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The funerary use of caves during the Holocene in the Atlantic Western Pyrenees: new information from Atxuri-I and Txotxinkoba caves (Biscay, Northern Iberian Peninsula)

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Abstract

The Atlantic Western Pyrenean area is exceptionally rich in archaeological evidence of funerary contexts dated to Late Prehistory. These funerary deposits are mainly recorded in caves and megalithic structures. Burials attributed to the Holocene have been recorded in more than 187 caves (177 just in Gipuzkoa and Bizkaia), reflecting the relevance of this phenomenon in the AWP. Nonetheless, just a few of these inhumation contexts have been properly studied, and even fewer have direct and systematic ¹⁴C dates. Here, we present the results from the analysis of two sepulchral caves from Biscay: Atxuri-I and Txotxinkoba, that preserve a minimum number of 9 and 14 individuals, respectively. Both caves present subadult individuals of different ages-at-death and among adults, both sexes are represented. Although the representation of osteological elements is roughly similar in both sites, small differences in the preservation of pelvic bones and the completeness of long bones suggest a potential bias in Atxuri-I. We provide six new radiocarbon dates on human remains. Two ¹⁴C dates from Atxuri-I show that the cave was used for funerary purposes at two very different times: the Mesolithic and the Bronze Age. The latter period is represented by a directly dated complete femur, which was also studied biomechanically, providing results similar with the available Bronze Age female sample from the Iberian Peninsula. The four dates from Txotxinkoba show that the cave was only used for a relatively short period during the Chalcolithic. When put within the Atlantic Western Pyrenean context, despite the limited amount of direct dates a pattern is evident, where most of the largest accumulations of human remains are found in sites with Chalcolithic burials (between 4,600 and 4,000 BP), such as Lacilla II, Pico Ramos, Urtao II and Abauntz, and Txotxinkoba would fit within this group. Those caves that show human burial chronologies spanning longer periods of time, such as Lumentxa, Santimamiñe, Marizulo or Aizpea, generally contain smaller numbers of individuals, and Atxuri-I would fit within this group.

Key-words: Funerary behaviour; Sepulchral caves, radiocarbon dates, MNI, Late Prehistory

1. Introduction

The Western Pyrenees (WP) has geographical and ecological particularities that make it of special interest for understanding the prehistory of Western Europe (Arrizabalaga and Rios-Garaizar, 2012). On the one hand, it has acted as an important cultural and biological corridor between the Iberian Peninsula, the largest of Europe's southern peninsulas and the rest of the continent, and functioned as a key refugium during glacial periods (Arrizabalaga and Rios-Garaizar, 2012; Gómez-Olivencia et al., 2014). In addition, this region encompasses coastal and mountainous areas, as well as the peripheral areas of the Iberian plateau, providing a diversity of landscapes and ecological conditions in a relatively small region. Geologically, the abundance of limestone outcrops (Bodego and López-Horgue, 2018, and references therein) has resulted in a large number of caves (e.g., Dorado et al., 2013), which have been used as a shelter by different human and animal species during the Quaternary (Gómez-Olivencia, 2018 and references therein). The present study focuses on the funerary practices in caves located in the westernmost area of the Pyrenees and the nearby Basque mountains, comprising sites from the provinces of Biscay, Gipuzkoa, Béarn, and the northern part of Navarre.

The study of funerary practices is of great interest because it provides important biological and cultural information about past societies (Pettit, 2011; Arias, 2012; López-Onaindia and Subirà, 2017). First, the archaeological study of burials and the associated archaeological remains (grave goods or other kinds of material deposits), and the synchronic and diachronic analysis of the burial sites/structures, provides information about the mortuary and funerary practices of social groups, and can provide important glimpses into their organization and degree of social stratification.

Additionally, the study of the skeletal remains not only provides important paleobiological information, including demographic characteristics, health status, etc., but the combined application of forensic and imaging techniques also reveals additional important cultural information regarding mortuary practices and past mobility patterns (e.g., Sala et al., 2015; Gómez-Olivencia et al., 2018; García-Sagastibelza et al., this volume). Furthermore, the systematic osteological study, including taphonomic analyses of the remains and representation patterns of the different anatomical elements, provides insight into the nature of the bone accumulation, the history of their context

and the funerary rituals performed at the sites (Ubelaker, 1973; Adams and Konigsberg, 2008; Gerdau Radonić and Makowski, 2011; Sala et al., 2015).

In the Atlantic Western Pyrenees (AWP), more than 187 caves (177 just in Gipuzkoa and Bizkaia) have yielded human remains, reflecting the importance of this phenomenon in the area. The Upper Palaeolithic record is very scarce (Gómez-Olivencia, 2018 and references therein) and most human remains from caves are traditionally related to Holocene funerary practices. In some of these caves, just one or a handful of individuals have been recovered while other deposits, such as Pico Ramos (n = 104) and Urtao II (n = 51) have yielded a large number of individuals (Etxeberria, 1989; Zapata, 1995). The sole (or main) function of the caves may have been funerary (e.g., Lacilla II; Gil Abad and Llamosas Rubio, 2016-2017). In some other cases, funerary practices occur sporadically across long periods of occupation of the cave (e.g., Lumentxa; Arribas and Berganza, 2018; García-Sagastibelza et al., in press). From a chronological point of view, the Mesolithic, ca. 8,000-5,000 cal BCE, is represented in this region by two paradigmatic burials: Linatzeta and J3 (Iriarte et al., 2005, 2010; Tapia et al., 2008). There is little evidence of mortuary contexts contemporary with the introduction of domesticated plants and animals during the 5th millennium cal BCE, as the main Neolithic sites (e.g., Marizulo and Ekain) date to the 4th millennia cal BCE (Laborde et al., 1966; Alday and Mujika, 1999; Altuna, 2009). Subsequently, ca. 4,300 to 3,900 cal BCE, funerary practices change with the introduction of megalithic structures, coexisting with cave burials (Armendariz, 1992, 1999; Fernández-Crespo, 2010; Arias, 2012).

Whether the human accumulations in these caves are the result of a single event or repeated funerary use is difficult to ascertain without either direct dates and/or evidence of violence or infectious disease which could justify the burial of multiple bodies in a single event (e.g., presence of violence in San Juan ante Portam Latinam; Vegas, 2007). The available (and scarce) radiocarbon dates on human bones support the long-term use of caves for funerary purposes (e.g., Pico Ramos; Zapata, 1995), although evidence of violence has been found in other contexts alongside longer term use as a burial site (e.g., San Juan Ante Portam Latinam, in Fernández-Crespo et al., 2018).

For many of the AWP cave sites, anthropological information is limited to brief inventories that, in many cases, lack basic information such as the determination of the minimum number of individuals and demographic profiles (sex and age-at-death) (Armendariz and Etxeberria, 1983; Ontañón and Armendáriz, 2005). Additionally, estimates of stature and body mass are all but absent for the majority of the human remains from AWP cave sites. This is generally due to the lack of complete long bones needed to generate such estimates and the absence until recently of reliable methods using other skeletal elements (e.g., regression equations based on feet remains; Pablos et al., 2013). While archaeological artefacts associated with the human remains may, in some cases, offer some chrono-cultural indications, many human remains have been attributed to the Chalcolithic-Bronze Age based solely on the greater frequency of burials from this period in the area (e.g., Atxuri-I, García-Sagastibelza, 2017).

Besides the obvious problems with interpreting the typological and chronological contexts of these caves, the lack of systematic bioarchaeological and chronological analysis also presents a problem when trying to understand more fully the prehistoric populations in the area. Analyses based on group frequencies or means, such as demography, non-metric traits, or interpretations of aDNA and stable isotope data are affected by the lack of information regarding the chronology of funerary activity in such caves. Despite the relatively large number of sites with human remains, there is a relative dearth of bioarchaeological and chronological studies of the human remains from caves or megalithic structures from the AWP, which are limited to a few betterdocumented sites (Izagirre and de la Rúa, 1999; Izagirre et al., 2001; Cardoso et al., 2011; Hervella et al., 2012; de la Rúa et al., 2015; Cubas et al., 2016; López-Onaindia, 2017; López-Onaindia and Subirà, 2017; García-Sagastibelza, 2017; Sarasketa-Gartzia, 2018; Villalba-Mouco et al., 2018; García-Sagastibelza et al., this volume). Surprisingly, the lack of thorough anthropological and/or chronological studies in some sites has not precluded sampling for DNA and/or isotopic analysis (e.g. Atxuri-I: Prieto, 2002; Fernández, 2005; Pico Ramos: Sarasketa-Gartzia et al., 2018). Additionally, new techniques that can provide important paleobiological information, such as biomechanical analyses, have not been performed, despite recent advances (García-Sagastibelza et al., this volume). In summary, we still know very little about the Holocene populations of the AWP.

The objectives of this work are two-fold. First, we present the anthropological study and new dates on the human remains from two caves of the AWP that were excavated more than 50 years ago: Atxuri-I and Txotxinkoba. We employ innovative

methods to determine the minimum number of elements and individuals (MNE and MNI respectively) represented in the collections using landmark-based inventories (Txotxinkoba) and biomechanical analysis of a complete directly dated femur (Atxuri-I). Second, we provide six new radiocarbon dates from human remains: two from Atxuri-I and four from Txotxinkoba, and provide a review of the currently available direct ¹⁴C dates from human remains recorded in caves in the AWP in order to contextualize our research. Finally, we discuss these results and compare them to: direct dates obtained in burials from megalithic structures from the same region, other nearby sites in the Mediterranean watershed, and to other sites from other regions of the Iberian Peninsula.

