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New evidences of the cave lion (*Panthera spelaea*) from the north of the Iberian Peninsula

Nuevos hallazgos de león de las cavernas en el norte de la Península Ibérica

KEY WORDS: Middle-Late Pleistocene lion, Systematics, Sexual dimorphism, Northern Iberian Peninsula.
PALABRAS CLAVES: León del Pleistoceno Medio-Superior, Sistemática, Dimorfismo sexual, Norte de la Península Ibérica.
GAKO-HITZAK: Erdi-Goi Pleistozenoko lehoia, sistematika, dimorfismo sexuala, Iberiar penintsulako iparraldea.

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ABSTRACT

The presence of the cave lion in the Iberian Peninsula is expanding with new finds on the Cantabrian coast. This update is recorded to a total of 56 sites from 44 locations and dated from MIS 10 to the end of the Upper Pleistocene. The new findings are studied and attributed to the *Panthera spelaea* species. Comparative analysis with other Eurasian sites confirms the trend of decreasing species size between the end of the Middle Pleistocene (MIS 6) and the Late Pleistocene. In addition, data on sexual dimorphism and new measurements of the deciduous teeth of one of the samples are offered.

RESUMEN

La presencia del león de las cavernas en la Península Ibérica se amplía con nuevos hallazgos en la Cornisa Cantábrica, actualizando su registro hasta un total de 56 yacimientos procedentes de 44 localidades y datados desde el MIS 10 hasta finales del Pleistoceno Superior. Se estudian los nuevos hallazagos y se atribuyen a la especie *Panthera spelaea*. Se confirma la tendencia a la disminución del tamaño de la especie entre finales del Pleistoceno Medio (MIS 6) y el Pleistoceno Superior, ya señalada en otros yacimientos eurasiáticos. Se ofrecen datos sobre el dimorfismo sexual y nuevas medidas de la dentadura decidua de una de las muestras.

LABURPENA

Iberiar penintsulako kobazuloetan aurkitutako lehoiaren aztarnak ugaritu egin dira Kantauri itsasoko ertzean topatutako azken aurkikuntzak direla eta. Hala, erregistroa eguneratu egin da eta 44 tokitako 56 aztarnategi daude. Aztarna horiek MIS 10etik Goi Pleistozenoaren amaierara arte datatu dira. Aurkikuntza berriak aztertu ondoren, *Panthera spelaea* espeziekoak direla ondorioztatu da. Hala, Erdi Pleistozenoaren (MIS 6) eta Goi Pleistozenoaren artean, espeziearen neurria gutxitu egin zela zioen joera baieztatu da (Eurasiako beste aztarnategi batzuetan ere aipatu zen joera hori). Dimorfismo sexualari eta laginetako baten hortzeria erorkorraren neurri berriei buruzko datuak jaso dira.

1. INTRODUCCIÓN

The lion, with different taxonomic attributions (*Panthera leo clueti, Panthera spelaea, Panthera leo*), was the largest carnivore present in the Iberian Peninsula during the Middle and Late Pleistocene. It is also the rarest feline species in archaeological (Villaluenga, 2016) and paleontological (Álvarez-Lao *et al.*, 2020) contexts. The largest number of evidences of this species is located in the Cantabrian Region (northern Spain), but it is also present, although less frequently, in other peninsular areas.

This work aims to update the records of the cave lion in the Iberian Peninsula and to present the chronological and morphometric data of the latest lion findings in northern Iberia.

2. UPDATED REVIEW OF THE CAVE LION IN IBERIA

The scarcity of lion finds in the Iberian Peninsula has generated reviews from the second half of the last century (Altuna, 1972; Castaños, 1990) to until the beginning of the current century (Castaños, 2005; Villaluenga, 2016; Álvarez-Laó, 2020). These reviews have never exceeded 25 references. However, new publications have significantly increased this record. Therefore, an update of this information is needed. Some references that lacked morphometric data or confirmations in subsequent revisions have been removed: Morín and Aizkirri (Altuna, 1972). In other cases, because of their dubious identification as Arlanpe (Arceredillo *et al.*, 2013), Gorham'cave (Zeuner & Sutcliffe, 1964) and Torralba-Ambrona (Marciszak & Stefaniak, 2010) or that

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have been the subject of discussion regarding their taxonomic attribution as Punta Lucero (Gómez-Olivencia *et al.*, 2015), La Arbreda (Nadal *et al.*, 2002), and Mollet (Alba & Maroto, 2002).

The result of this latest review is a set of 56 sites from 44 localities that far exceeds previous estimates and provides significant information about the lion's distribution in the extreme SW of Eurasia (Fig. 1).

