

The Koskobilo (Olazti, Navarre, Northern Iberian Peninsula) paleontological collection: New insights for the Middle and Late Pleistocene in Western Pyrenees

Asier Gómez-Olivencia^{a,b,c,*}, Mikel Arlegi^{a,d}, Diego Arceredillo^e, Eric Delson^{f,g,h,i,j}, Alfred Sanchis^k, Carmen Núñez-Lahuerta^{l,m,n}, Mónica Fernández-García^{o,p}, Mónica Villalba de Alvarado^{q,c}, Julia Galánⁿ, Adrián Pablos^{r,c}, Antonio Rodríguez-Hidalgo^{q,s,o}, Mikel A. López-Horgue^a, Manuel Rodríguez-Almagro^a, Virginia Martínez-Pillado^c, Joseba Rios-Garaizar^r, Jan van der Made^t

^a Dept. Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Euskal Herriko Unibertsitatea, UPV/EHU, Barrio Sarriena s/n, 48940, Leioa, Spain

^b Sociedad de Ciencias Aranzadi, Zorroagaina 11, 20014, Donostia-San Sebastián, Spain

^c Centro UCM-ISCIII de Investigación sobre Evolución y Comportamiento Humanos, Avda. Monforte de Lemos 5 (Pabellón 14), 28029, Madrid, Spain

^d Université de Bordeaux, UMR PACEA / 5199, Laboratoire d'Anthropologie des Populations du Passé, Université Bordeaux 1, avenue des Facultés, 33405, Talence Cedex, France

^e Facultad de Humanidades y Ciencias Sociales, Universidad Isabel I, c. Fernán González 76, 09003, Burgos, Spain

^f Department of Anthropology, Lehman College of the City University of New York, 250 Bedford Park Boulevard West, Bronx, NY, 10468, USA

^g Department of Vertebrate Paleontology, American Museum of Natural History, 200 Central Park West, New York, NY, 10024, USA

^h PhD Program in Anthropology, The Graduate Center of the City University of New York, 365 Fifth Avenue, New York, NY, 10016, USA

ⁱ New York Consortium in Evolutionary Primatology, New York, NY, USA

^j Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de La UAB, 08193, Cerdanyola del Vallès, Barcelona, Spain

^k Museu de Prehistòria de València, Servei d'Investigació Prehistòrica, Diputació de València, Corona 36, València, Spain

^l Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia, FCT, Universidade Nova de Lisboa, 2829-516, Caparica, Portugal

^m Museu da Lourinhã, Rua João de Moura 95, 2530-158, Lourinhã, Portugal

ⁿ Aragosaurus-IUCA, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, C/ Pedro Cerbuna, 12, 50009, Zaragoza, Spain

^o Institut Català de Paleocologia Humana i Evolució Social (IPHES), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007, Tarragona, Spain

^p Área de Prehistòria, Universitat Rovira i Virgili, Facultat de Lletres, Avinguda Catalunya 35, 43002, Tarragona, Spain

^q Departamento de Prehistoria, Historia Antigua y Arqueología, Universidad Complutense, Prof. Aranguren s/n, 28040, Madrid, Spain

^r Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo de la Sierra de Atapuerca, 3, 09002, Burgos, Spain

^s IDEEA (Instituto de Evolución en África), Calle Covarrubias 36, 28010, Madrid, Spain

^t Consejo Superior de Investigaciones Científicas, Museo Nacional de Ciencias Naturales, c. José Gutiérrez Abascal 2, 28006, Madrid, Spain

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ABSTRACT

The destroyed site(s) of Koskobilo (Olazti, Navarre, Northern Iberian Peninsula) have yielded unique archaeo-paleontological evidence in the Western Pyrenees region. The quarry uncovered a karstic site with faunal remains in 1940, and fossils were recovered both *in situ* and from the quarry dump. Ten years later, while the quarry was still working, a new visit to the dump yielded a large lithic assemblage and additional fossil remains with a different taphonomic pattern, which has been interpreted as the remains coming from a different site or zone within the same karst system. Here we re-study the paleontological evidence and provide new dating on a speleothem covering a *Stephanorhinus hemitoechus* tooth, which has yielded a minimum date of c. 220 ka for part of the assemblage. In total, the fossil assemblage comprises 38 mammal and six avian taxa and three fish remains. The faunal evidence indicates that in 1940 a mix of taxa from both the Middle and Upper Pleistocene were recovered, and it is difficult to assign most of them to a concrete period. However, based on biochronological criteria some of the identified taxa (e.g., *Ursus thibetanus*, *Ursus cf. deningeri*, *Cuon cf. priscus*, *Macaca sylvanus*, cf. *Megaceroides*) could be roughly contemporaneous with the dated rhino tooth, which would provide a new window to the Middle Pleistocene of the region, with deposits from MIS 7d and/or older. Despite the

* Corresponding author. Dpto. Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea. Barrio Sarriena s/n, 48940, Leioa, Spain.

E-mail address: asier.gomez@ehu.eus (A. Gómez-Olivencia).

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difficulties in studying this collection, recovered without stratigraphic context and in a salvage operation, Koskobilu has yielded an important paleontological assemblage which helps to understand the paleoecology of the Middle Pleistocene human occupations in the Western Pyrenees.

1. Introduction

The Western Pyrenees (henceforth WP) is a key area to understand the cultural and biological interchanges between the Iberian Peninsula and the rest of Europe (Arrizabalaga and Rios-Garaizar, 2012). It is located on the northern fringe of the Iberian Peninsula and acts as a natural corridor among the continent, the Ebro basin, the northern Meseta (plateau) and the Cantabrian fringe. Despite a relatively good record of Upper Pleistocene deposits, there is a dearth of Middle Pleistocene sites in this area (and in the rest of the Northern Iberian Peninsula) which has limited so far a good understanding of the paleoecological conditions of the oldest hominin occupations in this region. The nearby areas, on the contrary, have yielded a relatively well known record for this chronology (e.g., Atapuerca: Rodríguez et al., 2011; Arsuaga et al., 2014, 2015). In the last decade, new findings, the re-study of collections excavated a long time ago and the implementation of new geochronological dating methods have provided new insights into this important time period. However, there are still only three mid-Middle Pleistocene sites in the whole Cantabrian region, and late Middle Pleistocene paleontological information comes only from a handful of sites.

The mid-Middle Pleistocene is only represented by a single site in the WP (Punta Lucero) and only two additional sites are known in the Northern Iberian Peninsula: Llantrales and Mestas de Con (Álvarez-Lao, 2016). The Llantrales quarry (Asturias) has yielded a small assemblage including *Cervus* cf. *elaphus*, *Praemegaceros solilhacus*, and *Stephanorhinus* cf. *hundsheimensis*. A date of 0.8–0.5 Ma has been proposed for this site (Álvarez-Lao, 2016). The new study of the Mestas de Con assemblage (proposed age: 0.6–0.4 Ma) has yielded a more diverse assemblage including herbivores such as *C. elaphus*, *Praemegaceros*?, *Capreolus* cf. *capreolus*, a small sized bison (*Bison* sp.), *Equus* sp., and

Stephanorhinus hemitoechus, as well as two carnivore taxa: *Homotherium latidens* and *Ursus* sp. Punta Lucero was preliminarily studied by Castaños (1988). With a similar chronology to Mestas de Con (i.e., 0.6–0.4 Ma), it is currently the most important site in terms of number of fossils and species identified: it has yielded fossils from five herbivore (*C. elaphus*, a megacerine deer, cf. *Bos primigenius*, *Bison* sp., *Stephanorhinus* sp.) and four carnivore (*H. latidens*, *Panthera gombaszoegensis*, *Vulpes* sp., and *Canis mosbachensis*) taxa (Gómez-Olivencia et al., 2015). Additionally, a combined isotopic analysis and trophic modeling has provided important paleoecological information: resource partitioning, with bison and aurochs consuming vegetation from more open spaces when compared to red deer, evidence of high competition among the carnivore guild, with overlap between the two large cats, which probably did not compete with the wolf *C. mosbachensis* (Domingo et al., 2017).

The late Middle Pleistocene is slightly better represented in the WP: the c. 300 ka site of Santa Isabel de Ranero with the presence of *Ursus deningeri* and *Panthera spelaea* (Torres et al., 2001, 2014), the lower levels of Arlanpe (Rios-Garaizar et al., 2015), Lezetxiki (Altuna, 1972; Falguères et al., 2005) and Lezetxiki II (Castaños et al., 2011; Arriolabengoa et al., 2018), and the single dated rhinoceros tooth from Goikoetxe (Edeso et al., 2011). The sites of Astigarraga (Villaluenga et al., 2012) or Irrikaitz (Arrizabalaga and Iriarte, 2011) could also be pre-MIS 5 in age. North of the Pyrenees, there are several late Middle Pleistocene archaeological sites such as Duclos (Auriac, Pyrénées-Orientales) or Romentères (Le Vignau, Landes) (Hernandez et al., 2012). However, the archaeological sequences are still scarce, in some cases only preliminarily published, and only a single human remain has been found (the humerus from Lezetxiki; Basabe, 1966; de-la-Rúa et al., 2016) combined with some scant paleontological evidence, and a good chronological setting is still missing for many sites. In this context, the

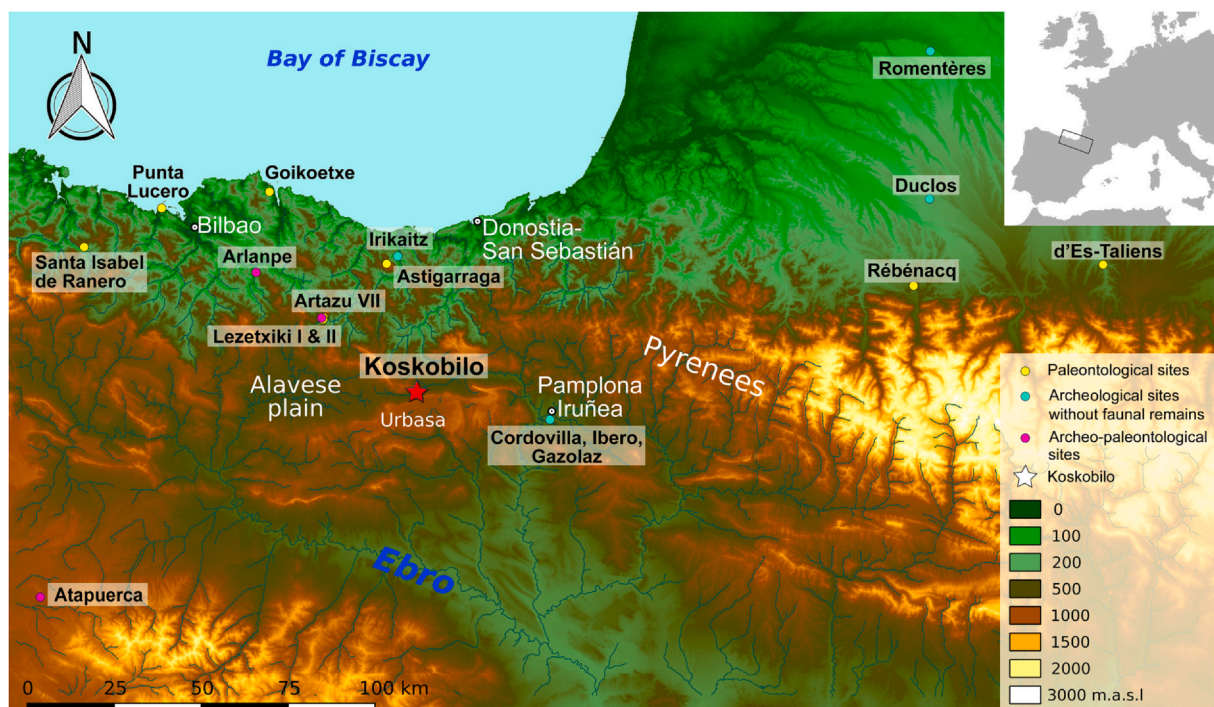


Fig. 1. Geographical location of the Koskobilu quarry together with other sites mentioned in the text.

presence in Koskobilo of *Hippopotamus* sp. (Ruiz de Gaona, 1941, 1952, 1958), a species which went extinct in western continental Europe c. 117 ka BP (Stuart and Lister, 2012); and of *U. thibetanus* (Arlegi et al., 2018), a taxon which enters Western Europe at different times during the Middle Pleistocene (Crégut-Bonnoure, 1997), provides a new window into the Middle Pleistocene in the northern Iberian Peninsula. The main objective of this report is to provide an in-depth analysis of the paleontological collection recovered from Koskobilo during the middle of the 20th century, including biochronological and taphonomic aspects.

1.1. Koskobilo: geological, geographic and historiographic context

The Koskobilo quarry (Olazti, Navarre, UTM: 30 T 565685 4747601; 42°52'N, 2°11'W; 556 m.a.s.l.) is located in the termination of the Aizkorri mountain range, in front of the Urbasa plateau, both flanking a natural corridor between the Alavan plain and the Sakana corridor, which is close to the limit between Atlantic and Mediterranean climates (Fig. 1; Supplementary Information Fig. S1). This quarry is located in the central part of the inverted Basque-Cantabrian Basin, which structurally is part of the southeastern end of the SE plunging Bilbao anticlinorium, a complex folded area that extends

along 100 km with a N125E strike between the study area and the west of Biscay province. The Koskobilo limestones and the coeval sedimentary units form the periclinal end of this structure, dipping around 60° towards SW, S and NE.

The currently abandoned Koskobilo and Olazti quarries were dug in a single limestone unit which stratigraphically changes laterally to coeval fine-grained siliciclastic deposits. This limestone was formed as an isolated shallow marine carbonate bank separated by siliciclastic deeper marine troughs from other coeval carbonate banks. These carbonates are included in the Egino Formation (García-Mondéjar, 1982) and more recently in the Albeniz Unit (López-Horgue et al., 1996) just to include the coeval deeper marine siliciclastics and a unit of calcarenites cropping out to the north of Altsasu. Sedimentary thickness varies between carbonate banks (max. 600 m) and troughs (max. 300 m), the Koskobilo bank being 250 m thick. The age of this unit is early Late Albian based on orbitolinids from the limestones and on ammonoids from the coeval siliciclastics (López-Horgue et al., 1996; Klompmaker, 2013).

The limestone facies are micritic floatstones of large planar corals, algae and sponges, with bioclastic floatstones atop some sequences and bioclastic debrites and breccias in the transition to deeper marine troughs. The limestones show features of early dissolution during the

Table 1
Composition of the Koskobilo faunal assemblage according to Ruiz de Gaona (1941).

Taxon ^a	Specimens ^a
<i>Equus caballus fossilis</i>	52 M and 6 incisors
<i>Rhinoceros megarhinus</i> / <i>R. tichorhinus</i> ^b	Nine upper and 6 lower molars (one within a jaw fragment)
<i>Sus (scrofa ferus?)</i>	Three incisors (2 of them broken, and within a mandibular fragment), two additional “jaw” fragments (one preserving the last 2 M and the other the first premolars), three first premolars and a second molar
<i>Hippopotamus</i>	Canine fragment
<i>Cervus elaphus</i>	Large-sized antler fragment and 5 M
<i>Cervus capreolus</i>	Two antler fragments
A cervid	An antler, 8 M, and 4 deformed molars
An “antilopid”	Two lower jaws, some isolated molars and incisors
Wild goat	Horn fragment
<i>Bos curvidens</i> ^c	Nearly as many molars as <i>Equus</i> and some incisors
<i>Bison</i> sp. ^c	[Number of specimens unknown]
<i>Lepus</i>	Upper jaw fragment with 4 M (sic)
<i>Mus</i>	Four right lower jaws
<i>Arvicola spelaea</i>	Two specimens preserving both upper jaws, many lower jaws and isolated molars and incisors
<i>Castor fiber</i> ^d	Nearly complete lower right jaw (including 4 M (sic) and incisor), 2 incomplete upper upper incisors, 2 M within the upper jaw, 14 isolated upper and lower molars
<i>Arctomys primigenia</i> (sic)	Five jaws, preserving their molars (and in some cases their incisors), and some isolated incisors
Rodentia indet.	Two jaws without teeth no corresponding to the previous species
<i>Felis catus</i>	Three mandibles, with all their teeth, and some isolated canines
<i>Felis pardus</i> ^e	[Number of specimens unknown]
<i>Hyaena spelaea</i>	Two canines, a lower carnassial, an upper carnassial, 5 M, and 3 claws
<i>Canis vulpes</i>	Some jaw fragments (both with and without teeth), isolated canines, premolars and molars
<i>Canis familiaris</i>	
<i>Canis lupus</i>	
<i>Ursus spelaeus</i>	Ten canines and at least 30 M, premolars and incisors
<i>Ursus</i> sp./ <i>U. arctos</i> ^f	[Number of specimens unknown]
<i>Mustella vulgaris</i>	Five more or less complete jaws and some canines
<i>Sorex</i> sp.	[Number of specimens unknown]
<i>Crocodyra</i> sp.	[Number of specimens unknown]
<i>Talpa</i> sp. ^g	[Number of specimens unknown]

^a Unless otherwise stated, these refer to the description made by Ruiz de Gaona (1941) based on the study by Federico Gómez Llueca (Museo Nacional de Ciencias Naturales, Madrid). Note that the term “jaw” was used by Ruiz de Gaona for both the maxilla (upper jaw) and mandible (lower jaw). Ruiz de Gaona (1941) mentioned that the fossil collection preserved cranial fragments, radii, metacarpals, femora, tibiae, tali, calcanei, metatarsals, etc. but suggested that the identification was based on the dental remains.

^b *Rhinoceros megarhinus* according to Ruiz de Gaona (1941, 1952) and *R. tichorhinus* according to Ruiz de Gaona (1958).

^c Ruiz de Gaona (1941) states the presence of three bovine species, but only provides the name of one: *Bos curvidens*. Ruiz de Gaona (1952) lists the presence of both *Bos curvidens* and *Bos-Bison*, while Ruiz de Gaona (1958) cites de presence of *Bos curvidens* and *Bison* sp.

^d Crusafont and Villalta (1948) described these castorid remains in detail.

^e Not mentioned in Ruiz de Gaona (1941) but subsequently listed in Ruiz de Gaona (1952, 1958).

^f Indeterminate bear species according to Ruiz de Gaona (1941), not mentioned in Ruiz de Gaona (1952) and identified as *Ursus arctos* according to Ruiz de Gaona (1958).

^g Ruiz de Gaona (1941) suggested that he was able to identify them among the faunal specimens sent to Gómez Llueca, but the latter did not include *Talpa* in his faunal list. Later, Ruiz de Gaona (1952, 1958) included “*Talpa* sp.” in the faunal list.

Late Albian following fractures. Later these fractures were filled with carbonate sediments and siliciclastics (e. g., López-Horgue et al., 1996). These smaller scale fractures originated at right angles with respect to the main synsedimentary SW-NE faults. During the Basque-Cantabrian Basin inversion (Bodego and López-Horgue, 2018), some old fractures were re-activated and played an important role in the alpine deformation. However, sedimentary units in the folded study area show a good lateral continuity only broken by a thrust to the north of the town of Altsasu. In the Koskobilo bank the Quaternary karstification follows in part some of the minor fractures with synsedimentary infillings. A more detailed analysis of the fractures with karst features is necessary to better understand the karst development in the area, but a main dissolution along NW-SE strike seems likely.

