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Recull d'estudis de fauna de jaciments valencians

V Jornades d'arqueozoologia



Museu de Prehistòria de València

REULL D'ESTUDIS DE FAUNA DE JACIMENTS
VALENCIANS

V JORNADES D'ARQUEOZOOLOGIA

RECULL D'ESTUDIS DE FAUNA DE JACIMENTS
VALENCIANS

V JORNADES D'ARQUEOZOOLOGIA
DEL MUSEU DE PREHISTÒRIA DE VALÈNCIA

Alfred Sanchis i Josep Lluís Pascual Benito
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THE LYNXES (*LYNX PARDINUS/SPELAEUS*, *LYNX LYNX*)
FROM THE MIDDLE PLEISTOCENE TO THE HOLOCENE
IN SOUTHERN FRANCE: A PALEONTOLOGICAL AND
TAPHONOMICAL OVERVIEW

*Philippe Fosse, Jean Philip Brugal, Evelyne Crégut-Bonnoure, Jean Baptiste
Fourvel and Stéphane Madelaine*

ABSTRACT

Paleontological data on lynx are relatively scarce in Pleistocene sites. However, in southern France and Monaco, samples from caves of Escale (NISP= 435; MNI= 15), Observatoire (NISP= 103; MNI= 9), Campefiel (NISP= 1532; MNI= 26) and Lunel-Viel (NISP= 37; MNI= 5) are some among the most important fossil series. Our paleontological revision indicates the presence of the cave lynx (here named *Lynx pardinus spelaeus*) considered as the Pleistocene form of the modern Iberian lynx. Taphonomic analysis suggest either a natural occupation of the caves by this species or caused of natural trapping. The French geo-chronological distribution of lynxes (*Lynx pardinus/spelaeus* and *Lynx lynx*) is also provided.

INTRODUCTION

The lynxes (European lynx, *Lynx lynx* Linné, 1758 and Iberian lynx, *Lynx pardinus* Temminck, 1827) are the largest extant felids in Europe. Their recent geographical distribution is highly fragmented due to the extreme anthropogenisation of ecosystems and their biotopes. In the Pleistocene record, the lynx *l.s.* were identified in paleontological (*i.e.* traps, carnivore dens) and archaeological (anthropogenic) sites. The European lynx, very rare in western Europe, is identified in some Late Glacial and Holocene

karstic infillings. The Iberian lynx is much more abundant in extra-steppic regions and has been described by a chronoform (*Lynx pardina* race *spelaea*) from Grimaldi (*i.e.* Enfants, Prince) caves (Boule, 1910 and not Boule, 1906). This cave lynx is seldom as large as the extant European lynx and presents characteristics of the extant Iberian one (teeth morphology, slenderness of postcranial elements). A third lynx species, called Issoire lynx, *Lynx issiodorensis* Croizet and Jobert, 1828, is identified mainly from fluvial deposits. Two distinct sized chronoforms (*Lynx issiodorensis issiodorensis* [large]/*Lynx issiodorensis valdernensis* [small] Werdelin, 1981) are respectively recorded in the Middle Late Pliocene - early Lower Pleistocene («villafanchian») and in the late Lower Pleistocene («epivillafanchian») sites. The systematic position as well as the geo-chronological distributions of all these species/forms have been debated over the last 50 years (Bonifay, 1971; Ficcarelli and Torre, 1977; Kurtén, 1978; Pons-Moyà, 1983; Blanc, 1984; Martínez-Navarro, 1992; Rustioni et al., 1995; Hemmer, 2001; Testu, 2006; Garrido, 2008; Lorfèvre, 2009; Cherin et al., 2013; Madurell-Malapeira et al., 2014; Ghezzi et al., 2015; Boscaini et al., 2016). More recently ancient DNA analyses provide interesting consideration to the biogeographical/sympatric range of the two lynx species (Rodríguez-Varela et al., 2015a, 2015b) or a progressive eurasian split between lynx populations (Lucena-Pérez et al., 2020).

Usually identified from few bones/site(s) in the Pleistocene faunal assemblages, important lynx samples from three caves in southern France and in the Principality of Monaco are presented in this contribution, with an updated paleontological and taphonomic overview. The lynx remains come from Escale cave (Bouches-du-Rhône; Bonifay, 1971; Fosse et al., 2020a, 2020b), dated to the end of the first half of the Middle Pleistocene, and from Campefiel cave (Gard; Paulus and Tron, 1945; Bonifay, *ibid*; Fosse and Crégut-Bonnoure, *pers. obs.*), Observatoire cave (Monaco; Boule and Villeneuve, 1927; Brugal et al., 2017), whose biostratigraphical fillings can be attributed to the Late Pleistocene. Furthermore, a fourth sample, from Lunel-Viel I and IV cave (Hérault; Bonifay, *ibid*; Fosse, *pers. obs.*), was also considered, due to interesting taphonomic context (hyena den). Finally, a survey on zooarcheological data is also performed for French and Spanish Paleolithic deposits (cutmarks, symbolism) for the *Lynx* ssp. remains.

SITES PRESENTATION

The fossil samples yielding lynx remains are clearly more abundant in South-East France (including Monaco area) (Paulus and Tron, 1945; Bonifay, 1971) than in western (such as Dordogne and the Pyrenees) or northern regions (figure 1). Our recent researches provide a detailed quantification and identification of these samples, including the complete osteometrical dataset (currently available online for Escale cave) as well as taphonomical observations about the site context (Brugal et al., 2017, 2020; Fosse et al., 2020a, 2020b).

Escale cave

Escale cave (Saint Estève, Bouches du Rhône) is located about 50 kilometers north of Marseille and was discovered in the early 1960s following a road construction. This karst infill (up to 23 meters of sedimentary deposit, see Bonifay and Bonifay, 1963), excavated over a decade (1962-1974), is divided into five main fossiliferous levels (from the base level B up to the top one), including numerous macromammalian remains (*Lynx pardinus spelaeus* (B, H), *Panthera gombazoegensis* (C-D), *Canis mosbachensis* (B), *Hyaena prisca* (B), *Gulo schlosseri* (H), *Ursus deningeri* (B), *Vulpes praeglacialis* (H), *Hemitragus bonali* (B): Bonifay, 1971, 1974-75; Coumont, 2006; Boudadi-Maligne, 2010; Fosse et al., 2020a). Biochronological information support an age estimation about the end of the first half of the Middle Pleistocene (~MIS 12). Lynx remains are mainly located within the cryoclastic levels H and B (*cf infra*). Mesofauna is scarce (lagomorphs, birds) and no lithic artefacts have been found.

Observatoire cave

The cave of L'Observatoire in Principality of Monaco yields one of the most important sample of non steppic Late Pleistocene carnivore species (such as *Canis lupus*, *Cuon alpinus*, *Panthera pardus*, *Lynx pardinus spelaeus*) and ibex (*Capra ibex*) in southern Europe (Boule and Villeneuve, 1927; Testu, 2006; Brugal et al., 2017, 2020). This karstic cave (over a hundred meters depth) located about 100 meters above sea level, has been excavated during the 1920s. Lynx remains come from the first upper section of the cave. Unfortunately no precise spatial data have been recorded. However,

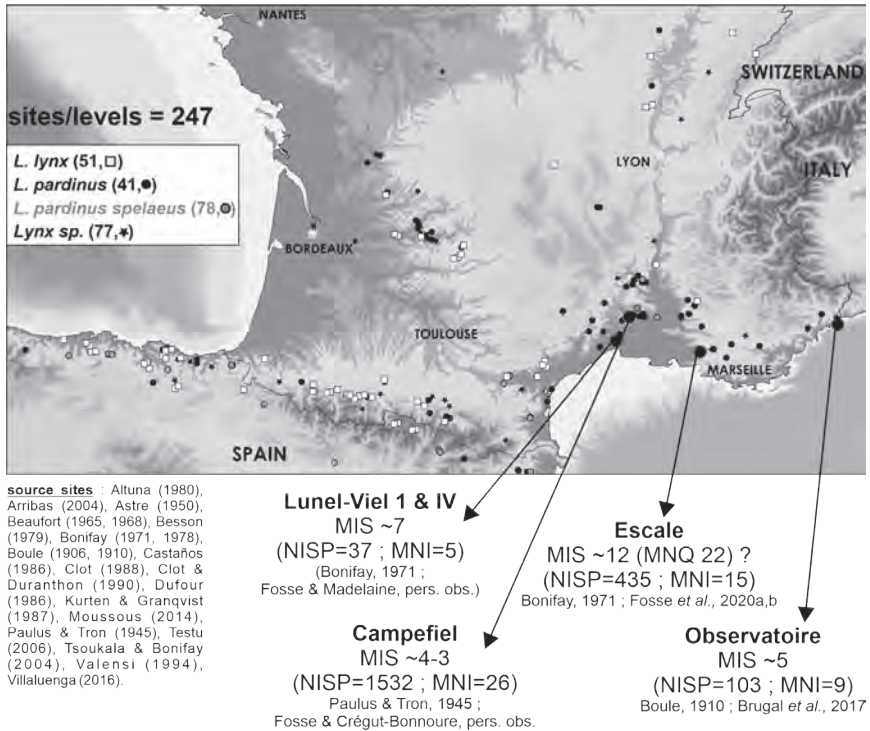


FIGURE 1. Location of samples currently studied and geographical distribution of lynxes in southern France.

the faunal composition and their specific evolutionary stages suggest an estimated age between the end of the Middle Pleistocene and the beginning of the Late Pleistocene (MIS 7?-5).