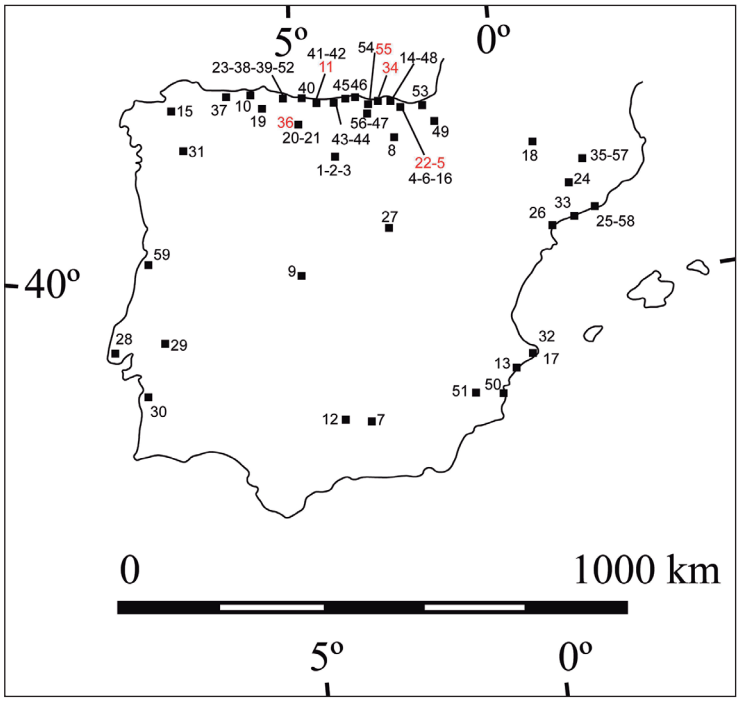

Fig.1. Records of *Panthera spelaea* in Iberian Peninsula (in red new findings). The localities are numered and listed at Table 1. / Distribución de los yacimientos con *Panthera spelaea* en la Península Ibérica (en rojo los nuevos hallazgos). Las localidades están numeradas en la Tabla 1

N	SITE	LOCALITIES	MIS	NISP/MNI	REFERENCES
1	Atapuerca TD	Ibeas de Juarros, Burgos	10	30/3	Morales *et al.*, 1987 Cervera, 1992 García, 2003
2	Atapuerca SH		9	10/3	
3	Atapuerca TG		9	65/5	
4	Lezetxiki I	Arrasate-Mondragón, Gipuzkoa	7	1/1	Altuna, 1972
5			6	1/1 52/2	Altuna, 1972 This paper
			4	128/2	Altuna, 1972
6	Lezetxiki II		4	12/2	Villaluenga *et al.*, 2012
7	S. de Zamborino	Fonelas, Granada	9	15/2	Martín Penela, 1988
8	Koskobilo	Olazti, Navarra	7-5	2/2	Gómez-Olivencia *et al.*, 2020
9	C. Descubierta	Pinilla del Valle, Madrid	6a	68/4	Baquedano *et al.*, 2023
10	La Parte	Siero, Asturias	6	1/1	Álvarez-Lao *et al.*, 2002
11	La Garma, P. Antiguo	Ribamontán al Monte, Cantabria	6	2/1	This paper
12	Carigüela	Piñar, Granada	6	1/1	Riquelme-Cantal *et al.*, 2024
13	Bolomor	Tavernes de la Valldigna, Valencia	5e	3/2	Blasco, 2011
14	Imanolen Arrobia	Deba, Gipuzkoa	5c	1/1	Castaños *et al.*, 2017
15	Valdevara 3	Becerreá, Lugo	5c	4/1	Vaquero *et al.*, 2018
16	Artazu VII	Arrasate-Mondragón, Gipuzkoa	5a-b	8/1	Castaños *et al.*, 2019
17	Cova Negra	Xátiva, Valencia	5-4	7/1	Pérez Ripoll, 1977
18	Moros de Gabasa	Peralta de Calasanz, Huesca	4	6/1	Blasco-Sancho, 1995
19	Jou'l Llobu	Onís, Asturias	4	1/1	Pinto Llona, 2007

N	SITE	LOCALITIES	MIS	NISP/MNI	REFERENCES
20	El Castillo Musteriense	Puente Viesgo, Cantabria	4	7/2	Carballo, 1910; Castaños, 2017
21	El Castillo Auriñ-Solutr		2	5/2	
22	Artazu VIII	Arrasate-Mondragón, Gipuzkoa	4	8/2	This paper
23	Torca del león	Llanes, Asturias	3	169/1	Álvarez-Lao *et al*., 2020
24	Cova d'El Toll	Moiá, Barcelona	3	2/2	Villalta & Thomas 1974
25	L'Abric de Romaní	Capellades, Barcelona	3	1/1	Cáceres *et al*., 1993
26	Cova Foradada	Calafell, Tarragona	3	2/1	Morales *et al*., 2019
27	Los Casares	Riba de Saelices, Guadalajara	3	1/1	Altuna, 1973
28	Pedreira da Salemas	Loures	3	4/3	Antunes & Cardoso,1987
29	Gruta do Escoural	Montemor-o-novo	3	1/1	Cardoso, 1993
30	Gruta da Figueira Brava	Brava, Setubal	3	1/1	Cardoso, 1993
31	Lorga de Dine	Vinhais	3	1/1	Cardoso, 1993
32	San Luis	Bunyol, Valencia	3	1/1	Fernández Peris & Martínez Valle, 1989
33	Riera del Caniars	Gavá, Barcelona	3	2/2	Daura *et al*., 2013
34	Kiputz IX	Mutriku, Gipuzkoa	2	25/1	Castaños, 2017; This paper
35	Reclau Viver	Serinyá, Girona	2	2/1	Villalta & Thomas, 1974
36	La Pasiega	Puente Viesgo, Cantabria	2-1	1/1	This paper
37	La Paloma	Soto de las Regueras, Asturias	1	5/2	Castaños, 1980
38	La Riera	Posada de Llanes, Asturias	1	4/1	Altuna, 1986
39	Balmorí	Llanes, Asturias	1	1/1	Alcalde del Río *et al*., 1911
40	Altamira	Santillana del Mar, Cantabria	1	1/1	Harlé, 1909; Castaños & Castaños, 2014
41	El Juyo	Igollo, Cantabria	1	1/1	Klein & Uribe, 1985
42	El Pendo	Camargo, Cantabria	1		Castaños, 2001
43	Garma, galería inferior	Ribamontán al Monte, Cantabria	1	9/1	Cueto *et al*., 2016
44	Garma, galería Weitzman-Kreger				M. Cueto (pers. com.)
45	El Mirón	Ramales, Cantabria	1		Harlé, 1909; Marín-Arroyo, 2008
46	Santimamiñe	Kortezubi, Bizkaia	1	1/1	Castaños, 1987
47	Amalda	Zestoa, Gipuzkoa	1	1/1	Altuna, 1990
48	Urtiaga	Deba, Gipuzkoa	1	8/1	Altuna, 1972
49	Abauntz	Arraiz, Navarra	1	1/1	Altuna *et al*., 2001-2002
50	Cova del Corb	Ondara, Alicante		1/1	Sarrión, 1990
51	Moli de Mato	Agres, Alicante		1/1	Sarrión *et al*., 1987
52	Quintanal,	Llanes, Asturias		1/1	Fraga Torrejón, 1958
53	Aitzbitarte IV	Rentería, Gipuzkoa		2/1	Harlé, 1908
54	Arrikrutz	Oñati, Gipuzkoa		70/1	Altuna, 1981
55	Arrikrutz			13/2	This paper
56	Azóleta	Gorbeia, Álava		27/1	Castaños, 2005
57	Cellera d'Amont	Serinyá, Girona		2/1	Maroto *et al*., 2017
58	Avenc de la Pepi	Gavá, Barcelona			Villalta & Thomas, 1974
59	Penacova	Penacova, Coimbra		1/1	Antunes & Cardoso,1987

