

## Article

# Southernmost Eurasian Record of Reindeer (*Rangifer*) in MIS 8 at Galería (Atapuerca, Spain): Evidence of Progressive Southern Expansion of Glacial Fauna Across Climatic Cycles

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## Abstract

During the Pleistocene, the successive ice ages prompted the southward expansion of the “Mammoth Steppe” ecosystem, a prevalent habitat that supported species adapted to cold environments such as the mammoth, woolly rhinoceros, and reindeer. Previously, the earliest evidence for such cold-adapted species in the Iberian Peninsula dated back to Marine Isotope Stage 6 (MIS 6, ~191–123 ka). This paper reports the discovery of a reindeer (*Rangifer*) tooth from Unit GIII of the Galería site at the Atapuerca-Trinchera site complex, dated to MIS 8 (~300–243 ka). This find is significant as it represents not only the oldest evidence of glacial fauna in the Iberian Peninsula but also the southernmost occurrence of reindeer in Europe of this age. The presence of *Rangifer* at this latitude (42°21' N) during MIS 8 suggests that the glacial conditions affected the Iberian fauna earlier and with greater intensity than previously understood. Over the subsequent climatic cycles, cold-adapted species spread further south, reaching Madrid (40°20') during the penultimate glacial period and the province of Granada (37°01') during the last glacial maximum. The coexistence of human fossils and lithic artefacts within Units GII and GIII at Galería indicates that early humans also inhabited these glacial environments at Atapuerca. This study elaborates on the morphological and archaeological significance of the reindeer fossil, emphasizing its role in understanding the biogeographical patterns of glacial fauna and the adaptability of Middle Pleistocene human populations.

**Keywords:** ice age; glacial environment; glacial refugia; biogeography; Pleistocene; Iberian Peninsula; paleoclimate; prehistory; early humans

## 1. Introduction

The Pleistocene witnessed several glacial periods, marked by significant expansions of ice sheets and cold environments pushing southward across Eurasia [1]. These climatic



Academic Editor: Leszek Marks

Received: 26 May 2025

Revised: 2 July 2025

Accepted: 21 July 2025

Published: 1 August 2025

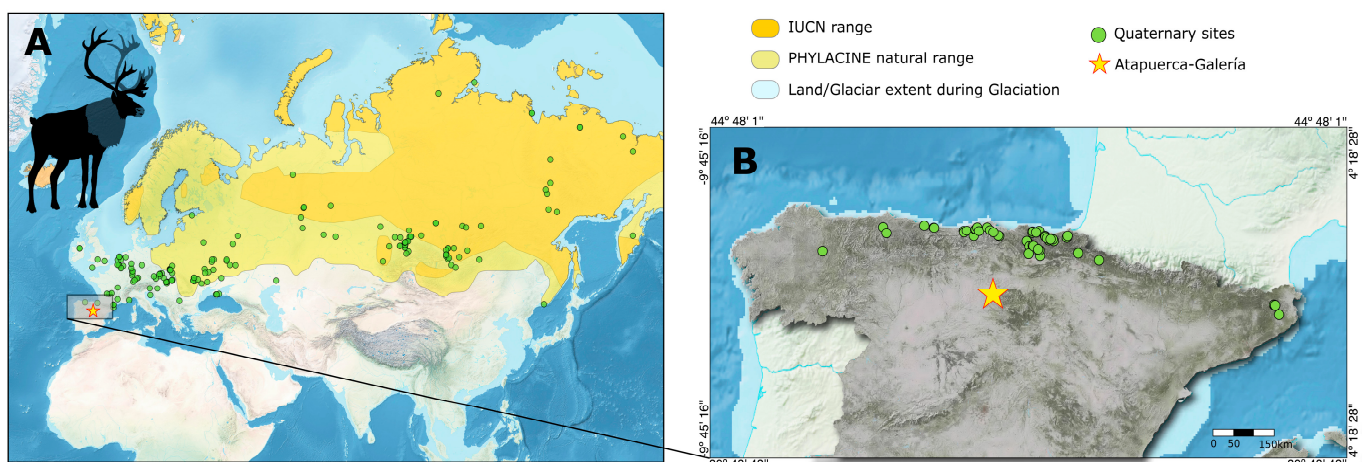
**Citation:** van der Made, J.; Lazagabaster, I.A.; García-Medrano, P.; Cáceres, I. Southernmost Eurasian Record of Reindeer (*Rangifer*) in MIS 8 at Galería (Atapuerca, Spain): Evidence of Progressive Southern Expansion of Glacial Fauna Across Climatic Cycles. *Quaternary* **2025**, *8*, 43. <https://doi.org/10.3390/quat8030043>

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shifts facilitated the spread of the steppe–tundra biome, which hosted its characteristic boreal and arctic faunal components, collectively referred to as the “mammoth fauna” or “*Mammuthus-Coelodonta* faunal complex” [2,3]. The iconic large mammals of this community included the woolly mammoth (*Mammuthus primigenius*), the woolly rhinoceros (*Coelodonta antiquitatis*), and the reindeer (*Rangifer tarandus*), alongside less prevalent species such as the wolverine (*Gulo gulo*), the arctic fox (*Alopex lagopus*), the muskox (*Ovibos moschatus*), and the saiga antelope (*Saiga tatarica*) [4]. These taxa thrived within the “mammoth steppe”, an extensive herbaceous ecosystem that dominated the glacial periods of the Pleistocene [5].

The glacial conditions during these periods reached as far south as the Iberian Peninsula. The extent and establishment of steppe–tundra ecosystems in Iberia, however, heavily depended on the intensity and duration of each glacial phase [4]. Consequently, the cold-adapted fauna in this region was less common than in northern Europe, with its presence often being episodic and geographically confined, largely restricted to mountainous areas where localized microclimates mirrored the colder conditions of higher latitudes [6,7]. Nevertheless, the geographical and topographical complexities of the Iberian Peninsula, including significant climatic barriers such as the Cantabrian Mountains and the Pyrenees, influenced the distribution and persistence of these species [8,9].

Here, we report the discovery of a reindeer (*Rangifer* sp.) tooth in the Galería site at Atapuerca, likely dated to MIS 8 (~300–240 ka). The Galería site, excavated since 1976 with few interruptions [10], has now yielded its first cold-adapted species and the first representative of the “mammoth fauna” across the entire site complex of Sierra de Atapuerca (Burgos, Spain). This specimen marks the southernmost documented presence of reindeer in MIS8 and significantly extends the known timeline of cold-adapted species in the Iberian Peninsula by one climatic cycle. By now, *Rangifer* is known from over 55 localities in Spain, concentrated in the Cantabrian Mountains and the eastern Pyrenees (Figure 1) [11]. *Rangifer* and other cold-adapted species are first known from Spain from MIS 6 [11,12]. The presence of reindeer during MIS 8 not only highlights the first southern extension of cold-adapted fauna into Iberia but also adds to the growing body of evidence demonstrating the adaptability of early humans to challenging glacial conditions [13].



