



# Pleistocene leopards in the Iberian Peninsula: New evidence from palaeontological and archaeological contexts in the Mediterranean region



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## ARTICLE INFO

### Article history:

Received 7 April 2015

Received in revised form

7 July 2015

Accepted 11 July 2015

Available online xxx

### Keywords:

*Panthera pardus*

Late Pleistocene

Taxonomy

Distribution

Taphonomy

Iberian Peninsula

## ABSTRACT

This study analyses the fossil record of leopards in the Iberian Peninsula. According to the systematic and morphometric features of new remains, identified mainly in Late Pleistocene palaeontological and archaeological sites of the Mediterranean region, they can be attributed to *Panthera pardus* Linnaeus 1758. The findings include the most complete leopard skeleton from the Iberian Peninsula and one of the most complete in Europe, found in a chasm (Avenc de Joan Guitón) south of Valencia. The new citations and published data are used to establish the leopard's distribution in the Iberian Peninsula, showing its maximum development during the Late Pleistocene. Some references suggest that the species survived for longer here (Lateglacial-Early Holocene) than in other parts of Europe. Finally, the contexts of appearance and origin of leopard remains are described and the processes of interaction with prehistoric human groups are assessed.

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## 1. Introduction

The leopard (*Panthera pardus* Linnaeus 1758) is a medium-sized member of the Felidae family with solitary, territorial habits. The males are usually heavier and have larger body dimensions than females. Their ubiquitous and eurythermal nature and their opportunistic behaviour allow them to adapt well to different biotopes. Nowadays, different subspecies are distributed throughout different areas of Africa and Asia (Turner and Antón, 1997; Bertram, 1999; Hayward et al., 2006; Macdonald et al., 2010; Stein and Hayssen, 2013).

The species is now extinct in Europe, but during the Pleistocene it was widely distributed (Sommer and Benecke, 2006), with occurrences throughout much of this continent (Bonifay, 1971;

Kotsakis and Palombo, 1979; Spassov and Raychev, 1997; Fischer, 2000; Cardoso and Regala, 2006; Baryshnikov, 2011; Marciszak et al., 2011; Testu et al., 2011; Altuna and Mariezkurrena, 2013; Diedrich, 2013; Sauqué and Cuenca-Bescós, 2013; Sauqué et al., 2014a; Ghezzeo and Rook, 2015). The earliest appearance of *P. pardus* in Europe could be the Early Pleistocene remains found at Le Vallonnet (Moullé et al., 2006), although most leopard identifications in ancient contexts have been questioned and the remains reassigned to *Puma pardoides* (Hemmer, 2001; Argant, 2004; Hemmer et al., 2004; Madurell-Malapeira et al., 2010; Cherin et al., 2013). The presence of other felines during this phase, such as the puma, jaguar or cheetah, could explain the later appearance of the leopard (Testu, 2006). The first confirmed European evidence of the leopard corresponds to the Middle Pleistocene, with its maximum expansion towards the end of this phase and the beginning of the Late Pleistocene (Turner, 1995; Crégut-Bonnouire, 1996; Testu, 2006). The species' survival in Europe is uneven and varies geographically; in France the last appearances correspond to the Early Upper Palaeolithic, before the Last Glacial Maximum

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(LGM) (Bonifay, 1971; Crégut-Bonnoure, 1996), in Jaurens (Ballesio, 1980) and Isturitz (Altuna, 1972). In Italy, the last occurrences appear in the MIS 3 levels of Equi Cave (Ghezzi and Rook, 2015), in the Aurignacian levels of Fumane Cave (Cassoli and Tagliacozzo, 1991) and the LGM levels of Arene Candide (Cassoli and Tagliacozzo, 1994; Sommer and Benecke, 2006). In central Europe it has been considered that the last appearance of the leopard would date to the Lower Pleniglacial (Wolsan, 1993), but two records in Ettingen, Switzerland, and Teufelsbrücke, Germany, suggest that the species may have survived in the area during the Lateglacial (cited in Sauqué and Cuenca-Bescós, 2013). In the Balkans (Triagalnata) the species is recorded during the Lateglacial

(Spassov and Raychev, 1997; Sommer and Benecke, 2006). The last appearance of leopard on the continent is documented in Greece (Vraona) (Nagel, 1999) and in the Iberian Peninsula (see sites listed in Sauqué and Cuenca-Bescós, 2013; see also Table 13 in this study), with several records during the Lateglacial and Early Holocene. Some marginal areas of the continent could have acted as a refuge for the species during the harshest phases (O'Regan, 2008).

In the Iberian Peninsula, the leopard's presence during the Middle Pleistocene is limited and most appearances are from the Late Pleistocene onward (Sauqué and Cuenca-Bescós, 2013). They are normally assemblages consisting of few remains (isolated teeth, metapodials or phalanges) that are found in Middle and Upper

**Table 1**  
New leopard remains from palaeontological and archaeological contexts of the Mediterranean Iberia (MNE and MNI). The age of the individuals is expressed in years (Ad: adult).

Elements	AJG	Malladetes	REC I	REC II	Bolomor	C. Negra	Horadada	C. Borràs	Meravelles
Cranium	1								
Maxilla				1					
Mandible	1								
C1			1						
i1	1								
m1		1							
Scapula	2								
Humerus	2			2					
Radius	2		1	2					
Ulna	2			2				1	
Scapholunate	2		1	1					
Pyramidal	2								
Pisiform	2		1	1					
Trapezium	2								
Trapezoid	2								
Capitate	2								
Hamate	2								
Mc I	2			1					
Mc II	2		2	1					
Mc III	2		1						
Mc IV	2		2	1		1			1
Mc V	2				2				
Hyoid	1								
Sternum	8								
Cervical V.	7								
Thoracic V.	13								
Lumbar V.	7			1					
Sacrum	1								
Caudal V.	22		8	1					
Ind. V.			1						
Ribs	25		2						
Pelvis	1	1							
Femur	2								
Tibia	2		1	1					
Fibula	1								
Patella	2		1						
Calcaneus	2			2		1			
Talus	1		1	1					
Cuboid	2			1					
Navicular	2			1					
Cuneiform I	2								
Cuneiform II	1								
Cuneiform III	2			1					
Mt I	2								
Mt II	2			1					
Mt III	1		1		1				
Mt IV	2		1	1	1				
Mt V	2		1	1					
1st phalanx	17	2	8	5			1		
2nd phalanx	16		5	5		1			
3rd phalanx	15		1	2					
Sesamoid	25								
Metapodial				2					
Total MNE	221	4	40	38	4	3	1	1	
Total MNI	1	2	2	1	2	1	1	1	1
Age	1.5 to 2	<1/Ad	Ad/7 to 10	3 to 4	Ad/Ad	Ad	Ad	Ad	Ad

Palaeolithic archaeological sites or palaeontological contexts, while partial or complete skeletons are rare (Arribas, 1997; Cardoso and Regala, 2006).

Various taphonomic studies have shown the leopard's ability to accumulate and modify bone remains in archaeological sites (de Ruiter and Berger, 2000; Domínguez-Rodrigo and Pickering, 2010; Sauqué et al., 2014b; Gidna et al., 2015) as a consequence of competition with hominins and other carnivores for access to prey and occupation of caves (Brugal and Fosse, 2004). The leopard is a solitary, territorial hunter (Bertram, 1999; Hayward et al., 2006) that acts on all types of prey, although it mainly targets those within a weight range of 20–80 kg (Mills and Harvey, 2001). Despite not being a selective hunter (Hart et al., 1996; Hayward et al., 2006), it prefers prey with an optimum size of 23 kg (Hayward et al., 2006).

As regards the taxonomy of the European Pleistocene leopard, the theory put forward by Diedrich (2013) is that there are four subspecies, the most recent being *P. pardus spelaea* Bächler 1936, also known as the “Ice Age Leopard”, a subspecies from the Late Pleistocene with its own skeletal morphology and differences with respect to the present-day leopard.

In contrast to this, Ghezzi and Rook (2015) recently suggested that all the European leopards belong to a single species, *P. pardus*, although there is no genetic analysis yet. This theory is based on morphological differences in the Equi population that they link to intraspecific variability.

This paper presents new leopard remains from Pleistocene palaeontological and archaeological contexts in the Mediterranean region of the Iberian Peninsula. Part of this study will describe a leopard skeleton recovered in Avenc de Joan Guitón (southern

Valencia), the most complete example found in this geographical area, which provides very valuable information and enables us to compare its morphometric characteristics with other findings. A review and study is also made of remains from ancient excavations in the Valencia area. Based on the morphometric characteristics of several of the remains studied here, they can be attributed to *P. pardus*, although they show many similarities with the subspecies *P. pardus spelaea*.

The purpose of this study is also to review and compile the information, so all citations of leopards in the Iberian Peninsula corresponding to archaeological and palaeontological contexts are recorded in order to analyse the chronology of the species' appearance, expansion and disappearance in the area. Attention is also given to the origin of the remains (natural or anthropogenic) and the characteristics of the contexts of appearance in order to describe the possible processes of interaction between leopards and prehistoric human groups.

## 2. Methods and materials

### 2.1. Methodology

The reference collections of the Museu de Prehistòria de València (MPV) and Universidad de Zaragoza were used for the taxonomic identification of the leopard remains, as was the bone collection of [archeozoo.org](http://archeozoo.org). The following fossil collections were consulted: Museu de Ciències Naturals de Barcelona, Museu Geològic del Seminari de Barcelona, Museo de Huesca, Museo de Ciencias Naturales de la Universidad de Zaragoza, Museo Nacional de Ciencias Naturales in Madrid, Instituto Alavés de la Naturaleza

**Table 2**

Cranial measurements of leopard fossils from the Iberian Peninsula compared to other European individuals. Avenc de Joan Guitón (AJG-1); Algar da Manga Larga (nn; Cardoso and Regala, 2006); Allekoitze and Aintzulo (nn; Altuna and Mariezkurrena, 2013); Abric Romaní (nn; Cáceres et al., 1993); Equi (IGF15111V/1, IGF15110V, IGF185V/1, IGF10036V; Ghezzi and Rook, 2015); Observatoire (nn; Boule and de Villeneuve, 1927); Vjetrenica (VJE-1; Diedrich, 2013); Monte Sacro (MPUR/V1191; Kotsakis and Palombo, 1979) [Approximate measurement]. nn (no number).

Crania	AJG	AML	ALL	AIN	ARO	EQC	OBS	VJE	MSA
1 Total L	195.2	183	221.7	[210.5]		191-196-255-239	223	214	250.5
2 Condylobasal L	184.8	165	204.6	[195]			209		
3 Basal L	166.5	152.6	192.6	184.5		170-175-210-195.8			
4 Basicranial axis	541		64.1						
5 Basifacial axis	110.9		130.2						
6 Neurocranium L	122	131.1	138	127					
7 Upper neurocranium L	106.7	[105.7]							
8 Viscerocranium L	100	[101.5]			97				
9 Facial L	67.2		94.5	[91]					
10 Lateral L snout	65.3	57.2							
11 Median palatal L	90.9						83		
11a Palatal L	94.1	76.2	100.5	[98.5]					
12 Cheektooth row L	48.5	45.7	53.4						
13 Premolar row L	46.6	43.4	48.9	52.5	49.9				
15 P4 alveolus L	23.1	21.3							
16 Greatest D auditory bulla	33	24	35.2	30					
17 Least D auditory bulla	22.4	18.8	25.3	20.5					
18 Greatest mastoid B	85.7	79.2	93	[86]			93		
19 Greatest B occip. condyles	[40]	[39]	42.9	[41]		39.6-41.6-49-48	43	44.7	48
20 Greatest B fora. magnum	22.7	21.7	23.7	19.2					
21 H foramen magnum	18.7	17.2	15.8	15.9					
22 Greatest neurocranium B	72.4	69.1				69.8-78.4-80-75.9			
23 Zygomatic B	130	>129.4					150		
24 Frontal B	70.6	>72.2					68		
25 Least B between the orbits	43.3	43.1					44		
26 Greatest palatal B	77.5	75.9				86.7-91.2-112-89.6	91		
27 B canine alveoli	52.8	[53]	60	56.5			60		
28 Least B aboral supraorb. p.	44.2	45.2	43.4	44.5			43		
29 Facial B between infraorb. f.	55.7	54.4	51.7	61					
30 Greatest inner L orbit	35.4	>33.1			36				
31 Greatest inner H orbit	41.6	40.4							
32 H occipital triangle	[52.9]	52.1	58.8						

**Table 3**  
Mandibular measurements of leopard fossils from the Iberian Peninsula compared to other European individuals. Avenc de Joan Guitón (AJG-1); Algar da Manga Larga (nn; Cardoso and Regala, 2006); Allekoaitze (nn; Altuna and Mariezkurrena, 2013); Torrejones (nn; Arribas, 1997); Abric Romaní (nn; Cáceres et al., 1993); Zafarraya (UC9/P14/B3/47; Barroso et al., 2006); Los Rincones (Ri10/C1/1; Sauqué and Cuenca-Bescós, 2013); L'Arago (E14EFN11000; Testu, 2006; Testu et al., 2011); Triagalnata (nn; Spassov and Raychev, 1997); Karañ E (17H26110, 18H26111; Testu, 2006). [Approximate measurement], nn (no number).

Mandible	AJG	AML	ALL	TOR	ARO	BZ	LR	ARA	TRI	KAR
1 Total L	135.1	123.7	150.2		141.5	151.5	132	137.7	134	
2 L ident. Condyle/ang proc-infradent	127.7	120.2	143.3				122			
3 L cond. Proc. aboral border c1 alveolus	[111.8]	107.1	129.2		123.7					
4 L ident. Cond./ang. Proc.-abo. Bor. c1 alv.	[108.4]	102.4	125.5		118.1					
5 L cheektooth row p3-m1 alveoli	45.7	44.3	51.1	44.7	49.2	53.8	49	43.7	49	50.5–50.3
7 L m1 alveolus		17.5					18.8			19.8–19
8 H vertical ramus	61.3	58.7					52.5	63.5		
9 H mandible behind m1	29.5	27.7	30				27.2	28.2	28	31.2
10 H mandible in front p3	27	28.9	28.2			33		27.4	26.5	31.3
L diasteme c1-p3	15.3	11.4				14.7		14.2	10.1	15.9
L p3-m1	[46.5]	44.3					32		49	49.3–49.5
L p3-p4	[29]	27.3						27.4		31.7–31.2

(IAN) in Vitoria and North Carolina Museum of Natural Sciences and Smithsonian National Museum of Natural History in the United States. Various articles were also used: Schmid (1940), Testu (2006), Sims (2005, 2012), Christiansen (2008), Diedrich (2013), Sauqué and Cuenca-Bescós (2013), Indu et al. (2013), Podhade et al. (2013, 2014a and b), Sauqué et al. (2014a) and Ghezze and Rook (2015). For the description of the cranial and mandibular material from Avenc de Joan Guitón (AJG), other well-preserved Late Pleistocene leopard skulls from the Iberian Peninsula were used as comparative paratypes: Algar da Manga Larga (Cardoso and Regala, 2006), Allekoaitze and Aintzulo (Corral, 2012; Altuna and Mariezkurrena, 2013). Where the remains of both sides are present, the best preserved element is used in the morphological description, provided that no differences are observed. The fossil remains presented in this paper are deposited in the MPV.

The new specimens were quantified according to the minimum number of elements (MNE) and the minimum number of

individuals (MNI) (Lyman, 2008). The age at death was estimated by the state of tooth wear (Stander, 1997) and the degree of joint fusion of the bones (Morris, 1972). The sex was determined according to the cranial features described by Ghezze and Rook (2015), although the cranial and postcranial dimensions of the remains were also taken into account as a guideline (Diedrich, 2013). Elements with trauma or fractures were described according to Bartosiewicz (2013).

Measurements are expressed in millimetres and were taken using digital callipers (TESA CAL-IP67, Swiss) according to the method proposed by von den Driesch and von (1976). All metric information is shown in Tables 2–12, where the dimensions of the new remains are presented alongside those of published materials, mainly from the Iberian Peninsula. For comparative purposes, we also present the skull and dentition measurements of present-day leopards, pumas and snow leopards, recorded by Testu (2006) and Cardoso and Regala (2006) (see Supplementary material).

**Table 4**  
Upper dentition measurements of leopard fossils from the Iberian Peninsula. DMD (mesial-distal diameter), DVL (vestibular-lingual diameter), and H (height). Avenc de Joan Guitón (AJG-1); Racó del Duc II (REC-586); Cova Negra (CN2013, LIMP/RTV); Allekoaitze and Aintzulo (nn; Altuna and Mariezkurrena, 2013); Abric Romaní (nn; Cáceres et al., 1993); S'Espasa (nn; Estévez, 1975–76); Zafarraya (P3: UE32/Q8/122/1, P9R493; Barroso et al., 2006) (P4: B2/93/Q6/263, B2/91/Q8/127/1, B2/91/P7/17/51; Testu, 2006); Torrejones (nn; Arribas, 1997); Cova del Gegant (nn; Viñas and Villalta, 1975); Bolinkoba (nn; Castaños, 1987); Algar da Manga Larga (nn; Cardoso and Regala, 2006); Figueira Brava, Gruta do Escoural and Lorga da Dine (nn; Cardoso, 1993, 1996). [Approximate measurement], nn (no number).

Upper dentition	AJG	REC II	CN3	ALL	AIN	ARO	ESP	BZ	TOR	GEG	BOK	AML	FB	ESC	LDD
I1 DMD															
DVL	3.7–3.2														
I2 DMD		5.7–5.7													
DVL	3.5–3.8	3.9–4.1													
I3 DMD		8.7–9													
DVL	4.4–4.5	7.6–7.7													
C1 DMD	14–14.1						12.5				14.1–12.1–14.3–13.5	12.3	12.9	14.7	14.3
DVL	[12.7]–[12.7]										11.5–11–9.3–10.6	9.8	10.5	10.2–12.2	10.3
P2 DMD	4.4														
DVL	3.1														
P3 DMD	16.4–16.2			18.7	19.2	18.7	19.4	17.3–20.3		17.5	19.1	15	16.2		
DVL			9.3	9.3	9.1	9.4	8.7–9.1	12.9–14		8	8.3	7.8	8		
DMD proto								5.8–7.3							
DMD talon															
P4 DMD ext	23.2–23.3		26.5		25.7	24.7	[24.8]	24.4–24.5–26.5	22.6	26		23.8	25.1	25.1–28.6	
DMD mid			25.1			24.4		23.1–24.2–25.5							
DMD int			25.8			25.6		24.1–24.2–26.4				23.4	25.1	26–27.9	
DVL ant			13.3	13.9	13.3	12.9	13.5	12.1–12.9–13.7	12			12	13	12.5–15	
DVL mid			9.5												
DVL post			8.2			8.3		7.9–7.7–9.4							
DMD para	9.8–9.7		10.1			10.1		11.2–9.9–11.3							
DMD meta	8.8–8.7		11.1			10.4		10.5–10.9–11.6				9.3	10.1	10.4–12.1	
DMD p + m	17.9–18.2		20			19.6		20–19.4–20.7							
H para	13.1		13	13.2	12.5	13.3		12.9–13.1–14.6							
H proto			5.5			5.6		4.3–3.8–4.7							



**Table 5**

Lower dentition measurements of leopard fossils from the Iberian Peninsula (also including Caune de l'Arago), DMD (mesial-distal diameter), DVL (vestibular-lingual diameter), and H (height), Avenc de Joan Guitón (AJG-1); Cova Negra (CN 6240; No. 30240); Lezeixiki (nn: Altuna, 1972); Aliekkoaitze (nn: Altuna and Maniezkurrena, 2013); Abric Romani (nn: Cáceres et al., 1993); S'Espasa (nn: Estévez, 1975–76); Zafarraya (c1: UC9/P14/B3/47, ind/R4947, UC42/Q8/I28/61, UB5/P6/4/118), (p3: UC9/P14/B3/47, P12/R174, UC36/Q15/E3/R50157, UA2/Q6/I2/R40100, UB5/P6/4/118), (p4: P7/N1R3740, R8/R2356, UE25/8/47/R40137, UC19/P8/11/R40136, UC19/P7/11/R40376), (m1: UC9/P14/B3/47, R8/R2356, UB36/I5/106, UC7/P6/16/318) (Bartoso et al., 2006); Torrejones (nn: Aribas, 1997); Amalda (nn: Altuna, 1990); Bolinkoba (nn: Castanos, 1987); Atxuri (nn: Castanos, 1987); Los Rincones (R10/C1/1; Sauque and Cuenca-Bescós, 2013); Algar da Manga Larga (nn: Cardoso and Regala, 2006); Figueira Brava, Escoural, Lorga da Dine, Fontainhas and Pedreira das Salemas (nn: Cardoso, 1993, 1996); L'Arago (E14/EFN1/1000, E14/EFN1/1001; Testu, 2006). [Approximate measurement], nn (no number).

