

## **Osteometric Analysis of the Scapula and Humerus of Rangifer tarandus and Cervus elaphus: a Contribution to the Discrimination of Late Pleistocene Cervids**

Authors: Castaños, Jone, Castaños, Pedro, Murelaga, Xabier, Alonso-Olazabal, Ainhoa, Ortega, Luis Angel, et al.

Source: Acta Palaeontologica Polonica, 59(4) : 779-786

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2012.0027>

---

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Osteometric analysis of the scapula and humerus of *Rangifer tarandus* and *Cervus elaphus*: A contribution to the discrimination of Late Pleistocene cervids

JONE CASTAÑOS, PEDRO CASTAÑOS, XABIER MURELAGA, AINHOA ALONSO-OLAZABAL, LUIS ANGEL ORTEGA, and MARIA CRUZ ZULUAGA



Castaños, J., Castaños, P., Murelaga, X., Alonso-Olazabal, A., Ortega, L.A., and Cruz Zuluaga, M. 2014. Osteometric analysis of the scapula and humerus of *Rangifer tarandus* and *Cervus elaphus*: A contribution to the discrimination of Late Pleistocene cervids. *Acta Palaeontologica Polonica* 59 (4): 779–786.

Fossil remains of reindeer (*Rangifer tarandus*) occurring outside their present range are an important indicator of formerly cold climatic conditions, but are easily confused with those of the red deer (*Cervus elaphus*). The locality of Kiputz IX has yielded one of the best-preserved Late Pleistocene reindeer populations of the southern Pyrenees, occurring in association with *Bison priscus* and the much more abundant *Cervus elaphus*. Fossil remains from this site are mostly complete and not affected by human intervention, thus creating the perfect conditions for reliable osteometric analyses. Here, we quantify diagnostic morphological features of the scapula and the humerus of *Cervus elaphus* and *Rangifer tarandus* to establish the potential of these bones to aid in interspecific discrimination. In the case of the scapula, the best species discriminator is the ratio of the minimum anteroposterior diameter of the scapular neck and the development of the articular process, while the breadth of the trochlea is the best discriminator in the case of the humerus.

**Key words:** Mammalia, *Rangifer tarandus*, *Cervus elaphus*, scapula, humerus, osteometric data, Pleistocene, southern Pyrenees.

Jone Castaños [jcastanosdlf@yahoo.es] and Xabier Murelaga [xabier.murelaga@ehu.es], Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea, UPV/EHU, Apdo. 644, E-48080 Bilbao, Spain;

Pedro Castaños [pedrocastanos@yahoo.es], Sociedad de Ciencias Aranzadi, Geo-Q, E-48940 Leioa, Spain;

Ainhoa Alonso-Olazabal [ainhoa.alonso@ehu.es], Luis Angel Ortega [luis.ortega@ehu.es], and Maria Cruz Zuluaga [mcruz.zuluaga@ehu.es], Departamento de Mineralogía y Petrología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea, UPV/EHU, Apdo. 644, E-48080 Bilbao, Spain.

Received 27 February 2012, accepted 18 November 2012, available online 7 December 2012.

Copyright © 2014 J. Castaños et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

## Introduction

Faunal assemblages from archaeological sites are an important source of climatic and environmental data. In some cases, specific taxa can be used to interpret environmental and/or climatic changes. In Europe, reindeer remains (*Rangifer tarandus*) are often abundant in assemblages from the Late Pleistocene (Weinstock 2000b; Sommer and Nadachowski 2006 and references therein), with the exception of the southern Pyrenees, where red deer (*Cervus elaphus*) are usually dominant (Altuna 1972, 1985, 1986; Altuna and Straus 1976; Castaños 1984; Altuna and Mariezkurrena 1985, 2000; Altuna et al. 2002; Álvarez-Lao and García-García 2006).

While this scarcity may indicate that reindeer were genuinely rare, it could also be a result of the difficulty of telling apart cervid remains. Most southern Pyrenean sites are human settlements, thus making most faunal assemblages a result of hunting activity (Altuna 1992; Domingo et al. 2005–06; Costamagno and Fano 2006; Marín Arroyo et al. 2009; Straus 2009; González Morales and Straus 2009; Kuntz and Costamagno 2011). Highly fragmented bones, the absence or scarcity of some skeletal elements (e.g., ribs and vertebrae), and an abundance of limb bones often characterize such anthropogenic assemblages (Binford 1978; Enloe 2003; Lam et al. 1998, 2003; Stiner 2002; Yeshurun et al. 2007; Rendu 2010), thus making it difficult to discriminate between taxa. Sexual dimorphism and the presence of differ-

ent age classes, as well as post-depositional alteration (e.g., attrition) may pose additional problems (Lyman 1984, 1985, 1994, 2006; Lam et al. 2003).

To address some of these issues, we performed a morphometric analysis of reindeer and red deer remains from the locality of Kiputz IX (Mutriku, Gipuzkoa), with the aim to identify osteometric criteria which could aid in their differentiation. In particular, our study focused on the humerus and scapula, owing to their relative abundance at the site. Cervid humeri, which owing to their robustness are commonly found as fossils, have been included in a variety of previous osteometric analyses (Lister 1996; Weinstock 2000a, b; Enloe 2003; Breda 2005; Lyman 2006; Liouville 2007; Puputti and Niskanen 2009; van Kolschoten et al. 2011). By contrast, scapulae are relatively rare, resulting in a lack of comparative data. The large number of preserved scapulae and humeri at Kiputz IX thus offers an opportunity to establish a set of diagnostic characters for the former, while at the same time allowing us to validate our results and compare them with previous studies based on the humerus.

*Institutional abbreviations.*—BGG, Basque Government official repository institution for the District of Guipuzkoa, San Sebastián, Spain.

*Other abbreviations.*—BT, breadth of the trochlea; Dd, anteroposterior depth; GLP, length of the glenoid process; LG, length of the glenoid cavity; SLC, diameter of the scapular neck (collum scapulae).