**Figure 1.** Geographic distribution of extant and fossil reindeer *Rangifer tarandus* in Eurasia (A) and the Iberian Peninsula (B). The extant distribution corresponds to the present-day range (in yellow) obtained from the International Union for Conservation of Nature (IUCN) Red List [14] and the natural range (in orange), which is an estimation of the possible distribution of the reindeer without anthropogenic impacts obtained from the PHYLACINE dataset v. 1.2 [15]. The Quaternary localities with the presence of fossil reindeer (green circles) sometimes represent clusters of sites, with a total of 178 sites in Eurasia obtained from the NOW Fossil Mammal Database [16] and 56 sites in the Iberian Peninsula obtained from Gómez-Olivencia et al. [11]. The approximate extent of the glaciers is represented in blue, and the Atapuerca-Galería site is represented with a star.

The Sierra de Atapuerca sites allow us to establish a general framework for analyzing the evolution of large and small vertebrate fauna, paleoenvironments, humans, and cultural subsistence strategies during the late Early to the late Middle Pleistocene [17]. The best known sites are Gran Dolina (type locality of *Homo antecessor* [18,19]), Sima del Elefante (with human presence dated to about 1.2–1.1 Ma [20,21]), and Sima de los Huesos (with thousands of human fossils of nearly 30 individuals [19,22]). Galería is another site in the Sierra de Atapuerca, which is well known for its Middle Pleistocene stratigraphic sequence and rich archaeological and paleontological record, including human remains. The fauna includes amphibians, reptiles, birds, and large and small mammals. The large mammals are listed in Table 1. The Galería site featured a vertical shaft in TN, serving as a natural trap for animals. The fossil assemblage was formed by animals that fell into this trap, with many carcasses later modified by humans through sporadic and repeated visits to exploit these remains. Consequently, the site was likely never used as a base camp [23,24].

**Table 1.** The large mammals from Galería in [25–29] and this paper.

| Taxon                             | GIIa | GIIb | GIIIa | GIIIb |
|-----------------------------------|------|------|-------|-------|
| <i>Homo</i>                       |      | X?   | X     |       |
| Acheulean industry                | X    | X    | X     | X     |
| <i>Vulpes vulpes</i>              | X    | X    | X     |       |
| <i>Canis lupus</i>                | X    |      |       |       |
| <i>Cuon alpinus europaeus</i>     | X    | X    | X     |       |
| <i>Mustela nivalis</i>            | X    | X    | X     |       |
| <i>Mustela putorius</i>           | X    | X    | X     |       |
| <i>Meles meles</i>                | X    | X    |       |       |
| <i>Ursus spelaeus</i>             |      |      |       | X     |
| <i>Lynx pardinus spelaeus</i>     | X    | X    | X     |       |
| <i>Panthera leo</i>               | X    | X    | X     |       |
| <i>Felis sylvestris</i>           |      |      | X     |       |
| <i>Stephanorhinus hemitoechus</i> | X    | X    | X     | X     |
| <i>Equus hydruntinus</i>          |      | X    | X     |       |
| <i>Equus torralbae</i>            | X    | X    | X     | X     |
| <i>Capreolus priscus</i>          |      |      | X     | X     |
| <i>Rangifer</i>                   |      |      | X     |       |
| <i>Megaceroides</i>               | X    | X    | X     |       |
| <i>Dama clactoniana</i>           | X    | X    | X     | X     |
| <i>Cervus elaphus</i>             | X    | X    | X     | X     |
| <i>Bison</i> sp.                  | X    | X    | X     | X     |
| <i>Hemitragus bonali</i>          | X    | X    | X     | X     |

The aim of this paper is to describe the *Rangifer* fossil from Galería and to discuss its significance. The specimen is indicative of the severity of the MIS 8 glacial, how far its effects reached into the Iberian Peninsula, and its relevance for humans living in this “glacial refuge”.

## 2. Materials and Methods

The *Rangifer* specimen, number Ata18/GIIIa/L25/103 as well as other fossils from Galería and other sites in the Sierra de Atapuerca are initially kept for study in the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA) in Tarragona (Spain), but they will be permanently deposited in the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH) in Burgos (Spain).

The *Rangifer* tooth from Galería was compared to the same teeth of *Rangifer*, *Capreolus*, *Cervus*, *Dama*, and other recent and fossil deer kept in the IPHES-CERCA, the Naturalis Biodiversity Center, Leiden (NBC), the Institut für Quartärpaläontologie (IQW, now

Forschungsstation für Quartärpaläontologie of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Weimar), and the Natuurhistorisch Museum, Maastricht (NMM). Measurements were taken in a standard way [30]. The maximum length (DAP) was taken at the occlusal surface and on the buccal side. The basal length (DAPb) was taken at the crown base and on the buccal side. The width of the anterior lobe (DTa) was taken at the widest point just above the crown base from the base of the antero-lingual cusp to the base of the antero-buccal cusp. The width of the posterior lobe (DTp) was taken in the same way from the base of the postero-lingual cusp to the base of the postero-buccal cusp.