Lower dentition	AJG	CN3	LEZ	ALL	ARO	ESP	BZ	TOR	AMA	BOK	ATX	LR	AMIL	FB	ESC	LDD	FON	PDS	ARA
i1	DMD 3.9																		
	DVL 1.9																		
	[13.5]–[14.8]																		
c1																			
	DVL 12.7–[12]																		
p3																			
	DVL 6.9–6.5																		
	H protoconid 7.7–7.4																		
p4																			
	DMD [15.7]	17	20	18.9	18.1	20	17.5–17.1–17.5–19.6–18.6												
	DVL	8	9.6	9.8	9.6	9.5	7.8–8.4–7.8–8.6–8.4												
	DVL ant	6.9					8.5–8.7–9.5–9.4												
	DMD protod.	8.2																	
	H protoconid	10.3																	
m1																			
	DMD [19]																		
	DVL																		
	DMD protod.																		
	DMD paracod.																		
	H protod.																		
	H paracod.																		
	H crown u. SM																		

All citations of Iberian Peninsula leopards are shown in Fig. 14 with further details in Table 13, showing the altitude of the site, context of appearance, chronology of the finding, number of remains/individuals/presence, taxonomic attribution, level, bibliographical references and an identification number for each site.

## 2.2. Sites and remains

### 2.2.1. Avenc de Joan Guitón

The chasm is located in the vicinity of Fontanars dels Alforins, in the south of the province of Valencia (Spain), in the east of the Iberian Peninsula (Fig. 1A). It is situated at approximately 770 masl in an area covered by typical Mediterranean vegetation of pine trees and holm oaks known as Racó del Colmenar (Fig. 1B), its former name, in the upper axis of an anticline formed by Cretaceous calcareous material on the SE face of the Serra Grossa mountain range. AJG lies on the crossover point of two faults; the chasm runs along the first of these faults in a N–S direction, while the second (NE–SW) affects its continuity to the south, cutting across the fracture perpendicularly (Fig. 1C).

This place has been frequented by many speleological groups and has been the subject of various descriptive and topographic studies. In 2013, two of the authors (VS and RD), from the *Club d'Espeleologia l'Avern d'Ontinyent*, found various bone remains in a new, unexplored area.

AJG is a very complex cave in terms of its development and morphology (Fig. 2A). It consists of various karst systems running N and S that reach –211 and –161 m, respectively, with horizontal galleries that form superimposed chambers. The *Leopard Gallery* is very difficult to access, as there are a number of technical difficulties with vertical sections that require speleological knowledge. After passing various pits, horizontal sections, slopes, loose blocks and narrow passages, we reach a small vertical fracture about 30 cm wide covered with boulders. After removing the boulders, we reach a flat-ceilinged gallery that is 40 m long ending in a 6-m vertical section, where the bone remains are located at a depth of about 150 m in an area far away from the current vertical mouth to the cave (Fig. 2B). It would have been impossible for the animal to reach this place by itself via the current entrance, so it can be assumed that the cave had other closer entrances in the past.

The photographs taken showed that the remains belonged to a feline of the *Panthera* genus, possibly a leopard. The MPV and the Museu Arqueològic d'Ontinyent i la Vall d'Albaida (MAOVA) therefore undertook an initiative in collaboration with the aforementioned speleologists. The material was recovered with the authorization of the Directorate General for Heritage of the Valencian Regional Government (2013/0697-V (SS.TT.)).

The feline skeleton was found in the area described (Fig. 2C). The materials were photographed and stored by anatomical group and side. The process was recorded by photography and video. The remains belong to an individual leopard and no other specimens were found. The different elements were found in anatomical semiconnection, some bones were joined by concretion and they are barely covered by sedimentation; others, such as the cranium, were somewhat displaced and half-buried.

Once the remains had been recovered and adequately packaged, they were moved to the MPV for cleaning and consolidation. Controlled drying was performed using ethyl alcohol and acetone impregnations to avoid stress. Some of the remains were in a very delicate state and they need to be consolidated with 10% and 20% Paraloid B-72. A complete consolidation and restoration plan was therefore developed. After these measures had been taken, it was observed that the front of the individual was better preserved than the rear and the right side was better than the left. Many of the remains presented different levels of concretion; the analyses

**Table 6**

Forelimb measurements of leopard fossils from the Iberian Peninsula. Scapula: Avenc de Joan Guitón (AJG-2, 29); El Salt (D6/X/La/Lev6/3). Humerus: AJG (AJG-3, 30); Racó del Duc II (REC-568); Aintzulo (nn; [Altuna and Mariezkurrena, 2013](#)); Cova Negra (nn; [Martínez, 1996](#)); Lezetxiki (nn; [Altuna, 1972](#)); Cova del Gegant (nn; [Viñas and Villalta, 1975](#)); Los Rincones (Ri10/N10/5, Ri10/GL1/33; [Sauqué et al., 2014d](#)). Radius: AJG (AJG-4, 31); Racó del Duc I (REC-614); Zafarraya (UB5/P6/14/123, Q6/R5143; [Barroso et al., 2006](#)); Bolinkoba (nn, [Castaños, 1987](#)); S'Espasa (nn; [Estévez, 1975–76](#)); Lezetxiki (nn; [Altuna, 1972](#)); Los Rincones (Ri10/N11/18, Ri10/N10/216, Ri10/O14/41; [Sauqué et al., 2014d](#)). Ulna: AJG (AJG-5, 32); Racó del Duc II (REC-569); Cova Negra (nn; [Martínez, 1996](#)); Zafarraya (UE29/Q7/I19/184; [Barroso et al., 2006](#)); Cau d'En Borràs (CBO-1); Aintzulo (nn; [Altuna and Mariezkurrena, 2013](#)); Los Rincones (Ri10/O13/120; [Sauqué et al., 2014d](#)). Scapholunate: AJG (AJG-6); Racó del Duc I (REC-634); Zafarraya (UB6/P6/15/299, UG39/P10/25/161; [Barroso et al., 2006](#)); Los Rincones (Ri10/GL1/53, Ri10/GL1/54; [Sauqué et al., 2014d](#)). Pyramidal: AJG (AJG-7). Pisiform: (AJG-8); Racó del Duc I (REC-653); Racó del Duc II (REC-593). Trapezium: Avenc de Joan Guitón (AJG-9). Trapezoid: AJG (AJG-10); Zafarraya (UC19/P7/I11/R40256, UE25/P10/2e/R5754b; [Barroso et al., 2006](#)). Capitate: AJG (AJG-11); Zafarraya (UE25/P19/D5/R40024; [Barroso et al., 2006](#)). Hamate: AJG (AJG-12). [Approximate measurement]. nn (no number).

Scapula	AJG	ESA						
BG	24.6–24	24.8						
GLP	38.1–38	42.4						
LG	31.5–30.1	34.8						
SLC	34–32	37						
Humerus	AJG	REC II	AIN	CN2	LEZ	GEG	LR	
GL	212–212		236.9					
Bp ap	53.4–54.2							
Bp t	42.6–42							
SD	19–18.4		18.4					
Bd ap	30.7–[31.8]					34.6		
Bd t	53–[54.7]	55.7	54.9	51.4	50	51		47.6–53.6
Radius	AJG	REC I	BZ	BOK	ESP	LEZ		LR
GL	183.5	184.3						
Bp ap	17.8–17.4	16.5	17.2–18.4					
Bp t	23.8–24.4	24.8	23.6–27.1	25.2	26.1	24–24.3		22.2–23.2
SD	16.8	15.8		17.8	17.1	18.8		15.8
Bd ap	20.6–[22.1]	21.3						
Bd t	34–[34.5]	35.7			37.2	40.7		40.6
Ulna	AJG	REC II	CN2	BZ	CBO	AIN		LR
GL	226							241
Bp ap	30.2–30	42.1		33.6				
Bp t	21	22		22.7				
LO	40.7							
SDO	28.5					28.2		
DPA	32.3–32.8				[36.4]	35.8		
BPC	28.8		27.8		[26.5]			30.81
Bd ap	21.8							
Bd t	10.5			12				
Scapholunate	AJG	REC I	BZ	LR				
DAP	20.3	21.9	25–25.6					
DT	27.8	28.4	29.3–32	29.9–28.8				
H	17.1	17.1	19.2–18.3					
Pyramidal	AJG							
DAP	11.3							
DT	15.4							
H	7.3							
Pisiform	AJG	REC I	REC II					
DAP	23.4	24.7	27.3					
DT	14.8	14.6	15.7					
H	14.2	14.9	16.3					
Trapezium	AJG							
DAP	10							
DT	15.9							
H	9.5							
Trapezoid	AJG	BZ						
DAP	12.6	15.6–13.8						
DT	14.4	17.4–18.2						
H	7	9.9–7.3						
Capitate	AJG	BZ						
DAP	20.2	22.1						
DT	13	10.1						
H	13.5	14.8						
Hamate	AJG							
DAP	17.7							
DT	12.5							
H	15.3							

carried out on two samples by Arte-Lab S. L. (XRD, FTIR, SEM-EDX) confirmed that it was calcium carbonate (aragonite) associated with contamination by clays, caused by external diagenetic processes. As a result of these processes the cranium and mandible were attached to each other, although for now their conservation is the priority and it has been decided that they should not be separated.

The skeleton is almost complete and the bones are fused ([Table 1](#); [Fig. 3](#)). All the teeth were still in the maxilla and mandible, except for a lower incisor that was found on its own. Some bones are missing from the hindlimb. As regards the age at death of the individual, it has all its permanent dentition but it is not worn, so it could have been between 1.5 and 2 years old ([Stander, 1997](#)).

Signs of trauma and/or fractures were found on several of the

**Table 7**

Metacarpal measurements of leopard fossils from the Iberian Peninsula. Mc I: Avenc de Joan Guitón (AJG-13); Racó del Duc II (REC-606); Zafarraya (UC21/P10/11R40141; Barroso et al., 2006); Bolinkoba (nn; Castaños, 1987). Mc II: AJG (AJG-14); Racó del Duc I (REC-612, 635); Racó del Duc II (REC-580); Cova Negra (nn; Pérez, 1977); Cueva Merino (CME-112; Sarrión, 1984); Zafarraya (UC33/P10/2e195, UG38/P10/2i/140, D22/P7/114/281; Barroso et al., 2006); Bolinkoba (nn; Castaños, 1987); Algar da Manga Larga (nn; Cardoso and Regala, 2006); Escoural (nn; Cardoso, 1993). Mc III: AJG (AJG-15); Racó del Duc I (REC-620); Lezetxiki (nn; Altuna, 1972); Los Rincones (Ri10/GL1/16; Sauqué et al., 2014d); Algar da Manga Larga (nn; Cardoso and Regala, 2006); Zafarraya (UG37/Q15/E3621, UB5/P6/14/84, UG39/Q89/127/57, ind/R1960; Barroso et al., 2006); Bolinkoba (nn; Castaños, 1987). Mc IV: AJG (AJG-16); Racó del Duc I (REC-622, 636); Racó del Duc II (REC-590); Cova del Corb (nn; Sarrión, 1990); Cova Meravelles (116235); Cova Negra (CN13/LIMP/RTV); S'Espasa (nn; Estévez, 1975–76); Lezetxiki (nn; Altuna, 1972); Zafarraya (UG36/Q15/E2/583; Barroso et al., 2006); Los Rincones (Ri10/O13/408, Ri10/GL1717; Sauqué et al., 2014d). Mc V: AJG (AJG-17); Cova del Bolomor (CB97/EI/SUB/XIII/negro/82244, CB13/G13/XIII/CU3/190669); Zafarraya (ind/R1029; Barroso et al., 2006); Bolinkoba (nn; Castaños, 1987); Gruta do Caldeirão and Escoural (nn; Cardoso, 1993). [Approximate measurement], nn (no number).

Mc I	AJG	REC II	BZ	BOK										
GL	26.3	29.9	29.3	28										
Bp ap	13.1	15.3	11.5											
Bp t	9.9	12.2	13.2											
SD	9.4	11	9.7											
Bd ap	9.6	11.5	10											
Bd t	8.7	10.9	11.5	10.6										
Mc II	AJG	REC I	REC II	CN1	MER	BZ	BOK	AML	ESC					
GL	62.9	67.5			65.1	67.6–58.5–66.7	66–66–67.5		69.3					
Bp ap	18.5	17.5–17.1	[19.7]		17.3	20.5–15–19.6		15.7						
Bp t	11.6	13.1–13	[14.2]		13.2	13–12–14.8		12.2						
SD	8.6	9.8–9.6			10.6	10–8.3–9.3	10.4–10–9.2		9.2					
Bd ap	13.3	[10.5]			13.5	14.7–10.5–13.7								
Bd t	13.8	14.3		13.6	14.7	14.3–13–15.7	15.3–15–13.9							
Mc III	AJG	REC I	LEZ	LR	AML	BZ	BOK							
GL	71.7		84	77	69.6	79.6–79.8–75.3–70.8	72–75.5							
Bp ap	15.4				14.3	18–17.2–17.7–16.5								
Bp t	14.5				15.6	16.1–18.4–16.6–16.1								
SD	9.6	10.8	11.6	10.5	9	10.9–11.7–10.8–10.2	10.7–11.5							
Bd ap	13.3	13.9			11.7	15–15.8–15.9–14.2								
Bd t	14.4	16.1		15.7	13.7	15.9–17.2–17.7–14.3	15.5–15.6							
Mc IV	AJG	REC I	REC II	COR	MEV	CN3	ESP	LEZ	BZ	LR	AML	FUR		
GL	69.3	73.9				68.6		84.5	77.8	70.5–74.7		78.8		
Bp ap	15.3	14.4–16	17	16.6	16.1	14.2	15.8		16.6		14			
Bp t	11.7	11.7–11.9	14.1	12.2–13.2	13	11.4	13.7		12.9		12.5			
SD	8.4	9.8				8.2			10	8.7–10.1		10.6		
Bd ap	12.9	13.9				12.6			14.5					
Bd t	12.9	14.4				12.1			14.8	13.7–13.8		15.4		
Mc V	AJG	BOL	BOL	BZ	BOK	CAL	ESC							
GL	55.9			59.4	64.2–74.6	79.2	70.3							
Bp ap	14.5			15.4										
Bp t	13.2			14.6										
SD	8.4	9.5		9.1	9.8–9.2	10.3	7.4							
Bd ap	12.4	12	11.9	14.2										
Bd t	13	14	12.7	12.9	14.7–13.8	13.9	11.9							

**Table 8**

Comparative analysis of the robustness index (SD/GL) based on measurements of metapodials of extant individuals of *Panthera pardus* and *Panthera uncia*, and *P. pardus vraelensis* with leopard fossils from the Mediterranean Iberia (number of remains of each sample).

Taxa	<i>P. pardus</i>	<i>P. uncia</i>	<i>P. p. vraelensis</i>	<i>Panthera pardus</i>					
Site	Extant	Extant	Vraona	AJG	REC I	REC II	CN3	BOL	MER
Reference	Nagel 1999			This study					
Mc I	32.64 (3)	32.63 (8)	37.05 (7)	35.74		36.78			
Mc II	11.96 (16)	13.22 (8)	14.61 (4)	13.67	14.51				16.28
Mc III	11 (16)	12.53 (8)	14.59 (3)	13.38					
Mc IV	10.89 (16)	12.16 (8)	12.92 (5)	12.12	13.26		11.95		
Mc V	13.56 (16)	15.21 (8)	15.65 (9)	15.02					
Mt II	9.33 (15)	11.36 (8)	12.18 (3)	11.58		11.5			
Mt III	10.65 (17)	10.81 (8)	13.45(2)	12.93	13.48			12.31	13.18
Mt IV	9.52 (16)	10.87 (8)	12.15 (3)			11.83			
Mt V	8.67 (15)	9.71 (8)	9.97 (3)		10.27	10.39			

remains. The cranium shows a 2-cm depression between the frontal and nasal bones. The right nasal bone appears to be partially sunken and has microfissures. The body of the left scapula has several fractures and cracks that have caused lateral torsion of the bone. All these cases correspond to an incomplete fracture. The left radius and ulna present complete oblique-spiral fractures on the

proximal diaphysis that occurred in fresh bone, which coincide anatomically and were caused at the same time. A similar fracture can be seen on the distal diaphysis of the left ulna. There is a fracture at the base of the spinous process of the first thoracic vertebra. Seven rib fragments present transverse fractures. No bone remodelling processes are observed, so these are perimortem

**Table 9**

Cervical vertebrae measurements of leopard fossils from the Iberian Peninsula. Vc I: Avenc de Joan Guitón (AJG-54); Abric Romani (nn; Cáceres et al., 1993). Vc II: AJG (AJG-55); Bolinkoba (nn; Castaños, 1987). Vc III: AJG (AJG-56); Abric Romani (nn; Cáceres et al., 1993). Vc IV: AJG (AJG-57). Vc V: AJG (AJG-58); Abric Romani (nn; Cáceres et al., 1993). Vc VI: AJG (AJG-59). Vc VII: AJG (AJG-60). [Approximate measurement], nn (no number).

1st cervical	AJG	ARO
GL	47.8	45.3
GB		
Lad	21.4	[22.5]
BFcr	41.2	43.8
BFcd	39.7	47.8
H	31	28.7
2nd cervical	AJG	BOK
H	54.7	
LAPa	54.8	
LCDe	[55]	
BFcr	[39.1]	45.5
3rd cervical	AJG	ARO
GLPa	37.4	
Bpacr		42.1
Bpacd	39.8	43
PL		
4th cervical	AJG	
GLPa		
Bpacr		
Bpacd	[55.2]	
PL	30.1	
5th cervical	AJG	ARO
GLPa		
Bpacr		43.5
Bpacd	39.5	43.2
6th cervical	AJG	
GLPa	31.7	
Bpacr	39.8	
Bpacd	39.9	
7th cervical	AJG	
GLPa	32.2	
Bpacr	40	
Bpacd	35.4	

alterations that occurred as a result of the animal falling (Bartosiewicz, 2013). There is no evidence of bite marks on the remains, so no carnivore had access to the carcass and fed on it.