Campefiel cave

Campefiel (Sainte Anastie, Gard) is a cave located along the Gardon valley in a particularly important area characterized by its numerous Pleistocene sites (Bonnet, 1945). Excavated in the early XXth century, Campefiel cave has two distinct entrances; the main one opens over a 50 meters length gallery followed by a shorter and narrowed corridor driving on a sinkhole. The main gallery was identified as a hyena den (abundant mandibles, coprolites) with no lynx remains. Just before the WWII (1939), new excavations were carried

out and a «Lynx level» was apparently found («Niveau à lynx» as written in French on a single manuscript note in a small box). The sinkhole, excavated then, provides numerous lynx remains (Paulus and Tron, 1945; Bonifay, 1971). A revision of lynxes remains has been realized recently (Fosse and Crégut-Bonnoure, pers. obs.). Lagomorphs are also abundant at Campefiel, which could maybe explain the abundance of lynx remains. However, no taphonomic study has been done yet and there is no spatial data available from all these paleontological galleries/levels.

Lunel-Viel cave

Lunel-Viel (Hérault) is a Middle Pleistocene palaeontological site known since the first half of the XIXth century. The most important excavations were leaded by E. and M. F. Bonifay during the 1970s (Bonifay, 1971) and restart two years ago (Brugal et al., forthcoming). This huge cave is one of the most important hyena den in Europe (Fosse, 1996). Cervids, equids, large bovids, hyenids and canids, are especially abundant and identified from well preserved cranial and postcranial skeletal elements (Bonifay, 1971; Brugal, 1983; Fosse, 1996; Boudadi-Maligne, 2010; Uzidinis, 2017). Few lynx remains have been identified among this important bone sample (over 6000 specimens) (Bonifay, 1971; Fosse, pers. obs.). Biochronological estimation from the vertebrates (mammalian, bird and chelonian species) attributed the temperate mammal association to MIS 9 or, more probably, to MIS 7.

MATERIAL AND METHODS

This paper is based on the revision of lynx remains from these four caves. Cranial and postcranial samples are abundant in the first three deposits (table 1). At Escale cave, 435 paleontological remains have been attributed to the lynx (Bonifay, 1971; Fosse et al., 2020a, 2020b). This sample might be slightly increased considering thoracic/lumbar vertebrae or ribs (not considered taxonomically yet due to the presence of the wolf, *Canis mosbachensis*, in all levels). The minimum number of individuals based on the right calcaneus is 15. At Observatoire cave, 103 complete lynx remains (skulls, mandibles and all appendicular skeletal elements) have been taxonomically identified, with a MNI of 9 (from left mandibles). The Campefiel cave yields so far the largest Pleistocene 'population' of lynx

Elements	Escale			Observatoire			Campeffel			Lunel-Viel						
	NISP	%NISP	%surv	MNI	NISP	%NISP	%surv	MNI	NISP	%NISP	%surv	MNI	NISP	%NISP	%surv	MNI
skull + maxil	10	2,3	22,2	5	4	3,9	14,8	4	10	0,7	12,8	1	2,7	6,7	1	1
mandible	19	4,4	63,3	8	17	16,5	94,4	9	25	1,6	48,1	10	27,0	100,0	5	5
teeth	37	8,5	8,8	6	33	32,0	13,1	129	8,4	17,7	19	4	10,8	2,9	1	1
atlas	1	0,2	6,7	1				9	0,6	34,6	9					
axis	3	0,7	20,0	3				8	0,5	30,8	8					
vertebrae								60	3,9	5,1						
ribs								5	0,3	0,7						
scapula								17	1,1	32,7	9					
humerus	30	6,9	100,0	11	3	2,9	16,7	39	2,5	75,0	16	4	10,8	40,0	3	3
radius	22	5,1	73,3	8	5	4,9	27,8	3	51	3,3	98,1	24	3	8,1	30,0	2
ulna	20	4,6	66,7	9	7	6,8	38,9	2	80	5,2	100,0	26				
carpals	18	4,1	8,6	3				49	3,2	13,5	22					
metacarpals	32	7,4	21,3	6	14	13,6	15,6	156	10,2	60,0	22	1	2,7	2,0	1	1
innominate	6	1,4	20,0	5				36	2,3	69,2	10	2	5,4	20,0	1	1
femur	20	4,6	66,7	11	3	2,9	16,7	22	1,4	42,3	9					
patella	4	0,9	13,3	3				19	1,2	36,5	19					
tibia	27	6,2	90,0	7	3	2,9	16,7	3	37	2,4	71,2	19	3	8,1	30,0	2
fibula								15	1,0	28,8						
calcaneus	21	4,8	70,0	15	2	1,9	11,1	35	2,3	67,3	18	2	5,4	20,0	2	2
astragalus	15	3,4	50,0	8				40	2,6	76,9	20	1	2,7	10,0	1	1
tarsals	19	4,4	12,7	4				72	4,7	27,7	16					
metatarsals	29	6,7	19,3	7	12	11,7	13,3	163	10,6	62,7	25	1	2,7	2,0	1	1
phalanges	102	23,4	12,6					455	29,7	32,4	5	5	13,5	1,9		
Total	435			15	103			9	1532		26	37			5	5

TABLE 1. Frequencies (NISP, %NISP, %survival) of lynx skeletal parts in Escale, Observatoire, Campeffel and Lunel-Viel caves (southern France). source: Fosse et al., 2020 (Escal); Brugual et al., 2017 (Observatoire); Fosse and Crégut-Bonnoure, pers. obs. (Campeffel), Fosse, pers. obs. (Lunel-Viel).

in Europe, with 1532 identified teeth/bones belonging to 26 individuals (from left ulnas). Although no complete skull has been found, all skeletal elements are present in similar proportions. Finally, a minimum of 37 cranial and postcranial elements from Lunel-Viel I-IV cave belonging to five individuals (from right lower carnassials) have been also studied. These bone and teeth samples were analyzed from a paleontological and taphonomical point of view (identification, measurements, morphology, bone breakage, toothmarks). The measurements carried out on teeth and post-cranial skeletal elements generally follow von den Driesch's (1976) code measurements, with additional data for small bones (carpals, tarsals) taken on Felids (Sarrión, 1978; Argant, 1980 2010) or Ursids (Tsoukala and D'Anglade, 2002). Teeth terminology follows Hemmer (1966) which is commonly used by Bonifay (1971) and others. The extensive osteometrical data from lynx samples have been compared from literature as follows: extant European lynx (Hagmann, 1899; Harlé, 1910; Miller, 1912; Kurten and Rausch, 1959; Terzea, 1963; Bonifay, 1971; Van Bree and Clason, 1971; Clot and Besson, 1974; Ficcarelli and Torre, 1977; Valensi, 1994; Testu, 2006; Moussous, 2014), extant Iberian lynx (Ficcarelli and Torre, 1977; García-Perea et al., 1985; Cervera, 1992; Valensi, 1994; Testu, 2006), Pleistocene and Holocene European lynx (Hagmann, 1899; Clot and Besson, 1974; Altuna, 1980; Werdelin, 1981; Clot, 1988; Clot and Duranthon, 1990; Ballésio et al., 1991; Sablin, 2001; Testu, 2006; Moussous, 2014), the cave lynx *l.s.* (Harlé, 1910; Paulus and Tron, 1945; Bonifay, 1971, 1978; Pillard, 1972; Ficcarelli and Torre, 1977; Pérez-Ripoll, 1977; Sarrión, 1978, 1990; Pons-Moyà, 1983; Ruiz-Selfa and Laurino, 1986; Dufour, 1989; Cervera, 1992; Cardoso, 1993; Castañós, 1993; Valensi, 1994; Testu, 2006; Madurell-Malapeira et al., 2014; Moussous, 2014; Ghezzeo et al., 2015; Boscaini et al., 2016) and the Issoire lynx (Ficcarelli and Torre, 1977; Kurten, 1978; Blanc, 1984; Koufos, 1992; Hemmer, 2001; Montoya et al., 2001; Argant, 2004; Garrido, 2008; Cherin et al., 2013; Petrucci et al., 2013).

Graphical projections were made with R v.3.6.3 (R Core Team, 2019) and the packages dplyr v.0.8.5 (Wickham et al., 2020) and ggplot2 v.3.3.0 (Wickham, 2016). Individual ages are estimated from García-Perea (1996) and Marti and Ryser-Degiorgis (2018).