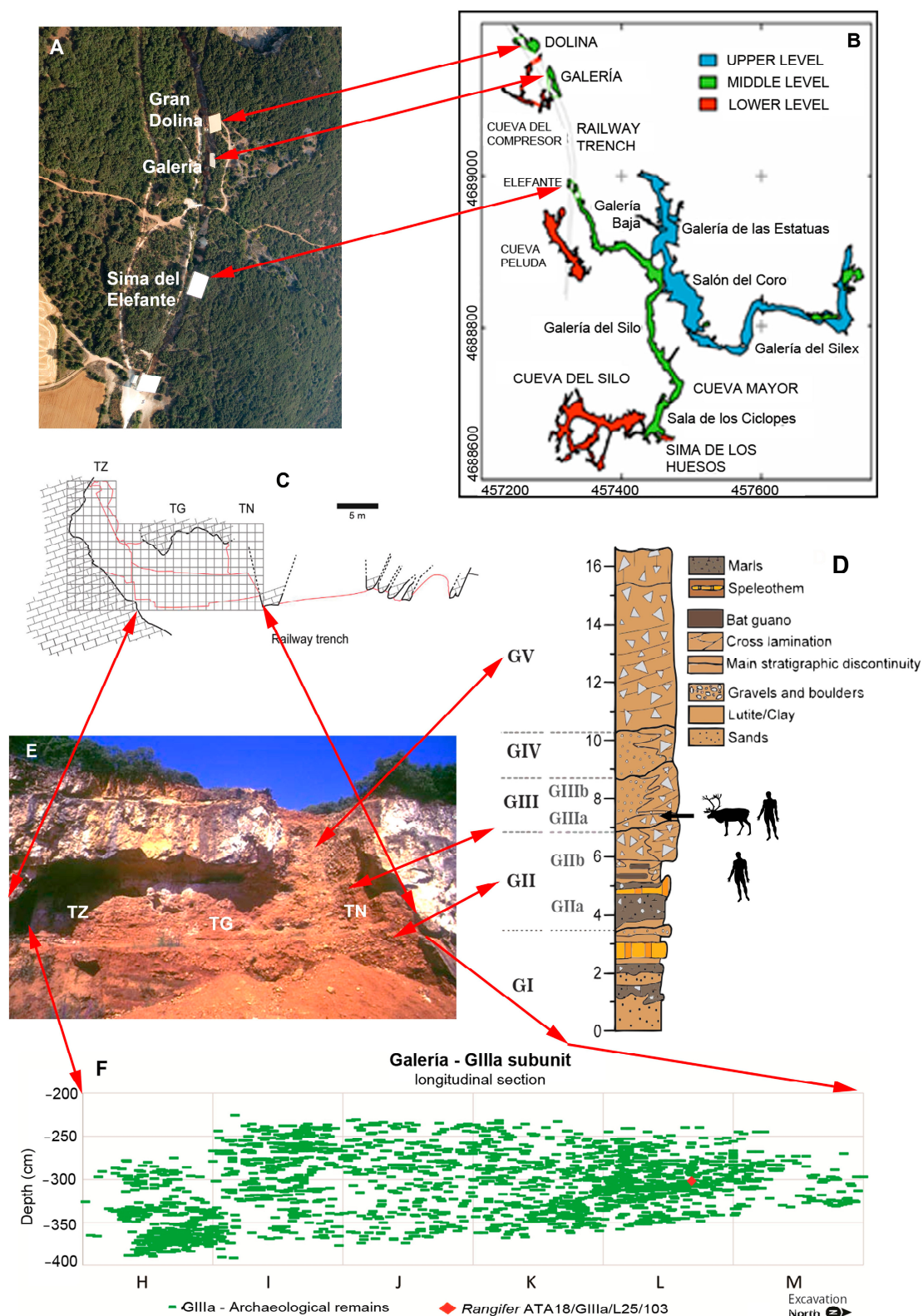
### 3. Stratigraphy and Dating of Galería—Exact Provenance of the Specimen

The Galería site ( $42^{\circ}21'5''$  N and  $3^{\circ}31'11''$  W) is located on the western side of the Sierra de Atapuerca. It is one of the sites that became exposed when a railway trench was cut through the Sierra de Atapuerca in the late 19th century. The cavity is roughly 14 m high, 18 m wide and over 12 m deep. The name Galería is used to refer to the entire cave system, which comprises three different areas: a central area (TG), joined at the northern end to a small chamber (TZ), and a vertical shaft at the southern end (TN).

Five main infilling phases (GI to GV) and one paleosol (GVI) have been distinguished in the Galería stratigraphic sequence [31–34]. Only units GII to GIV contain archaeological and paleontological remains. Unit GI is formed by archeologically sterile endokarstic detrital sediment, dated to  $>350$  ka (U/Th) and  $317 \pm 60$  ka (ESR) [35]. The Matuyama–Brunhes boundary has been identified less than half a meter below the chronometric samples. Unit GII is divided into two subunits, separated by a continuous organic layer. The earliest of these, GIIa, contains evidence of the cave’s first exposure to the outside and is correlated with MIS 11 [36]. However, TL dates provide older chronologies ( $503 \pm 95$  ka and  $422 \pm 55$  ka for TG9) [37]. Further data from ESR-US give an age of 350–363 ka [38]. The more recent dates were obtained using TT-OSL and pIR-IR<sub>225</sub> (330 ka and 230 ka) [39]. The youngest subunit, GIIb, has recently been dated by ESR-US to 237–269 ka [38]. Unit GIII is also divided into two subunits, which have been dated using different methods (TL, ESR, ESR-US, TT-OSL, pIR-IR<sub>22</sub>, and pIR-IR<sub>290</sub>), providing dates between 460 ka and 220 ka for the GIIIa subunit and 300–250 ka for the GIIIb subunit [37–41]. The final infilling event corresponds to the edaphic relict formation that sealed the cave (units GIV to GVI). A stalagmite from the top of GIV has been dated to between 250 ka and 87 ka (ESR, U/Th, TT-OSL, and pIR-IR<sub>225</sub>). In addition to dating, curves of the goethite and ferromagnetic minerals from the Galería sequence were used to correlate GI–IV to the marine oxygen isotope curve and to MIS 10–7 [42].

Specimen Ata18/GIIIa/L25/103 comes from unit GIIIa, from square L25 in the TN, with  $z = 302$  cm (recorded excavation depth with respect to reference point  $z = 0$ ). Its stratigraphic position is indicated in Figure 2.