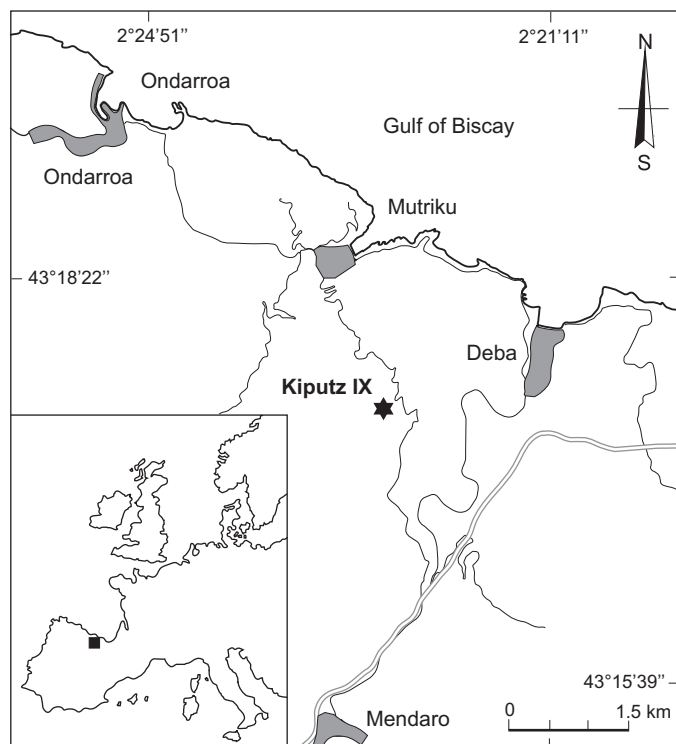


Fig. 1. Geographic location of Kiputz IX (Mutriku, Gipuzkoa).

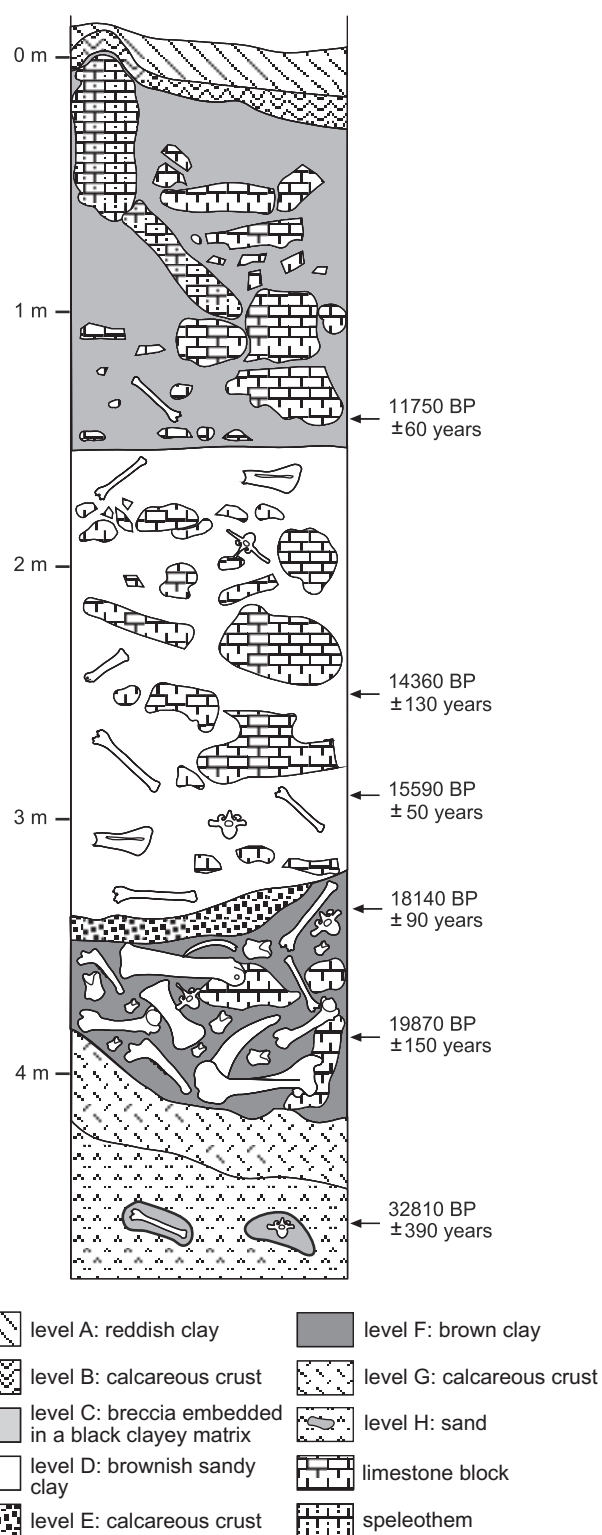


Fig. 2. Stratigraphic section and radiocarbon dates for the locality of Kiputz IX.

## Geological setting

The locality of Kiputz IX (Mutriku, Gipuzkoa) is one of several, mostly Late Pleistocene, archaeological sites located in caves and rock shelters along the Cantabrian Cornice (Fig. 1;

Table 1. Faunal assemblage preserved at the locality of Kiputz IX, southern Pyrenees, Spain. n, number of identified specimens.

	Level C		Level D		Level F		Level H	
	n	%	n	%	n	%	n	%
<i>Cervus elaphus</i>	8	19.5	1164	32.6	5319	52.3	150	63.6
<i>Rangifer tarandus</i>	8	19.5	647	18.1	1620	15.9	15	6.4
<i>Bison priscus</i>	5	12.2	959	26.8	2532	24.9	9	3.8
<i>Rupicapra pyrenaica</i>	2	4.9	42	1.2	94	0.9	23	9.7
<i>Equus caballus</i>		0.0	87	2.4	108	1.1	1	0.4
<i>Ursus arctos</i>		0.0	23	0.6	13	0.1	4	1.7
<i>Vulpes vulpes</i>	5	12.2	249	7.0	46	0.5	6	2.5
<i>Lepus europaeus</i>		0.0	5	0.1	7	0.1	2	0.8
<i>Pica pica</i>	1	2.4	61	1.7	24	0.2	3	1.3
Indeterminate	8	19.5	128	3.6	164	1.6	11	4.7
Total	41		3573		10178		236	

Table 2. Identified elements of *Rangifer tarandus* and *Cervus elaphus* preserved at the locality of Kiputz IX, southern Pyrenees, Spain. MNI, minimum number of individuals; n, number of identified elements.

