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The mandible of Salbatore II: A new *Ursus deningeri* site in the northern Iberian Peninsula ✡

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Highlights

- Identification of a new remain of *Ursus deningeri*, a scarse species in the Iberian Peninsula.
- Detailed comparison with late Early to late Middle Pleistocene *U. deningeri* specimens illustrates the morphological complexity of this species.
- Presence of a Middle Pleistocene site in the Cantabrian Region adds to the paleontological record prior to the Late Pleistocene.

Abstract

Ursus deningeri, together with *Ursus spelaeus sensu lato*, are chronospecies that belong to the Quaternary iconic cave bear lineage. They inhabited Iberia from the late Early to the late Middle Pleistocene. Here we describe a complete bear mandible recovered from Salbatore II cave (Basque Country). To assess its taxonomy, we compared it with other European Pleistocene cave and brown bears. Comparisons were made concerning its morphology and using both traditional and 3D geometric morphometrics analyses. The mandible has several morphological similarities with the cave bears such as a high corpus and deep masseter fossa. However, it exhibits a coronoid process that leans backwards, a pointed pterygoid process, and the p1 and p3 are present. These are characteristics customarily associated with *U. deningeri* and *U. arctos*. Metric analyses show that Salbatore II fits within the cave bears variation, with a minimum overlap with brown bears once size is accounted for. However, geometric morphometric analyses show that Salbatore II is similar to *U. arctos*, but within *U. deningeri* variation. Based on the overall size and the morphological characteristics, Salbatore II displays *U. deningeri* affinities with many ancestral characteristics, suggesting a minimum mid-Middle Pleistocene age rarely recorded in the Cantabrian region.

Keywords:

Cave bear

Geometric morphometrics

Evolution

Early Pleistocene

Middle Pleistocene

1. Introduction

The Deninger bear *Ursus deningeri*, together with *Ursus spelaeus sensu lato*, are chronospecies that belong to the cave bear lineage, which inhabited Eurasia from the late Early Pleistocene to the Late Pleistocene. This lineage experienced a progressive increase in size and a gradual acquisition of traits indicative of an herbivorous diet, with several transitional taxa having been described from ca. 200 ka, including *Ursus spelaeus deningeroides* Mottl, 1964, and *Ursus deningeri-spelaeus* from sites such as Repolust (Kurtén, 1959), Azé I-2 and Azé I-3 (Argant, 1991), and Nauterie (La Romieu, Level 7; Prat and Thibault, 1976).

The molecular history of cave bears, based on mitochondrial and nuclear DNA studies, is complicated. During the Late Pleistocene, five putative species/subspecies inhabited Europe, the Urals and the Caucasus – *U. s. spelaeus*, *U. ingressus*, *U. kudarensis* (Knapp et al., 2009; Stiller et al., 2014), *U. spelaeus eremus*, and *U. kanivetz* (Barlow et al., 2021). Some of these coexisted in the same region such as *U. s. spelaeus* and *U. ingressus* in eastern France (Gretzinger et al., 2019) and *U. ingressus* and *U. s. eremus* in the Alps (Rabeder et al., 2004). Paleogenome studies of Palearctic bears have also suggested the presence of admixing among these five taxa (Barlow et al., 2021).

During the Middle Pleistocene, the cave bear *U. deningeri* inhabited Europe, coexisting with a genetically different species, *Ursus kudarensis praekudarensis*, found in the Caucasus and northeastern Asia (Baryshnikov, 1998; Knapp et al., 2009; Baryshnikov and Puzachenko, 2019). The European *U. deningeri* fossils show a large intraspecific variability and sexual dimorphism, which has led to the description of several subspecies such as *Ursus deningeri hundsheimensis*, based on remains from the Hundsheim site (Austria; Zapfe, 1946), *Ursus deningeri suevicus* based on fossils found at Jagsthausen (Germany; Koby, 1951), and *Ursus deningeri romeviensis* based on remains found at Nauterie (France; Prat and Thibault, 1976).

In the Iberian Peninsula, eight sites have yielded *U. deningeri* remains so far, spanning the late Early Pleistocene to Middle Pleistocene. Compared to the Late Pleistocene *U. spelaeus*, the number of sites containing, and specimens of *U. deningeri* are scarce, except at Sima de los Huesos, Santa Isabel de Ranero, and La Lucia. The oldest remains date from the late Early Pleistocene and belong to the Vallparadís section (Terrasa, Barcelona; Madurell-Malapeira et al., 2009, 2010), whose levels belong to the Epivillafranchian biochron (1.2–0.8 Ma). The largest Middle Pleistocene fossil bear accumulation in Iberia is found in the karst system of the Sierra de Atapuerca site complex (Burgos). The most extensive assemblage has been excavated from here, encompassing fossils from various locations such as Sima de los Huesos, dated at 416 ± 17 ka and 428 ± 13 ka BP (LU-7; Arnold et al., 2014) and 434 +36/-24 ka BP (LU-6; Arsuaga et al., 2014), Sala de los Cíclopes and Sala de las Oseras (García et al., 1997; García García, 2003). Additionally, bear remains from Galería have been classified as *Ursus* cf. *U. deningeri* (Rodríguez et al., 2011). Other *U. deningeri* remains have also been found at Santa Isabel de Ranero (Biscay; ca. 300 ka BP; Torres et al., 2001, 2014), Cueto de la Lucia (Cantabria; 247 ± 26 ka BP; Torres et al., 2005), and Lezetxiki (Gipuzkoa; 115 +9/-8 ka and > 260 by U-Th and 225 ± 40 ka by ESR; Falguères et al., 2005), although U-Th ages of 309 ± 92 ka BP and 303 ± 114 ka BP have also been reported (Altuna, 1992).

In this context, the description of new *U. deningeri* fossil remains is vital in order to improve our understanding of the intra-specific variation and evolution of the cave bear lineage. The aim of this work is to describe a recently found cave bear mandible with primitive features from the Salbatore II cave, and to compare it morphometrically with *U. deningeri* remains of the late Early and Middle Pleistocene.

2. Geographic and geological setting

The Salbatore II cave is located in the municipality of Itziar, Deba (Gipuzkoa). It was catalogued as Salvatore II by the Club Deportivo (CD) Eibar in 1971. The cave lies in Upper Aptian reef limestones and is surrounded by a network of faults that juxtapose the limestones with adjacent materials (Garrote et al., 1989). The cave is located on the northwestern slope of the karstic pinnacle of the same name, and is currently intersected by the Highway A8. Part of the entrance (ca. 15 m) was razed to the ground during construction of the motorway, which led to a partial collapse of the cave and the debris observed inside. The fossil remains discovered here were found at the base of a cone of blocks of limestone debris, in an area that corresponds to the original topography of the cave (Fig. 1).

The Salbatore karstic pinnacle is characterised by an extensively developed endokarstic network that hosts caves such as Salbatore I, Urtiaga, Urtiaga II and Surgencia de Urtiaga (Fig. 1). All these caves exhibit morphologies indicative of horizontal phreatic conduits, and they collectively constitute a multi-level system comprising a minimum of three cave levels (Aranburu et al., 2015). Salbatore II may correspond to one or two cave levels in this system, although it is presently not possible to assign specific levels due to its almost complete collapse.

The current entrance to the cave is located between the intersection of the highway cut and the karstic pinnacle. Based on the 1971 topography records from the CD Eibar, ca. 15 m of gallery have been destroyed by the construction of the highway. Consequently, the prevailing deposit in the cave is a colluvial deposit extending from the entrance. As a result of this, the state of preservation of any indicators related to cave’s evolution is poor. Near the entrance, a flat and sub-horizontal cave ceiling has been preserved, providing evidence of paragenetic processes in its formation and suggesting a possible cave level at that height. However, the floor has collapsed, contributing to the colluvium accumulation and the formation of a large chamber. It is not possible to see if there are any more cave levels. Moving towards the lower part of the cave, the influence of colluvial processes diminishes as the topography becomes more horizontal. A floor composed of silts and clays containing siliciclastic gravels and ferruginous nodules starts to appear, indicating the ingress of soils into the cave, a phenomenon that is not currently occurring. The paleontological remains studied herein were collected from the surface of these sediments. The cave terminates in a horizontal surface bearing very fine sediment, featuring morphologies that indicate the intermittent presence of stagnant water. Based on clay traces on the walls, this water level does not usually reach the location where the bones were found. Finally, it is worth noting the presence of some bioerosion cupolas on the ceiling at the bottom of the cave, created by bat colonies.

3. Material and methods

3.1. Material

The Antxieta Arkeologia Taldea recovered five fossil remains from the Salbatore II cave: a complete adult bear mandible, a fragmentary left adult bear rib, a left bear navicular, a fragmentary immature artiodactyl metapodial, and a nearly complete immature thoracic vertebra (indeterminate taxon). All these fossil remains are housed at the Gordailua-Gipuzkoako Foru Aldundiaren Ondare Bildumen Zentroa (Heritage Collections Centre of the Provincial Council of Gipuzkoa, Irún). Here we focus on the complete bear mandible. The samples used for comparative morphometrical analyses are given in Table S1 (Appendix A).

Abbreviations: i, lower incisor; m, lower molar; p, lower premolar.

3.2. Taxonomic and age-at-death assessment

The age-at-death was determined based on the eruption-wear stages published by Stiner (1998). Measurements were taken according to Tsoukala and Grandal d'Anglade (2002). A univariate comparative analysis using z-scores was performed on the mandible. Significant values, i.e., z-score values greater than 1.96 ($p < 0.05$) and 2.576 ($p < 0.01$) standard deviations (Sokal and Rohlf, 1981) were highlighted, as well as the Salbatore II measurements outside the range of our comparative fossil samples. Bivariate analyses were performed on the mandible and teeth. Principal component analysis (PCA) was used to compare the Salbatore II mandible to specimens from *U. deningeri*, *U. spelaeus* and *U. arctos* using eight variables taken from García García (2003), and then was run again using only five selected variables in order to increase the comparative sample size (Fig. S1; Appendix A). A second PCA was performed dividing all the used variables by the geometric mean (Arsuaga and Carretero, 1994). The bivariate analyses and PCA were performed using R software (R Core Team, 2020).