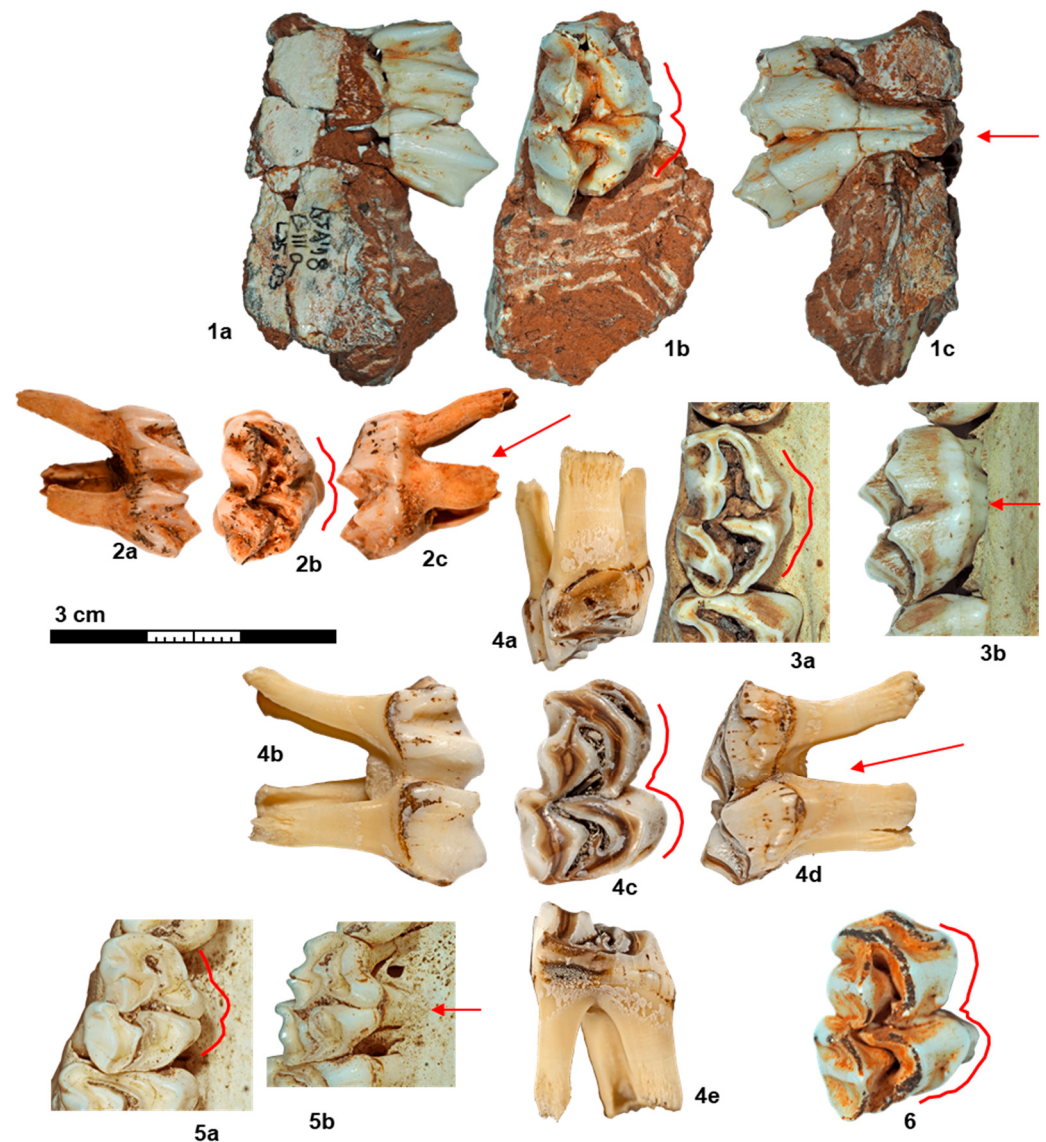
During the first intervention in the site, a human mandible was found, but its exact position is not known, though it came from unit GII in the TZ area [45]. Much later, in 1995, a human cranial fragment was found in the base of unit GIII in the transition of the TZ and TG areas [46]. Its stratigraphic provenance is close to that of the *Rangifer* tooth (Figure 2).



**Figure 2.** (A) Location of the Sierra de Atapuerca (Burgos, Spain) on Iberian Peninsula. (B) Map of the Atapuerca multilevel cave system (modified from Ortega et al. [43]). (C) Location of the Galería site and other main sites in the Trinchera del Ferrocarril. The sites stand out due to the roofs that were constructed above them, which are visible as whitish rectangles. (D) General view of Galería with different sectors of the site (© EIA). (E) Stratigraphy of Galería site (modified from Nuñez-Lahuerta et al. [44]) and the position of fossils of *Homo* and *Rangifer*. (F) Planimetry of Galería (R. Pérez-EIA). G Longitudinal section of the GIIIa subunit with the projections of the finds, highlighting the stratigraphic position of the *Rangifer* fossil (red).

#### 4. Results: Description and Comparison

Specimen Ata18/GIIIa/L25/103 (Figure 3(1a–1c)) is a selenodont upper tooth (with lingual root) and four main cusps. The anterior lobe is markedly narrower, as is common in the D3 and uncommon in the D4 and permanent molars. The anterior cingulum is damaged.



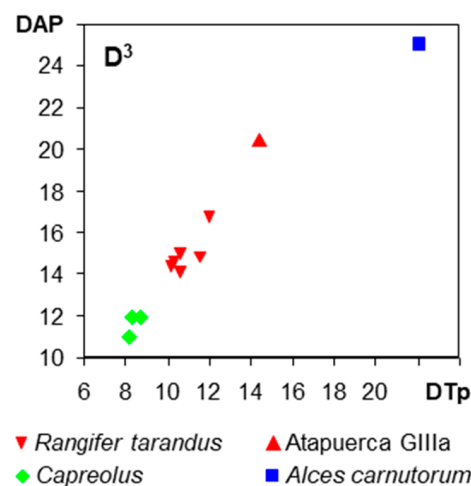
**Figure 3.** Third upper deciduous molars (D<sup>3</sup>) of selected Cervidae: (1) Ata18/GIIIa/L25/103—*Rangifer* from Atapuerca Galería GIIIa: (a) buccal, (b) occlusal, and (c) lingual views. (2) Ata22/E7c/G23/32—*Capreolus* from Atapuerca Sima del Elefante TE7: (a) buccal, (b) occlusal, and (c) lingual views. (3) IPHES O235—recent *Rangifer tarandus*: (a) occlusal and (b) lingual views. (4) MNCN 17959—recent *Cervus elaphus*: (a) anterior, (b) buccal, (c) occlusal, (d) lingual, and (e) posterior views. (5) IPHES O234—recent *Capreolus capreolus*: (a) occlusal and (b) lingual views (reversed). (6) Ata22/GIIIa/H20/7—*Cervus elaphus* from Atapuerca Galería GIIIa: occlusal view (reversed). Red arrows indicate the presence or absence of fused lingual roots under the two lingual cusps. Red lines highlight the position of the two lingual cusps: well separated or close together.

In the occlusal view, the bases of the two lingual cusps are close together, separated by a narrow and shallow indentation. This is different from the D<sup>3</sup> of *Cervus elaphus*, both recent and fossil from the same site (Figure 3(4a–4e,6)) and has the base of the first lobe extending lingually much more anteriorly; the first and second lobes are separated by a wide and deep indentation. The same differences were found between recent and fossil

*Rangifer* (Figure 3(3a,3b,6) [47], Figure 10/6) and recent and fossil *Capreolus* on the one hand (Figure 3(2a–2c,5a,5b)) and recent *Cervus elaphus* (Figure 3(4a–4e)) on the other. We also observed the same differences between several other Capreolinae, such as *Alces*, and other Cervinae, such as *Dama*.