Tabla 1: Records of Panthera spelaea from Iberian Peninsula. / Distribución de los hallazgos de Panthera spelaea en la Península Ibérica.

The chronology of the remains has been homologated to the Marine Isotopic stages (MIS) (Table 1). Its presence during the Middle Pleistocene is recorded in 10 sites relatively well distributed between the Cantabrian coast (La Parte, La Garma-P.Antiguo, Lezetxiki, Koskobilo), the plateau (3 Atapuerca'sites, C. descubierta) and the south (Solana de Zamborino, La Carigüela). Geographically, almost half of the samples (60.7%) are concentrated in the eastern half of the Cantabrian Region (northern Spain) and 10 are below the

38th parallel. It is interesting to note that the two better southern Iberia sites are the southernmost records of this species in the Pleistocene of Europe.

3. MATERIAL

Recently, the cave lion record from the Middle and Late Iberian Pleistocene has increased with three new sites (La Garma, La Pasiega, Artazu VIII) and with new findings in three already known others (Arrikrutz, Lezetxiki, Kiputz IX). All are located in the Cantabrian Region, the area with the highest density of this species on the Iberian Peninsula (Fig. 1).

3.1. La Garma

On Mount La Garma (Ribamontán al Monte, Cantabria,Spain) there is a group of sites whose chronology extends from the Middle Pleistocene to the Holocene. The oldest human occupation is La Garma A (Old Palaeolithic), which has been excavated under the direction of P. Arias and R. Ontañón (1995-2022) (Arias Cabal, Ontañón Peredo, 2008). At level SI 1 has been recovered a lower left P4 and a proximal phalanx of cave lion. This sample is associated with other remains of megafauna *(Palaeoxodon antiquus, Stephanorhinus hemitoechus, Megaceros megaceros)*, ungulates *(Bos/Bison, Equus caballus, Cervus elaphus, Rangifer tarandus, Capreolus capreolus, Capra pyrenaica, Rupicapra pyrenaica, Sus scrofa)* and carnivores *(Ursus spelaeus, Canis lupus, Cuon alpinus, Vulpes vulpes, Lynx sp., Felis silvestris, Lutra lutra, Martes martes)*. This level has been dated by amino acid racemisation from 2 molars of *Stephanorhinus hemitoechus* in 174,5 ±4,5 ky (Torres & Ortiz, 2010, using).

3.2. La Pasiega

La Pasiega is an archaeological site located on Mount El Castillo (Puente Viesgo, Cantabria, Spain) that includes a group of caves with rock art. In 1993 C. González (University of Cantabria) collected a sample of fauna on the surface in the so-called Gallery A. The material lacks stratigraphic context. The study of the sample indicates the presence of a middle phalanx of cave lion along with a deer antler and 17 cave bear remains.

The phalanx exhibits the torsion typical of felids and its measurements fall within the domain of variation of the cave big cat. The cave paintings in the area of the find have been attributed to the Upper Palaeolithic (Solutrean-Magdalenian) and it seems reasonable to assume that the remains found from MIS 2-1.