2. Archaeological context

2.1. Atxuri-I

The cave of Atxuri-I (43°08'28.6"N, 2°39'19.3"W, 225 m.a.s.l.), located on the mountain of the same name in a gorge between the Mugarra (964 m) and Untzillatx (934 m) mountains and close to the town of Mañaria (Biscay; Figure 1), no longer exists due to the activities of the Markomin Goikoa quarry (Nolte, 1957; Castaños, 1986) (Supplementary Figure S1). The entrance (2 m high, 2.50 m wide) was oriented to the south and gave passage to a single gallery of *ca.* 17-18m in length (Apellániz, 1973).

The site was discovered by José Miguel de Barandiarán in 1929, and an excavation was directed by E. Nolte in 1957 (Nolte, 1957; Garate, 2012). Subsequently, between 1960-1961 (Barandiarán, 1964; Castaños, 1986), or finishing in 1962 (Apellániz, 1973; Garate, 2012), J.M. de Barandiarán organized salvage excavations due to the imminent destruction of the cave by the quarry.

Regarding the stratigraphy, the only evidence is the assessments made by José Miguel de Barandiarán of the first part of the 1961 excavation (Barandiarán, 1964) (Supplementary Figure S1). Unfortunately, the available information is incomplete and the stratigraphy seems to be mixed, possibly because of the actions of treasure hunters (Garate, 2012). The subsequent destruction of the cave makes it impossible to reconstruct its stratigraphic sequence.

Despite the lack of a clear stratigraphy due to both the presence of mixed deposits and the urgent way it was excavated (Garate, 2012), there are archaeo-

palaeontological evidence and direct dates indicating that Atxuri-I was occupied during both the Late Pleistocene and Holocene. The typological assessment of the lithic remains demonstrates occupations at least during the Solutrean (Garate, 2012). Additionally, a piece of portable art (an antler fragment with relief decoration) was directly dated by ¹⁴C to 9,625 ± 80 B.P., relating it to the Azilian culture (Euskal Arkeologia Etnografia eta Kondaira Museoa/Museo Arqueológico, Etnográfico e Histórico Vasco, 1995). While it has been suggested that parietal art was present at the site (Fernández, 1971), the lack of graphic recording precludes any further assessment. For post-Palaeolithic occupations, based on the lithic industry and pottery remains there is reliable evidence only for the Late Chalcolithic (Arias, 1989).

In terms of faunal remains, the site has yielded both domestic taxa (e.g., sheep and goat), indicating Neolithic or recent occupations and other taxa that disappeared at the end of the Pleistocene (reindeer) or at the beginning of the Holocene (e.g., leopard; Sanchis et al., 2015). One *Rangifer tarandus* bone has been directly dated to $13,030 \pm 60$ B.P. (Gómez-Olivencia et al., 2014), indicating the presence of faunal bone deposits with Upper Palaeolithic chronologies. Nevertheless, the lack of a clear stratigraphy precludes any assumptions regarding the possible associations with other archaeological materials (Gómez-Olivencia et al., 2014) or relating the location of the reindeer remains to any specific layer of the Pleistocene. Thus, the limited studies performed in this site have relied on both direct dating and typological features of the archaeological remains.

Several human remains from Atxuri-I have been included in analyses of mitochondrial DNA (Prieto, 2002; Fernández, 2005). Prieto (2002) studied 12 samples, assuming that the funerary deposit spanned from the 5th to the 4th millennia BCE. (i.e., roughly from the Neolithic until the Chalcolithic). Fernández (2005) analysed 13 samples and considered that the sepulchral use of the cave occurred roughly between the 3rd to the 2nd millennia BCE (Valdés, personal communication), which would correspond to the Chalcolithic/Bronze Age. However, to our knowledge, no radiocarbon dates have been published by these scholars.

2.2. Txotxinkoba

Txotxinkoba cave (43°20'10.81"N, 2°31'42.86"W, 72 m.a.s.l.) is located on Lariz mountain in Gizaburuaga (Lea-Artibai, Biscay; Figure 1), and is reached by taking an abandoned road that leaves the main road from Lekeitio to Gizaburuaga, and then climbing the mountain (Apellániz and Nolte, 1967). The cave entrance is 3 m tall and 1.90 m wide at the base, leading to a single 7.5 m-long gallery (Supplementary Figure S1).

The cave was discovered by E. Nolte in 1963 and was subsequently excavated by Nolte and J.M. Apellániz between 1966 and 1967 (Apellániz and Nolte, 1967), who emptied the whole cave. The human remains from this cave site have been mentioned in a previous publication (Armendariz, 1990), but a systematic study of these remains has not yet been performed.

Apellániz and Nolte (1967) provide preliminary descriptions of the stratigraphy of the site: it was filled with ochre clays, with a uniform type of sediment, which was covered by the modern soil with a distinct black colour. The human remains appeared in the upper part of the clayish levels, while lower levels were archaeo-paleontologically sterile. According to the excavators, the inhumations occurred in a single, probably short, and discrete time span. They identified the formation of a stalagmitic crust in a small extension at the end of the cave, which covered some remains, and therefore identified two potential archaeological levels (Levels I and II), but they concluded that the burials occurred during the time that this crust was being formed (Supplementary Figure S1). In the field notes and the two publications where the excavators mention the cave (Apellániz and Nolte, 1967, Apellániz, 1973), they considered that there were no differences in the nature and chronology of the materials between Levels I and II. In fact, they remarked that most of the human bones and associated archaeological remains appeared away from the zone affected by the crust; in Level II, they hardly discovered any associated archaeological remains, and after our inventory the number of osteological elements recorded in this level is 134. The associated materials found in the site include mainly Chalcolithic pottery fragments, a few jet beads (cylindrical and barrel-shaped), and some lithic blades. Amongst the lithic material, an archaic trapezoid microlithic tool was also reported (Apellániz and Nolte, 1967). Faunal remains were also recovered, but a systematic study has not yet been performed.

3. Materials and Methods

3.1. Materials

We studied the whole assemblage of human remains from Atxuri-I and Txotxinkoba, currently housed at the Arkeologi Museoa (Bilbao, Biscay). The Atxuri-I collection currently comprises 387 fragments, the majority from the 1960-1961 excavation. A subadult human femur without any specific information (i.e., label) and with a different external appearance compared to the rest of the Atxuri-I collection was excluded from this study. The Txotxinkoba human remains derive from the 1966-1967 excavations and comprise 1,234 fragments.

Stature and body mass data from the Argar populations of Terrera del Reloj (2 males and 2 females) and Castellón Alto (15 males and 15 females) (Ruff and Garvin, 2018), as well as several other sites from the Iberian Peninsula were used as comparative data. The latter sample comprises stature and/or body mass estimations from Abittaga (1 female; Ríos-Garaizar et al., in press), Cova de Montanissell (1 male and 2 females; Armentano et al., 2014), Galería del Sílex (1 male and 2 females; Galera Olmo, 1987), Caserío de Perales (1 male and 2 females), La Loma del Lomo (4 males), Los Berrocales (4 males and 3 females), Soto del Henares (1 male) (Aliaga Almeda, 2012), Motilla del Azuer (Martín-Flórez 2010; Nájera et al., 2010, 2012) and Cerro de la Encina (3 males and 3 females; Jiménez Brobeil y Sánchez 1989-1990).

For the biomechanical study, comparative samples from the Iberian Peninsula, France and Italy were used (Holt et al., 2018a; Ruff and Garvin, 2018). Additionally, a sample dating to the 7th-8th century AD from the Jau-Dignac-et-Loirac commune, near the Gironde estuary (Nouvelle Aquitaine, France: Cartron and Castex, 2006, 2010, Deguilloux et al., 2014; d'Incau et al., 2015), was also analysed for this study. CT-scans of 14 of the 65 individuals from this site were available for analyses (7 males and 7 females). An early Medieval sample from Santa María de Hito (Iberian Peninsula) was also used (Ruff and Garvin, 2018).

3.2. Minimum number of individuals

The Minimum Number of Individuals (MNI) was determined in both collections based on the highest Minimum Number of Elements (MNE) from a single side and

taking age category into account (Knüsel and Outram, 2004). Due to the highly fragmented state of the remains from Txotxinkoba, the *Landmark method* was preferred to determine MNE: we registered all the bone fragments by element, side, age and described landmarks (Mack et al., 2016). All points were evaluated as present or absent, and they are only used to count the MNE if at least 50% of the landmark is observable (Lambacher et al., 2016).

3.3. Sex assessment

Sex estimation for adult remains used morphological features of the pelvis when available (Martin and Saller, 1957; Ferembach et al., 1980; Krogman and Iscan, 1986; Schutowski, 1993). Since few pelvis or complete cranial bones and mandibles are present in the collection, discriminant analyses based on measurements of the humeri and femora of adult individuals were used (Bass, 2005).

As a preparatory step for the stature estimation, an approach to the sex assessment of the first and second metatarsals was performed using the k-means cluster analysis based on the maximum length (see also Arceredillo et al., 2011) using Past (Hammer et al., 2001).

