Azorit, C., Blondel, C., Ruiz, M.S.T., Merceron, G., 2017. Deer in an arid habitat: dental microwear textures track feeding adaptability. Hystrix 28, 222–230.
Brown, W.A.B., Chapman, N.G., 1991a. Age assessment of fallow deer (Dama dama): from a scoring scheme based on radiographs of developing permanent molariform teeth. J. Zool. 224, 367–379. https://doi.org/10.1111/j.1469-7998.1991.tb06031.x.
Brown, W.A.B., Chapman, N.G., 1991b. Age assessment of red deer (Cervus elaphus): from a scoring scheme based on radiographs of developing permanent molariform teeth. J. Zool. 225, 85–97. https://doi.org/10.1111/j.1469-7998.1991.tb03803.x.
Brown, W.A.B., Chapman, N.G., 1991c. The dentition of red deer (Cervus elaphus): a scoring scheme to assess age from wear of the permanent molariform teeth. J. Zool. 224, 519–536. https://doi.org/10.1111/j.1469-7998.1991.tb03783.x.
Brugal, J.-P., David, F., 1993. Usure dentaire, courbe de mortalité et "saisonnalité" : les gisements du Paléolithique moyen à grands bovidés. In: Anthropozoologica. Presented at the Exploitation des animaux sauvages à travers le temps : XIIIe rencontres internationales d'archéologie et d'histoire d'Antibes – IVe colloque international de l'Homme et l'Animal. Société de recherche interdisciplinaire, Antibes, pp. 63–77.
Bunn, H.T., Gurtov, A.N., 2014. Prey mortality profiles indicate that Early Pleistocene Homo at Olduvai was an ambush predator. Quat. Int. 322– 323, 44–53. https://doi.org/10.1016/j.quaint.2013.11.002.
Bunn, H.T., Pickering, T.R., 2010a. Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running–hunting and passive scavenging by early Pleistocene hominins. Quat. Res. 74, 395–404. https://doi.org/10.1016/j.yqres.2010.07.012.
Bunn, H.T., Pickering, T.R., 2010b. Methodological recommendations for ungulate mortality analyses in paleoanthropology. Quat. Res. 74, 388–394. https://doi.org/10.1016/j.yqres.2010.07.013.

Burke, A., 2002. Palaeoethology as an archaeological tool: a model for the social and spatial behaviour of E. hydruntinus. In: Equids in Time and Space Papers in Honour of Véra Eisenmann. Presented at the Proceedings of the 9th Conference of the International Council of Archaeozoology, Durham, August 2002 Series Editors: Umberto Albarella, Keith Dobney and Peter Rowley-Conwy. Oxbow Books, Park End Place, Oxford, pp. 62–69.

Burke, A., Castanet, J., 1995. Histological Observations of cementum growth in horse teeth and their application to Archaeology. J. Archaeol. Sci. 22, 479–493. https://doi.org/10.1006/jasc.1995.0047.

Clutton-Brock, T.H., Guinness, F.E., Albon, S.D., 1982. Red Deer: Behavior and Ecology of Two Sexes, Wildlife Behavior and Ecology Series. University of Chicago Press.

Daujeard, C., Moncel, M.-H., 2010. On Neanderthal subsistence strategies and land use: a regional focus on the Rhone Valley area in southeastern France. J. Anthropol. Archaeol. 29, 368–391. https://doi.org/10.1016/j.jaa.2010.05.002.

Domínguez-Rodrigo, M., Barba, R., Soto, E., Sesé, C., Santonja, M., Pérez-González, A., Yravedra, J., Galán, A.B., 2015. Another window to the subsistence of Middle Pleistocene hominins in Europe: a taphonomic study of Cuesta de la Bajada (Teruel, Spain). Quat. Sci. Rev. 126, 67–95. https://doi.org/10.1016/j.quascirev.2015.08.020.

Fernandez, P., 2009. De l'estimation de l'âge individuel dentaire au modèle descriptif des structures d'âge des cohortes fossiles: l'exemple des" Equidae" et du time-specific model en contextes paléobiologiques pléistocenes. Bull. Société Préhistorique Fr. 5–14.

Fernandez, P., Legendre, S., 2003. Mortality curves for horses from the Middle Palaeolithic site of Bau de l'Aubesier (Vaucluse, France): methodological, palaeo-ethnological, and palaeo-ecological approaches. J. Archaeol. Sci. 30, 1577–1598. https://doi.org/10.1016/S0305-4403(03)00054-2.

Fichant, R., 2003. Le Cerf: Biologie, Comportement, Gestion. Editions du Gerfaut, Paris.

Frison, G.C., 1984. The Carter/Kerr-McGee Paleoindian site: Cultural resource management and archaeological research. Am. Antiq. 49, 288–314. https://doi.org/10.2307/280020.