3.3. Geometric morphometrics

Landmarks were chosen following van Heteren et al. (2016) (Table S2; Appendix A). The landmarks were placed using the Landmark software package (Wiley et al., 2005). To calculate the measurement error, three individuals of each species were digitised three times. A Generalized Procrustes Analysis (GPA) and an analysis of variance (ANOVA) based on the procrustes coordinates were performed (Klingenberg et al., 2002; Arlegi et al., 2017) using MorphoJ v.1.07a. software (Klingenberg, 2011). We tested for the measurement error variation being less than the variation among the individuals belonging to all three species, which was only 2.40%, and also less than individuals of the same species: *U. deningeri*, *U. spelaeus* and *U. arctos*, constituting 2.03%, 3.99%, and 3.18%, respectively. Raw 3D coordinates were scaled, rotated and translated by Procrustes superimposition in order to remove all information unrelated to shape (Rohlf, 1990) using MorphoJ v.1.07a. A PCA was performed in both analyses in order to compare the mandible from Salbatore II to the *U. deningeri*, *U. spelaeus* and *U. arctos* specimens.

4. Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Genus *Ursus* Linnaeus, 1758

Ursus deningeri Von Reichenau, 1904

Referred specimen: Complete right mandible SLT.20.0.1.

Description:

Mandible. Both hemimandibles in the studied mandible were fused and the p4-m3 dental series in the right hemimandible and the p1, p4 and m2 in the left hemimandible were preserved (Fig. 2). The specimen belongs to an old adult (Stage VIII *sensu* Stiner, 1998), with the wear on both canines affecting not only the crowns, but also the roots. This high degree of wear may have been the cause of the periostitis in the sockets of all teeth and the evident periodontal disease, which was especially visible on the buccal surface of the left hemimandible, affecting the m1 and, to a lesser degree, the m2. Other lesions of pathological origin include the presence of an abscess in the root of the right i1 and abnormal bone regrowth in the mental foramina located at the level of the diastema of the right hemimandible.

In buccal view, the profile of the mandible ventral corpus is straight, but beginning to curve upwards at the posterior edge of the m3. This profile is similar to some bear specimens assigned to *U. deningeri*, such as one of the specimens from Nauterie (LR 59; Fig. 3), one individual from Mosbach (von Reichenau, 1906; Fig. S2, Appendix A) and the most complete mandible from Vallparadís Section (IPS 14950; Fig. 3), to the *U. dolinensis* from Trinchera Dolina (García García, 2003) and to *U. arctos* (Fig. 3). In other *U. deningeri* specimens, such as Nauterie (LR 120) and Santa Isabel de Ranero (SI-1234), and in *U. spelaeus*, the mandible displays a curved profile at the anterior edge of the m3 (Fig. 3).

In the Salbatore II specimen, the coronoid process leans slightly towards the posterior part of the mandible. The coronoid process morphology is variable in *U. deningeri* (Fig. 3), being slightly posteriorly oriented in some *U. deningeri* specimens from Sima de los Huesos, in the Nauterie specimen LR 59 and Vallparadís Section specimens IPS 14950 and IPS 110415, whereas it is anteriorly oriented in Santa Isabel de Ranero specimen SI-1234, in the Grotte de la Carrière S1 (Prat-Vericat et al., 2020), and Cueva Mayor (García García, 2003). The ramus of the Salbatore II specimen differs from that of *U. spelaeus*, which shows the coronoid process oriented forwards and divided into two sections, the first being vertical and forming a right-angle to the mandibular body and the second leaning backwards (Torres Pérez-Hidalgo, 1988; García García, 2003). The *incisura semilunaris superior* of the mandible from Salbatore II is straight, but curves at the contact with the coronoid crest. In *U.*

deningeri, it is usually straight (Torres Pérez-Hidalgo, 1988; García García, 2003), whereas a slightly curved morphology has been observed in *U. deningeri* from Nauterie (specimen LR 59; Fig. 3). The Salbatore II mandible differs from *U. spelaeus*, in which the *incisura semilunaris superior* tends to slope forwards, and from *U. arctos* which is curved due to the backwards inclination of the coronoid process.

The insertion of the internal pterygoid muscle in the Salbatore II mandible ends in a protruding tip, similarly to *U. arctos* (Torres Pérez-Hidalgo, 1988) and *U. dolinensis* from Trinchera Dolina (García García, 2003). However, in *U. deningeri*, the insertion of the internal pterygoid muscle is wide and does not protrude from the corpus (Torres Pérez-Hidalgo, 1988). We observed a protruding tip in Santa Isabel de Ranero specimen V7119, Nauterie specimen LR 120 and Vallparadís section specimen IPS 14950 (Fig. 4).

The raw dimensions of the Salbatore II mandible, together with the summary statistics of the comparative samples of *U. deningeri*, *U. dolinensis*, *U. spelaeus* and *U. arctos*, and the results of the *z*-score analyses are shown in Table 1. The dimensions of the Salbatore II mandible fits well within the variation of the comparative Middle Pleistocene *U. deningeri* sample, although it is significantly larger than the late Early Pleistocene *U. deningeri* sample. While the Salbatore II mandible also fits within the variation in *U. spelaeus*, it is more gracile and displays shorter dental series than the comparative sample. However, the Salbatore II specimen is larger than the mandible of *U. dolinensis,* both in terms of the height of the ramus and of the condyle. It is also more robust than the comparative Pleistocene *U. arctos* mandible sample with the length and total height of the Salbatore II mandible being significantly larger, and the height of the vertical branch falling outside the range observed in the *U. arctos* sample. Also, the mandibular body in our specimen is significantly wider at the m2-m3 and the diastema is significantly longer. The mandibular condyle is relatively smaller in relation to its width compared to the mean values for *U. deningeri* (Fig. S3; Appendix A). However, it is within the variation of cave bears and outside the variation of *U. arctos*.

The results of the first PCA based on traditional measures are shown in Fig. 5(A, B) and Table S3 (Appendix A). The Salbatore II mandible plots consistently within, albeit at the limit of, the variation in the Middle Pleistocene *U. deningeri* and does not overlap with the late Early Pleistocene *U. deningeri*. Except for a very few instances, the variation in *U. deningeri* also falls within the 95% equiprobability ellipse of *U. spelaeus*. Cave bears and brown bears are distributed along PC1 (92.2% of the variance) with minimum overlap, which relates to overall size, as all the variables studied correlate with this PC, having similar values. All species overlap in PC2, which is related to the mandibular corpus height, and PC3, related to length of the dental series. When compared to only the *U. deningeri* specimens from different chronologies (Fig. S4 and Table S4; Appendix A), the Salbatore II mandible shows PC1 values close to 0, separating it from the late Early Pleistocene *U. deningeri* in PC2, which is related to thickness of the mandibular corpus, and PC3, related to length from the canine to the m3.

The results of the second PCA, in which we divided the raw variables by the geometric mean, are shown in Fig. 5(C, D), and Table S5 (Appendix A). In this analysis, the overlap between the specimens increases. The mandible of Salbatore II falls within the variation of *U. deningeri*, close to the centroid of *U. spelaeus*, and also at the edge of the 95% equiprobability ellipse of *U. arctos*. These species are distributed along PC1 (40.9% of the variance), relating to the general length and thickness of the corpus and height of the ramus. There is a complete overlap between the different species in PC2 (22.3% variance) and PC3 (11.9% variance), related to height of the corpus.

The results of the shape space PCA, based on geometric morphometrics, are shown in Fig. 5(E). The Salbatore II mandible is closer to the limit of the variation in *U. arctos* than to *U. deningeri*, and occurs in the same space as a *U. deningeri* mandible from Sima de los Huesos (SH), which belongs to a young adult (Stage IV *sensu* Stiner, 1998). The Salbatore II and the SH mandibles show PC1 values close to 0, while the *U. deningeri* and *U. spelaeus* specimens have positive PC1 values, relating to a relatively wide dorsoventral (superoinferior) corpus, a relatively curved corpus profile under the m3, a relatively thick condyle and a relatively more anterior tip of the coronoid process. Although there is overlap between *U. deningeri* and *U. spelaeus*, the former (and the Salbatore II specimen) tend to have more positive PC2 values, related to a relatively more posterior tip of the coronoid process. As shown by the PC1 and PC3 values displayed in Fig. S5 (Appendix A), the Salbatore II mandible and one *U. deningeri* specimen from Nauterie plotted separately from the others, showing highly negative PC3 values relating to a relatively wide dorsoventral corpus, whereas the rest of the specimens fall along all the PC. When the landmark information regarding the inferior aspect of the corpus is deleted (Fig. S6; Appendix A), larger (but still minimal) degree of overlap become apparent between cave bears and *U. arctos* in PC1. The mandibles from Salbatore II and one of the specimens from the late Early Pleistocene show negative PC1 values related to a relatively more posterior tip of the coronoid process. In addition, *U. deningeri* and the Salbatore II specimens have negative PC2 values related to a relatively short ramus. The Salbatore II mandible have a centroid size similar to that of the Middle Pleistocene *U. deningeri* median, but this also fits within the variation of *U. spelaeus* (Fig. S7; Appendix A).

Dentition. The mandible from Salbatore II includes a preserved p1, the alveolus of the p3, the p4 and the m2 in the left hemimandible, and the alveolus of p1 and p3, and the p4-m3 in the right hemimandible. The p1 is present in some *U. deningeri* specimens from Sima de los Huesos and Vallparadís Section. It is normally present in *U. dolinensis* (García García, 2003) and *U. arctos*, whereas it is absent in *U. spelaeus*. All teeth are worn, especially the m1 and m2, where the cuspulids are not preserved, and so they can only provide information on the morphology of the occlusal outline.