In the lingual view, it can be seen that Ata18/GIIIa/L25/103 has a root below each lingual lobe, but they are close together and fused over their whole length but have a furrow from the crown to the tip of the roots (Figure 3(1c)). Near the tips, the furrow becomes wider and the roots diverge slightly. Recent *Rangifer* and *Capreolus* (Figure 3(3b,5b)) have also fused lingual roots. In contrast, *Cervus elaphus* (Figure 3(4d)) has a root below the posterior lingual cusp, while there is one wide root below the two anterior cusps.

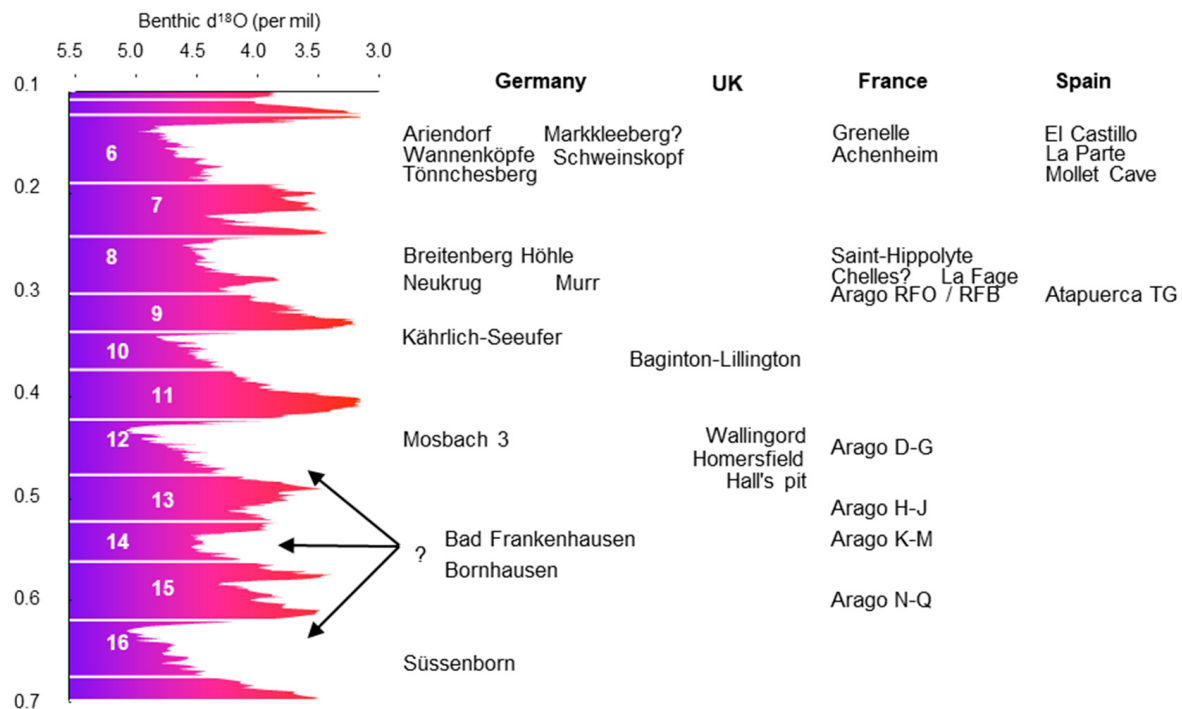
The dimensions (in mm) of Ata18/GIIIa/L25/103 are maximum length (DAP) 20.4, basal length (DAPb) 18.3, width of the first lobe (DTa) 12.8, width of the second lobe (DTp) 14.4. The specimen is much larger than the recent and fossil *Capreolus* and is much smaller than *Alces carnutorum* (Figure 4), which was much smaller than *Alces latifrons* and smaller than or equal to the living species *Alces alces* [48]. It is a little larger than the recent *Rangifer* we studied but closer to a specimen from Maastricht-Belvédère 5 (the Netherlands), which dates to the early Weichselian [49].



**Figure 4.** The length (DAP) and width (DTp) of the third upper deciduous molar (D<sup>3</sup>) comparing *Rangifer tarandus*, both recent and fossil from Maastricht-Belvédère (Netherlands, Weichselian), *Capreolus* spp. from Atapuerca TE7 (Spain, about 1.2 Ma), Voigtstedt (Germany, about 0.7 Ma and recent), *Alces carnutorum* from Untermassfeld (Germany, Jaramillo Subchron), and the specimen from Galería. Raw data in Table A1.

## 5. Discussion

Morphologically, Ata18/GIIIa/L25/103 is similar to the Capreolinae; while it is much too large for *Capreolus* and too small for *Alces*, it fits *Rangifer*. Reindeer live today in the Arctic and other cold parts of Eurasia and North America. After more than 40 years of excavation, the first fossil of a cold-adapted species was found in Galería. There are many sites with *Rangifer* in Europe, but by far most of them date to the last glacial period, and there are relatively few Middle Pleistocene sites. The NOW database gives 181 sites with *R. tarandus* from Eurasia, with only Süssenborn (Germany, about 0.65 Ma) and three levels at Arago (France) being older than MIS 6. Figure 5 shows more occurrences of Middle Pleistocene *Rangifer*, based on the literature.