Frison, G.C., Reher, C.A., 1970. Appendix I: age determination of buffalo by teeth eruption and wear. Plains Anthropol. 15, 46–66.

Garutt, N.V., 1992. Ontogenez zubnoj sistemy scerstistogo nosoroga coelodonta antiquitatis (Blumenbach, 1799). Istor. Krupnyh Mlekopit Ptiz Sev. Evrazii Skt Petersburg Ross. Akad Nauk Zool Inst 246, 81–102.

Gaudzinski, S., Roebroeks, W., 2000. Adults only. Reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, Northern Germany. J. Hum. Evol. 38, 497–521. https://doi.org/10.1006/jhev.1999.0359.

Hill, M.G., 2008. Paleoindian Subsistence Dynamics on the Northwestern Great Plains: Zooarchaeology of the Agate Basin and Clary Ranch Sites. British Archaeological Reports Limited.

Klein, R.G., 1982. Age (mortality) profiles as a Means of distinguishing hunted species from scavenged ones in stone age archeological sites. Paleobiology 8, 151–158. https://doi.org/10.1017/S0094837300004498.

Klein, R.G., 1978. Stone age predation on large African bovids. J. Archaeol. Sci. 5, 195–217. https://doi.org/10.1016/0305-4403(78)90040-7.

Klein, R.G., Cruz-Uribe, K., 1984. The Analysis of bones from archaeological sites. Chicago University Press, Chicago.

Klein, R.G., Wolf, C., Freeman, L.G., Allwarden, K., 1981. The use of dental crown heights for constructing age profiles of red deer and similar species in archaeological samples. J. Archaeol. Sci. 8, 1–31. https://doi.org/10.1016/0305-4403(81)90010-8.

Kolb, C., Scheyer, T.M., Lister, A.M., Azorit, C., de Vos, J., Schlingemann, M.A., Rössner, G.E., Monaghan, N.T., Sánchez-Villagra, M.R., 2015. Growth in fossil and extant deer and implications for body size and life history evolution. BMC Evol. Biol. 15, 1–15.

Kurtén, B., 1953. On the Variation and Population Dynamics of Fossil and Recent Mammal Populations.

Levine, M.A., 1982. The use of crown height measurements and eruption-wear sequences to age horse teeth. In: Ageing and Sexing Animal Bones from Archaeological Sites. Oxford, pp. 223–250.

Livraghi, A., Rivals, F., Rendu, W., Peresani, M., 2022. Neanderthals' hunting seasonality inferred from combined cementochronology, mesowear, and microwear analysis: case studies from the Alpine foreland in Italy. Archaeol. Anthropol. Sci. 14, 51. https://doi.org/10.1007/s12520-022-01514-5.

Louguet-Lefebvre, S., 2005. Les mégaherbivores (éléphantidés et rhinocérotidés) au Paléolithique moyen en Europe du Nord-Ouest: paléoécologie, taphonomie et aspects palethnographiques. BAR Publishing.

Lowe, V.P.W., 1967. Teeth as indicators of age with special reference to Red deer (Cervus elaphus) of known age from Rhum. J. Zool. 152, 137–153. https://doi.org/10.1111/j.1469-7998.1967.tb01881.x.

Lubinski, P.M., O'brien, C.J., 2001. Observations on seasonality and mortality from a recent catastrophic death assemblage. J. Archaeol. Sci. 28, 833–842. https://doi.org/10.1006/jasc.2000.0603.

Mariezkurrena, K., 1983. Contribucioón al conocimiento del desarollo de la denticioón y el esqueleto poscraneal de Cervus elaphus. Munibe Soc. Cienc. Aranzadi 35, 149–202.

Marín, J., Daujeard, C., Saladié, P., Rodríguez-Hidalgo, A., Vettese, D., Rivals, F., Boulbes, N., Crégut-Bonnoure, E., Lateur, N., Gallotti, R., Arbez, L., Puaud, S., Moncel, M.-H., 2020. Neanderthal faunal exploitation and settlement dynamics at the Abri du Maras, level 5 (south-eastern France). Quat. Sci. Rev. 243, 106472 https://doi.org/10.1016/j.quascirev.2020.106472.

Marín, J., Rodríguez-Hidalgo, A., Vallverdú, J., Gómez de Soler, B., Rivals, F., Rabuñal, J. R., Pineda, A., Chacón, M.G., Carbonell, E., Saladié, P., 2019. Neanderthal logistic mobility during MIS3: zooarchaeological perspective of abric Romaní level P (Spain). Quat. Sci. Rev. 225, 106033 https://doi.org/10.1016/j.quascirev.2019.106033.