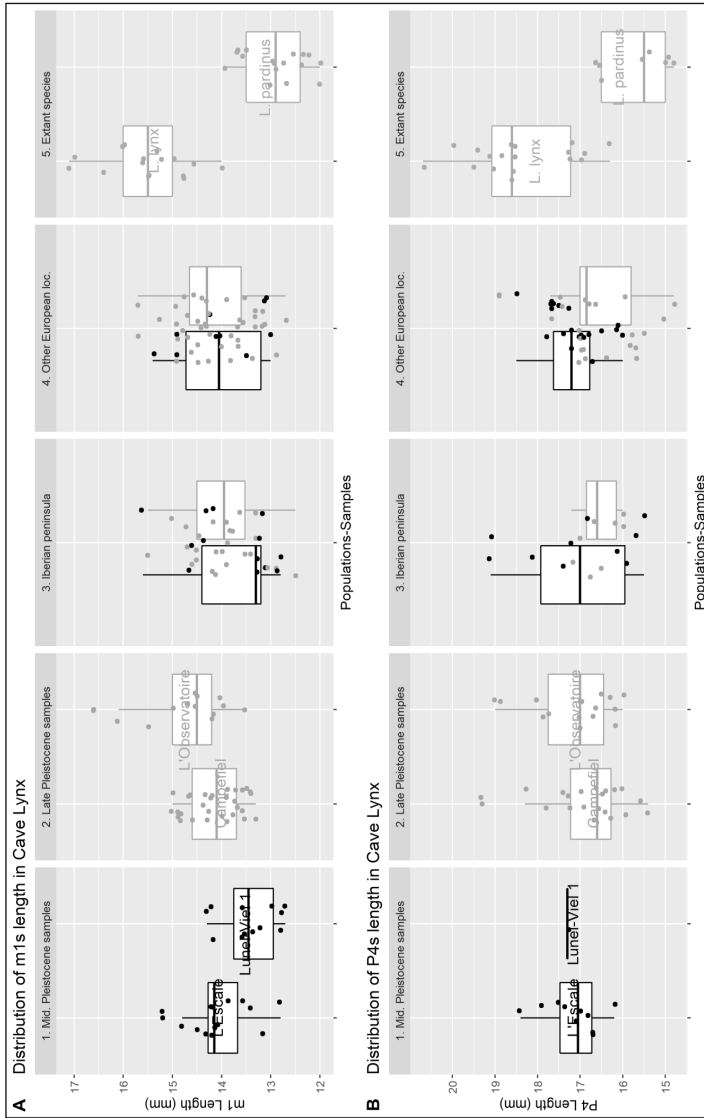
RESULTS

Paleontological data

The lynx remains identified in the four caves are relatively homogeneous in size and have been all identified as fossil Iberian lynx (cave lynx). Some bones are sometimes quite robust (one skull in Observatoire, two complete tibiae in Campefiel), but can reflect the intraspecific variability.

On the upper carnassial (P4), the protocon is high and massive. The anterior part of this tooth is composed of a well developed parastyl, overhanging, in a lingual position, an ectoparastyl. An elongated metacon is always present behind the protocon. Comparative measurements on this tooth reveal two size groups of Pleistocene lynx (figure 2, table 2): one including samples from large lynxes (*L. issiodorensis issiodorensis* and most of *L. lynx*) and the other from smaller lynxes (*L. spelaeus*, *L. pardinus spelaeus*, *L. issiodorensis valdarnensis*). All upper carnassials studied (Escale, Observatoire, Campefiel) fit well with this latter group.

The lower carnassials (m1) are robust teeth, commonly well preserved in fossil deposits. The paraconid and protoconid are particularly developed and secant, with a deeper and wider blade as tooth is worn. This blade, always well developed on Escale specimens, does not appear on extant European lynx lower carnassials (MNP sample) nor on the fossil material of Vallparadis (Boiscani et al., 2016) or Quibas (Montoya et al., 2001), whereas it is not very developed on the Pantalla specimen (Cherin et al., 2013) but stronger from the mandibles of Untermassfeld (Hemmer, 2001) as well as on some figured material from the Val d'Arno sites (Fabrini, 1896: figure 1). Beyond the odontometric aspect (figure 2, table 2), the differences between the two extant lynx are mainly based on very few morphological criteria, especially the profile of the posterior edge of the tooth and the presence of a metaconid above a talonid. Their taxonomic value, which is based on too much restricted samples, difficult to evaluate from a biochronological base (Boule, 1910; Bonifay, 1971; Hemmer, 2001; Testu, 2006; Madurell-Malapeira et al., 2014), have suggested different phyletic hypotheses for this zoological group considered as "heterogeneous" (sensu Ficcarelli and Torre, 1977). In Escale sample, only three m1 (n= 15) do not present a metaconid; the frequency of this denticule is therefore significant (~80%) and could



source : samples studied by the Authors (and see Fosse *et al.*, 2020b) ; comparative data : see refs in « material and method ». 1. *L. pardinus spelaeus* (black dots) from L'Escaud and Lunel-Viel 1 (Middle Pleistocene) ; 2. *L. pardinus spelaeus* (black dots) from Campéfiel and L'Observatoire (Late Pleistocene) ; 3. *L. pardinus spelaeus* from Spain and Portugal (black dots = Middle Pleistocene ; grey dots = Late Pleistocene) ; 4. *L. pardinus spelaeus* from Europe (black dots = Middle Pleistocene ; grey dots = Late Pleistocene) ; 5. extant European lynx and Iberian lynx.

FIGURE 2. Metrical data (in mm) on lower (A) and upper (B) carnassials from Lynx samples currently studied and from comparative data.

P4	Breadth					Length				
	min	max	Mean	n	SD	min	max	Mean	n	SD
Escale	7,7	8,3	7,9	9	0,2	16,2	18,4	17,2	10	0,6
Lunel-Viel	-	-	8,0	1	-	-	-	17,3	1	-
Observatoire	7,3	9,2	7,9	18	0,6	16,0	19,0	17,1	16	0,9
Campefiel	6,6	9,5	8,0	21	0,6	12,7	19,3	16,6	21	1,3

m1	Breadth					Length				
	min	max	Mean	n	SD	min	max	Mean	n	SD
Escale	5,5	6,7	6,1	15	0,3	12,8	15,2	14,0	15	0,6
Lunel-Viel	5,7	6,7	6,1	10	0,3	12,8	14,3	13,4	12	0,6
Observatoire	5,5	7,0	6,3	13	0,4	13,5	16,6	14,7	13	0,9
Campefiel	5,4	6,8	6,0	30	0,4	13,3	15,0	14,1	30	0,5

TABLE 2. Measurements (in mm) of upper (P4) and lower (m1) carnassials belonging to the cave lynx (*Lynx pardinus spelaeus*) from studied samples.

constitute a biochronological stage. Indeed, this particularity is only very rarely found on the m1s from Late Pleistocene populations (Observatoire and especially Campefiel) or on the m1s from extant Iberian lynx. This criterion is considered too variable by Boule (1910: 274) who does not take it into account as a specific diagnose, whereas Bonifay (1971) does consider this difference as a notable evolutionary stage. Our revision of Pleistocene lynxes would suggest that both authors are partly right, i) considering the cave lynx as a subspecies of the Iberian lynx on one hand, and ii) validating the frequency of the metaconid as an evolutionary step on the other.

The measurements from the lower carnassials do not provide any precise information dealing with a specific identification (*Lynx lynx/Lynx pardinus* ssp.), despite important comparative data. The archaic form of the Issoire lynx (*L. issiodorensis issiodorensis*) from Les Etouaires and Saint Vallier appears again to be at least as robust as extant male European lynx are and as some Late Pleistocene specimens were. All carnassials from Escale, Observatoire and Campefiel caves are much smaller and better match with «spelean» samples and extant Iberian lynxes. This tooth does not allow any study of sexual dimorphism.

With the exception of the archaic Issoire lynx (*L. issiodorensis issiodorensis*) from the Middle-Late Pliocene (and/or earlier: Alcalá, 1994; Arribas and Antón, 1997; Ginsburg, 1998) and from the earliest Lower Pleistocene deposits (Les Etouaires), all lynxes from the second half of the Lower Pleistocene up to the Late Pleistocene deposits are small

sized in (southern) Europe. The Issoire lynx subspecies *L. issiodorensis valdarnensis* is very similar to the cave lynx and these two forms should be probably considered as synonymous. The group of small lynxes from the early Lower Pleistocene (Fonelas P-1), late Lower Pleistocene (Ceysseguet, Untermassfeld, Vallparadís) and all remains of *Lynx pardinus spelaeus* from the Middle Pleistocene (Escale) are in all respects similar and form a homogeneous group from the teeth morphometry. This latter period corresponds to the widest geographical distribution of the fossil Iberian lynx in Western Europe, from southern Spain to Germany. During the Late Pleistocene, the distribution range of the fossil Iberian lynx retracted towards the Mediterranean areas; most of the remains identified specifically come from Spain, southern France and Italy, out of the tundra-steppe biome. In the second half of the Late Pleistocene, during interstadial climatic phases, the European lynx gradually expanded in Western Europe (Central Europe, Germany, Belgium, England) until to reach the French (Aran) and Spanish (Pagosulieta) Pyrenees and Italy at the end of the Late Glacial period to the beginning of the Holocene. In these last two regions, ancient DNA analyses suggest locally a sympatry between both species (Rodríguez-Varela et al., 2015a, 2015b). The Mediterranean region is the main geographical area for Pleistocene and Holocene Iberian lynx and there is no gap in lynx paleontological records from the Late Pleistocene to the Holocene. The expansion of the European lynx, probably linked to the arrival/increasing frequency of woodland ungulates (roe deer, red deer), reached all of non-Mediterranean Europe as far as Scotland. No size difference can be noted between the “spelean” lynx (both interstadial - Lunel-Viel - and from the end of the Late Glacial) and the Holocene Iberian lynx; some specimens from the Late Pleistocene are sometimes larger than the modern Iberian lynx (ecotypical variability? sexual dimorphism?). For all of these reasons, we suggest that the “spelean” lynx cannot be maintained at a specific rank. Nevertheless, it might be considered as a subspecies of the Iberian lynx which shows some morphological peculiarities during its long history. At Escale cave, the high frequency of the metaconid on the m1 distinguishes this lynx population from the Late Pleistocene one (Campefiel, Observatoire): the former can be identified as *Lynx pardinus spelaeus* (i.e. Middle Pleistocene) and the latter to *Lynx pardinus pardinus*.