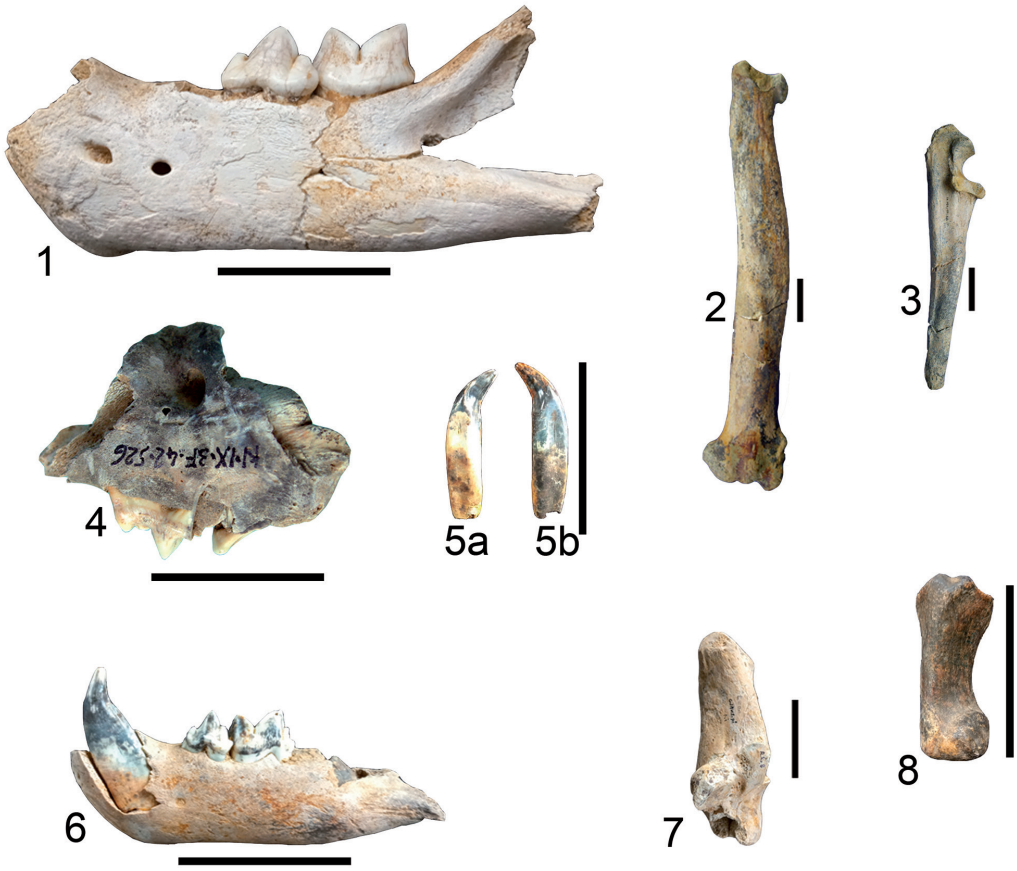

Fig.2 *Panthera spelaea* cranial and postcranial remains from the new Cantabrian discoveries. Left mandible (1) from Artazu VIII in lateral view; rigth radius (2) and rigth ulna (3) from Lezetxiki in medial views; rigth upper jaw (4), left (5a) and rigth (5b) upper deciduous canines and left mandible (6) from Kiputz IX; left calcaneum (7) from Arrikrutz; phalanx 2 (8) from La Pasiega. Scale Bar= 5 cm. / Restos craneales y postcraneales de Panthera spelaea de los nuevos hallazgos cantábricos. Mandíbula izquierda (1) de Artazu VIII en vista lateral; radio derecho (2) y ulna derecha (3) de Lezetxiki en vista mesial; serie dentaria lacteal derecha (4), canino deciduo superior izquierdo (5a) y derecho (5b) y mandíbula izquierda (6) de Kiputz IX; calcáneo izquierdo (7) de Arrikrutz; falange 2 (8) de la Pasiega. Escala=5 cm.

S. C. Aranzadi. Z. E. Donostia/San Sebastián
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3.3. Artazu VIII

The Artazu VIII site was discovered by chance during work at the Kobate Quarry (Arrasate-Mondragón, Gipuzkoa, Spain) in 2013 and was excavated in the summers from 2014 to 2016 under the direction of Xabier Murelaga. It is located in Mt. Artazu at 351m above sea level, at the head of the Deba valley (Fig. 1). The site is in the form of a pothole shaped like an inverted tunnel, with an entrance 8-10m in diameter and a depth of over 20m containing a fill consisting of 8 layers of sediment. Ten dates have been obtained by the amino-acid racemization method in the Molecular Stratigraphy Laboratory at the Polytechnic University of Madrid. The samples were taken from the third lower molars of bison in each layer and the first two upper molars from the same woolly rhinoceros specimen found in the lower part of Layer 8. The results range from 65.05±1.95 ka for Layer 1 to 101.7±1.9 ka for Layer 8 (Suárez-Bilbao *et al.*, 2021).

Cave lion remains come from level 1 (right upper canine, vertebra, scapula, humerus, talus, cuneiform tarsal) (65.05±19.5 ka) and level 4 (pisiform carpal, left mandible with P4 and M1) (73.1 ka) (MIS 4). This sample is associated with other remains of *Coelodonta antiquitatis, Bos/Bison, Equus caballus, Cervus elaphus, Rangifer tarandus, Capreolus capreolus, Capra pyrenaica, Rupicapra pyrenaica, (Ursus spelaeus, Canis lupus, Vulpes vulpes).*

3.4. Arrikrutz

In 1967 an almost complete skeleton of a cave lion was found in one of the galleries of the Arrikrutz cave (Oñate, Gipuzkoa, Spain) (Altuna, 1981). Later, a speleologist M. Laurino collected mammal remains in other galleries of this karst system that he gave us for study. The remains were located on the ground without stratigraphic context. 15 remains of this cave lion have been identified that belong to three adult individuals (Table 2). They were associated with the remains of ungulates (*Cervus elaphus, Capreolus capreolus, Capra pyrenaica, Rupicapra pyrenaica*) and other carnivores (*Panthera pardus, Lynx sp., Ursus spelaeus, Canis lupus, Cuon alpinus, Vulpes vulpes*).