	Kiputz IX total		Level D			Level F		
	n	MNI	n		MNI	n		MNI
			left	right		left	right	
<i>Rangifer tarandus</i>								
Scapula	22	12	2	2	2	8	8	8
Humerus	27	17	1	1	1	12	12	12
Femur	28	14	2	1	2	9	9	9
Astragalus	42	21	9	7	9	13	12	13
Calcaneum	27	14	5	4	5	9	10	10
Radius	30	15	2	2	2	7	7	7
Metacarpal	32	16	3	4	4	8	8	8
Metatarsal	21	11	2	2	2	8	8	8
Tibia	32	16	3	3	3	11	12	12
<i>Cervus elaphus</i>								
Scapula	42	24	4	4	4	17	17	17
Humerus	27	16	7	6	7	19	19	19
Femur	31	16	2	3	3	13	13	13
Astragalus	44	22	10	10	10	33	33	33
Calcaneum	19	10	3	2	3	12	12	12
Radius	53	27	6	7	7	25	25	25
Metacarpal	39	20	3	4	4	26	27	27
Metatarsal	34	17	6	4	6	26	25	26
Tibia	40	20	3	4	4	28	29	29

see also references summarized in Sommer and Nadachowski 2006 and Sommer et al. 2007). At Kiputz IX, the presence of a karstic cavity with a floor area of 6 m<sup>2</sup> has acted as a natural faunal trap (pit-fall) and now contains 4.2 m of sediment infill, divided into eight stratigraphic levels (levels A to H). The age of the sequence was established by radiocarbon dating of red deer bones (performed at Beta Analytic, Florida, USA), and falls into oxygen isotope stage 2 (OIS-2). The radiocarbon ages for level F range from 19870 ± 150 years BP to 18140 ± 90 years BP, and for level D from 15590 ± 50 years BP to 14360 ± 130 years BP (Fig. 2). The site contains a well-preserved fossil bone assemblage, consisting of mostly complete material and hardly affected by post-depositional

alteration, and with no signs of animal or human predation (Castaños et al. 2006).

All bone remains were systematically retrieved and recorded, and are now housed at BGG. The highest density of fossil material occurred within levels D and F (Castaños et al. 2006; Fig. 2, Table 1). Isolated elements dominate the assemblage and indicate the presence of a variety of mammals, including: *Cervus elaphus*, *Bison priscus*, *Rangifer tarandus*, *Rupicapra pyrenaica*, *Equus caballus*, *Ursus arctos*, *Vulpes vulpes*, *Lepus europaeus*, *Microtus agrestis-arvalis*, *M. (Alexandromys) oeconomicus*, *Terricola* sp., *Arvicola terrestris*, *Sorex* sp., *Crociodura* sp., *Apodemus* sp., and *Talpa* sp., as well as several birds and amphibians (Castaños et al. 2006). *Bison priscus*, *Cervus elaphus*, and *Rangifer tarandus* are the most common species (Table 1), with red deer clearly (at least 27 individuals) dominating the site. Nevertheless, the locality also contains one of the best-preserved reindeer populations (2290 elements, equaling 16% of the total) of the southern Pyrenees (Altuna 1992; Sommer and Nadachowski 2006; Kuntz and Costamagno 2011), representing at least 21 individuals (Table 2).

## Material and methods

We started by visually comparing the humerus and scapula of *Rangifer tarandus* and *Cervus elaphus* to identify their most diagnostic features, following which the latter were quantified (Fig. 3) and, where possible, compared to previously

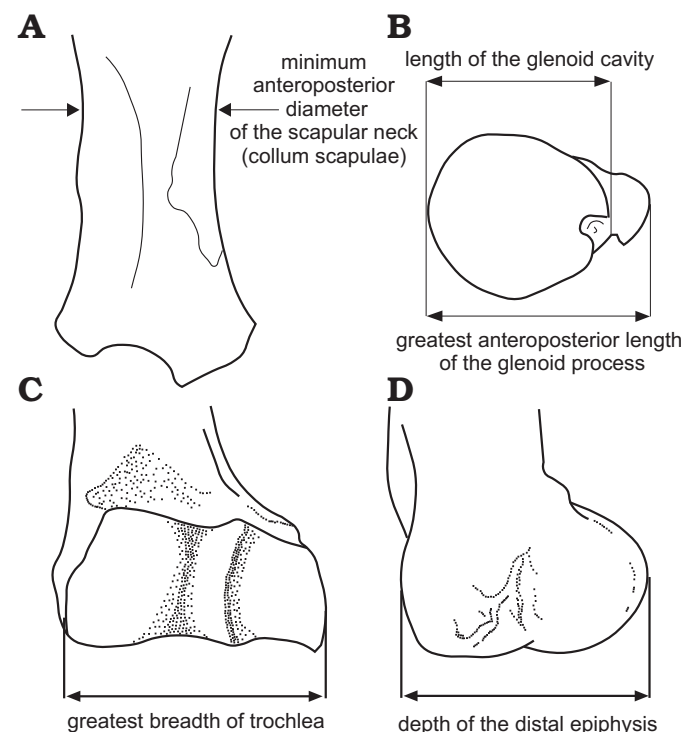


Fig. 3. Osteological measurements of the scapula (A, B) and the humerus (C, D) (modified from Weinstock 2000a). All drawings are based on *Rangifer tarandus*.