The skeleton was sent for radiocarbon dating to VERA-laboratorium (Vienna), but this was impossible due to the very low collagen content of the fossils. This is common in other carnivores found on the surface inside caves with little sedimentation, such as the specimens found at Algar da Manga Larga (Cardoso and Regala, 2006) and Los Rincones (Sauqué et al., 2014b).

### 2.2.2. Cova de les Malladetes

This cave is situated in the vicinity of Barx (Valencia), 631 masl in the Mondúver mountains in the south of the province of Valencia. This site has been the subject of archaeological research during the 20th century (Fortea and Jordá, 1976; Davidson, 1989) and beginning of the 21st century (De la Peña, 2013). Four leopard specimens (Table 1) were found at the basal levels of the 1940s excavations (Sector D, E, I): pelvis (Fig. 4A), m<sub>1</sub> germinal (Fig. 4B) and two first phalanges (Fig. 4C, D). The remains are those of two individuals (an adult and a juvenile aged < 1 year) and they are linked to lithic materials and the bone industry of the Aurignacian and the faunal remains of different species, including *Capra pyrenaica*. The archaeozoological and taphonomic study of the fauna is still in progress, but it seems likely that the accumulation is mainly due to the action of carnivores, with minor human involvement. As regards the chronology of the lower levels, AMS dating for layer 12 of sector E (25.1 ky) corresponds to the Gravettian period in the region (Arsuaga et al., 2002), above the

level where the leopard remains lay. There is another date for level XII (eastern section of the 1970s excavations), with associated lithic material, with a result of  $29.6 \pm 0.5$  ky (Fortea and Jordá, 1976).

### 2.2.3. Cova del Racó del Duc

This cave is located in a ravine with very vertical walls in the vicinity of Vilallonga, next to the river Serpis at 200 masl, in the south of the province of Valencia. It has a small vestibule that leads to an inner chamber, at the back of which there is a pit (Juan-Cabanilles, 1991, 1997). The leopard materials, which were recovered by I. Sarrión in 1970, come from an area of the vestibule (REC I) and the bottom of the pit (REC II).

REC I consists of 40 well-preserved ossified remains (dark colour) belonging to two adult individuals, one larger than the other (Table 1; Fig. 5A-AN). They were located in level G-F of sector B associated with *C. pyrenaica* remains which may have been accumulated by leopards, although the taphonomic study is yet to be concluded. Human presence in the cave at the end of the Solutrean corresponds to levels C, D and E of sector A, which means that the leopard-Spanish ibex association of levels G-F precedes the archaeological level. A very worn canine from the largest individual indicates that its age was 7–10 years (Stander, 1997).

REC II consists of 38 poorly preserved ossified remains (light colour) of a large individual (Table 1; Fig. 6A-AO), published preliminarily by Sarrión (1976). The upper incisors are worn and indicate an age of 3–4 years (Stander, 1997).

### 2.2.4. Other sites in the Valencia area

New leopard remains are presented from archaeological and palaeontological sites in the Valencia area (Table 1).

From an Early Late Pleistocene (MIS 5e) level of Cova del Bolomor (Tavernes de la Valldigna, Valencia), an ossified distal fragment of Mc V has been identified (Fig. 7A) (Fernández, 2004, 2007). Recently, another three remains were recovered from level XIII of the northern sector (Middle Pleistocene, MIS 7, 190–200 ky): distal half of Mc V, complete Mt III and distal fragment of Mt IV, all of which were ossified and probably belonged to the same individual (Fig. 7B–D).

At Cova Negra (Xàtiva, Valencia), leopard remains were identified by various investigators (Royo, 1942; Pérez, 1977; Martínez, 1996, 2009). The sequence of this Middle Palaeolithic site (Villaverde, 2009) is being studied and its origin may be put back to the end of the Middle Pleistocene (MIS 7-6) and beginning of the Late Pleistocene (MIS 5e), with its maximum development during the Middle Pleistocene (Villaverde et al., 2014). Three new ossified remains are presented from disturbed levels of the 2013 excavation: Mc IV, calcaneus and second phalanx (Fig. 7E–G), and also Mt V (Fig. 7H) and two premolars (P4 and p4) published (Pérez, 1977) but not described (Fig. 7I–J).

In the province of Castellón, two new remains of leopard have been found without any context: a proximal fragment of ulna (Fig. 7K) from Cau d'En Borràs (Orpesa), where there was already a previous citation (Carbonell et al., 1979; Fernández, 2004), and a first phalanx (Fig. 7L) from Cueva Horadada (Azuébar).

A leopard Mc IV (Fig. 7M) without any context from Cova de les Meravelles (Alzira, Valencia) is associated with fauna of natural origin (Breuil and Obermaier, 1914).

## 3. Systematic and morphometric study of the new leopard remains

Order Carnivora Bowdich, 1821  
 Family Felidae Fischer, 1817  
 Genus *Panthera* Oken, 1816  
 Species *P. pardus* Linnaeus, 1758

**Table 10**

Hindlimb measurements of leopard fossils from the Iberian Peninsula. Pelvis: Malladetes (No. 134343). Femur: Avenc de Joan Guitón (AJG-138, 148); Aintzulo (nn; [Altuna and Mariezkurrena, 2013](#)); Escoural (nn; [Cardoso, 1993](#)); Los Rincones (Ri100-13.225; [Sauqué et al., 2014d](#)). Tibia: AJG (AJG-139); Racó del Duc I (REC-613); Racó del Duc II (REC-581); Aintzulo (nn; [Altuna and Mariezkurrena, 2013](#)); Furninha and Escoural (nn; [Cardoso, 1993](#)). Fibula: AJG (AJG-140); Zafarraya (UB6/Q6/15/144; [Barroso et al., 2006](#)). Patella: AJG (AJG-141, 150); Racó del Duc I (REC-637); Zafarraya (UC18/P6/11/954; [Barroso et al., 2006](#)); Amalda (nn; [Altuna, 1990](#)); Los Rincones (Ri10/GL1/174, Ri10/GL1/39; [Sauqué et al., 2014d](#)). Calcaneus: AJG (AJG-142, 151); Cova Negra (CN13/LIMP/RTV); Racó del Duc II (REC-576); Zafarraya (UC9/P6/17/626; [Barroso et al., 2006](#)); S'Espasa (nn; [Estévez, 1975–76](#)); Bolinkoba (nn; [Castaños, 1987](#)). Talus: AJG (AJG-143); Racó del Duc I (REC-633); Racó del Duc II (REC-574); Bolinkoba (nn; [Castaños, 1987](#)); Escoural (nn; [Cardoso, 1993](#)); Zafarraya (UB6/P6/15/301, UB6/P6/14/283, UC8/P6/16/405, Q8/R3044, UF35/Q15/E2/362; [Barroso et al., 2006](#)). Cuboid: AJG (AJG-153); Racó del Duc II (REC-584); Zafarraya (ind/R4444; [Barroso et al., 2006](#)). Navicular: AJG (AJG-152); Racó del Duc II (REC-594); Zafarraya (UB5/P6/14/164b; [Barroso et al., 2006](#)). First cuneiform: AJG (AJG-147). Second cuneiform: AJG (AJG-155). Third cuneiform: AJG (AJG-154); Racó del Duc II (REC-598); Zafarraya (UB/P7/14/R40389, UB5/Q6/14/89, R7/R2558, UC7/P6/15/375, UB5/P6/14/115; [Barroso et al., 2006](#)). [Approximate measurement]. nn (no number).

Pelvis	MAL								
LAR	28.2								
LA	30.7								
SB	13.9								
GL	[180]								
L ilion	[106]								
Femur	AJG	AIN	ESC	LR					
GL		261.5	266.7						
Bp ap									
Bp t	51.2–49.1	54.8							
SD	21.5	20.6	21.7						
Bd ap									
Bd t		51.9	51.9	44.3					
DC	24.6	27.6							
Tibia	AJG	REC I	REC II	AIN	FUR	ESC		LR	
GL		[232]		[239]					
Bp ap	47.4	56.4							
Bp t	[47.2]	54.4		56.2					
SD	18	21.9		19.3	22.2	24.9			
Bd ap	20.6	[26.8]	[27.6]						
Bd t	35	[35.2]	[35.9]		38.4	42.1–43.3		39.9–42.4	
Fibula	AJG	BZ							
GL		220							
Bp ap		13.6							
Bp t		24.6							
Bd ap	19.6	11.6							
Bd t	9.9	5.5							
Patella	AJG	REC I	BZ	AMA	LR				
GL	32.1	35.6	31.5	38.5	36.2–36.6				
GB	23.5–23.6	27.6	24	27.5	27.5–27.5				
Calcaneus	AJG	CN3	REC II	BZ	ESP	BOK		FUR	LR
Bp ap	20.6–21.2	25.7							
Bp t	17.4	25.3							
GL	60.4–[60]	62.1	71.8	69.3	67.5	79–67–70.5		59.8	72
DT	26.6–25.9	26.1	31.5	33.6		36.5–33.5–35		26.1	33.1
KD	11.1–11.7	11.2	13						
KD/GL	18–19.5	18	18						
Talus	AJG	REC I	REC II	BOK	ESC	BZ		LR	
GL ext		37.6	41.9	38.2–38.6	40.7	41.7–36.5–36.8–35.8–40.2		39.6	
GL int		26.4	27.9			29.9–25.7–25.1–26.1–27.5			
B troclea	22.1	21.9	25.8			22.8–21–17.9–19.3–21.3			
B neck		17.1	20.2			17.2–16.9–15.1–16–16.1			
B head		21.6	24.6			21.9–21.7–20.2–20.2–23.1			
Cuboid	AJG	REC II	BZ						
DAP	17.7	20.1	18.2						
DT	18.2	21.1	18.4						
H	18.2	20.1	18.6						
Navicular	AJG	REC II	BZ						
DAP	23.4	29.7	21.9						
DT	[19.9]	25.5	19						
H	17.9	18.8	16.6						
Cuneif. I	AJG								
H	14.9								
Cuneif. II	AJG								
DAP	13.3								
DT	7.1								
H	8.2								
Cuneif. III	AJG	REC II	BZ						
DAP	24.7	31.4	27.1–28.7–28.2–26.7–24.3						
DT	14.9	17.7	16.4–16.1–16.1–14.4–14.8						
H	12.6	15.4	13–15–13.5–13.2–12.4						

**Table 11**

Metatarsal measurements of leopard fossils from the Iberian Peninsula. Mt I: Avenc de Joan Guitón (AJG-157). Mt II: AJG (AJG-158); Racó del Duc II (REC-566); Lezetxiki (nn; Altuna, 1972); Escoural (nn; Cardoso, 1993); Zafarraya (UG45/Q10/2em/116, P8/R3415; Barroso et al., 2006). Mt III: AJG (AJG-159); Cova Merino (MER-113; Sarrion, 1984); Racó del Duc I (REC-616); Lezetxiki (nn; Altuna, 1972); Zafarraya (UF35/Q8/I25/9, UE32/P10/2e/R40122, UE23/R7/I15/4; Barroso et al., 2006); Amalda (nn; Altuna, 1990); Furninha (nn; Cardoso, 1993); Bolomor (CB13/G12/XIII/CU3/191231). Mt IV: Racó del Duc I (REC-626); Racó del Duc II (REC-567); Zafarraya (UB6/P6/I5/317, UG43/Q17/E6/142; Barroso et al., 2006); Bolinkoba (nn; Castaños, 1987); Lezetxiki (nn; Altuna, 1972); Bolomor (CB13/E13/XIII/CU21/191262). Mt V: Cova Negra (nn; Martínez, 1996); Cova Negra (CN 10952); Racó del Duc I (REC-567); Racó del Duc II (REC-577); Zafarraya (UG7/Q6/I6/148, UC21/Q10/11/61; Barroso et al., 2006); Lezetxiki (nn; Altuna, 1972); Escoural (nn; Cardoso, 1993); Los Rincones (Ri10/GL1/18). [Approximate measurement]. nn (no number).

Mt I	AJG								
GL	19.4								
Bp ap	11								
Bp t	8								
SD	4.4								
Mt II	AJG	REC II	LEZ	ESC	BZ				
GL	76.8	87.8		86.9–89.4	60–77.9				
Bp ap	16.4	19.8			17.4–16.8				
Bp t	10.2	13.3			12–10.2				
SD	8.9	10.1	9.3	9.8–10.2	9.8–9.2				
Bd ap	[11.5]	14.6			13.3–13.8				
Bd t	12.5	15.5		14.1–15.9	13.3–16.8				
Mt III	AJG	MER	REC I	LEZ	BZ	AMA	FUR	BOL	
GL	88.1	91.8	91.2	101.2	99.7–97.8–90.9	104	91.5	88.5	
Bp ap		19.6	21		22.5–22.5–18.6				
Bp t	15.5	16.7	17		17.3–17.8–16.6			15	
SD	11.4	12.1	12.3	13	11.7–12.9–12.8	15.3	12.5	10.9	
Bd ap	13.9	15	14.8	3	15.9–15.2–15			13.2	
Bd t	15.4	16.2	17.2	3	16.9–15.8–15.8		16.5	[13.9]	
Mt IV	REC I	REC II	BZ	BOK	LEZ	BOL			
GL		99.7	96.2–100.4	94	[104]				
Bp ap	17	21.5	18.1–20.2						
Bp t	15.6	17.7	17.9–17						
SD	10.9	11.8	11.2–11.6	10.5	11.7				
Bd ap		15.8	15.8–15.5			12.5			
Bd t		15.7	15.4–15.3	14.7		[12.5]			
Mt V	CN2	CN3	REC I	REC II	BZ		ESC	LR	
GL			82.7	88.5	84.7–91.7	[97]–83.2	88.2	87.6	
Bp ap		14	12.6	11.6	13.9–13				
Bp t	13.4	11.4	15.7	17.4	15.5–16.5				
SD		9.1	8.5	9.2	9.0–9.0	9.3	8.2	8.3	
Bd ap			13.7	15.1	14–14.2				
Bd t			12.4	13.6	12.9–14		12.4	13.1	

**Table 12**

First and second phalanges measurements of leopard fossils from Avenc de Joan Guitón. First phalanx; forelimb: I (AJG-18, 45), II (AJG-19, 46), III (AJG-20), IV (AJG-21, 48), V (AJG-22, 49); hindlimb: II (AJG-166, 173), II (AJG-167), IV (AJG-168). Second phalanx; forelimb: II (AJG-23, 50), III (AJG-24, 51), IV (AJG-25, 52), V (AJG-26, 53); hindlimb: II (AJG-176), III (AJG-170, 177), IV (AJG-171), V (AJG-172). [Approximate measurement].

1st phalanx AJG		GL	Bp ap	Bp t	SD	Bd ap	Bd t	
Fore limb	I	19.3–19.1	9.7–9.8	12.5–12.7	10.2–9.6	8.9–8.1	10.9–10	
	II	32.7–32.1	10.8–10.8	12.7–11.7	7.2–7.5	7.6–8.1	9.6–9.9	
	III	38.4	10.8	13.8	9.3–8.7	8.5–8.5	10.4–10.3	
	IV	36.8–36.8	10.4–11.8	13.4–13.2	8.5–9.2	8.4–8.9	10.3–10.8	
	V	33–32.3	10.4–10.8	12.9–11.8	7.9–7.4	7.7–8.5	9.6–9.8	
Hind limb	II	33.4–[33.2]	11.1–[9]	13	9–9.2	8.9–8.3	10.5–10.4	
	III	37.1	11.7–11.5	14.2–13.7	10.6–9.8	8.4	[11.8]	
	IV	[35.9]	11	[13.1]	9.5	8.7–8.7	11.2–11.4	
2nd phalanx AJG			Bp ap	Bp t	SD	Bd ap	Bd t	
	Fore limb	II	25.4–25.6	11.8–11.4	11.5–11.3	6.4–6.2	8–8.6	10.5–10.6
		III	30–30.2	10.5–11.3	10.7–11.2	6.5–6.7	8.3–8.2	10.4–10.5
		IV	28.7–28.8	10.2–10.4	10.7–10.8	6.5–6.5	7.6–8.2	9.6–10.1
		V	24–23.2	10–9.9	10.4–10.5	7.3–7.2	7.3–7.5	9.2–9.5
Hind limb	II	24	10	[11.3]–10.8	7.9	7.3	9.6	
	III	27.6–27.2	[10.4]–[10]	[10]–[11.1]	6.7–6.7	8–8.2	10.4–10.4	
	IV	27	10.2	10.9	6.9	8.2	10.1	
	V	22.3	[9.2]–9.5	10.6–10.9	7.5	7.5	9.3	

### 3.1. Avenc de Joan Guitón

#### 3.1.1. Cranium

The cranium from AJG has a convex nasal profile in lateral view (Fig. 8C), a feature of *P. pardus* and *Puma concolor*, whereas in *Panthera uncia* and *Panthera onca* it is concave. The auditory bulla

presents a flat projection of the ectotympanic bone (Fig. 8B), which is typical of *P. pardus* and *P. onca*. These features enable us to attribute the cranium found at AJG to the leopard (Sims, 2005, 2012).

The neurocranium shows a globular profile that projects backward at the level of the occipital bone (Fig. 8C, F), which is wider



**Table 13**

Palaeontological and archaeological sites of the Iberian Peninsula with leopard remains. The numbers refer to the sites of the Fig. 14. Context: A (archaeological); P (palaeontological). Chronology: P (Pleistocene); MP (Middle Pleistocene); ELP (Early Late Pleistocene); LP (Late Pleistocene); EH (Early Holocene); MPal (Middle Palaeolithic); EUPal (Early Upper Palaeolithic); UPal (Upper Palaeolithic); Ms (Mousterian); Chat (Chatelperronian); Per (Perigordian); Au (Aurignacian); Gr (Gravettian); So (Solutrean); Mg (Magdalenian); Az (Azilian); Mes (Mesolithic).