A detailed history of the discovery of the archaeo-paleontological assemblage from the Koskobilo quarry can be found in Arlegi et al. (2018), which will be briefly summarized here. In 1940, work at the Koskobilo quarry revealed the presence of a vertical cavity of 12–14 m (height), with a base of c. 6 m, divided into two compartments by a rocky crest. This cavity was filled with sediment where paleontological remains were found and shown to Máximo Ruiz de Gaona. This researcher visited the site and realized that part of the paleontological assemblage from the infilling of the cavity had been thrown into the dump (Ruiz de Gaona, 1941). Ruiz de Gaona recovered fossil remains not only from the dump but also *in situ* from the infilling itself. He sent these remains to the paleontologist Federico Gómez Lluca (Museo Nacional de Ciencias Naturales, Madrid) in order to make the first identification of the Koskobilo findings, which resulted in a list of more than 25 taxa (Table 1; Ruiz de Gaona, 1941). In 1948, Crusafont and Villalta (1948) described in more detail the beaver (*Castor fiber*) remains from Koskobilo, which represented the first mention of this taxon in the Iberian Peninsula. In 1950, Ruiz de Gaona returned to the dump with the objective of recovering additional faunal remains. During this visit, he basically recovered a large assemblage of lithic remains, with the presence of both Middle Paleolithic and Upper Paleolithic typologies; he considered the Solutrean to be very abundant (but see Maluquer de Motes, 1954 for an alternative classification). Thereafter, some of the quarry workers told him about the potential presence of a horizontal gallery from which the archaeological material would derive (Ruiz de Gaona, 1952). Maluquer de Motes and Uranga also recovered lithic materials in 1954 (Vallespí Pérez and Ruiz de Gaona, 1971). In 1955, the renown Basque archaeologist J.M. de Barandiarán recovered 1155 flint remains, a sandstone pebble and a small bone assemblage (Beguiristain Gúrpide, 1974). Subsequently, Ruiz de Gaona published five Solutrean foliate points (Vallespí and Ruiz de Gaona, 1969) and three bifacial tools (Vallespí Pérez and Ruiz de Gaona, 1971; see also Beguiristain Gúrpide, 1974; García Gazólaz, 1994). In 2016 we recovered 134 faunal remains and 425 lithics from dump “a” and 25 additional lithics from dump “b” (*sensu* Ruiz de Gaona, 1952; see also Arlegi et al., 2018). Our preliminary revision of the paleontological collection from Koskobilo, new archaeo-paleontological findings and a critical evaluation of the literature led us to propose that the archaeo-paleontological collection probably derives from two different cavities, with both the Middle Pleistocene and the Late Pleistocene represented: most of the archaeological material probably derives from a second cavity (or cave sector), different from that which yielded the paleontological remains described in 1941 by Ruiz de Gaona (Arlegi et al., 2018).

The lithic assemblage of Koskobilo, recovered by Ruiz de Gaona, Barandiarán, and ourselves, reinforces the interpretation of different occupation episodes at the site(s). The presence of a handaxe and other large cutting tools, now lost, suggests the existence of Middle Pleistocene Middle Paleolithic occupations at Koskobilo, while there are other lithics that can be attributed to a generic Middle Paleolithic. Other pieces, like carinated end-scrapers, backed points, and some characteristic burin types, such as Noailles burins, suggest a human presence in Koskobilo during the Early Upper Paleolithic. The bulk of

the lithic collection can be attributed to the Solutrean. The presence of almost finished foliate points, foliate point roughouts, and many waste products generated during the foliate fabrication process, suggest the presence of a solutrean flint workshop at the site. Finally there are some elements that can be attributed to the Final Upper Magdalenian/Azilian (Arlegi et al., 2018 and references therein).

2. Material and methods

2.1. Material

The Koskobilo paleontological collection is currently divided among three different institutions. Most of the paleontological remains ($n = 680$) are housed at the Museo de Navarra (Pamplona-Iruñea), with smaller samples at the Sociedad de Ciencias Aranzadi (Donostia-San Sebastián; $n = 32$), and at the Museo Nacional de Ciencias Naturales (MNCN, Madrid; $n = 9$). The latter sample is probably part of the original collection studied by Federico Gómez Lluca (Ruiz de Gaona, 1941) that was never returned to Navarre. The Museo de Navarra sample does not have an official label, so we have “virtually” labeled all the specimens using numbers. The small paleontological sample housed at the S.C. Aranzadi was collected by J.M. de Barandiarán in 1955 (Beguiristain Gúrpide, 1974); it was given to the paleontologist J. Altuna, who never actually studied this sample (Altuna, personal communication). The 134 remains recently found by us (Arlegi et al., 2018) are not included in this study, but we nonetheless discuss them. Many collections have been visited to examine comparative materials (see Supplementary Text S1, Supplementary Tables S1–S2).

2.2. Paleobiological analysis

The taxonomic assessment was conducted using both modern and fossil samples housed in different research centers as well as osteological atlases. Upper teeth are indicated by uppercase letters, lower teeth by lowercase. To distinguish between *Canis* and *Cuon* the morphometric differences between these two genera present in the dentition and in the mandibular morphology have been taken into consideration based on published reports of Middle and Late Pleistocene wolves and dholes from France and the Iberian Peninsula (e.g., Altuna, 1972, 1983; Sarrión Montañana, 1984, 1990; García, 2003; Boudadi-Maligne, 2010; Pérez Ripoll et al., 2010). The canid remains were also compared to *Canis mosbachensis* and to fossils attributed to *Lycaon* (Madurell-Malapeira et al., 2013; Bartolini Lucenti et al., 2017). None of the diagnostic features found in the latter genus were found in the Koskobilo canid assemblage (see Supplementary Text S2). The identification criteria and the metrics considered during small-mammal analysis were based on Crusafont and Villalta (1948), Chaline (1972), Nadachowski (1982), Menu and Popelard (1987), Cuenca-Bescós (1988), Sevilla (1988), van Cleef Roders and van den Hoek Ostende (2001), and López-García (2011). Various keys were used for taxonomic identification of the birds (Woolfenden, 1961; Kraft, 1972; Jánossy, 1983; Cohen and Serjeantson, 1996; Tomek and Bochenki, 2000; Bochenki and Tomek, 2009). For the analysis of the paleontological record of the avian species, the works of Mlíkovský (2002) and Tyberg (2007) were used.

The biometrical assessment generally follows the standard approaches (Driesch, 1976). The measurements of the Rhinocerotidae and Suidae fossils were taken following Van der Made (1996, 2010). Measurements of the fossils of *Megaceroides* follow Van der Made (2019). Nomenclature of the tooth morphology in the descriptions of the Suidae, *Cervus elaphus* and *Megaceroides* follow Van der Made (1996, 2019). In the case of the human remains, the anatomical variables studied in the present work are linear measurements employed in other studies of foot remains, largely following the Martin system (Bräuer, 1988; but see also Trinkaus, 1975, 1983, 2016; Pablos et al., 2012, 2013a, 2014). The metrical variables were selected in order to describe the general morphology and articular size of each bone, some of which

allow the differentiation of Neandertal pedal remains from other samples. The *Lyrurus tetrax* remains were measured following Erbersdobler (1968).

In order to offer some insights into the paleobiology of the Koskobilu human foot bones (Supplementary Text S3) we tried to determine the sex using the multivariate formulae offered by Alonso-

Llamazares and Pablos (2019) using both talar and calcaneal variables. Stature was estimated using European male formulae based on both the talus and the calcaneus (Pablos et al., 2013b). Body mass was estimated based on the medio-lateral breadth (M5) of the trochlea of the talus, using the regression formula derived from a recent human sample (McHenry, 1992).

Table 2
Composition of the Koskobilu faunal assemblage.

Taxa	NISP			MNI	
	Museo Navarra	Aranzadi	MNCN	Total	
Mammalia indet.	86	22		108	–
<i>Equus ferus</i>	42		1	43	4
<i>Stephanorhinus hemitoechus</i>	22		3	25	3
Artiodactyla indet.	2	3		5	–
<i>Sus scrofa</i>	11			11	3 + 1 modern
Cervidae indet. + <i>Cervus/Megaceroides</i>	9			9	–
<i>Capreolus capreolus</i>	22			22	3
<i>Cervus elaphus</i> spp.	13			13	2
cf. <i>Megaceroides</i>	12			12	4
Caprinae indet.	2			2	–
<i>Capra</i> sp.	21			21	3
<i>Rupicapra</i> sp.	50			50	6
<i>Bos/Bison</i>	52	4	1	57	4
Carnivora indet.	9			9	–
<i>Felis silvestris</i> + <i>Felis</i> sp.	6			6	1 + 1 modern
<i>Panthera pardus</i>	1			1	1
<i>Panthera spelaea</i>	2			2	2
<i>Crocuta</i> sp.	2			2	1
<i>Vulpes vulpes</i>	16			16	3
<i>Canis/Cuon</i>	7			7	–
<i>Cuon</i> sp./ <i>Cuon</i> cf. <i>priscus</i>	3			3	3
<i>Cuon</i> cf. <i>alpinus europaeus</i>	2			2	1
<i>Canis</i> sp.	4			4	1
<i>Canis</i> cf. <i>lupus</i>	2			2	3
<i>Ursus</i> sp.	39	1		40	–
<i>Ursus arctos</i>	12			12	2
<i>Ursus</i> cf. <i>deningeri</i>	1			1	1
<i>Ursus deningeri/Ursus spelaeus</i>	5			4	1
<i>Ursus spelaeus</i>	31			31	4
<i>Ursus thibetanus</i>	2			2	1
<i>Meles meles</i>	2			2	2 modern
<i>Mustela nivalis</i>	9			9	6
<i>Talpa</i> sp.	18			18	6
cf. <i>Erinaceus</i>	1			1	1
Chiroptera indet.	1			1	1
<i>Myotis myotis</i>	4			4	2
<i>Miniopterus schreibersii</i>	1			1	1
Rodentia indet.	71			71	–
<i>Rattus</i> sp.	3			3	1 modern
Arvicolidae indet.	3			3	–
<i>Arvicola</i> sp.	1			1	–
<i>Arvicola amphibius</i>	15		1	16	7
<i>Microtus arvalis</i>	2			2	1
<i>Microtus agrestis</i>	2		1	3	2
<i>Microtus (Terricola)</i> cf. <i>lusitanicus</i>			1	1	1
<i>Plomys coronensis</i>	3		1	4	2
<i>Marmota marmota</i>	22			22	4
<i>Castor fiber</i>	5	1		6	2
Lagomorpha indet.	1			1	1
<i>Homo sapiens</i>	3			3	1
<i>Macaca sylvanus</i>	1			1	1
Aves indet.	12				–
Columbiformes indet.	1				–
<i>Columba livia/oenas</i>	1				1
<i>Lyrurus tetrax</i>	3				1
<i>Lagopus muta</i>	1				1
<i>Perdix perdix</i>	1				1
Passeriformes indet.	2				–
Alaudidae indet.	1				1
Corvidae indet.	3				–
<i>Pyrrhocorax pyrrhocorax</i>	2				1
Actinopterygii indet.	3			3	1

NISP = Number of identified specimens. MNI = Minimum number of individuals.

2.3. Taphonomic analysis

The taphonomic analysis of the assemblage was done using standardized methods and techniques reported elsewhere (Lyman, 1994). Three hundred ninety-four specimens (NSP) were studied. The bone cortical surface is well preserved, which allowed us to analyze the potential modifications present on its surfaces. All the remains were studied using a binocular microscope (x20) and hand-lenses (x4), using oblique light (Blumenschine et al., 1996). Additional observations on the small-mammal assemblage were done following Andrews (1990).

2.4. Uranium series dating

A speleothem crust covering a *Stephanorhinus hemitoechus* left p3 (specimen number 50 of our catalogue; henceforth just the number will be given) was dated. In order to eliminate the potential contamination by the surrounding clays and to better visualize the internal structure of the carbonatic crystals, the most external part of the crust was scraped away on the occlusal part of the tooth and also, to a smaller extent, on the lingual part, using a tungsten carbide elongated drill (width = 1 mm) at 17,000 rpm. From the occlusal surface of the tooth a translucent and whitish layer was chosen to be sampled for the U/Th dating (Supplementary Fig. S2). The powder extraction (c. 95 mg; Supplementary Fig. S3) was performed using tungsten carbide drill

burrs (width = 0.5 mm) at 10,000 rpm following the lamination of the speleothem growth. The sampling was done under a laminar flow chamber to avoid contamination and with clean drills (purification using HCl 0.6M and ethanol). The U/Th dating was carried out at the Xi'an Jiaotong University (China) following the methodology of Cheng et al. (2013).

3. Systematic paleontology-Mammals

A total of 694 remains have been identified as mammals, belonging to a total of 8 orders and 22 different families.

3.1 Order Perissodactyla Owen, 1848

Perissodactyls are represented by a total of 68 remains belonging to two families (Table 2). Selected perissodactyl remains are shown in Fig. 2.

3.1.1 Family Equidae Gray, 1821

Equus ferus Boddaert, 1785

Ruiz de Gaona (1941) cited the presence of 52 M and 6 incisors belonging to *Equus caballus fossilis* (Table 1). The current collection is smaller (NISP = 43), with the presence of 10 permanent incisors, a

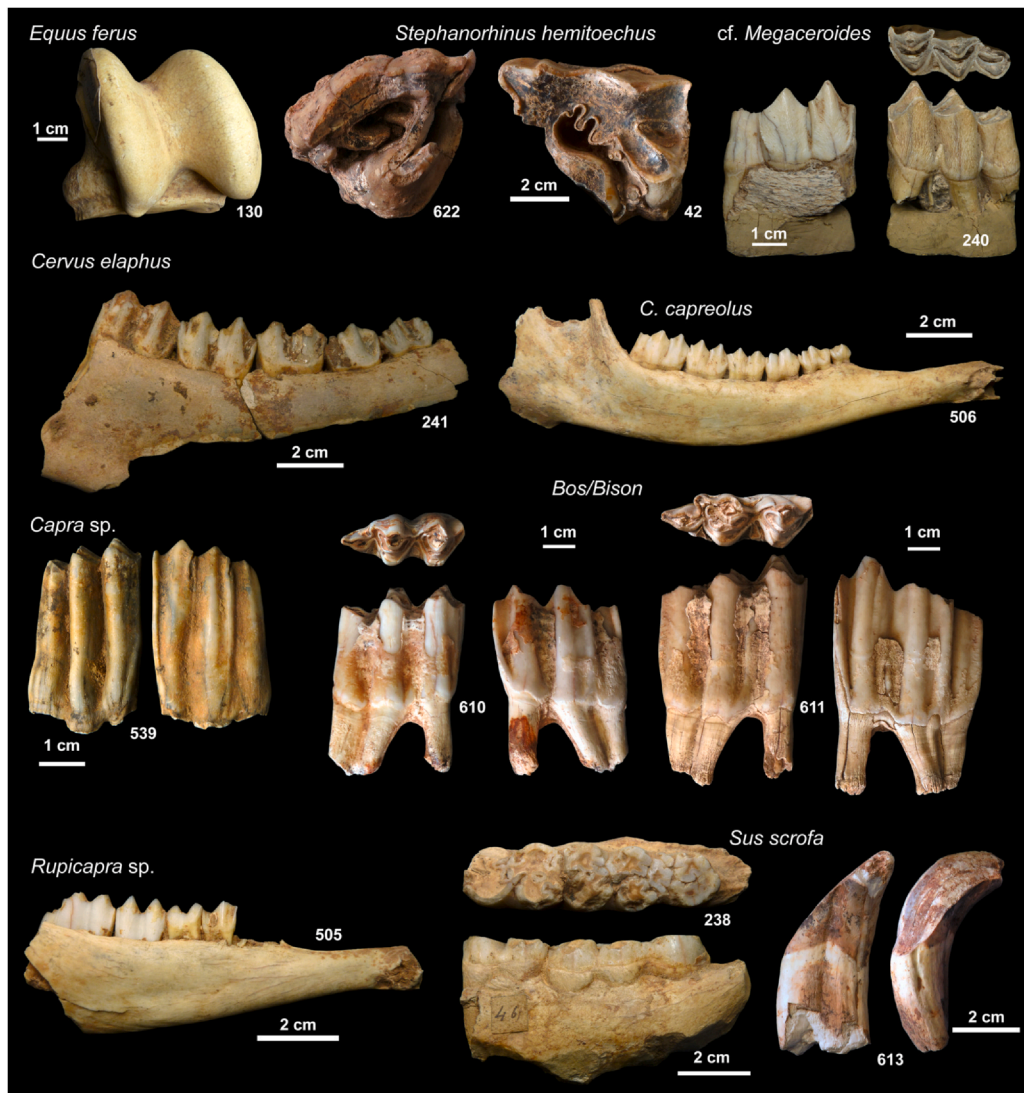


Fig. 2. Selected herbivore remains from Koskobilu. From left to right and from top to bottom: horse (*Equus ferus*) left talus (130) in anterior view; steppe rhinoceros (*Stephanorhinus hemitoechus*) right M3 (622) and left M1-2 (42) in occlusal view; cf. *Megaceroides* left mandibular fragment with m3 (240) in different views; red deer (*Cervus elaphus*) hemimandible fragment preserving the p3-m3 series (241) in lingual view; roe deer (*Capreolus capreolus*) left hemimandible preserving the whole p2-m3 series (506) in lingual view; goat (*Capra sp.*) right m3 (539) in labial (left) and lingual (right) views; two right large bovid (*Bos/Bison sp.*) m3s (610 and 611) in different views; chamois (*Rupicapra sp.*) left hemimandible preserving p4-m3 (505) in lingual view; wild boar (*Sus scrofa*) right hemimandible (238) in occlusal and labial views, and dorsal and anterior views of a right upper canine (613).

deciduous incisor, 28 upper and lower molariforms, one upper canine, a talus (Fig. 2), a calcaneus, and a proximal phalanx. The measurements and morphology of these elements are compatible with *Equus ferus*. These teeth represent a minimum of four individuals, based on the presence of three left i3 and a di2.

3.2 Family Rhinocerotidae Gray, 1821

Stephanorhinus hemitoechus (Falconer, 1860)

The rhinoceros from Koskobillo (Fig. 2, Supplementary Fig. S4) was first assigned to *Rhinoceros megarhinus* (Ruiz de Gaona, 1941, 1952) and later to *Rhinoceros tichorhinus* (= *Coelodonta*) (Ruiz de Gaona, 1958). This assignment to *Coelodonta* was later repeated elsewhere (Altuna, 1972; Arsuaga Ferreras and Aguirre Enríquez, 1979). Guérin (1980) assigned the three teeth from Koskobillo housed at MNCN to

Dicerorhinus hemitoechus, and Cerdeño (1990) and Álvarez-Laó and García (2011) assigned them to *Stephanorhinus hemitoechus*, and we agree with this determination and extend it to the rest of the collection (see below). The Koskobillo collection currently includes 25 rhinoceros remains: a mandibular fragment preserving (partially) three teeth and 24 isolated teeth. Therefore, the collection preserves 10 additional remains above the 15 initially reported by Ruiz de Gaona (1941), which represent a minimum of three individuals: two adults are represented based on the repetition of the left p3 (48 and 50) and p4 (571 and 573) and an immature based on the presence of a d3-4 (576). The speleothem overlying one *Stephanorhinus* specimen (50) has been dated using U/Th, which provides a minimum age for this specimen and hence for part of the deposit. The Koskobillo *Stephanorhinus* measurements are compared in Figs. 3–4 and shown in Supplementary Tables S3–S4.