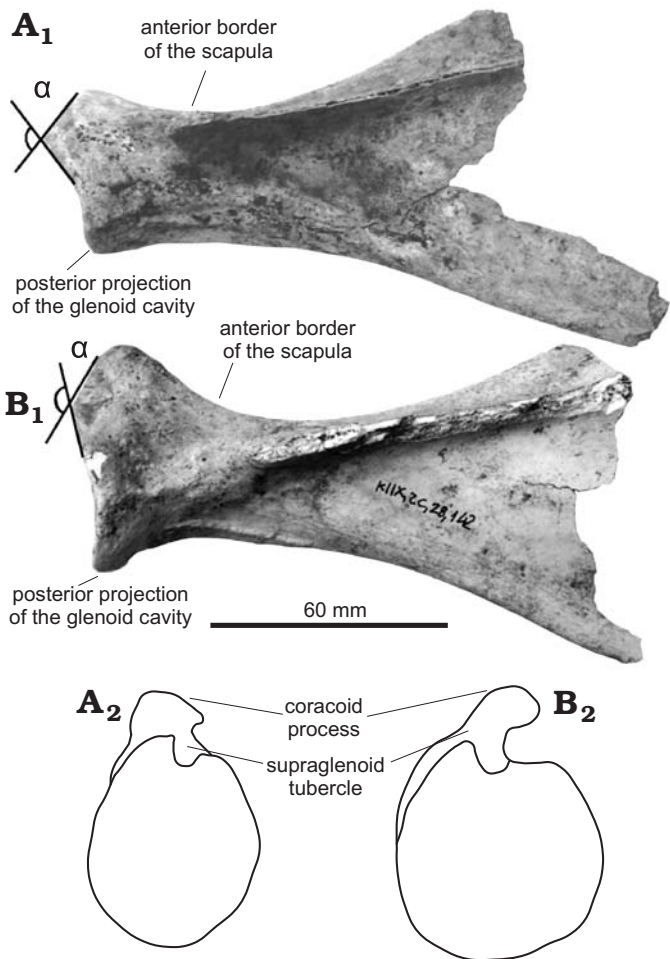


Fig. 4. Morphological features distinguishing the scapulae of the cervid mammals *Rangifer tarandus*, BGG KI-IX.2D.39.618 (A) and *Cervus elaphus*, BGG KI-IX.2C.28.142 (B), from Kiputz IX (southern Pyrenees, Spain), Late Pleistocene, in lateral (A<sub>1</sub>, B<sub>1</sub>) and distal (A<sub>2</sub>, B<sub>2</sub>) views; α, the angle formed by the glenoid cavity and the supraglenoid tubercle.

published data from the Western European Late Pleistocene (Weinstock 2000a; Liouville 2007). Only well-preserved bones were chosen for measurement. Tooth wear stages indicate a predominance of adult reindeer, compared to a wider range of differently-aged red deer individuals. To minimize age effects, we restricted our analysis to humeri with fused

distal epiphyses and scapulae with fused supraglenoid processes. While sexual dimorphism may also have an influence on body size, previous studies only reported slight gender differences in the size of the humerus and scapula (Weinstock 2000b; Enloe 2003; Mariezkurieta and Altuna 1983). In addition, analyses of coeval remains from other sites did not reveal any significant body-size variations in either taxon. Specimens from levels D and F were generally similar in size, and hence were analyzed together. In total, we measured 27 reindeer and 27 red deer humeri, and 22 reindeer and 42 red deer scapulae (Supplementary Online Material available at [http://app.pan.pl/SOM/app59-Castanos\\_et\\_al\\_SOM.pdf](http://app.pan.pl/SOM/app59-Castanos_et_al_SOM.pdf)). All measurements (in mm) were taken following the criteria in Driesch (1976). We used two different calipers depending on the size of the bone, resulting in an error margin of <0.25 mm for measurements over 20 mm, and <0.1 mm for measurements less than 20 mm. Finally, we compared our data for both species using student t-tests, carried out in SPSS® 19.

Results and discussion

**Scapula.**—We found the shape of the scapula (triangular or subtriangular) and the relative breadth of the supraspinous and infraspinous fossae to be of little diagnostic value, as they are rarely preserved. By contrast, the articular process is relatively robust and comprises several species-specific features. In lateral view, the anterior border of the scapula is clearly concave in *Rangifer tarandus*, but almost straight in *Cervus elaphus* (Fig. 4A<sub>1</sub>, B<sub>1</sub>). Similarly, the lateral profile of the supraglenoid tubercle and the outline of the glenoid cavity essentially form a right angle in *R. tarandus* (Fig. 4A<sub>2</sub>, B<sub>2</sub>), but an obtuse angle in *C. elaphus*. The posterior border of the glenoid cavity is located at the same level as the posterior border of the scapula in *R. tarandus*, while being projected far posterior to the latter in *C. elaphus* (Fig. 4A<sub>3</sub>, B<sub>3</sub>). The rim of the glenoid cavity varies from circular to ellipsoidal in both species, but the circular shape occurs more commonly in *C. elaphus*. Finally, the coracoid process is twisted medially (Fig. 4A<sub>4</sub>), and the supraglenoid tubercle is transversely broad and barely protrudes from the outline of the glenoid cavity in proximal view in *R. tarandus* (Fig. 4A<sub>5</sub>).

Table 3. Descriptive statistics and results of the Student’s t-tests performed on the scapular measurements of *Rangifer tarandus* and *Cervus elaphus* from Kiputz IX (southern Pyrenees, Spain), Late Pleistocene. Abbreviations: CV, coefficient of variation (in %); GLP, greatest anteroposterior length of the glenoid process; LG, greatest anteroposterior length of the glenoid cavity; Min, minimum; Max, maximum; n, sample number; p, p-value arising from the Student’s t-test; s.d., standard deviation; SLC, minimum anteroposterior diameter of the scapular neck (collum scapulae); t, Student’s t-test statistic.

Measurement/ Index	<i>Rangifer tarandus</i>						<i>Cervus elaphus</i>						t	p
	n	Min	Max	Mean	s.d	CV	n	Min	Max	Mean	s.d.	CV		
GLP	20	43.5	50.5	47.4	2.22	4.7	40	58	73	62.5	3.99	6.4	12.07	<0.001
LG	22	34.0	41.0	37.9	1.82	4.8	40	44	57	48.2	3.05	6.3	12.40	<0.001
SLC	22	30.5	40.5	36.7	2.92	8.0	41	31.5	44.5	35.7	3.16	8.9	0.74	0.234
I1	20	76.3	84.8	80.5	0.02	3.1	40	70.4	83.5	77.3	0.02	3.2	4.41	<0.001
I2	20	69.1	83.5	77.6	0.04	5.4	39	50	65.9	57.4	0.04	6.4	14.92	<0.001
I3	22	92.5	116.4	103.7	0.06	6.0	39	118	160.6	135.1	0.08	5.9	15.13	<0.001

By contrast, the coracoid process is less twisted, and the supraglenoid tubercle is transversely narrow and protrudes strongly in *C. elaphus* (Fig. 4B<sub>4</sub>, B<sub>5</sub>).

