

A complete hyoid bone of a woolly rhinoceros (*Coelodonta antiquitatis*) from the Late Pleistocene at Artazu VIII (Gipuzkoa, northern Iberian Peninsula)

Un hioideo entero de rinoceronte lanudo (*Coelodonta antiquitatis*) del Pleistoceno Superior en Artazu VIII (Gipuzkoa, norte de la Península Ibérica)

KEY WORDS: Hyoid bone, morphology, osteometry, *Coelodonta antiquitatis*, Iberian Peninsula.

PALABRAS CLAVES: Hioideo, morfología, osteometría, *Coelodonta antiquitatis*, Península Ibérica.

GAKO-HITZAK: Hioidea, morfología, osteometria, *Coelodonta antiquitatis*, Iberiar penintsula.

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ABSTRACT

The presence of *Coelodonta antiquitatis* has been only confirmed at 25 sites in the Iberian Peninsula, and 20 of them are in the Cantabrian region. Among the skeletal remains recovered so far, the hyoid bone of this species has never been described at the Iberian Peninsula, and it is also very scarce in the rest of Europe. Artazu VIII site is presented in this work as the most important location known for this species in the Iberian Peninsula, yielding the first complete hyoid bone attributable to *Coelodonta antiquitatis*.

The morphology and the measurements of the hyoid bone from Artazu VIII is described in detail in this work, and its dimensions are compared with a specimen found at Neumark-Nord site (Germany), whose attribution to the woolly rhinoceros is not certain. Metric differences seem statistically significant, which can be attributed either to sexual dimorphism or taxonomic differences at the specific level.

RESUMEN

Actualmente, la presencia de rinoceronte lanudo está confirmada en 25 yacimientos de la Península Ibérica y la mayoría de ellos (20) se sitúan en la cornisa Cantábrica. El hioideo es un hueso del esqueleto de esta especie ausente hasta ahora en Iberia y muy escaso en el resto de Europa. Artazu VIII ha proporcionado la muestra más rica de esta especie en la Península con el primer hioideo completo de *Coelodonta antiquitatis*.

En este artículo se ofrece una descripción detallada de la morfología del hioideo de Artazu VIII y las medidas de sus distintos elementos, comparándolos con un ejemplar del yacimiento alemán de Neumark-Nord cuya atribución al rinoceronte lanudo no es segura. Las diferencias métricas son estadísticamente significativas y pueden atribuirse al dimorfismo sexual o a diferencias taxonómicas.

LABURPENA

Gaur egun, errinozero iletsuaren presentzia Iberiar Penintsulako 25 aztarnategitan baieztatuta dago, eta horietako gehienak (20) Kantauri isurialdean kokatzen dira. Espezie honen hioidea, orain arte Iberiar penintsulan ez da aurkitu, eta oso urria da Europako beste aztarnategietan. Artazu VIIIan *Coelodonta antiquitatis* espeziazen Penintsulako laginik aberatsena eta lehen hioide osoa aurkitu dira. Artikulu honetan, Artazu VIIIaren hioidearen morfologiaren deskribapen zehatzta eta haren elementuen neurriak ematen dira. Neumark-Nordeko aztarnategi alemania-rraren aurkitutako errizonero iletsua izan daitzekeen ale batekin konparatu da. Desberdintasun metrikoak estatistikoki esanguratsuak dira eta hauek dimorfismo sexualagatik edo desberdintasun taxonomikoagatik izan dakizkieke.