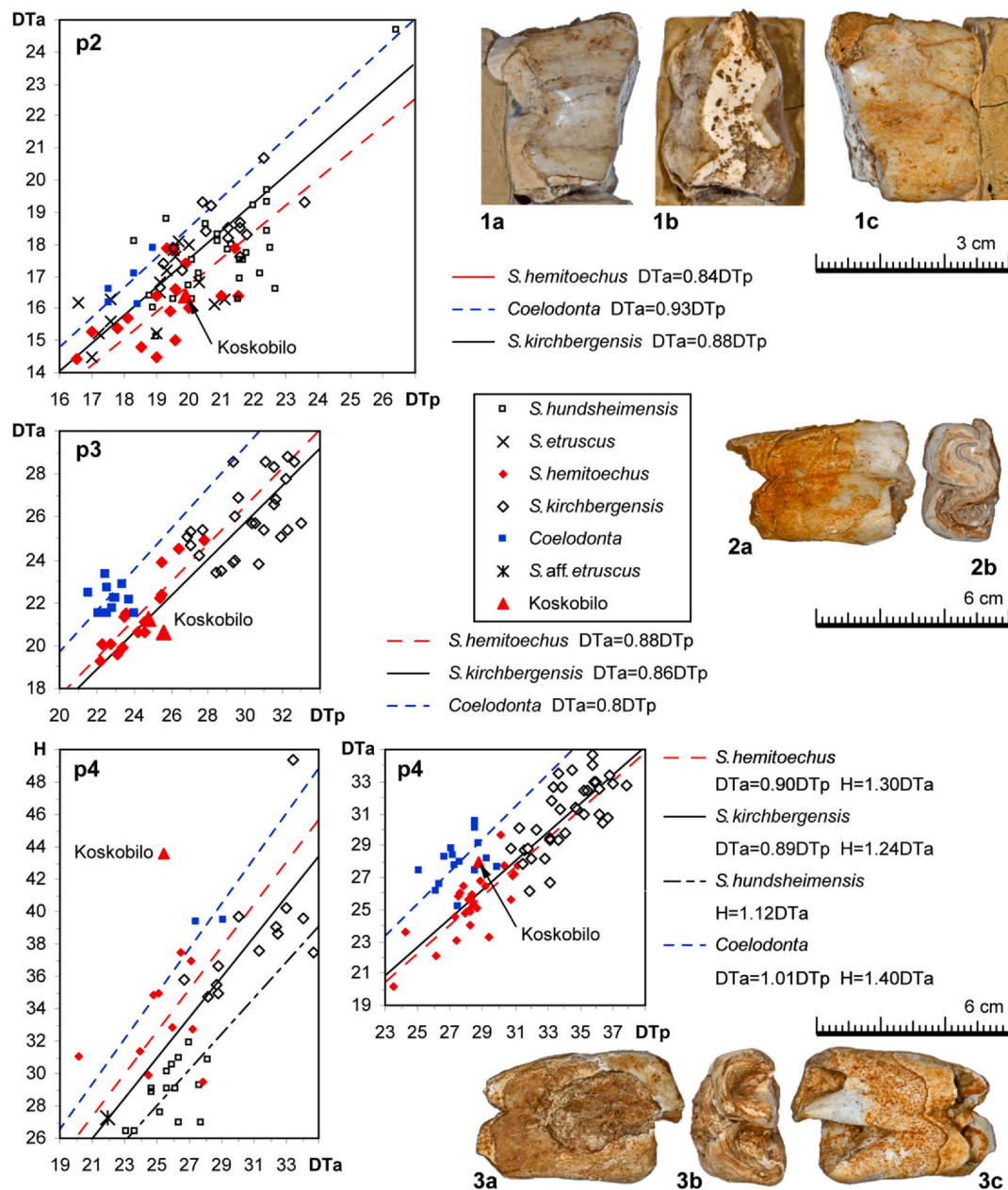


Fig. 3. Comparison (in mm) of the *Stephanorhinus hemitoechus* lower premolars from Koskobillo to other rhinoceros samples. Bivariate plots of the height (H), width of the anterior lobe (DTa) and width of the posterior lobe (DTp) of the p2 (top), p3 (center) and p4 (bottom). Lines indicate average proportions. Provenance of data as indicated in Supplementary Table S1. Specimens: 1) left p2 (575): a) lingual, b) occlusal, and c) buccal views. 2) Left p3 (50): a) buccal, and b) occlusal views (note that this specimen shows a speleothem crust on its labial side; see Supplementary Fig. S3). 3) Left p4 (40): a) buccal, b) occlusal, and lingual views.

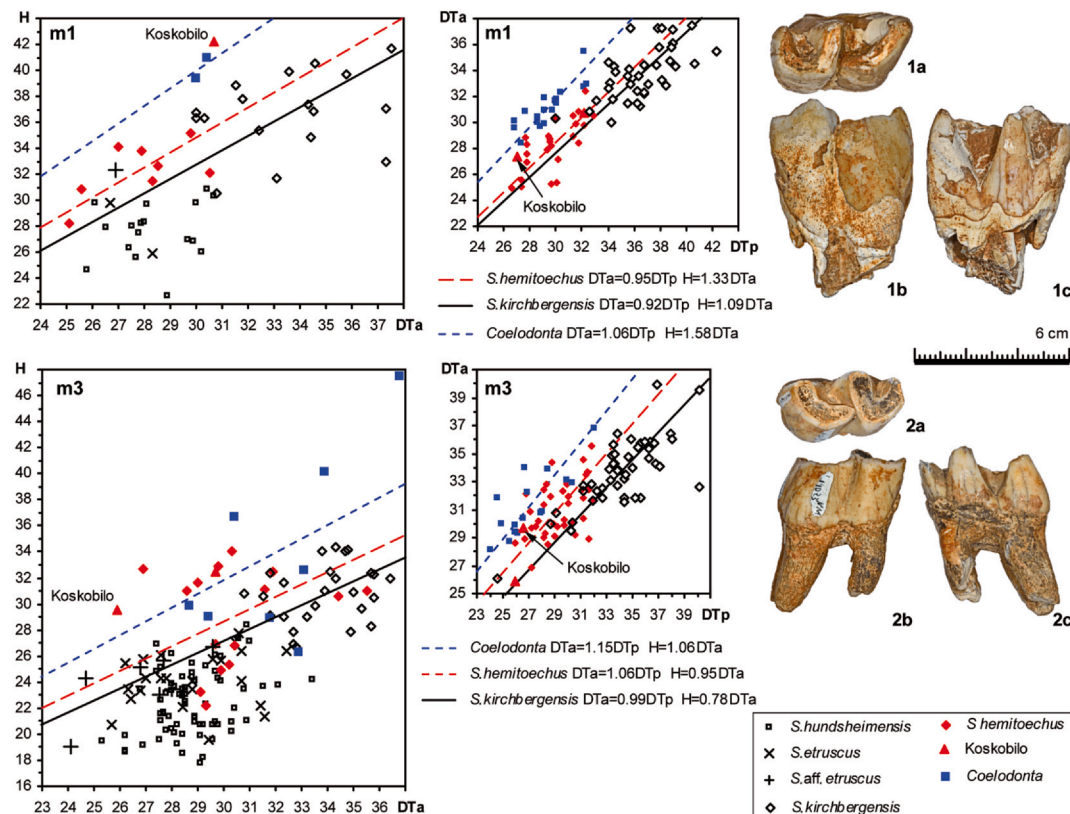


Fig. 4. Comparison (in mm) of the *Stephanorhinus hemitoechus* lower molars from Koskobillo to other rhinoceros samples. Bivariate diagrams of the height (H), width of the anterior lobe (DTa) and width of the posterior lobe (DTp) of the m1 and m3. Lines indicate average proportions. Provenance of data as indicated in [Supplementary Table S1](#). *Stephanorhinus hemitoechus* specimens from Koskobillo: 1) left m1 (40): a) occlusal; b) buccal; and c) lingual views; 2) right m3 (MNCN 46062): a) occlusal; b) buccal; and c) lingual views.

The Koskobillo remains do not belong to the genus *Coelodonta* due to the absence of characteristics typical of this taxon: e.g., a relatively wider (relative to *Stephanorhinus*) anterior lobe of the lower cheek teeth, which are shorter near the base and much longer at the occlusal surface of m1/2 (resulting in very divergent anterior and posterior sides

when regarded lingually), a heavy crenellated enamel, a crochet isolating a middle fossa from the lingual valley in upper teeth, and the presence of a metaloph and hypocone which together with the posterior end of the ectoloph enclose a post fossa in M3. On the other hand, the Koskobillo specimens are not as large as *Stephanorhinus kirchbergensis*,

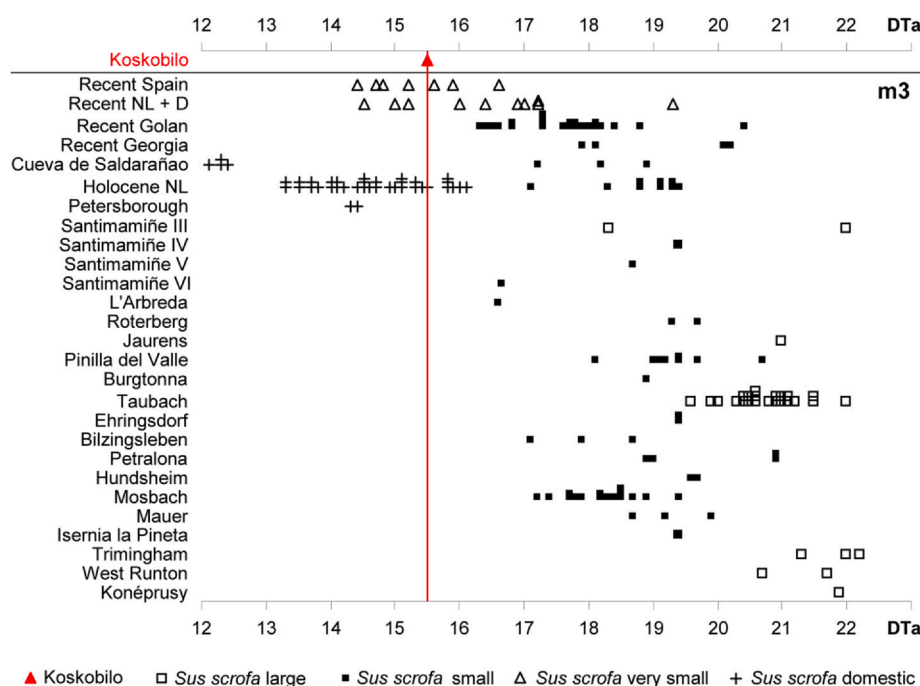


Fig. 5. Comparison (in mm) of the *Sus scrofa* from Koskobillo to other *Sus* samples: size changes, as indicated by the width of the anterior lobe (DTa) of the m3 of wild and domestic *Sus scrofa*. The samples are arranged according to approximate age, old at the bottom and recent at the top. The fossil represented in the bottom of the images is a right mandible fragment preserving the m2-m3 (label: 238). Provenance of data as indicated in [Supplementary Table S1](#). Data for the Santimamiñe sample according to [Castaños \(1986\)](#). Note that the current fossil record from Iberian Peninsula is very limited. NL = Netherlands; D = Germany.

and the m3s do not show a U-shaped posterior valley (in lingual view). We also consider that the Koskobilo specimens do not belong to *S. hundsheimensis* as the P2 may be very large in the latter species. Moreover, the teeth from Koskobilo, not having the *Coelodonta* features, are very hypsodont, consistent with (and even above) *S. hemitoechus*, the most hypsodont species within *Stephanorhinus*, and of course above *S. hundsheimensis*, *S. etruscus* and *S. aff. etruscus*. The Koskobilo specimens being so hypsodont compared to the *S. hemitoechus* (Fig. 4) sample could be due to the low number of *S. hemitoechus* in which hypsodonty could be measured.

3.3 Order Artiodactyla Owen, 1848

The artiodactyls are represented by 202 remains belonging to 7 taxa (Table 2). Selected artiodactyl remains are shown in Fig. 2.

3.3.1 Family Suidae Gray, 1821

Sus scrofa Linnaeus, 1758

The collection currently comprises all the elements listed by Ruiz de Gaona (1941; Table 1) plus a canine previously assigned to *Hippopotamus* sp. (total NISP = 11; Table 1; Fig. 2). They belong to a minimum of two adults (239 and 476) and a younger adult (474) based on the repetition of the left P3. A fragment of left maxilla preserving the M1-M2 (289), not listed previously, is probably recent. All these remains (Supplementary Table S5) fit well within the metric and morphological range of variation of recent and/or Pleistocene *Sus scrofa* and are different from both *S. strozzi* and the domestic pigs (Fig. 5; Supplementary Fig. S5). However, we lack information about the range of variation and any potential size trend in the Pleistocene of Iberia.

3.3.2 Family Cervidae Goldfuss, 1820

Ruiz de Gaona (1941) mentioned the presence of several cervid

fossil remains: 6 belonging to red deer, two antler fragments belonging to roe deer and 13 additional fossils to an indeterminate cervid (Table 1). Apart from the indeterminate cervid remains (NISP = 10), we attribute the cervid fossils to three different taxa: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and a giant deer (cf. *Megaceros*).

Capreolus capreolus (Linnaeus, 1758)

Twenty-two remains have been attributed to roe deer: two antler fragments (listed by Ruiz de Gaona, 1941), a distal phalanx, and 19 maxillary/mandibular fragments and isolated dental remains. We suppose that the complete roe deer mandible (506; Fig. 2) was likely previously classified by Ruiz de Gaona (1941) as one of the two “antilopid” lower jaws (Table 1), although we cannot discount that it could have been added to the collection after his first publication. The roe deer remains from Koskobilo correspond to a minimum of three individuals based on the repetition of the right m3s (248, 253, and 386).

Cervus elaphus Linnaeus, 1758

Thirteen remains have been attributed to red deer, seven more than those listed by Ruiz de Gaona (1941). Most of these remains are mandibular, maxillary and isolated dental remains with the exception of an intermediate phalanx (which could be recent) and an antler fragment with the characteristic bez tine of this species. A minimum of two individuals are represented in the Koskobilo red deer sample, a juvenile known by a left maxilla preserving D3-M1 (494), and an adult hemimandible (241).

Cervus elaphus appeared in western Europe at the end of the Early Pleistocene. It is present at Dorn Dürkheim 3 (Germany; Franzen et al., 2000) and in Atapuerca TD4 to 7 (Van der Made et al., 2017), levels which have reversed polarity and are situated between the Jaramillo and Brunhes-Matuyama boundary (Álvarez-Posada et al., 2018). It is also cited from Mosbach 1, which is situated in the Jaramillo (Von Koenigswald and Tobien, 1987). Initially, the antlers of the adults lacked a crown, but after about 500 ka crowns are known. There are marked size changes as seen in the m3, astragali and phalanges (Van

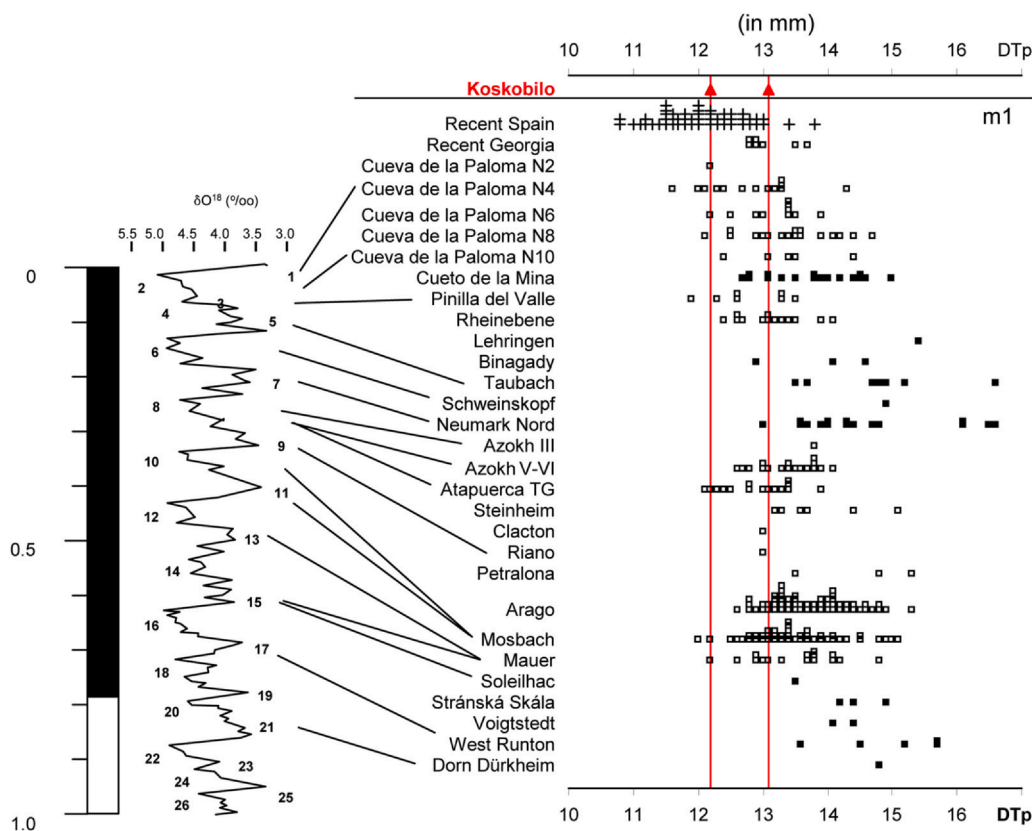


Fig. 6. Size changes (in mm), as indicated by the width of the posterior lobe (DTp) of the m1 of the red deer *Cervus elaphus*. The samples are arranged according to approximate age, with older at the bottom and recent at the top. The two Koskobilo remains (red lines) are consistent with the size present in the c. 300 ka site of Galería (Sierra de Atapuerca), but also with the most recent Late Pleistocene and Holocene Iberian samples. Cueva de la Paloma level 2 is of Early Holocene age. Provenance of data as indicated in Supplementary Table S1.

der Made, 2011; Van der Made et al., 2014). The species was large until about 650 ka, then it became smaller, from MIS 7 to the earlier part of MIS 5 it was large again, and then it was generally smaller, although during MIS 2 it was also larger. During the Holocene it became very small in western Europe but retained its size further to the east. The same size change trends can be observed in the m1 (Fig. 6), despite the limited size of the samples. The two m1s from Koskobilob probably represent different individuals. The smaller of the two is smaller than any specimen of the populations with larger body size, which suggests that at least this individual does not derive from such a population. This specimen and the m3 (Fig. 7) are similar in size to the MIS 8–9 *Cervus elaphus* from Galería (Sierra de Atapuerca), and thus the small *Cervus* from Koskobilob could have been contemporary to the *Megaceroides* and *Stephanorhinus*, but it is also consistent in size with other Late Pleistocene/Holocene samples.