Based on these observations, we measured the greatest anteroposterior length of the glenoid cavity (LG), the greatest anteroposterior length of the glenoid process including the supraglenoid tubercle (GLP), and the minimum anteroposterior diameter of the scapular neck (collum scapulae) (SLC) (Fig. 3, Table 3; SOM: table S1). Of these three measurements, GLP best discriminates between *Rangifer tarandus* and *Cervus elaphus* (Fig. 5; student t-test  $p < 0.001$ ; Table 3). Within the respective populations, the bimodal distribution of the reindeer data might reflect sexual dimorphism, whereas the multimodal distribution of the red deer data might be the result either sexual dimorphism and/or intraspecific vari-

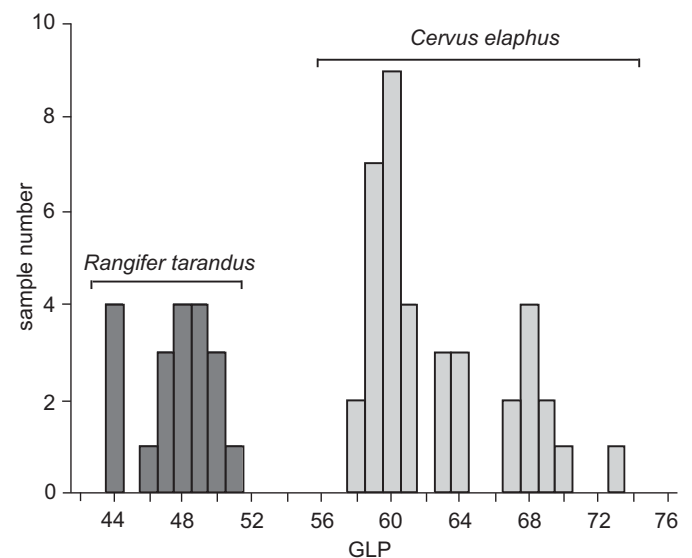


Fig. 5. Histogram of the greatest anteroposterior length of the glenoid process of *Rangifer tarandus* and *Cervus elaphus* from Kiputz IX (southern Pyrenees, Spain), Late Pleistocene. GLP, greatest anteroposterior length of the glenoid process (in mm).

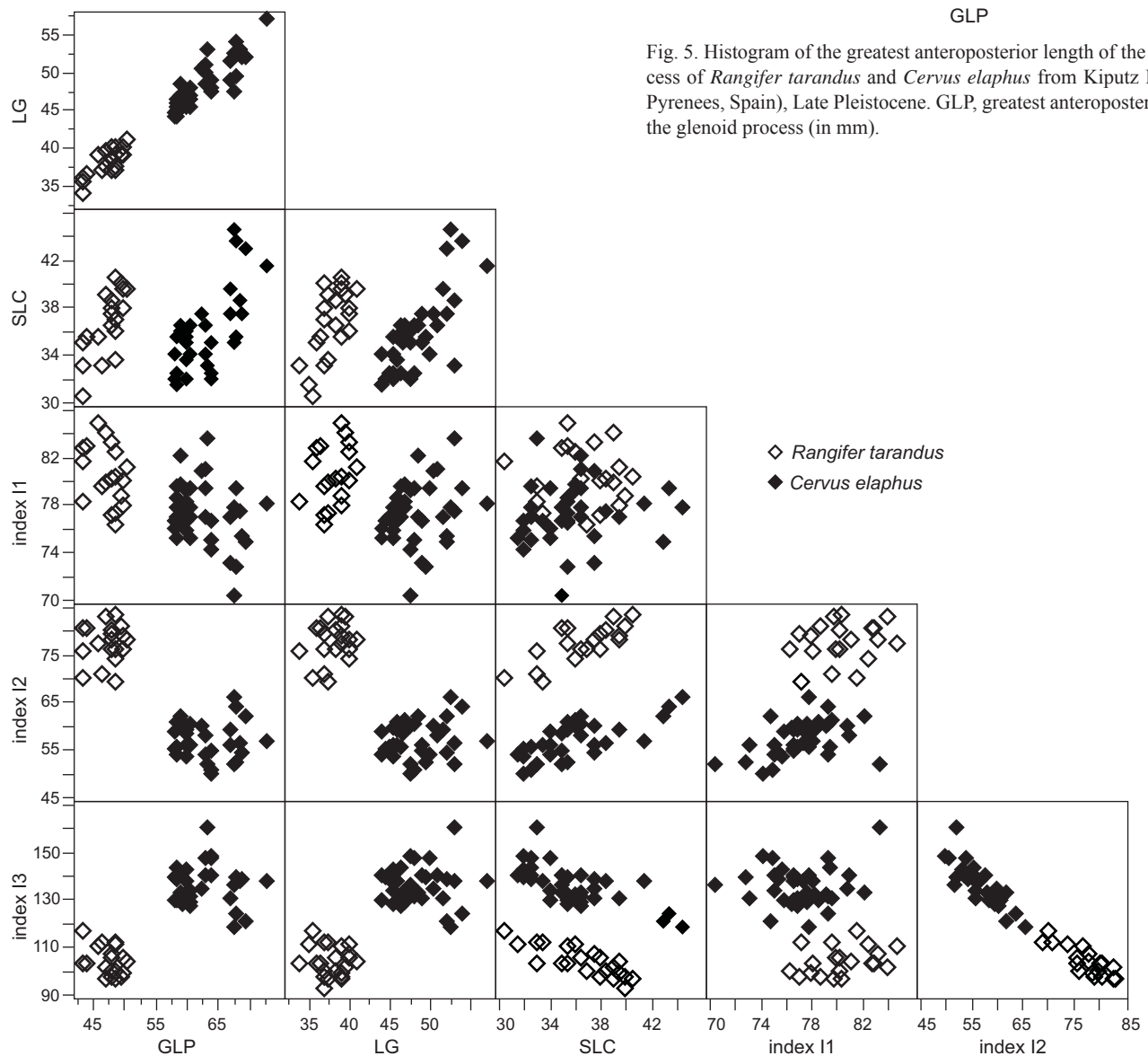


Fig. 6. Scatterplots of different combinations of scapular measurements and indices for *Rangifer tarandus* and *Cervus elaphus* from Kiputz IX (southern Pyrenees, Spain), Late Pleistocene. Abbreviations: GLP, greatest anteroposterior length of the glenoid process; LG, greatest anteroposterior length of the glenoid cavity; SLC, minimum diameter of the scapular neck.

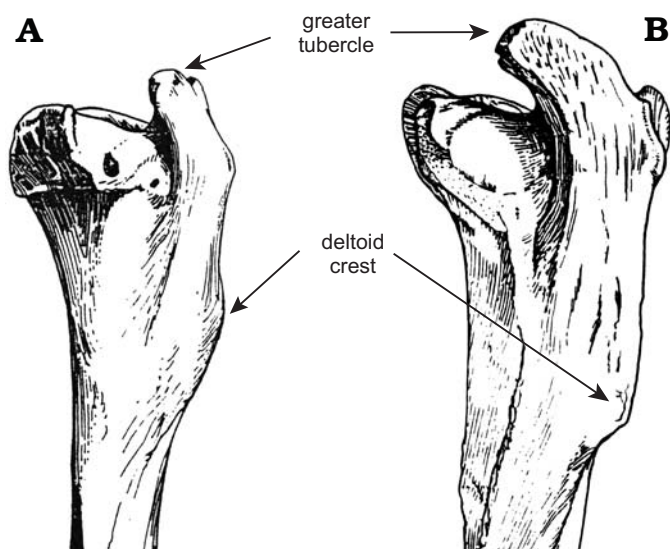


Fig. 7. Morphological features distinguishing the proximal portion of the humerus of *Rangifer tarandus* (A) and *Cervus elaphus* (B) (modified from Pales and García 1981).

ation. Besides GLP, LG also performs well in discriminating the two species ( $p < 0.001$ ), whereas SLC fails to do so at a statistically significant level ( $p = 0.234$ ; Table 3).