Site	Age	NISP	MNI	Source
Escale	Middle Pleistocene	435	15	Fosse et al., 2020a
Lunel-Viel	Middle Pleistocene	37	5	Fosse, pers. obs.
Observatoire	Middle/Late Pleistocene	103	9	Brugal et al., 2017
Campefiel	Late Pleistocene	1532	26	Fosse and Crégut-Bonnouire, pers. obs.
Ingarno	Late Pleistocene	416		Mecozzi, 2019
Cova del Gegant	Late Pleistocene	299	6	Rodríguez-Hidalgo et al., 2020

TABLE 3. Major Pleistocene lynx (*Lynx pardinus spelaeus*) samples in southern Europe.

Taphonomy

The studied sites provide some of the largest lynx populations for the Pleistocene in Europe (table 3). Such an abundance of lynx remains appears specific of Mediterranean karstic infillings. Two main types of lynx sites can be distinguished: natural traps and lynx dens. The first one are characterized by (sub)adult complete skeleton(s) embedded with other taxa (ungulates) remains whereas the latter are, recently described (Cova del Gegant IIIa: Rodríguez-Hidalgo et al., 2020), from various taphonomical criteria (highly abundant lagomorph remains, very few gnawed and/or digested bones, regularly complete lynx limbs, presence of new-born/very young lynx, lynx, coprolites). This taphonomical characterization is partially supported by the coproscopical analysis of scat contents (Lloveras et al., 2008).

Taphonomical data are scarce for the studied samples. Previous taphonomical analysis from Escale *Hemitragus* assemblage suggests the importance of natural trapping process in site formation (Coumont, 2006). Escale site differs from Cova del Gegant in its topography (sedimentary deposits, chimney) and by the total absence of juvenile lynx (no milk teeth), a sex-ratio consisting in several females and a single male, some anatomical connexions, the absence of coprolites as well as the scarcity of mesomammals (lagomorphs, birds) in B and H levels. All along the stratigraphical sequence, at least 15 adults and sub-adults lynxes have been recognized. The taphonomical context suggests that these animals have probably died from their fall within the trap. However, very few toothmarks are visible on *Hemitragus* bones and have been attributed to small carnivores (foxes) whereas no lynx remain does present any modification by carnivores (Fosse et al., 2020a).

Contextual data are missing in the case of Observatoire: no spatial information, probable selection during the excavation, no collection of

small remains (lagomorphs) are available ... The lynx skeletal distribution (see table 1) highlights an over-representation of cranial remains (including both skulls and mandibles) as well as complete limbs and metapodials, without any anthropogenic (cutmarks) or carnivores and rodents (toothmarks, gnawing marks) activity (Brugal et al., 2017). Young adults and a few (very) old individuals characterize the mortality pattern (figure 3). Even though we suppose that the Observatoire cave was not used as a lair although the general/main site function is still difficult to precise (and the huge caprid sample suggests some natural trapping processes).

Campefiel, excavated at the beginning of the XXth century, was interpreted as a hyena den (coprolites, abundant cave hyena remains) and no lynx skeletal elements were firstly identified. Excavations in the deepest part of the cavity were focused on a sinkhole containing a very important sample of cave lynx remains (cf. above). Unfortunately, no informations neither publications provide any details on this unique exceptional lynx sample. We recently notice that there is an important lagomorph sample coming from the same area, material curated at the MHNN. The lynx sample consists in 26 lynx individuals which are mainly young adults as well as a few older ones (figure 3); long bones are almost all complete and undamaged neither by humans nor by carnivores. Accordingly, Campefiel cave could have been used as a lair (in the main gallery) and the bone accumulation (thanatocenosis) were probably reworked into the sinkhole (natural trap, yielding hyena remains as well) by natural processes. Lynx age-classes are similar to those of Cova del Gegant and could represent a lynx lair specifically occupied by adult lynx female breeding cubs/young.

In Lunel-Viel, five adult individuals have been identified by forelimb and hindlimb elements probably brought back within the cavity by the cave hyena. Long bones (ulna, tibia) and innominates show typical large carnivore toothmarks and a complete first phalanx has been digested and show acid-etched modification (figure 4). Lunel-Viel is one of the rare Pleistocene sites allowing to consider lynxes preyed by larger predators.

Natural traps are relatively rare in the Pleistocene record but more obvious during the Holocene (unembedded lynx remains oftently discovered, lying on the floor). Few instances show that only one lynx individual usually was trapped, sometimes in the deepest part of the

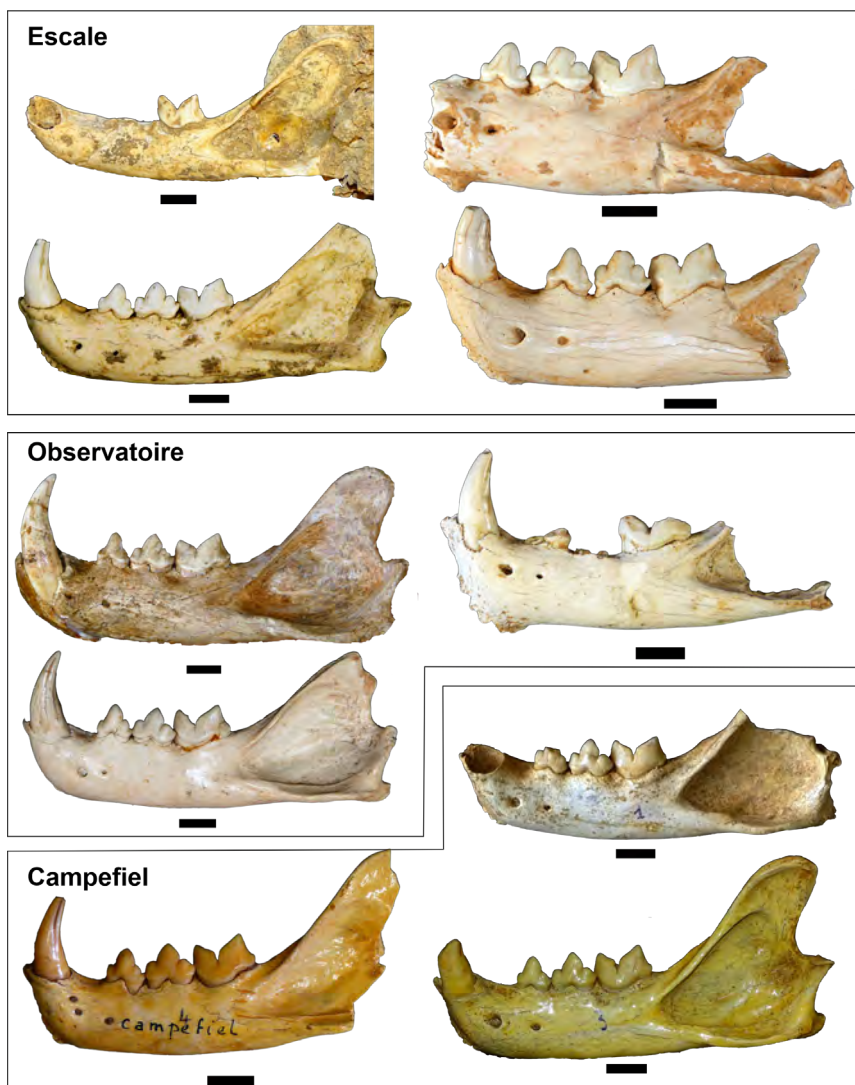


FIGURE 3. Selected left mandibles from Escale, Observatoire and Campefiel caves respectively. Bar scale = 1cm. Pictures Ph. Fosse.

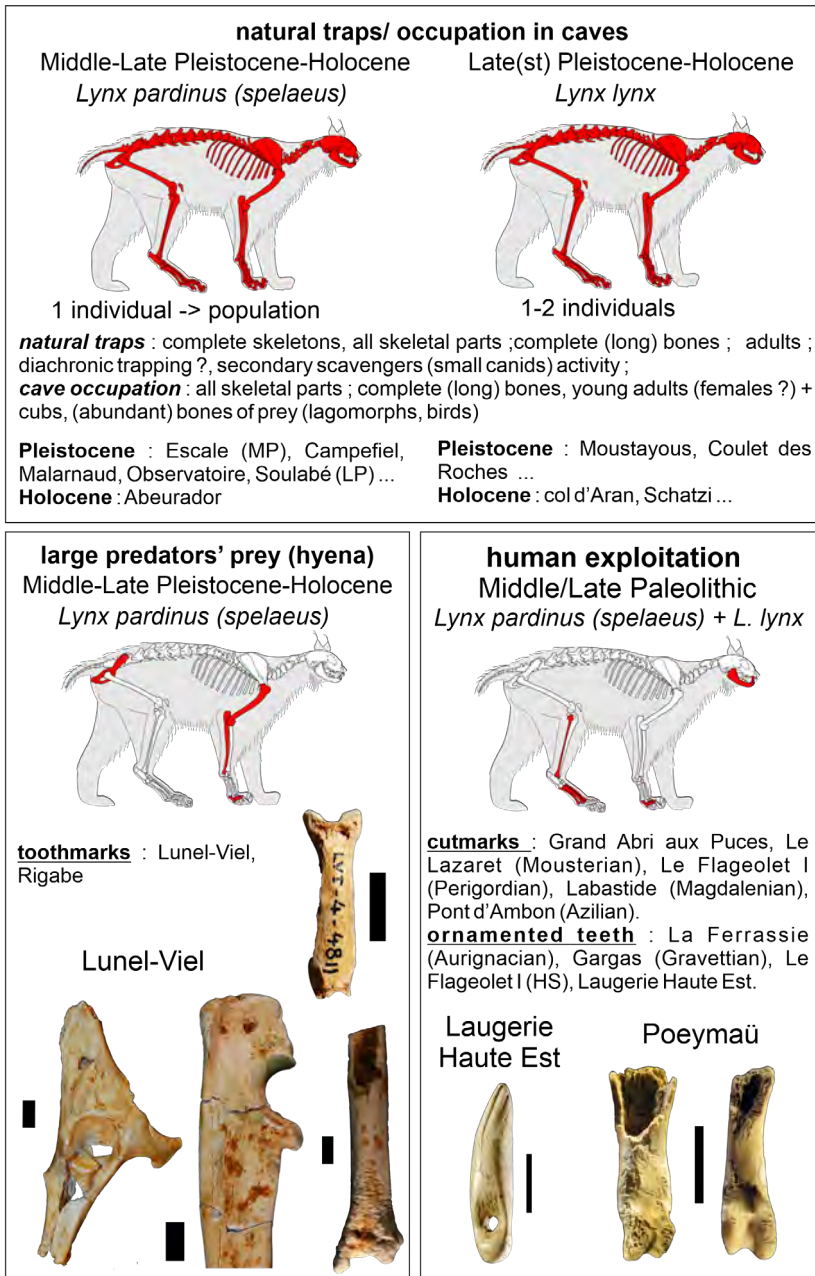


FIGURE 4. Taphonomical and zooarchaeological survey of *Lynx* remains in french Pleistocene sites. Bar scale= 1 cm. Pictures Ph. Fosse and J. B. Fourvel.