cf. *Megaceroides* Joleaud, 1914

Twelve mandibular fragments and isolated teeth have been assigned to a minimum of four cf. *Megaceroides* individuals based on the

repetition of the left m3 belonging to three young adult individuals (Figs. 2 and 7) and a fourth individual (M3, 493; Fig. 8), with a greater degree of wear. The identification is based on four different criteria. First, a relatively wide mandible (243) when compared to the teeth (i.e., pachystosis) which is a common feature of giant deers (*Megaloceros*, *Megaceroides*, etc.), while *Cervus elaphus* has normal narrow mandibles (Fig. 7). Second, unlike *Cervus*, all the m3s attributed to *Megaceroides* (240, 243, and 252; Figs. 2 and 7), have the lingual wall of the third lobe placed clearly more buccally than the lingual wall of the first and second lobes, the back of the anterior fossid is open towards the lingual side, and there is no connection between the proto-postcrisid and meta-postcrisid or metaendocrisid. Moreover, the three specimens are smaller than *Megaloceros giganteus* m3s, but fit exactly in the range of variation of *Megaceroides* specimens (Fig. 7), and are larger than their homologues in *Megaloceros savini*, *M. matritensis*, *Cervus* or *Dama* and *Haploidoceros* (the latter being close in size to *Cervus* and *Dama*). Fourth, the m3s (Figs. 2 and 7) differ from those of *Alces* in having a higher crown and lack the typical morphology of this taxon,

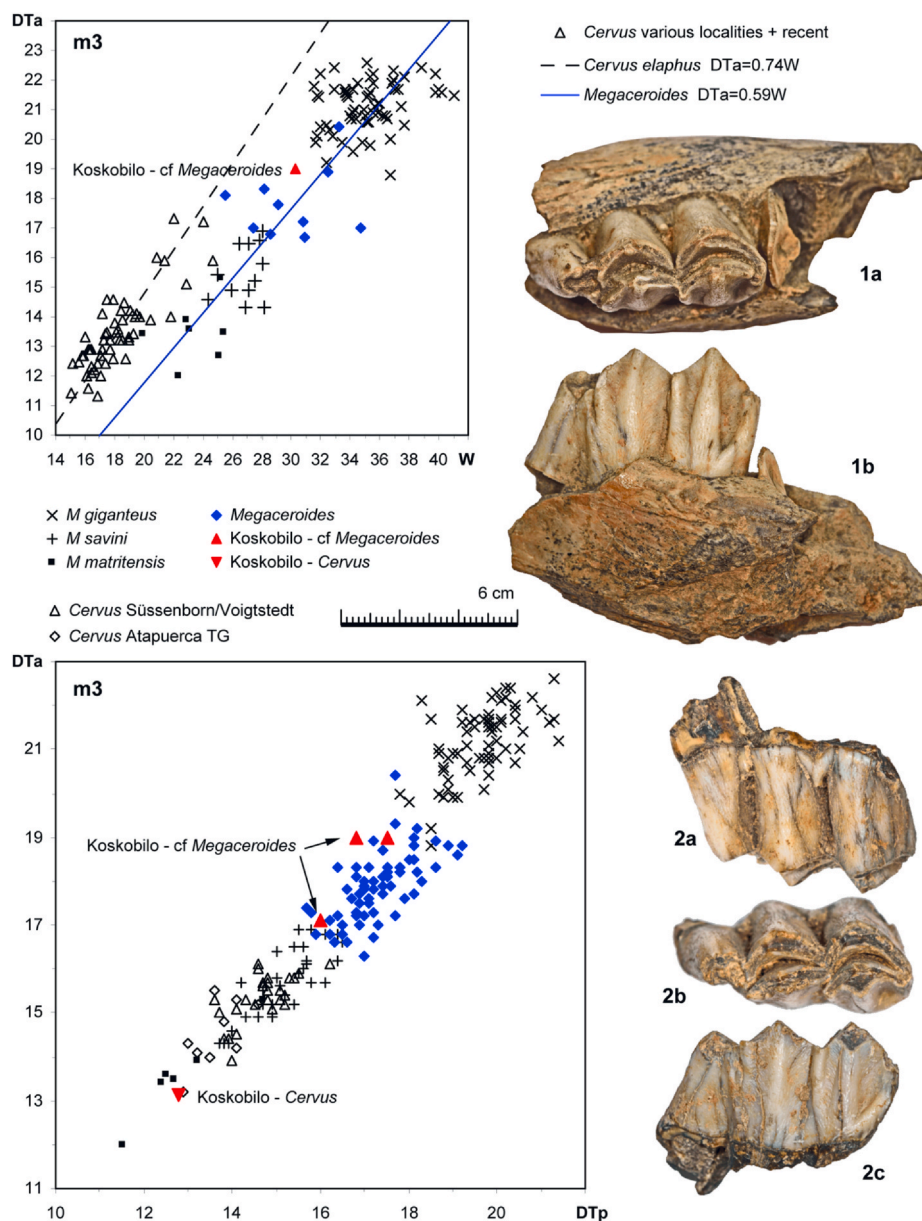


Fig. 7. Comparison of the cf. *Megaceroides* m3 and mandibular fragments from Koskobilob to other cervid samples: left m3 in a mandible fragment (243): a) occlusal, and b) lingual views; 2) left m3 (252): a) buccal, b) occlusal, and c) lingual views. Bivariate diagrams of the width of the anterior and posterior lobes of the m3 (DTa and DTp, respectively) and width of the mandible below the M3 (W). Lines indicate average proportions. Provenance of data as indicated in [Supplementary Table S1](#).

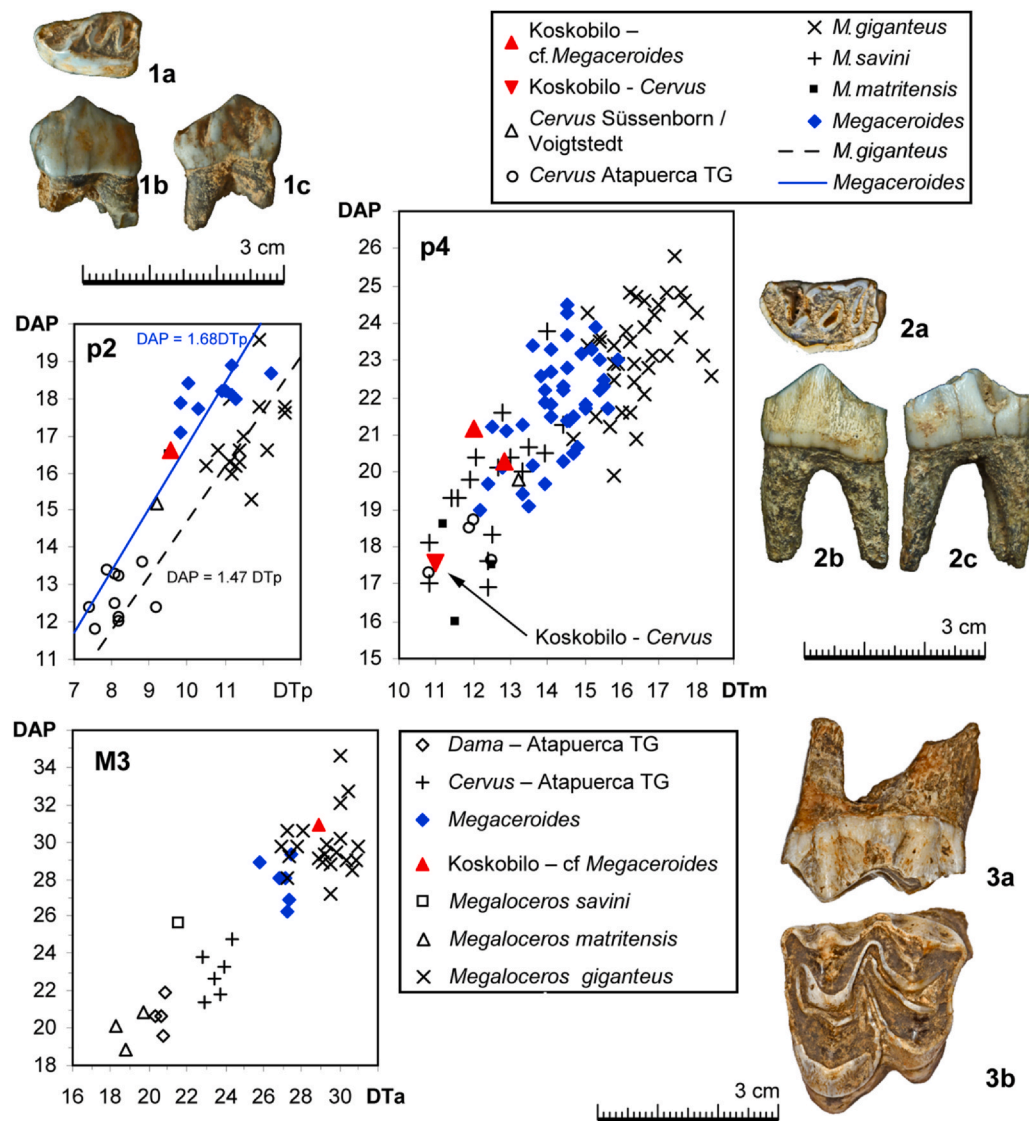


Fig. 8. Comparison of the cf. *Megaceroides* lower premolars and M3 from Koskobillo to other cervid samples. Bivariate diagrams of the length (DAP) and width of the anterior (DT) or posterior lobe (DTp) of the M3, p2 and p4. Lines indicate average proportions. Provenance of data as indicated in [Supplementary Table S1](#). Specimens: 1) left p2 (68): a) occlusal b) buccal, and c) lingual views; 2) left p4 (70): a) occlusal, b) buccal, and c) lingual views; 3) left M3 (493): a) buccal, and b) occlusal views.

such as a well-developed lingual cusp in the third lobe (hexaconid). Several other molars and premolars also fit within the *Megaceroides* range of variation ([Fig. 8](#), [Supplementary Table S6](#)).

3.3.3 Family Bovidae Gray, 1821

[Ruiz de Gaona \(1941\)](#) recognized the presence of both Caprini and Bovini. With regards to caprins, he attributed two lower jaws and some isolated dental remains to an “antilopid” and a horn fragment to wild goat. He also recognized the presence of two different large bovids: *Bos curvidens*, with a large number of specimens, and an unknown number of specimens attributed to *Bison* sp. We recognize the presence of wild goat (*Capra* sp.), chamois (*Rupicapra* sp.), and large bovids ([Fig. 2](#)).

Genus *Capra* Linnaeus, 1758

Capra sp.

The horn fragment attributed by [Ruiz de Gaona \(1941\)](#) to a wild goat actually belonged to a red deer. Currently, 21 dental remains have been assigned to *Capra* sp. ([Fig. 2](#)) representing at least two adult individuals based on the presence of two left M2s (367 and 369) and two right m3s (373 and 539), and an immature individual based on the

presence of a right (503) and a left dp4 (454).

Genus *Rupicapra* Blainville, 1816

Rupicapra sp.

[Ruiz de Gaona \(1941\)](#) cited the presence of two mandibles and some isolated molars and incisors belonging to “an antilopid”. A total of 50 remains have been assigned to chamois representing a minimum of 6 individuals ([Fig. 2](#)) based on the repetition of the left m3 (295, 371, 381, 451, 502, and 505). Except for an intermediate phalanx, the rest are cranio-mandibular/dental remains, mostly isolated teeth.

Genus *Bos* Linnaeus, 1758

Genus *Bison* Hamilton Smith, 1827

Bos/Bison.

While [Ruiz de Gaona \(1941\)](#) proposed the presence of two large bovid species, *Bos curvidens* and bison, the difficulties of distinguishing between these two taxa, and the diachrony of the deposit has led us to classify all the large bovid remains as *Bos/Bison* sp. The large bovid assemblage is composed of 56 isolated dental remains and an intermediate phalanx belonging to a (conservative) minimum of four individuals of different ages-at-death based on the presence of eight m1-2s.

3.4 Order Carnivora Bowdich, 1821

A total of 156 remains have been attributed to the Order Carnivora, with 5 families represented (Table 2; Figs. 9–11).

3.4.1 Family Felidae Fischer von Waldheim, 1817

Genus *Felis* Linnaeus, 1758

Felis silvestris Schreber, 1777

Felis sp.

Ruiz de Gaona (1941) cited the presence of three mandibles and some isolated canines belonging to *Felis catus*. The current collection preserves two hemimandibles, probably belonging to the same individual (Fig. 9), a nearly complete canine, a fibular fragment and a proximal phalanx identified as *Felis silvestris*. Additionally, the collection includes a cat cranium belonging to an immature individual (*Felis* sp.; Supplementary Fig. S6) which is recent and was not mentioned by Ruiz de Gaona (1941).

Genus *Panthera* Oken, 1816

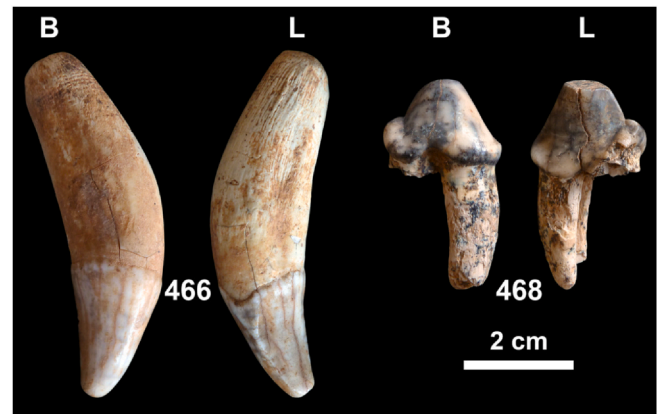


Fig. 10. Spotted hyena (*Crocuta* sp.) remains from Koskobillo: upper right canine (466) in buccal (B) and lingual (L) views; p3 (468) in buccal (B) and lingual (L) views.

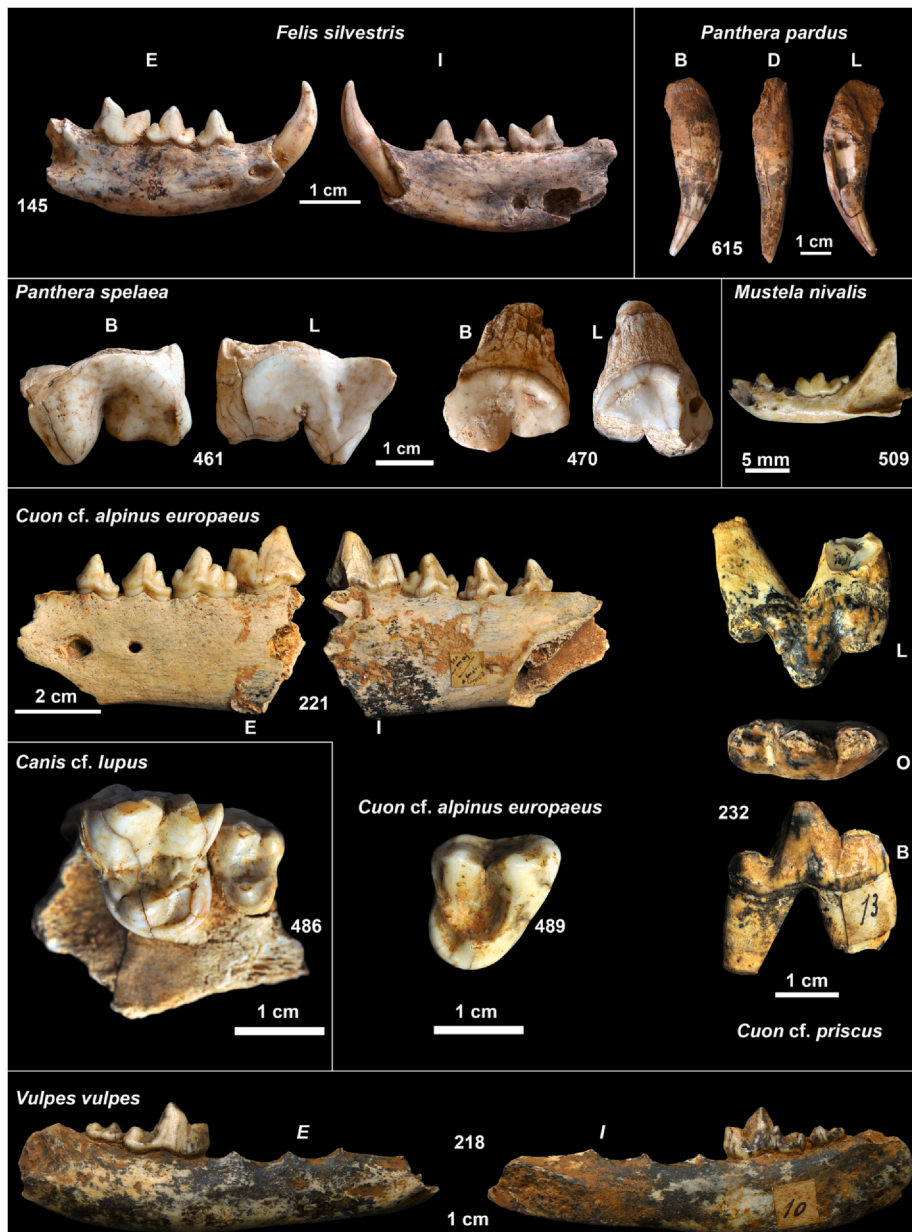


Fig. 9. Selected felid, mustelid, and canid remains from Koskobillo. From left to right and from top to bottom: right hemimandible (145) of wild cat (*Felis silvestris*) in external (E) and internal (I) views; right upper canine (615) of leopard (*Panthera pardus*) in buccal (B), distal (D) and lingual (L) views; two left P4s (461 and 470) of *Panthera spelaea* in buccal (B) and lingual (L) views; left *Mustela nivalis* hemimandible preserving p3, m1-2 (509) in buccal view; different dhole remains: left hemimandible preserving p2-m1 (221) attributed to *Cuon* cf. *alpinus* europaeus, right m1 (232) attributed to *Cuon* cf. *priscus* in lingual (L), occlusal (O) and buccal (B) views, and right M1 (489) attributed to *Cuon* cf. *alpinus europaeus* in occlusal view; left maxilla preserving the M1-M2 (486) of a wolf (*Canis* cf. *lupus*) in occlusal view; right hemimandible (218) of a fox (*Vulpes vulpes*) in external (E) and internal (I) views.