1. INTRODUCTION

From the second half of the middle Pleistocene to the upper Pleistocene three species of rhinoceros occupied the greater part of the Palearctic region. One of these species was the woolly rhinoceros (*Coelodonta an-*

tiquitatis Blumenbach, 1799) (Guérin, 1980, 2010) which is one of the most remarkable taxa in the Pleistocene *Mammuthus-Coelodonta* faunal complex (Kahlke, 1999). This genus has an Asian origin, evolved progressively from *C. thibetana* (Deng *et al.*, 2011), followed by *C. ni-*

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howanensis Benshun 1978 (Deng, 2008; Tong & Wang, 2014), to *C. tologojensis* Beliaeva 1966, considered by some authors as a subspecies *C. antiquitatis praecursor* (Guérin, 1980). Finally, this species concluded the evolution in *C. antiquitatis* (Tong, 2001), also attributed to the nominal subspecies *C. antiquitatis antiquitatis* (Guérin, 1980). Thus, *C. antiquitatis* extended throughout Asia and entered Europe at the end of the middle Pleistocene (MIS10) and disappeared in Europe in the Last Glacial Maximum (LMG) (MIS 2) (Kahlke & Lacombat, 2008; Stuart & Lister, 2012), surviving only in Siberia until the Younger Dryas (MIS 1) (Orlova *et al.* 2008).

The first finds of the woolly rhinoceros in the Iberian Peninsula date back to the second half of the 19th century. These were two upper molars from the La Gándara site (Udías, Cantabria) (Naranjo & Garza, 1875). During the last century, references were made to eleven sites in the Cantabrian region, two in Catalonia and three in Madrid (Alvarez-Laó, 2007). Most of them were finds with an unknown context and uncertain chronology except for Lezetxiki (Altuna, 1972) and Legintxiki (Castaños, 1996), which correspond to the Gravettian-Solutrean. The samples with the largest number of specimens were published with the present century. Labeko koba (Altuna & Mariezkurrena, 2000) is the first important assemblage regarding the number of remains. Later, La Parte (Alvarez-Laó & García-García, 2006) was published, containing the oldest chronology for this species in the Iberian Peninsula.

In the Cantabrian region (north of Spain) is where the largest concentration of bones of this species has been recorded from all the Iberian Peninsula. In particu-

lar, the site of Artazu VIII contains 610 woolly rhinoceros remains, which is larger than other samples in its close environment, such as Lezika (NISP = 144; Castaños *et al.*, 2009), Jou Puerta (NISP = 125; Alvarez-Laó, 2014), Labeko koba (NISP = 122; Altuna and Mariezkurrena, 2000) and Rexitxiki (NISP = 36; Alvarez-Laó *et al.*, 2015). Thus, Artazu VIII provides the most numerous bone collection of this species currently known in the Iberian Peninsula. In addition, the Artazu VIII woolly rhinoceros sample includes a hyoid bone, which is a very significant find considering the scarcity of this skeletal part in the sites studied until now. Keeping this in mind, the objective of this paper is to present the woolly rhinoceros hyoid apparatus mentioned before, including morphological and metric description and a comparison with the only hyoid recovered from Europe (Neumak-Nord specimen).

2. GEOGRAPHICAL AND GEOLOGICAL SETTING

The palaeontological site of Artazu VIII was discovered in 2013 and it was located at the Kobate Quarry (Arrasate, Gipuzkoa, Spain), at 351 m above sea level with the UTM coordinates: X: 538241, Y: 4769155; datum WGS84 and Zone 30T (Fig. 1) (Suárez-Bilbao, 2019). This site is part of a Cretaceous limestone karst system that includes numerous anticlinal and synclinal folds on a NW-SE alignment.

The cave of Artazu VIII took the shape of an inverted funnel, with a shaft 4-5 m in diameter and 18 m deep connecting the entrance to the inner cave. Moreover, the maximum length of the cave was 12 m and the width