3.4. Age-at-death

In subadult individuals, the degree of calcification and eruption of the dentition was assessed, as well as the general size and degree of fusion of the secondary centres of ossification (Buikstra and Ubelaker, 1994; Scheuer and Black, 2000; White and Folkens, 2005; AlQathani et al., 2010). In adult individuals, the study was focussed on the assessment of the dental wear (Lovejoy, 1985) or the auricular surface of the coxal bones following Lovejoy et al. (1985).

3.5. Stature and body mass estimation

Stature was estimated in adult individuals using the maximum length of the femur (n = 1; Ruff et al., 2012) and from the first and second metatarsals (Pablos et al., 2013). Body mass (BM) was estimated in a single adult individual from Atxuri-I using

femoral head diameter (FHD = 40 mm). The average of three formulae (Ruff et al. 1991; McHenry, 1992; Grine et al., 1995) was used (Auerbach and Ruff, 2004; Trinkaus and Ruff, 2012; Sparacello et al., 2018).

3.6. CT-scans

The complete femur from Atxuri-I was CT-scanned at the IMQ Zorrotzaurre Hospital (Bilbao) using the Siemens Definition As 20, with a source energy setting of 120 kv/180 mAs. Slice thickness was collimated to 0.6 mm and the slice increment was 0.6 mm. This CT scan is available with the identifier https://doi.org/10.6084/m9.figshare.12319565. The Jau-Dignac-et-Loirac femora, on the other hand, were scanned in Tivoli Medical Center in Bordeaux.

3.7. Biomechanical analysis

Due to preservation, the study of the biomechanical properties was restricted to one adult femur from Atxuri-I. The studied parameters are summarized in Supplementary Table S1.

The 3D models of the bones derived from the CT-scans were aligned and the plugins Bone J (Doube et al., 2010) and MomentMacroJ (Ruff, 2006; www.hopkinsmedicine.org/fae/mmacro.html) of ImageJ were used to quantify the cross-sectional geometric properties (CSGP) of the bones.

The CSGP analysed in detail are percent cortical area (%CA) and the polar section modulus (Z_p). Percent cortical area (%CA= (CA/TA) x 100) is a measure of cortical area relative to the total area of the cross section that reflects not only activity, but other lifestyle factors including nutrition and demographic factors such as age (e.g. Garn et al. 1967; Mays et al 2009; Robbins Schug, 2011; Ruff, 2008, 2018a). The polar section modulus (Z_p) represents the torsional and average bending strength and is considered the most appropriate indicator of the overall mechanical loading on bone (Ruff, 2002, 2008, 2018a; Trinkaus and Ruff, 2012; Rodríguez et al., 2018).

In the case of the femur, the midshaft (at 50% of biomechanical length) was studied (Ruff and Hayes, 1983; Trinkaus and Ruff, 2012; Ruff, 2008; Gosman et al.,

2013; Macintosh et al., 2013), as it reflects habitual activity most strongly (Ruff, 2018b), but data from other cross-sectional locations are reported for reference.

The robusticity of the long bones is influenced by body mass and/or limb lengths and physical activity (Ruff et al., 1991; Marchi et al., 2006; Ruff, 2008), therefore, CSGP data must be standardised to remove the effects of body size and bone lengths in order to study patterns of habitual activity (Ruff et al., 1991; Ruff, 2000; Davies and Stock, 2014). The polar section modulus (Z_p) was standardized by dividing by the product of body mass and bone length (Ruff, 2000, 2002, 2018a; Sparacello et al., 2018). %CA is by its nature self-standardising.

Univariate comparative analysis was done on both %CA and Z_p using z-scores, which were calculated by subtracting the comparative sample mean from the Atxuri-I value and dividing by the standard deviation (SD) of the comparative sample (Gómez-Olivencia et al., 2009). In a normal distribution, the values beyond 1.96 and 2.576 SD from the mean indicate that the variable is significant at p<0.05 and p<0.01 respectively (Sokal and Rohlf, 1981).

3.8. Paleopathology

All the bones were examined macroscopically for any anomalies that could constitute pathological lesions, and differential diagnoses were made where possible (Buikstra and Ubelaker, 1994; Rogers and Waldron, 1995; White and Folkens, 2005).

3.9. Direct radiocarbon dating of the human remains

Two human remains from the site of Atxuri-I were selected: a rib fragment and a femur fragment. In the case of Txotxinkoba, four right human bones were selected for dating. All the samples were sent to Beta Analytics Inc (Florida, USA) and dated using AMS methodology, which is more suitable for this material since it requires smaller samples. Standard collagen extraction methodology, including alkali pretreatments, was applied.

Dates were calibrated using Oxcal v.4.4. software (Bronk Ramsey, 1998, 2009) and the Intcal120 calibration curve for terrestrial samples and Marine20 curve for samples showing marine protein in the diet (Heaton et al., 2020; Reimer et al., 2020; see Table 1).

3.10. Taphonomic observations

To consider the taphonomic history of the deposits we studied different indicators based on bone representation and completeness. To evaluate the survival of skeletal elements, we calculated the Bone Representation Index (BRI) by comparing expected and observed values following the following formula:

BRI = (MNEobserved/MNEexpected)*100

** where MNE expected corresponds to the N of elements expected in the context if all individuals were complete.

As in many cases subadult individuals are underrepresented, we calculated this index twice: including only adults, and the second including subadults (teeth were not included in these calculations).

The percentage completeness of preserved elements was calculated following Morlan (1994) and Mack et al. (2016):

Percentage of Completeness = ((Ppreserved/NISP)/Pdefined)*100

** where Ppreserved stands for "Portions Preserved" in each bone (all landmarks/zones/segments recorded for an element), Pdefined stands for "Portions Defined" (the total number of landmarks/zones/segments defined on a complete bone), and NISP is the total Number of Identified Specimens for that element (Lyman, 1994).

4. Results

4.1. Direct radiocarbon dating of the Atxuri-I and Txotxinkoba human remains in the Atlantic Western Pyrenees context

Here we present for the first time six new dates from the two studied sites (Table 1, Supplementary Table S2). The two human samples from Atxuri-I have yielded two very different dates: the rib fragment dates to 7,290 ± 30 BP (6,224-6,076 cal BCE), which corresponds to the Mesolithic in the region and is similar to the date obtained in Linatzeta (Tapia Sagarna et al., 2008; Table 1). The complete femur yielded a date of 3,570 ± 30 BP (2,023-1,778 cal BCE), corresponding to the Early Bronze Age. This date is similar to that obtained in Kobaederra, and one of the individuals from Lumentxa, among others (Ibañez et al., 1999; García-Sagastibelza et al., in press; Table 1). The four radiocarbon dates, belonging to four different individuals, from Txotxinkoba are similar to one another ranging from 4,420 to 4,250 BP (3,322-2,704 cal BCE), indicating funerary use of the cave during the Chalcolithic. These dates are similar to those from Lacilla II (Euskal Arkeologia Etnografia eta Kondaira Museoa/Museo Arqueológico, Etnográfico e Histórico Vasco, 1995; Gil Abad and Llamosas Rubio, 2016-2017), Arantzazu (Armendariz and Etxeberria, 1996; Armendariz et al., 1998) and Abauntz (Utrilla et al., 2015) (Table 1).

In the AWP area there are more than 187 sepulchral caves with presumed Holocene burials, and there are 74 direct dates on human bones from a total of 38 sites including the novel data presented in this study (Table 1). These dates show that the funerary use of the caves during the Holocene spanned, at least, from 8,300 BP to 1,130 BP. These direct dates include certain cases of human remains found on the surface of a site with long chronologies and not directly associated with any archaeological artifact (e.g., Arlanpe; Gómez-Olivencia, 2013; Rios-Garaizar et al., 2013), to sites where the human remains have been found in layers which are both chronologically and technotipologically consistent with the direct radiocarbon date from the human remains (e.g., Lumentxa; García-Sagastibelza et al., this volume).

Based on the still limited number of directly dated individuals relative to the total number of individuals found in caves, we can observe two patterns. First, most of the largest accumulations of human remains are found in sites with Chalcolithic burials, such as Lacilla II, Pico Ramos, Urtao II and Abauntz. All of these caves present similar dates between 4,600 and 4,000 BP. Urtiaga also contained a large MNI (25) but its three ¹⁴C dates correspond to the Bronze Age (3,475-3,430 BP) (Altuna and de la Rúa, 1989). The caves that show long-term use, such as Lumentxa, Santimamiñe, Marizulo or

Aizpea generally contain small numbers of individuals, roughly between five and nine (Table 1).

[INSERT TABLE 1 HERE]

4.2. Atxuri-I

4.2.1 Minimum number of individuals, age-at-death and sex assessment

The total number of human bone fragments recovered from Atxuri-I is 387, which correspond to 366 identifiable bone specimens (neurocrania were not taken into account due to fragmentation), which represent a minimum of nine individuals (Table 2). Six adults and one immature individual were identified based on the number of 1st right metatarsals (Figure 2). Two additional subadults were identified based on age-at-death incompatibilities. The anatomical elements assigned to each individual can be seen in Table 2, and the full bone inventory in Table 3.