3.5. Lezetziki I

Lezetxiki I is an archaeological site (Arrasate-Mondragón, Gipuzkoa, Spain) excavated by J.M. de Barandiarán (1956-1968) with fauna associated with hunter-gatherer occupations from the ancient Mousterian to the Magdalenian and with remains of cave lion on MIS levels 7, 6 and 4 (Altuna, 1972).

Subsequently, during the excavations led by Álvaro Arrizabalaga and María José Iriarte-Chiapusso (1996-2018), 53 cave lion remains (Table 2) have been recovered, representing a minimum of three adult individuals. These remains come from levels attributed to MIS 6 (Álvarez & Arrizabalaga, 2012).

	LG	LP	A VIII	ARR	LZ	KIX
Skull						4
Upper maxilla						1
P^4	1				1	
C^1			1			2
D^3						
Mandible			1	1	1	2
P_3				1	1	
P_4				1	1	
M_1				1		
Vertebrae			1		1	
V. lumbar					9	
V. caudal					5	
Rib					1	
Skapula			1			2
Humerus			1			2
Radius				2	2	1
Ulna					1	
Carpal			1			1
Metacarpals						
Mc II					2	
Mc III				1		
Mc IV				1	1	
Pelvis						1
Femur					2	1
Patella						1
Tibia						
Fibula					1	
Talus			1		1	
Calcaneum				2	1	2
Cuneiform			1		1	
Mt 2					2	
Mt IV					1	
Mt V				1	1	
Metapodia				4		2
Phalanx 1	1				3	2
Phalanx 2		1			3	1
Phalanx 3					1	
Sesamoid					12	
NISP	2	1	8	15	53	25
MNI	1	1	2	3	3	1

Tabla 2: Anatomical distribution of cave lion remains from the new Cantabrian sites: (LG) La Garma; (LP); La Pasiega; (A VIII) Artazu VIII; (ARR) Arrikrutz; (Lz) Lezetiki I; (K IX) Kiputz IX. / Distribución anatómica de los restos de león de las cavernas de los nuevos yacimientos cantábricos: (LG) La Garma; (LP); La Pasiega; (A VIII) Artazu VIII; (ARR) Arrikrutz; (Lz) Lezetiki I; (K IX) Kiputz IX.

3.6. Kiputz IX

The palaeontological site of Kiputz IX is formed by the sedimentary filling in the cave of the same name. (Mutriku, Gipuzkoa, Spain). It is divided into 7 levels whose chronology ranges from 32,810 ± 390 BP to 11,750 ± 60 BP (Beta Analytic, Florida, USA) (Castaños *et al*., 2012). 25 cave lion remains have been recovered, belonging to the same juvenile individual, from level F (19,870 ± 150 BP) (MIS 2). Among them are a left upper jaw with dI^3, D^3 y D^4, the two upper canines and the two hemimandibles with their corresponding canines and deciduous molariforms (Fig.). The rest of the sample is composed of postcranial elements (Table 2).

4. METHODS

The identification of the lion remains has been carried out from the morphometric characters of both the teeth and the bones. Morphological terminology and osteometric methodology have been taken from Schmid (1940), Argant (1988), Marciszak & Stefaniak (2010) and Marciszak *et al*. (2019). All measurerents are given in millimeters.

In the systematics section, the dental and postcranial material hve been compared with samples from Eurasia of the three subspecies (*Panthera spelaea fossilis, Panthera spelaea intermedia, Panthera spelaea spelaea*) of the Pleistocene. Compilations have been used that collect the most up-to-date database in this regard, indicating the tables used. (Argant & Brugal, 2017; Marciszak *et al*., 2019, 2023; Prat-Vericat *et al*., 2022).

Sexual dimorphism has been determined by comparing the dimensions of the humerus and radius with those of Diedrich (2009) and for the rest with Marciszak *et al*. (2023).

Abbreviations used in the text: **B,** breadth; **Bd,** distal breadth; **Bp,** proximal breadth; **BT,** breadth of trochlea; **GB,** Greates breadth; **GL,** Greates length; **f,** female; **L,** length; **m,** male; **M,** Mean; **MIS,** Marine Isotopic Stage; **MNI,** minimum number of individuals; **N,** number for localities; **NISP,** number of identified specimens; **SD,** smallest breadth of diaphysis.

5. RESULTS AND DISCUSSION

5.1. Osteometry of the new cave lion findings

A part of the new cave lion finds are teeth. Except for one isolated lower P/4 from La Garma, the rest are part of two jaw fragments from adult individuals (Arrikrutz, Artazu VIII) and of a jaw with the two hemimandibles of the same juvenile individual (Kiputz IX) (Fig. 2). The rest of the measurements are of appendicular bones, highlighting the sample from Lezetxiki I (Table 3).