The p4 has a broad elliptical outline, which is recurrent in *U. deningeri* (García García, 2003). It shows a parastyle in the mesial part of the tooth and three small cuspulids forming a row from the protoconid to the posterior part of the tooth. The presence of a parastyle is a frequent characteristic in cave bears (Torres Pérez-Hidalgo, 1988; García García, 2003; Wagner and Cemárk, 2012; Fig. S8, Appendix A), whereas the brown bears develop a cuspulid in the distal part of the p4. The m1 displays a buccolingually wide talonid in relation to the trigonid, with the buccal edge being concave and the lingual edge being straight. The occlusal surface is worn, but the cementum can provide us an idea of the number of cuspulids that may have been present. The metaconid can be triple and the entoconid double. Both m2 have concave buccal edges and straight lingual edges. This is a primitive characteristic that frequently occurs in *U. arctos* and is present in some *U. deningeri* (Torres Pérez-Hidalgo, 1988; Fig. S8, Appendix A). On the right m2, small cuspulid is preserved on the metaconid that is in contact with the entoconid, and the left m2 displays this small cuspulid in the most mesial part of the tooth. Based on the presence of these cusps and the cementum, we can assume the metaconid is triple. Despite the wear, the morphology of the entoconid can be observed in the left m2 being double. Finally, the m3 has a pentagonal shape with a pointed distal part.

The raw dimensions of the lower dentition of the Salbatore II specimen, together with the summary statistics of the comparative samples of each *U. deningeri* from the Middle

Pleistocene, *U. deningeri* from the late Early Pleistocene, *U. spelaeus* and *U. arctos*, as well as the results of the *z*-score analyses are shown in Table 2. The dimensions of the Salbatore II mandible fit well within the variation of the Middle Pleistocene *U. deningeri*.

5. Discussion

The *U. deningeri* fossil record is relatively scarce and covers a relatively broad range of time, from 1.2 Ma (Vallparadís Section; Madurell-Malapeira et al., 2009, 2010) to transitional forms towards the end of the Middle Pleistocene (ca. 200 ka). Concerning the Iberian Middle Pleistocene *U. deningeri* record, the SH fossil remains have been dated ca. 430 ka (Arsuaga et al., 2014), and the rest of the Iberian *U. deningeri* record is ca. 300 kyr old or younger. Therefore, there is a significant gap of paleontological information on the mid-Middle Pleistocene cave bears history of the Iberian Peninsula. In this context, the morphology of the Salbatore II mandible, despite the lack of a chronological context, can provide vital clues to improve our understanding of the evolution of the cave bear lineage.

5.1. Morphology of the Salbatore II mandible

The Salbatore II mandible is similar in size to most of the European *U. deningeri* and *U. spelaeus* mandibles, based on the greater length and thickness of the mandible, together with the greater length of the diastema. However, it has some primitive features, such as the insertion of the internal pterygoid in a pointed shape and exempt from the mandibular body, that have also been observed in a few Middle Pleistocene *U. deningeri* specimens, such as those from Santa Isabel de Ranero (V7119) and Nauterie (LR 59), the late Early Pleistocene *U. deningeri* from Vallparadís Section, and *U. arctos* (Torres Pérez-Hidalgo, 1988). Also, the Salbatore II specimen possesses a corpus similar to those of some *U. deningeri* mandibles from Mosbach (von Reichenau, 1906; Fig. S2(A, D), Appendix A) and Vallparadís Section (Madurell-Malapeira et al., 2009, 2010). However, its size is larger overall than the mentioned late Early Pleistocene *U. deningeri* bears.

There is a large degree of morphological variability in *U. deningeri* (García García, 2003; van Heteren et al., 2018). The latest Middle Pleistocene forms were increasingly similar to *U. spelaeus*, as opposed to the archaic forms from the latest Early Pleistocene, which are closer to the *U. etruscus* morphotype. Because this species encompasses bears that occur nearly 1 myr apart, the intraspecific differences could be attributed to chronological factors. In addition, we also observed morphological variability within the same population. If we extrapolate the genetic complexity and morphometric variation of cave bears s.l. during the Late Pleistocene – where cave bears comprised several genetically differentiated lineages (Barlow et al., 2021) which also show metrical and morphological differences (Vereschagin and Baryshnikov, 2000; Rabeder et al., 2004; Baryshnikov and Puzachenko, 2011, 2019; Spassov et al., 2017) – to the Middle Pleistocene, a large degree of morphological variation would not be surprising. This would be consistent with the more flexible diet of *U. deningeri* than the herbivorous diet of *U. spelaeus* (Vila Taboada et al., 2001; van Heteren et al., 2019). The effects of allometry (both evolutionary and static) as observed in *U. spelaeus* (Baryshnikov and Puzachenko, 2011, 2019; van Heteren et al., 2016) still need to be explored in *U. deningeri*.

In sum, the cave bear evolution is likely to be more complicated, and therefore a more detailed comparative analysis with additional middle Middle Pleistocene specimens is required, using additional methodologies that could help to better contextualise the morphology of the Salbatore II mandible as part of the evolution of the cave bear lineage.

5.2. Regional implications of the taxonomic determination of the Salbatore II mandible

At the regional level, the eastern Cantabrian region hosts an important Late Pleistocene continental record due to the abundance of karts environments, including important cave sites with extended archeo-paleontological sequences from different moments in time in the Late Pleistocene. However, the paleontological record prior to the Marine Isotope Stage MIS 6 is very restricted. The Salbatore II mandible shows morphological features that are more evolved than those of the late Early Pleistocene bears from Vallparadís Section and more primitive than those of the Santa Isabel de Ranero. Therefore, our specimen likely represents a mid-Middle Pleistocene *U. deningeri*. The Salbatore II site would contribute to the existing record of *U. deningeri* in the eastern Cantabrian region that also includes sites such as Santa Isabel de Ranero (Biscay; Torres et al., 2001, 2014) and Koskobilo (Navarre; Gómez-Olivencia et al., 2020), and reinforces the growing evidence for Middle Pleistocene sites in the eastern Cantabrian region (Gómez-Olivencia et al., 2015, 2020).

Regarding the evolution of the cave bear lineage in the eastern Cantabrian region, Altuna (1992) indicated the presence of *Ursus spelaeus deningeri* in the lowermost layers of the Lezetxiki site. The analysis of new bear remains from this site have suggested the presence of transitional characteristics. However, a detailed study remains to be conducted on the bear remains from Lezetxiki to ascertain whether they "*belong to* Ursus spelaeus*, the transitional form* Ursus spelaeus deningeroide *or* Ursus deningeri" (Villaluenga et al., 2012: p. 539).

6. Conclusions

The *U. deningeri* fossil record is relatively scarce and covers a very broad range of time. Specifically, on the Iberian Peninsula, there are both late Early Pleistocene and late Middle Pleistocene cave bear remains, but there is a gap in the mid-Middle Pleistocene. The Salbatore II mandible is similar in size to those of the Middle Pleistocene cave bears, and also displays some primitive features observed in some archaic *U. deningeri* specimens. A significant morphological variability is observed in this species both over time and at the same sites, which can be attributed to intraspecific variability and sexual dimorphism. Therefore, unravelling the evolution *U. deningeri* is complex. Consequently, it is necessary to obtain further genetic and ecological information on mid-Middle Pleistocene cave bears in order to better understand the morphology of the Salbatore II mandible. Our study underscores the value of detailed metric and morphological analyses, using different methodologies, on out-of-context fossil remains. Also, we have provided further evidence of the presence of Middle Pleistocene faunal remains in the eastern Cantabrian region.

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Appendix A. Supplementary information

Supplementary information (including Tables S1-S5, Figs. S1-S8 and supplementary references) associated with this article can be found, in the online version, at:

References

Altuna, J., 1992. Le paléolithique moyen de la région cantabrique. L'anthropologie (Paris) 96, 87-102.

Aranburu, A., Arriolabengoa, M., Iriarte, E., Giralt, S., Yusta, I., Martínez-Pillado, V., del Val, M., Moreno, J., Jiménez-Sánchez, M., 2015. Karst landscape evolution in the littoral area of the Bay of Biscay (north Iberian Peninsula). Quaternary International 364, 217–230.

Argant, A., 1991. Carnivores quaternaires de Bourgogne. Documents des laboratoires de Géologie, Lyon 115, 1-301.

Arlegi, M., Gómez-Olivencia, A., Albessard, L., Martínez, I., Balzeau, A., Arsuaga, J.L., Been, E., 2017. The role of allometry and posture in the evolution of the hominin subaxial cervical spine. Journal of Human Evolution 104, 80–99.

Arnold, L.J., Demuro, M., Parés, J.M., Arsuaga, J.L., Aranburu, A., Bermúdez de Castro, J.M., Carbonell, E., 2014. Luminescence dating and palaeomagnetic age constraint on hominins from Sima de los Huesos, Atapuerca, Spain. Journal of Human Evolution 67, 85–107.

Arsuaga, J.L., Carretero, J.M., 1994. Multivariate analysis of the sexual dimorphism of the hip bone in a modern human population and in early hominids. American Journal of Physical Anthropology 93, 241–257.

Arsuaga, J.L., Martínez, I., Arnold, L.J., Aranburu, A., Gracia-Téllez, A., Sharp, W.D., Quam, R.M., Falguères, C., Pantoja-Pérez, A., Bischoff, J., Poza-Rey, E., Parés, J.M., Carretero, J.M., Demuro, M., Lorenzo, C., Sala, N., Martinón-Torres, M., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Gómez-Olivencia, A., Moreno, D., Pablos, A., Shen, C.-C., Rodríguez, L., Ortega, A.I., García, R., Bonmatí, A., Bermúdez de Castro, J.M., Carbonell, E., 2014. Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. Science 344, 1358–1363.

Barlow, A., Paijmans, J.L.A., Alberti, F., Gasparyan, B., Bar-Oz, G., Pinhasi, R., Foronova, I., Puzachenko, A.Y., Pacher, M., Dalén, L., 2021. Middle Pleistocene genome calibrates a revised evolutionary history of extinct cave bears. Current Biology 31, 1–9.

