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

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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.

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; Ghezzo 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-Bonnoure, 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 (Ghezzo 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