PERMANENT TEETH								
	LP_3	BP_3	LP_4	BP_4	LM_1	BM_1	LP^4	BP^4
La Garma			32	15.4				
Arrikrutz	20.4	12.1	29	14.9	32.4	16.3		
Artazu VIII			26.3	13.4	29.5	15.2		
Lezetxiki I	20.5	11.5	30.5	15.8			37.5	20.5
MILK TEETH								
		L	B			L	B	
	dC^1l	10.2	6.7		dC_1l	13.5	5.5	
Kiputz IX	dC^1r	10.3	6.8		dC_1r	13	5.4	
	D^3l	20.5	7.5		D_3l	13.6	6.3	
	D^3r				D_3r	14	6.1	
	D^4l	5.3	9		D_4l	18.9	7.4	
	D^4r				D_4r	19.2	7.9	
LIMB BONES								
		GL	GB	Bp	SD	Bd	BT	
Artazu VIII	Humerus					87.5	65	
	Talus	57	46.5					
Arrikrutz	Radius	338		47	37	74.6		
	Radius			49.6				
	Calcaneum	119.5	54.5					
	Calcaneum	126.5	60					
	Mt V	134			14.3			
Lezetxiki I	Radius	324			39	75		

LIMB BONES								
	Radius	376		54.1	43.2	71.5		
	Mc II	118		29.5				
	Mc II	120.5		18.5	19	24.2		
	Mc IV	134		26.5	19.1	28		
	Calcaneum	143	59					
	Talus	74.6	31.7					
	Mt II	140.5		29.5	20.3	25.5		
	MT II	132.5		27.5	18.3	26		
	Mt IV	158.5		25.5	20.5	29		
	Prox. phal.	48,5		25,2	16,9	18,4		
	Prox. phal.	62,4		27,4	20,4	20,4		
	Prox. phal.	51.3		22.4	15.6	21.3		
	Mid.phal.	49.5		22.5	14.6	21		
La Pasiega	Mid.phal.	47.5		22.5	14.4	20.5		

Tabla 3: Cave lion measurements from new Iberian finds. / Medidas del león de las cavernas de los nuevos hallazgos ibéricos.

Measurment	***P. spelaea fossilis***			***P. spelaea spelaea***			***P. spelaea intermedia***		
	Marciszak *et al.*, 2019: t. S2			Marciszak *et al.*, 2019: t. S4 Marciszak *et al.*, 2023: t. S2			Argant & Brugal, 2017: t. 1 Marciszak *et al.*, 2019: t. S4		
	n	min-max	mean	n	min-max	mean	n	min-max	mean
LP^4	9	40.7-45,9	43,28	142	33.7-44.5	38.41	25	35.2-44	39.11
							Lz 37.5 m		
	Prat-Vericat *et al.* 2022: t. 1, S1			Marciszak *et al.*, 2019: t. S7 Marciszak *et al.*, 2023: t. S4			Argant & Brugal, 2017: t. 2 Marciszak *et al.*, 2019: t. S4		
LP_3	15	20.5-22.7	21.72	125	15-22	18.45	21	16.8-22.9	18.97
				Arr 20.4 m **Lz 20.5 m**					
	Prat-Vericat *et al.*, 2022: t. 1, S1			Marciszak *et al.*, 2019: t. S8 Marciszak *et al.*, 2023: t. S4			Argant & Brugal, 2017: t. 2 Marciszak *et al.*, 2019 t. S4		
LP_4	22	26.5-34.7	31.0	220	22.9-34.7	27.72	26	25.2-31.8	28.4
				Arr 29 m **Art 26.3**			**LG 32 m** **Lz 30.5 m**		
	Marciszak *et al.*, 2023: t. S9								
LM1	90	25.2-36.1	30.86	345	23.2-32.2	29.09	57	25.1-33.6	30.2
				Arr 32.4 m **Art 29.5 m**					
	Marciszak *et al.*, 2023: t. S10								
Humerus Bd	21	84.1-129.7	103.7	119	64.8-117.7	92.86	7	79.3-100.4	92.58
				Art 87.5 f					
Radius GL	8	290.4-400.4	350.86	63	282-375.7	319.4	5	300.4-332.7	306.9
				Arr 338 m **Lz 324, 376 m**					
	Marciszak *et al.*, 2023: t. S11								
Mc II	23	116.5-154.6	126.85	129	95.4-147.4	117.24	18	103.5-144.5	120.03
				Lz 118-120.5 m					
Mc IV	32	100-157.8	133.5	89	103.4-156.9	125.15	15	117.2-140.4	130.17
							Lz 134 m		
	Marciszak *et al.*, 2023: t. S12								

Measurment	*P. spelaea fossilis*			*P. spelaea spelaea*			*P. spelaea intermedia*		
Calcaneum	63	111.4-157.6	142.6	147	107.8-142.2	127.51	23	113.7-141.4	126.5
				Arr 119.5, 126.5 f Lz 143 m					
MT II	23	132.6-169.6	147.2	101	108.6-153.5	130.23	10	126.1-143.5	134.38
							Lz 132.5, 140.5		
MT IV	20	133.2-181.7	162.8	86	120.8-176.4	148.3	9	135.5-171.2	156.2
							Lz 158.5 m		
MT V	12	122.5-163.3	151.92	78	115.4-157.9	139.74	11	117.4-145.4	136.03
				Arr 134 m					
Prat-Vericat *et al.* 2022: t. 1, S1									
Talus GL	21	50.1-77	71.07	17	56-70	63.75			
				Art 57 f Lz 74.6 m					
	Marciszak *et al.*, 2019: t. S12			Marciszak *et al.*, 2019: t. S32-40					
Prox. Phal. Marc2019	29	39.5-78.6	66.14	99	35.2-76.9	60.41			
	Lz 48.5, 62.4								
	Marciszak *et al.*, 2019: t. S13			Marciszak *et al.*, 2019: t. S41-48					
Mid. Phal. Marc 2019	21	42.3-58.5	49.87	83	32.7-59.3	48.22			
	Lz 49 LP 47.5								

Tabla 4: Comparison of the measurements of Pleistocene lion subspecies in Europe with new findings in northern Iberia (Lz: Lezetxiki; LP: La Pasiega; LG: La Garma; Art: Artazu VIII; Arr: Arrikruz; m: male; f: female)./ Comparación de medidas de subespecies de león pleistoceno europeo con los hallazgos del norte de Iberia (Lz: Lezetxiki; LP: La Pasiega; LG: La Garma; Art: Artazu VIII; Arr: Arrikruz; m: macho; f: hembra).