cave. In gouffre d'Aran n°1 and puits Schatzi in the French Pyrenees, an adult male skeleton was found at -140m and -70m from the entrance respectively (Clot and Besson, 1974; Delmasure, pers. com.). In Navarre (Pagolusieta), another adult male skeleton has been discovered at the bottom of a ~60 m deep pit (Altuna, 1980). Similar natural traps are known in the Alps (Karholeschacht: Blant et al., 2018). In these sites, (European) lynx are mainly old individuals, according to the canine toothwear. The Coulet des Roches site is an important natural trap, yielding 3 European lynx (Crégut-Bonnoure, pers. obs.; Rodríguez-Valera et al., 2015b). Few similar sites yielding a skeleton from *Lynx pardinus spelaeus* or *Lynx* sp. are also known (Crégut-Bonnoure and Guérin, 1979-81; Reggiani and Ghezzi, 2015 respectively). Sporadic site occupation by lynx could be suggested for some caves (Malarnaud, Soulabé in Ariège: Fosse and Madelaine, pers. obs.; Moustayous in Hautes Pyrénées: Clot, 1988) and/or from the mesofaunal record. In the Postglacial period, the important Abeurador deposit yield a complete Iberian lynx skeleton (Vaquer, pers. com.) in association with partridge bones.

Lynx remains in hyena dens are also scarce; in Rigabe cave (Var) lynx sample is important (NISP= 68, MNI= 7: Fosse and Fourvel, pers. obs.) mainly in an anthropogenic context. However, a left ulna shows carnivore toothmarks on its olecrania, probably gnawed by the cave hyena. In Spain, Gabasa cave, occupied by hyenas and/or wolves, contains an important sample of cave lynx (NISP= 77, MNI= 12: Blasco Sancho, 1995) but no taphonomic data are available for this felid.

Zooarchaeological overview dealing with human modifications at the Paleolithic times show little evidence of lynx exploitation, both for utilitarian or non-utilitarian (perforated teeth, ornaments, art, symbolism) aspects (Fosse et al., 2019). Evidences of consumption seems more frequent in Spanish record than in France (table 4 and references therein). The lynx stays quite uncommon in southwestern France during the Later Palaeolithic, period of a tundra-steppe climatic context. A few remains (maxillae, phalanges) from Poeymau cave (Fourvel, pers. obs.) bear some cutmarks (figure 4). Other examples come from Mousterian sites of Lazaret (Valensi and Psathi, 2004) and Grotte aux Puces (Fourvel, pers. obs.) but most of human exploitation/use come from Latest Paleolithic archeosequences (figure 4, table 4). Finally, we can mention

Country	Site	Level	Chronoculture	Species	Bone (n)	Marks	Source
France	Gargas		Gravetian	<i>L. lynx</i>	tooth, canine	ornament	San Juan-Foucher et al., 2013
Italy	Grotta Paglicci	6d, 8b	Epigravetian	<i>L. lynx</i>	skull (n=2)	cutmarks	Boschin, 2019
France	Iboussières, aven des		Epipaleolithic	<i>L. lynx</i>	mandible + phalanges	ochred	Chaix, 2005
France	Labastide		Magdalenian, Middle	<i>L. lynx</i>	fibula	cutmarks	Cloet, 1988
Italy	Riparo Mochi		Gravetian	<i>L. lynx</i>	phalanx 1	cutmarks + burnt	Tagliacozzo et al., 2012
Spain	Angel		Mousterian	<i>L. pardinus</i>	radius	cutmarks	García-Solano, 2014
Spain	Arbreda	H	Aurignacian	<i>L. pardinus</i>	skull, condyles	cutmarks	Maroto et al., 2017
Spain	Cendres, Cova de les		Epipaleolithic	<i>L. pardinus</i>	multi (n=32)	cutmarks	Maroto et al., 2017
Spain	Cova Foradada	Vb + VI	Aurignacian, Latest	<i>L. pardinus</i>	tooth, canine (n=2) + calc.	ornaments + cutmarks	Pantoja et al., 2011
Spain	Estebanvela, abrigo del	I, 6	Magdalenian, Late	<i>L. pardinus</i>	fibula	industry	Pascual Benito, 2017
Portugal	Gruta de Lapa do Suão		Solutrean, Late	<i>L. pardinus</i>	tooth, canine (n=3)	ornaments	Pascual Benito, 2017
Spain	Maltravieso, S. Huesos		Mousterian	<i>L. pardinus</i>	scapula	cutmarks	Rodríguez-Hidalgo, 2008
Spain	Nerja		Gravetian	<i>L. pardinus</i>	fibula + tooth, canine	industry + ornament	Pascual Benito, 2017
Spain	Nerja	IX + VIII	Solutrean	<i>L. pardinus</i>	mandible + other (n=6)	burnt	Riquelme Cantal et al., 2005
Spain	Parpallo, El		Magdalenian, Middle (III/II)	<i>L. pardinus</i>	fibula / ultra	industry	Pascual Benito, 2017
Spain	Peña de Estebanvela	I	Magdalenian, Late	<i>L. pardinus</i>	femur, tibia, metapodials	cutmarks	Yravedra, 2005-2006
Spain	Reclau Vivier	D	Gravetian	<i>L. pardinus</i>	tooth, canine (n=2)	ornament	Maroto et al., 2017
Spain	Romani	DC-N2	Mousterian	<i>L. pardinus</i>	radius	cutmarks	Cáceres Cuello de Oro, 2002
Spain	Santa Maira, Coves de	SM 4-ia	Magdalenian, late/Epip.	<i>L. pardinus</i>	multi (rib)	cutmarks + industry	Morales-Pérez, 2015
Spain	Altamira	mi/inf	Solutrean	<i>L. spelaeus</i>	tooth, canine	ornament	Álvarez Fernández, 2000
France	Grand abri aux Puces		Mousterian	<i>L. spelaeus</i>	multi	cutmarks	Simak et al., 2010
France	Flageolet I, Le	VII + ?	Perigordian ?	<i>L. spelaeus</i>	metatarsal + phalanx 1	cutmarks	Lorffèvre, 2009
France	Lazaret, Le		Mousterian	<i>L. spelaeus</i>	skull + mandible	cutmarks	Valensi and Psathi, 2004
Spain	Abautz	e	Magdalenian, Middle/Late	<i>Lynx</i> sp.	tooth, canine (n=2)	ornaments	Álvarez Fernández, 2000
Spain	Altamira		Magdalenian	<i>Lynx</i> sp.	tooth, canine	ornament	Pascual Benito, 2017
Spain	Ambrosio, cueva de	VI	Solutrean	<i>Lynx</i> sp.	tooth, canine	ornament	Pascual Benito, 2017
Spain	Axlor	III	Mousterian	<i>Lynx</i> sp.	femur	cutmarks	Gómez-Olivencia et al., 2018
Spain	Beneito, Cova de		Aurignacian, Early	<i>Lynx</i> sp.	tooth, canine (n=3)	ornaments	Pascual Benito, 2017
Spain	Beneito, Cova de		Solutrean	<i>Lynx</i> sp.	tooth, canine	ornament	Pascual Benito, 2017
Spain	Buho/Zarzamora		Aurignacian III	<i>Lynx</i> sp.	humerus	cutmarks	Sala et al., 2012
France	Ferrassie, La		Aurignacian III	<i>Lynx</i> sp.	tooth, upper canine	ornament	Fosse and Madelaine, p. obs.
France	Flageolet I, Le	?	Aurignacian III	<i>Lynx</i> sp.	tooth, upper canine	ornament	Fosse and Madelaine, p. obs.
France	Laugerie Haute Est		Magdalenian, Middle	<i>Lynx</i> sp.	tooth, upper canine	ornament	Fosse and Madelaine, p. obs.
France	Pair non Pair		Aurignacian/Gravetian	<i>Lynx</i> sp.	tooth, canine	ornament	Fosse and Madelaine, p. obs.
France	Poeymau		Magdalenian, Late	<i>Lynx</i> sp.	phalanx 1 (n=3)	cutmarks	Fourvel, pers. obs.
France	Pont d'Ambon	c3	Azilian	<i>Lynx</i> sp.	maxillary	cutmarks	Fosse and Madelaine, p. obs.
Spain	Reclau Vivier		Solutrean	<i>Lynx</i> sp.	tooth, canine (n=3)	ornaments	Pascual Benito, 2017

TABLE 4. European sites yielding anthropogenic evidence on *Lynx* (ssp) teeth and bones.

the presence of lynx from few archaeological level/context, based on perforated teeth (canines) used as ornaments (see figure 4). Concerning the rock art, only one mention is documented, as the single engraved lynx from Late Magdalenian site of La Madeleine (Tosello, 2003).