Different combinations of our three measurements provide additional diagnostic indices: (i) the ratio of LG to GLP (Index I1) is higher in *Rangifer tarandus* than in *Cervus elaphus* because of the greater protrusion of the supraglenoid tubercle in the latter; (ii) the ratio of SLC to GLP (Index I2) is also higher in *R. tarandus*, owing to its more massively built caudal border of the scapular neck and its smaller glenoid process; and (iii) the ratio of LG to SLC (Index I3) is higher in *C. elaphus* than in *R. tarandus*. While I1 reveals a statistically significant difference between the two species, their ranges of variation broadly overlap (*R. tarandus*: 76.3–84.8 mm; *C. elaphus*: 70.4–83.5), possibly because the larger supraglenoid tubercle of *C. elaphus* is counteracted by its equally enlarged glenoid cavity (Fig. 4). By contrast, I2 and I3 clearly distinguish the two taxa (Fig. 6, Table 3).

**Humerus.**—The main difference between the humeral diaphyses of *Rangifer tarandus* and *Cervus elaphus* consists of its slightly flattened shape in *R. tarandus*, which is barely measurable. However, several diagnostic traits are present in the epiphyses. The proximal epiphysis shows three significant features: (i) the greater tubercle protrudes only slightly above the head in *R. tarandus*, whereas it is more pronounced in *C. elaphus* (Fig. 7A<sub>1</sub>, B<sub>1</sub>); (ii) the articular head is narrower in *R. tarandus* than in *C. elaphus*; and (iii) the deltoid crest, which extends from the lateral region of the base of the greater trochanter down to the dorsal half of the diaphysis, is nearly continuous in *R. tarandus*, whereas it forms a sharp corner in *C. elaphus* (Fig. 7A<sub>2</sub>, B<sub>2</sub>).

The narrowness of the reindeer humerus forms the basis of the interspecific differences expressed in the distal epiphysis. In anterior view, the radial (or coronoid) fossa

consists of a single, long cavity in *Rangifer tarandus* (Fig. 8A<sub>1</sub>), whereas it comprises two pits and a small bridge in *Cervus elaphus* (Fig. 8B<sub>1</sub>). In distal view, the lateral epicondyle of *R. tarandus* is less developed than the medial epicondyle (Fig. 8A<sub>2</sub>), whereas they are of similar size in *C. elaphus* (Fig. 8B<sub>2</sub>). In posterior view, the olecranon fossa of *R. tarandus* is narrower (Fig. 8A<sub>3</sub>, B<sub>3</sub>) and its medial epicondyle is transversely thicker than in *C. elaphus* (Fig. 8A<sub>4</sub>, B<sub>4</sub>). In addition, the medial and lateral epicondyles are almost parallel in *R. tarandus*, as opposed to being slightly curved or concave in *C. elaphus* (Fig. 8A<sub>4</sub>, B<sub>4</sub>). Finally, in

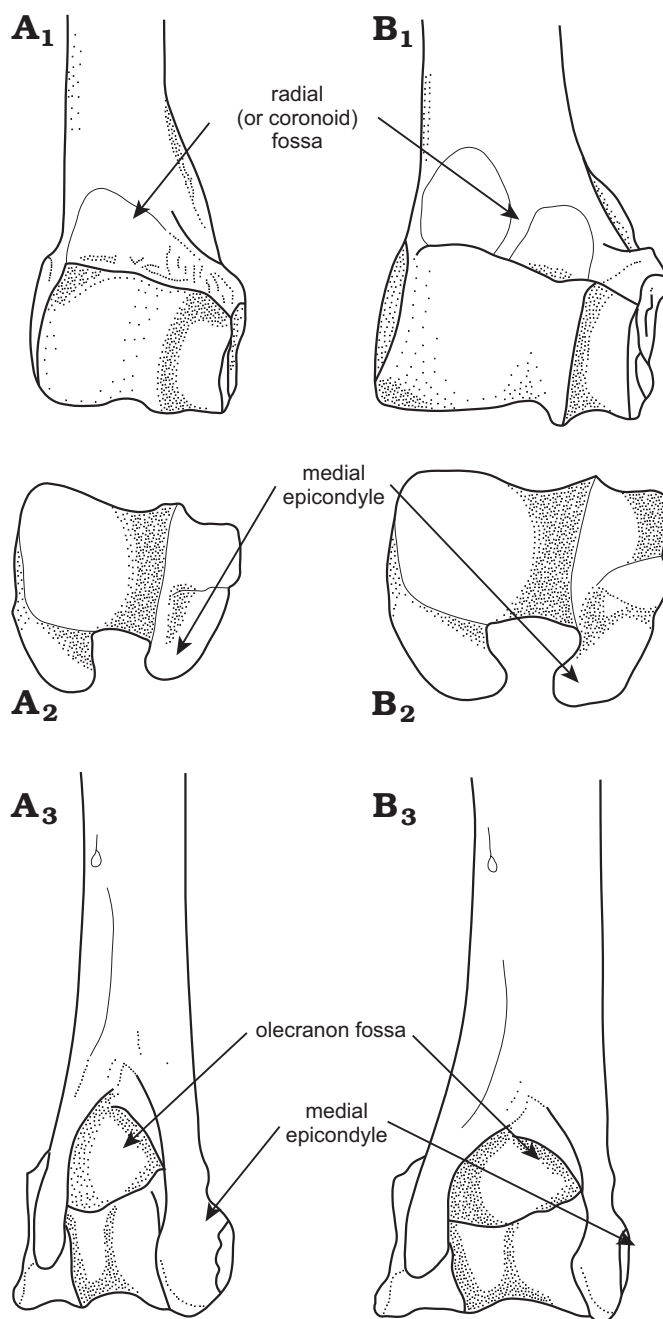


Fig. 8. Morphological features distinguishing the distal portion of the humerus of *Rangifer tarandus* (A) and *Cervus elaphus* (B), in anterior (A<sub>1</sub>, B<sub>1</sub>), distal (A<sub>2</sub>, B<sub>2</sub>), and posterior (A<sub>3</sub>, B<sub>3</sub>) views (modified from Breda 2005).