Baryshnikov, G.F., 1998. Cave Bears from the Paleolithic of the Greater Caucasus. In: Saunders, J.J., Styles, B.W., Baryshnikov, G.F. (Eds.), Quaternary Paleozoology in the Northern Hemisphere. llinois State Museum Scientific Papers, Springfield, pp. 69–118.

Baryshnikov, G.F., Puzachenko, A.Y., 2011. Craniometrical variability in the cave bears (Carnivora, Ursidae): Multivariate comparative analysis. Quaternary International 245, 350–368.

Baryshnikov, G.F., Puzachenko, A.Y., 2019. Morphometry of upper cheek teeth of cave bears (Carnivora, Ursidae). Boreas 48, 581–604.

Falguères, C., Yokoyama, Y., Arrizabalaga, Á., 2005. La Geocronología del yacimiento pleistocénico de Lezetxiki (Arrasate, País Vasco). Crítica de las dataciones existentes y algunas nuevas aportaciones. Munibe (Antropologia-Arkeologia) 57, 93–106.

García García, N., 2003. Osos y otros carnívoros de la Sierra de Atapuerca. Fundación Oso de Asturias, Oviedo, 575 p.

García, N., Arsuaga, J.L., Torres, T., 1997. The carnivore remains from the Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain). Journal of Human Evolution 1997, 155–174.

Garrote, E., García, J., Fernández, J., Cerezo A., Tijero, F., Zapata, M., 1989. Mapa geológico del País Vasco 1:25.000 hoja 63-II Zumaia. Ente Vasco de la Energía.

Gómez-Olivencia, A., Sala, N., Arceredillo, D., García, N., Martínez-Pillado, V., Rios-Garaizar, J., Garate, D., Solar, G., Libano, I., 2015. The Punta Lucero Quarry site (Zierbena, Bizkaia): a window into the Middle Pleistocene in the Northern Iberian Peninsula. Quaternary Science Reviews 121, 52–74.

Gómez-Olivencia, A., Arlegi, M., Arceredillo, D., Delson, E., Sanchis, A., Núñez-Lahuerta, C., Fernández-García, M., Villalba de Alvarado, M., Galán, J., Pablos, A., Rodríguez-Hidalgo, A., López-Horgue, M.A., Rodríguez-Almagro, M., Martínez-Pillado, V., Rios-Garaizar, J., van der Made, J., 2020. The Koskobilo (Olazti, Navarre, Northern Iberian Peninsula) paleontological collection: New insights for the Middle and Late Pleistocene in Western Pyrenees. Quaternary International 566-567, 113–140.

Gretzinger, J., Molak, M., Reiter, E., Pfrengle, S., Urban, C., Neukamm, J., Blant, M., Conard, N.J., Cupillard, C., Dimitrijević, V., Drucker, D.G., Hofman-Kamińska, E., Kowalczyk, R., Krajcarz, M.T., Krajcarz, M., Münzel, S.C., Peresani, M., Romandini, M., Rufí, I., Soler, J., Terlato, G., Krause, J., Bocherens, H., Schuenemann, V.J., 2019. Large-scale mitogenomic analysis of the phylogeography of the Late Pleistocene cave bear. Scientific Reports 9, 10700.

Klingenberg C. P., 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources 11, 353–357.

Klingenberg, C.P., Barluenga, M., Meyer, A., 2002. Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. Evolution 56, 1909–1920.

Knapp, M., Rohland, N., Weinstock, J., Baryshnikov, G., Sher, A., Nagel, D., Rabeder, G., Pinhasi, R., Schmidt, H.A., Hofreiter, M., 2009. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. Molecular Ecology 18, 1225–1238.

Koby, F., 1951. Un nouveau gisement a *Ursus deningeri* von REICH. Eclogae Geologicae Helvetiae 44, 398–403.

Kurtén, B., 1959. On the bears of the Holsteinian interglacial. Stockholm Contributions in Geology 2, 73–102.

Madurell-Malapeira, J., Alba, D.M., Moyà-Solà, S., 2009. Carnivora from the late Early Pleistocene of Cal Guardiola (Terrassa, Vallès-Penedès Basin, Catalonia, Spain). Journal of Paleontology 83, 969–974.

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., Berástegui, X., 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. Quaternary Science Reviews 29, 3972–3982.

Prat, F., Thibault, C., 1976. Le gisement de La Nauterie à la Romieu (Gers). Fouilles de 1967 à 1973. Nauterie I. Mémoires du Muséum National d'Histoire Naturelle, Série C – Science de la terre 35, 3–83.

Prat-Vericat, M., Rufí, I., Llenas, M., Madurell- Malapeira, J., 2020. Middle Pleistocene *Ursus deningeri* from Grotte de la Carrière (Réseau Lachambre, Têt Valley, Eastern Pyrenees). Journal of Iberian Geology 46, 163-175.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rabeder, G., Hofreiter, M., Nagel, D., Withalm, G., 2004. New Taxa of Alpine Cave Bears (Ursidae, Carnivora). Actes du 9e symposium international sur l'ours des cavernes, cahiers scientifiques du Muséum d'histoire naturelle de Lyon, H.-s. 2 (2004), 49–67.

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Van der Made, J., Pérez González, A., Blain, H.A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quaternary Science Reviews 30, 1396–1412.

Rohlf, F.J., 1990. Rotational fit (Procrustes) methods. In: Rohlf, F.J., Bookstein, F.L. (Eds.), Proceedings of the Michigan Morphometrics Workshop. Special Publication, University of Michigan, Museum of Zoology, pp. 227–236.

Sokal, R.R., Rohlf, F.J., 1981. Biometry. W.H. Freeman and Company, New York.

Spassov, N., Latinka, H., Stefanka, I., Ivan, G., 2017. First record of the "small cave bear" in Bulgaria and the taxonomic status of bears of the *Ursus savini* Andrews – *Ursus rossicus* Borissiak group. Fossil Imprint 13, 275–291.

Stiller, M., Molak, M., Prost, S., Rabeder, G., Baryshnikov, G., Rosendahl, W., Münzel, S., Bocherens, H., Grandal-d'Anglade, A., Hilpert, B., 2014. Mitochondrial DNA diversity and evolution of the Pleistocene cave bear complex. Quaternary International 339, 224–231.

Stiner, M.C., 1998. Mortality analysis of Pleistocene bears and its paleoanthropological relevance. Journal of Human Evolution 34, 303–326.

Torres Pérez-Hidalgo, T., 1988. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Ibérico (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmüller-Heinroth, *U. arctos* Linneo): VI. Dentición inferior. Boletín Geológico y Minero XCIX-VI, 886–940.

Torres, T., Nestares, T., Cobo, R., Ortiz, J.E., Cantero, M.A., Ortiz, J., Vidal, R., Prieto, J.O., 2001. Análisis morfológico y métrico de la dentición y metapodios del oso de Deninger (*Ursus deningeri* Von Reichenau) de la Cueva Sta. Isabel de Ranero. Aminocronología (Valle de Carranza - Bizkaia - País Vasco). Munibe (Ciencias Naturales - Natur Zientziak) 51, 107–141.

Torres, T., Ortiz, J., Cobo, R., Julià, R., Camacho, A., Puch, C., Llamas, J.F., 2005. Presence of two cave bear species in La Lucia cave (Lamasón, Cantabria, N Spain): *Ursus deningeri* von Reichenau and *Ursus spelaeu*s Rosenmüller-Heinroth. Munibe (Antropologia-Arkeologia) 57, 103–122.

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.

Tsoukala, E., Grandal-d'Anglade, A., 2002. Système de mesures du squelette des Ursidés. Études et Recherches Archéologiques de l'Université de Liège (ERAUL) 100, 265–287.

van Heteren, A.H., Arlegi, M., Santos, E., Arsuaga, J.L., Gómez- Olivencia, A., 2019. Cranial and mandibular morphology of Middle Pleistocene cave bears (*Ursus deningeri*): implications for diet and evolution. Historical Biology 31, 485–499.

van Heteren, A.H., MacLarnon, A., Soligo, C., Rae, T.C., 2016. Functional morphology of the cave bear *(Ursus spelaeus*) mandible: a 3D geometric morphometric analysis. Organisms Diversity & Evolution 16, 299–314.

Vereschagin, N., Baryshnikov, G., 2000. Small cave bear *Ursus (Spelearctos) rossicus uralensis* from the Kizel Cave in the Ural (Russia). Geoloski zbornik 15, 53–66.

Vila Taboada, M., Fernández Mosquera, D., Grandal-d'Anglade, A., 2001. Cave bear's diet: a new hypothesis based on stable isotopes. Cadernos Lab. Xeolóxico de Laxe 26, 431–439.

Villaluenga, A., Castaños, P., Arrizabalaga, A., Mujika-Alustiza, J.A., 2012. Cave Bear (*Ursus spelaeus* Rosenmüller Heinroth, 1794) and Humans During the Early Upper Pleistocene (Lower and Middle Palaeolithic) in Lezetxiki, Lezetxiki II and Astigarragako Kobea (Basque Country, Spain). Preliminary Approach. Journal of Taphonomy 10, 521-543.

von Reichenau, W., 1906. Beiträge zur näheren Kenntnis der Carnivoren aus den Sanden von Mauer und Mosbach. Abhandlungen der Grossherzoglich Hessischen Geologischen Landesanstalt zu Darmstadt 4, 185–313.

Wagner, J., Čemárk, S., 2012. Revision of the early Midle Pleistocene bears (Ursidae, Mammalia) of Central Europe, with special respect to possible co-occurrence of spelaoid and arctoid lineages. Bulletin of Geosciences 87, 461–496.

Wiley, D.F., Amenta, N., Alcantara, D.A., Ghosh, D., Kil, Y.J., Delson, E., Harcourt-Smith, W., Rohlf, F.J., St John, K., Hamann, B., Piscataway: IEEE, 2005. Evolutionary morphing. VIS 05. IEEE visualization 2005, 431–438.

Zapfe, H., 1946. Die altplistozanen Baren von Hundsheim in Niederosterreich. Jahrbuch der geologischen Bundesanstalt 91, 95–164.