CONCLUSIONS

The lynx is relatively frequent and sometimes abundant in the Middle and Late Pleistocene bone assemblages from the Mediterranean area (France, Spain, Portugal, Italy). Our study is based on four large collections of Lynx remains from Southeastern France and Monaco, and a wide comparative analysis mainly on teeth materials. The specific attribution systematically indicates the cave lynx, here named *Lynx pardinus spelaeus*, as a subspecies of the extant Iberian lynx. However, a enlarge revision with early Lower Pleistocene and Pliocene forms would be requisite to clarify the evolution and phyletic positions of medium-sized felines of Europe (Issoire lynx; Caracal ssp.: Morales et al., 2003; Werdelin and Peigné, 2010) and Asia (*Lynx shansius*; Kurten and Werdelin, 1984) ... The paleobiological analysis (paleontology, taphonomy) carried out on the most important samples in France and Monaco (Escale, Lunel-Viel, Campefiel, Observatoire) underlines similarities between Middle Pleistocene and Late Pleistocene specimens. The distinction with *L. lynx*, seems to be ascertained on the basis of odontometrical characters. Finally, we need to question the almost exclusive presence of the Iberian lynx during the Quaternary regarding and in relation with the absence of the European lynx until MIS 3. Only the integration of new contextual data (geotopographic, paleoenvironmental backgrounds, vegetation, faunal assemblages, direct radiocarbon dates, ancient DNA) will contribute to the better understanding of the expansion of the Iberian lynx during the Pleistocene until its progressive regression up to the extinction of most of the geographical areas. From a taphonomic point of view, lynxes are identifiable as predators and bone collectors from mesofauna remains whereas only few data are known concerning the predation on macrofaunal species (see ex. Arceredillo et al., 2018). Revision of important paleontological series suggests that the lynx is another species connected with karstic contexts during the Pleistocene in the same way than other larger predators (hyenas, wolves or leopards).

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BIBLIOGRAPHY

- Alcalá, L. (1994): *Macromamíferos neogenos de la fosa de Alfambra-Teruel*. Museo Nacional de Ciencias Naturales.
- Altuna, J. (1980): Hallazgo de un lince nordico (*Lynx lynx* L. Mammalia) en la sima de Pagolusieta, Gorbea (Vizcaya). *Munibe* 32, 3-4, 317-322.
- Álvarez Fernández, E. (2000): *Los objetos de adorno colgantes del Paleolítico superior y del Mesolítico en la cornisa cantábrica y en el valle del Ebro: una visión europea*. Tesis, Universidad Salamanca.
- Arcercedillo, D., Brugal, J. P., Peyrouse, J. B., Aubry, T. (2018): Paléolithique moyen et supérieur à Buraca Escura (Redinha, Pombal, Portugal): comparaisons taphonomique et archéozoologique. *Quaternaire* 29, 1, 53-60.
- Argant, A. (1980): *Une brèche fossilifère du Pléistocène moyen de Saône-et-Loire: étude paléontologique du gisement de Château*. DEA Université Lyon I.
- Argant, A. (2004): Les carnivores du gisement Pliocène final de Saint-Vallier (Drôme, France). *Geobios* 37, suppl. 1, 133-182.
- Argant, A. (2010): Carnivores (Canidae, Felidae et Ursidae) de Romain-la-Roche (Doubs, France). *Revue de Paléobiologie* 29, 2, 495-601.
- Arribas, A., Antón, M. (1997): Los carnívoros de los yacimientos pliocenos de las Higuieruelas y Piedrabuena (Ciudad Real, España). *Boletín Geológico y Minero* 108, 2, 111-120.
- Arribas, O. (2004): *Fauna y paisaje de los Pirineos en la era glaciár*. Lynx edicions.
- Astre, G. (1950): Faune magdalénienne et azilienne de Rochereil (Dordogne). *Bull. soc. Hist. Nat. Toulouse* 85, 3-4, 151-171.
- Beaufort de, F. (1965): Lynx des Pyrénées, *Felis* (L.) *Lynx lynx* (L.). *Mammalia* 29, 4, 598-601.
- Beaufort de, F. (1968): Survivance du lynx dans le parc national des Pyrénées occidentales. *Mammalia* 32, 2, 207-210.

- Besson, J. P. (1979): Le lynx dans les Pyrénées. In, C. Dendaletche (dir.), *La grande faune pyrénéenne et des montagnes d'Europe*, Université de Pau, FIEP, 193-198.
- Blanc, A. (1984): *Les genres Lynx, Acinonyx, Viretailurus (Carnivora, Felidae) dans les séries plio-pléistocènes de France. Etude biométrique et chrono-stratigraphique*. Maitrise Université Paris I.
- Blant, M., Hasler, C., Häuselmann, P., Müller, W. (2018): Assemblage faunistique découvert dans la grotte du Karholenschacht (Habkern, BE). *Stalactite* 68, 1, 19-29.
- Blasco Sancho, M. F. (1995): *Hombres, fieras y presas. Estudio arqueozoológico y tafonómico del yacimiento del Paleolítico Medio de la cueva de Gabasa 1 (Huesca)*. Monografías Arqueológicas 38.
- Bonifay, E., Bonifay, M. F. (1963): Un gisement à faune épi-villafranchienne à Saint-Estève-Janson (Bouches-du-Rhône). *Comptes-Rendus de l'Académie des Sciences* 256, 1136-1138.
- Bonifay, M. F. (1971): *Carnivores quaternaires du Sud-Est de la France*. *Museum national d'Histoire naturelle (Paris)*, série C, Mémoires 21, 2, 43-377.
- Bonifay, M. F. (1974-1975): *Hemitragus bonali* Harlé et Stehlin Caprinae de la grotte de l'Escale, (Saint Estève-Janson, Bouches-du-Rhône). *Quaternaria* 18, 215-302.
- Bonifay, M. F. (1978): Le gisement de la Baume de Valorgues a Saint-Quentin-La-Poterie (Gard) (Paléolithique supérieur final et Epipaléolithique). *Gallia Préhistoire* 21, 1, 123-142.
- Bonnet, A. (1945): Les faunes pléistocènes du Gard. *Bulletin de la Société préhistorique française* 42, 1, 43-48.
- Boscaini, A., Alba, D., Beltran, J., Moyà-Solà, S., Madurell-Malapeira, J. (2016): Latest Early Pleistocene remains of *Lynx pardinus* (Carnivora, Felidae) from the Iberian Peninsula: taxonomy and evolutionary implications. *Quaternary Science Reviews* 143, 96-106.
- Boschin, F. (2019): Exploitation of carnivores, lagomorphs and rodents at Grotta Paglicci during the Epigravettian: The dawn of a new subsistence strategy? *Journal of Archaeological Science: Reports* 26, 101871.
- Boudadi-Maligne, M. (2010): *Les Canis pléistocènes du Sud de la France: approche biosystématique, évolutive et biochronologique*. Doctorat Université Bordeaux 1.
- Boule, M. (1906): II. La grotte du Prince. In: Villeneuve de, L. (dir.), *Les grottes de Grimaldi (Baoussé-Roussé)*, Paris, Institut de Paléontologie Humaine, tome I, 1, 85-115.
- Boule, M. (1910): Paléontologie. In: Boule, M. (dir.), *Les grottes de Grimaldi (Baoussé-Roussé)*, Paris, Institut de Paléontologie Humaine, tome I, 3, 157-357.

- Boule, M., Villeneuve de, L. (1927): La grotte de l'Observatoire à Monaco. Archives de l'Institut de Paléontologie humaine, 1.
- Brugal, J. P. (1983): *Application des analyses multidimensionnelles à l'étude du squelette des membres des grands Bovidés pléistocènes (Grottes de Lunel-Viel, Hérault), perspectives évolutives*. Thèse Université Aix-Marseille.
- Brugal, J. P., Fourvel, J. B., Fosse, P. (2017): Premières observations sur les guildes de carnivores de la grotte de l'Observatoire (Principauté de Monaco). *Bulletin du Musée d'Anthropologie Préhistorique de Monaco* 57, 35-48.
- Brugal, J. P., Fourvel, J. B., Fosse, P. (2020): Carnivores pléistocènes de la principauté de Monaco: les grottes de l'Observatoire et de Saint Martin. *Bulletin du Musée d'Anthropologie Préhistorique de Monaco* 59, 63-67.
- Cáceres Cuello de Oro, I. (2002): *Tafonomía de yacimientos antrópicos en karst. Complejo galería (sierra de Atapuerca, Burgos), Vanguard cave (Gibraltar) y Abric Romani (Capellades, Barcelona)*. Tesis Universitat Rovira i Virgili Tarragona.
- Castaños, P. M. (1986): *Los Macromamíferos del Pleistoceno y Holoceno de Vizcaya*. Tesis Universidad San Sebastián.
- Castaños, P. M. (1993): Estudio de los macromamíferos de los niveles paleolíticos de Chaves. *Bolskan* 10, 9-30.
- Cervera, J. (1992): Nuevos hallazgos de carnívoros en el complejo de yacimientos mesopleistocenos de la Sierra de Atapuerca, Burgos. *Revista Española de Paleontología*, Extra, 21-27.
- Chaix, L. (2005): Hétéroclite et éclectique: la faune épipaléolithique de l'Aven des Iboussières (Drôme, France). *Munibe* 57, 411-420.
- Cherin, M., Iurino, D. A., Sardella, R. (2013): New well-preserved material of *Lynx issiodorensis valdarnensis* (Felidae, Mammalia) from the Early Pleistocene of Pantalla (central Italy). *Bollettino della Società Paleontologica Italiana* 52, 103-111.
- Clot, A. (1988): Le lynx pléistocène (*Lynx lynx* (L.)), Felidae, Carnivora) des Moustayous (Saint-Pé-de-Bigorre, Hautes-Pyrénées). *Bull. Soc. Hist. Nat. Toulouse* 124, 107-110.
- Clot, A., Besson, J. P. (1974): Nouveaux restes osseux de lynx dans les Pyrénées. *Bull. Soc. Hist. Nat. Toulouse* 110, 1-2, 157-169.
- Clot, A., Duranthon, F. (1990): *Les Mammifères fossiles du Quaternaire dans les Pyrénées*. Toulouse, Accord (eds), 159 p.
- Coumont, M. P. (2006): *Taphonomie préhistorique: mammifères fossiles en contexte naturel, les avens-pièges, apport pour l'étude des archéofaunes*. Doctorat, Université Aix-Marseille I.
- Crégut-Bonnoure, E., Guérin, C. (1979-1981): Le gisement pléistocène de l'aven de la Terrasse à Aiguèze (Gard): première découverte dans le Midi méditerranéen de