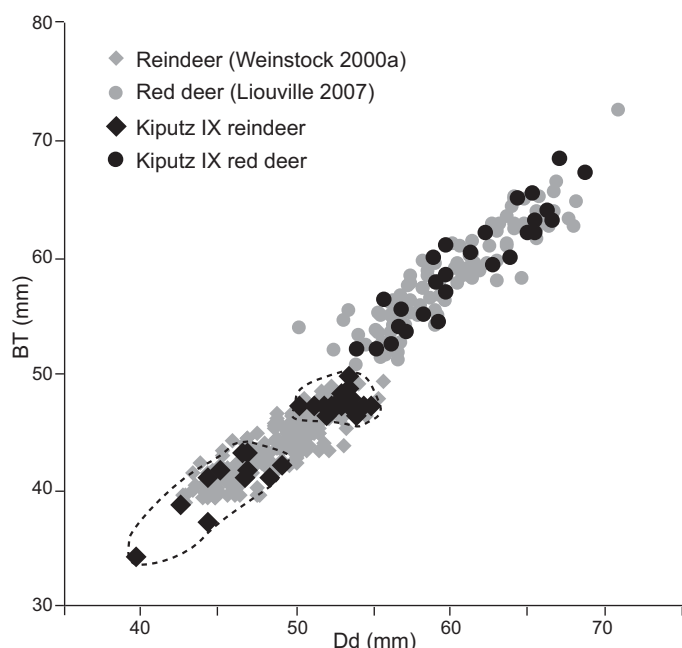


Fig. 9. Scatterplot of the greatest breadth of the trochlea (BT) vs. the depth of the distal epiphysis (Dd) of the humerus of *Rangifer tarandus* and *Cervus elaphus* from Kiputz IX and other European sites.

ventral view, the epicondylar crest terminates 10–15 mm before the nutrient foramen in *C. elaphus*, but extends all the way to the foramen in *R. tarandus*.

In order to quantify these observations, we measured the breadth of the trochlea (BT) and the anteroposterior depth (Dd) of the distal epiphysis (SOM: table S1; see also Weinstock 2000a; Liouville 2007; Puputti and Niskanen 2009), and compared our data to the 228 measurements of *Rangifer tarandus* reported by Weinstock (2000a) and the 111 measurements of *Cervus elaphus* of Liouville (2007). For both measurements, the values for *R. tarandus* are generally smaller than those for *C. elaphus* (Fig. 9). Although there is some overlap of the two species in terms of the depth of the distal epiphysis, they are clearly distinguished by the breadth of the trochlea. Within the reindeer population, the grouping of the data into two distinct clusters might be the result of sexual dimorphism.

## Conclusions

Our results reveal the scapulae of *Rangifer tarandus* and *Cervus elaphus* to be highly diagnostic, and provide several morphological and osteometric features distinguishing these two species. In particular, we observed clear differences in the greatest anteroposterior length of the glenoid process and the greatest anteroposterior length of the glenoid cavity. In addition, we propose two additional diagnostic indices based on ratios of these two measurements and the minimum anteroposterior diameter of the scapular neck. Overall, our findings provide a novel way of distinguishing between the fossil remains of different cervids, based on scapular data. Although

scapulae tend to be relatively rare in the fossil record, our results are applicable even in cases when only few and/or fragmentary remains are available. In terms of the humerus, we found the breadth of the trochlea to outperform the depth of the distal epiphysis as a useful species indicator.

## Acknowledgements

The authors would like to thank Miguel Sasieta and Juan Mari Aruabarrena (both Munibe Group, Azkoitia, Spain) for providing local support and collaboration in the excavation of the Kiputz IX site. Thanks also to Christine Laurin for providing linguistic assistance. The authors would like to express gratitude to Julià Maroto (Universitat de Girona, Spain), Claude Guérin (Université de Lyon, France) and two anonymous reviewers, as well as the Associate Editor Felix G. Marx (National Museum of Nature and Science, Tsukuba, Japan) for critical remarks and recommendations that improved the manuscript. This work was financially supported by UNESCO 09/01 and EHU10/32 research projects of the Basque Country University, Spain (UPV/EHU) and by the BFI.09.21/AE F.P.U. Ph.D. research grant of Basque Country Government.

## References

- Altuna, J. 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa. *Munibe* 24: 1–464.
- Altuna, J. 1985. Dataciones de carbono 14 del yacimiento de Erralla. Comparación con las dataciones de otros yacimientos próximos. *Munibe* 37: 25–28.
- Altuna, J. 1986. The mammalian faunas from the prehistoric site of La Riera. In: L.G. Straus and G.A. Clark (eds.), *La Riera Cave. Stone Age Hunter – Gatherer Adaptations in Northern Spain*, 237–497. Anthropological Research Papers, Arizona State University, Mesa.
- Altuna, J. 1992. El medio ambiente durante el Pleistoceno superior en la región Cantábrica con referencia especial a sus faunas de mamíferos. *Munibe (Antropología-Arkeología)* 43: 13–29.
- Altuna, J. and Mariezkurrena, K. 1985. Bases de subsistencia de los poblados de Erralla: Macromamíferos. *Munibe* 37: 87–117.
- Altuna, J. and Mariezkurrena, K. 2000. Macromamíferos del yacimiento de Labeko Koba (Arrasate, País Vasco). *Munibe (Antropología-Arkeología)* 52: 107–181.
- Altuna, J., Mariezkurrena, K., and Elorza, M. 2002. Arqueozoología de los niveles Paleolíticos de la Cueva de Abauntz (Arraiz, Navarra). *Saldvie* 2: 1–26.
- Altuna, J. and Straus, L.G. 1976. The Solutrean of Altamira: The artifactual and faunal evidence. *Zephyrus* 26/27: 175–182.
- Álvarez-Lao, D. and García-García, N. 2006. A new site from the Spanish Pleistocene with cold-resistant faunal elements: La Parte (Asturias, Spain). *Quaternary International* 142–143: 107–118.
- Binford, L.R. 1978. *Nunamiut Ethnoarchaeology*. 509 pp. Academic Press, New York.
- Breda, M. 2005. The morphological distinction between the postcranial skeleton of *Cervalces/Alces* and *Megaloceros giganteus* and comparison between two Alceini genera from the Upper Pliocene–Holocene of Western Europe. *Geobios* 38: 151–170.
- Castañós, J., Castañós, P., and Murelaga, X. 2006. Estudio osteométrico preliminar de los restos de ciervo (*Cervus elaphus*) del yacimiento paleontológico del Pleistoceno Superior de Kiputz IX (Mutriku, Gipuzkoa). *Geogaceta* 40: 163–166.
- Castañós, P. 1984. Estudio de los macromamíferos de la cueva de Santimamiñe (Vizcaya). *Kobie (Serie Paleoantropología y C. Naturale)* 14: 235–318.