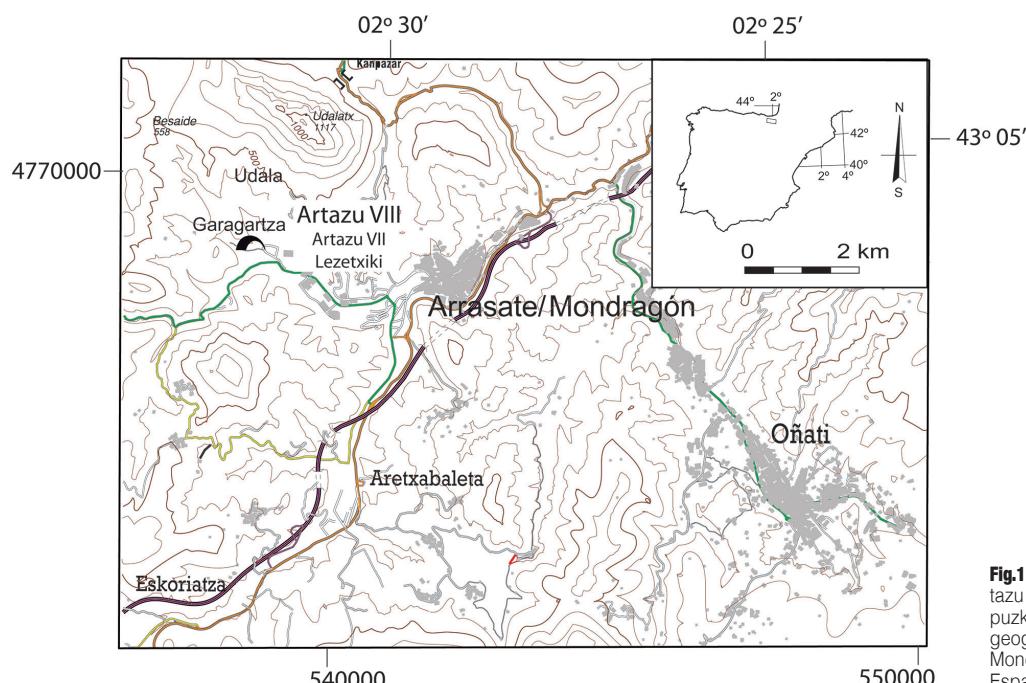


Fig.1. Geographic situation of Artazu VIII (Arrasate/Mondragón, Gipuzkoa, northern Spain). / Situación geográfica de Artazu VIII (Arrasate/Mondragón, Gipuzkoa, norte de España).

differed from 1 to 5 m in width (at the bottom of the site). The cavity was filled by silt and clay sediment, limestone blocks and accumulations of fauna consisting on small vertebrate remains, large mammals, avifauna and malacofauna (Suárez-Bilbao, 2019). This site acted as a natural trap, since noanthropic and predator marks were conserved (Suárez-Bilbao, 2019). Furthermore, the good state of preservation of bones allow us to identify more than 95 % of large mammal bones.

In Artazu VIII 12 levels were differentiated, covering a temporal range of at least 36 ka (Fig. 1). The hyoid bone came from Level 8, which has provided two dates obtained for rhinoceros molars by the amino acid racemization (AAR) method in the Biomolecular Stratigraphy Laboratory (LEB) in the Higher School of Mining Engineers in Madrid (E.T.S.I de Minas). The AAR results were based on the D/L relationships for each amino acid identified and the total contents (pmol/mg) of each enantiomer (Torres *et al.*, 2014). One of these (LEB-14071) gave an age of 99,800 ka, while the other (LEB-14072) was dated to 103,600 ka. Hence, the mean value for the level 8 are 101.7 ± 1.9 ka. This data supposes the oldest dating from Artazu VIII.

3. MATERIAL AND METHODS

The hyoid bone of woolly rhinoceros recovered from Artazu VIII was found inside an almost complete viscerocranum of a subadult individual in anatomical position between the two jaws. The hyoid was recovered during the extraction of the clay filling that occupied the oral cavity. The exceptional state of preservation of bone was result of clay protection.

The basihyoid with the two thyrohyoid cornua, the lingual process and the articulation tubers with the ceratohyoïds are conserved. The ceratohyoïds are

missing and the presence of epihyoid bones is doubtful for reasons indicated below. The stylohyoid bones of the suspensory apparatus are also preserved although with some deterioration in the stylidian angles (Fig. 2).

The measurements have been made following the methodology of van der Made (2010) and stylohyoid measurements have been added (Fig. 3). All measurements are given in mm with their corresponding abbreviations (Table 1).