- Mustela (Putorius) eversmanni* (Mammalia, Carnivora). *Bull. Soc. Et. Sci. Nat. Vaucluse* 1979-1981, 135-164.
- Driesch von den, A. (1976): *A guide to the measurement of animal bones from archaeological sites*. Peabody Museum Bulletins, 1.
- Dufour, R. (1989): *Les Carnivores pléistocènes de la caverne de Malarnaud (Ariège)*. D.E.S.S. Université de Bordeaux I.
- Fabrini, E. (1896): La lince del Pliocene italiano. *Palaeontographia italica* II, 1-24.
- Ficcarelli, G., Torre, D. (1977): Phyletic relationships between *Lynx* group *issiodorensis* and *Lynx pardina*. *Bollettino della Società Paleontologica Italiana* 16, 2, 197-202.
- Fosse, P. (1996): La grotte n° 1 de Lunel-Viel 1 (Hérault, France): repaire d'hyènes du Pléistocène moyen. Etude taphonomique du matériel osseux. *Paleo* 8, 41-84.
- Fosse, P., Fleury, G., Fourvel, J. B., Madelaine, S. (2019): *L'exploitation des grands carnivores au Paléolithique (supérieur): quelques données archéo(zoo)logiques. Animaux rares, gibiers inattendus. Reflets de la biodiversité*, Musée national de Préhistoire (ed.), 61-72.
- Fosse, P., Fourvel, J. B., Madelaine, S. (2020a): Le lynx *Lynx pardinus spelaeus* Boule, 1910 du Pléistocène moyen de la grotte de l'Escale (Bouches-du-Rhône, France): données paléontologiques et taphonomiques. *Paleo* 30, 2, 108-137.
- Fosse, P., Fourvel, J. B., Madelaine, S. (2020b): *Cave lynx Osteometrical Datasets from L'Escale Palaeontological site (South-East France) (Version 1.0)* [Data set]. Zenodo, doi.org/10.5281/zenodo.3936484.
- García-Perea, R. (1996): Patterns of postnatal development in skulls of lynxes, genus *Lynx* (Mammalia: Carnivora). *Journal of Morphology* 229, 3, 241-254.
- García-Perea, R. Gisbert, J., Palacios, F. (1985): Review of the biometrical and morphological features of the skull of the iberian lynx, *Lynx pardina* (Temminck, 1824). *Säugetierk. Mitteil.* 32, 249-259.
- García Solano, J. A. (2014): *La persistencia en las estrategias de subsistencia de los grupos humanos del Pleistoceno medio Ibérico, a partir del registro fosil de la Cueva del Ángel (Lucena, Cordoba)*. Tesis Universidad Granada.
- Garrido, G. (2008): Linces y guepardos (Felidae, Carnivora, Mammalia) en el Plioceno superior terminal del Fonelas P-1 (cuena de Guadix, Granada). In, A. Arribas (dir.), *Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas*, Cuadernos del Museo Geominero 10, 231-249.
- Ghezzo, E., Boscaini, A., Madurell-Malapeira, J., Rook, L. (2015): Lynx remains from the Pleistocene of Valdemino cave (Savona, Northwestern Italy), and

- the oldest occurrence of *Lynx spelaeus* (Carnivora, Felidae). *Rendiconti Lincei* 26, 2, 87-95.
- Ginsburg, L. (1998): Le gisement de vertébrés pliocènes de Çalta, Ankara, Turquie. 5. Carnivores. *Geodiversitas* 20, 3, 379-396.
- Gómez-Olivencia, A., Sala, N., Núñez-Lahuerta, C., Sanchis, A., Arlegi, M., Rios-Garaizar, J. (2018): First data of Neandertal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Nature, scientific reports* 8, 14 p.
- Hagmann, G. (1899): Die diluviale Wirbeltierfauna von Völklinshofen. *Abhandlungen zur Geologischen Specialkarte von Elsass-Lothringen, Neue Folge* 3.
- Harlé, E. (1910): Les mammifères et oiseaux quaternaires connus jusqu'ici en Portugal. *Service géologique du Portugal VIII*.
- Hemmer, H. (1966): Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). Teil I. *Veröff. Zool. Staatssamml. München* 11, 1-121.
- Hemmer, H. (2001): Die Feliden aus dem Epivillafranchium von Untermassfeld. In: R.D. Kahlke (dir.), *Das Pleistozan von Untermassfeld bei Meiningen (Thüringen)*, Teil 3, *Romisch-Germanischen Zentralmuseums Mainz* 40, 699-782.
- Koufos, G. D. (1992): The Pleistocene carnivores of the Mygdonia Basin (Macedonia, Greece). *Annales de Paléontologie* 78, 4, 205-257.
- Kurten, B. (1978): The lynx from Etouaires, *Lynx issiodorensis* (Croizet and Jobert), late Pliocene. *Ann. Zool. Fennici* 15, 314-322.
- Kurten, B., Werdelin, L. (1984): The relationships of *Lynx shansius* Teilhard. *Ann. Zool. Fennici* 21, 129-133.
- Kurten, B., Granqvist, E. (1987): Fossil pardel lynx (*Lynx pardina spelaea* Boule) from a cave in southern France. *Ann. Zool. Fennici* 24, 39-43.
- Kurten, B., Rausch, R. (1959): Biometric comparisons between North American and European Mammals. II. A comparison between the northern lynxes of Fennoscandia and Alaska. *Acta Arctica* XI, 21-44.
- Lloveras, L., Moreno-García, M., Nadal, J. (2008): Taphonomic analysis of leporid remains obtained from modern Iberian lynx (*Lynx pardinus*) scats. *Journal of Archaeological Science* 35, 1, 1-13.
- Lorfèvre F. (2009): *Les lynx plio-pléistocènes: examen critique de leur phylogénie et intérêt paléoenvironnemental*. Master 2 Université Bordeaux 1.
- Lucena-Pérez, M., Marmesat, E., Kleinman-Ruiz, D., Martínez-Cruz, B., Wecek, K., Saveljev, A. P., Seryodkin, I. V., Okhlopov, I., Dvornikov, M. G., Ozolins, J., Galsandorj, N., Paunovic, M., Ratkiewicz, M., Schmidt, K., Godoy, J. (2020): Genomic patterns in the widespread Eurasian lynx shaped by Late Quaternary climatic fluctuations and anthropogenic impacts. *Molecular Ecology* 29, 812-828.

- Madurell-Malapeira, J., Morales, J., Vinuesa, V., Boscaini, A. (2014): Úrsidos, hienidos y félidos del Pleistoceno inferior de Cueva Victoria (Cartagena, Murcia). *Mastia* 11-13, 401-432.
- Maroto, J., Millan, F., Rufí, I., Albizuri, S., Soler, J., Soler, N. (2017): Contextualización arqueológica y paleontológica de los félidos pleistocenos de Serinyà. In, A. Sanchis and J. L. Pascual Benito (eds.), *Interaccions entre Felins i Humans. III Jornades d'arqueozoologia del Museu de Prehistòria de València*, 49-79.
- Marti, I., Ryser-Degiorgis, M. P. (2018): Morphometric characteristics of free-ranging eurasian lynx *Lynx lynx* in Switzerland and their suitability for age estimation. *Wildlife Biology* 2018, 1, doi: 10.2981/wlb.00432.
- Mecozi, B. (2019): *Le faune a mammiferi del Pleistocene Medio-Superiore della Puglia: biocronologia, paleoecologia, paleobiogeografia*. Tesis Universita Sapienza Rome.
- Miller, G. S. (1912): *Catalogue of the Mammals of Western Europe (Europe exclusive Russia) in the collection of the British Museum*. Londres, British Museum, 830 p.
- Montoya, P., Alberdi, M. T., Barbadillo, L. J., Van der Made, J., Morales, J., Murelaga, X., Peñalver, E., Robles, F., Ruiz Bustos, A., Sánchez, A., Sanchiz, B., Soria, D., Szyndlar, Z. (2001): Une faune très diversifiée du Pléistocène inférieur de la Sierra de Quibas (province du Murcia, Espagne). *C. R. Acad. Sci. Paris* 332, 387-393.
- Morales, J., Soria, D., Montoya, P., Perez, B., Salesa, M. J. (2003): *Caracal depereti* nov. sp. y *Felis* aff. *silvestris* (Felidae, Mammalia) del Plioceno inferior de Layna (Soria, España). *Estudios Geol.* 59, 229-247.
- Morales-Pérez, J. V. (2015): *Explotació dels mamífers i economia de les darreres comunitats caçadores-recol·lectores del vessant mediterrani ibèric durant la transició Tardiglacial-Holocé*. Tesis Universitat Valencia.
- Moussous, A. (2014): *Approche biostratigraphique et évolution des paléoenvironnements au cours du Pléistocène supérieur, d'après l'étude des grands mammifères des grottes de Balzi Rossi (Ligurie, Italie)*, doctorat Université Perpignan.
- Pantoja, A., Sala, N. García, N., Ruiz Zapata, B., Gil García, M. J., Aranburu, A., Arsuaga, J. L., Casabó, J. (2011): Análisis paleontológico del yacimiento del Pleistoceno superior de Cova Foradada (Xàbia, Alicante, España). *Boletín de la Real Sociedad Española de Historia Natural* 105, 53-66.
- Pascual Benito, J. L. (2017): Industria ósea sobre huesos y dientes de lince en la prehistoria de la península ibérica. In, A. Sanchis and J. L. Pascual Benito (eds.), *Interaccions entre felins i humans. III Jornades d'arqueozoologia del Museu de Prehistòria de València*, 189-212.