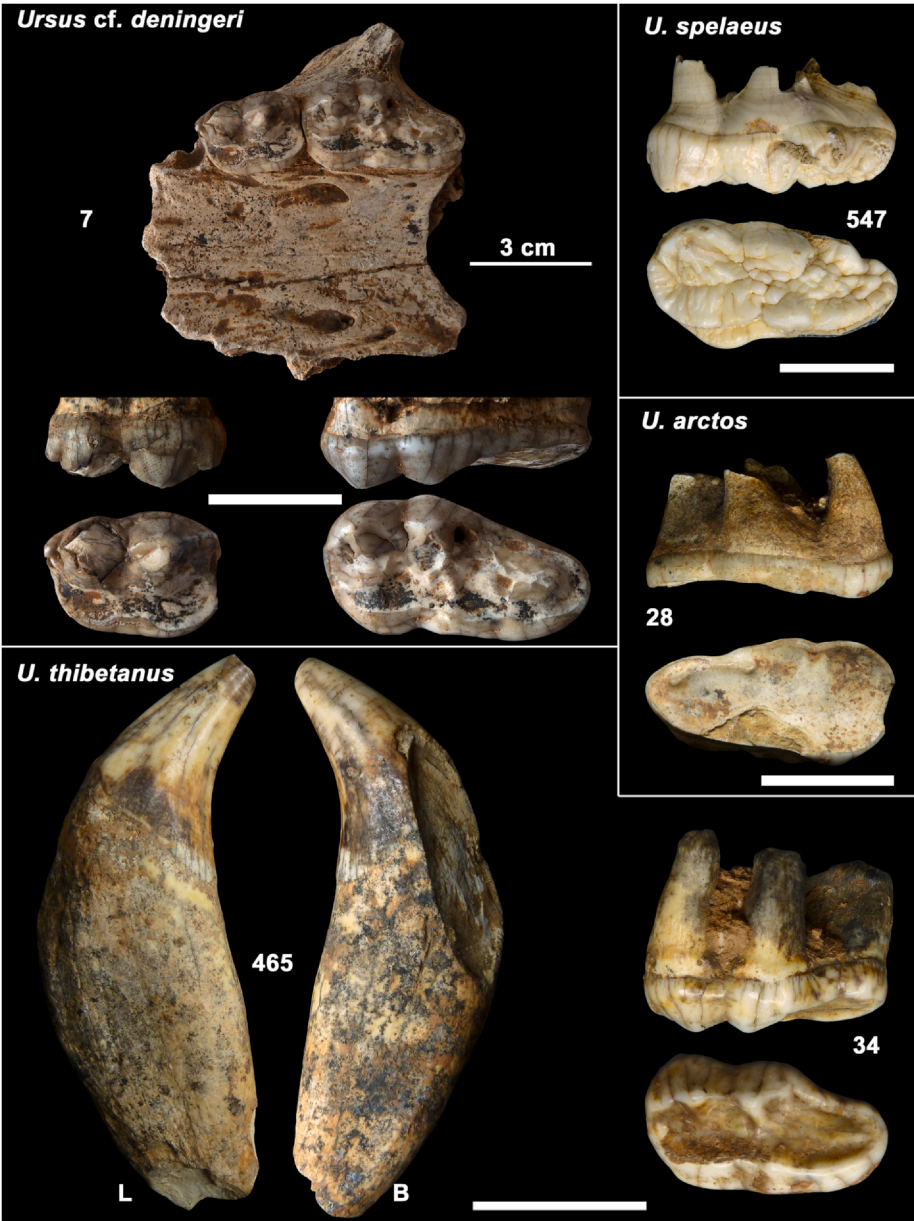


Fig. 11. Selected bear remains from Koskobilo. Deninger's bear (*Ursus cf. deningeri*): incomplete maxilla and nasal bones (not shown) preserving the left M1-M2 (7) in occlusal view; both teeth are shown in more detail in buccal (top) and occlusal (bottom) views. Brown bear (*Ursus arctos*): right M2 (28) in buccal (top) and occlusal (bottom) views. Asian black bear (*Ursus thibetanus*): lower right canine (465) in labial (L) and buccal (B) views, and left M2 (34) in buccal (top) and occlusal (bottom) views. Scale bars = 2 cm, unless otherwise indicated.

Panthera pardus (Linnaeus, 1758)
The leopard is represented by a single upper right canine (Fig. 9). The measurements of this specimen fit well with other Iberian leopards (Table 3).
Panthera spelaea Goldfuss, 1810
The cave lion is represented by two fragmentary left P4s, corresponding to two adult individuals of different age-at-death based on the

degree of wear (Fig. 9). These two remains were likely attributed to hyaena by Ruiz de Gaona (1941), however their size and morphology are those of a lion.

3.4.2 Family Hyaenidae Gray, 1821

Genus *Crocota* Kaup, 1828

Table 3
Measurements (in mm) of the upper canine (C) of leopard (*Panthera pardus*) from Koskobilo and other individuals from the Iberian Peninsula used as comparative sample in this study.

Site/Sample/	Chronology	L	W	Reference
Koskobilo	Late Middle or Late Pleistocene	12.8	10.5	This study
Iberian sites	Late Middle and Late Pleistocene	13.53 ± 0.92 (12.10–14.7) n = 12	10.98 ± 1.15 (9.3–12.7) n = 12	Supplementary Table S7 and references therein

L = length; W = width.

Crocota sp.

Ruiz de Gaona (1941) cited the presence of 12 remains belonging to *Hyaena spelaea*. The spotted hyena is represented by two specimens: an upper right canine and a right p3 (Fig. 10; Table 4), both of which are within the range of variation of the Iberian spotted hyenas and below the range of a relatively large sample of European *Pachycrocota brevirostris*. The carnassials attributed to this taxon by Ruiz de Gaona (1941) have been reidentified as belonging to *Panthera spelaea*. Moreover, the permanent exposition of the Museo de Navarra had some bear distal phalanges also identified as belonging to hyena (Arlegi et al., 2018). We do not rule out that the other remains identified by Ruiz de Gaona (1941) as hyena were either misidentified or are currently lost.

3.4.3 Family Canidae Fischer von Waldheim, 1817

Genus *Canis* Linnaeus, 1758*Canis* cf. *lupus* Linnaeus, 1758*Canis* sp.

Six fossil remains are identified as belonging to genus *Canis* based on their morphology and size greater than those of fossil *Cuon*. Additionally, they are larger and morphologically different from *Canis mosbachensis* (Tables 5–6). A left maxilla fragment preserving M1–M2 (486; Fig. 9) is identified as belonging to an adult individual of *Canis* cf. *lupus*. A second older *Canis* cf. *lupus* adult would be represented by a left M1 (485). The remaining four fossils are identified as *Canis* sp., and one of them represents an additional individual: based on both size and shape, the morphology of the right M1 487 does not correspond to either 485 or 486. Finally, a left hemimandible fragment preserving p3–p4 (222), and two isolated upper premolars are also present in the collection (216: P3; 224: P2). Metrically, all these remains fit within modern *Canis lupus* variation (Tables 5–6) and are larger than all the known Iberian *Cuon* records.

Cuon Hodgson, 1838*Cuon* cf. *priscus* Thenius, 1954*Cuon* cf. *alpinus europaeus* (Bourguignat, 1868)*Cuon* sp.

Five remains have been attributed to genus *Cuon*. Based on the current knowledge of this genus in the Iberian Peninsula, a tentative identification is proposed here: three of them (MNI = 3) could belong to Middle Pleistocene populations, while the remaining two remains (MNI = 1) show Late Pleistocene characteristics.

The Late Pleistocene dhole populations, assigned to either *Cuon alpinus* or *C. alpinus europaeus*, depending on the author and site, show smaller teeth with more derived traits that are normally related to a higher degree of hypercarnivorism: a reduced metaconid and narrower

m1 talonids, and simpler m2. Two remains from Koskobilo have been identified within this group attributed to a single *Cuon* cf. *alpinus europaeus* individual: a left hemimandible preserving the dental series p2–m1 (221; Fig. 9) and a right M1 (489). The M1 shows the typical characteristics of *Cuon* and a size similar to the specimens from Obarreta, Zafarraya (Table 7) and Llonin (Asturias; Sanchis et al., 2020). The hemimandible presents small premolars with pointed cuspids and the anterior denticle on p4 (typical of Late Pleistocene dholes, and variable in Middle Pleistocene dholes) (Table 8).

The dhole assemblage assigned to the Middle Pleistocene comprises a mandibular fragment (229, *Cuon* sp.) preserving the distal half of the m1, the alveolus for the m2 and the ramus nearly complete, and two right m1: one preserving the mesial half (230, *Cuon* sp.), and one preserving the complete crown and very complete roots (232, *Cuon* cf. *priscus*). The mandible is robust (body height behind the m1), and shows some archaic features such as a m2 with two roots and the development of the metaconid. The measurements of the m1 are close to the Middle Pleistocene dhole from Cova Negra recently identified as *Cuon* cf. *priscus* (Table 8; Sanchis et al., 2020). Two of these fossils (229, 230) are assigned to *Cuon* sp. due to their incompleteness.

Vulpes vulpes (Linnaeus, 1758)

Sixteen fossil remains, comprising isolated teeth ($n = 9$), hemimandibles ($n = 5$), a maxilla and a proximal phalanx have been attributed to the red fox (Fig. 9). A minimum of 3 individuals have been estimated based on the repetition of the left hemimandible. One of the mandibles was directly labeled as belonging to a dog by Ruiz de Gaona. Metrically, the *Vulpes* remains from Koskobilo fit within the range of variation of Middle Pleistocene and recent *V. vulpes* and are larger than recent *V. lagopus* remains (Supplementary Table S12).

3.4.4 Family Mustelidae Fischer von Waldheim, 1817

Meles meles Linnaeus, 1758

Ruiz de Gaona did not mention the presence of badger remains among the Koskobilo paleontological collection. Currently there are two complete badger crania (including their mandibles in articulation; 8 and 9) of modern aspect in the Koskobilo collection (Supplementary Fig. S6).

Genus *Mustela* Linnaeus, 1758*Mustela nivalis* Linnaeus, 1766

Ruiz de Gaona (1941) mentioned the presence of five more or less complete jaws that he assigned to “*Mustella vulgaris*”. The collection currently includes 9 hemimandibles belonging to a minimum of six individuals based on the repetition of the left hemimandible (507, 508, 509, 512, 513, and 514) that we attribute to *Mustela nivalis* based on

Table 4

Measurements (in mm) of the upper canine (466) and p3 (468) of spotted hyenas (*Crocota* sp.) from Koskobilo compared to other recent and fossil hyena samples.

Site/Sample	Chronology	Upper canine		p3		Reference
		L	W	L	W	
Koskobilo (<i>C. crocuta</i> / <i>C. spelaea</i>)	Late Middle or Late Pleistocene	16.6	13.3	21.0	15.3	This study
Iberian sites (<i>C. crocuta</i> / <i>C. spelaea</i>)	Late Middle and Late Pleistocene	16.8 ± 1.3 (14.4–18.9) $n = 12$	12.9 ± 1.4 (9.1–14.6) $n = 13$	22.5 ± 1.4 (20.0–26.3) $n = 47$	16.2 ± 1.0 (14.4–18.7) $n = 47$	Supplementary Tables S8–S9
Masai Mara (<i>Crocota crocuta</i>)	Recent	15.81 ± 1.28 (13.4–21.0) $n = 34$	11.74 ± 1.03 (9.8–16.2) $n = 34$	20.0 ± 0.68 $n = 37$	13.8 ± 0.73 $n = 37$	García (2003)
<i>Crocota crocuta praespelea</i>				22.9 ± 0.32 $n = 10$	17.6 ± 0.25 $n = 10$	Kurtén and Poulanos (1977)
<i>Crocota crocuta petralonae</i>				22.4 ± 0.41 $n = 4$	17.1 ± 0.54 $n = 4$	Kurtén and Poulanos (1977)
<i>Pachycrocota brevirostris</i> (European sites)	Early and Middle Pleistocene	22.0 ± 1.2 (20.1–24.0) $n = 8$	15.6 ± 0.5 (15.0–16.3) $n = 7$	24.3 ± 1.3 (22.0–27.5) $n = 36$	17.9 ± 0.9 (15.6–19.4) $n = 33$	Supplementary Tables S8–S9

L = length; W = width.

Table 5
Measurements (in mm) of the upper dentition of the *Canis* remains from Koskobillo compared to other samples.

Taxon	Site	Side	Number	P2		P3		M1		M2		Reference
				L	W	L	W	L	W	L	W	
<i>Canis</i> sp.	Koskobillo	Left	224	12.9	5.2							This study
<i>Canis</i> sp.	Koskobillo	Right	216									This study
<i>Canis</i> cf. <i>lupus</i>	Koskobillo	Left	485			14.2	6.5	15.7	18.8			This study
<i>Canis</i> cf. <i>lupus</i>	Koskobillo	Left	486					15.8	17.1			Pérez Ripoll et al. (2010)
<i>Canis</i> <i>lupus</i>	Recent							16.54 ± 1.09 (14.9–19.6)	18.25 ± 1.46 (15.0–20.95)	9.2	12.0	
								n = 23	n = 23	8.7*	13.6*	
<i>Canis mosbachensis</i>	Iberian Peninsula			11.27 ± 0.47 (10.9–11.8)	4.48 ± 0.21 (4.2–4.7)	12.83 ± 0.63 (11.7–13.5)	5.01 ± 0.22 (4.7–5.3)	13.48 ± 0.65 (12.7–14.7)	15.98 ± 0.82 (14.6–17.4)	7.63 ± 0.57 (6.4–8.6)	10.24 ± 1.11 (8.9–12.9)	Supplementary Table S10
				n = 3	n = 4	n = 6	n = 7	n = 15	n = 16	n = 16	n = 16	

L = length; W = width.

*Measurements from individual EBD 15981 (Estación Biológica de Doñana).

size (Fig. 9; Supplementary Table S13).

3.4.5 Family Ursidae Fischer von Waldheim, 1817

Genus *Ursus* Linnaeus, 1758

Ruiz de Gaona (1941) mentioned the presence in Koskobillo of 10 canines and at least 30 M, premolars and incisors belonging to cave bears and an indeterminate number of specimens belonging to an indeterminate ursid (*Ursus* sp.), later identified as *U. arctos* (Ruiz de Gaona, 1958). A total of 91 specimens have now been identified as bears belonging to a minimum of nine individuals. Thirty-nine specimens have been identified as *Ursus* sp. Five specimens (a very complete mandible and four upper teeth) have been classified as belonging to the speleoid clade (*U. deningeri*-*U. spelaeus*) without specifying the species due to the lack of enough information (Supplementary Figs. S7-S11; Supplementary Tables S14-S17).

Ursus arctos Linnaeus, 1758

Twelve remains (nine isolated dental remains, two phalanges and a scapholunate) have been attributed to two different brown bear individuals based on the presence of two M2s with very different degrees of wear (27 and 28; Fig. 11) and two right upper canines (233 and 235). The dental remains are smaller than those from the speleoid lineage (Supplementary Tables S16-S17). The phalanges are within the *U. arctos* variation: medio-laterally narrower at both the proximal end and at the mid-part of the diaphysis, relative to their greatest length. The scapholunate shows a convex anterior border and a pointed posterior end of the palmar protuberance, typical of *U. arctos* and different from *U. spelaeus* (more flattened with a quadrangular protuberance).

Ursus cf. *deningeri* von Reichenau, 1904

This species is represented by a maxilla (7) that preserves the undeformed palate with the left M1-M2 and crushed nasal bones. The teeth are worn on their lingual borders. The M1 displays a trapezoidal shape with rounded borders, and labial and lingual cingula. The parastyle and the metastyle are wide, clearly distinguishable from the paracone and metacone, and are oriented outwards. These are characteristics of speleoid bears that distinguish them from *U. arctos*, where they are oriented vertically and the metastyle might be small or absent (García, 2003). The lingual cusps are worn, but the metacone/mesocone seems to be narrow in comparison to the protocone and hypocone, which is rather common in *U. deningeri* and not a characteristic of *U. spelaeus* (Supplementary Table S18). The M2 shows a wide talon with a rounded tip and a very pronounced sulcus between paracone and metacone, which is a morphology common in speleoid bears, but not uncommon in *U. arctos* (Torres, 1988; García, 2003). The paracone has no parastyle and the metacone is posteriorly worn but seems not to have accessory cusps. Thus, the cusps are less complex than in *U. spelaeus*. The lingual and the internal cusps are worn and cannot be distinguished. Metrically the teeth are similar to and/or fall within the range of variation of the *U. deningeri* from Sima de los Huesos, Santa Isabel de Ranero and Lezetxiki (Iberian Peninsula), and other European sites such as Grotte de la Carrière, Mauér, Mosbach, Jagsthausen and Petralona (Supplementary Table S16; Supplementary Figs. S10-S11). They are also below the mean from Troskaeta, which has yielded a small-sized *U. spelaeus* with an early Late Pleistocene chronology (Torres et al., 1991, 2014). Finally, this maxilla shows a palate thickness at the M2 which is above the range of a *U. arctos* sample and below the range of a *U. spelaeus* sample (Supplementary Table S19).

Ursus spelaeus Rosenmüller, 1794

Thirty-six fossils, mostly cranio-dental remains but including six metapodials and three proximal phalanges, have been attributed to cave bear, representing a minimum of four individuals based on the M2s (35, 500, 544, and 547), due to their morphological and age-at-death incompatibilities. The teeth show speleoid-like features not only in their larger size (Supplementary Tables S16-S17), but also in the multiplication of their cusps (Fig. 11). The metapodials and phalanges are wider relative to their maximum length, which makes them more

Table 6Measurements (in mm) of the lower dentition of the *Canis* remains from Koskobilo compared to other samples.

Taxon	Site	Side	Number	p3		p4		Reference
				L	W	L	W	
<i>Canis</i> sp.	Koskobilo	Left	222	12.9	6.0	15.0	7.1	This study
<i>Canis lupus</i>	Recent			13.5 ± 0.63 (12.4–14.4) <i>n</i> = 12	6.6 ± 0.34 (6.0–7.0) <i>n</i> = 12	15.3 ± 0.53 (14.4–16.3) <i>n</i> = 14	7.6 ± 0.37 (6.9–8.4) <i>n</i> = 14	
<i>Canis mosbachensis</i>	Iberian Peninsula			11.94 ± 1.27 (10.9–14.6) <i>n</i> = 7	5.15 ± 0.91 (4.3–6.9) <i>n</i> = 6	13.53 ± 0.70 (12.4–14.2) <i>n</i> = 7	6.14 ± 0.49 (5.6–7.0) <i>n</i> = 7	

L = length; W = width.

Table 7Measurements (in mm) of the upper dentition of the *Cuon* remains from Koskobilo compared to other samples.

Taxon	Site	Chronology	Side	Label	M1		Reference
					L	W	
<i>Cuon</i> cf. <i>alpinus europaeus</i>	Koskobilo		Right	489	13.1	14.1	This study
<i>Cuon alpinus</i>	Obarreta	LP?			12.6	13.4	
<i>Cuon alpinus europaeus</i>	Zafarraya	LP	Right	91-P7-I3741	12.7	13.9	Geraads (1995)
<i>Cuon alpinus</i>	Galería	MP		ATA1	14.5	14.7	García (2003)
		MP		ATA2	13.9	14.1	García (2003)
<i>Cuon alpinus</i>	Puits de Ronzes				12.7	13.4	García (2003)
<i>Cuon alpinus</i>	Recent				12.53 ± 0.15 (12.4–12.7) <i>n</i> = 6	15.6 ± 0.37 (15.1–16.2) <i>n</i> = 6	Sanchis, own data
					12.84 ± 0.76 (11–13.8) <i>n</i> = 33	13.3 ± 0.6 (12–14.4) <i>n</i> = 33	

L = length; W = width; LP = Late Pleistocene; MP = Middle Pleistocene.

robust than the arctoid species.