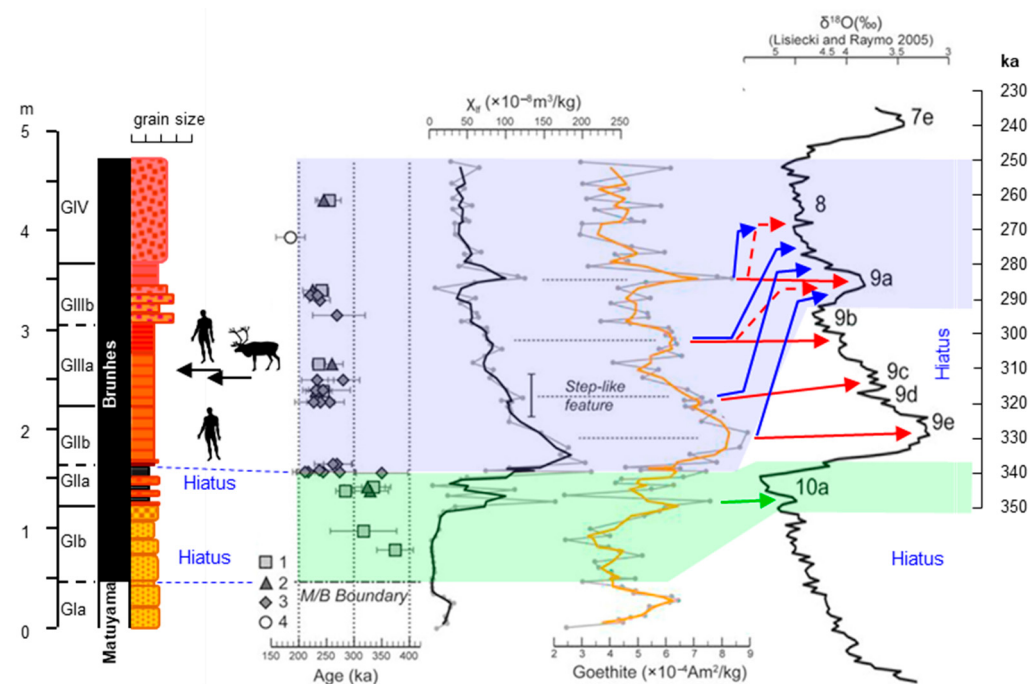


**Figure 5.** Middle Pleistocene occurrences of *Rangifer* in Europe mentioned in multiple sources [4,50–53]. The stratigraphic positions relative to the MIS stages and oxygen isotope curve [54] are approximate.

### 5.1. Age of the *Rangifer* Find from Galería

As indicated above, Galería has been dated many times using different methods. One of the most recent studies was conducted by Bógalo et al. [42] (Figure 8), who studied goethite and ferromagnetic mineral proxies to estimate annual precipitation and used datings as well as the peaks of the curves of their proxies to correlate the Galería sequence with the marine oxygen isotope curve and MIS stages (red arrows in Figure 6). Such a correlation would imply that the reindeer fossil dates to MIS 9, around the transition of 9b and 9c. However, *Rangifer*, being a cold-adapted species, would be expected to date to a cold stage, such as MIS 8. These authors mentioned that the magnetostratigraphic reversal observed in the section does not correspond to the Brunhes–Matuyama boundary but to a hiatus. The dating results suggest the possibility of a second hiatus: the dates immediately below the GIIa–GIIb boundary are significantly older than the dates immediately above it, indicating an apparent gap from about 340 to 290 ka. Accepting such a gap, GIIb and GIIa can be correlated with MIS 10 and the beginning of MIS 9e (green area and arrow in Figure 6) and GIIb to GIV with MIS 9a to MIS 8 (blue area and arrows).

Up to now, the oldest known records of *Rangifer* in Spain have been found in Mollet Cave, La Parte, and El Castillo, dated around 200, 150, and 120 ka, respectively, within MIS 6 [4]. The antiquity of the remains found at El Castillo has been known for a long time [55,56]. Spanish sites that date to or are correlated to MIS 8 or MIS 10 do not have *Rangifer*, such as TD10.2 [25] and various sites in the Manzanares Valley [30,57]. Whether dating to MIS 9 or MIS 8, the specimen from Galería is the oldest reindeer fossil from Spain.



**Figure 6.** Lithostratigraphy of Galería (Atapuerca), the stratigraphic distribution of lithic industry and the position of the fossils of *Homo* and *Rangifer*, dating results, low-field magnetic susceptibility, total goethite content, and the marine oxygen isotope curve adapted from Bógalo et al. [42]. Red arrows indicate the correlations by Bógalo et al. [42]. Added here are the positions of two possible hiatuses and an alternative correlation in blue and green, which fit the numerical dating better.

## 5.2. *Rangifer* from Galería in the Biogeographic Context of the Genus

Cervidae first dispersed from Asia to North America during the early Blancan (Pliocene) [58,59]. *Rangifer*'s closest relative is the North American *Navahoceros*, while the closest living relatives are the South American *Hippocamelus* and *Blastoceros* [60], suggesting that reindeer originated in North America. The *Rangifer* remains from Cape Deceit and Fort Selkirk (Yukon, Alaska) date to 1.8–1.6 Ma [2,3,47,61]. Fossil reindeer are found as far south as in the Late Pleistocene of Yarbrough Cave (Georgia), about 34° N [62]. This is at a similar latitude to Rabat, Morocco. In Europe, they are known from Süssenborn [63], which is still with *Mimomys* and dates probably to MIS 16, and Arago unit Q4, with an age close to 580 ka [64].

The geographic distribution of *Rangifer* has been well studied, and maps of the maximum distribution of *Rangifer* based on fossils have been published for more than a century [2,3,56]. The southernmost areas where it lived are northern Spain, followed by the area near Vladivostok in Russia. Recently, the Spanish fossil record of *Rangifer* received much attention, and fossils from 55 sites are known in the Cantabric Mountains and Pyrenees [7,11] (Figure 1). The southernmost of these are L'Arbreda and some other Late Pleistocene sites in Catalonia, all in the forelands of the Pyrenees. The Pyrenees are situated here a little further south than the Cantabric Mountains. It has been proposed that the Cantabrian–Pyrenees Mountain range formed a barrier for reindeer (see discussion in [11]), and the find from Galería is special in that it is clearly south of it. There are three sites in the Cantabric Mountains that are situated south of the watershed that forms the northern limit of the Ebro basin [11], and Arrillor cave is the one closest to Atapuerca. It is about 93 km from Galería and 64 km more to the north. Rock art depicting reindeer is known from nearly 20 sites [9,11] and includes the sites Siega Verde (province of Salamanca) and Cueva del Reno and Cueva de la Hoz (both Guadalajara). Interestingly, the published maps

of the distribution of *Rangifer* do not show its presence in the Balkans or Italy south of the Po valley [2,3] nor is it mentioned by Sardella et al. [65].