Marín, J., Saladié, P., Rodríguez-Hidalgo, A., Carbonell, E., 2017. Neanderthal hunting strategies inferred from mortality profiles within the Abric Romaní sequence. PLoS One 12, e0186970. https://doi.org/10.1371/journal.pone.0186970.

Moclán, A., Huguet, R., Márquez, B., Laplana, C., Galindo-Pellicena, M.Á., García, N., Blain, H.-A., Álvarez-Lao, D.J., Arsuaga, J.L., Pérez-González, A., Baquedano, E., 2021. A neanderthal hunting camp in the central system of the Iberian Peninsula: a zooarchaeological and taphonomic analysis of the Navalmaíllo Rock Shelter (Pinilla del Valle, Spain). Quat. Sci. Rev. 269, 107142 https://doi.org/10.1016/j.quascirev.2021.107142.

Payne, S., 1987. Reference codes for wear states in the mandibular cheek teeth of sheep and goats. J. Archaeol. Sci. 14, 609–614. https://doi.org/10.1016/0305-4403(87)90079-3.

Payne, S., 1973. Kill-off patterns in sheep and goats: the mandibles from aşvan kale. Anatol. Stud. 23, 281–303. https://doi.org/10.2307/3642547.

Pérez-Barbería, F.J., Carranza, J., Sánchez-Prieto, C., 2015. Wear fast, die young: more worn teeth and shorter lives in iberian compared to scottish red deer. PLoS One 10, e0134788. https://doi.org/10.1371/journal.pone.0134788.

Pike-Tay, A., 1991. Red Deer Hunting in the Upper Paleolithic of South-West France: A Study in Seasonality. BAR Publishing. https://doi.org/10.30861/9780860547181.

Riglet, P.H., 1977. Contribution aÁ l'eÂtude de l'aÂge du Cerf eÂlaphe (Cervus elaphus L.). In: Doctoral Thesis, 1±75. Ecole veÂteÂrinaire de Maison-Alfort (France).

Rodríguez-Hidalgo, A., Saladié, P., Ollé, A., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2017. Human predatory behavior and the social implications of communal hunting based on evidence from the TD10.2 bison bone bed at Gran Dolina (Atapuerca, Spain). J. Hum. Evol. 105, 89–122. https://doi.org/10.1016/j.jhevol.2017.01.007.

Rolett, B.V., Chiu, M., 1994. Age estimation of prehistoric pigs (Sus scrofa) by molar eruption and attrition. J. Archaeol. Sci. 21, 377–386. https://doi.org/10.1006/jasc.1994.1036.

Steele, T.E., 2002. Reed deer: their ecology and how they were hunted by late Pleistocene hominids in Western Europe. Department of Anthropology, Stanford University. Ph. D. dissertation.

Steele, T.E., 2004. Variation in mortality profiles of red deer (Cervus elaphus) in Middle Palaeolithic assemblages from western Europe. Int. J. Osteoarchaeol. 14, 307–320. https://doi.org/10.1002/oa.763.

Steele, T.E., Weaver, T.D., 2012. Refining the Quadratic Crown Height Method of age estimation: do elk teeth wear quadratically with age? J. Archaeol. Sci. 39, 2329–2334. https://doi.org/10.1016/j.jas.2012.02.017.

Stiner, M.C., 2006. Middle paleolithic subsistence ecology in the mediterranean region. In: Hovers, E., Kuhn, S.L. (Eds.), Transitions before the Transition: Evolution and Stability in the Middle Paleolithic and Middle Stone Age. Springer US, Boston, MA, pp. 213–231. https://doi.org/10.1007/0-387-24661-4_12.

Stiner, M.C., 1990. The use of mortality patterns in archaeological studies of hominid predatory adaptations. J. Anthropol. Archaeol. 9, 305–351. https://doi.org/10.1016/0278-4165(90)90010-B.

Terlato, G., Lubrano, V., Romandini, M., Marín-Arroyo, A.B., Benazzi, S., Peresani, M., 2021. Late neanderthal subsistence at san bernardino cave (berici hills-NORTHEASTERNITALY) inferred from zooarchaeological data.: neanderthal subsistence in northeastern Italy. Alp. Mediterr. Quat. 34, 213–235.

Ugarte, P.M.C., 2021. Estudio de la fauna de macromamíferos de la cueva de Covalejos. Presented at the La cueva de Covalejos (Velo de Piélagos, Cantabria): ocupaciones neandertales y sapiens en la cueva baja del río Pas. Actuaciones arqueológicas, 1997-1999 y 2002. Museo de Prehistoria y Arqueología de Cantabria, pp. 106–125.

Valensi, P., Psathi, E., 2004. Faunal exploitation during the Middle palaeolithic in south-eastern France and north-western Italy. Int. J. Osteoarchaeol. 14, 256–272. https://doi.org/10.1002/oa.760.