[INSERT TABLES 2 AND 3 HERE]

[INSERT FIGURE 2 HERE]

The three subadult individuals have different estimated ages-at-death (Table 2). The youngest individual was 3-4 years old based on the maximum length of the ulna. The second individual has an estimated age-at-death between 6 and 8 years old, based on the erupted first permanent molar and the presence of the second molar still in the crypt. The third individual has an estimated age-at-death between 13 and 16 years old based on the lack of fusion of the proximal epiphysis of the first metatarsal. Among the adults, age-at-death was estimated based on dental wear. Two of the mandibles belonged to individuals older than 35 years, and another individual was between 21 and 35 years old when he/she died. Regarding the maxillae, age-at-death estimates range between 18-24, 20-30 and 40-50 years for the three individuals in which it has been possible to estimate the age-at-death by this method (Supplementary Table S3).

Sex assessment for two humeri suggests the presence of both males and females in the Atxuri collection. One femur, which was biomechanically studied, was also assessed as probably female. The assessment of sex based on the k-means analysis

using the maximum length of the first and second metatarsals indicates the presence of at least two males and five females (Table 4).

[INSERT TABLE 4 HERE]

4.2.2. Stature and body mass estimation

The complete femur, previously determined as probably female, provided an estimated stature of 160.4 cm and a body mass estimate of 53.1 kg. The stature for the female individuals using the first metatarsals ranged between 158.8 and 163.0.5 cm (Table 4). The second metatarsal, presumably belonging to a female individual, gives an estimated stature of 151.85 cm. In contrast, the stature in males has been estimated between 175.3 and 176.6 cm.

[INSERT TABLE 5 HERE]

4.2.3. Biomechanical analysis

Due to the uncertainty regarding the sex assessment of the femur (probably female), the data were compared to both male and female samples. The results of the standardised and non-standardised biomechanical analyses of the Atxuri-I femur are summarized in Table 5 and Supplementary Tables S4 and S5. The mid-shaft section and other sections of the femur are illustrated in Figure 3. The comparison of Atxuri-I to different samples is represented in Figure 4. The comparative sample database of different chronologies from the Iberian Peninsula, and France and Italy and the results of the z-score analysis are summarized in Supplementary Table S6.

[INSERT FIGURES 3 & 4 HERE]

Relative cortical area (%CA)

The %CA value of the Bronze Age Atxuri-I femur, is similar to the both Bronze age male comparative sample medians and shows an intermediate value between the female comparative samples from the same period (Figure 4). The z-score analysis shows that the Atxuri-I is closer to the female mean than to the male mean (Supplementary Table S6). The z-score analysis also shows that the %CA value of Atxuri-I femur is significantly greater than the Early Medieval male sample from Jau-Dignac-et-Loirac and the female sample from the Iberian Peninsula (Supplementary Table S6).

Polar section modulus (Z_p)

The relative strength (Z_p) of the Bronze Age Atxuri-I femur shows an intermediate value between the Bronze age male comparative sample medians and is similar to the Iberian female comparative sample median (Figure 4). The z-score analysis shows that, when compared to the Bronze Age Iberian samples, the Z_p value of Atxuri-I is significantly below the male mean and very close (z-score = 0.07) to the female mean (Supplementary Table S6). The z-score analysis also shows that the Z_p value of Atxuri-I femur is also significantly below the two Early Medieval male samples (Supplementary Table S6).

In summary, the Bronze Age individual Atxuri-I shows the strong affinities with the Bronze age female sample from the Iberian Peninsula, but falls within the range of samples from most other periods and locations.

4.2.4. Pathological lesions and anomalies

The majority of pathological anomalies were observed in the cranio-dental remains, including caries and plaque affecting a large number of teeth from different individuals. Regarding the postcranial remains, a proximal foot phalanx shows osteochondritison the proximal surface. A cervical vertebra also shows the presence of osteophytes and porosity, as well as deformation of the vertebral body and lower left articular facet, that could indicate arthrosis (Campillo, 2001). Finally, one of the maxillae shows a rotated first upper left premolar (P³) (Figure 5).

[INSERT FIGURE 5 HERE]

4.3. Txotxinkoba

4.3.1. Minimum number of individuals, age-at-death, sex assessment and stature estimation

The total number of human bone fragments recovered from Txotxinkoba is 1,234, which correspond to 578 identifiable bone specimens and 290 identifiable human teeth (NISP=868). Once analysed, these specimens gave a total (both left and right side) of 668 identified bones excluding fragments that could not be lateralised (Table 3). The

anatomical elements assigned to each individual can be seen in Table 1, and the full bone inventory in Table 3.

A minimum of 14 individuals are represented in the collection, including three subadult individuals (Table 2), based on the repetition of four dental remains (12, 32, 34 and 44). From the postcranium, the highest MNI is eight individuals based on the number of left clavicles (Figure 6). One individual was <6 years old at death based on the absence of fusion between the vertebral body and the neural arch. The other subadult is an individual between the ages 6 and 16. Using the coxal bones recovered from the cave we have been able to estimate the sex and approximate age-at-death of some of the adults. This collection includes five left coxal bones and two from the right side: all of them, except for one of the right coxae, belong to adult individuals as all have fused epiphyses. Amongst the left coxal bones, sex could be accurately estimated for two of them, both males. The adult right coxal corresponds to a female aged around 30 years. There was also a left coxal that despite being robust, shows a well delimited pre-auricular sulcus, and which corresponds to an individual older than 30 (Table 2). The k-means analysis on the maximum length of nine metatarsals suggest the presence of at least two females and two males (Table 4).

The estimated stature for the putative female individuals from Txotxinkoba ranged between 152.4 and 163.0 cm, while the males ranged from 167.8 to 170.1 cm (Table 4).

[INSERT FIGURE 6 HERE]

4.3.2. Pathological lesions and anomalies

The fragmentary nature of the bones prevents a systematic analysis of the pathologies present in this sample. Nonetheless, some lesions and anomalies were identified (Figure 7). There is an individual that shows Baastrup syndrome in several of the lumbar vertebrae, a degenerative condition generally produced by excessive lordosis or extensive disk-space loss, which derives in the close proximity and contact of the spinous processes (Resnick, 1985). In addition, there is a fifth right metacarpal showing an antemortem and completely healed oblique fracture. Several foot phalanges also show signs of inflammation at the distal end, and osteochondritis was observed in the

proximal facet of one first foot phalanx. Finally, a well-preserved maxilla shows a severe caries on the first molar and a probably related abscess that affects the palatal area of the bone (Figure 7).

[INSERT FIGURE 7 HERE]

4.4. Preliminary taphonomic observations

At a macroscopic level, the bones presented no evidence of cut-marks or anthropic modifications at either site. Some chemical alteration due to the composition of the soil and running water was present, although not widespread on the bones. Also, some bones showed evidence of being burned or in contact with fire, but there was no evidence of incineration.

Regarding the representation of different bones, in Atxuri-I there is an evident underrepresentation of crania, vertebrae, and bones from the pelvis (Supplementary Figure S2). In fact, most of the preserved bones are phalanges (Table 3). From the bones where we have calculated the BRI, MT1 is the most represented in the whole sample (78%), and is present in 100% of the adults (Supplementary Figure S2). Regarding the bone completeness index, most of the Atxuri-I bones are highly complete (most of them above 50%) (Supplementary Figure S2). Unsurprisingly, long bones are less complete than metacarpals, metatarsals and tarsal bones.

Bone representation is higher and more even in Txotxinkoba, where the least represented bones are the hyoid, sacrum and the distal phalanges of the foot (Supplementary Figure S2). The clavicles and arm bones are relatively frequent in the sample. In fact, in adults, clavicles and ulnae are represented for all the individuals (Supplementary Figure S2). Nevertheless, compared to Atxuri-I, the bones are overall less complete (Supplementary Figure S2). In this case too, the more complete bones are small bones, such as metacarpals, metatarsals and phalanges.

5. Discussion

Atxuri-I has yielded the remains of a minimum of nine individuals, two of which have been dated giving disparate results (Mesolithic and Bronze Age). Txotxinkoba has

yielded 14 individuals and the four ¹⁴C dates show that they were inhumed during the Chalcolithic. Both caves contain the remains of a similar number of individuals, with variable degrees of representation and completeness.

5.1. Skeletal representation and possible biases in Atxuri-I and Txotxinkoba

In many cases, the reconstruction of the inhumed population, including variation in element representation and demographic profile, can help identify the mortuary behaviours and taphonomic factors that have resulted in the commingling of the remains (Ubelaker, 1973; Adams and Konigsberg, 2008; Gerdau Radonić and Makowski, 2011). In both Atxuri-I and Txotxinkoba we have identified individuals of all ages and both sexes, thus their demographic profiles were roughly similar, although the disparity in the dates of Atxuri-I precludes any meaningful comparison, as the demographic profile in this cave could be the result of accumulation over a long period of time. In the case of Txotxinkoba, this study provides a new determination of the number of inhumed individuals that is larger than the previous estimate (14 vs. 2; Apellániz and Nolte, 1967; Armendáriz, 1990).