N°	Site	Level	masl	Context	Chronology	Taxon	NISP	MNI	References
1	Cueva Eirós (Triacastela, Lugo)	2	780	A	LP (EUPal)	<i>P. pardus</i>	Presence		De Lombera-Hermida et al., 2014
2	Valdavara 3 (Becerreá, Lugo)	Depósito	600	P	ELP (120–100 ka)	Leopard	Presence		Alonso et al., 2014
3	Cueva de las Caldas (Priorio, Asturias)	–	160	A	LP (So.)	Leopard	Presence		Corchón, 2014
4	Cueva de la Güelga (Cangas de Onís, Asturias)	D, level 9	200	A	LP (Ms., 45–48 ka)	<i>P. pardus</i>	Presence		Menéndez et al., 2014
5	Cueva de La Riera (Posada de Llanes, Asturias)	Azilian	30	A	EH (Az.)	<i>P. pardus</i>	Presence		Vega del Sella, 1930; Fraga, 1958; Álvarez-Laó, 2003
6	Cueva de Jou Puerta (Llanes, Asturias)	–	28	P	LP (MIS 3, 36.6–30.2 ka)	cf. <i>P. pardus</i>	1	1	Álvarez-Laó, 2014
7	Cueva de Llonín (Peñamera Alta, Asturias)	VI (conjunto II)VI (conjunto II)VI (conjunto II)	ca. 200	A	LP (EUPal)	<i>P. pardus</i>	30	1	Fortea et al., 1992, 1995, 1999; De la Rasilla and Santamaría, 2011–2012
8	Cueva de Hornos de la Peña (S. F. de Buelna, Cantabria)	E	280	A	LP (Au.)	<i>P. pardus</i>	5	1	Yravedra, 2010b
9	Cueva del Castillo (Puente Viesgo, Cantabria)	22	190	A	LP (Ms.)	<i>Felis pardus</i>	Presence		Cabrera, 1984
9	Cueva del Castillo (Puente Viesgo, Cantabria)	Must A		A	LP (Ms.)	<i>P. pardus</i>	3	1	Dari, 1999; Quesada, 2006
9	Cueva del Castillo (Puente Viesgo, Cantabria)	18–14		A	LP (Au.–Per.)	<i>P. pardus</i>	Presence		Cabrera, 1984
9	Cueva del Castillo (Puente Viesgo, Cantabria)	Aur. B		A	LP (Au.)	<i>P. pardus</i>	5	2	Dari, 1999; Quesada, 2006
9	Cueva del Castillo (Puente Viesgo, Cantabria)	12_14		A	LP (Gr.)	<i>P. pardus</i>	7	2	Bernaldo de Quirós et al., 2014
10	Cueva de El Juyo (Igollo, Cantabria)	4	35	A	LP (Mg.)	<i>P. pardus</i>	1	1	Klein and Cruz Uribe, 1985
11	Cueva Morín (Villaescusa, Cantabria)	5b–5c	50	A	LP (Au.)	<i>P. pardus</i>	1	1	Altuna, 1971, 1994
12	Cueva de El Mirón (Ramales de la Victoria, Cantabria)	108	260	A	LP (Mg.)	<i>P. pardus</i>	1	1	Marín-Arroyo, 2009
13	Cueva de las Pajucas (Lanestosa, Vizcaya)	Infra-Eneolithic	400	A	LP/EH? (UPal/Mes?)	<i>P. pardus</i>	1	1	Altuna, 1972
14	Covacho de Arenillas (Islares, Cantabria)	II	15	A	LP (Au.)	<i>P. pardus</i>	Presence		Bohigas and Muñoz, 2002; Rasines del Río et al., 2011
15	Abrigo del Cuco (Castro Urdiales, Cantabria)	XIII	43	A	LP (Au.)	<i>P. pardus</i>	1	1	Castaños and Castaños, 2007; Rasines del Río et al., 2011
16	Cueva de Arlanpe (Lemoa, Vizcaya)	3,4,D	204	A	MP (MPal, 180 ka)	<i>P. cf. pardus</i>	5	3	Arcecedillo et al., 2013
16	Cueva de Arlanpe (Lemoa, Vizcaya)	II		A	LP (So.)	<i>Panthera sp.</i>	1	1	Arcecedillo et al., 2013
17	Cueva de Atxuri (Mañaria, Vizcaya)	V–VII	188	A	LP (UPal)	<i>P. pardus</i>	1	1	Castaños, 1987
18	Cueva de Oyalkoba (Abadiano, Vizcaya)	V	ca. 410	A	LP (UPal)	<i>P. pardus</i>	1	1	Castaños, 1987
19	Cueva de Bolinkoba (Abadiano, Vizcaya)	VI	430	A	LP (Gr.)	<i>P. pardus</i>	79	–	Castaños, 1983, 1987
19	Cueva de Bolinkoba (Abadiano, Vizcaya)	IV–V		A	LP (So.)	<i>P. pardus</i>	49	–	Castaños, 1983, 1987
19	Cueva de Bolinkoba (Abadiano, Vizcaya)	III		A	LP (Mg.)	<i>P. pardus</i>	14	–	Castaños, 1983, 1987
20	Cueva de Axlor (Dima, Vizcaya)	III-I/D	300	A	LP (Ms./Au.)	<i>P. pardus</i>	1	1	Altuna, 1980, 1994; Castaños, 2005
21	Cueva de Arrillor (Murua, Álava)	Lmc	710	A	LP (Ms., 37,1 ka)	<i>P. pardus</i>	4	–	Castaños, 2005
22	Cueva de Prailleaitz I (Deba, Guipúzcoa)	Exterior	55	P	LP	<i>P. pardus</i>	7	–	Castaños, 2010
22	Cueva de Prailleaitz I (Deba, Guipúzcoa)	Vestíbulo		A	LP (Mg., 15,4 ka)	<i>P. pardus</i>	6	–	Castaños, 2010
23	Cueva de Astigarraga (Deba, Guipúzcoa)	II	425	A	LP (So., 16,9 ka)	<i>P. pardus</i>	2	1	Castaños, 2010; Villaluenga et al., 2012a
24	Cueva de Ekain (Deba, Guipúzcoa)	X a	90	A	LP (Chat.)	<i>P. pardus</i>	3	1	Altuna and Mariezkurrena, 1984; Altuna, 1994; Villaluenga et al., 2012b
24	Cueva de Ekain (Deba, Guipúzcoa)	IX b		A	LP (Au.)	<i>P. pardus</i>	1	1	Altuna and Mariezkurrena, 1984; Altuna, 1994

(continued on next page)

Table 13 (continued)

N°	Site	Level	masl	Context	Chronology	Taxon	NISP	MNI	References
25	Cueva de Amalda (Zestoa, Guipúzcoa)	VII	205	A	LP (Ms.)	<i>P. pardus</i>	3	–	Altuna, 1990; Altuna and Mariezkurrena, 2010
25	Cueva de Amalda (Zestoa, Guipúzcoa)	VI–V		A	LP (Gr.)	<i>P. pardus</i>	4	–	Altuna, 1990; Altuna and Mariezkurrena, 2010
25	Cueva de Amalda (Zestoa, Guipúzcoa)	VI		A	LP (Gr.)	<i>P. pardus</i>	11	1	Yravedra, 2010a
26	Cueva de Baio (Zestoa, Guipúzcoa)	–	100	P	LP	<i>P. pardus</i>	3	–	Altuna and Mariezkurrena, 2010
27	Cueva de Aintzulo (Errezil, Guipúzcoa)	–	215	P	LP (21,7 ka)	<i>P. pardus</i>	5	1	Altuna and Mariezkurrena, 2011, 2013
28	Cueva de Lezetxiki (Arrasate, Guipúzcoa)	VI	345	A	MP (MPal, 234 ka)	<i>P. pardus</i>	9	–	Altuna and Mariezkurrena, 2010; Falguères et al., 2005–2006
28	Cueva de Lezetxiki (Arrasate, Guipúzcoa)	III–IV		A	LP (Au.)	<i>P. pardus</i>	18	–	Altuna, 1972
28	Cueva de Lezetxiki (Arrasate, Guipúzcoa)	N		A	LP (Ms.)	<i>P. pardus</i>	3	1	Villaluenga et al., 2012a
29	Cueva de Iruaxpe I (Aretxabaleta, Guipúzcoa)	II	675	P	LP	<i>P. pardus</i>	10	1	Mariezkurrena, 1987
30	Cueva-Sima de Allekoaitze (Ataún, Guipúzcoa)	–	635	P	LP (34,8 ka)	<i>P. pardus</i>	2	1	Corral, 2012; Altuna and Mariezkurrena, 2011, 2013
31	Escombrera de Coscobillo (Olazagutía, Navarra)	–	ca. 540	?	LP	<i>P. pardus</i>	Presence		Altuna, 1972; Mariezkurrena, 2011
32	Cueva de Aitbitarte III (L. de Rentaría, Guipúzcoa)	III	220	A	LP (Gr.)	<i>P. pardus</i>	1	1	Altuna and Mariezkurrena, 2011
33	Cueva de Abauntz (Arraitz, Navarra)	25D-E, 27D-E-F, 33F	650	A	LP (Ms.)	<i>P. pardus</i>	31	–	Mazo et al., 2011–2012; Utrilla et al., 2014
34	Cueva de Prado Vargas (Cornejo, Burgos)	4	620	A	LP (MIS 3, 46,2 Ka)	<i>P. pardus</i>	1	1	Arceredillo, 2010
35	Cueva de Valdegoba (Huérmeces, Burgos)	4.3–4.4	930	A	LP (Ms.)	<i>P. pardus</i>	–	2	Diez et al., 1988–89; Quam et al., 2001
36	Cueva de la Ermita (Hortigüela, Burgos)	5a	935	A	LP (Ms.)	<i>P. pardus</i>	6	1	Delibes, 1972
37	Cueva de los Rincones (Purujosa, Zaragoza)	Main gallery	1010	P	LP	<i>P. pardus</i>	110	4	Sauqué and Cuenca-Bescós, 2013; Sauqué et al., 2014a, b, c
38	Cueva de Aguilón P-7 (Aguilón, Zaragoza)	–	683	A	LP (MIS 3)	<i>P. pardus</i>	8	1	Sauqué et al., 2014d
39	Cuevas de Zarzamora-Búho (Perogordo, Segovia)	Upper unit	ca. 980	P	LP (44.4–32.5 ka)	cf. <i>P. pardus</i>	1	1	Sala et al., 2011, 2012
39	Cuevas de Zarzamora-Búho (Perogordo, Segovia)	Gallery		P	LP (Würm I-II)	<i>Panthera</i> sp.	1	1	Molero et al., 1989; Íñigo et al., 1998
40	Cueva de Pinarillo-1 (Segovia)	–	ca.1000	P	LP (Ms.)	<i>P. pardus</i>	Presence		Arribas, 1997; Arribas et al., 2008
41	Cueva del Camino (Pinilla del Valle, Madrid)	North–Central (5)	1114	A	ELP (Ms., MIS 5e)	<i>Panthera</i> sp.	1	1	Alfárez et al., 1982; Arsuaga et al., 2012
N°	Site	Level	masl	Context	Chronology	Taxon	NISP	MNI	References
42	Cueva de los Torrejones (Tamajón, Guadalajara)	E–5	1100	A	LP	<i>P. pardus</i>	51	1	Arribas, 1997
43	Cueva de los Casares (Riba de Saelices, Guadalajara)	7_12	1162	A	LP (Ms.)	<i>P. pardus</i>	8	1	Altuna, 1973
44	Cueva de los Moros de Gabasa (P. de Calasanz, Huesca)	e-f-g	780	A	LP (Ms.)	<i>P. pardus</i>	7	3	Blasco Sancho 1995; Utrilla et al., 2010
45	Cova dels Muricecs (Llimiana, Lleida)	–	390	A	LP (MPal)	<i>P. pardus</i>	14	–	Estévez, 1979
46	Cova de S'Espasa (Oix-Sadernes, Girona)	–	370	A	LP (Würm inicial)	<i>P. pardus</i>	17	1	Estévez, 1975–76
47	Cova dels Ermitons (Sales de Llierca, Girona)	IV	470	A	LP (Ms., 33.1 ka)	<i>P. pardus</i>	Presence		Estévez, 1979; Maroto, 1993
48	Cova de L'Arbreda (Serinyà, Girona)	C-E	210	A	LP (Gr., So.)	<i>P. pardus</i>	2	2	Estévez, 1987; Nadal et al., 2002
49	Cau del Duc d'Ullà (Ullà, Girona)	–	280	A	MP (MPal)	<i>P. pardus</i>	2	–	Estévez, 1979
50	Abric Romaní (Capellades, Barcelona)	E (SO)	310	A	LP (44.9 ka)	<i>P. pardus</i>	6	1	Cáceres et al., 1993
51	Cova del Gegant (Sitges, Barcelona)	II a, II b	0	A	LP (MPal)	<i>F. (P.) pardus</i>	5	1	Viñas and Villalta, 1975; Daura et al., 2005
52	Terrasses de la Riera dels Canyars (Gavà, Barcelona)	MLU unit	9	A	LP (Au.)	<i>P. pardus</i>	4	1	Daura et al., 2013; Rosado-Méndez et al., 2014
53	Cova Foradada (Calafell, Tarragona)	–	46	A	LP (Au)	<i>P. pardus</i>	Presence		Morales, Rodríguez-Hidalgo and Saladié, personal communication
54		–	140	P	MP	Panther	Presence		

Table 13 (continued)

N°	Site	Level	masl	Context	Chronology	Taxon	NISP	MNI	References
	Cau d'En Borràs (Orpessa, Castelló)								Carbonell et al., 1979; Fernández, 2004
54	Cau d'En Borràs (Orpessa, Castelló)	–		P	MP	<i>P. pardus</i>	1	1	This study
55	Cueva Horadada (Azuebar, Castelló)	–	ca.300	A	LP (UPal)	<i>P. pardus</i>	1	1	This study
56	Cueva Merino (Dos Aguas, València)	Salita interior	ca.400	P	LP	<i>P. pardus</i>	2	1	Sarrión, 1984; Fernández, 2004
57	Cova de les Meravelles (Alzira, València)	–	60	?	P	<i>P. pardus</i>	1	1	This study
58	Cova del Bolomor (Tavernes de Valldigna, València)	XIII	90	A	MP (MIS 7)	<i>P. pardus</i>	3	1	This study; Fernández, personal communication
58	Cova del Bolomor (Tavernes de Valldigna, València)	El sub XIII		A	LP (MIS 5e)	<i>P. pardus</i>	1	1	Fernández, 2004; Fernández, personal communication; this study
59	Cova Malladetes (Barx, València)	SE c16–17, SD c22, SI c28	631	A	LP (Au.)	<i>P. pardus</i>	4	2	This study
60	Cova Negra (Xàtiva, València)	–	100	A	P	<i>Felix pardus</i>	2	1	Royo, 1942
60	Cova Negra (Xàtiva, València) CN1	S/N, SE c4, c24, SF c7, SB c29, c5		A	P	<i>P. pardus</i>	10	2	Pérez, 1977
60	Cova Negra (Xàtiva, València) CN2	VI, IIIa, II		A	P	<i>P. pardus</i>	6	1	Martínez, 1996, 2009
60	Cova Negra (Xàtiva, València) CN3	Messed level		A	P	<i>P. pardus</i>	3	1	This study
61	Cova de Racó del Duc I (Vilallonga, València)	Infra-Solutrian level	ca. 200	A	LP (UPal)	<i>P. pardus</i>	41	2	This study
61	Cova de Racó del Duc II (Vilallonga, València)	Chasm bottom		P	P	<i>P. pardus</i>	47	1	This study
62	Cova del Corb (Ondara, Alacant)	External breccia; IV	200	A	MP (MIS 7)	<i>P. pardus</i>	1	1	Sarrión, 1990; Fernández, personal communication
62	Cova del Corb (Ondara, Alacant)	Internal breccia		A	LP (UPal)	<i>P. pardus</i>	1	1	Sarrión, 1990; Fernández, personal communication
63	Cova Foradada (Xàbia, Alacant)	VII, VI, V	40	A	LP (Au)	<i>P. pardus</i>	7	3	Pantoja et al., 2011
64	Cova de les Calaveres (Benidoleig, Alacant)	–	131	A	LP (UPal)	<i>P. pardus</i>	1	1	Aparicio et al., 1982
65	Cova del Parat (Tollos, Alacant)	–	ca. 776	A	ELP	<i>P. pardus</i>	3	1	Martínez, personal communication
66	El Salt (Alcoi, Alacant)	D6, X La, Lev 6 n°3 (2006)	700	A	LP (Ms.)	<i>P. pardus</i>	1	1	Morales, Brugal and Pérez, personal communication; this study
67	Abric del Pastor (Alcoi, Alacant)	A. clean profiles, AP-1633 (2005)	800	A	LP (Ms.)	<i>P. pardus</i>	1	1	Morales and Pérez, personal communication; this study
68	Avenc de Joan Guitón (Fontanars dels Alforins, València)	Leopard gallery	774	P	P	<i>P. pardus</i>	221	1	This study
69	Sima de las Palomas (Torre Pacheco, Murcia)	–	75	A	LP (Ms.)	<i>P. pardus</i>	1	1	Walker, 2001; Walker et al., 2012
70	Cueva de Carigiuela (Darro, Granada)	–	1020	A	LP (Ms.)	<i>P. pardus</i>	3	1	Bouchud, 1969
71	Boquete de Zafarraya (Alcaucín, Málaga)	A, B, C, D, E, F, G	ca. 1000	A	LP (Ms.)	<i>P. pardus</i>	247	18	Barroso et al., 2006
72	Devil's Tower (Gibraltar)	–	<10	A	LP (Ms.)	<i>P. pardus</i>	Presence		Currant, 2000
73	Genetista Cave (Gibraltar)	–	<10	A	LP (Ms.)	<i>P. pardus</i>	Presence		Currant, 2000
74	Vanguard Cave (Gibraltar)	C–D units	<5	A	LP (Ms.)	<i>P. pardus</i>	7	–	Stringer et al., 2008
75	Gorham's Cave (Gibraltar)	IV	<5	A	LP (Ms.)	<i>P. pardus</i>	4	–	Currant, 2000; Rodríguez et al., 2010
75	Gorham's Cave (Gibraltar)	III		A	LP (So.)	<i>P. pardus</i>	2	–	Currant, 2000; Carrión et al., 2008; Rodríguez et al., 2010
76	Gruta do Escoural (Montemor-o-Novo)	–	350	A	P	<i>P. pardus</i>	19	1	Cardoso, 1993, 1996
77	Gruta da Figueira Brava (Setúbal)	C.2	<5	A	LP (Ms., 30,9 ka)	<i>P. pardus</i>	3	1	Cardoso, 1993, 1996
78	Pego do Diabolo (Loures)	2	250	A	LP (Au.)	cf. <i>P. pardus</i>	1	1	Zilhão et al., 2010a; Valente, 2004a, b
79	Pedreira das Salemas (Loures)	C.2	240	A	LP (Au., 29,8 ka)	<i>P. pardus</i>	1	1	Antunes et al., 1989
80	Gruta das Fontainhas (Cadaval)	–	400	A	LP (So., 22,7 ka)	<i>P. pardus</i>	2	1	Cardoso, 1993, 1996
81	Furninha (Peniche)	4–4.5; 7–7.5; 8.8–9.3	<5	A	LP (Ms.)	<i>P. pardus</i>	4	1	Cardoso, 1993, 1996; Brugal et al., 2012

(continued on next page)

Table 13 (continued)

N°	Site	Level	masl	Context	Chronology	Taxon	NISP	MNI	References
82	Casa da Moura (Óbidos)	–	160	A	LP (Au., 25 ka)	<i>P. pardus</i>	1	1	Valente, 2004a
83	Algar da Manga Larga (Porto de Mós)	–	460	P	LP	<i>P. pardus</i>	ca. 10	1	Cardoso and Regala, 2006
84	Gruta da Oliveira (Torres Novas)	13	ca. 115	A	LP (Ms.)	<i>Panthera</i> sp.	1	1	Zilhão et al., 2010b
85	Gruta do Caldeirão (Tomar)	Ms. level	120	A	LP (Ms.)	<i>P. pardus</i>	1	1	Davis, 2002
85	Gruta do Caldeirão (Tomar)	So. level		A	LP (So.)	<i>P. pardus</i>	6	1	Davis, 2002; Cardoso, 1996
86	Lorga de Dine (Vinhais)	–	787	A	LP (Ms.)	<i>P. pardus</i>	2	1	Cardoso, 1993, 1996

than that of the African leopard. This feature also appears in other crania found in the Iberian Peninsula such as Abric Romaní, Algar da Manga Larga and Allekoaitze (Cáceres et al., 1993; Cardoso and Regala, 2006; Corral, 2012; Altuna and Mariezkurrena, 2013), which for some authors may be typical of female leopards (Ghezzo and Rook, 2015). In the present-day African leopard this area is more elongated and does not project backwards (Sims, 2012). Likewise, the zygomatic bones of AJG do not open up laterally as much as in the African species and they run more parallel to the neurocranium (Fig. 8A, B). The maxilla presents a very hypsodont P4 (Fig. 8C, E).