Ursus thibetanus Cuvier, 1823

This small sized bear is represented by two specimens: a left M2 (34) and a lower right canine (465; Fig. 11). Apart from its size, the M2 displays several morphological features consistent with other European *U. thibetanus* and different from speleoid species and *U. arctos* (Supplementary Fig. S12). The M2 shows a small-sized talon with an acute tip shape, and unlike speleoid species, it shows a low number of internal cusps, contrary to what is seen in *U. arctos* and in cave bears. The cusps have a low height and are oriented toward the internal surface of the crown (Crégut-Bonnouire, 1997). The paracone has no parastyle as in 88.46% of extant and fossil *U. thibetanus* (*n* = 26), 85.96% of a large sample of Pleistocene, Holocene and extant *U. arctos* (Regourdou and Sima de Illobi; *n* = 57) but only 25.8% of a large sample of *U. deningeri* (Santa Isabel de Ranero, Lezetxiki, La Romieu, Mauer and Jagsthausen; *n* = 31). The metacone is simple and in lingual view has almost the same height as the paracone, as in 64% of *U. thibetanus* (*n* = 25), 27.27% of *U. arctos* (*n* = 55), and 12.12% of *U. deningeri* (*n* = 33). The protocone and hypocone are simple and form a thin continuous ridge (Crégut-Bonnouire, 1997), the hypocone is small and subtle, and there is no post-hypocone. This pattern appears in 77.77% of *U. thibetanus* (*n* = 18) but only in 24.32% of *U. arctos* (*n* = 37) from the mentioned sites and it is not observed in *U. deningeri* (*n* = 23). However, in both the arctoid and speleoid species the hypocone is usually more differentiated and there might be multiple cuspids and/or the presence of a post-hypocone. Metrically the Koskobilo M2 is similar to the Middle Pleistocene specimen from Gajtan (Albania; Supplementary Table S20) and within the known range of variation for European *U. thibetanus* (Table 9). The lower canine shows the typical bear morphology and a very small size, similar to one specimen from Mosbach and one individual from Ehringsdorf (Supplementary Table S21) and in the lower range of the known fossil record for Europe and Western Asia (Table 9).

3.5 Order Eulipotyphla

3.5.1 Family Talpidae Fischer von Waldheim, 1817

Talpa sp.

Eighteen remains (seven hemimandibles, seven humeri, three ulnae, a tibiofibula) have been assigned to moles (Fig. 12), representing a minimum of six individuals (six left humeri). During the Late Pleistocene (and still today), two species of *Talpa* can be found in the Iberian Peninsula: the smaller Iberian mole (*T. occidentalis*) and the European mole (*T. europaea*). The best character to distinguish between these two species is the width of the humeral diaphysis (López-García, 2011). The measurements of the Koskobilo sample are in the overlap zone between these two species, but closer to the *T. europaea* measurements. Three of the mandibles show evidence of strong digestion which would indicate that these remains were accumulated either by a diurnal raptor or a small carnivore.

3.5.2 Family Erinaceidae Fischer von Waldheim, 1817

cf. *Erinaceus* Linnaeus, 1758

We have attributed the distal fragment of a humerus preserving the distal articulation to a hedgehog (Fig. 12).

3.6 Order Chiroptera Blumenbach, 1779

Bats are represented by five remains belonging to two vespertilionoid species.

3.6.1 Superfamily Vespertilionoidea Gray, 1821

Family Vespertilionidae Gray, 1821

Myotis myotis (Borkhausen, 1797)

Three hemimandibles and a distal fragment of a humerus are

Table 8
Measurements (in mm) of the lower dentition of *Cuon* from Koskobilo compared to other samples.

Taxon	Site	Chronology	Side	Number	p2		p3		p4		m1		Reference
					L	W	L	W	L	W	L	W	
<i>Cuon cf. alpinus europaeus</i>	Koskobilo	LP?	Left	221	10.2	5.7	11.4	6.3	14.7	7.4	–	9.6	This study
<i>Cuon</i> sp.	Koskobilo	MP?	Right	229	–	–	–	–	–	–	–	9.1	This study
<i>Cuon</i> sp.	Koskobilo	MP?	Right	230	–	–	–	–	–	–	–	10.0	This study
<i>Cuon cf. priscus</i>	Koskobilo	MP?	Right	232	–	–	–	–	–	–	25.3	9.6	This study
<i>Cuon alpinus</i>	Obarreta	LP?	Left/Right	8.7/8.7	4.2/4.2	–	–	–	–	–	23.0/23.0	8.8/8.6	Altuna (1983)
<i>Cuon alpinus</i>	Zafarraya	LP	Right	P10-R1005	–	–	–	–	14.4	7.1	–	–	Geraads (1995)
		LP		R7/8-R2369	–	–	–	–	–	–	22.4	9.1	Geraads (1995)
		LP		90-P7-16-37	–	–	–	–	–	–	22.3	9.0	Geraads (1995)
		LP	Left	91-P7-1-3050	–	–	–	–	–	–	22.0	9.0	Geraads (1995)
		LP		92-Q6-16-164	–	–	–	–	–	–	22.2	9.0	Geraads (1995)
<i>Cuon alpinus fossilis</i>	Heppenloch			1	–	–	–	–	–	–	24.0	9.0	Adam, 1959 in Bonifay (1971)
				2	–	–	–	–	–	–	24.5	9.0	Adam, 1959 in Bonifay (1971)
				3	–	–	–	–	–	–	24.6	9.3	Adam, 1959 in Bonifay (1971)
				5	–	–	11.1	9.9	14.8	7.2	24.5	9.6	Adam, 1959 in Bonifay (1971)
<i>Cuon alpinus</i>	Parpalló		Right		8.73	4.82	–	–	–	–	22.21	9.81	Pérez Ripoll et al. (2010)
<i>Cuon alpinus</i>	Duranguésado				10.05	5.31	–	–	14.94	7.26	22.89	9.17	Pérez Ripoll et al. (2010)
<i>Cuon alpinus</i>	Amalda V				–	–	–	–	–	–	22.7	9.0	Pérez Ripoll et al. (2010)
<i>Cuon alpinus</i>	Escoural				–	–	–	–	13.0	6.5	–	–	Pérez Ripoll et al. (2010)
<i>Cuon alpinus</i>	Malamaud				–	4.8	9.7	5.2	14	5.9	–	8.4	Harlé (1891)
<i>Cuon alpinus</i>	TG1	MP	Right	Ata-84-GSU11-F17-1	10.4	5.0	11.2	5.6	13.6	7.3	22.2	8.7	García (2003)
<i>Cuon alpinus</i>	TG2	MP	Right	ATA90 TG10a	–	–	–	–	14.8	6.7	23.6	8.9	García (2003)
<i>Cuon alpinus</i>	TG3	MP	Left	ATA89-GSU12-F26-1	10	5.3	11.9	5.7	15.2	7.5	24.2	9.6	García (2003)
<i>Cuon priscus</i>	Mosbach				–	–	–	–	–	–	25.1	9.7	Tobien (1957)
<i>Cuon priscus</i>	Hundshelm			IV-495	9.1	4.6	10.6	5	13.7	6.8	23.2	9.8	Thenius (1954)
				IV-74	8.9	5.2	10.7	5	14	6.8	23.3	9.8	Thenius (1954)
<i>Cuon cf. priscus</i>	Cova Negra				10	5.2	12	5.7	14.6	7	24.8	9.7	Pérez Ripoll et al. (2010); Sanchis et al. (2020)
<i>Cuon priscus</i>	Lumel-Viel			9-1103	–	–	–	–	14.8	7	23.3	9.2	Bonifay (1971)
				9-1165	–	–	–	–	–	–	23.9	9.2	Bonifay (1971)
				9-2932	–	–	–	–	–	–	24.2	9.5	Bonifay (1971)
<i>Cuon alpinus</i>	Recent	Mean (min-max)			–	–	–	–	–	–	21.31	8.65	Sanchis et al. (2020)
		<i>n</i>			–	–	–	–	–	–	(20.8–22.2)	(7.9–9.0)	
					8.52 ± 0.63	4.32 ± 0.28	9.81 ± 0.64	4.75 ± 0.35	12.37 ± 0.81	6.01 ± 0.46	21.42 ± 1.06	8.27 ± 0.49	García (2003)
		Mean ± SD (min-max)			(7.4–10.4)	(3.8–5)	(7.8–11.2)	(4.1–5.6)	(10.7–13.6)	(5.1–7.3)	(18.8–23.3)	(7.1–9.3)	
		<i>n</i>			<i>n</i> = 42	<i>n</i> = 42	<i>n</i> = 42	<i>n</i> = 42	<i>n</i> = 42	<i>n</i> = 42	<i>n</i> = 42	<i>n</i> = 42	

L = length; W = width; LP = Late Pleistocene; MP = Middle Pleistocene.

Table 9

Measurements (in mm) of the *Ursus thibetanus* remains from Koskobilo^a, summary statistics for different *U. thibetanus* and *U. arctos* samples compared to other fossil and extant *U. thibetanus* samples and results of the z-score between the Koskobilo specimen and the different recent samples.

Species	Site/Sample	Upper M2		Lower canine		References
		L	Anterior W	L	W	
<i>U. thibetanus</i>	Koskobilo	27.6	16.2	(17.1)	12.3	This study
<i>U. thibetanus</i>	Fossil (Europe and Western Asia)	27.7 ± 1.33 (24.7–29.29) n = 11	15.66 ± 0.64 (14.6–16.62) n = 11	20.68 ± 2.16 (17.1–25.9) n = 22	13.6 ± 1.55 (10.5–16.2) n = 21	Supplementary Tables S19-S20
<i>U. thibetanus</i>	Z-score	–0.08	0.84	–1.66	–0.84	
<i>U. thibetanus</i>	Recent (Asia)	25.36 ± 2.43 (21.55–30.03) n = 22	13.94 ± 0.79 (12.71–15.52) n = 22	17.91 ± 1.84 (12.66–22.26) n = 22	11.8 ± 1.45 (10.03–16.23) n = 22	This study
<i>U. arctos</i>	Z-score	0.92	<u>2.86**</u>	–0.44	0.34	
<i>U. arctos</i>	Pleistocene (Regourdou)	35.92 ± 2.25 (32.24–40.81) n = 12	18.57 ± 1.58 (16.54–22.4) n = 12	24.57 ± 0.79 (23.44–25.5) n = 5	16.21 ± 0.99 (14.9–17.22) n = 5	This study
<i>U. arctos</i>	Z-score	<u>–3.70**</u>	<u>–1.50</u>	<u>–9.45**</u>	<u>–3.94**</u>	
<i>U. arctos</i>	Holocene/Recent/no dating	33.56 ± 3.09 (25.66–42.7) n = 140	17.41 ± 1.57 (14.3–22.66) n = 126	19.77 ± 2.43 (15.19–26.56) n = 98	13.9 ± 1.9 (10.5–18.5) n = 109	This study
	Z-score	–1.92	–0.77	–1.10	0.84	

The z-score analyses values with an * or two ** are significantly different from the comparative samples (* = $p < 0.05$; ** = $p < 0.01$). Underlined means that Koskobilo is outside the range of the comparative sample.

^a Labels (side): Lower canine: 465 (right); Upper M2: 34 (left). Values between parentheses are estimated.

identified as belonging to two individuals of the greater mouse-eared bat (Fig. 12). The myotodont lower molars and the dental formula of the mandibles (3.1.3.3), as well as the humerus distal epiphysis lacking a styloid process, are diagnostic of genus *Myotis*. The large size of the remains allows to assign them to *Myotis myotis*, as the size of the lower molars is larger than Iberian populations of the sibling species *Myotis blythii* (Galán et al., 2019). This bat prefers deciduous and mixed forests as well as transitional woodland and woodland margins and is a typical cave-dwelling species (Dietz et al., 2009; Palomo et al., 2007).

Family Miniopteridae Mein and Tupinier, 1977

Miniopterus schreibersii (Kuhl, 1817)

Schreiber's long-fingered bat is represented by a complete left m1. The molar is nyctalodont and presents a narrow but irregular labial cingulum together with a relatively closed trigonid with lingual cingulum that characterize this species among nyctalodont Iberian bats. This species inhabits a variety of Mediterranean landscapes although it seems to favor broadleaved forests, and it mainly roosts in karstic cavities (Dietz et al., 2009; Palomo et al., 2007).

3.7 Order Rodentia Bowdich, 1821

A total of 125 remains have been assigned to four families and eight different taxa of rodents.

3.7.1 Family Muridae Illiger, 1811

Genus *Rattus* Fischer von Waldheim, 1803

Rattus sp.

A cranium and two hemimandibles (right-left) have been assigned to this taxon. These remains are modern based on their different color pattern, and on the surface of the cranium it was still possible to observe hair.

3.7.2 Family Cricetidae Fischer von Waldheim, 1817

Arvicola amphibius (Linnaeus, 1758)

Sixteen cranial/mandibular remains have been identified as belonging to a minimum of seven European water voles (Fig. 12). The SDQ values of these specimens are similar to those from other Late Pleistocene sites (Supplementary Fig. S13).

Microtus arvalis (Pallas, 1778)

Two hemimandibles have been identified as belonging to a single common vole (Fig. 12).

Microtus agrestis (Linnaeus, 1761)

Three hemimandibles have been identified as belonging to a minimum of two field voles (Fig. 12).

Microtus (Terricola) cf. lusitanicus (Gerbe, 1879)

A left hemimandible has been identified as belonging to the Lusitanian pine vole (Fig. 12).

Plomys coronensis Mehely, 1914

A left hemimandible has been identified as belonging to this vole species (Fig. 12).

3.7.3 Family Sciuridae Fischer von Waldheim, 1817

Marmota marmota (Linnaeus, 1758)

The marmot collection comprises 22 elements, all except a talus being cranio-dental remains, representing a minimum of four individuals (Fig. 12). The measurements of these remains can be found in Supplementary Tables S22-S23.

3.7.4 Family Castoridae Hemprich, 1820

Castor fiber Linnaeus, 1758

Ruiz de Gaona (1941) mentions the presence of 19 beaver remains. Crusafont and Villalta (1948) studied 12 remains from Koskobilo which would indicate a minimum of four individuals based on their anatomical determinations. The current collection comprises only six remains (one of them recovered by J.M. Barandiarán in 1955; Table 1; Fig. 12), including a left maxilla preserving P4-M3 (154), a very complete right mandible with all the teeth (477), and two P4s (right and left; 155 and AR.6) which would represent two individuals. The measurements of these remains can be found in Supplementary Table S24. Two proximal phalanges (345 and 353) are also tentatively attributed to this taxon.

3.8 Order Lagomorpha Brandt, 1855

3.8.1 Family Leporidae Fischer von Waldheim, 1817

Leporidae indet.

A single leporid fossil is represented by a right maxilla preserving

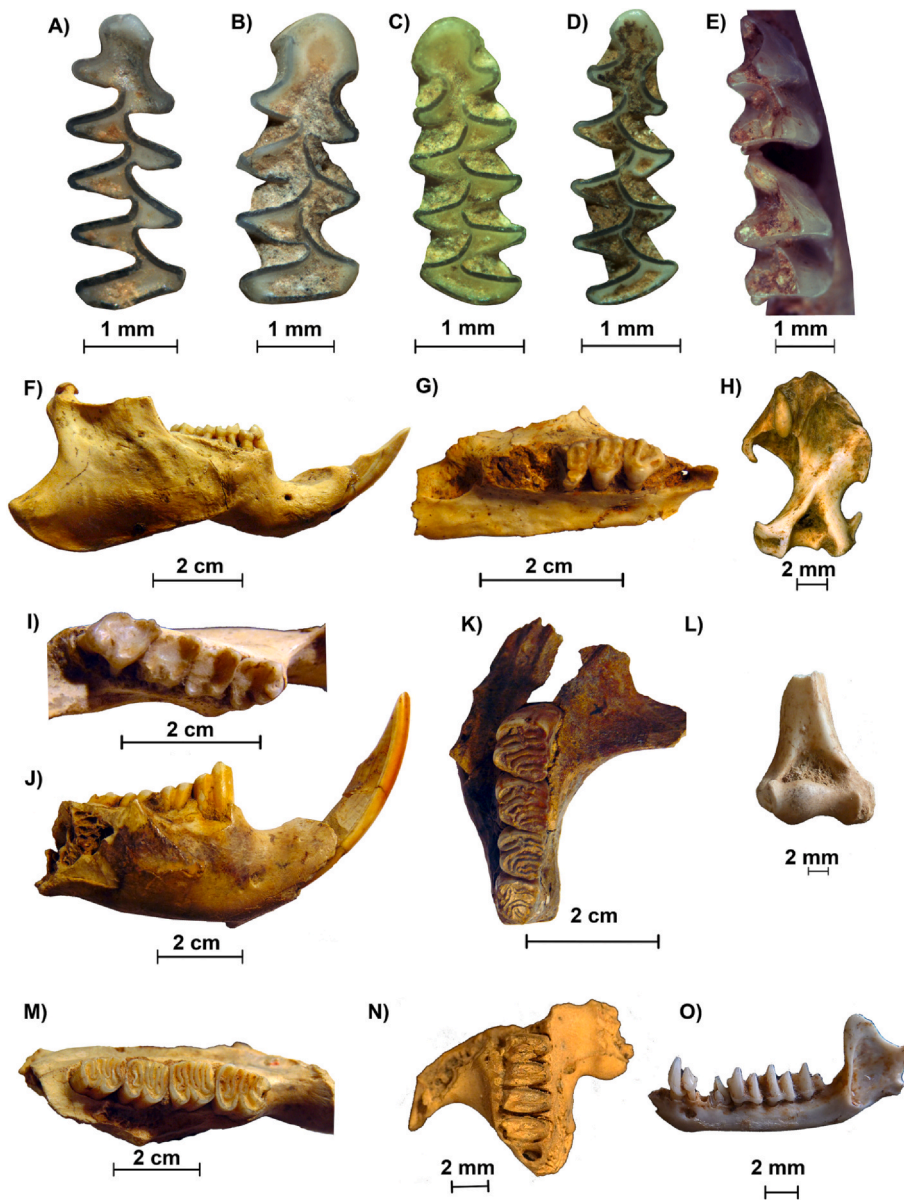


Fig. 12. Selected micromammals from Koskobilo. A) *Pliomys coronensis* right m1; B) *Arvicola amphibius* right m1; C) *Microtus arvalis* left m1; D) *Microtus agrestis* right m1; E) *Talpa* sp. right mandible fragment with m1-m2; F) *Marmota marmota* right mandible; G) *M. marmota* left maxilla preserving M1-M3; H) *Talpa* sp. left humerus; I) *M. marmota* right mandible with p4-m3; J) *Castor fiber* right mandible; K) *C. fiber* left maxilla with P4-M3; L) cf. *Erinaceus*, right humerus; M) *C. fiber* right mandible preserving p4-m1; N) Leporidae indet right maxilla preserving P3-M2; O) *Myotis myotis* left mandible. A-E, G, I, K, M-N: occlusal views; F, J, O: labial views; H: posterior view; L: anterior view.

P3-M2 (Fig. 12), which would be consistent with the only leporid described by Ruiz de Gaona (1941).