L	length
DT	transverse diameter
Lip	length of the lingual process measured from the back of the basihyoid
Hip	height of the lingual process
DTlp	greatest width of the lingual process
DAPbh	minimal antero-posterior diameter of the section of the body of the basihyoid
DTbh	transverse diameter of the basihyoid, or maximum width of the bone at the place of the tubercles for articulation with the ceratohyoïd
DTthmi	transverse diameter of thyrohyoid
DAPtch	greatest diameter of the tubercle for articulation with ceratohyoïd
DTtch	width of the tubercle for articulation with ceratohyoïd, measured perpendicular to DAPtch
Lth	length of the thyrohyoid
Hth	height of the thyrohyoid
DTth	transverse diameter of the thyrohyoid
Hstfl	height of stylohyoid in the middle of the flex
DTstfl	transverse diameter of thyrohyoid in the middle of the flex
Hst	maximum height of stylohyoid
DTst	transverse diameter of stylohyoid

Tabla 1: Measurements and abbreviations of hyoid bone. / Medidas y abreviaturas del hioídes.

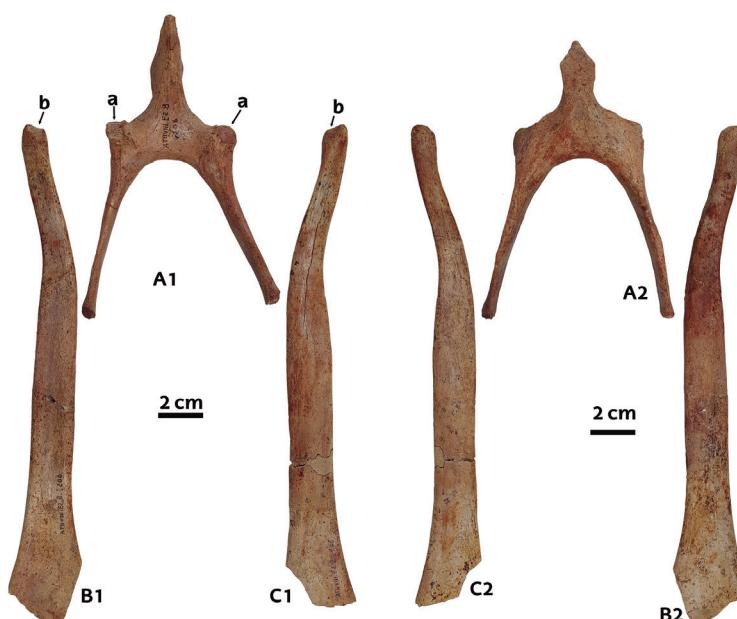


Fig.2. A1 basihyoid: lingual process + 2 thyrohyoides (dorsal view); B1 stylohyoid left and C1 stylohyoid right (mesial view); A2 basihyoid: lingual process + 2 thyrohyoides (ventral view); B2 stylohyoid left and C2 stylohyoid right (lateral view); a, b (ceratohyoïd articulations) / A1 basihyoides: proceso lingual + 2 tirohoides (vista dorsal); B1 estilohoides izquierdo y C1 estilohoides derecho (vista mesial); A2 basihyoides: proceso lingual + 2 tirohoides (vista ventral); a, b (articulaciones ceratoideas).

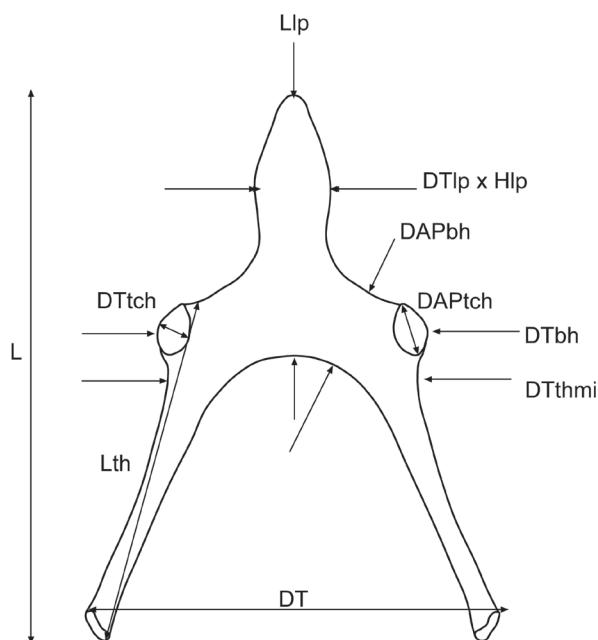


Fig.3. The way of measuring the hyoid. / Toma de medidas del hioideo.