The temporal sutures join further back from the post-orbital process, the sagittal crest shows little development, the braincase is short and wide and there is no clear post-orbital constriction (Fig. 8A, C), which are typical features of females (Ghezzo and Rook, 2015). The relatively small size of the cranium appears to be the consequence of sexual dimorphism (Christiansen and Harris, 2012) and confirms that it is a female, like the one found at Algar da Manga Larga (Cardoso and Regala, 2006).

The cranium is not as long as that of African females, a feature that it shares with *P. uncia*. In contrast, AJG has a greater frontal and nasal width than that of the African leopard (Fig. 8A, D), a feature which is typical of *P. pardus spelaea* and *P. uncia* (Sims, 2012;

Diedrich, 2013) and which can be interpreted as an adaptation to mountainous areas (Diedrich, 2013). This greater nasal width would allow them to heat the air in cold atmospheres (Hemmer, 1972).

As regards the cranial dimensions of AJG, the total length is within the range of female *P. pardus* and is almost the minimum for males. Compared with other fossil material (Table 2), AJG is longer than Algar da Manga Larga, but shorter than Allekoaitze and Aintzulo, and very similar to the smallest female from Equi. Present-day *P. pardus* specimens show a high degree of biometric variability according to sexual dimorphism, with males generally being larger than females, although there may be overlaps. This variability is also seen in the fossil material. AJG is close to the maximum for *P. uncia*, greater than the maximum for female *Puma* and similar to the minimum for males.

The condylobasal length of AJG is shorter than the minimum for male *P. pardus* and is within the upper range for females. In the case of felines, this cranial measurement appears to be strongly related to the overall size of the animal (Turner and O'Regan, 2002). AJG is clearly larger than Algar da Manga Larga but smaller than Aintzulo and Allekoaitze. AJG is larger than the maximum for *P. uncia*, it is within the range of male and larger than the maximum for female *Puma*.

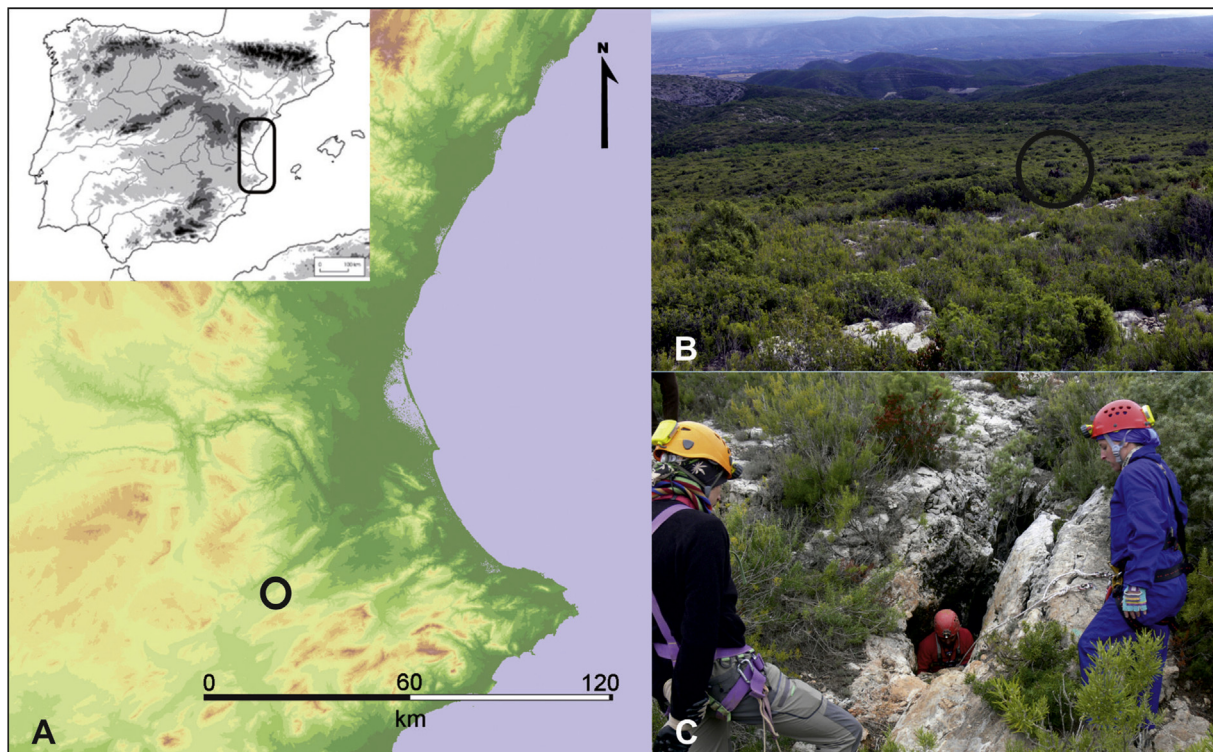


Fig. 1. A) Geographical location of Avenc de Joan Guitón chasm; B) Immediate environment; C) View of the entry to the chasm.



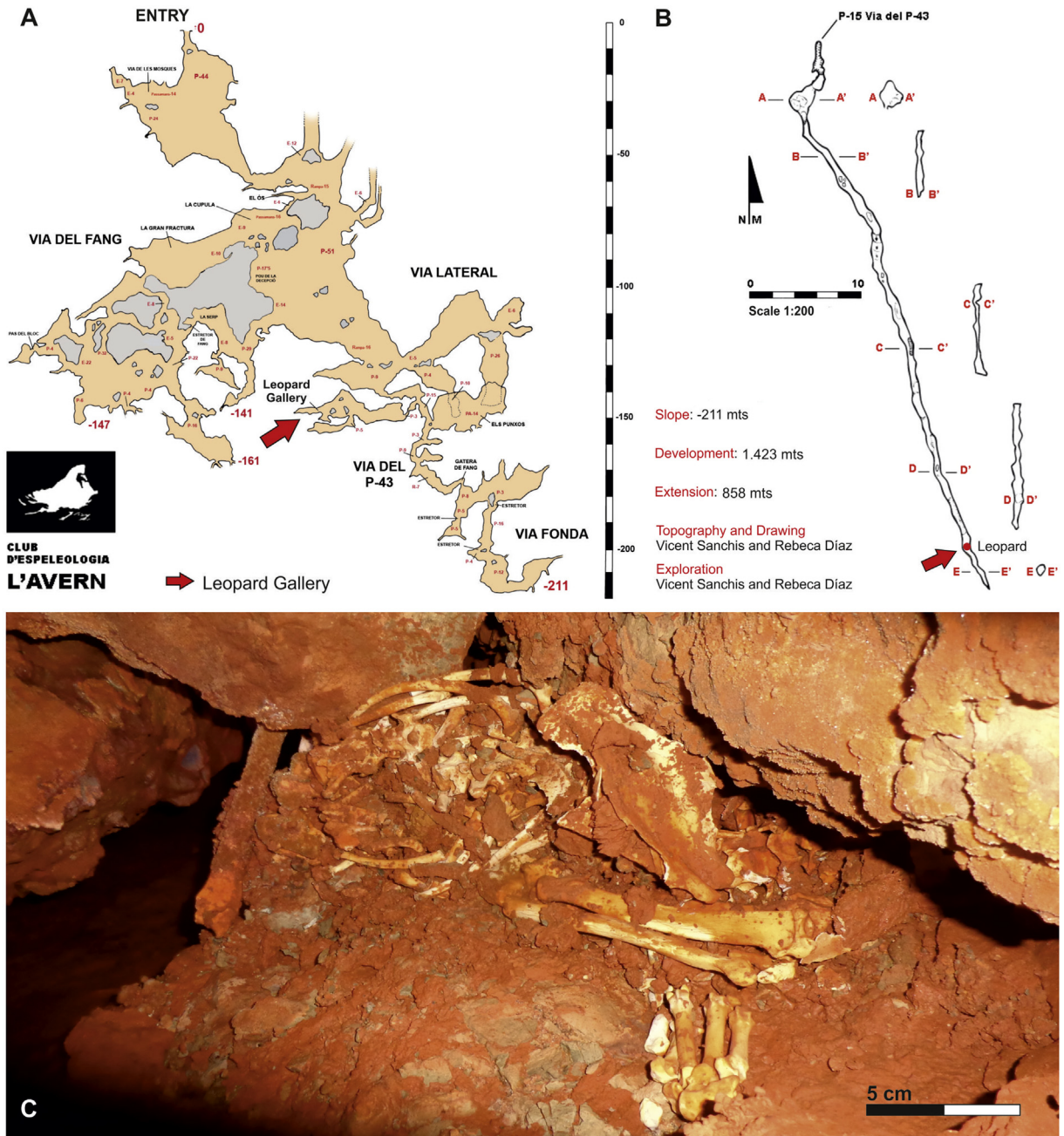


Fig. 2. A) Chasm topography section (Avenç de Joan Guitón); B) Leopard Gallery plant; C) Leopard remains before their recovery.

The zygomatic width is similar to Algar da Manga Larga. This value is within the lower range of male and upper range of female *P. pardus*, close to the maximum for *P. uncia* and greater than the maximum for female *Puma*.

The minimum distance between the orbits is within the range of female and male *P. pardus*. This measurement is similar to that of Algar da Manga Larga, equal to the minimum for *P. uncia* and greater than the maximum for *Puma*.

The post-orbital constriction width is very similar to Algar da Manga Larga, Allekoaitze and Aintzulo, greater than the maximum for female *P. pardus* and within the range of males. This value in AJG is smaller than the minimum for *P. uncia* and greater than that of female and within the range of male *Puma*.

The cranial lengths situate the AJG leopard within the range of female *P. pardus*, which is consistent with the crania of female fossils (Algar da Manga Larga and the smallest individual from Equi) (Fig. 9). The crania from Allekoaitze and Aintzulo present dimensions that are more consistent with males, although recently the first of them has been classified as a female based on its morphology (Ghezzeo and Rook, 2015).

AJG has a short, wide cranium typical of female *P. pardus* fossils from southern areas of Europe. If we compare AJG with fossils such as Algar da Manga Larga, the zygomatic width is similar. The same applies to the minimum width of the orbits or the neurocranial width. Post-orbital constriction in AJG is similar to fossil values and greater than for female *P. pardus*. The frontal width of Pleistocene

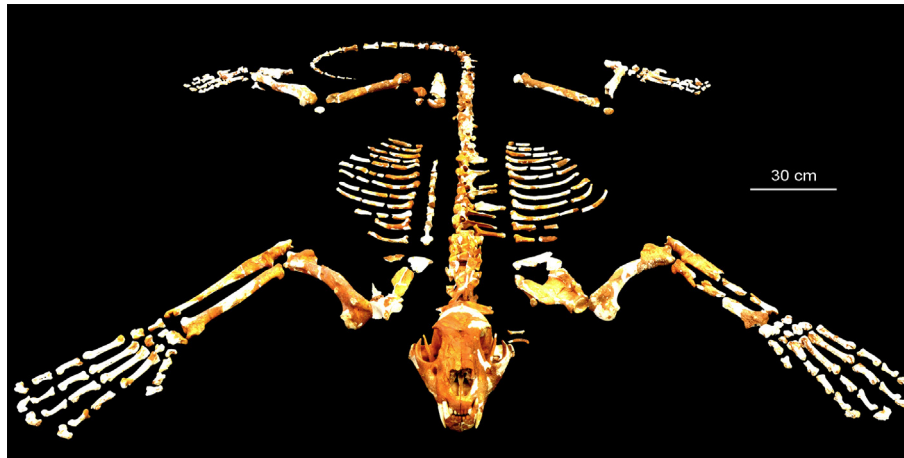


Fig. 3. Leopard skeleton from Avenc de Joan Guitón (No. 30464). The white bits are due to differential preservation.



Fig. 4. Leopard remains from Cova de les Malladetes: A) right pelvis in lateral view (No. 134343); B) germ of m1 in occlusal view (No. 134292-1); C-D) first phalanges in dorsal view (No. 134292-2; 134574).

crania is greater than that of female *P. pardus*.

If we consider the idea put forward by [Diedrich \(2013\)](#) and [Sauqué et al. \(2014a\)](#), the AJG cranium has morphometric features that lie somewhere between *P. uncia* and present-day African leopards, which would be typical of the European subspecies *P. pardus spelaea*. For [Ghezzi and Rook \(2015\)](#) the features of the AJG cranium could be explained by the intraspecific variability and sexual dimorphism that exist in *P. pardus*. Considering that the sample of leopards from the Iberian Peninsula does not provide a large enough number of crania from both the Middle and Late Pleistocene with morphological or metric differences that demonstrate the existence of a subspecies, we maintain the specific attribution for the AJG specimen.

### 3.1.2. Mandible

The AJG mandibles have two mental foramina in the buccal view, the mesial in the middle of the diastema and the distal under p3 (Fig. 8C). A similar number is observed in other mandibles found in the Mediterranean area (Abric Romaní and Boquete de Zafarraya), whereas those found in the rest of the peninsula show three (Algar da Manga Larga, Allekoaitze, Torrejones and Los Rincones). Some authors have used this criterion to distinguish *P. pardus* from *P. uncia* (three foramina) ([Madurell-Malapeira et al., 2010](#)), although others consider that this characteristic is part of intraspecific variability and therefore lacks systematic value ([Cardoso and Regala, 2006](#); [Testu et al., 2011](#); [Sauqué and Cuenca-Bescós, 2013](#)), as Iberian examples seem to confirm.

The angle formed by the basal and anterior border of the ramus is obtuse ( $>90^\circ$ ) and shows a receding symphysis that is characteristic of *P. pardus* (Fig. 8C, E), whereas in *P. uncia* it is almost at a right angle and the symphysis is semivertical ([Testu, 2006](#); [Christiansen, 2008](#); [Testu et al., 2011](#)). Some of the Iberian leopards present the morphology described for *P. pardus* (Abric Romaní, the large specimen from Zafarraya, Allekoaitze and AJG); however, others are more similar to that of *P. uncia* (Algar da Manga Larga, Los Rincones and the small specimen from Zafarraya) ([Cáceres et al., 1993](#); [Barroso et al., 2006](#); [Cardoso and Regala, 2006](#); [Altuna and Mariezkurrena, 2013](#); [Sauqué and Cuenca-Bescós, 2013](#)).

The basal profile of the horizontal ramus is convex at the level of m1 (Fig. 8C, E), which is typical of the present-day and Late Pleistocene (Los Rincones) *P. pardus*, whereas *P. uncia* has a straight profile ([Hemmer, 1972](#); [Testu, 2006](#)). This may also be a non-defining feature, as a European leopard fossil specimen (Caune de l'Arago) appears without this convexity ([Testu, 2006](#)).

The masseteric fossa is deep and reaches the level of the protoconid of m1. This feature is observed in various European Pleistocene leopards ([Testu, 2006](#); [Testu et al., 2011](#); [Sauqué and Cuenca-Bescós, 2013](#)), although it also appears in *Puma concolor* and *P. uncia* ([Madurell-Malapeira et al., 2010](#)).

The coronoid process is quite vertical, projecting backwards less than in the present-day *P. pardus* ([Testu, 2006](#)). Likewise, the condyle is positioned somewhat further back than the posterior border of the coronoid process (Fig. 8C).

The mandible is higher behind m1 than in front of p3 (Table 3),





**Fig. 5.** Leopard remains from Racó del Duc I (No. 115782): A) right radius in dorsal view (REC-614); B) left tibia in cranial view (REC-613); C) C1 in lateral view (REC-628); D–K) caudal vertebrae in dorsal and ventral views (REC-629, 631, 632, 615, 621, 648, 650, 651); L) left patella in dorsal view (REC-637); M–O) rib fragments in lateral view (REC-617, 630–647, 638); P) left Mc II in dorsal view (REC-612); Q) right Mc II in dorsal view (REC-635); R) left Mc III in dorsal view (REC-620); S) right Mc IV in dorsal view (REC-636); T) left Mc IV in dorsal view (REC-622); U) left Mt III in dorsal view (REC-616); V) left Mt IV in dorsal view (REC-626); W) right Mt V in dorsal view (REC-619); X) right talus in dorsal view (REC-633); Y) left scapholunate in proximal view (REC-634); Z) left pisiform in proximal view (REC-653); AA–AH) first phalanges in dorsal view (REC-641, 645, 644, 627, 649, 625, 624, 643); AI–AM) second phalanges in dorsal view (REC-642, 623, 639, 640, 652); AN) third phalanx in lateral view (REC-655).

which is observed in all the Iberian *P. pardus* fossils except that of Algar da Manga Larga (Sauqué and Cuenca-Bescós, 2013).

As regards the dimensions of the AJG mandible (Table 3), the total length is very similar to that of Abric Romaní, Los Rincones and Caune de l'Arago (Cáceres et al., 1993; Testu, 2006; Sauqué and Cuenca-Bescós, 2013) and greater than that of Algar da Manga Larga (Cardoso and Regala, 2006). This measurement in the AJG specimen is close to average for present-day leopards and greater than for *P. uncia* and *Puma*.

The diastema index (length of the diastema relative to that of p3) (Hemmer, 1971) is long (120.5), with values close to those of Karañ E (122.3), Observatoire (118.4) and present-day *P. pardus* (121), while it differs considerably from *P. uncia* (89.7) and *Puma pardoides* of Stránská Skála (62.5), which have a short diastema. But some Late Pleistocene *P. pardus* specimens also have a short diastema, such as those from Los Rincones, Algar da Manga Larga, Zafarraya and Triagalnata (Spasov and Raychev, 1997; Barroso et al., 2006; Cardoso and Regala, 2006; Testu, 2006; Testu et al.,



**Fig. 6.** Leopard remains from Racó del Duc II (No. 115781): A) premaxilla in frontal view (REC-586); B) lumbar vertebra in ventral view (REC-578); C) caudal vertebra in dorsal view (REC-573); D) right humerus in medial view (REC-587); E) right humerus in caudal view (REC-568); F) right ulna in lateral view (REC-569); G) right ulna in lateral view (REC-592); H) right ulna in lateral view (REC-589); I) left radius in palmar view (REC-570); J) right radius in lateral view (REC-575); K) right tibia in proximal view (REC-588); L) right tibia in caudal view (REC-581); M) right calcaneus in dorsal view (REC-576); N) left calcaneus in dorsal view (REC-602); O) left talus in dorsal view (REC-574); P) left pisiform in lateral view (REC-593); Q) right scapholunate in proximal view (REC-608); R) left navicular in distal view (REC-594); S) right cuboides in lateral view (REC-584); T) third cuneiform in proximal view (REC-598); U) left Mc I in lateral view (REC-606); V) right Mc II in dorsal view (REC-580); W) left Mc IV in dorsal view (REC-590); X) left Mt II in dorsal view (REC-566); Y) left Mt IV in dorsal view (REC-567); Z) left Mt V in dorsal view (REC-577); AA-AB) indeterminate metapodials in dorsal view (REC-596, 607); AC-AH) first phalanges in dorsal view (REC-597, 585, 583, 603, 605, 599); AI-AM) second phalanges in dorsal view (REC-600, 595, 591, 612, 610); AN-AO) third phalanges in lateral view (REC-611, 604).

2011; Sauqué and Cuenca-Bescós, 2013).