3.9 Order Primates Linnaeus, 1758

3.9.1 Family Hominidae Gray, 1825

Homo sapiens Linnaeus, 1758

Our species is represented by three specimens belonging to the same adult individual: the two calcanei from both sides and a left talus, which perfectly articulates with the calcaneus. While these remains are relatively complete, their surface is eroded and trabecular bone is exposed in many places (Fig. 13; Supplementary Figs. S14-S16). Twelve of 15 of the multivariate discriminant functions analyzed suggest that the talus and calcanei from Koskobilo probably belonged to a male individual, with an estimated stature of c. 170 cm and estimated body mass of 67.8 kg. From a metrical point of view (Supplementary Tables S25-S26; Fig. 14) these remains are close to the mean of recent humans, with the talus being more useful than the calcaneus to establish taxonomic affinities (Fig. 14). The bivariate plot (Fig. 14-A) of lateral malleolar breadth (M7a) and total talar breadth (M2) indicates that the Koskobilo talus is different from the Middle Pleistocene sample from

Sima de los Huesos (SH) and Upper Paleolithic modern humans. The bivariate plot of the talar head breadth (M9) and talar length (M1) separates Koskobilo from both Neandertals and Upper Paleolithic modern humans (Fig. 14-B). The bivariate plot of the anterior trochlear breadth (M5-2) and posterior trochlear breadth (M5-1) separates Koskobilo from Upper Paleolithic modern humans (Fig. 14-C).

3.9.2 Family Cercopithecidae Gray, 1821

Macaca sylvanus (Linnaeus, 1758)

One specimen can be attributed to a macaque: a distal half of a right m3 of a papionin monkey (200; Fig. 15). The area of breakage passes through the mesial ends of the hypoconid and entoconid, which present only slight amounts of surface wear. The cusp tip of the entoconid shows a small subcircular dentine exposure, while the remainder of that cusp, the hypoconid, the hypoconulid and two (or three) lingually placed accessory cusps show planar wear surfaces. The entoconid and hypoconid are elevated above the more distal cusps, which lie behind a meandering transverse groove. The hypoconulid is directly buccal to the accessory cusps, rather than protruding distally as is more often the case. Columnar roots under each cusp are fused into a single

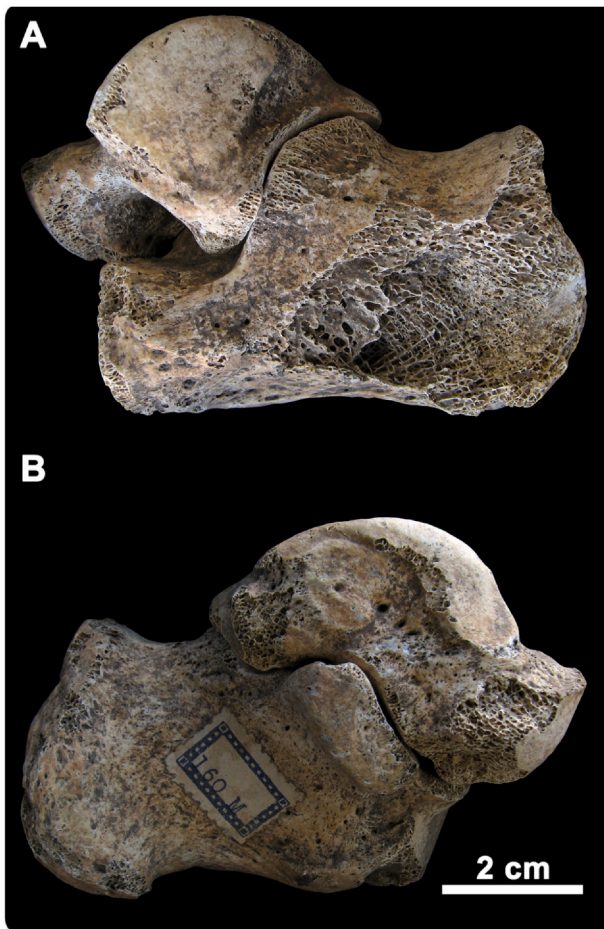


Fig. 13. Lateral (A) and medial (B) views of the *Homo sapiens* left talus and calcaneus from Koskobilu showing their articulation.

structure, whose apex is broken away.

Only a few standard measurements can be taken of the tooth fragment (Table 10) as other landmarks are too damaged to use for measurement. The preserved metrical values of the Koskobilu specimen are consistent with those for *Macaca sylvanus*, the only papionin known in the European later Pleistocene. The values for extant *M. sylvanus* do not differ from those for samples of Early or Middle to Late Pleistocene macaques. It has been proposed that European macaques might be divided into three time-successive subspecies (Szalay and Delson, 1979; Delson, 1980), but metrical differences among these have not been supported (see also Alba et al., 2011). Of two other known Early Pleistocene European papionins, *Macaca majori* is slightly smaller, while *Paradolichopithecus arvernensis* is rather larger (the ranges of these two taxa hardly overlap those of *Macaca sylvanus*). Thus, the Koskobilu tooth can be reliably identified as *Macaca sylvanus*.

4. Systematic paleontology-Birds

The Ruiz de Gaona collection preserves 27 avian remains, and it was possible to taxonomically assess 15 of them, which belong to three different orders (Fig. 16). Twelve indeterminate remains (*Aves* indet.) belong to different anatomical regions, including a vertebra, two synsacra, a coracoid, a phalanx, and seven long bones.

4.1 Order Galliformes Temminck, 1820

4.1.1 Family Phasianidae Horsfield, 1821

Perdix perdix (Linnaeus, 1758)

A distal fragment of a right tarsometatarsus has been attributed to a

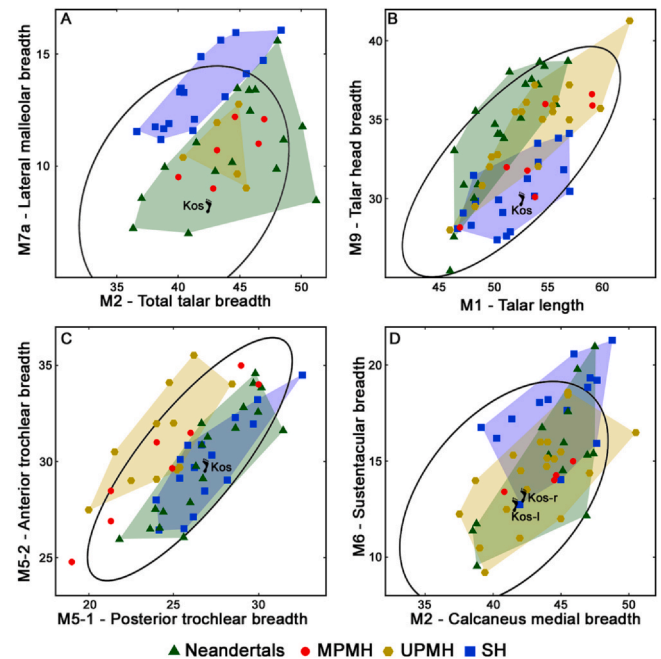


Fig. 14. Bivariate scatter plot of selected measurements (in mm) of the *Homo sapiens* talus (A–C) and calcaneus (D), comparing the Koskobilu (Kos) remains to Neandertals, Middle Paleolithic modern humans (MPMH), Upper Paleolithic modern humans (UPMH) and the Sima de los Huesos (SH) Middle Pleistocene sample. The solid line indicates the 95% equiprobability ellipse of modern human variation. Kos-r = Koskobilu right calcaneus, Kos-l = Koskobilu left calcaneus.

gray partridge (Fig. 16c).

Lagopus muta (Montin, 1776)

A complete right tarsometatarsus from a rock ptarmigan has been identified (Fig. 16b).

Lyrurus tetrax (Linnaeus, 1758)

A left carpometacarpus and both tarsometatarsi from a single black grouse have been identified (Fig. 16a). The measurements of the Koskobilu black grouse expand the known range variation of this species in the WP (Table 11; Suárez-Bilbao et al., 2020).

4.2 Order Columbiformes Latham, 1790

Columbiformes indet.

A complete left coracoid has been attributed to an indeterminate dove.

4.2.1 Family Columbidae Leach, 1820

Columba livia/oenas group (*Columba livia* Gmelin, 1789 or *Columba oenas* Linnaeus, 1758)

A nearly complete carpometacarpus has been attributed to a rock or stock dove (Fig. 16e).

4.3 Order Passeriformes Linnaeus, 1758

4.3.1 Passeriformes indet

A complete right humerus belongs to an indeterminate passerine bird.

4.3.2 Family Alaudidae Vigors, 1825

A complete right humerus belongs to an indeterminate lark (Fig. 16f).

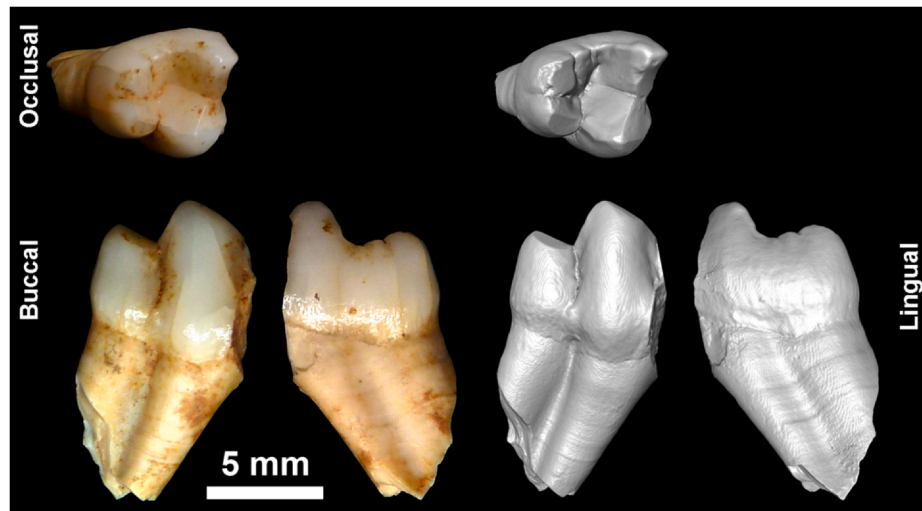


Fig. 15. Barbary macaque (*Macaca sylvanus*) partial m3 (200) from Koskobilob: original fossil (left) and 3D surface model (right) in occlusal, buccal and lingual views.

4.3.3 Family Corvidae Vigors, 1825

Corvidae indet.

An immature (very porous) complete right femur, a complete (but eroded) right humerus and a complete right carpometacarpus have been attributed to indeterminate corvids.

Pyrrhocorax pyrrhocorax Linnaeus, 1766

The proximal half of a right ulna and the complete left coracoid bone (Fig. 16d) have been attributed to a red-billed chough.

5. Taphonomic analysis

5.1. Large-mammal assemblage

Of the 394 studied large vertebrate specimens (NSP), 99% were determined at both anatomical and taxonomic levels (Number of Identified Specimens, NISP). Anatomically, the skeletal representation of the paleontological assemblage is dominated by cranial, dental and basipodial bone remains, supporting an artificial selection of the recovered remains (Arlegi et al., 2018). Regarding the fragmentation, this assemblage displays a high number of complete remains (54% of the

NSP). Many are dental or cranio-mandibular remains with several teeth (NISP = 267; 67.7%). The results of the taphonomic analysis are displayed in Table 12.

The most abundant modifications are those related to the diagenetic phase and indicate a fossil-diagenesis associated to karstic environments (Fernández-Jalvo and Andrews, 2016). We can underscore the presence of manganese oxide (black) staining (23.1% NSP) and to a lower extent, fissures, cracking and flaking due to changes of humidity (2.8% NSP) and CaCO_3 cementations (1.8% NSP). The same pattern is also observed in the small-mammal assemblage. However, and taking into consideration that this is a selected assemblage, a significant percentage of the non-dental remains (NISP = 17; 7.1%) show tooth-marks (Supplementary Fig. S17). Pits, punctures and scores have been recorded on bear, canid, felid, red-deer like cervid, bovid and especially bird remains, which constitute 28% of the tooth-marked NISP. Despite the low amount of carnivore tooth marks, which preclude the statistical treatment of the data in order to establish the carnivore(s) responsible for these modifications, the width of some pits (5.5 mm) and of some scores (4.2 mm) in cortical bone indicate the presence of a large carnivore (i.e., bear, lion, hyena and/or wolf) chewing the macro-mammal bones (Domínguez-Rodrigo and Piqueras, 2003). Among the bones

Table 10

Measurements (in mm) of the partial m3 (200) of *Macaca sylvanus* from Koskobilob compared to other extant and fossil samples.

Taxon/Population		Distal width (PW) ^a	Distal intercuspal distance (ICP) ^b	Hypoconulid width (HW) ^c	Reference(s)
Koskobilob		6.3	3.9	5.0	This study
<i>Macaca sylvanus</i> (extant)	mean (range) <i>n</i>	6.78 (5.67–7.92) <i>n</i> = 44	3.54 (2.8–4.3) <i>n</i> = 10	4.77 (3.8–5.8) <i>n</i> = 10	PRIMO ^d
<i>M. sylvanus pliocena</i> (Middle-Late Pleistocene)	mean (range) <i>n</i>	7.21 (6.0–8.4) <i>n</i> = 12	3.57 (3.2–4.1) <i>n</i> = 7	5.19 (3.5–7.1) <i>n</i> = 10	PRIMO ^d
<i>M. sylvanus florentina</i> (early Pleistocene)	mean (range) <i>n</i>	7.19 (6.4–7.9) <i>n</i> = 9	3.46 (2.9–4.6) <i>n</i> = 8	5.28 (4.2–6.1) <i>n</i> = 9	PRIMO ^d
<i>M. majori</i> (early Pleistocene)	mean (range) <i>n</i>	6.33 (5.5–6.7) <i>n</i> = 12	2.62 (1.8–3.2) <i>n</i> = 13	3.84 (2.7–4.2) <i>n</i> = 12	PRIMO ^d
<i>Paradolichopithecus arvernensis</i> (early Pleistocene)	mean (range) <i>n</i>	10.51 (9.5–11.1) <i>n</i> = 7	5.63 (4.7–6.5) <i>n</i> = 6	7.4 (6.6–8.5) <i>n</i> = 7	PRIMO ^d

^a Maximum buccolingual width across the base of the hypolophid (hypoconid to entoconid).

^b Distance between cusp tips of hypoconid and entoconid (only taken if there is no enamel perforation or just point wear through to dentine on each cusp).

^c Maximum buccolingual width across the base of the hypoconulid.

^d PRIMO data are available in the NYCEP PRimate Morphometrics Online database, at <https://primo.nycep.org/>.



Fig. 16. Avian remains from Koskobillo. a) Black grouse (*Tetrao tetrix*) right tarsometatarsus (268), dorsal view. b) Rock ptarmigan (*Lagopus muta*) right tarsometatarsus (272), dorsal view. c) Gray partridge (*Perdix perdix*) right tarsometatarsus (397), dorsal view; d) Red-billed chough (*Pyrrhocorax pyrrhocorax*) left coracoid (271), ventral view; e) Rock/Stock dove (*Columba livia/oenas*) right carpometacarpus (401), dorsal view; f) lark (*Alaudidae* indet.) right humerus (264), caudal view.

modified by carnivores, the presence of crenulated edges (40% of the bones with tooth marks) and digested bones (35% of the bones modified by carnivores) stand out. The high incidence of crenulated edges is here related to the anatomical selection of the remains because out of 17 remains with tooth marks seven correspond to mandibles. The level of digestion ranges between subtle to moderate, and principally affect the avian remains (5 out of 6). Among the biostratinomic modifications, three remains shows cut-marks, and one shows modifications compatible with the use of a bone blank as bone retoucher (Supplementary Fig. S18). An equid calcaneus presents two groups of slicing marks. The first group comprises nine short, straight, and parallel slicing marks located on the medial side of the bone (Arlegi et al., 2018). The second group comprises five straight, parallel (though in some cases overlapping) deeper cut-marks, located on the dorsal edge. The location of these marks is related to the disarticulation of the basipodial (Nilssen, 2000). Two large-sized long limb shaft fragments show groups of slicing marks, oblique to the axis of the element and parallel to each other. Both groups of butchering marks are related to the exploitation of large packages of meat, and the two bone fragments present fracture edges compatible with green breakage (Binford, 1981; Nilssen, 2000). Finally, one shaft fragment of long bone of a large-sized animal (Aranzadi AR-16, Supplementary Fig. S18) shows deep-short cuts (like small chop marks), centered in the bone blank, concentrated and superposed, generating a hatched area. All these features have been related to the use of bones as retouchers (e.g. Mallye et al., 2012).

5.2. Small-mammal assemblage

The small-mammal assemblage shows a bias with cranial and larger post-cranial elements being preferentially represented, which we

Table 12

Number and percentage of bone surface modifications observed over the total number of specimens (NSP = 394) in the assemblage of Koskobillo.

Taphonomic phase	Surface modification	NSP	% NSP
Biostratinomic	Cut-marks	3 ^a	0.8
	Retoucher?	1 ^b	1.8
	Tooth-marks	17	4.3
	Digested	6	1.5
	Rodent-gnawing	1	0.3
	Root etching	6	1.5
	Trampling	7	1.8
	Polished	2	0.5
	Rounded	6	1.5
	Fissures-Weathering	11	2.8
Fossildiagenetic	Manganese staining	91	23.1
	Cementation	7	1.8

^a Two of them in the Aranzadi collection.

^b Aranzadi collection.

interpret as the result of the recovery techniques used. Otherwise, the three remains of rat (*Rattus* sp.) are not fossils. The rest of the small-mammal remains show a homogeneous taphonomic pattern, which consist on fissures, cracks and manganese oxide stains on most of the bones. This pattern is similar to what is found with larger mammals, consistent with a humid fossiliferous environment. Regarding the origin of the accumulation, digestion modifications are not observed, indicating that they have not been accumulated by the action of a predator or, more likely, that they were accumulated by a predator which does not leave significant signs of digestion (Category 1; Andrews, 1990), such as the barn owl (*Tyto alba*). Digestion was only detected in

Table 11

Measurements (in mm) of the *Lyrurus tetrix* remains from Koskobillo compared to another Western Pyrenees sample.

Site	Number (side)	Carpometacarpus		Tarsometatarsus				Reference
		Height of the symphysis (HS)	Diameter of the distal end (DD)	Greatest length (GL)	Breadth of the proximal end (BP)	Breadth of the distal end (BD)	Smallest breadth of the shaft (KS)	
Koskobillo	270 (left)	6.1	9.4	–	–	–	–	This study
	268 (right)	–	–	46.1	9.9	10.5	4.0	
	267 (left)	–	–	46.5	–	–	4.1	
Artazu VII	Mean ± SD	5.9 ± 0.7	8.65 ± 0.63	48.61 ± 1.83	10.33 ± 0.79	10.89 ± 0.87	4.22 ± 0.1	Suárez-Bilbao et al. (2020)
	Range	5.4–6.61	7.86–8.98	46.6–53.62	9.77–11.23	10.3–11.99	4.21–4.23	
	n	n = 5	n = 6	n = 4	n = 4	n = 4	n = 3	

three remains of mole (*Talpa* sp.; [Supplementary Fig. S19](#)), including one mandible with strong digestion marks, which could indicate the intervention of a small carnivore. Some common predators of moles are red foxes, but also wildcats, genets and martens ([Hernández, 2005](#)). Nevertheless, the scarce number of remains and their selected origin do not allow going further in these inferences. The origin of the accumulation of groundhogs and beavers, larger than the rest of the small vertebrates, cannot be readily determined given the absence of digestion or other predator modifications, but no anthropic marks were found.