Bone Representation Index (BRI) (without taking into consideration isolated teeth) gives an idea of whether any elements were disproportionately represented in the collection (Mack et al., 2016). We calculated BRI twice, one without including subadults and the other including them as usually they are less completely preserved. This underrepresentation of subadult individuals may occur due to the fragility of their bones, which can be more easily fragmented and/or decomposed. Alternatively, the bias could be the result of differential funerary practices, in which only a certain part of the population is inhumed (e.g., Fernández-Crespo and de la Rúa, 2015; Alt et al., 2016). The very long chronology for the Atxuri-I human assemblage precludes a detailed assessment. In the case of Txotxinkoba, the main limitation to fully assessing any potential bias in the demographic profile is the relatively small number of individuals represented (MNI = 14). Zapata (1995) provides information on the demographic profile of the largest Chalcolithic accumulation in the AWP (MNI = 104): Pico Ramos. This site preserves individuals of all ages-at-death with the following percentages: <13 years (40%); 13-21 years (29%); >21 years (31%) (Zapata, 1995). Future studies could use resampling methods (e.g., bootstrapping) in order to assess whether smaller samples could be accommodated within the age-at-death profiles of larger sites. The differences in bone representation between the two studied sites are evident mainly in the long bones and clavicles. Also, in Atxuri-I there is a clear underrepresentation of the vertebrae and hip bones. Logically, at both sites the BRI values decrease when adding the subadult bones, but not dramatically. Similar studies carried out on other prehistoric commingled burials have shown a higher representation of the cranium in comparison to the two sites analysed here (Mack et al., 2016). Metatarsals, metacarpals and both hand and foot phalanges are represented similarly to other skeletal elements, and in Atxuri-I they are the most represented postcranial elements, indicating that in both sites that the burials were overall primary, as in secondary burials these elements are less likely to persist (Duday, 2011; Knüsel, 2014; Knüsel and Robb, 2016; Mack et al., 2016). In addition, the fact that the elements with the lowest percentages of recovery correspond to those from the axial skeleton might be explained due to their thinner cortical bone, which makes them more susceptible to taphonomic damage. Lastly, the low preservation of long bones in Atxuri-I might indicate that these were selectively taken from the deposit during prehistoric cleaning episodes of the cave (Knüsel, 2014; Knüsel and Robb, 2016). Another hypothesis is that due to the fast intervention, only better-preserved remains were recovered during the excavation of Atxuri-I.

The Percentage Completeness indicates that for those bones that were comparable, elements from Atxuri-I are more complete than those from Txotxinkoba. This evidence is clearest in the metacarpals and metatarsals, which could indicate differences in the physical-chemical conditions prior to the recovery of these bones. Txotxinkoba shows relatively low completeness percentages for the cranium, mandible and axial bones. Also, similar to the values reported by Mack and collaborators (2016) for the Bolores site, the major long bones do not exceed 30% completeness, and the most complete bones are metacarpals and metatarsals. The fact that long bones recovered from Atxuri-I are fewer but more complete may suggest selection of more complete elements at the time of excavation.

5.2-The new Atxuri-I and Txotxinkoba chronologies in the Iberian context

Despite the lack of stratigraphy for Atxuri-I (Garate, 2012) different chronologies had been suggested for the inhumations at this site: Neolithic/Chalcolithic

(Prieto, 2002) and Chalcolithic/Bronze Age (Fernández, 2005). In the case of Txotxinkoba, the excavators suggested that it belonged to the Chalcolithic Age and although they identified two levels, they argued that all burials corresponded to the same period (Apellániz and Nolte, 1967). The ¹⁴C dates that we have obtained for each of the sites have shown that Atxuri-I, in contrast to previous assumptions (Prieto, 2002; Fernández, 2005) had a diachronic series of burials, from at least the Mesolithic to the Late Bronze Age. In contrast, at Txotxinkoba all the dates (4 out of 14 individuals) correspond to a relatively restricted time period (3,322-2,704 cal BCE) consistent with previous interpretations of the deposit as most probably pertaining to the Chalcolithic and with the typology of the associated archaeological artefacts. Moreover, in our study we have found bones from both levels that refit and bones corresponding to the same individuals that come from both levels, reinforcing the suggestion that all the burials correspond to a relatively short period of time. Both cases demonstrate how apparently similar commingled contexts can have contrasting origins (Ubelaker, 2002; Gerdau Radonić and Herrera, 2010; Gerdau Radonić and Makowski, 2011).

Considering the archaeological evidence available in the AWP, there are examples of both diachronic commingling and also of synchronic collective burials. Caves for which we have evidence of a funerary function across different time periods include Santimamiñe, Lumentxa, Marizulo, Aizpea (Laborde et al., 1967; Cava, 1978; Altuna et al., 1995; Alday and Mujika, 1999; Barandiarán and Cava, 2001; Herrasti and Etxeberria, 2011; López Quintana, 2011; López Quintana et al., 2015; García-Sagastibelza et al., this volume), each of which contain a total of 5-9 individuals (Table 1). In caves that were only used for burial purposes during the Chalcolithic, the number of inhumed individuals varies and in many cases, they comprise very large accumulations of individuals. Amongst these caves, Pico Ramos and Abauntz stand out, with more than 100 individuals deposited in them (Baraybar and de la Rúa, 1995; Utrilla et al., 2015). While not synchronous strictly speaking these accumulations occurred during a relatively shorter time with a more intense use than at the former sites.

Near the AWP, San Juan Ante Portam Latinam (Biasteri, Araba, in the Mediterranean watershed) is a rock-shelter where 338 individuals were buried in a short period of time during the Chalcolithic. Although it has been debated (de la Rúa et al., 1995), this burial has been interpreted by most authors as a single event related to a

massacre due to the fact that many of the skeletons showed evidence of violence (Etxeberria and Vegas, 1988; Etxeberria and Herrasti, 2007; Fernández-Crespo, 2007; Fernández-Crespo et al., 2018).

In this study, we have not found any bias regarding sex or age-at-death in the inhumed individuals. This is consistent with previous studies of sites from the same region (Armendariz and Etxeberria, 1983; Ontañón and Armendáriz, 2005; Fernández-Crespo and de la Rúa, 2015, 2016).

Funerary practices in caves in the region are well recorded since the Mesolithic (Santimamiñe, Linatzeta, Atxuri-I). The Neolithisation process in the 5th millennium cal BCE and spread of the megaliths at the end of the 4th millennium cal BCE (Supplementary Table S7) did not involve the disappearance of funerary events in caves. Current archaeological evidence clearly indicates that both funerary phenomena are coeval both in the AWP (Supplementary Table S7) and Cantabrian region (Cubas et al., 2016). This behaviour is well recorded in the AWP and the Cantabrian region during the 3rd and 2nd millennia cal BCE.

There are 38 caves in this region with direct ¹⁴C dates on human remains. This represents around 20% of the total number of sepulchral caves found in the WP region to date. Moreover, from these dated caves, 32 contained multiple burials but only one individual was directly dated from each of 13 of these cases. In the case of Biscay, more than 50% (18 out of 32) of these dates were only obtained in the last decade (Herrasti and Etxebarria, 2011; López-Quintana and Guenaga, 2011; Arias, 2012; Gómez-Olivencia, 2012, 2013; Rios-Garaizar and Garate, 2012; Rios-Garaizar et al., 2013; Gómez-Olivencia et al., 2015; López-Quintana et al., 2015; Arribas and Berganza, 2018; García-Sagastibelza et al., this volume). Sepulchral caves from the Holocene are usually archaeological palimpsests, demonstrating recurrent use over long time periods, sometimes with evidence of clearing activities. The Iberian Peninsula has an extensive record of caves being used for funerary purposes in different periods, as does the AWP as demonstrated by the dates compiled in the present paper. For example, caves like Lumentxa and Santimamiñe have been used for funerary purposes over several millennia (López-Quintana et al., 2015; García-Sagastibelza et al., this volume). Moreover, some caves were not only used for funerary purposes, but present evidence of different uses at different points in time. In this sense, like in Lumentxa (García-Sagastibelza et al., this volume), caves like Can Sadurní (Begues, Barcelona) present

different layers of burials from different Holocene periods which alternated with habitation and penning (Blasco et al., 2005, 2011; Edo et al., 2019), and in Cueva de Chaves (Bastarás, Huesca) the habitation and burial areas are horizontally separated only by a few metres (Sánchez Cebrán, 2015; Utrilla and Laborda, 2018). At Cova Bonica (Vallirana, Barcelona), there is evidence of use both as a burial place during the Cardial Neolithic and also for habitation and penning at different times (Oms et al., 2017; Daura et al., 2019). Finally, some stratigraphies are easier to understand and interpret, while others present more complexities and mixed levels: this is the case of sites like Gruta do Caldeirão, where the Neolithic burials appear mixed with Palaeolithic artefacts (Zilhão, 1992, 2001). In this sense, the repeated use of the caves over long periods, and the creation of burial pits for funeral purposes may alter already complex stratigraphies.

In the Iberian Peninsula, caves that were fully excavated at the beginning of the 20th century or in the 1960's due to quarry activities or construction of water dams are abundant, as is the case of Atxuri-I. The salvage excavation of the Cova del Pantà de Foix (Castellet i la Gornal, Barcelona) was performed in 1926 before the construction of a dam. Direct dating of four individuals suggest a consistent funerary use of the cave for a limited time during the Chalcolithic (Cebrià et al., 2013; Subirà et al., 2016). Systematic dating programs are demonstrating their importance in these especially complicated contexts as shown in the present paper, where thanks to the new dates we have been able to determine the longer-term funerary use of Atxuri-I but a more chronologically limited use of the cave in the case of Txotxinkoba.