The fossil is currently held in the Laboratorio de Paleontología de Vertebrados de la Sociedad de Ciencias Aranzadi but will shortly be deposited in the Centro de Patrimonio Cultural Mueble de Gipuzkoa, Gordaillu (Irún, Gipuzkoa).

4. RESULTS AND DISCUSSION

4.1. Backgraound

Bibliographic references about the hyoid bone morphology of the woolly rhinoceros are very scarce. It is quite significant that in the monumental thesis of Guérin (1980) were not included the description of the hyoid bone, either in current nor in fossil rhinos. Three years later Guérin cited a stylohyoid discovered at Jaurens site (France) and he affirmed that the hyoid bone is an anatomical part that had hardly ever been described (*presque jamais décrite*) in rhinos, which was the reason for his omission in his thesis (Guérin, 1983: 69). This bone is not described in two doctoral theses dedicated to the Rhinoceratidae family (Antoine, 2002; Lacombat, 2003). Regarding publications of other authors, only one other stylohyoid fragment has been published in Europe (Germany) (Diedrich, 2008).

The only rhinoceros hyoid described and measured comes from the Newmark-Nord (Germany) site where remains of Stephanorhinus kirchbergenis, *Stephanorhinus hemitoechus* and *Coelodonta antiquitatis* have been found. In this author's opinion, the absence of criteria to differentiate this bone does not allow a certain attribution of this specimen to the woolly rhino (van der Made, 2010: 480).

The most recent references to this anatomical element come from East Asia. A rich sample of woolly rhinoceros (1064 remains) has been recently published at the Wulanmulum site (Ordos, Nei Mongol, northern China), including three hyoid bones from the Late Pleistocene levels (Li-min-Zhang *et al.*, 2016). In addition, there is an almost complete skeleton from Ondorkhaan (eastern Mongolia) that preserves a stylohyoid with a date of 45-40 ka (Handa *et al.*, 2022). In both cases, the metric data is missing.

With this background, these antecedents, the specimen from Artazu VIII, both for its conservation and for its certain specific attribution, acquires a special interest for knowledge and discrimination of this part of the cephalic skeleton of the woolly rhinoceros.

4.2. Age and systematics

The hyoid belongs to an individual who preserves the upper jaws and mandibles with complete dental series. The last upper milk molars are still preserved, although the lower counterparts have already been replaced. M^1, P^2 and P^3 already show a first degree of wear and an age of 8-10 years can be estimated and included in the C-IV group of Garutt (1994).

The upper dentition presents a typical morphology of the woolly rhinoceros. The teeth have a very angular occlusal contour, rough enamel, strong hypsodontia, oblique internal valleys with respect to the axial axis and great development of internal folds to achieve a larger crushing surface.

4.3. Morphological description

The hyoid bone from Artazu VIII has the general structure of the Perissodactyla but with more robust bones. The basihyoid is the only transverse bone that occupies the lower and central base of the complex and forms a single bone with the lingual process and the thyrohyoid pair (Fig. 2, A1). The thyrohyoid cornua and the distal border of the basihyoid form a parabolic shape. In *D. bicornis* the insertion between the horns and the basihyoid is angled. The basihyoid has a dorsoventrally flattened section with a slightly concave dorsal face and flat ventral face. In the middle of its cranial border it has an extension (lingual process) that dorsally is more or less convex and progressively narrows until it ends at the tip, but ventrally it is formed by two flat surfaces: the caudal is horizontal and forms a trapezoid while the cranial is triangular and oblique. The cross-section of the lingual process is triangular. On the basihyoid dorsal surface, two joint tubers articulate with the ceratohyoid, which has an elliptical shape (Fig. 2a). The thyrohyoid cornua is divergent and extends backward and upward from the basihyoid to the thyroid cartilage of the larynx.