Table and Figure captions

Table 1. Comparison of the Salbatore II *Ursus deningeri* mandible raw measurements (in mm) to those from other specimens and results from the *z*-score analysis. †: Affected by

pathology. Values in bold and underlined indicate that the Salbatore II value falls outside the range of variation of the comparative sample. Values in bold with * or ** are significantly different in the *z*-score analysis (*: $p < 0.05$; **: $p < 0.01$). Measured variables taken from Tsoukala and Grandal d'Anglade (2002).

Site/Species		**Length**	**Length between the lower canine and the m3**	**Length of the dental series**	**Length of the diastema**	**Length of the molar series**	**Height of the mandible under the p4**	**Height of the mandible under the m1**	**Height of the mandible under the m3**	**Height of the mandibular condyle**	**Thickness of the mandible between the p4 and m1**	**Thickness of the mandible between the m2 and m3**	**Height of the vertical ramus**	**References**
Salbatore II	Left/right	291.1/293.9	148.7/147.3	93.9/92.5	54.0/55.0	78.1/77.1	66.6/65.3	61.8/64.5	65.7†/69.6	23.2/22.9	20.3/21.2	30.9/30.1	158.1/158.2	This study
U. deningeri (Middle Pleistocene, Europe)	Mean ± SD (Min-Max) (n)	285.48 ± 19.56 (245.0-320.0) (n = 32)	145.49 ± 8.95 (128.3-168.3) (n = 20)	94.47 ± 5.35 (82.9-106.1) (n = 30)	53.96 ± 7.33 (35.9-69.4) (n = 31)	78.75 ± 4.10 (69.8-87.2) (n = 22)	61.82 ± 6.65 (49.2-7) (n = 34)	61.70 ± 7.17 (51.7-72.8) (n = 23)	67.39 ± 7.71 (54.2-81.0) (n = 27)	23.63 ± 2.99 (17.3-30.8) (n = 28)	21.30 ± 3.14 (15.9-29.8) (n = 24)	24.85 ± 4.00 (19.5-34.0) (n = 26)	143.76 ± 19.23 (104.0-174.5) (n = 20)	Table S1 (Appendix A)
	Z-score Salbatore II vs MP *U. deningeri*	0.29/0.43	0.36/0.20	-0.12/-0.38	0.00/0.15	-0.16/-0.41	0.73/0.52	0.09/0.39	-0.22/0.29	-0.15/-0.26	-0.33/-0.02	1.50/1.30	0.75/0.75	-
U. deningeri (Early Pleistocene, Europe)	Mean ± SD (Min-Max) (n)	273.67 ± 12.34 (260.0-284.0) (n = 3)			40.58 ± 3.40 (34.7-46.4) (n = 7)	80.38 ± 4.63 (75.8-84.9) (n = 4)	53.03 ± 5.33 (45.5-60.2) (n = 7)	55.02 ± 5.92 (48.5-62.4) (n = 5)	62.79 ± 6.95 (48.5-72.3) (n = 8)	20.02 ± 0.54 (19.4-21.0) (n = 6)	16.87 ± 1.86 (14.3-19.1) (n = 6)	20.26 ± 1.85 (17.0-22.1) (n = 8)	114.32 ± 4.60 (107.2-118.6) (n = 5)	Table S1 (Appendix A); Madurell-Malapeira et al. (2009)
	Z-score Salbatore II vs EP *U. deningeri*	**1.41/1.64**			**3.94**/4.26****	-0.49/-0.71	**2.55**/2.30***	1.02/**1.60**	0.42/0.98	**5.84**/5.24****	**1.82/2.35***	**5.75**/5.31****	**9.52**/5.54****	-
U. dolinensis (Trinchera Dolina)	Ata96-TDW4-E9-1									19.1		28.2	104.2	García García (2003)

U. spelaeus (Europe)	Mean ± SD (Min-Max) (n)	297.52 ± 25.06 (248.5-358.4) (n = 91)	155.51 ± 10.93 (131.4-203.6) (n = 115)	102.72 ± 6.13 (84.9-115.9) (n = 122)	52.23 ± 8.06 (30.2-73.8) (n = 132)	86.68 ± 5.37 (71.5-103.0) (n = 123)	63.78 ± 9.55 (45.4-82.0) (n = 134)	64.59 ± 8.21 (47.1-83.7) (n = 130)	71.03 ± 9.31 (43.7-92.4) (n = 132)	26.05 ± 3.66 (20.7-33.9) (n = 111)	22.73 ± 2.99 (16.8-37.7) (n = 139)	27.07 ± 3.32 (20.5-36.9) (n = 145)	158.98 ± 21.03 (122.5-207.4) (n = 68)	Table S1 (Appendix A)
	Z-score Salbatore II vs *U. spelaeus*	-0.26/-0.14	-0.62/-0.75	-1.45/-1.67	0.22/0.35	-1.59/-1.79	0.30/0.16	-0.43/-0.01	-0.57/-0.15	-0.78/-0.87	-0.82/-0.5	1.14/0.90	-0.04/-0.04	-
U. arctos Pleistocene (Europe)	Mean ± SD (Min-Max) (n)	257.06 ± 16.8 (232.6-295.0) (n = 17)	126.49 ± 7.24 (112.7-142.1) (n = 22)	87.58 ± 4.65 (80.0-99.7) (n = 33)	40.65 ± 6.14 (28.3-54.0) (n = 24)	72.20 ± 3.52 (66.6-81.3) (n = 26)	49.93 ± 5.53 (37.7-57.2) (n = 24)	48.92 ± 10.6 (36.9-57.4) (n = 28)	56.15 ± 6.78 (42.0-65.2) (n = 25)	18.12 ± 1.66 (15.2-21.4) (n = 17)	17.96 ± 2.89 (13.5-24.4) (n = 23)	22.04 ± 3.73 (16.1-31.0) (n = 24)	119.53 ± 5.56 (112.8-128.1) (n = 9)	Table S1 (Appendix A)
	Z-score Salbatore II vs *U. arctos*	**2.03*/2.19***	**3.06**/2.87****	1.36/1.06	**2.17*/2.34***	1.68/1.39	**3.01**/2.78****	1.22/1.47	1.41/**1.98***	**3.01**/2.87****	0.81/1.12	**2.38*/2.16***	**6.94**/6.96****	-

Table 2. Comparison of the Salbatore II *Ursus deningeri* lower dentition raw measurements (in mm) to those from specimens and results from the *z*-score analysis. Numbers in parentheses are estimates. Values in bold and underlined indicate that the Salbatore II value falls outside the range of variation of the comparative sample. Values in bold with * or ** are significantly different in the *z*-score analysis (*: $p < 0.05$; **: $p < 0.01$). L, Length; TD, Transverse diameter.

Species	**Site**	**Level/Label (side)**	**Lower canine**		**Lower p4**		**Lower m1**			**Lower m2**			**Lower m3**		**References**
			L	**TD**	**L**	**TD**	**L**	**TD-anterior**	**TD-posterior**	**L**	**TD-anterior**	**TD-posterior**	**L**	**TD**	
	Salbatore II	left/right	-/(22.0)	16.9/17.0	14.2/14.2	8.7/8.5	-/26.0	-/11.5	-/14.3	28.0/27.3	17.9/17.8	18.8/18.62	-/24.82	-/17.3	This study

U. deningeri	Middle Pleistocene (Europe)	Mean ± SD (Min-Max) (n)	22.29 ± 3.63 (17.1-29.8) n = 30	16.97 ± 2.65 (13.0-22.3) n = 38	14.08 ± 1.26 (10.9-15.9) n = 34	8.86 ± 0.74 (7.4-10.2) n = 34	27.44 ± 1.96 (23.4-32.5) n = 46	10.94 ± 1.36 (8.9-17.6) n = 48	13.58 ± 1.20 (11.4-18.0) n = 50	27.84 ± 1.66 (24.7-33.3) n = 54	16.52 ± 1.19 (14.2-19.9) n = 53	17.13 ± 1.21 (14.7-19.5) n = 53	24.80 ± 1.98 (19.6-29.2) n = 40	18.32 ± 1.19 (16.1-20.9) n = 37	Table S1 (Appendix A)
		Z-score Salbatore II vs *U. deningeri* MP	-/-0.08	-0.02/0.01	0.10/0.10	-0.22/-0.49	-/-0.74	-/0.41	-/0.60	0.10/-0.33	1.16/1.07	1.39/1.24	-/0.01	-/-0.86	-
U. deningeri	Early Pleistocene (Europe)	Mean ± SD (Min-Max) (n)	24.80 ± 3.08 (19.2-28.4) n = 9	17.07 ± 2.28 (13.5-20.0) n = 9	13.95 ± 1.11 (11.6-16.1) n = 32	8.09 ± 0.70 (6.8-9.4) n = 31	26.90 ± 1.74 (22.9-30.9) n = 35	10.19 ± 0.96 (7.9-11.9) n = 33	11.85 ± 1.13 (9.5-15.0) n = 33	27.96 ± 4.84 (24.0-32.5) n = 39	16.03 ± 1.52 (13.5-18.8) n = 36	16.85 ± 1.51 (14.0-19.2) n = 35	22.44 ± 1.50 (19.0-25.8) n = 47	17.32 ± 1.34 (14.1-21.1) n = 47	Table S1 (Appendix A)
		Z-score Salbatore II vs *U. deningeri* EP	-/-0.91	-0.07/-0.03	0.22/0.22	0.87/0.58	-/-0.52	-/1.36	-/2.17*	0.01/-0.14	1.23/1.17	1.29/1.18	-/1.59	-/-0.02	-
U. spelaeus	Pleistocene (Europe)	Mean ± SD (Min-Max) (n)	23.69 ± 3.62 (17.2-33.9) n = 211	18.13 ± 2.6 (13.2-26.3) n = 229	15.55 ± 1.35 (12.3–19.4) n = 233	10.91 ± 1.26 (8.3–10.2) n = 238	30.11 ± 2.48 (26.4–34.2) n = 267	12.29 ± 1.2 (9.4–18.6) n = 259	14.56 ± 1.23 (10.0–19.1) n = 285	30.58 ± 1.86 (26.5–36.6) n = 320	17.97 ± 1.14 (14.5–21.4) n = 319	18.67 ± 1.32 (15.5–22.8) n = 314	26.23 ± 1.95 (20.1–31.3) n = 113	19.4 ± 1.37 (16.6–23.8) n = 108	Table S1 (Appendix A)
		Z-score Salbatore II vs *U. spelaeus*	-/-0.47	-0.47/-0.44	-1.00/-1.00	-1.74/-1.90	-/**-1.66**	-/-0.66	-/-0.21	-1.38/-1.75	-0.06/-0.15	0.10/-0.04	-/-0.72	-/-1.53	-
U. arctos	Pleistocene (Europe)	Mean ± SD (Min-Max) (n)	21.69 ± 2.89 (15.4-27.9) n = 48	15.42 ± 1.64 (12.9-18.8) n = 48	13.60 ± 1.26 (11.2-16.8) n = 44	7.74 ± 0.81 (6.5-9.4) n = 42	25.11 ± 1.72 (21.1-31.0) n = 91	10.18 ± 1.10 (8.2-12.9) n = 54	12.33 ± 1.00 (10.5-14.8) n = 53	25.97 ± 2.06 (21.9-32.0) n = 80	16.0 ± 1.77 (12.6-20.6) n = 49	16.26 ± 1.79 (13.1-21.8) n = 47	21.69 ± 1.98 (17.0-25.3) n = 71	16.19 ± 1.73 (12.0-23.6) n = 68	Table S1 (Appendix A)
		Z-score Salbatore II vs *U. arctos*	-/0.11	0.89/0.96	0.48/0.48	1.17/0.93	-/0.51	-/1.19	-/1.97*	0.98/0.61	1.07/1.01	1.41/1.31	-/1.58	-/0.64	-