5.2. Systematics

The morphometric variability of Middle and Upper Pleistocene Eurasian cave lion has been a recurring theme since the first findings as early as the nineteenth century. In the second half of the 20th century, some authors, due to the cranial similarities with the current lion, have proposed the existence of successive extinct species attributed to *Panthera leo*. From DNA studies (Barnett *et al.*, 2009), currently most of the authors support the existence of two species: *Panthera fossilis* (Reichenau, 1906) during the first half of the Middle Pleistocene (MIS 19-9) and *Panthera spelaea* (Goldfuss, 1810) during the Late Pleistocene (Sotnikova and Nikolskiy 2006; Marciszak and Stefaniak, 2010; Sabol 2014). Argan and Brugal, from Igue-des- Rameaux sample, propose a new subspecies *Panthera spelaea intermedia* related to upper Middle Pleistocene (MIS 10-6), although the classification of this subspecies is based more on the teeth than on postcranial elements (Argan & Brugal, 2017). Since then, it has been common to attribute lion remains to the latter subspecies, with MIS 8-6 chronology, from regions with high lion density such as Poland (Marciszak *et al.*, 2019) and Ukraine (Marciszak *et al.*, 2023).

For many authorsthat the presence of *P. fossilis* does not exceed the MIS 11-9 range. The new findings, for their chronology, it is not reasonable to attribute them to this ancient form of cave lion but to *P. spelaea* present in Europe from the end of the Middle Pleistocene to the Late Pleistocene. Therefore, it seems coherent that most of its measures are below the minimum value of *P.s. fossilis*. Only the calcaneus and astragalus of Lezetxiki exceed the maximum value of *P. spelaea*. However, they are in the overlap zone between the two species and are far from the average values of *P. s. fossilis*. Therefore, its attribution to *P. spelaea* does not seem problematic. (Table 4). The measurements of the phalanges lack systematic value due to their great variability associated with their anatomical position.

However, some differences are observed between the specimens of La Garma and Lezetxiki (MIS 6) compared to those of Artazu VIII (MIS 4), La Pasiega and Arrikrutz. These differences are reflected when comparing their dental and postcranial measurements with European samples of the three subspecies mentioned (Table 4).

The dimensions of the specimens from Lezetxiki and La Garma, with some exceptions resulting from sexual dimorphism, are larger than those from Arrikrutz and Artazu VIII. The decrease in size of *Panthera spelaea* in Europe between the end of the Middle Pleistocene (MIS 8-6) and the Late Pleistocene (MIS 5-2) is confirmed once again.

The scarcity of dental remains in Lezetxiki and La Garma does not allow their attribution to *Panthera spelaea intermedia* (Argant & Brugal, 2017) with sufficient reliability. Therefore, the presence of this subspecies in the Iberian Peninsula is a question to be resolved in the future with new findings.

5.3. Sexual dimorphism

The cave lion, like other Felidae, presents a clear sexual dimorphism that is manifested in a larger size of the limb bones of males compared to females. These differences are even observed in teeth such as the lower carnassial. Comparing the measurements of humerus, radius (Diedrich, 2009), molars, metapodia and tarsals from European samples (Marciszak *et al*. 2023) with the new findings, the sex of some individuals can be estimated (Table 5).

The distal radius breadth and the length of the calcaneus and metapodia of two Lezetxiki individuals fall within the domain of variation of males. However, the length of an Mc II, it belongs to a female. The dimensions of the LP_4 of La Garma correspond to a male (Table 4). In Arrikrutz the lower dental series and the radius belong to a male and the two calcanei to a female. The humerus and talus of Artazu VIII belong to a female and the rest of the remains to males (Table 4).

5.4. Comparative study of deciduous dentition

The morphometry of the deciduous dentition of the cave lion is a little-known question due to the scarcity of findings unlike permanent dentition. The Atapuerca sites have provided a good sample of deciduous lion dentition in Eurasia.: Trinchera Galería (1 C^s, 1 D^3, 2 D_3, 2 D_4), Sima de los Huesos (2 C^s, 2 D^3, 1 D^4) and Trinchera Dolina (1 I^2, 1 D_3,1 D_4) (García, 2003). This assemblage is only comparable witd the English site of Wookey Hole Caves in Somerset (Dawkins & Sandford, 1866) and the French site of Igue-des-Rameaux (Argant & Brugal, 2017).

The presence of an almost complete skeleton of an immature individual at the Kiputz IX site, which preserves most of the deciduous dentition (except for the incisors), is an interesting contribution. The two lower deciduous canines are very flat (except at the apex) (Fig. 2). It has a strong depression on the lingual side that facilitates the emergence of the permanent canine. In Kiputz IX, the two canines have a well-developed mesolingual cusp that does not occur in other specimens (Broom, 1948). The mesial face is convex and the distal face has a well-marked ridge that separates the lingual and vestibular sides.