The stylohyoid bones are not completely straight since they display a slight flexion in their lower third. They are shaped like a blade, laterally flattened and possess

a shallow fossa at the mesial side. They are the longest bones in the hyoid complex and are lower and shorter before the flexion and higher and longer between the flexion and stylidian angle. At the inferocranial mesial end they present a concave facet for articulation with the ceratohyoid bones in a slightly oblique position (Fig. 2b). It is not possible to describe the epihyoid bone since this small bone can form a small patella between the ceratohyoid and stylohyoid at an early age but very soon merges with the lower end of the stylohyoid. Given the age of the individual to which this hyoid belongs, it is likely that the epihyoid of this specimen is already fused and forms the concave joint surface described above.

4.4. Osteometry

The way to measure the different elements of the hyoid bone as well as its nomenclature and abbreviations is taken from van der Made (2010) (Fig. 2), together with some additions to this suspensory apparatus. Table 2 shows the measurements of the hyoid bone from Artazu VIII and those of the Neumak-Nord specimen (van der Made, 2010). The values of the hyoid bone from the German site are significantly higher than those of the specimen from Artazu VIII.

The difference observed is hardly attributable to age since all bones are definitively formed in both cases. It may also be assumed that differences in size are a consequence of sexual dimorphism. There are two circumstances that make it difficult to test the second hypothesis. First the absence of osteometric information

for this part of the skeleton in the different rhino species. Secondly palaeontologists are not unanimous about the existence of a statistically significant dimorphism in the woolly rhinoceros. Some do not admit metric differences between males and females greater than 10% (Prothero, 2005: 9) but others claim a sexual dimorphism that can translate into differences greater than 28% in bone measurements (Guérin, 1983).

In the specimens compared here, metric differences exceed 10% (Table 1). In the lingual process the differences range from 17% in width (DTlp), 18.9% in length (Lip) and 30% in height (Hlp). In the basihyoid width, the differences are 20.8% (DTthmi) and 24.1% (DTbh). Therefore, if the existence of sexual dimorphism in *Coevodonta* is accepted, both the Neumark-Nord hyoid bone and the specimen from Artazu VIII can be attributed to the woolly rhinoceros, the German specimen belonging to a male and the Spanish specimen to a female. If this degree of sexual dimorphism is not accepted, it would be necessary to admit that they belong to two different rhino species. Apart from this question, the measurements of the hyoid bone from Artazu VIII are useful for the metric characterization of this part of the woolly rhino skeleton.

5. CONCLUSION

Artazu VIII site (Arrasate, northern Iberian Peninsula) has become a late Pleistocene palaeontological referent due to its nature, the continuous stratigraphy, the high number of skeletal remains (small and large vertebrates) and the exceptional state of preservation of fossil skeletal remains. Besides that, the outstanding amount of woolly rhinoceros bones recovered from Artazu VIII makes this site the deposit with the highest number of *C. antiquitatis* from the whole Iberian Peninsula. On top of that, Artazu VIII presents the only woolly rhino hyoid bone from the Iberian Peninsula for the late Pleistocene and one of the three remains recovered from Europe. Apart from European rhino hyoids, only other three fragmented remains have been discovered in northern China. Here Artazu VIII hyoid bone morphological description and osteometry is presented, contributing substantially to the knowledge of this skeletal remain from woolly rhino. Moreover, a comparison between Neumak-Nord deposit to Artazu VIII site specimens have been performed, revealing a larger size for those from Germany. Keeping in mind the absence of osteometric data for his bone and this species, this difference has provisionally attributed to sexual dimorphism.