Fig. 1. A. Location of the Salbatore II cave (red) in relation to Urtiaga and Urtiaga II caves. **B.** Current entrance to the cave. **C.** View of the area where the mandible was found. **D.** View of the cone from the back of the cave. **E.** Topography of the cave and position of the mandible (Topography from the CD Eibar; geographical North; March 2020; magnetic declination: 0°-1'-E included).

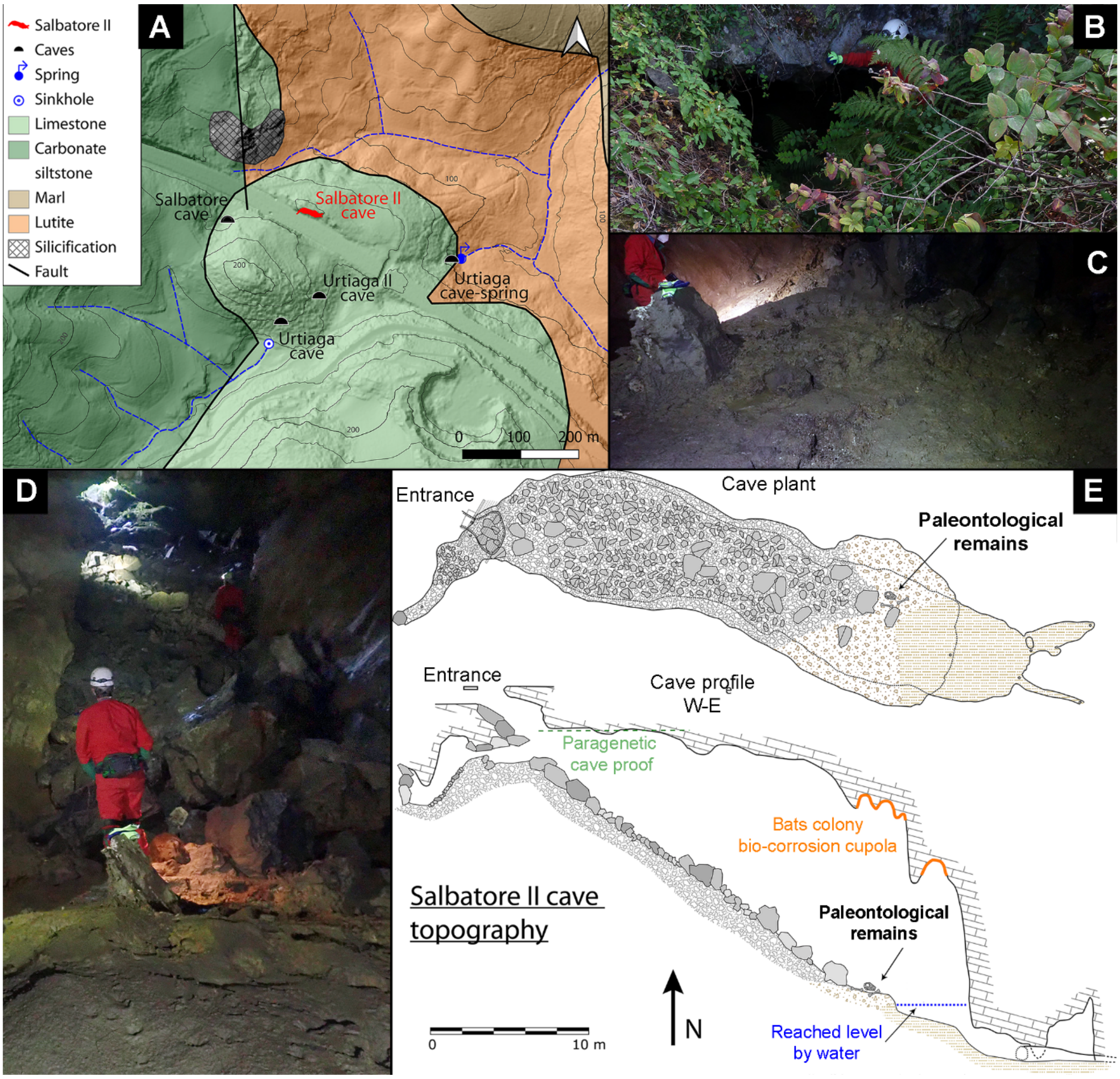
Fig. 2. Salbatore II mandible (SLT.20.0.1). **A.** Upper/occlusal view. **B.** Occlusal view of the dental series (top: left side; bottom: right side). **C.** External view of the right hemimandible. **D.** Detail of the pathology of the external view of the mandibular corpus. **E.** Posterior view. **F.** Anterior view and detail of the pathology of the alveolus of the incisor. **G.** Lateral view of the left hemimandible. **H.** Detail of the p1 and the periodontal disease in the alveolus of the m1of the left hemimandible. Scale bars: 5 cm (A, C, E, G), 2 cm (B, D, F, H).

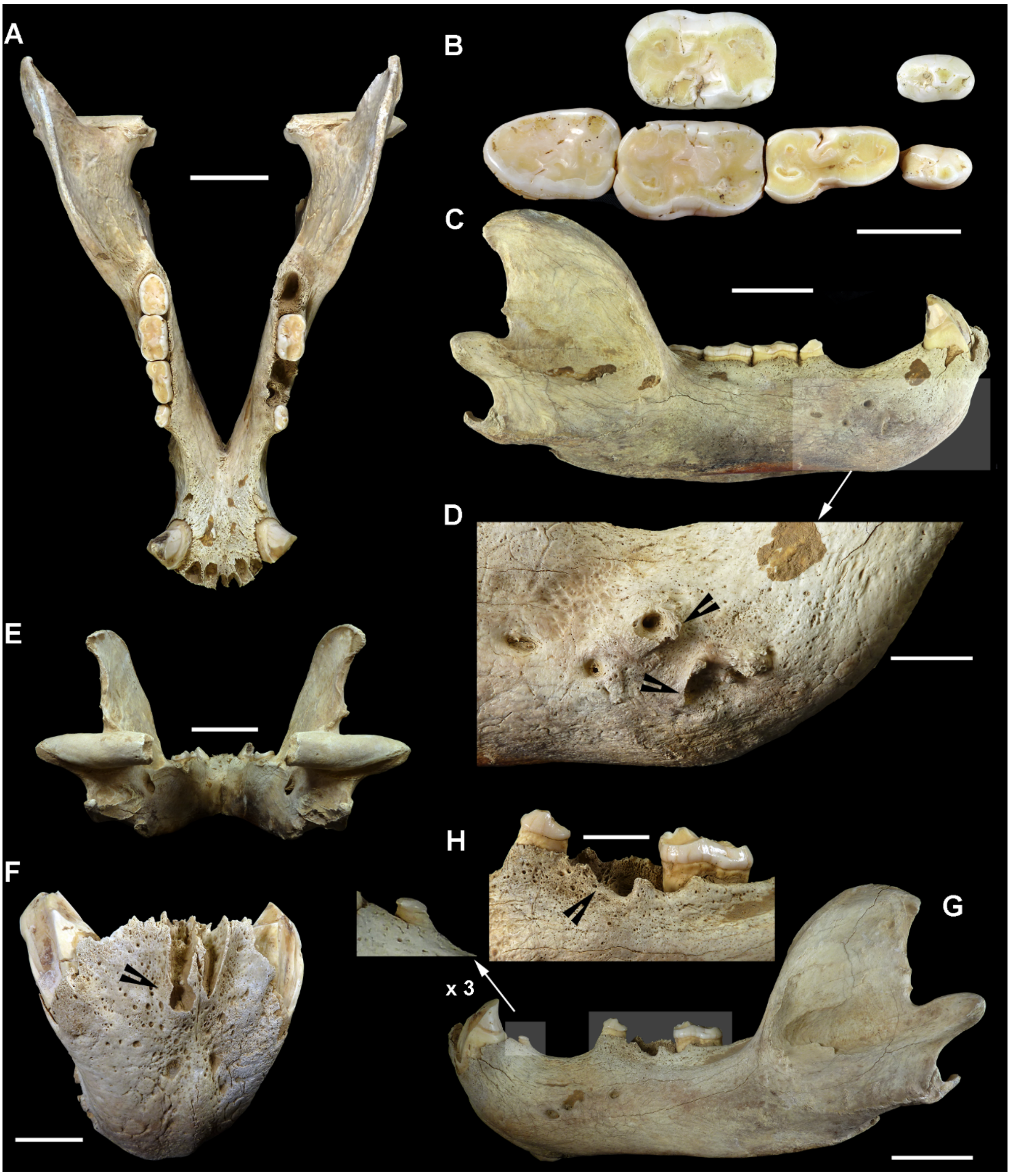
Fig. 3. Comparison of the Salbatore II *U. deningeri* right hemimandible (SLT.20.0.1) with *U. deningeri* hemimandibles from Vallparadís Section (IPS 110415: left, mirror image; IPS 14950: left, mirror image), Nauterie (LR 59: right; LR 120: right), Santa Isabel de Ranero (SI-1234: left, mirror image; image from a CT-scan), Sima de los Huesos (SH2: right), and Lezetxiki (Lz.5A.750: left, mirror image); *U. spelaeus* from Askondo (13120: left, mirror image); and *U. arctos* from Maspino (Ch.698; right; image from a surface scan). Blue line: coronoid process leaning towards the posterior part of the mandible; orange line: coronoid ridge oriented forwards and divided into two sections; green line: straight mandibular corpus; pink line: curved mandibular corpus under the m3. Scale bar: 10 cm.