The deciduous lower molars have a number of cusps that are not present in permanent teeth at both the mesial and distal ends. The mandibular body is very robust, especially in the area of the symphysis and there is a clear space between the distal end of the D4 and the ascending ramus of the mandible to allow the eruption of the carnassial molar (Fig. 2).

D3 has similar structure to permanent premolars with a well-marked main cusp (protoconid), a small me-

	MALES			FEMALES			References
	n	min-max	mean	n	min-max	mean	
LM_1	6	29.7-34.7	31.38	5	22-26.1	24.84	Marciszak *et al*., 2023: t. S9
	Arr 32.4 Art 29.5						
Humerus Bd	13	92-103	97.5	5	80-90	84.4	Diedrich, 2009: Fig. 10 A
	53	90.4-115.4	97.2	45	64.8-90.5	82.6	Marciszak *et al*., 2023: t. 10
				Art 87.5			
Radius Bd	5	70-76	74.8	6	64-69	66.1	Diedrich, 2009: Fig. 10 B
	Lz 71.5, 75 Arr 74.6						
Mc II	32	120.6-147.4	130.2	9	110.8-119.7	116.3	Marciszak *et al*., 2023: t. 11
	Lz 120.5			**Lz 118**			
Mc IV	25	122.6-156.9	138.6	36	103.4-119.4	113.3	Marciszak *et al*., 2023: t. 11
	Lz 134						
Calcaneum	24	130.5-142.2	136.4	8	110.3-123.5	117.5	Marciszak *et al*., 2023: t. 12
	Lz 143			**Arr 119.5, 125.6**			
Mt II	30	127.3-153.5	145.2	5	119.8-122.4	121.2	Maciszak *et al*., 2023: t. 12
	Lz 132.5, 140.5						
Mt IV	32	153.6-176.4	164.2	5	114.9-144.1	133.4	Marciszak *et al*., 2023: t. 12
	Lz 148.5						
Mt V	36	129.2-157.9	149.7	11	115.4-125.6	119.8	Marciszak *et al*., 2023: t. 12
	Arr 134						

Tabla 5: Sexual dimorphism in lower carnasial and the postcranial long bones. / Dimorfismo sexual en la carnicera inferior y en huesos largos postcraneales.

sial cusp and two small distal cusps. The morphology of D4 is similar to that of permanent carnassial (M1). There are two main cusps (paraconid and protoconid), separated by a notch, as in the other felines. The protoconid is longer and higher than the paraconide, it has a clear metaconid on its distal edge and a small talonid.

The dimensions of the Kiputz IX specimen fall within the variation of several European samples: Somerset (Dawkins & Sandford, 1866), Atapuerca (García, 2003), Kudaro (Baryshnikov, 2011) and L'Escale (Bonifay, 1971) (Table 6).

6. CONCLUSION

The description and study of cave lion remains from 3 new sites and unpublished materials from other already known sites, has significantly increased the presence of this during the Middle and Upper Pleistocene of the Iberian Peninsula.

The comparative analysis of the dental and postcranial material of the new findings has allowed their attribution to *Panthera spelaea* (Goldfuss, 1810). The metric differences between the specimens of Lezetxiki and La Garma (MIS 6) and those of Artazu VIII (MIS 4) and Arrikrutz, confirm the decrease in size of the species between the end of the Middle Pleistocene and the Late Pleistocene. However, the scarcity of data does not yet allow us to establish with certainty the presence of *Panthera spelaea intermedia* (Argant & Brugal, 2017) in Iberia.

The dimensions of the long bones of the legs allow sexual attributions of some individuals to be made following the criteria applied in other Eurasian sites. The presence of an upper jaw and the two hemimandibles with the dental series in the cub of Kiputz IX, provides metric data of interest taking into account the scarcity of data on the deciduous teeth of this species.

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	LdC^u	WdC^u	LD^3	WD^3	LdCi	WdCi	LD_3	WD_3	LD_4	WD_4
Atapuerca										
SH1	9	5.7	24.8	8.3						
SH2	8.9	5.7								
TD1									18,5	7,3
TD2									19,7	8
TG10d141									18,4	7,1
TG10d54							13.5	6		
TG10bG17-51									20,5	8
Kiputz IX	10.2	6.7	(20.5)	(7.5)	13.5	5.5	13.6	6.3	18.9	7.4
	10.3	6.8			13	5.4	14	6.1	19.2	7.9
Somerset										
P spelaea 1					12,7	5,3				
P spelaea 2					12,2	5,6				
P spelaea 3					14	6,4	15,24	6,4	20,3	7,7
P spelaea 4							13	5,6	17	6,4
P spelaea 5									17,8	6,9
P spelaea 6							15,2	6,4		
P spelaea 7									21,6	6,4
Westb1							12,7	6,4		
Westb2							12,2	6,6		
Westb3							11,2	5,3		
Kudaro							13	5,8		
L'Escale							13.2	6.2	17.8	7.1

Tabla 6: Deciduous tooth measurements of cave lion. Atapuerca (García, 2003), Somerset (García, personal communication), Kudaro (Baryshnikov, 2011), L'Escale (Bonifay, 1971). / Medidas de dientes de leche de león de las cavernas. Atapuerca (García, 2003), Somerset (García, comunicación personal), Kudaro (Baryshnikov, 2011), L'Escale (Bonifay, 1971).

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