6. ACKNOLEGMENTS

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	Artazu VIII		Neumark-Nord	
	left	right	left	right
L	123.5	123.0		
DT	82.6			
Lip	57.8		71.3	
Hlp	12.6		18.0	
DTlp	14.6		17.6	
DAPbh	20.7	19.9	23.5	23.0
DTbh	55.4		73.0	
DTthmi	52.6		66.4	
DAPtch	13.1	14.2	18.6	16.6
DTtch	8.1	8.9	12.1	11.3
Lth	85.6	81.2		
Hth	14.0	14.9		
DTth	5.5	5.6		
Hstfl	14.9	13.9		
DTstfl	6.0	5.7		
Hst	19.9	19.4		
DTst	5.6	5.8		

Tabla 2: Neumak-Nord and Artazu VIII hyoid measurements. / Medidas del hioideo de Neumak-Nord y Artazu VIII.

7. BIBLIOGRAPHY

- Altuna, J., 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa. *Munibe* 24, 1-464.
- Altuna, J., Mariezkurrena, K., 2000. Macromamíferos del yacimiento de Labeko Koba (Arrasate, País Vasco). En: Arrizabalaga, A., Altuna, J. (Eds), *Labeko Koba (País Vasco) Hienas y Humanos en los albores del Paleolítico Superior*. *Munibe Antropología-Arqueología* 52, 107-151.
- Alvarez-Laó, D.J., 2006. A new site from the Spanish Middle Pleistocene with cold-resistant faunal elements: La Parte (Asturias, Spain). *Quaternary International* 142-143, 107-118.
- Alvarez-Laó, D.J., 2007. Revisión paleontológica de los macromamíferos indicadores de clima frío en el Pleistoceno de la Península Ibérica. Tesis Doctoral Universidad de Oviedo, pp. 413.
- Alvarez-Laó, D.J., 2014. The Jou Puerta cave (Asturias, NW Spain): A MIS 3 large mammal assemblage with mixture of cold and temperate elements. *Palaeogeography, Palaeoclimatology, Palaeoecology* 393, 1-19.
- Alvarez-Laó, D.J., Ruiz-Zapata, M.B., Gil-García, M.J., Ballessteros, D., Jiménez-Sánchez, M., 2015. Palaeoenvironmental research at Rexistora Cave: New evidence of cold and dry conditions in NW Iberian during MIS 3. *Quaternary International* 379, 35-46.
- Antoine, P.O., 2002. Phylogénie et évolution des Elasmotherriina (Mammalia, Rhinocerotidae). *Mémoires du Muséum national d'Histoire naturelle* 188.
- Castaños, P., 1996. Hallazgos de rinoceronte lanudo en Le-gintxiki (Etxauri, Navarra). *Príncipe de Viana. Suplemento de Ciencias* 14-15, 77-80.
- Castaños, P., Murelaga, X., Bailón, S., Castaños, J., Sáez de la Fuente, X., Suárez, O., 2009. Estudio paleontológico de la fauna de Lezikako Koba (Kortezubi, Bizkaia). *Kobie Paleoantropología* 28, 25-50.
- Deng, T., 2008. Comparison between wolly rhino forelimbs from Longdan, Northwestern China and Tologoi, Transbaikalian region. *Quaternary International* 179, 196-207.
- Deng, T., Wang, X., Fortelius, M., Li, Q., Wang, Y., Tseng, Z.J., Tajuechi, G.T., Saylor, J.E., Säila, L.K., Xie, G., 2011. Out of Tibet: Pliocene Woolly Rhino Suggests High Plateau Origin of Ice Age Megaherbivores. *Science* 333, 1285-1288.
- Diedrich, C., 2008. A skeleton of an injured Coelodonta antiquitatis from the Late Pleistocene of north-western Germany. *Cranium* 25, 1-16.
- Garutt, N.V., 1994. Dental ontogeny of the woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799). *Cranium* 14(1), 37-48.
- Guérin, C., 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. *Documents des Laboratoires de Géologie de Lyon* 79.
- Guérin, C., 1983. Le gisement pléistocène supérieur de la grotte de Jaurens à Nespouls, Corrèze, France: les Rhinocerotidae (Mammalia, Perissodactyla). *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon* 21, 65-85.