5.3. The paleobiology of the Bronze Age individual from Atxuri-I in context

The presence of a directly dated complete femur from Atxuri-I provides the opportunity to compare some paleobiological data from this individual (stature, body, mass, biomechanical properties) to other sites from the Iberian Peninsula, although it should be noted that comparisons based on this single individual must be interpreted very cautiously. The sex of this individual was estimated as female but with reservations. Thus, we compared the data to both male and female samples. Estimated stature from this femur (160.4 cm) was shorter than most of the Bronze Age males but taller than, though within the range of variation, of most other Bronze Age females from

the Iberian Peninsula (Supplementary Table S8). The body mass estimate for the Atxuri-I individual (53.1 kg) is below that of the Bronze Age male comparative samples (Martin-Flórez, 2010; Nájera, 2010, 2012; Ruff and Garvin, 2018), but similar to that of the female comparative samples (52 kg) (Supplementary Table S8).

The femur of Atxuri-I shows a more similar pattern of percent cortical area (%CA) to the Mesolithic and Bronze Age male and female samples from the Iberian Peninsula. This similarity can also be observed with the Neolithic male individual of Lumentxa (García-Sagastibelza et al., in press). This situation tentatively suggests that the mobility pattern did not change drastically in the Iberian Peninsula during the Late Prehistory, although clearly larger samples are needed to draw firm conclusions and both Atxuri-I and Lumentxa lie within the range of variation for various time periods and locations. Moreover, the similarity between our individual and the Lumentxa individual, both from different periods, also needs more investigation to examine the extent to which the Basque Atlantic orography plays a role in this similarity. Comparative samples from nearby areas like the Northern Iberian plateau or the Ebro Valley could be helpful to deal with this issue, as lower limb bone biomechanics are influenced by the nature of terrain (Marchi et al., 2006). The availability of complete long bones is a limiting factor to more extensive analyses. As we have observed, none of the Txotxinkoba individuals preserved a complete long bone suitable for biomechanical analysis.

Regarding the comparative samples from France and Italy, our individual had a lower value in %CA compared with Upper Palaeolithic and Mesolithic samples of both sexes, suggesting lower habitual mobility, although the influence of age, diet or other factors on cortical bone content of long bone cross-sections may also affect %CA (e.g., Garn et al., 1967; Mays et al., 2009; Robbins Schug, 2011; Ruff, 2008, 2018a). This is compatible with the decrease in bone robusticity observed from the Palaeolithic until the present in other studies, associated with increased sedentarism with the adoption of agriculture (Holt, 2018b; Cox et al., 2019; Ruff et al., 2015). In contrast, it seems that our individual was more mobile than the Neolithic examples, but less than the Bronze Age individuals. Furthermore, the Atxuri-I individual was slightly more robust than the average individual from the Iron Age/Roman Age and Early Medieval samples (including the Early Medieval sample from Iberian Peninsula), consistent with the interpretation that these later populations were more sedentary.

For the polar section modulus (Z_p) , more differences can be seen depending on whether the individual is assumed to be male or female. Our individual has a higher value for this parameter than Mesolithic sample of both sexes from Iberian Peninsula, which would be consistent with the progressive increase in lower bone strength during the Bronze Age documented elsewhere (Ruff and Garvin, 2018), although a much larger Bronze Age sample would be required to demonstrate any such pattern. The similarity observed between the Atxuri-I femur with the Bronze Age female sample would be consistent with the (cautious) sex assessment. The Atxuri-I femur suggests higher mechanical loading than individuals from the Upper Palaeolithic samples from both sexes, and the Mesolithic male sample. Nevertheless, compared with the Mesolithic female sample and the Neolithic and Bronze Age samples from both sexes, our individual demonstrates greater robusticity, and similar to the Iron Age/Roman Age male sample. The Atxuri-I individual is less robust than both male samples from Jau-Dignac-et-Loirac and the Early Medieval from the Iberian Peninsula, but similar, though slightly above the median values of the female samples of these periods.

In summary, based on the available information, we consider it most likely that the complete femur from Atxuri-I belonged to a relatively tall female individual from the Bronze Age, which should be further tested with nuclear DNA analysis.

6. Conclusions

In this work we provide the results of the anthropological study of human remains from two sites in the Atlantic Western Pyrenees: Atxuri-I and Txotxinkoba, which yielded a minimum number of 9 and 14 individuals, respectively. Both caves present subadult individuals of different ages-at-death and among adults, both sexes are represented. Although the representation of osteological elements is roughly similar in both sites, small differences in the preservation of pelvic bones and the completeness of long bones suggest a potential bias in Atxuri-I.

We provide six new radiocarbon dates on human remains. Two ¹⁴C dates from Atxuri-I show that the cave was used for funerary purposes during at least two very different periods: the Mesolithic and the Bronze Age, which contrast with previous assumptions about the chronology of the human remains of this cave. A complete femur

from Atxuri-I, directly dated to the Bronze Age, was also studied biomechanically, providing results similar to the available Bronze Age samples from the Iberian Peninsula, especially the female sample, which would fit with changes in habitual mobility during the recent Prehistory proposed elsewhere. The four dates from Txotxinkoba show that the cave was only used for a relatively short span of time during the Chalcolithic.

When these dates are put within the Atlantic Western Pyrenean context, and despite the still limited number of direct dates, it is evident that most of the largest accumulations of human remains are found in sites with Chalcolithic burials (between 4,600 and 4,000 BP), such as Lacilla II, Pico Ramos, Urtao II and Abauntz. Txotxinkoba would fit within this group. Those caves that show human burial chronologies spanning longer periods of time, such as Lumentxa, Santimamiñe, Marizulo or Aizpea, generally contain smaller numbers of individuals, and Atxuri-I would fit within this group.

This study underscores the necessity to combine paleobiological studies with systematic radiocarbon dating before attempting other analyses such isotopic analysis or ancient DNA due to the long chronologies in which caves were used for funerary purposes in the Atlantic Western Pyrenees.

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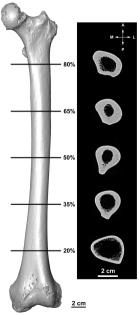
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Figure legends

- **Figure 1**. Location of Atxuri-I and Txotxinkoba in relation to other cave sites in the Western Pyrenees with Holocene dated human remains. 1: Las Pajucas, 2: Lacilla II, 3: Pico Ramos, 4: Covachon III, Punta Lucero II, 5: Urratxa II, 6: Arlanpe, 7: Askondo, 8: Atxuri-I, 9: Santimamiñe, 10: Txotxinkoba, 11: Lumentxa, 12: Langatxo; 13: Ekain, Linatzeta, Urtiaga; 14: Iruaxpe I, 15: Arantzazu, Nardakoste IV, Urtao II, 16: San Adrian, 17: Aintzulo, 18: Karea B, 19: Marizulo, 20: J3, 21: Abauntz, 22: Aizpea. Padre Areso, Laà 3, Bordedela 1 and 2, Houn de Laà, Laplace and Larrun 1 are situated further east of the area shown in the map.
- **Figure 2**. Minimum number of individuals (MNI = 9) represented in the Atxuri-I human bone assemblage (see Table 2). Individuals 1-3 are subadults, while individuals 4-9 are adults. Individual 1 (3-4 years old) is represented by an ulna (mesial view) and a second upper deciduous molar (buccal view). Individual 2 (6-8 years old) is represented by a deciduous canine (lingual view) and a mandible (occlusal view). Individual 3 (13-16 years old) is represented by two metatarsals (mesial views). Individuals 4-9 (adults) are represented by right first metatarsals (medial view).
- **Figure 3**. Anterior view of the 3D surface model of the femur from Atxuri I (label: ATXI.27B.70). Five sections along the diaphysis of the bone were studied (20%, 35%, 50%, 65% and 80% of biomechanical length measured from the distal end).
- **Figure 4**. Percentage cortical area and relative strength of the femur (mid-shaft) of the Bronze Age individual from Atxuri-I compared to a temporal male and female series from Western Europe. Grey boxes: France and Italy (Holt et al., 2018); open boxes: Iberian Peninsula (Ruff and Garvin, 2018). J refers to the 7th -8th century Early Medieval sample from the Jau-Dignac-et-Loirac (this study). The Early Medieval sample from the Iberian Peninsula is from Santa María de Hito (Ruff and Garvin, 2018).
- **Figure 5**. Selected examples of anomalies and pathological lesions in the skeletal remains from Atxuri-I. Dorsal view of a foot phalanx with osteophytes and osteochondritis on the proximal surface (top); cranial view of a cervical vertebra with evidence of osteoarthrosis on the cranial surface of the vertebral body and the lower left articular facet (middle); occlusal view of a maxilla with the first upper left premolar (P³) rotated (bottom).
- **Figure 6**. Representation of the eight adult left clavicles from Txotxinkoba. Shaded region in the drawing represents the bone part preserved in each clavicle.
- **Figure 7**. Examples of pathological lesions in the Txotxinkoba sample. Maxilla with evidence of acute caries affecting the M¹ (top left), and the subsequent abscess in the palatal area (top right). A considerable calculus deposit is visible on the M³ of the maxilla too (arrow). Posterior view of lumbar vertebra (second row left): articular modifications can be observed, as well as well-defined evidence of Baastrup syndrome on the spinous process. Medial foot phalanx with signs of inflammation of the distal epiphysis (second row right). Medial view of the fifth right metacarpal showing a healed antemortem fracture at the midshaft (bottom left). First foot phalanx showing evidence of osteochondritis on the mesial epiphysis (bottom right). All scale bars correspond to 1 cm.