The mandibular robustness (height of the mandibular ramus behind m1 relative to the length of m1) (155.3) is similar to that of various Late Pleistocene specimens such as those of Abric Romaní (156.4), Algar da Manga Larga (149.3), Torrejones (158.2) and Triguernada (154.6) (data compiled by Sauqué and Cuenca-Bescós, 2013), differing from the present-day *P. uncia* (137.2) (Testu, 2006).

The length of the molar row of some fossils found in the Iberian Peninsula, which is very similar to the regression line of the present-day *P. uncia* (Fig. 10), could indicate the adaptation of both species to a similar mountain habitat with scarce prey, which they would have to exploit to the full (Spassov and Raychev, 1997; Sauqué and Cuenca-Bescós, 2013).

Despite some similarities with *P. uncia*, the other features



**Fig. 7.** Leopard remains from several archaeological and palaeontological sites of Valencia area. Cova del Bolomor: A) left Mc V in ventral view (No. 82244); B) left Mc V in dorsal view (No. 190669); C) left Mt III in dorsal view (No. 191231); D) Mt IV in dorsal view (No. 191262). Cova Negra (CN13, LIMP, RTV): E) right Mc IV in dorsal view; F) right calcaneus in dorsal view; G) second phalanx in dorsal view. Cova Negra (Pérez, 1977): H) right Mt V in dorsal view with cut marks (CN 10952); I) left P4 in lingual and occlusal views (CN 11013; No. 30239); J) left p4 in buccal and occlusal views (CN 6300; No. 30240). Cau d'En Borràs: K) right ulna in lateral view (CBO-1; No. 115954). Cueva Horadada: L) first phalanx in dorsal view (No. 115922). Cova Meravelles: M) right Mc IV in dorsal view (No. 116235).

confirm that the AJG mandible belongs to *P. pardus*.

### 3.1.3. Upper teeth

The incisors are inserted into the premaxilla (Fig. 8D), are frontally flat, have a posterior cusp and increase in size from I1 to I3, a common morphology in leopards (Table 4) (Testu, 2006). There is a short diastema between incisors and canines.

The canines have a rounded cross section and are massive and laterally flattened. The crown, which is straight, shows some backwards torsion. There is a well-defined ridge on the distal edge of the crown. On the buccal and lingual surfaces of the crown there are two prominent longitudinal grooves, a feature that rules out *P. onca* and *Puma concolor* (Sims, 2005, 2012) (Fig. 8C, E). These grooves are also seen in Aintzulo, Algar da Manga Larga and Caune de l'Arago (Testu, 2006; Cardoso and Regala, 2006; Altuna and Mariezkurrena, 2013). The dimensions of the canines vary somewhat between the different fossil specimens found in the Iberian Peninsula; they are within the range of present-day leopards and are larger than those of *P. uncia* (Table 4).

Both P2 are present (Fig. 8C, E) and the crown has a low cusp and two ridges, the posterior one being more prominent. A slight cingulum is visible in the distal area (Table 4).

P3 has a paracone followed by a weakly developed hypocone bordered by a cingulum (Fig. 8C). On the mesial-lingual border there is a weakly developed parastyle, which is rare in *P. onca*

(Baryshnikov, 2011). The mesial-distal length is similar to the present-day *P. pardus*, greater than that of Algar da Manga Larga and *P. uncia*, and shorter than most fossils of Iberian leopards (Table 4).

P4 has a very high crown (Fig. 8C). The parastyle is round and the paracone is slightly curved backwards and has two well-defined vertical ridges; the posterior ridge of the paracone and the anterior ridge of the metacone form an open angle. The protocone is round and well developed. The outer length is similar to that of Algar da Manga Larga and is smaller than that of most Iberian leopards (Table 4). All these features appear to be common to Late Pleistocene leopards (Diedrich, 2013).

M1 is a small oval residual tooth (mesial-distal GL: 7.3).

### 3.1.4. Lower teeth

The left i1 is displaced and has a compressed root in the buccal-lingual direction with some lateral torsion. It has a well closed apex. The upper third of the crown is broken. The other incisors are inserted into the mandible and increase in size from i1 to i3 (Table 5; Fig. 8D).

The lower canines are shorter than the upper ones (Fig. 8D). They have a groove on the buccal surface (Fig. 8C), although it is possible there may be two and they may also be present on the lingual surface, hidden by the occlusion (the cranium and the mandible are attached to each other). The mesial-distal length is





**Fig. 8.** Leopard cranial remains (cranium and mandible) from Avenc de Joan Guitón (AJG-1): A) dorsal view; B) ventral view; C) right lateral view; D) cranial view; E) left lateral view; F) caudal view.

greater than that of most Iberian leopard fossils and also that of the present-day *P. pardus* and *P. uncia* (Table 5).

A long diastema separates the canine from p3 (Fig. 8C, D). The jugal teeth are very close together. p3 is trilobed and has a clearly visible circular paraconid, a feature which is seen in *P. uncia* and *Puma concolor* (Madurell-Malapeira et al., 2010). There is a well-developed protoconid and well-differentiated metaconid with a distal cingulum on the buccal surface. The tooth narrows slightly in the middle section. The dimensions of AJG coincide with the range found in Iberian fossils and are generally greater than average for present-day *P. pardus* and *P. uncia* (Table 5).

p4 is trilobed. It is difficult to describe (only seen from the lingual surface). It has a well-differentiated paraconid that slopes forward slightly. There is a well-developed, almost vertical protoconid (Table 5).

m1 has two main crests (paraconid and protoconid). There is no evidence of any metaconid on the distal border of the protoconid on

the buccal side of the talonid, a typical feature of *P. uncia* (O'Regan and Turner, 2004). This is a discriminating criterion that confirms its attribution to *P. pardus*. The paraconid is less developed than the protoconid that has a small talonid, which is also typical of *P. pardus* (Schmid, 1940).

The ratio between the length of m1 (Table 5) and that of the mandible (Table 3) is very similar (0.140) to the average for European fossils (Algar da Manga Larga, Observatoire, Los Rincones, Abric Romaní and Zafarraya), exceeds the maximum for the present-day *P. pardus* and is within the range of *P. uncia* (Cardoso and Regala, 2006; Testu, 2006; Sauqué and Cuenca-Bescós, 2013).

### 3.1.5. Forelimb

The scapula has an oval glenoid cavity and very weakly developed coracoid process. The spine is well differentiated from the body and the acromion is very curved medially (Fig. 11A, B). There are few examples of this bone in the Iberian fossil record (Table 6).

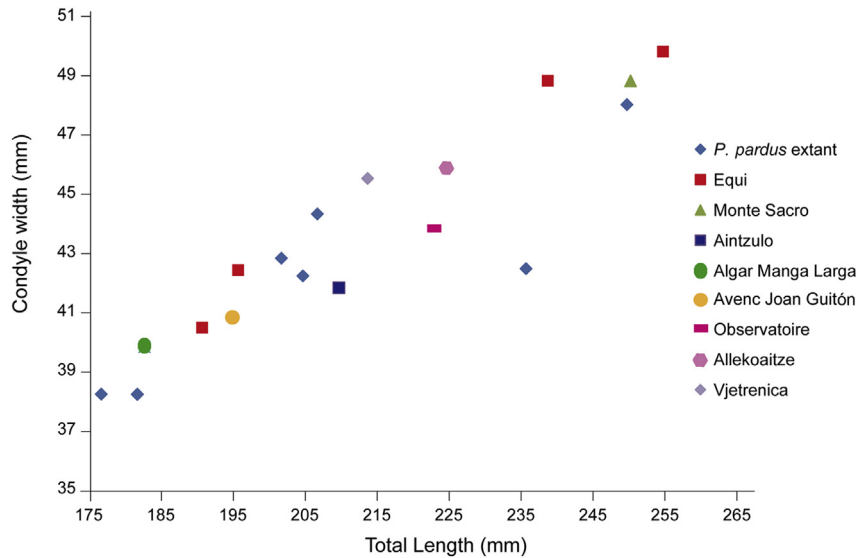


Fig. 9. Graph representing total length versus condyle width of fossil and extant leopard crania from several regions (measurements from Appendix A).

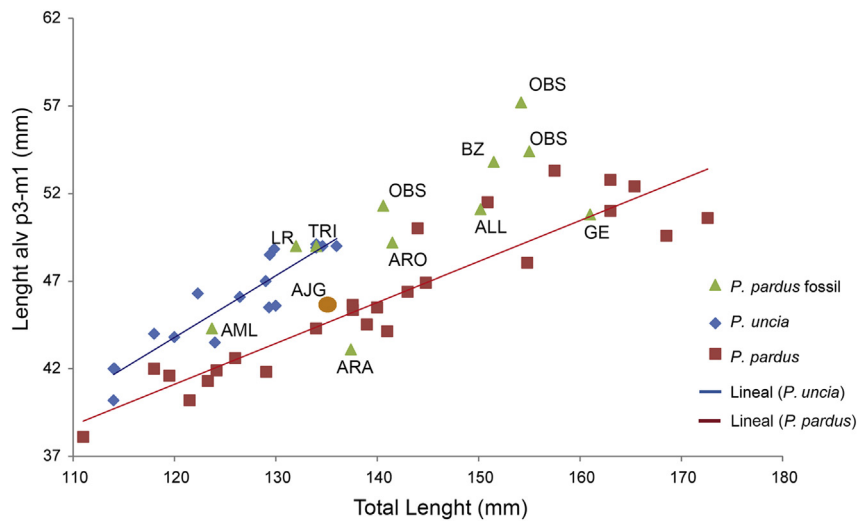


Fig. 10. Graph representing total length versus alveolar length p3-m1 of fossil and extant leopard and snow leopard mandibles from several regions (measurements from Appendix B).

As regards the proximal epiphysis (humerus), the greater tubercle is higher than the lesser tubercle, separated by a very deep intertubercular groove that runs along the medial surface (Fig. 11C). The proximal articular head projects backwards craniocaudally and shows an oval morphology in proximal view. In cranial view the diaphysis is very straight, thin and laterally flattened, with backwards torsion in the proximal third. The deltoic crest is not very prominent and is reduced to a small lateral ridge that connects with the cranial margin of the diaphysis. The distal epiphysis has a well-developed medial epicondyle with a long oval supracondylar foramen above it. The distal trochlea is wide with a long, slender, cylindrical *capitulum*. The olecranon fossa is quite deep, which is not a feature of *P. uncia* and *Puma pardoides* (Madurell-Malapeira et al., 2010). The radial fossa (medial side) is wide and shallow. The specimen from Aintzulo is longer and more robust than AJG. The dimensions of AJG are within the range of leopard fossils (Table 6).

The radius has an oval proximal epiphysis with some medial

torsion. The bicipital tuberosity is oval, very prominent and is located on the lateral-palmar side of the proximal diaphysis, below the joint. There is backwards torsion in the distal part of the bone. The diaphysis has a semicircular cross section and is dorsopalmarly flattened. The distal extremity is well developed and is wider than the diaphysis. There is a very pronounced styloid process that is pointed and projects vertically. The distal articular surface is sub-rectangular with a very prominent transverse ridge. The dimensions of the radius are within the range of Iberian fossils (Table 6; Fig. 11D).

The olecranon process of the ulna is highly developed and is forked. The proximal caudal edge is rounded and presents medial torsion. The lower border of the trochlear notch has a distally oriented facet. Below the radial notch the diaphysis is flat or even slightly convex. The diaphysis, which is very straight and has a triangular cross section, is flattened laterally, narrowing in a proximal-distal direction. The distal extremity, which is also flattened, has an oval cross section. It has a subcircular styloid process,



**Fig. 11.** Leopard forelimb remains from Avenc de Joan Guitón: A–B) left scapula in dorsal and distal views (AJG-29); C) right humerus in cranial view (AJG-3); D) right radius in palmar view (AJG-4); E) right ulna in medial view (AJG-5); F) right scapholunate in proximal view (AJG-6); G) right pyramidal in proximal view (AJG-7); H) right pisiform in proximal view (AJG-8); I) right trapezium in proximal view (AJG-9); J) right trapezoid in proximal view (AJG-10); K) right capitate in proximal view (AJG-11); L) right hamate in proximal view (AJG-12); M) right Mc V in dorsal view (AJG-17); N) right Mc IV in dorsal view (AJG-16); O) right Mc III in dorsal view (AJG-15); P) right Mc II in dorsal view (AJG-14); Q) right Mc I in dorsal view (AJG-S13); R) right first phalanx (V) in dorsal view (AJG-22); S) right first phalanx (IV) in dorsal view (AJG-21); T) right first phalanx (III) in dorsal view (AJG-20); U) right first phalanx (II) in dorsal view (AJG-19); V) right first phalanx (I) in dorsal view (AJG-18); W) right second phalanx (V) in dorsal view (AJG-26); X) right second phalanx (IV) in dorsal view (AJG-25); Y) right second phalanx (III) in dorsal view (AJG-24); Z) right second phalanx (II) in dorsal view (AJG-23); AA–AE) third phalanges in lateral view (AJG-28, 189, 188, 190, 191).

with a rounded articular circumference that projects dorsally. The distal crest is pronounced on the dorsal side. The dimensions are smaller than those of Los Rincones (Table 6; Fig. 11E).

There are very few carpal bones in the Iberian fossil record (Table 6).

The scapholunate is subrectangular and mediolaterally elongated. It has a very robust posterior-medial process. In the proximal

side, it has a convex facet that articulates with the radius (Fig. 11F). In distal view, the surface is divided into four facets at an oblique angle that articulate with the carpal bones of the distal segment.

The pyramidal is small and oval and articulates with the scapholunate, pisiform and hamate. In proximal view, the surface forms an obtuse angle, divided lateromedially by a facet, and the articulation with the pisiform is situated on the palmar margin





**Fig. 12.** Leopard axial remains from Avenc de Joan Guitón: A) sternum in dorsal view (AJG-104 to 111); B) cervical vertebrae in dorsal view (AJG-54 to 60); C) second thoracic vertebra in cranial and lateral views (AJG-62); D) third thoracic vertebra in cranial and lateral views (AJG-63); E) fifth thoracic vertebra in cranial and lateral views (AJG-65); F) eleventh thoracic vertebra in cranial and lateral views (AJG-71); G) hyoid bone (AJG-218); H–I) ribs in lateral view (AJG-114, 112); J–R) caudal vertebrae in dorsal and ventral views (AJG- 90, 91, 92, 93, 94, 96, 98, 100, 102).

(Fig. 11G). In distal view, the articular facet with the hamate is subrectangular.

The pisiform is subtriangular. The articular surface is divided into two facets; the one that articulates with the pyramidal is subrectangular and that of the hamate is triangular. The posterior process is well developed (Fig. 11H).

The trapezium is rectangular. In proximal view there is a small concave triangular facet that articulates with the scapholunate (Fig. 11I). On the medial surface of the bone there are two small suboval facets, separated by a groove, which articulate with the

trapezoid, the capitate and Mc I and II. In distal view, a concave surface articulates with the proximal epiphysis of Mc I.

The trapezoid is subtriangular. In proximal view a lateromedial groove separates the surface into two facets that articulate with the scapholunate (Fig. 11J). On the medial margin, a small trapezoid facet articulates with the trapezium. On the lateral margin, another small rectangular facet articulates with the capitate. In distal view, the convex articulation matches the concavity of the proximal area of Mc II.

The capitate is subrectangular. In proximal view it presents a



**Fig. 13.** Leopard hindlimb remains from Avenc de Joan Guitón: A) right pelvis in lateral view (AJG-137); B) left femur in cranial view (AJG-148); C) right tibia in cranial view (AJG-139); D) right fibula in medial view (AJG-140); E) right patella in dorsal view (AJG-141); F) right talus in lateral view (AJG-143); G) right calcaneus in dorsal view (AJG-142); H) right cuboid in proximal view (AJG-153); I) left navicular in proximal view (AJG-152); J) left first cuneiform in proximal view (AJG-147); K) left second cuneiform in proximal view (AJG-155); L) right third cuneiform in proximal view (AJG-154); M) left Mt III in dorsal view (AJG-159); N) left Mt II in dorsal view (AJG-158); O) left Mt I in dorsal view (AJG-157); P–S) second phalanges in dorsal view (AJG-176, 170, 171, 172); T–V) third phalanges in medial view (AJG-184, 185, 186).

facet that runs obliquely in a dorsopalmar direction, which articulates with the scapholunate and ends in a well-developed posterior process (Fig. 11K). In distal view the articular facet with Mc III is rectangular and concave. On the palmar-lateral margin of this facet is another very small triangular facet that partially articulates with Mc IV. On the lateral side there is a concave surface that serves to articulate the hamate.

The hamate is subtriangular. In proximal view there is a slightly curved, elongated facet that is convex on its dorsal margin and

concave on the palmar surface, which articulates with the scapholunate (Fig. 11L). In distal view a suboval concave facet articulates with the proximal epiphysis of Mc IV and partially with that of Mc V. On the medial side there is a subtriangular facet that articulates with the capitata.

Mc I is small and has a subtriangular proximal area. The articulation with Mc II is sinuous. The articular facet with the trapezium is triangular and convex and narrows distally. The diaphysis is very short. The distal articulation projects vertically in an oblique plane

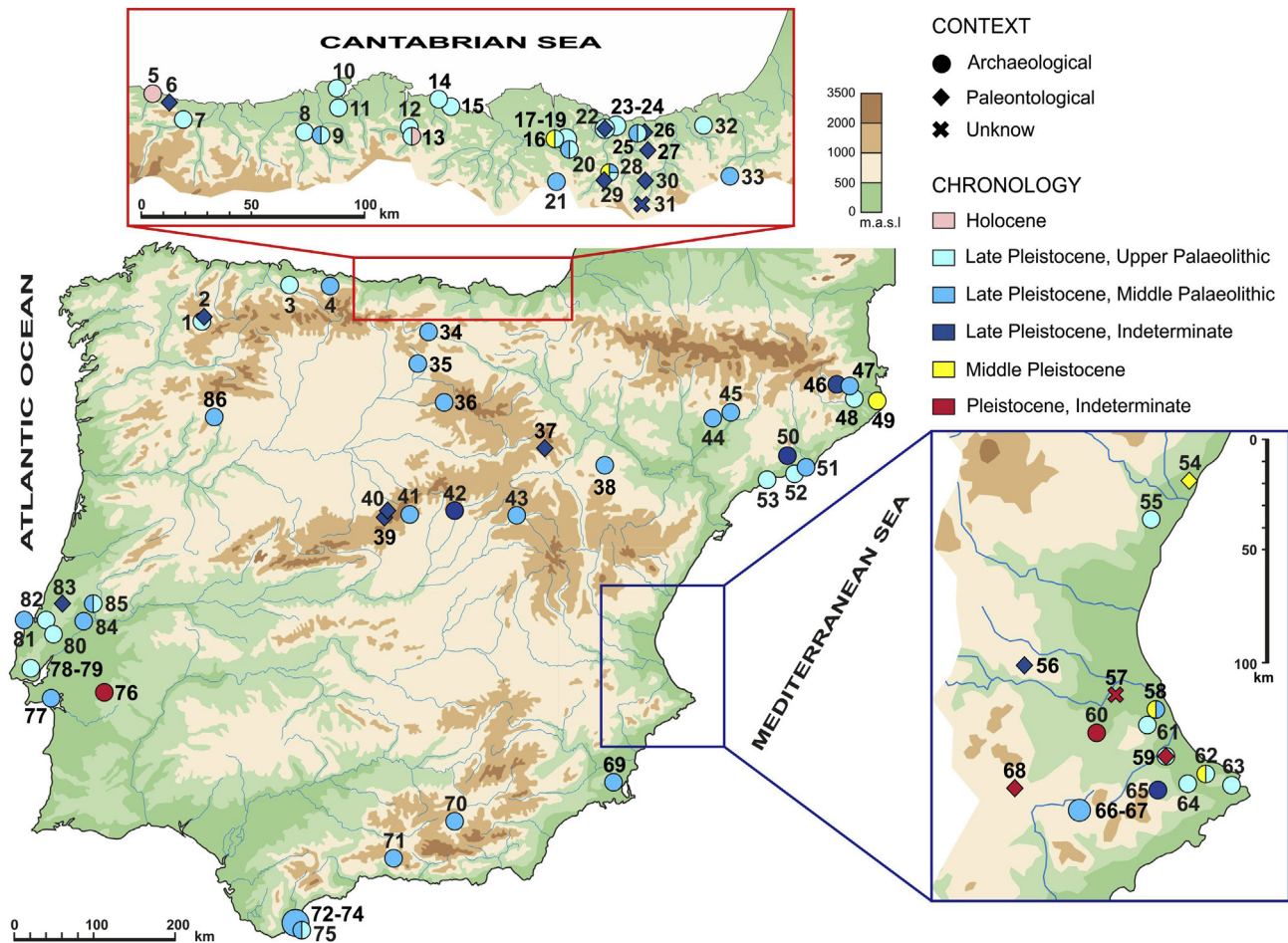


Fig. 14. Palaeogeographic and diachronic distribution of the leopard in the Iberian Peninsula. The numbers refer to the sites of the Table 13.

with a convex articular facet with the first phalanx (Table 7; Fig. 11Q).