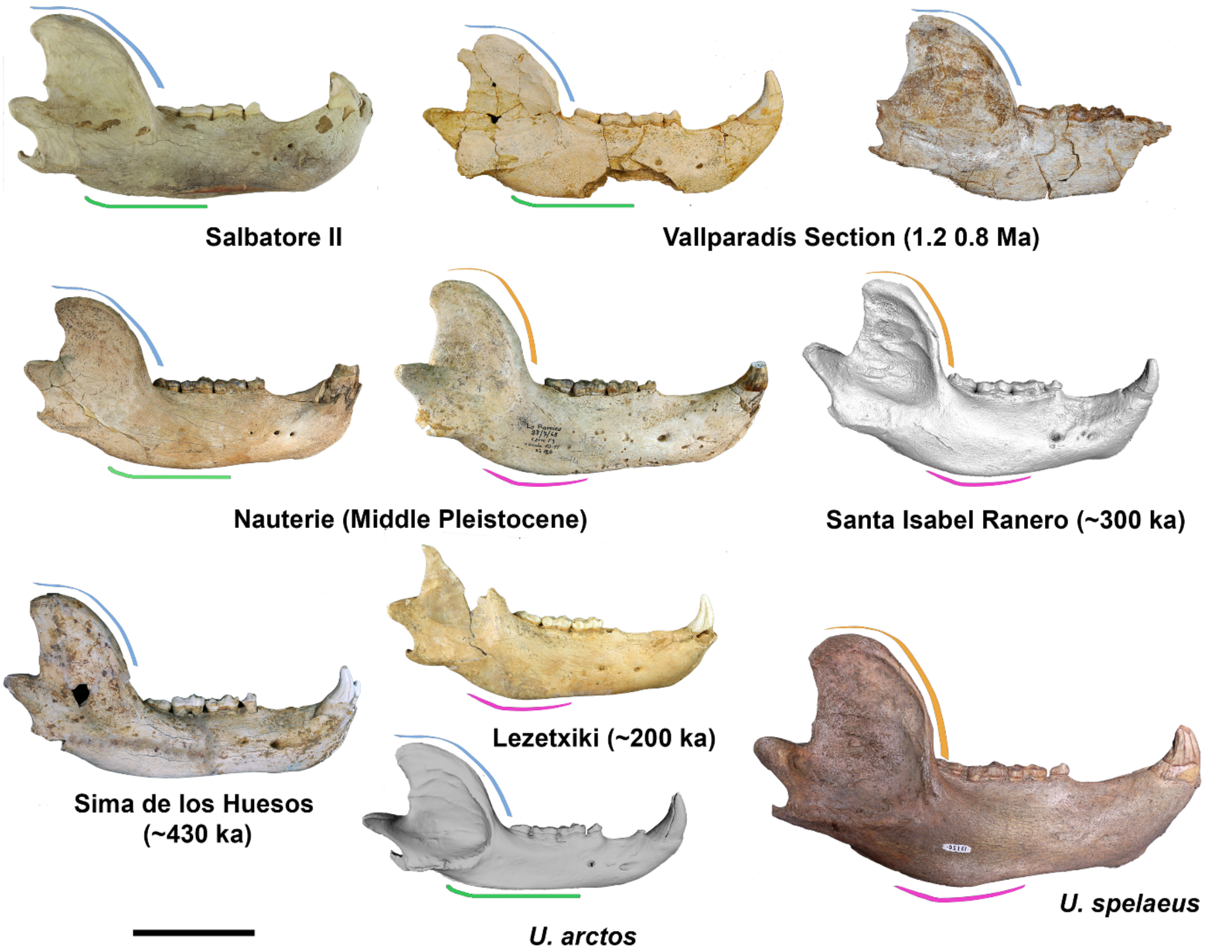
Fig. 4. Comparison of the pterygoid process of the Salbatore II hemimandible (right), with those of *U. deningeri* hemimandibles from Vallparadís Section (IPS 14950: left, mirror image; IPS 14950: right), Sima de los Huesos (right), Santa Isabel de Ranero (V7119: left, mirror image; SI-1234: left, mirror image), La Lucia (LU R 2089: right), Nauterie (LR 120: right; LR 59: right), Mosbach (32854/5: right), and Lezetxiki (Lz. 13c-960: left, mirror image; Lz. 5A.750: left, mirror image); *U. arctos* from Maspino (Ch.698: right); and *U. spelaeus* from Askondo (13120: left, mirror image). All images derived from surface scans except for the specimens from Vallparadís section (photo) and Santa Isabel de Ranero SI-1234 (CT-scan). Scale bar: 3 cm.

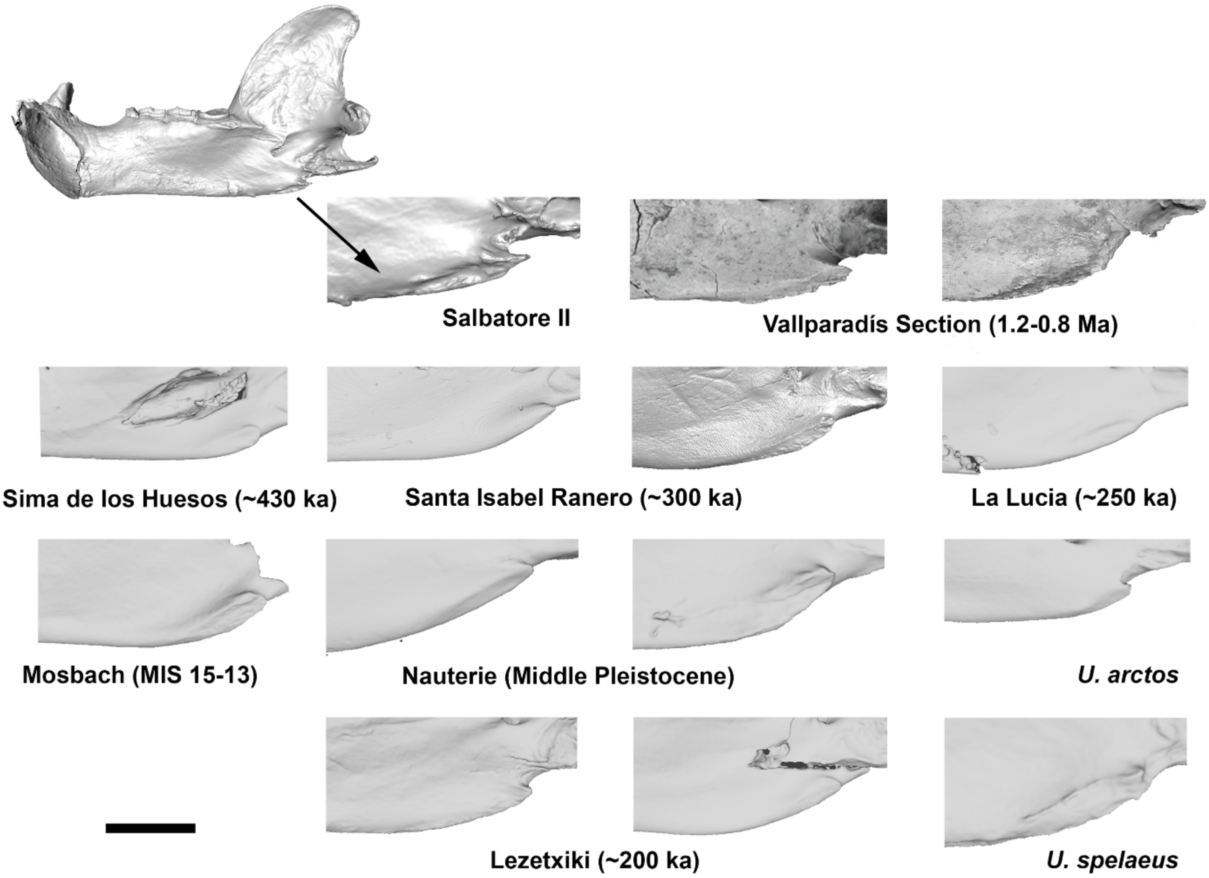
Fig. 5. Principal Component Analyses (PCA) of selected measurements of the Salbatore II mandible (red triangle), compared with *U. deningeri* from the Middle Pleistocene (grey circles), *U. deningeri* from the Early Pleistocene (green squares), *U. spelaeus* (black circles) and *U. arctos* (blue circles). Ellipse: 95% equiprobability. **A, B.** PCA using traditional measurements (selected variables shown in Table S3; Appendix A). **C, D.** PCA using measurements divided by the geometric mean (selected variables shown in Table S5; Appendix A). **E.** PCA based on shape space (selected landmarks shown in Fig. S1; Appendix A).