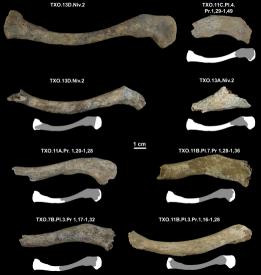


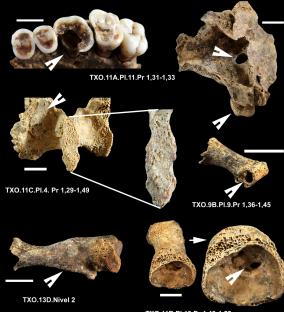












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Table 1. Cave sites in the Atlantic Western Pyrenees with directly dated human remains.

Site ^a	Location	Lab. Code	Radiocarbon date (BP)	Calibrated BCE age (95%)	Minimum number of individuals	Age at death	Sex determination	References	
					Biscay				
Abittaga	Amoroto	Ua-64120	$3,478 \pm 36$	1,895-1,689	1	1 adult	1 adult Female? Rios-Garaizar et al., in p		
		Beta-339110	$3,580 \pm 30$	2,028-1,782					
Arlanpe	Lemoa	Beta-299200	$3,510 \pm 30$	1,922-1,746	2 2 adults - Gómez-Oliv		Gómez-Olivencia, 2013; Rios-Garaizar et al., 2013		
		Beta-272221	3.180 ± 40	1,519-1,321					
Askondo	Mañaria	Beta-303669	$3,290 \pm 40$	1,677-1,452	2	10 years old individual	-	Gómez-Olivencia, 2012; Rios-Garaizar and Garate Maidagan, 2012	
		Beta-443326	$7,290 \pm 30$	6,224-6,076			At least 1 male and 1		
Atxuri I	Mañaria	Beta-493406	$3,570 \pm 30$	2,023-1,778	9	3 subadults and 6 adults	female	García Sagastibelza, 2017; This study	
Covachón III	Zierbena	Ua-50093	$4,065 \pm 32$	2,847-2,475	1	adult	-	Gómez-Olivencia et al., 2015	
Gerrandixo	Ibarrangelu	I-3197	3,090 ± 100	1,598-1,048	2	-	-	Apellániz and Nolte., 1967	
Kobaederra	Kortezubi	AA-29109	$3,545 \pm 60$	2,113-1,694	1	-	Male	Ibañez et al., 1999	

Lacilla II	Sopuerta	Ua-44279	4,335 ± 60	3,321-2,783	57	6 infants, 7 juveniles and 44 adults	-	E.A.E.K.M., 1995; Gil Abad and Llamosas Rubio, 2016- 2017.
Las Pajucas	Lanestosa	I-3513	$3,710 \pm 130$	2,469-1,751	2	2 At least 1 subadult -		Apellániz and Nolte., 1967
		OxA-18236 *	6,122 ± 38	4,952-4,726				
		CNA-5114.1.1	6,110 ± 35	4,936-4,726				
Lumentxa	Lekeitio	Ua-12665	$5,105 \pm 80$	4,157-3,657	7	2 subadults, 1 subadult- adolescent, 1 adolescent-	1 male and 1 female	Arias, 2012; García Sagastibelza et al., this volume
Lunientxa	Leketuo	CNA-5113.1.1	4,810 ± 35	3,646-3,526	,	young adult and 3 adults	I male and I female	Alias, 2012, Galeia Sagastibelza et al., uns volume
		Beta-493405	$4,780 \pm 30$	3,640-3,518				
		Beta-493404	$3,550 \pm 30$	2,014-1,771				
		I-16798	4,790 ± 110	3,913-3,345				
Pico Ramos	Muskiz	I-16501	4,210 ± 110	3,092-2,474	104	All the age ranges	At least 8 females and 8 males	Baraybar and de la Rúa, 1995; Zapata, 1995
		I-16797	4,100 ± 110	2,912-2,346				
Punta Lucero II	Zierbena	Ua-50094	4,687 ± 34	3,617-3,369	1	1 subadult	Indeterminate	Gómez-Olivencia et al., 2015
Santimamiñe	Kortezubi	Beta-307665	$6,130 \pm 40$	4,980-4,730	9	2 infants, 3 young adults and 1 old adult	At least 3 males and 1	Herrasti and Etxeberria, 2011; López-Quintana and
Santimanine	Konezuoi	Beta-240896	$3,710 \pm 40$	2,275-1,973	9	and 1 Old addit	female	Guenaga, 2011; López Quintana et al., 2015

		Beta-307664	$3,370 \pm 30$	1,743-1,542				
		Beta-307667	$3,370 \pm 30$	1,743-1,542				
		Beta-307669	$3,240 \pm 30$	1,607-1,433				
		Beta-307666	$3,130 \pm 30$	1,496-1,298				
		Beta-307668	$1,740 \pm 30$	245-402				
		Beta-542719	4,310 ± 30	3,011-2,885				
Txotxinkoba	Gizaburuaga	Beta-542720	$4,250 \pm 30$	2,916-2,704	- 14	At least 2 subadults and 8	At least 2 males and 2	This study
TAUTAHIKUDA	Gizabui uaga	Beta-542721	$4,400 \pm 30$	3,265-2,913	14	adults	females	Tills study
		Beta-542722	$4,420 \pm 30$	3,322-2,921				
		Ua-11430	$3,405 \pm 70$	1,886-1,520				
Urratxa III	Orozko	Ua-11431	$3,475 \pm 80$	2,022-1,546	12	1 phoetus, 6 subadults and 5 adults,	-	Muñoz Salvatierra and Berganza, 1997; de la Rúa et al., 1997
		Ua-11432	$3,365 \pm 80$	1,881-1,463				
					Gipuzkoa			
Aintzulo	Errezil	Ua-21155	4,495 ± 50	3,362-3,025	-	-	-	Altuna-Etxabe and Mariezkurrena-Gastearena, 2013

Arantzazu	Oñati	Ua-11849	$4,390 \pm 55$	3,330-2,898	2	1 infant and 1 adult	-	Armendariz and Etxeberria, 1996; Armendariz et al., 1998
Ekain	Deba	Ua-36855	$4,960 \pm 60$	3,945-3,639	-	-	-	Altuna, 2009
Iruaxpe I	Aretxabaleta	I-14097	4,130 ± 110	3,008-2,350	15	4 infants, 4 juveniles and 7 adults	At 2 males	Armendariz, 1987
J3	Hondarribia	GrA-23733*	8,300 ± 50	7,594-7,379	1	adult (20-40 years old and maybe 30-40 years old)	male	Iriarte et al., 2005
Karea B	Aia	OxA-33771	$4,125 \pm 35$	2,871-2,578	-	-	-	Aranburu-Mendizabal et al., 2018
Langatxo	Mutriku	Ua-3328	$3,820 \pm 55$	2,462-2,066	-	-	-	Zumalabe, 1993
Linatzeta	Deba	KIA-33193*	7,315 ± 35	6,086-5,925	3	1 infant	-	Tapia Sagarna et al., 2008
		Ua-4818	5,315 ± 100	4,346-3,960				
Marizulo	Urnieta	GrN-5992	5,285 ± 65 (individual)	4,319-3,976	5	1 infant, 1 juvenile and 2 adults (1 of them with 25 years old)	At least 1 male	Laborde et al., 1967; Cava, 1978; Altuna et al., 1995
		Ua-10374	$4,585 \pm 80$	3,617-3,027				
Nardakoste IV	Oñati	Ua-11848	$3,810 \pm 65$	2,463-2,041	14	5 subadults (1 foetus, 3 infants and 1 juvenile) and 9 adults	At least 6 males and 2 females	Armendariz et al. 1998
San Adrian	Aizkorri	Ua-44255	$3,311 \pm 30$	1,670-1,505	2	1 infant and 1 adult		Tapia et al., 2016
Urtao II	Oñati	I-14822	4,610 ± 120 (north gallery)	3,639-3,011	9	4 adults, 2 juveniles and 3 infants		Armendariz, 1989; Etxeberria, 1989

		I-14821	4,490 ± 170 (south gallery)	3,638-2,703	42	At least 3 infants, 2 juveniles and 31 adults,	both sexes		
		Ua-426	3,475 ± 120	2,134-1,506					
Urtiaga	Deba	Ua-506	3,445 ± 110	2,110-1,500	25	At least 1 infant and 5 adults	At least 1 male	Altuna and de la Rúa, 1989; López-Onaindia and Subirà, 2017	
		Ua-505	3,430 ± 100	2,014-1,504					
					Navarre	Navarre			
Abauntz	Arraiz	CSIC 785	$4,370 \pm 70$	3,332-2,885	>100	At least 1 infant, 2 children, 1 subjuvenile, 3 young and 6 adults (1	At least 5 male and 4	Utrilla et al., 2015	
Abauntz	Allaiz	GrA-37325	$4,025 \pm 35$	2,662-2,465	>100	individual with 50 years old and 1 older than 30 years old)	female		
		GrA-779	$6,600 \pm 50$	5,622-5,478					
		GrN-16620	$5,840 \pm 70$	4,892-4,506					
Aizpea	Arive	GrN-16621	$5,210 \pm 70$	4,244-3,805	1	At least 1 adult (30 years old)	At least 1 female	Barandiarán and Cava, 2001; de la Rúa et al., 2001	
		GrN-16622	$4,880 \pm 70$	3,932-3,518					
		GrN-18421	$4,420 \pm 70$	3,338-2,910					
Padre Areso	Bigüézal	GrN-14597	3,020 ± 35 B.P.	1,397-1,128	At least 2	At least 1 young adult	At least 1 male	Begiristain, 1997	
Tudio Meso	Diguezai	GrN-14596	1,130 ± 60 B.P.	772-1,025	I I IOUST 2	. w rease 1 young adult	7 K louge 1 Haire	Degrindin, 1771	