In relation to Mc II, the proximal articulation is triangular and slightly angled medially, with a deep dorsopalmar groove. The articular facet with Mc I is oval and slightly concave, like that of Mc III or even deeper, and is typical of *P. pardus*, whereas in *P. uncia* it is triangular (Nagel, 1999). The diaphysis presents a triangular cross section in the proximal area that is more circular at the distal end. The distal articulation has a semicircular morphology and is slightly angled medially, with a very prominent sagittal crest on the palmar surface that separates two asymmetrical areas; on the dorsal surface of the distal articulation there are two grooves and two protrusions for insertion of the ligaments. It is a straight bone, except for the distal part, which projects backwards (Table 7; Fig. 11P).

Mc III is very straight and is the longest fore metapodial bone (Table 7; Fig. 11O). The proximal articulation is triangular and is divided in two by a dorsopalmar groove. The articular facet with Mc II has a small triangular fossa and an oval one in the articulation with Mc IV. Almost the entire length of the diaphysis has an oval cross section, except for the most proximal part, which is subtriangular. On the dorsal surface of the proximal diaphysis there is a rough surface that fades halfway along the bone. The distal articulation is semicircular, forms a straight line and has a ridge on the palmar surface that separates two symmetrical areas; on the dorsal margin there are two grooves and protrusions for insertion of the ligaments (Nagel, 1999).

The proximal articulation of Mc IV is rectangular-trapezoid and

has an oblique surface that is higher on the medial side. The articular facet with Mc III is elongated, while the articular facet with Mc V is a deep oval fossa with quite a pronounced ridge on the dorsal margin. The diaphysis is straight and has a circular cross section throughout its length. On the dorsal side of the proximal diaphysis there is a rough surface that disappears towards the middle of the bone. The distal articulation is very similar to that of Mc III (Table 7; Fig. 11N).

Mc V is the smallest of the metacarpal bones (Table 7; Fig. 11M). The longitudinal axis of the bone shows some degree of torsion towards the medial side. The proximal articulation is semicircular. The articular facet with Mc IV has a curved groove with a somewhat pointed protrusion in the centre. The diaphysis has an oval cross section. The distal articulation is very similar to that of Mc II.

The Mc from Valencian sites are very robust if compared with those of the present-day leopard, with similar or greater values in relation to those of *P. uncia* (Table 8), which may be a consequence of adaptation to a mountain environment.

### 3.1.6. Axial skeleton

The sternum is complete and is divided into eight sternbrae (Fig. 12A). The first is elongated and laterally flattened (GL: 54.6) and has a flatter proximal section, where the articular facets with the first pair of ribs are situated (Fig. 12H–I). Sternebrae II to VII are more similar, quadrangular and with wider ends but of varying sizes; IV and V are longer. The last one (VIII) is the longest and thinnest, with two dorsoventrally flattened ends.



Due to the state of preservation of the vertebrae, only the cervical vertebrae are described (Fig. 12B), and there are few items to compare them with in the Iberian fossil record (Table 9).

The atlas is formed by a ring of bone in the area that joins the dorsal arch to the ventral arch. The cranial articular surface has two cotyloid cavities that articulate with the occipital condyles of the cranium (Indu et al., 2013). It has a circular vertebral foramen. The wings, which are well distinguished from the body and displaced backwards, are rectangular with a rounded edge on the caudal margin. There is a weakly developed tubercle on the dorsal side.

The axis has a dorsoventrally flattened body and is laterally compressed. It has a well-developed odontoid process that almost reaches the occipital bone (Indu et al., 2013). The transverse processes project backwards. The spinous process is ventrally oblique. In ventral view, the bone presents a triangular shape. The caudal articular process is well developed, oblique and projects backwards.

As regards the remaining cervical vertebrae, their body decreases in size from the third to the seventh. The third and fourth cervical vertebrae are poorly preserved. The fifth, sixth and seventh are connected by concretion. In general they present a convex cranial articulation, while the caudal articulation is concave (Indu et al., 2013). The sixth has a poorly developed dorsal spinous process. The morphology of these vertebrae is similar to that of the present-day *P. pardus*.

Only one fragment of hyoid bone remains (Fig. 12G), the basi-hyoid, a single transverse bony plate in the form of a curved proximodistally flattened arch, with two suboval articular facets at each end. It is the first remains of a hyoid bone preserved in the Iberian fossil record (GL: 24).

### 3.1.7. Hindlimb

The pelvis is highly fragmented (Fig. 13A). The femora are poorly preserved (Fig. 13B). It is a very straight bone, the diaphysis of which has a circular cross section, except at the ends. The proximal articulation has a very spherical head, with an oval fovea capitis. The head is separate from the rest of the articulation and is connected to it by the neck. The greater trochanter is at the same height as the head, while in present-day individuals the head is higher (Podhade et al., 2013). The lesser trochanter is a small tuberosity. Between the greater trochanter and the neck is a deep trochanteric fossa. The dimensions are within the range of Iberian fossils (Table 10).

The proximal end of the tibia has caudal torsion (Fig. 13C). The proximal articulation is triangular and this morphology continues throughout the diaphysis except for the distal portion, where it is more oval. The tibial crest is wide and very prominent. The tibial tuberosity is more receding and is more developed than in the present-day *P. pardus*. The caudal margin of the proximal part has a certain concavity, which is less than that seen in the present-day *P. pardus*. The caudal surface of the diaphysis has a well-marked popliteal line that runs lateromedially. The distal articulation is subrectangular, with a well-distinguished, vertically projecting medial malleolus. The dimensions are within the range of Iberian fossils (Table 10).

The patella is almond shaped, decreasing in width and thickness from the base to the apex (Fig. 13E). In caudal view it presents two articular surfaces; the lateral surface is wider (Table 10).

A proximal fragment of talus remains (Fig. 13F). The margins of the trochlea are subparallel; in distal view the lateral margin projects and is more developed. The concavity of the trochlea is dissymmetrical in distal view. The tarsal sinus is deep and separates the articular surface with the calcaneus into two areas (Podhade et al., 2014b). The width of the trochlea is average for Iberian leopard fossils.

The plantar border of the body of the calcaneus is curved and wide, while the dorsal border is narrower and more pronounced. The tuber calcanei is quite well developed and becomes thicker at the proximal end, with a groove for the Achilles tendon. This area is asymmetrical as in *P. pardus*, whereas in *P. uncia* it is symmetrical. The coracoid process is subrectangular and somewhat convex. The articular facet with the talus is oval and concave, like the distal articulation with the cuboid. The dimensions are small, similar to other possibly female Iberian fossils (Cova Negra and Furninha) (Table 10; Fig. 13G).

There are very few other tarsal bones in the Iberian fossil record (Table 10).

The cuboid has a trapezoid shape. In proximal view there is a flat rectangular facet that articulates with the calcaneus (Fig. 13H). On the medial margin there is a small triangular facet that articulates with the navicular. In distal view, a concave oval surface articulates with the proximal epiphysis of Mt IV and V.

The navicular is suboval and quite flat except for the posterior process, which projects proximally. In proximal view we see the articulation with the talus, which is very concave (Fig. 13I). In distal view, the surface is flatter and there are two facets separated by a triangular fossa for the articulation of the cuneiform bones; on the lateral margin there is a larger semicircular facet for the third cuneiform, and on the lateral surface there is a smaller, sub-rectangular facet for the second cuneiform.

The first cuneiform in proximal view presents a semicircular concave facet that articulates with a small posterior facet of the navicular (Fig. 13J). In distal view it presents an elongated facet that articulates with Mt I.

The second cuneiform is subrectangular and is the smallest tarsal bone. In proximal view it has a somewhat concave oval facet that articulates with the navicular (Fig. 13K). In distal view, a flatter, elongated, semicircular facet articulates with the proximal part of Mt II.

The third cuneiform is subtriangular. In proximal view there is a concave triangular surface that articulates with the navicular and that ends in a distally projecting posterior process (Fig. 13L). In distal view another flatter triangular facet serves as an articulation for Mt III.

It has been possible to describe Mt I, II and III.

Both Mt I have been preserved, which constitutes the first citation of this in the Iberian fossil record. It is a small triangular residual bone (Fig. 13O). It decreases in width from the proximal to the distal end. In proximal view there is a flat oval facet that articulates with the first cuneiform. It flattens in the distal direction and ends with a rounded edge.

The main axis of Mt II shows medial torsion (Fig. 13N). The proximal articulation is triangular and runs obliquely in dorsal view. The articulation with Mt I (oval concavity) is on the medial surface of the proximal area. On the lateral side, the articulation with Mt III forms two suboval fossae. The distal articulation is semicircular, forms a straight line and has a ridge on the plantar margin that separates two asymmetrical areas; on the dorsal margin there are two grooves and two protrusions for insertion of the ligaments.

Mt III has a dorsoplantarly flattened and transversely widening diaphysis. The articulation with Mt II is an oval fossa flanked by two protrusions. The articulation with Mt IV is a deeper triangular fossa. The proximal end has a characteristic "T" shape, while the distal articulation is semicircular, forms a straight line and has a ridge on the plantar surface that separates two symmetrical areas; on the dorsal surface there are two grooves and two protrusions for insertion of the ligaments (Fig. 13M).

The metatarsals exhibit significant robustness (Tables 8 and 11), greater than the values for *P. pardus* and similar to or greater than

*P. uncia*, as suggested by Nagel (1999) and Sauqué et al. (2014a), which has been associated with a process of convergence between Pleistocene leopards and *P. uncia* because they inhabited a similar environment.

### 3.1.8. Phalanges

All the first phalanges have been described except for the posterior phalanges of digit V (Table 12). In general, the first phalanges of the hindlimb are longer and more robust, with the exception of the forelimb phalanges of digits III and IV, which are somewhat longer. In lateral view they all present the characteristic curvature.

The longest of the first phalanges of the forelimb (Fig. 11R–V) are those of digit III, followed by those of digits IV, V, II and I. The vestigial first phalanx of digit I is a short bone with an oval, medially oblique proximal articulation. The distal articulation is wide. The first phalanx of digit II is narrow with some curvature, the proximal articulation has a half-moon shape and the distal articulation tapers, both are asymmetrical and have a more developed lateral side; their body has a circular cross section. The first phalanx of digit III is large, with a dorsopalmarly flattened body and a wide, half moon-shaped proximal joint; the distal articulation is straight and symmetrical, with a deep distal trochlea. The first phalanx of digit IV is very similar to that of digit III but is shorter and thinner. The first phalanx of digit V is similar to that of digit II but with torsion in the opposite direction, and the ends are more developed on the medial side than on the lateral side.

The morphology of the first phalanges of the hindlimb is similar to that of the forelimb but they are more robust.

The second phalanges of the forelimb (Fig. 11W–Z) are longer than those of the hindlimb (Fig. 13P–S). The articulation is also wider in those of the forelimb, but the width of the body is greater in those of the hindlimb. As in the first phalanges, the longest phalanges are those of digits III and IV. The second phalanges have a very curved body with a triangular cross section that ends in a trochlea that is laterally displaced to allow lateral retraction of the third phalanx. The half moon-shaped proximal articulation is a concavity separated by a ridge that serves as an articulation with the first phalanx. There is quite a deep fossa on the plantar/palmar border of the proximal articulation. In the second phalanges of the forelimb the most well-developed articular process is that of digit II, while it is digit III in the hindlimb.

Six right third phalanges and all the left ones (five of the forelimb and four of the hindlimb) have been preserved. In general the forelimb ones (Fig. 11AA–AE) are larger and more robust than the hindlimb ones (Fig. 13T–V); in the forelimb those of digits II, III and IV are largest, while those of digits III and IV are largest in the hindlimb. The articular surface with the second phalanx is deep and oval.

### 3.2. Cova de les Malladetes

The right pelvis is almost complete and very well preserved (Table 10; Fig. 4A). The acetabulum, which is very circular, is fused, although the iliac crest and ischial tuberosity are not yet fused (late fusion). The bone is very straight. The ilium is subrectangular and elongated, and the wing has a curved border. In medial view, the auricular surface is divided into two areas by a triangular fossa, the dorsal one larger than the ventral. The ischium is shorter than the ilium and is slightly twisted, while the ilium is on a straight plane. The ischium has a very thin cranial border, while the caudal border is wider. The characteristics coincide with those of the pelvis of present-day leopards in India (Podhade et al., 2014a), although the one found at Malladetes is longer.

### 3.3. Cova del Racó del Duc

The leopard remains found at this site show morphological similarities to AJG. We therefore describe some elements that are poorly preserved or not found at AJG (talus and Mt IV and V). In REC I the remains correspond to two individuals, one senile and larger than the other, and in REC II to a third, large individual.

In REC I, the set of large remains comprise tibia, canine, carpal, patella, four metacarpals and two metatarsals. The smaller remains that may correspond to a female (radius, talus, metacarpal and metatarsal) have similar dimensions to AJG (Fig. 5). It has not been possible to attribute the other elements to a specific individual (caudal vertebrae, phalanges and ribs). All the remains from REC II are large (Fig. 6).

Two talus bones are described, one large one from REC II (Fig. 6O) and another smaller one from REC I (Fig. 5X). The margins of the trochlea are subparallel, but the lateral margin projects and is more developed. The concavity of the trochlea is dissymmetrical. Both features appear in AJG. The neck is not very elongated and the head is medially oblique. The trochlea and neck are not aligned. The head is oval and has a bony ridge. In plantar view, the sinus is deep and separates the articular surface with the calcaneus into two areas. The dimensions of REC I are very similar to those of AJG and Bolinkoba. The talus from REC II is among the largest in the Iberian fossil record, similar to the more robust examples from Zafarraya (Table 10).

Two Mt IV are described from two large individuals, one larger and more robust (Fig. 6Y) than the other (Fig. 5V). The bone is large and straight, with some torsion towards the lateral side. The proximal epiphysis is rectangular. The articulation with Mt III has two oval facets separated by a deep groove, while that of Mt V is a very deep oval fossa. The cross section of the diaphysis is more quadrangular at the proximal end and becomes more oval towards the distal end. The distal articulation is semicircular, forms a straight line and has a ridge on the plantar border that separates two symmetrical areas; on the dorsal surface there are two grooves and protrusions for insertion of the ligaments. The measurements of the larger individual are similar to those of the robust forms of Zafarraya (Table 11).

Two Mt V are described, one more slender (Fig. 5W) and the other more robust (Fig. 6Z). The bone is curved in a dorsoplantar direction and is the smallest of the functional metatarsals. The diaphysis has a round cross section. The proximal epiphysis is triangular. The articulation with Mt IV consists of a pointed oval projection. In plantar view the proximal area presents two lobes (forked). The distal joint, which is displaced laterally, is semicircular and has a ridge on the plantar border that separates two asymmetrical areas. The dimensions are consistent with those of other specimens from sites in the Iberian Peninsula (Table 11).

### 3.4. Cova del Bolomor

The morphology, dimensions and robustness of the Mt III (Fig. 7C) found in level XIII (Middle Pleistocene) coincide with those of other Middle and Late Pleistocene remains from the Iberian Peninsula (Tables 8 and 11).

### 3.5. Cova Negra

A calcaneus found in the 2013 excavation presents the same morphometric characteristics as AJG and may correspond to a female (Table 10; Fig. 7F). A P4 from an adult and a p4 from a 1.5- to 2-year old individual are presented (Stander, 1997) (Tables 4 and 5), but not described (Pérez, 1977).

The P4 has a very high crown, a well-differentiated rounded

parastyle and a paracone or main crest with a well-marked, vertical anterior ridge (Fig. 7I). The posterior edge of the paracone and that of the metacone form a narrow angle. The cusp of the paracone presents some wear. The protocone is rounded and well developed, a typical characteristic of Late Pleistocene European leopards. The mesial-distal outer length is similar to that of Escoural and Aintzulo, but greater than for the females of AJG and Algar da Manga Larga (and possibly Torrejones) and that of present-day leopards.

p4 has a poorly differentiated, reduced paraconid, unlike that of AJG, similar to Caune de l'Arago (Testu, 2006). There is a well-developed almost vertical protoconid that shows no wear. The posterior cusp is reduced like the anterior one. Behind the posterior cusp there is a well-marked cingulum on the lingual side. In occlusal view, the tooth is widest in the distal third, with some narrowing in the middle (Fig. 7J). The tooth has a mixture of archaic features (Middle Pleistocene) and others that are more typical of present-day and Late Pleistocene individuals. The dimensions coincide with those of some Late Pleistocene (Los Rincones and Algar da Manga Larga) and present-day leopards.

## 4. Discussion

### 4.1. Pleistocene *Panthera pardus* in the Iberian Peninsula

The new cranium found at AJG, together with those from Allekoaitze and Aintzulo in the north of the Iberian Peninsula (Mariezcurrera, 2011; Corral, 2012; Altuna and Mariezcurrera, 2013), Algar da Manga Larga in Portugal (Cardoso and Regala, 2006), Equi in Italy (Ghezzo and Rook, 2015) and Vjetrenica in Bosnia-Herzegovina (Diedrich, 2013) represent Late Pleistocene European leopards. Although the remains from AJG could not be dated, the cranium is very similar to that of other European specimens from the Late Pleistocene, so it is provisionally attributed to that period. The cranium of these leopards is of a medium length, with wide nasal and frontal areas, a globular neurocranium and variable dimensions that for Diedrich are associated with strong sexual dimorphism, which would explain the existence of more elongated morphotypes in males (close to those of African leopards) and shorter morphotypes in females (more similar to *P. uncia*), corresponding to the subspecies *P. pardus spelaea* (Diedrich, 2013). For Ghezzo and Rook (2015), the crania of male and female *P. pardus* differ in terms of their morphological features and size is a criterion that can be more variable.