In Arago, on the northern side of the Pyrenees, cold-adapted species are found in almost all levels, which, according to the datings, range in age from MIS 16 to 11 [64]. *Rangifer* is abundant in the lowest levels, Q-N, peaks in levels M-K, and in levels J-C, while *Praeovibos* appears first in I, peaks in G, is still common in D, but later becomes rare [50]. One would expect the existence of levels that correlate to MIS 15, 13, and 11 that would have no cold-adapted fauna, but this is not the case. This either implies that these warm stages are not represented in the Arago sequence, or that the cold-adapted species were present during these interglacials. Perhaps they were not yet so well adapted to low temperatures. If the latter were the case, it is strange that they do not appear in other interglacial fauna. It is widely accepted that, during the warm stages, cold-adapted species lived in boreal, mountainous, and steppe refugia [2,3,66]. The *Rangifer* and *Praeovibos*, found at Arago, may have lived during the interglacials at a greater altitude in the Pyrenees. Caprinae tend to be adapted to mountainous environments, and the habitats in which reindeer live today include “mountain summit meadows” and “high arctic desert up to 2700–3000 m above sea level” [67]. It has been suggested that *Rangifer* originated as adapted to alpine meadows and later spread to the tundra [68]. The northern side of the Pyrenees has shorter days, less sunlight, and lower temperatures than flat land at the same latitude and may have served as an interglacial refuge for cold-adapted species. This could explain its apparent presence in Arago in warm MIS stages.

The Sierra de Atapuerca is a low hill and is situated at some distance from the Pyrenees but is closer to the Sierras de la Demanda and Urbión, which have peaks close to 2300 m. However, these are probably not extensive enough to maintain a viable population of reindeer during an entire interglacial. Given the datings of GIII, it seems more likely that *Rangifer* extended its range southward during a cold period, MIS 8 in this case.

The question could be asked whether the reindeer tooth from Galería was brought there by humans from further north. The formation of the site has been studied [23]. Large mammals fell into the natural trap that was formed by the TN conduct, when it opened to the surface. Humans exploited the carcasses that arrived in this way into the cave, but their presence was mostly limited to these events. They took bones out of the cave, but there is no evidence of them bringing bones or teeth into the cave. The reindeer tooth from Galería has a similar aspect as other isolated teeth from there and does not show any indication of weathering, natural transport (like rounding or abrasion), and or signs of modification by humans. At present, there is no reason to believe that it arrived at Galería post mortem.

### 5.3. *Rangifer* from Galería in the Context of the Cold-Adapted Fauna

Süssenborn is generally considered to be the oldest or one of the oldest European fauna with cold-adapted species: *Rangifer*, *Ovibos suessenbornensis*, *Soergelia elisabethae*, and, from possibly a slightly higher level, *Coelodonta* [63,69–71]. It is considered to be early Elsterian and still has *Mimomys* [72] and probably dates to MIS 16 (about 650 ka). The *Rangifer* and *Praeovibos* from Arago date to at least MIS 14 and 12, respectively [64].

Álvarez Lao and García (2010) [4] listed the Iberian sites with cold-adapted fauna and discussed their ages. *Mammuthus primigenius* is known from 25 sites, half of which are dated. The oldest records are not dated but could be late Middle Pleistocene (MIS 6) and are from near Madrid. The southernmost site with *Mammuthus primigenius* is Padul, in the province of Granada [73], and dates to about 40–30 ka. *Coelodonta antiquitatis* is known from 21 sites; the oldest one is from La Parte in the Cantabric Mountains (Asturias) and was dated to around 150 ka. The southernmost are from the Madrid area [74] and are not dated, but some of them could be MIS 6. *Ovibos*, *Gulo*, *Alopex*, and *Saiga* are known from

Spain but just from one, two, or three sites, all in the Cantabric Mountains or Pyrenees, and all are of Late Pleistocene age. There are no unequivocal cold elements among the small mammals from Galería [25], and we are not aware of their presence at other sites of similar age. Up to now, the first recorded entry of a cold-adapted species in the Iberian Peninsula dates to MIS 6, making the MIS 8 *Rangifer* tooth from Galería the oldest of all. Although the Iberian Middle Pleistocene fossil record is not very dense, there are some sites dating to MIS 10, that do not have cold-adapted fauna, supporting the idea that such fauna appeared later in MIS 8. These are Atapuerca TD10.2 and the sites from the Manzanares valley mentioned above.

#### 5.4. The Expansion of Glacial Fauna into the Southern Refugia

It has long been observed that certain taxa became restricted to southern or tropical regions, and various explanations have been proposed, including global cooling and alternating climatic regimes [75,76]. Penck and Brückner (1909) [77] introduced the classification of the Günz, Mindel, Riss, and Würm glacial periods. In response, paleontologists and archaeologists sought to identify the corresponding alternations of glacial and interglacial fauna [55,56]. However, much later Penck [78] argued that such faunal alternations did not exist. This view was strongly criticized by Soergel (1940, 1943) [66,79], who pointed to the tundra, steppe, and mountainous regions as the original habitats of glacial faunas—areas that also function as refugia during warmer climatic phases.

In the debate above and in the later literature, the refugia for the interglacial fauna were not mentioned. Apparently, it was taken for granted that these were the southern peninsulas of Europe. As glacial fauna extended progressively further into the Iberian Peninsula, it is to be expected that the glacial refuge shrank accordingly. While *Rangifer* and *Praeovibos* at Arago on the northern side of the Pyrenees mark the southernmost limit of the glacial fauna in MIS 12–14 (16?), *Rangifer* from Galería (42°21' N) marks the first expansion into the Iberian refugium as early as MIS 8. In MIS 6, cold-adapted species are known to have reached Madrid (40°20') and in the last glacial the province of Granada (37°01'). Warm-adapted large mammals that most depended on the refuge areas of southern Europe included *Palaeoloxodon antiquus*, *Hippopotamus*, *Sus scrofa*, *Dama*, and *Bos primigenius*. *Bubalus murrensis* and possibly *Stephanorhinus kirchbergensis* recolonized Europe from Asia. It would be worthwhile to systematically map the distribution of these taxa during the different glacial times, as has been conducted for the glacial fauna.

#### 5.5. Human Distribution During the Glacial Periods

The human colonization of Europe began in the south [80–83], while the higher latitudes were reached later [84–86]. Like many other mammal species, humans had refugia in the southern peninsulas of Europe during the glacial periods and spread northward during the subsequent interglacial periods. By MIS 14 and MIS 12, humans had acquired anatomical, physiological, and cultural adaptations that allowed them to live as far north as the U.K., northern France, and Germany [13]. This suggests that they were less dependent on refugia, such as the Iberian Peninsula. However, the possibility of a late “bottleneck”, as evidenced by the reduction in variability of the Neanderthal DNA [87], would suggest that refugia may have been important. Human fossils from Atapuerca play a role in the debate and so will the site of Galería, where the coincidence with *Rangifer* is proof that the human fossils and abundant lithic industry date to a glacial period. Eventually, reindeer became abundant in northern Spain [88], and there is evidence that they were hunted [11]. The European sites where reindeer is the predominant prey species gave rise to a discussion as to whether humans became specialized reindeer hunters during the Middle Paleolithic [89,90].