6. Uranium/thorium dating

The dating of the speleothem covering the *S. hemitoechus* p3 (50; [Supplementary Figs. S2-S3](#)) has yielded an age of $219,561 \pm 9,153$ yr, placing its formation during Marine Isotope Stage 7 (MIS 7), at the limit between substages 7d (~228-220 ka BP) and 7c (~220-215 ka BP), well within the Middle Pleistocene ([Table 13](#)). MIS 7, also known as the penultimate interglacial complex, (ca 245-186 ka; [Roucoux et al., 2008](#)), is marked by an alternation of five warm and cold periods (MIS 7e to MIS 7a; [Railsback et al., 2015](#)). During this stage, a combination of high eccentricity, maximum precession and low obliquity gave rise to insolation changes of very high amplitude ([Berger, 1978](#); [Jouzel et al., 2007](#)), but temperature and ice volume do not appear to respond proportionally to precessional insolation forcing. Thus, MIS 7 is one of several examples in the paleoclimatic record which could challenge the classical Milankovitch theory of astronomical climate forcing ([Paillard, 2001](#)). In summary, the speleothem formation over the *S. hemitoechus* premolar marks the transition between cold to warm conditions and implies that part of the Koskobilu assemblages was accumulated during or before MIS 7d.

7. Discussion

7.1. The Koskobilu paleontological collection

The difficulties in the study of the Koskobilu paleontological collection include both collection and curation problems. First, the original paleontological collection (published in 1941) was recovered without any stratigraphic control ([Ruiz de Gaona, 1941](#)). The preliminary faunal analysis ([Arlegi et al., 2018](#)) suggested a diachrony in the paleontological deposit, which was compatible with the size of the original cave-site (vertical cavity of 12–14 m, with a base of c. 6 m, divided into two compartments by a rocky crest; [Ruiz de Gaona, 1941](#)). This is further confirmed both on a geochronological basis, due to the direct dating of a speleothem covering a rhinoceros tooth, which provides a MIS 7d or pre-MIS 7d date for part of the deposit, and the presence of taxa more compatible with the Late Pleistocene on both size and morphological bases (e.g., some cave bear specimens and a significant part of the small-mammal assemblage). The lack of stratigraphic control does not permit dividing the faunal collection on this basis and makes it more difficult to understand potential changes in the faunal association. Second, the large percentage of identifiable remains in the macro-vertebrate assemblage points to a selective paleontological collection and/or discarding process afterwards ([Arlegi et al., 2018](#)), in which micro-vertebrate remains were specifically collected (by hand-picking or dry-sieving). Third, [Ruiz de Gaona \(1941\)](#) provides an inventory, which is quite accurate for some of the taxa ([Tables 1-2](#)), but rather vague for other species. Moreover, he did not cite whether the collection also preserves indeterminate faunal remains. Fourth, some of the studied remains (e.g., the castorids; [Crusafont and Villalta, 1948](#)) have been lost and are not currently in the collection. Fifth, the presence of readily recognizable taxa, not listed previously ([Ruiz de Gaona, 1941](#)), is in our opinion clear evidence that additional fossil specimens have been incorporated into the collection. We include in this group the human remains, the badger crania, the cat skull, the rat remains, and a

Table 13
U/Th dating results of the speleothem covering the *Stephanorhinus hemitoechus* tooth. The error is 2σ.

Sample	238U (ppb)	232Th (ppt)	230Th/232Th (ppt) x10 ⁻⁶	230Th/232Th (atomic)	D234U* (measured)	230Th/238U (activity)	230Th Age (yr) (uncorrected)	230Th Age (yr) (corrected)	D ²³⁴ Uinitial** (corrected)	230Th Age (yr BP)*** (corrected)
Koskobilu 50	28.1 ± 0.1	12,721 ± 255	36 ± 1		93.0 ± 2.5	0.9837 ± 0.0044	231,459 ± 3,979	219,629 ± 9,153	173 ± 6	219,561 ± 9153

U decay constants: $\lambda_{238} = 1.55125 \times 10^{-10}$ ([Jaffey et al., 1971](#)) and $\lambda_{234} = 2.82206 \times 10^{-6}$ ([Cheng et al., 2013](#)). Th decay constant: $\lambda_{230} = 9.1705 \times 10^{-6}$ ([Cheng et al., 2013](#)).
* $d^{234}U = ((^{234}U/^{238}U)_{activity} - 1) \times 1000$. ** $d^{234}U_{initial}$ was calculated based on ^{230}Th age (T), i.e., $d^{234}U_{initial} = d^{234}U_{measured} \times e^{234\lambda T}$.
Corrected ^{230}Th ages assume the initial $^{230}Th/^{232}Th$ atomic ratio of $4.4 \pm 2.2 \times 10^{-6}$. Those are the values for a material at secular equilibrium, with the bulk earth $^{232}Th/^{238}U$ value of 3.8. The errors are arbitrarily assumed to be 50%.
***B.P. stands for “Before Present” where the “Present” is defined as the year 1950 C.E. (common era).

Sus fossil. Additionally, many of these remains have a very “modern” aspect and could belong to animals that were living around the quarry dumps and/or included in recent egagropiles, so that their bone remains were mixed with the sediment. Unfortunately, we lack museum/collection records to test when each specimen was incorporated into the collection. The presence of some labels (pieces of paper with numbers glued onto the fossil surfaces) in part of the fossil assemblage points toward some kind of record similar to what Ruiz de Gaona provided with other invertebrate collections (Arlegi and Gómez-Olivencia, personal observation).

The dumps from where Ruiz de Gaona (1941, 1958) recovered part of the original collection were probably used to receive the cave sediments as the work of the quarry advanced. No lithic remains were found in the first collection in the 1940s, but 10 years later a large collection of lithic remains were recovered from the dumps, and the quarry workers mentioned a possible horizontal cave, different from the vertical infilling from where Ruiz de Gaona (1941) recovered part of the materials. This led Arlegi et al. (2018) to propose the presence of two caves or cave sectors from which the archaeo-paleontological evidence derived, with at least four different time intervals represented based on the diachrony in the paleontological collection and the typological differences in the lithic assemblage.

The small faunal collection recovered by J.M. de Barandiarán in 1955, similar to the bone remains recovered by Arlegi et al. (2018) in 2016, shows a different taphonomic aspect due to its anthropogenic origin in contrast to the taphonomic signal from the original collection, with a larger abundance of carnivore marks. In fact, only a single bone from the Museo de Navarra collection shows cut-marks: a horse calcaneus. This bone is not mentioned in the first faunal list by Ruiz de Gaona (1941), and it cannot be discounted that it might have been recovered during the 1950s. Thus, excluding the horse calcaneus (for which we lack information on when it was found) and those remains that are recent/sub-recent, it is noteworthy to underline that the faunal remains found in 1955 and most of those found by us in 2016 were recovered together with lithic remains in the quarry dump. As most of these lithic remains have been attributed to the Upper Paleolithic, a comparable age could be proposed for the associated fossils. However, for the largest part of the paleontological collection, including taxa belonging to the Middle and Late Pleistocene, it has not been possible to find distinct taphonomic traits that could help to distinguish between these ages.

In any case, despite the difficulties, Koskobilu has yielded the presence of new taxa unknown in the region and/or very rare in the Iberian Peninsula. The salvage excavation and the recovery of fossil remains from the quarry dump performed by M. Ruiz de Gaona in 1940 has provided a new window into the Middle Pleistocene of Western Pyrenees.

7.2. The age of the fossils

We have already listed the difficulties of studying the Koskobilu fossil collection, due to the lack of stratigraphical control and the likely presence of more than one time mixed together. The speleothem formation implies that part of the Koskobilu assemblage was accumulated during or before MIS 7d, and some of the species would be consistent with this chronology. Despite the presence of some species that appeared during the Early Pleistocene (*Castor fiber*, *Marmota marmota*, *Talpa* sp.) or the Middle Pleistocene (*Microtus arvalis*, *Microtus agrestis*, *Pliomys coronensis*), they are especially abundant in the Late Pleistocene (Cuenca-Bescós et al., 2010, 2017; López-García, 2011; Sesé, 2017). Moreover, there are taxa, such as *Microtus (Terricola) lusitanicus* and *Arvicola amphibius*, that only appeared during the Late Pleistocene (López-García, 2011). The size and SDQ results for *A. amphibius* (mean: 82.6; range: 72.8–103.9; Supplementary Fig. S13) are consistent with central European sites and Cova Eirós during MIS 3 (Maul et al., 2014; López-García et al., 2017; Rey-Rodríguez et al., 2016). Indeed, all these

species can be found nowadays in northern Iberia (Blanco, 1998), with the sole exception of *Pliomys coronensis*, which went extinct at the end of the Pleistocene (Cuenca-Bescós et al., 2010; López-García et al., 2012). In a previous work we also mentioned that the size of some of the *Ursus spelaeus* M2 from Koskobilu are similar to Late Pleistocene samples of the same species (Supplementary Table S15; Arlegi et al., 2018). Finally, the metric study of the human remains suggest that they belonged to Holocene modern humans.

We will refer here in detail to the giant deer, the macaque, the Asian black bear and the dhole. The giant deer specimens from Koskobilu are different from *Megaloceros giganteus*, larger than the Middle Pleistocene species *Megaloceros savini* and *M. matritensis*, but fit within the known range of variation of *Megaceroides* very well. There is no consensus on the classification of this genus. The use of the name *Megaceroides* (e.g., Van der Made, 2019) implies that these European deer are related to the Late Pleistocene type species *M. algericus* from North Africa. Many prefer the name *Praemegaceros* (e.g., Croitor, 2006; Vislobokova, 2013), which has a European type species. It has also been included in *Megaloceros* (e.g., Azzaroli, 1953, 1979; Lister, 1993). Various species of *Megaceroides* are recognized (*M. boldrini*, *M. obscurus*, *M. pliotarandoides*, *M. verticornis*, *M. solihacus*, *M. dawkinsi*, as well as some endemic species on the islands of Corsica and Sardinia), but the identifications are mainly based on antlers and generally do not take variability into account. Size and morphology of the specimens from Koskobilu do not show much variation and are compatible with derivation from a single population of a species of this genus, even though the species cannot be identified. The genus appeared in Europe in the Early Pleistocene, it is generally assumed to have disappeared after 400–500 ka, but there are some later records at Azokh V (~MIS 9) and Atapuerca TG10 (~MIS 8) (Fernández-Jalvo et al., 2016; Van der Made et al., 2016; Demuro et al., 2014). An endemic lineage in Corsica and Sardinia survived until the Holocene (Van der Made and Palombo, 2006; Benzi et al., 2007). However, if we assume that the Koskobilu *Megaceroides* remains are not the most recent ones, then MIS 8 would be the latest possible age for them.

The Barbary macaque (*Macaca sylvanus*) is known in Iberia from around a dozen sites (Marigó et al., 2014, and references therein; Alba et al., 2019), including sites well dated to the Early Pleistocene (e.g., level TE9, Sima del Elefante, Sierra de Atapuerca; the Vallparadis section, Terrassa); and Middle Pleistocene (e.g., Aroeira; level TD-8, Gran Dolina, Sierra de Atapuerca) (Alba et al., 2008, 2019; Rodríguez et al., 2011). Castaños et al. (2011) attributed a partial left hemimandible from Lezetxiki II to *M. sylvanus* cf. *pliocena* based on an MIS 5 age for the level where it was found, which would have represented one of the most recent occurrences of this species for Europe and therefore for Iberia. This specimen was found in level J, which is now dated to MIS 7-6 based on sedimentological and geochronological grounds: it overlies a TT-OLS date of 215 ± 15 ka in the upper part of level K (Arriolabengoa et al., 2018). Bolomor has also yielded a macaque fossil in level IV and two additional remains from level XII, both in MIS 6 (Blasco et al., 2010; Blasco and Fernández Peris, 2012). Cova Negra has also yielded two *M. sylvanus* remains: an m3 and an m2 from sector B, layers 9 and 11, respectively (Pérez Ripoll, 1977), which would correspond to the late Middle Pleistocene (Richard et al., 2019; Eixea, personal communication). Finally, Koskobilu is located in a zone modelled between “very high” and “excellent” probability of occurrence of *M. sylvanus* for both the Middle and Late Pleistocene (Elton and O'Regan, 2014).

The Asian black bear (*Ursus thibetanus*) has only been found in three additional sites in the Iberian Peninsula. A total of three remains have been found in Bolomor (Tavernes de la Valldigna, Valencia): a left M2, a left p4 (of uncertain date) and a left radius (MIS 7), which are associated with other taxa present in Koskobilu such as *Macaca* and *Stephanorhinus* (Sarrión Montañana and Fernández Peris, 2006). The dental remains were attributed to MIS 5e and the postcranial remain to MIS 7 (Sarrión Montañana and Fernández Peris, 2006). In Cau d'en Borràs (Orpesa del Mar, Castellón), Carbonell et al. (1979) cite the

presence of a small-sized ursid in a Middle Pleistocene deposit, together with the presence of *Hemitragus*. [Sos Baynat \(1975\)](#) reported the presence of a small-sized bear from Villavieja (Castellón; Middle Pleistocene, contra [Sarrión Montañana and Fernández Peris, 2006](#)): an m1 and an m2 attributed to *Helarctos arvernesis*? (sic). Other authors (e.g., [Torres Perezhidalgo, 1996](#)), while other authors cite the presence of an m2 and two metacarpals attributed to *Ursus mediterraneus*. The *U. thibetanus* remains from Europe are attributed to two subspecies: *U. thibetanus stehlini* from the early Middle Pleistocene, and *U. t. mediterraneus* from the late Middle and Late Pleistocene ([Baryshnikov, 2010](#) and references therein).

Among the dhole remains, a complete m1 from Koskobilo has been attributed to *Cuon cf. priscus*, together with two other specimens that also show a large size. The closest parallel to this specimen is the dhole mandible from Cova Negra ([Pérez-Ripoll et al., 2010](#)), recently attributed to *Cuon cf. priscus* ([Sanchis et al., 2020](#)). This mandible was found in the Entrance slope, layer VII (Middle Pleistocene; MIS 8-7; [Richard et al., 2019](#)).

7.3. Additional paleobiogeographical and paleoclimatic implications

The bird association found in Koskobilo is not unusual during the Pleistocene in the Western Pyrenees and is consistent with the landscape around the site. Koskobilo is within the current range of distribution ([Svensson et al., 2010](#)) of most of the species found in the site with only two exceptions. Koskobilo is outside of the current range of distribution of the rock ptarmigan (*Lagopus muta*) though this species is very abundant throughout Europe during the Late Pleistocene ([Lagerholm et al., 2017](#)). On the other hand, the black grouse (*Lyrurus tetrix*) does not currently inhabit the Iberian Peninsula, although it is relatively abundant along the northern face of the Pyrenees during the Late Pleistocene and its oldest record, from the Middle Pleistocene, can be found in Montoussé ([Clot and Mourer-Chauviré, 1986](#)). In the Pleistocene of the Iberian Peninsula, it has been found in the MIS 5 records from Artazu VII ([Suárez-Bilbao et al., 2016, in press](#)), in the Late Pleistocene records from Urutiaga ([Elorza, 1990](#)), and in the Middle Paleolithic levels of Valdegoba ([Sánchez-Marco, 2004](#)).

Most of the small-mammal species recovered point to an open and humid environment that would be consistent with alpine or subalpine meadows, with humid soils that can be burrowed and the presence of water masses ([Blanco, 1998](#); [Palomo et al., 2007](#)). All the species identified are related to mid-European environments, although some are tolerant of Mediterranean conditions and relatively cold climate. With the exception of *Pliomys coronensis*, all taxa can be found nowadays in the studied area, which corresponds for most of them to their southern peninsular limit ([Palomo et al., 2007](#)). Assuming that the recovered small-mammal species belonged to a concrete time period, the absence of Mediterranean species could point to a deposition during a cold period. However, the absence of a stratigraphic context and the bias induced by the selected small-mammal sample limits the inferences that can be drawn from it.

7.4. The Middle Pleistocene in Koskobilo: parallels

Based on the dating of the speleothem and the paleontological association, some parallels can be drawn to connect the Middle Pleistocene deposit from Koskobilo with other sites in WP and northern Iberian Peninsula. The closest would be the nearby sites of Lezetxiki II, based on the presence of *Macaca sylvanus*, the lower levels of Lezetxiki, with deposits older than 200 ka ([Falgüeres et al., 2005](#); [de-la-Rúa et al., 2016](#)) and the site of Santa Isabel de Ranero ([Torres et al., 2001, 2014](#)). The lower levels of Arlanpe ([Ríos-Garaizar et al., 2015](#)) are probably younger. In this context, additional information on the taxonomy of the dated rhinoceros tooth from Goikoetxe ([Edeso et al., 2011](#)) would allow establishing better parallels. Another possible parallel is the MIS 7c site of Mollet, which has also yielded a human fossil ([Maroto et al., 2012](#);

[López-García et al., 2014](#)). The best parallels for Koskobilo are larger, more complete stratigraphic sequences, such as the Middle Pleistocene assemblages from the Sierra de Atapuerca, especially Trinchera Galería ([Rodríguez et al., 2011](#)), and those present in the Iberian levant, at the site of Bolomor with the presence of *Macaca*, *Cuon*, *Stephanorhinus* and *U. thibetanus* ([Sarrión Montañana and Fernández Peris, 2006](#); [Blasco et al., 2010](#); [Blasco and Fernández Peris, 2012](#); [Sanchis et al., 2020](#)).

It is very difficult to relate the Middle Pleistocene faunal remains from Koskobilo to potential human occupations in surrounding areas due to the difficulties explained above. However, there is evidence of Middle Pleistocene occupation in the surroundings of Koskobilo. First, one of the bifaces and the convergent scraper from Koskobilo, initially described by [Vallespí Pérez and Ruiz de Gaona \(1971\)](#) and recovered by the latter in the quarry dump, could also be of Middle Pleistocene age ([Arlegi et al., 2018](#)). Additionally, there are several bifacial tools found mainly in Quaternary terrace contexts that are probably roughly contemporaneous to the Middle Pleistocene record from Koskobilo (e.g., [Armendáriz Martija, 1988](#); [García Gazólaz, 1994](#), and references therein). However, we still lack a good chronological context for the terraces in which some of these finds were made.

8. Conclusions

Despite the limitations in the recovery of the paleontological assemblage, the Koskobilo collection is one of the richest in the Western Pyrenees, especially in terms of macro-mammal species diversity, which could be (partially) related to the fact that different time periods from the Middle and Late Pleistocene are represented. Nonetheless, the Koskobilo paleontological assemblage is very important in the Iberian context for two reasons: 1) the presence of several taxa with a very limited representation in the Iberian Peninsula such as *Megaceroides*, *Cuon cf. priscus*, *Ursus thibetanus*, *U. cf. deningeri*, *Macaca sylvanus*, and *Lyrurus tetrix*; and 2) the dating of a speleothem crust on a rhinoceros tooth which indicates that part of the Koskobilo assemblages was accumulated during or before MIS 7d, being one of the limited Middle Pleistocene sites in the Western Pyrenees.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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