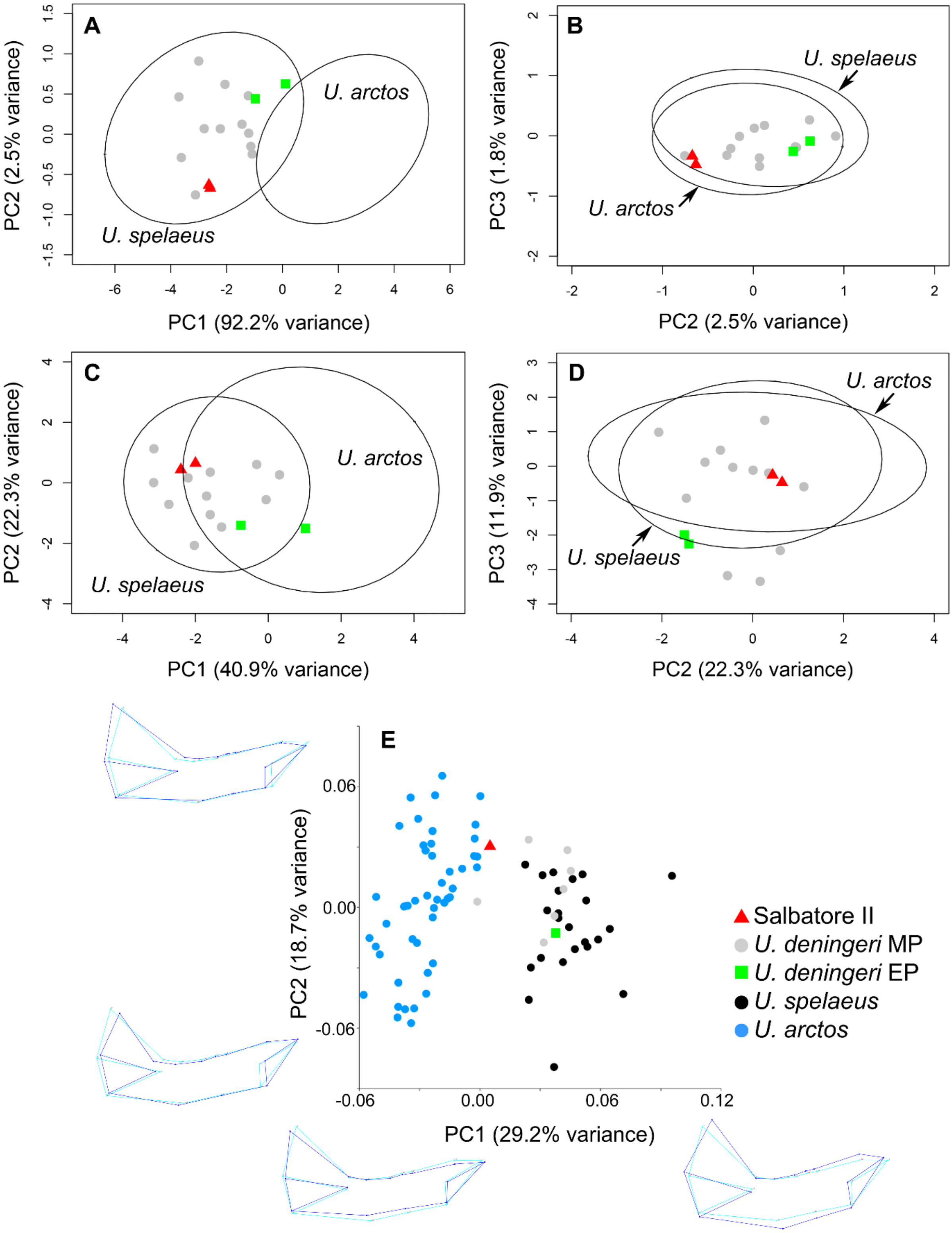
Fig. 6. Bivariate scatter plot of selected measurements of the *Ursus deningeri* lower canine-m3 from Salbatore II (red triangle) compared with Middle Pleistocene *U. deningeri* (grey circle), *U. deningeri* from Sima de los Huesos (Sierra de Atapuerca, Burgos; Torres Pérez-Hidalgo, 1988; grey cross: mean ± 1 std. dev.), Early Pleistocene *U. deningeri* (black cross: mean ± 1 std. dev.), *U. spelaeus* (90% equiprobability ellipse), and Pleistocene *U. arctos* (90% equiprobability ellipse).

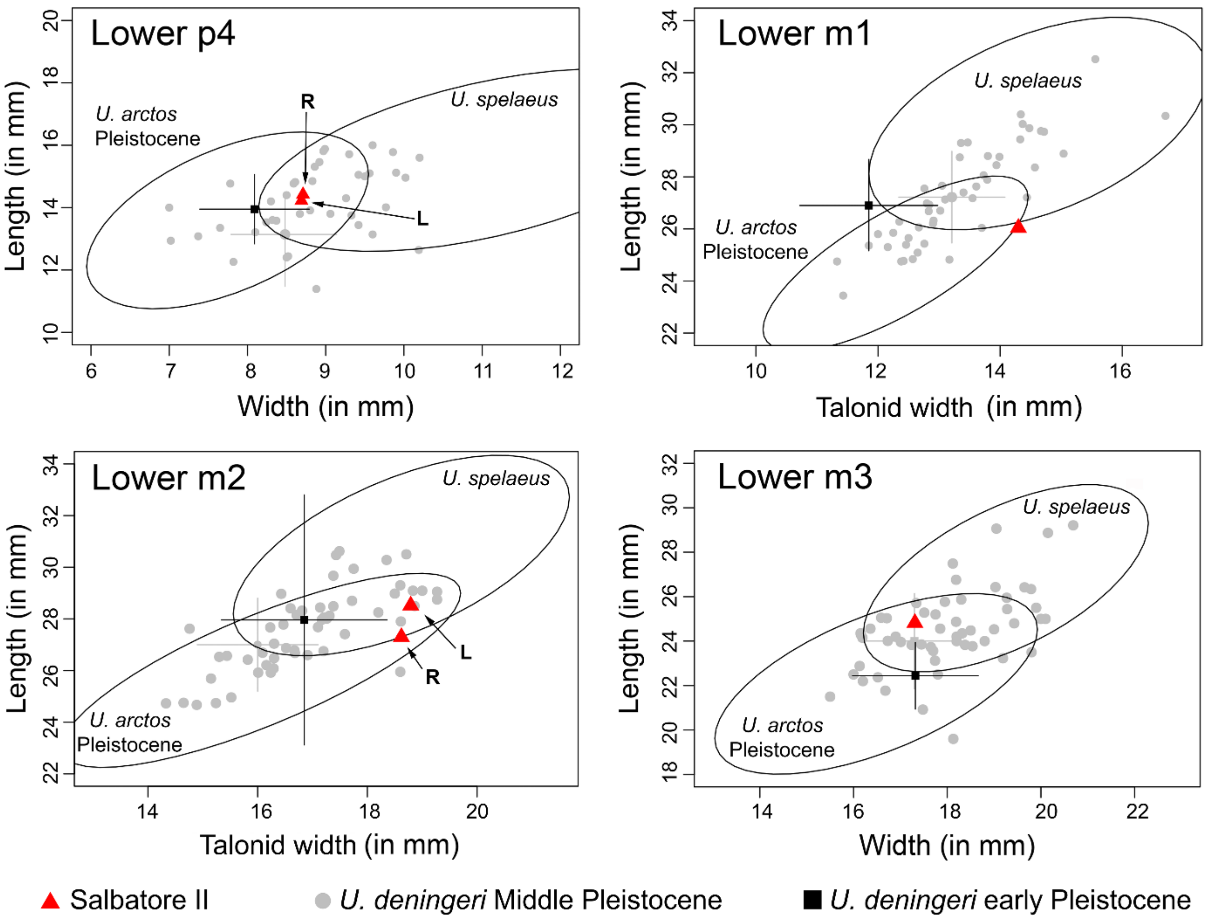



A
B
C
D
E
F
H
G
x 3


Salbatore II
Vallparadís Section (1.2 0.8 Ma)
Nauterie (Middle Pleistocene)
Santa Isabel Ranero (~300 ka)
Lezetxiki (~200 ka)
Sima de los Huesos
(~430 ka)
U. arctos
U. spelaeus


Salbatore II
Vallparadís Section (1.2-0.8 Ma)
Sima de los Huesos (~430 ka)
Santa Isabel Ranero (~300 ka)
La Lucia (~250 ka)
Mosbach (MIS 15-13)
Nauterie (Middle Pleistocene)
U. arctos
Lezetxiki (~200 ka)
U. spelaeus


A
PC1 (92.2% variance)
PC2 (2.5% variance)
U. arctos
U. spelaeus
B
PC2 (2.5% variance)
PC3 (1.8% variance)
U. spelaeus
U. arctos
C
PC1 (40.9% variance)
PC2 (22.3% variance)
U. arctos
U. spelaeus
D
PC2 (22.3% variance)
PC3 (11.9% variance)
U. arctos
U. spelaeus
E
PC1 (29.2% variance)
PC2 (18.7% variance)
-0.06
0.00
0.06
0.12
🟥 Salbatore II
● U. deningeri MP
🟩 U. deningeri EP
● U. spelaeus
● U. arctos


Lower p4
U. arctos Pleistocene
U. spelaeus
R
L
Length (in mm)
10
12
14
16
18
20
Width (in mm)
6
7
8
9
10
11
12
Lower m1
U. spelaeus
U. arctos Pleistocene
Length (in mm)
22
24
26
28
30
32
34
Talonid width (in mm)
10
12
14
16
Lower m2
U. spelaeus
U. arctos Pleistocene
L
R
Length (in mm)
22
24
26
28
30
32
34
Talonid width (in mm)
14
16
18
20
Lower m3
U. spelaeus
U. arctos Pleistocene
Length (in mm)
18
20
22
24
26
28
30
32
Width (in mm)
14
16
18
20
22
▲ Salbatore II
● U. deningeri Middle Pleistocene
■ U. deningeri early Pleistocene