- Guérin, C., 2010. Coelodonta antiquitatis praecursor (Rhinocerotidae) du Pléistocène moyen final de l'aven de Romain-la-Roche (Doubs, France). In: Guérin, C., Malvesy, T. (Eds.), *L'aven de Romain-la-Roche (Doubs)*. *Revue de Paléobiologie* 29(2), 697-746.
- Guérin, C., 2018. *Dicerorhinus hemitoechus* (Rhinocerotidae) du Pléistocène supérieur de la grotte du Castillo. In: Castaños Ugarte, P. (Coord.), *El Castillo: Historia de una fauna olvidada*. Monografías del Museo de Prehistoria y Arqueología de Cantabria 1, 192-218.
- Handa, N., Izuhara, M., Takahashi, K., Iizuka, F., Tsogtbaatar, B., Gunchinsuren, B., Odosuren, D., Ishitseren, L., 2022. The woolly rhinoceros (*Coelodonta antiquitatis*) from Ondorkhaan, eastern Mongolia. *Boreas* 51, 584-605.
- Kahlke, R. D., 1999. The history of the origin, evolution and dispersal of the Late Pleistocene Mammuths-Coelodonta faunal complex in Eurasia (large mammals). *Fenske Rapid City*.
- Kahlke, R.D., Lacombat, F., 2008. The earliest immigration of woolly rhinoceros (*Coelodonta tolojagensis*, Rhinocerotidae, Mammalia) into Europe and its adaptative evolution in Palearctic cold stage mammal faunas. *Quaternary Science Reviews* 27, 1951-1961.
- Lacombat, F., 2003. Etude des rhinocéros du Pléistocène de l'Europe méditerranéenne et du Massif Central. Paléontologie, phylogénie et biostratigraphie. Thèse de Doctorat du Muséum National d'Histoire Naturel, Paris.
- Made, J. van der., 2010. The rhinos from the Middle Pleistocene of Neumark-Nord (Saxony-Anhalt). *Veröffentlichungen des Landesmuseum für Vorgeschichte* 62, 433-527.
- Naranjo y Garza, F., 1875. Observaciones sobre molares fósiles de rinoceronte del criadero de calamina de Comillas (Santander). *Actas de la Sociedad Española de Historia Natural. Anales* 4, 3-9.
- Orlova, L.A., Vasil'ev, S.K., Kuz'min, Y.V., Kosintsev, P.A., 2008. New data on the time and place of extinction of the Wolly Rhinoceros *Coelodonta antiquitatis* Blumenbach 1799. *Doklady Biological Sciences* 423, 403-405.
- Prothero, D.R., 2005. *The Evolution of North American Rhinoceroses*. Cambridge University Press, Cambridge.
- Stuart, A.J., Lister, A.M., 2012. Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of late Quaternary megafaunal extinctions in northern Eurasia. *Quaternary Science Reviews* 51, 1-17.
- Suárez-Bilbao, A., 2019. Late Pleistocene vertebrate assemblage from Artazu VII and Artazu VIII sites (Arrasate, northern Iberian Peninsula): Palaeobiology and Palaeoecology. Tesis Doctoral. Universidad del País Vasco.
- Tong, H.W., 2001. Rhinocerotids in China. Systematics and material analysis. *Geobios (Lyon)* 34(5), 585-591.
- Tong, H.W., Wang, X.M., 2014. Juvenile skulls and other postcranial bones of *Coelodonta niowanensis* from Shanshenmiaozui, Nihewan Basin, China. *Journal of Vertebrate Paleontology* 34 (3), 710-724.
- Torres, T., Ortiz, J.E., Fernández, E., Arroyo-Pardo, E., Grün, R., Pérez-González, A., 2014. Aspartic acid racemization as a dating tool for dentine: a reality. *Quaternary Geochronology* 22, 43-56.
- Zhang, L., Griggo, C., Dong, W., Hou, Y., Zhang, Sh., Yang, Z., Liu, Y., Wang, X., 2016. Preliminary taphonomic analyses on the mammalian remains from Wulanmulun Paleolithic site, Nei Mongol, China. *Quaternary International* 400, 158-165.