					Béarn				
Laà 3	Arudy		4,197 ± 50 BP	2,901 - 2,629	1	Adult		Dumotier et al., 2014, 2016; Courtaud et al., 2018	
D 11111	Arudy	Ly-11876	4,470 ± 30 BP	3,340 - 3,026	7	1 subadult (<5 years old)		D :	
Bordelela 1	Ly-11875 4,035 ± 35 BP 2,834 -2,467		and 6 adults						
Bordelela 2	Arudy	Poz-69595	4,075 ± 35 BP	2,857 - 2,476	3	1 subadult (around 1 year old) and 2 adults		Dumotier et al., 2014, 2016; Courtaud et al., 2018	
Houn de Laà	Arudy	Erl-19174	4,449 ± 51 BP	3,340- 2,928	- 15	5 subadults (1 perinatal and 4 infants) and 10		Dumotier et al., 2014, 2016; Courtaud et al., 2018	
Houli de Laa	Ailudy	Erl-19173	4,401 ± 49 BP	3,329 - 2,906	13	adults		2 among et an, 2011, 2010, Command et al., 2010	
Grotte Laplace	Arudy	Ly-11874	4,150 ± 35 BP	2,879 - 2,586	5	3 subadults and 2 adults		Blanc, 1989; Dumotier et al., 2014, 2016; Courtaud et al.,	
Grotte Laplace	Aludy	Ly-11873	4,105 ± 35 BP	2,868 - 2,501				2018	
Grotte de Garli	Arudy	Erl-19171	4,986 ± 49 BP	3,945 - 3,648	4	3 subadults and 1 adult		Ébrard, 2013; Dumotier et al., 2014, 2016; Courtaud et al., 2018	
	•	Beta-308779	3,970 ± 30 BP	2,575 - 2,350				2016	
Larrun I	Arudy	Erl-19170	4,661 ± 48 BP	3,622 - 3,356	2	2 subadults (3 ± 1) and $8.5 \pm 1)$		Dumotier et al., 2014, 2016; Courtaud et al., 2018	

^a Organized alphabetically by province.

^{*}Calibrated using the curve Marine 20.

Table 2. Minimum number of individuals (MNI) represented at Atxuri I and Txotxinkoba.

Site	Developmental state	Individual number	Estimated age-at-death ^a (years)	Sex assessment	Associated elements
Atxuri I	Subadults	1	3-4	-	2 nd upper deciduous molar, thoracic vertebra, lumbar vertebra, ulna, indeterminate metatarsus
	2 6-8		-	mandible, canine, 1st lower deciduous mola indeterminate metatarsus	
		3	13-16	-	2 thoracic vertebrae, 2 lumbar vertebrae, 1 st metatarsus, 3 rd metatarsus
	Adults	4	18-22/20-24	2 males (1 humerus and 2 metatarsals) and 4 females	see Table 3
		5	20-24/24-30	(1 humerus, 1 femur and 6 metatarsals)	
		6	>40-50		
		7-9	-		
Txotxinkoba	Subadults	1	<6	-	unfused vertebral arches, several teeth on early stages of development
		2	6-16	÷	vertebrae with fused arches but unfused rings
	Adults	3-14	At least one individual >30 (right coxal)	At least 2 males (2 left coxal boness, 4	see Table 3

arsals), 3 females oxal, 5 metatarsals)

^a See Supplementary Table S3.

Table 3. Anatomical representation, Number of remains (NR) and minimum number of elements (MNE) by age-at-death of the Atxuri I and Txotxinkoba osteological collections.

			Atxuri-I				7	xotxinkoba	1	
Anatomical region	MNE NR						MNE NR			
		Adult	Subadu lt	Indet.	Total		Adult	Subadu lt	Indet.	Total
Cranium	44				*	90	3	1		4
Maxillae	7	3			3	3		2	1	3
Mandibles	5	3	1		4	21	5	1		6
Teeth**	112				140	243				293
Hyoid						2		1		1
Cervical vertebrae	4	4			4	28	13	7		21
Thoracic vertebrae	12	9	3		12	33	24	4		28
Lumbar vertebrae	9	6	3		9	22	14	2		16
Sternum	1	1			1	4	3			3
Ribs	2	2			2	90				2
Clavicles	3	3			3	12	12			12
Scapulae	1	1			1	12	6			6
Humeri	4	4			4	27	10	2		12
Radii	2	2			2	19	8	1		9
Ulnae	6	5	1		6	23	15			15
Carpal Bones						9	9			9
Metacarpals	28	24	3	1	28	38	38			38

Hand phalanges	72	56	12	4	72	80	35			35
Coxae						21	5	1		6
Sacrum						4	1			1
Femora	3	3			3	32	5	1		6
Patellae						6	6			6
Tibiae	4	4			4	11	5	1		6
Fibulae	1	1			1	5	4			4
Tarsal bones	4	4			4	42	42			42
Metatarsals	28	20	5	3	28	45	43	1		44
Foot phalanges	35	24	9	2	35	43	43			43
Total identified bone elements	387	179	37	10	366	1,234	642	25	1	668

^{*} In the case of Atxuri-I the fragmentation of the cranium has not allowed to determine the MNE.

^{**} The NR in teeth only accounts for isolated teeth, the MNE accounts for both isolated and *in situ* (mandibular and/or maxillary) teeth.

Table 4. The estimation of stature (± SEE; all in cm) from the first and seconde metatarsal bones (Pablos et al., 2013) for individuals from Atxuri-I and Txotxinkoba.

Anatomical region	Label	Side	Determined sex	Maximum length (mm)	Pooled sex ^a	Male ^b	Female ^b
			Atxu	ri I			
1° metatarsal	ATXI.19C.V.50	R	F	61.35	165.1 ± 4.85		163.0 ± 2.91
1° metatarsal	ATXI.21B.II.20.4	L	F	61.35	165.1 ± 4.85		163.0 ± 2.91
1° metatarsal	ATXI.21C.I.10	R	M	66.1	172 ± 4.85	175.3 ± 3.68	
1° metatarsal	ATXI.25B.90	R	M	67.45	174 ± 4.85	176.6 ± 3.68	
1° metatarsal	ATXI.27B.100	R	F	59.45	162.3 ± 4.85		160.4 ± 2.91
1° metatarsal	ATXI.29B.100	R	F	59.00	161.7 ± 4.85		159.8 ± 2.91
1° metatarsal	ATXI.29B.110	R	F	58.25	160.6 ± 4.85		158.8 ± 2.91
2° metatarsal	ATXI.25B.35	R	F	63.95	152.6 ± 5.485		151.8 ± 3.80
	Total				164.2 ± 6.73	176.0 ± 0.92	159.5 ± 4.13
					(152.6- 174)	(175.3- 176.6)	(151.8- 163.0)
					n = 8	n = 2	n = 6
			Txotxii	ıkoba			
1° metatarsal	11B plano 10 1,36-1,42	R	F	60.2	163.4 ± 4.85		161.4 ± 2.91
1° metatarsal	11C plano4 1,29- 1,49	L	F	61.3	165 ± 4.85		162.9 ± 2.91
1° metatarsal	13D Nivel2	R	F	61.4	165.2 ± 4.85		163.0 ± 2.91
1° metatarsal	9B pl 23 1,60- 1,72	L	F	59.4	162.2 ± 4.85		160.3 ± 2.91
2° metatarsal	11a. 1,31-1,33	L	F	64.51	153.3 ± 5.49		152.4 ± 3.80

2° metatarsal	11a. 1,31-1,34	L	М	70.1	160.5 ± 5.49	168.4 ± 3.44	
2° metatarsal	11B 1,28-1,36	R	М	69.4	159.6 ± 5.49	167.8 ± 3.44	
2° metatarsal	13D Nivel3	R	M	73.3	164.6 ± 5.49	170.1 ± 3.44	
2° metatarsal	9B 1,54-1,60	L	М	71.24	161.9 ± 5.49	169.3 ± 3.44	
	Total				161.7 ± 3.73	168.9 ± 1.01	160.0 ± 4.39
					(153.3- 165.2)	(167.8- 170.1)	(152.4- 163.0)
					n = 9	n = 4	n = 5

SEE= Standard error of estimate

^a Using formulae derived from a pooled sex and ancestry sample.

^b Using formulae derived from Euroamerican samples.

^{*} Two estimates are provided for each bone: one using formulae based on a pooled sex sample and another using sex-specific formulae based on the results of the k-means analyses

Table 5. Raw (non-standardised) and standardised cross-sectional geometric properties of the left femur of the site of Atxuri I (label: ATXI.27B.70).

Section level	%CA	$Z_{p} \ (non-standardised)$	\mathbf{Z}_{p} (standardised)
20	40.43		
35	63.60		
50	77.98	2513.01	1092.77
65	83.84		
80	69.59		

Estimated stature from this bone = 160.4 cm and estimated body mass = 53.11 kg.

Maximum length of the femur: 433 mm.

Polar section modulus (Z_p) is measured in mm^3 .