- Costamagno, S. and Fano, M.A. 2006. Pratiques cynégétiques et exploitation des ressources animales dans les niveaux du Magdalénien supérieur-final de El Horno (Ramales, Cantabrie, Espagne). *Páleo* 17: 31–56.
- Domingo, M.S., Alberdi, M.T., Sánchez Chillón, B., and Cerdeño, E. 2005–06. La fauna cuaternaria de la cornisa cantábrica en las colecciones del Museo Nacional de Ciencias Naturales. *Munibe (Antropología-Arkeología)* 57: 325–350.
- Driesch, A. von den 1976. *A Guide to the Measurement of Animal Bones from Archaeological Sites*. 136 pp. Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge.
- Enloe, J.G. 2003. Acquisition and processing of reindeer in the Paris Basin. In: S. Costamagno and V. Laroulandie (eds.), *Zooarchaeological Insights into Magdalenian Lifeways*. *British Archaeological Reports International Series* 1144: 23–31.
- González Morales, M.R. and Guy Straus, L. 2009. Extraordinary Early Magdalenian finds from El Mirón Cave, Cantabria (Spain). *Antiquity* 83: 267–281.
- Kolfschoten, T. van, Jagt, I. van der, Beeren, Z., Argiti, V., Leije, J. van der, Essen, H. van, Busschers, F.S., Stoel, P., and Plicht, H. van der 2011. A remarkable collection of Late Pleistocene reindeer (*Rangifer tarandus*) remains from Woerden (The Netherlands). *Quaternary International* 238: 4–11.
- Kuntz, D. and Costamagno, S. 2011. Relationships between reindeer and man in southwestern France during the Magdalenian. *Quaternary International* 238: 12–24.
- Lam, Y.M., Chen, X., Maream, C.W., and Frey, C. 1998. Bone density and long bone representation in archaeological faunas: Comparing results from CT and photon densitometry. *Journal of Archaeological Science* 25: 559–570.
- Lam, Y.M., Pearson, O.M., Curtis, C.W., and Chen, X. 2003. Bone density studies in zooarchaeology. *Journal of Archaeological Science* 30: 1701–1708.
- Liouville, M. 2007. *Variabilité du Cerf elaphe (Cervus elaphus L. 1758) au cours du Pléistocène Moyen et Supérieur en Europe occidentale: approches morphométrique, paléocologique et cynégétique*. Unpublished Ph.D. thesis, Museum National d'Histoire Naturelle, Paris.
- Lister, A.M. 1996. The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). *International Journal of Osteoarchaeology* 6: 119–143.
- Lyman, R.L. 1984. Bone density and differential survivorship of fossil classes. *Journal of Anthropological Archaeology* 3: 259–299.
- Lyman, R.L. 1985. Bone frequencies: Differential transport, in situ destruction, and the MGUI. *Journal of Archaeological Science* 19: 221–236.
- Lyman, R.L. 1994. *Vertebrate Taphonomy*. 524 pp. Cambridge University Press, Cambridge.
- Lyman, R.L. 2006. Identifying bilateral pairs of deer (*Odocoileus* sp.) bones: How symmetrical is symmetrical enough? *Journal of Archaeological Science* 33: 1256–1265.
- Mariezkurrena, K. and Altuna, J. 1983. Biometría y dimorfismos sexual en el esqueleto de *Cervus elaphus* würrmiense, postwürmiense y actual del Cantábrico. *Munibe* 35: 203–246.
- Marín Arroyo, A.B., Fosse, P., and Vigne, J.D. 2009. Probable evidences of bone accumulation by Pleistocene bearded vulture at the archaeological site of El Mirón Cave (Spain). *Journal of Archaeological Science* 36: 284–296.
- Pales, L. and Garcia, M. 1981. *Atlas ostéologique pour servir à l'identification des mammifères du Quaternaire*. 77 pp. Éditions du Centre national de la recherche scientifique, Paris.
- Puputti, A.K. and Niskanen, M.N. 2009. Identification of semi-domesticated reindeer (*Rangifer tarandus tarandus*, Linnaeus 1758) and wild forest reindeer (*R.t. fennicus*, Lönnberg 1909) from postcranial skeletal measurements. *Mammalian Biology* 74: 49–58.
- Render, W. 2010. Hunting behavior and Neanderthal adaptability in the Late Pleistocene site of Pech-de-l'Azé I. *Journal of Archaeological Science* 37: 1798–1810.
- Sommer, R.S. and Nadachowski, A. 2006. Glacial refugia of mammals in Europe: Evidence from fossil records. *Mammal Review* 36: 251–265.
- Sommer, R.S., Zachos, F.E., Street, M., Jöris, O., Skog, A., and Benecke, N. 2007. Late Quaternary distribution dynamics and phylogeography of the red deer (*Cervus elaphus*) in Europe. *Quaternary Science Reviews* 27: 714–733.
- Stiner, M.C. 2002. On in situ attrition and vertebrate body part profiles. *Journal of Archaeological Science* 29: 979–991.
- Straus, L.G. 2009. The Late Upper Paleolithic-Mesolithic-Neolithic transitions in Cantabrian Spain. *Journal of Anthropological Research* 65: 287–298.
- Weinstock J. 2000a. Late Pleistocene reindeer populations in Middle and Western Europe. An osteometrical study of *Rangifer tarandus*. *BioArcheologica* 3: 1–307.
- Weinstock J. 2000b. Osteometry as a source of refined demographic information: Sex-ratios of reindeer, hunting strategies, and herd control in the Late Glacial site of Stellmoor, Northern Germany. *Journal of Archaeological Science* 27: 1187–1195.
- Yeshurun, R., Bar-Oz, G., and Weinstein-Evron, M. 2007. Modern hunting behaviour in the early Middle Paleolithic: Faunal remains from Misliya cave, mount Carmel, Israel. *Journal of Human Evolution* 53: 656–677.