In this regard, and in the light of new work, the material from Los Rincones could be reassigned to *P. pardus*, although the remains present similarities with the subspecies *spelaea* described by Diedrich (2013).

The mandibles of Late Pleistocene *P. pardus* specimens from the Iberian Peninsula are longer than those of *P. uncia*, with a mixture of features of both species, as seen at Los Rincones (Sauqué and Cuenca-Bescós, 2013).

The dentition of Late Pleistocene *P. pardus* from the Iberian Peninsula is similar in size to that of present-day leopards. P4 has a very hypsodont crown. For Diedrich (2013), the morphology of the upper carnassial has undergone a process of evolution across the different European leopards. The height of the crown increases from the Middle Pleistocene subspecies to *P. pardus spelaea*, *P. pardus ciscaucasica* and, in particular, *P. uncia*. The presence of a rounded protocone is characteristic of the last European Pleistocene leopards and *P. uncia*, an area that tends to decrease from ancient forms to the end of the Late Pleistocene. In general, the morphology of P4 in Late Pleistocene leopards has similarities with *P. uncia* (Sauqué et al., 2014a).

The Late Pleistocene *P. pardus* of the Iberian Peninsula is a leopard that has similarities with *P. uncia*. The specimens found at

Algar da Manga Larga, Los Rincones, AJG, Allekoaitze, Aintzulo and Zafarraya (Sauqué et al., 2014a) present uncoid features and some of them have been reassigned by Diedrich (2013) to the subspecies *spelaea*. This could be related to the adaptation of both species to a mountain habitat, showing that these species may have a similar ethology.

Variations in size between the different leopard remains found in the Iberian Peninsula may be a consequence of both sexual dimorphism and climatic factors, as it is very likely that they were larger during cold phases than in milder periods (Diedrich, 2013). In any case it should be taken into account that there may be some overlap between the dimensions of males and females; some authors therefore believe it is better to assign the sex on the basis of morphological rather than metric criteria (Ghezzo and Rook, 2015).

As regards the age structure of the leopards, almost all the material found to date in the Iberian Peninsula corresponds to adult individuals, which is why we believe it is more plausible that they used the caves as storage places to protect their catches from other predators (de Ruiter and Berger, 2000; Diedrich, 2013; Sauqué et al., 2014c). This scenario is consistent with leopard breeding patterns, as they do not use caves (Diedrich, 2013). The presence of cubs in the Iberian Peninsula record is limited to one deciduous tooth at Jou Puerta (Álvarez-Laó, 2014), to which the m1 germinal from Malladetes has now been added. These remains may indicate a possible use as breeding areas, as is the case of Equi (Ghezzo and Rook, 2015) and Vraona (Nagel, 1999).

During the Late Pleistocene, leopards in the Iberian Peninsula fed mainly on small ungulates, particularly *Capra pyrenaica*, a species that inhabits rocky areas. The association between leopards and Spanish Ibex is present in many Pleistocene sites such as Los Rincones (Sauqué et al., 2014c), Zafarraya (Barroso et al., 2006), Amalda (Yravedra, 2010a) and Racó del Duc (currently being studied). For their part, snow leopards are also specialised in domestic or wild goats (Anwar et al., 2011; Diedrich, 2013), prey that they do sometimes carry to their dens (Oli et al., 1993; Diedrich, 2013).

As regards leopard remains found in Middle Pleistocene sites of the Iberian Peninsula (Cueva de Lezetxiki, Cueva de Arlanpe, Cau del Duc d'Ullà, Cau d'En Borràs, Cova del Corb and Cova del Bolomor), as in the rest of Europe there are few specimens and no good morphometric descriptions. For Diedrich (2013) the remains from this period correspond to the subspecies *P. pardus antiqua* Cuvier 1835, which migrated to Europe about 300 ky BP. In order to confirm the existence of different Pleistocene subspecies in Europe (Diedrich, 2013) or that of a single chronospecies with significant variability (Ghezzo and Rook, 2015), we would need a larger record of leopard remains in Middle and Late Pleistocene contexts.

In our case, despite the characteristics of Mediterranean leopards being very similar to those presented by Diedrich (2013) and Sauqué et al. (2014a) for *P. pardus spelaea*, in addition to having certain similarities or common features with *P. uncia*, we believe that, in view of the recent publication by Ghezzo and Rook (2015), intraspecific variability may also account for the variations seen in the leopards of the Iberian fossil record and we therefore classify the remains as *P. pardus*.

### 4.2. Diachronic and palaeogeographic distribution of the leopard in the Iberian Peninsula

The earliest presence of the leopard in the Iberian Peninsula corresponds to the Middle Pleistocene levels of Lezetxiki (234 ky). The few citations from this phase are distributed throughout the Mediterranean and Cantabrian regions (Table 13; Fig. 14). In some cases (Cova del Mollet I), the initial determinations (Maroto et al., 1987) have not been confirmed (Maroto et al., 2012). There are



even two possible remains from the transition between the Lower and Middle Pleistocene that would push back the leopard's appearance in the Iberian Peninsula until this time, a calcaneus (*Panthera cf. pardus*) from Venta Micena (Pons-Moyà, 1987) and a metapodial (*Panthera sp.*) from Gran Dolina (García, 2003), but they do not have a clear assignation. The leopard's presence in the Iberian Peninsula appears to be later than in the rest of Europe (Sauqué and Cuenca-Bescós, 2013).

The vast majority of references from the Iberian Peninsula come from the Late Pleistocene (Table 13; Fig. 14), mainly during MIS 2 (49.4%) and MIS 4–3 (45.9%), while there are few references from the Early Late Pleistocene or MIS 5e (4.7%). The information collected enables us to distinguish three points during MIS 2. Most references come from the beginning of this period and coincide with the Early Upper Palaeolithic (25.9%), with fewer citations during the Solutrean/LGM (11.8%) and Magdalenian (4.7%). This tells us that the phase of greatest distribution of the leopard in the Iberian Peninsula coincides with Mousterian Neanderthal occupations and early modern humans from the beginning of the Upper Palaeolithic. The leopard's ubiquitous nature explains its presence in both harsh phases and times when the climate was milder.

Two very late records in the Cantabrian region (Cueva de las Pajucas and Cueva de la Riera) suggest that the species survived in Europe into the Early Holocene (Altuna, 1972; Álvarez-Laó, 2003). These Holocene references together with those from the end of the Lateglacial period confirm the idea that the species survived for longer in the Iberian Peninsula than in other parts of Europe (LGM), mainly in the Cantabrian region (Sauqué and Cuenca-Bescós, 2013).

The main areas of distribution of the species in the Iberian Peninsula are areas of karst relief near the coast, with many of the findings concentrated in the eastern part of the Cantabrian coast, the Catalan coastal mountain range, the foothills of the Betic system close to Cabo de la Nao in the Mediterranean and Portuguese Estremadura. The rest of the peninsula, which has fewer or no records, has little karst development and preservation of the remains is difficult. The new findings from the Mediterranean region confirm a particularly dense distribution of the leopard, very similar to that of the Cantabrian region, during the Late Pleistocene.

The leopard's distribution can be analysed in relation to the two broad biogeographic regions of the peninsula, the Euro-Siberian and Mediterranean regions (Rivas-Martínez, 1987; Rivas-Martínez et al., 2002). The sites with records in the Euro-Siberian region are mainly located below 600 masl (approx. 79%) and secondarily between 540 and 780 masl. The sites at a higher altitude in the region (Arrillor and Eirós) are barely more than 700 masl. As regards the Mediterranean region, citations in the east of the peninsula are concentrated in areas below 200 masl and in sites near the coast, while on the Portuguese Atlantic coast they reach 460 masl (approx. 44%). Thirty-seven per cent of the findings in this Mediterranean region appear in areas between 115 and 1000 masl. Nineteen per cent of the records correspond to places at a higher altitude in the mountains of the Iberian and Guadarrama mountain ranges, except for Lorga de Dine, in the Portuguese part of the Montes de León. These are approximate estimates and are based on the current sea level, and it must be kept in mind that Pleistocene transgression–regression episodes would have affected the coastline (Álvarez-Laó and García, 2010, 2011).

The leopard is a common taxon in the Iberian Peninsula during the Late Pleistocene, although in general there are a small number of remains compared with other carnivores (Sauqué and Cuenca-Bescós, 2013; Sauqué et al., 2014a). This is due to their solitary, territorial behaviour, with large areas of distribution (Nowell and Jackson, 1996; Kingdon, 1997; Turner and Antón, 1997). Another factor that influenced the frequency of this taxon in cave sites was the high degree of competition with other carnivores during the

Late Pleistocene. *P. pardus* had to compete with the hyena (*Crocuta crocuta spelaea*), the cave lion (*Panthera leo spelaea*), the wolf (*Canis lupus*), the dhole (*Cuon alpinus*) and with two species of bear, the cave bear (*Ursus spelaeus*) in the northern half of the Iberian Peninsula and the brown bear (*Ursus arctos*) in the rest of the territory (Diedrich, 2009, 2011; Villaluenga, 2009; Pérez et al., 2010; Morales et al., 2012; Sauqué et al., 2014a).

During the Late Pleistocene the leopard was distributed throughout the Iberian Peninsula, and it is the part of Europe with the highest concentration of remains. This may be due to the fact that there were fewer carnivores such as hyenas and lions than in other areas of Europe (Diedrich and Zák, 2006; Diedrich, 2007, 2011, 2014). In the Cantabrian region most of the caves were occupied by bears during the Late Pleistocene (Villaluenga, 2009). Bears and hyenas were less common in the Mediterranean region, meaning that leopards competed mainly with humans and dholes (Pérez et al., 2010; Morales et al., 2012) for the use of caves, which resulted in the Mediterranean area having a significant density of sites containing leopard remains (Fig. 14).

#### 4.3. Contexts of appearance and origin of the leopard remains

During the Pleistocene in the Iberian Peninsula there was interaction between hominins and felines: from the lion (Blasco López et al., 2010), leopard (Arribas, 1997; Camarós et al., 2015) and different species of lynx (Yravedra, 2005) to the wild cat (Gabucio et al., 2014). Hominins hunted them for their meat, skin and bones, as well as to defeat a direct competitor for prey and for the use of caves and shelters (Brugal and Fosse, 2004). Hominins would also have been prey to some of these carnivores (Kruuk, 2002; Camarós et al., 2015).

In the case of leopards, these processes can be seen in several sites of the Iberian Peninsula. Sometimes the bones found in archaeological contexts, mostly as isolated elements, exhibit cut marks, indicating that these animals were hunted and/or processed by humans. For example, the incisions on the cranium of the leopard discovered at Torrejones (Guadalajara), which was found in the Middle Palaeolithic level, were made while the skin was being removed (Arribas, 1997). The same interpretation has been made of the marks observed on a leopard metapodial from Cova Foradada (Alacant) belonging to an Early Upper Palaeolithic level (Pantoja et al., 2011). On examination of a partially burnt Mt V from Cova Negra (CN 10952; Pérez, 1977), several cut marks were identified on the dorsal surface of the diaphysis, which could also be from skinning (Fig. 7H). Other evidence includes a leopard ulna from Cova Foradada, from the same level as the aforementioned metapodial, which shows intentional polishing on the distal end that could correspond to a bone awl (Pantoja et al., 2011). The remains found at Sima de las Palomas (Murcia) included a burnt leopard bone and various articulated appendicular elements associated with human remains, and it is possible that the Neanderthals hunted them (Walker et al., 2012). The leopard remains found at Llonín (assemblage II from the “Cono Posterior” section), which are currently being studied, do not present direct signs of human action, but they could be placed within a context that is considered anthropogenic. It is a partial leopard skeleton surrounded by five carefully arranged stalactite fragments and associated with other faunal and lithic remains (Forkea et al., 1999). In this case the leopard remains may be related to symbolic behaviours or acts.

Leopard attacks on humans can be seen as another type of interaction. Recently, a possible leopard attack on a Neanderthal has been documented in Cova Negra. Two punctures on a parietal fragment bone are likely to have been produced by two canines of a carnivore (Camarós et al., 2015).

Apart from predation, other interaction processes can also occur

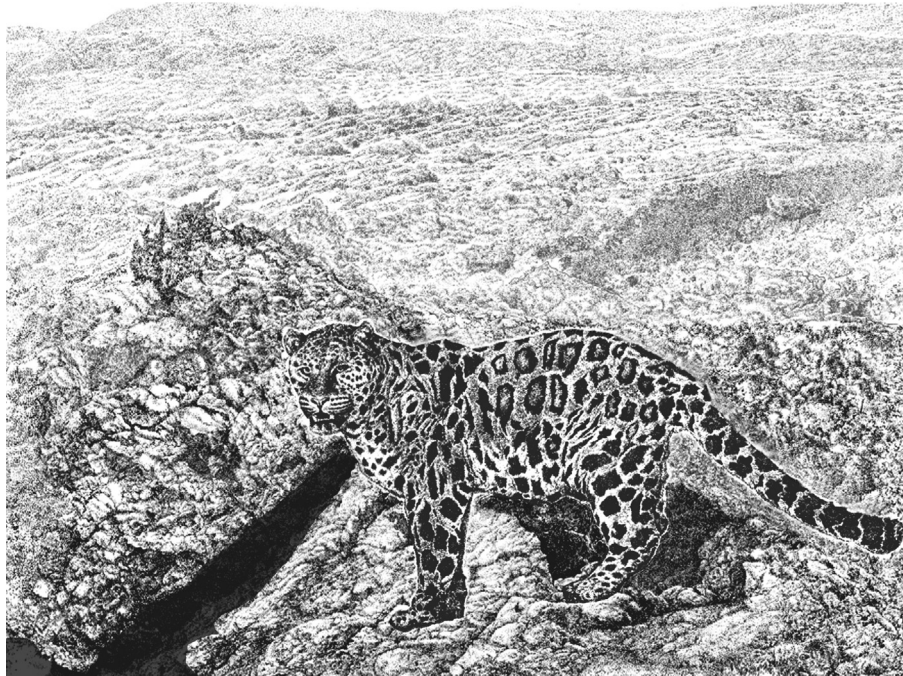


Fig. 15. Leopard (*Panthera pardus*) close to the Avenc de Joan Guitón chasm (Illustration of Gianfranco Messi).

when leopards occupy the same locations as humans (breeding dens, shelters, feeding or storage areas) and carry their prey there, creating bone accumulations that could be mixed with materials from anthropogenic sources (for example, in the Iberian Peninsula, Sauqué et al., 2014b). The latter may have also been scavenged by leopards as well. The phenomenon of prey being transported to caves by leopards has been documented in several areas (de Ruiter and Berger, 2000). Sometimes, leopard remains of natural origin are associated or interspersed with archaeological material during phases when humans did not occupy the sites, as is the case of Abric Romaní (Cáceres et al., 1993) or Furninha (Brugal et al., 2012). In palaeontological contexts, the accumulations are natural and result from predation or natural death as in AJG (Fig. 15), in this case a complete skeleton, where the fragmentation is perimortem and post-depositional.

In the Valencian region (central Mediterranean area of the Iberian Peninsula), there are few leopard remains in the archaeological contexts, with the exception of some Early Upper Palaeolithic levels of sites like Cova Foradada (Pantoja et al., 2011) and Malladetes (this study). These were times when there was little human presence in the area, with small or highly scattered groups and a great proliferation of carnivores, such as those documented in other areas of the Iberian Peninsula (Valente, 2004a,b). For some authors, this scenario may be due to a hiatus when humans were not present that coincided with the disappearance of the last Neanderthals and the arrival of the first anatomically modern humans (AMH) (Wood et al., 2013; Galván et al., 2014). However, it could also be a reflection of the low population density at the beginning of the Aurignacian expansion in the Iberian Mediterranean, as archaeological contexts bear witness to the interaction of humans and felines in the same caves.

## 5. Conclusions

The Mediterranean leopards presented in this paper have morphological characteristics similar to those of other European remains that have been attributed to the subspecies *P. pardus*

*spelaea*, with features representing a mixture between the present-day leopard and the snow leopard, showing strong sexual dimorphism. Despite this morphological similarity, with so few remains and no genetic analysis of Pleistocene leopard populations to corroborate or refute the existence of subspecies, we consider it prudent to classify the remains at species level (*P. pardus*).

The leopard skeleton found at AJG is the best preserved Pleistocene specimen of this kind in the Iberian Peninsula and one of the most complete specimens in the European and global fossil record. We believe it to be a reference for future studies. In this regard, we present an exhaustive morphological description of the cranial and postcranial elements that will be of great use, as leopard remains are usually found fragmented and it is difficult to establish the relationship between the different features of the cranial and postcranial skeleton.

The greatest expansion of the leopard in the Iberian Peninsula took place during the Late Pleistocene, between MIS 4 and MIS 2. Moreover, the species survived for longer in this geographical region than in other areas of Europe, with records from the Lateglacial period, possibly even reaching the Early Holocene.

Our review of the leopard's distribution in the Iberian Peninsula includes many new records, of which there are now 86, making the Iberian Peninsula one of the areas with the highest density of sites containing Pleistocene leopard remains in Europe.

The most complete and best preserved leopard remains in the Iberian Peninsula appear in palaeontological sites, but such findings are in the minority. The majority of leopard records correspond to Middle and Upper Palaeolithic archaeological contexts. In this case there are signs of processes of interaction between these carnivores and prehistoric human groups, Neanderthals and early AMH, based on competition, feeding and other behaviours.

## Acknowledgements

With respect to the finding, recovery and restoration of the skeleton from AJG and the analyses, photographs, video, X-rays and scanning of the remains, we would like to thank: Àngel Cambra,



Josep A. Ribera, Juan Salazar, João Zilhão, Mara Peiró, Juan Navarro, Trinidad Pasies, María Perales, Clínica Dental Adeslas, José Madrid, Elvira Aura, Mari Carmen Díaz and Xerea Films.

Various investigators have provided us with information about leopard remains in the Basque Country (Asier Gómez-Olivencia), Asturias (Javier Fortea and Marco de la Rasilla), Catalonia (Jordi Nadal, Juan Ignacio Morales, Antonio Rodríguez-Hidalgo and Palmira Saladié), Valencia (Inocencio Sarrion, Josep Fernández, J. Emili Aura, Joaquim Juan-Cabanilles, Bertila Galván, Cristo Hernández, Juan V. Morales, Leopoldo Pérez and Rafael Martínez), France (Agnès Testu and Jean Philip Brugal) and Portugal (João L. Cardoso). A particular thanks to palaeoartist Gianfranco Mensi for his precise reconstruction. Thanks to Jaime Vives for the revision of the text.

The text has been translated into English by Grace Horsley and Jordi Sanchis.

We would like to thank Helena Bonet, the director of the Museu de Prehistòria de València, for the support and interest she has shown for this project.

This work forms part of the following projects: (HAR-2011-24878) “Paleolítico medio final y Paleolítico superior inicial en la región central mediterránea ibérica (Valencia y Murcia)” (End of the Middle Palaeolithic and beginning of the Upper Palaeolithic in the central Mediterranean region of the Iberian Peninsula (Valencia and Murcia)) and (PROMETEOII/2013-016) “Más allá de la Historia. Origen y consolidación del poblamiento paleolítico valenciano” (Beyond history. Origin and consolidation of the Valencian Palaeolithic settlement).

The authors also thank the reviewers for the useful suggestions that greatly improved the manuscript. Finally, the authors thank the work of the editorial team of Quaternary Science Reviews.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2015.07.013>.

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