## 6. Conclusions

A recent find from Galería in the Sierra de Atapuerca is described and discussed. We draw the following conclusions:

- A single tooth demonstrates the presence of *Rangifer* in Galería unit GIII;
- This tooth, along with other fossils from the same stratigraphic level, dates to MIS 8;
- The accompanying fauna represents a typical “interglacial fauna” that inhabited the glacial refugium that was Spain back then;
- This finding constitutes the southernmost record of a reindeer in Eurasia during MIS 8;
- It also represents the oldest record of a cold-adapted large mammal in the Iberian Peninsula;
- During the subsequent glacial periods, cold-adapted mammals spread further into the Iberian glacial refugium;
- Humans inhabited the Sierra de Atapuerca during a period likely characterized by challenging local climatic conditions, as testified by the presence of reindeer.

**Author Contributions:** Conceptualization, J.v.d.M.; methodology, I.A.L. and J.v.d.M.; investigation, J.v.d.M., I.A.L., P.G.-M. and I.C.; direction of the excavation, I.C. and P.G.-M.; preparation of figures, J.v.d.M. and I.A.L.; writing—original draft preparation, J.v.d.M., I.A.L., P.G.-M. and I.C.; writing—review and editing, J.v.d.M., I.A.L., P.G.-M. and I.C. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the Spanish Ministerio de Ciencia, Innovación y Universidades, grant numbers PID2021-122355NB-C33 and PID2021-122355NB-C32, MCIN/AEI/10.13039/501100011033/FEDER, UE; by the Agència de Gestió d’Ajuts Universitaris I de Recerca, grant number 2021 SGR 01238; and by the Universitat Rovira i Virgili, grant number 2023PFR-URV-01238. I. A. L. was funded by the Ministerio de Ciencia e Innovación de España under grant No. RYC2021-034991-I, MCIN/AEI/10.13039/501100011033, and European Union NextGenerationEU/PRTR. P.G.-M. was supported by the ERC Lateurope project (grant agreement ID 101052653).

**Data Availability Statement:** The original data used here for comparison are given in Table A1.

**Acknowledgments:** We thank the three anonymous reviewers for their constructive criticism, which helped to improve the paper and the persons who gave access to the material that was used here for comparison. We thank all the volunteers, technicians, researchers, and other personnel who have contributed to the excavation and preservation of the paleontological and archaeological finds at Atapuerca.

**Conflicts of Interest:** The authors declare no conflicts of interest. The funders had no role in the design of this study; in the collection, analyses, or interpretation of data; in the writing of this manuscript; or in the decision to publish the results.

## Abbreviations

The following abbreviations are used in this manuscript:

|        |                                                                            |
|--------|----------------------------------------------------------------------------|
| CENIEH | Centro Nacional de Investigación sobre la Evolución Humana                 |
| DAP    | Antero-posterior diameter (maximum)                                        |
| DAPb   | DAP at the base of the crown                                               |
| DTa    | Transverse diameter of the anterior lobe                                   |
| DTp    | Transverse diameter of the posterior lobe                                  |
| ESR    | Electron spin resonance                                                    |
| ESR-US | ESR-uranium series                                                         |
| IPHES  | Institut Català de Paleoecologia Humana i Evolució Social                  |
|        | Institut für Quartärpaläontologie Weimar, now Forschungsstation für        |
| IQW    | Quartärpaläontologie of the Senckenberg Forschungsinstitut und Naturmuseum |
|        | Frankfurt, Weimar                                                          |

|         |                                                                                                     |
|---------|-----------------------------------------------------------------------------------------------------|
| MIS     | Marine isotope state                                                                                |
| NBC     | Naturalis Biodiversity Center, Leiden                                                               |
| NMM     | Natuurhistorisch Museum, Maastricht                                                                 |
| pIR-IR  | Post infrared-infrared stimulated luminescence                                                      |
| TD      | Trinchera Dolina, the site of Gran Dolina                                                           |
| TG      | Trinchera Galería, the site or central part of Galería                                              |
| TL      | Thermo Luminisence                                                                                  |
| TT-OSL  | Thermally transferred optically stimulated luminescence                                             |
| TN      | Trinchera Norte, a part of TG                                                                       |
| TZ      | Trinchera Zarpazos, Covacha de los Zarpazos, a part of Galería                                      |
| ZPALUWr | Division of Palaeozoology, Department of Evolutionary Biology and Ecology,<br>University of Wrocław |

## Appendix A

**Table A1.** The measurements of the D<sup>3</sup> (mm), used for comparison in Figure 4.

| Taxon                   | Locality             | Collection/Reference | Number                    | Side | DAP  | DAPb | DTa  | DTp  |
|-------------------------|----------------------|----------------------|---------------------------|------|------|------|------|------|
| <i>Rangifer</i>         | Atapuerca TG         | IPHES                | Ata18/GIIIa/L25/103       |      | 20.4 | 18.3 | 12.8 | 14.4 |
|                         | Maastricht-Belvedere | NMM                  | 2195                      | d    | 16.7 | 16.4 | 10.5 | 12.0 |
|                         | Recent Greenland     | NBC                  | 20389                     | s    | 14.8 | 14.8 | 10.2 | 11.6 |
|                         |                      | NBC                  | 11665                     | s    | 14.3 | 13.0 | 9.1  | 10.2 |
|                         | Recent zoo           | NBC                  | NAM55                     | s    | 14.6 | 12.4 | 8.8  | 10.3 |
|                         |                      | NBC                  | 1                         | s    | 14.9 | 13.3 | 9.4  | 10.6 |
|                         | Recent Lacunacha     | IPHES                | O-235                     | s    | 14.1 | 12.4 | 9.7  | 10.6 |
| <i>Procapreolus</i>     | Weze (Poland)        | ZPALUWr [91]         | MZ370                     | d    | 11.2 | 10.2 | 7.8  | 9.8  |
| <i>Capreolus</i>        | Atapuerca TE7        | IPHES                | Ata22/TE7c/G23/32         | d    | 11.9 | 10.9 | 7.4  | 8.3  |
|                         | Voigtstedt           | IQW [92]             | 1966/7411/Voi3595         | s    | 11.9 | 10.9 | 8.4  | 8.7  |
|                         | Recent Lacunacha     | IPHES                |                           | d    | 11.0 | 9.7  | 7.1  | 8.2  |
| <i>Alces carnutorum</i> | Untermassfeld        | [93]                 | IQW 1987/22044 (Mei21563) | d    | 25.0 |      |      | 22.1 |

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