- Paulus, M., Tron, C. (1945): Etude sur la faune quaternaire de la vallée inférieure du Gard ou Gardon. I. Les lynx. *Bulletin du Museum d'Histoire naturelle de Marseille* V(3), 41-72.
- Pérez-Ripoll, M. (1977): *Los mamíferos del yacimiento musteriense de Cova Negra (Játiva, Valencia)*. Serie de Trabajos varios del SIP 53.
- Petrucci, M., Cipullo, A., Martínez-Navarro, B., Rook, L., Sardella, R. (2013): The late Villafranchian (Early Pleistocene) carnivores (Carnivora, Mammalia) from Pirro Nord (Italy). *Palaeontographica Abteilung A Paläozoologie, Stratigraphie* 298, 113-145.
- Pons-Moyà, J. (1983): Presencia de *Lynx spelaea* (Fissipeda, Mammalia) en el Pleistoceno inferior de la Península Ibérica. *Paleontologia i Evolució* 18, 39-42.
- R Core Team (2019): *R: A language and environment for statistical computing*. <https://www.R-project.org/>.
- Real, C., Morales-Pérez, J. V., Aura, J. E., Villaverde, V. (2017): Aprovechamiento del lince por los grupos humanos del Tardiglaciario. El caso de Cova de les Cendres y Coves de Santa Maira. In, A. Sanchis and J. L. Pascual Benito (eds.), *Interaccions entre Felins i Humans. III Jornades d'arqueozoologia del Museu de Prehistòria de València*, 161-187.
- Reggiani, P., Ghezzi, E. (2015): Dal sequestro al completo recupero: il restauro della lince della "Grotta del Gattopardo" (Savona). *Museologia scientifica* 9, 62-68.
- Riquelme Cantal, J. A., Simón Vallejo, M. D., Cortés Sánchez, M. (2005): La fauna de mamíferos del Solutrense en la cueva de Nerja. *Munibe* 57, 255-263.
- Rodríguez-Hidalgo, A. J. (2008): *Zooarqueología de los yacimientos kársticos del Complejo Cacereño (Cueva de Santa Ana y Cueva de Maltravieso)*. Master Erasmus Mundus, Universitat Rovira i Virgili.
- Rodríguez-Hidalgo, A. J., Sanz, M., Daura, J., Sánchez-Marco, A. (2020): Taphonomic criteria for identifying Iberian lynx dens in quaternary deposits. *Nature, scientific reports*, doi.org/10.1038/s41598-020-63908-6.
- Rodríguez-Varela, R., García, N., Norez, C., Álvarez-Lao, D., Barnett, R., Arsuaga, J. L., Valdiosera, C. (2015a): Ancient DNA reveals past existence of Eurasian lynx in Spain. *Journal of Zoology* 298, 2, 94-102.
- Rodríguez-Varela, R., Tagliacozzo, A., Ureña, I., García, N., Crégut-Bonnoure, E., Mannino, M. A., Arsuaga, J. L., Valdiosera, C. (2015b): Ancient DNA evidence of Iberian lynx palaeoendemism. *Quaternary Science Reviews* 112, 172-180.
- Ruiz-Selfa, S., Laurino, M. (1986): Estudio biométrico de la mandíbula del lince de la cueva de Arrillor *Felis (Lynx) spelaea* ... ? (Boule 1906). *Estudios del Instituto Alavés de la Naturaleza* 1, 35-43.
- Sablin, M. (2001): Late Pleistocene lynx from Kostenki 21 (Voronezh Region, Russia). *Deinsea* 8, 27-31.

- Sala, M. T. N., Algaba, M., Arsuaga, J. L., Aranburu, A., Pantoja, A. (2012): A taphonomic study of the Búho and Zarzamora caves. Hyenas and humans in the Iberian plateau (Segovia, Spain) during the Late Pleistocene. *Journal of Taphonomy* 10, 3-4, 477-497.
- San Juan-Foucher, C., Foucher, P., Cap, H. (2013): Découverte d'une dent perforée de Lynx boréal dans les niveaux gravettiens de la grotte de Gargas (Hautes-Pyrénées, France). *Bull. Soc. Hist. Nat. Toulouse* 148, 83-92.
- Sarrión, I. (1978): Un lince de las cavernas en la cueva del Puerto (Calasparra, Murcia) y otros restos ineditos. *Lapiaz* 2, 7-26.
- Sarrión, I. (1990): El yacimiento del Pleistoceno medio de la Cova del Corb (Ondara-Alicante). *Archivo de Prehistoria Levantina* XX, 43-75.
- Slimak, L., Lewis, J., Crégut-Bonnoure, E., Metz, L., Vincent, O., André, P., Chravzev, J., Giraud, Y., Jeannet, M., Magnin, F. (2010): Le Grand Abri aux Pucés, a Mousterian site from the Last Interglacial: paleogeography, paleoenvironment, and new excavation results. *Journal of Archaeological Science* 37, 2747-2761.
- Tagliacozzo, A., Zeppleri, F., Fiore, I., Spinapolice, E., Del Lucchese, A. (2012): Archaeozoological evidence of subsistence strategies during the Gravettian at Riparo Mochi (Balzi Rossi, Ventimiglia, Imperia-Italy). *Quaternary International* 252, 142-154.
- Terzea, E. (1963): Observatii asupra morfologiei lui *Felis (Lynx) lynx* L. fossi citeva consideratii asupra raspindirii speciei pe teritoriul R.P.R. Studii siceretari de biologie. Academia republicii populare Romine. *Seria Biologie animala* 15, 3, 353-364.
- Testu, A. (2006): *Etude paléontologique et biostratigraphique des Felidae et Hyaenidae pléistocènes de l'Europe méditerranéenne (sites de la Caune de l'Arago, Orgnac 3, le Portel-Ouest, Bize-Tournal, l'Hortus, la Crouzade en France, la Cova de l'Arbreda en Espagne, Karain E en Turquie)*. Doctorat Université Perpignan.
- Tosello, G. (2003): Pierres gravées du Périgord magdalénien. Art, symbols, territories. *Gallia Préhistoire* XXXVIème suppl.
- Tsoukala, E., Grandal D'Anglade, A. (2002): Système de mesures sur le squelette d'Ursidae. In, Tillet, T. and Binford, L.R. (dir.), *L'Homme et l'Ours*, ERAUL 54, 265-287.
- Tsoukala, E., Bonifay, M. F. (2004): The Early Pleistocene carnivores (Mammalia) from Ceyssegues (Haute-Loire, France). *Paleo* 16, 193-241.
- Valensi, P. (1994): *Les grands mammifères de la grotte du Lazaret, Nice: étude paléontologique et biostratigraphique des carnivores: archéozoologie des grandes faunes*. Doctorat Museum national d'Histoire naturelle.

- Valensi, P., Psathi, E. (2004): Faunal exploitation during the Middle Palaeolithic in South-eastern France and North-western Italy. *International Journal of Osteoarchaeology* 14, 256-272.
- Van Bree, P. J. H., Clason, A. T. (1971): On the skull of a lynx, *Lynx lynx* (Linnaeus, 1758), found in the roman castellum at Valkenburg, province of Zuid-Holland, *The Netherlands. Bijdragen Tot de Dierkunde* 41, 2, 130-135.
- Villaluenga, A. (2016): Presencia de felinos (*Felis*, *Lynx* y *Panthera*) en el registro arqueológico de la Península Ibérica durante el Pleistoceno superior. *Archaeofauna* 25, 185-204.
- Werdelin, L. (1981): Evolution of lynxes. *Acta Zoologica Fennica* 18, 37-71.
- Werdelin, L. Peigné, S. (2010): 32. Carnivora. In, *Cenozoic Mammals of Africa*, University of California Press, 603-657.
- Wickham, H. (2016): *ggplot2: Elegant Graphics for Data Analysis*. New York.
- Wickham, H., François, R., Henry, L., Müller, K. (2020): *dplyr: A Grammar of Data Manipulation, package R v.o.8.5*. <https://CRAN.R-project.org/package=dplyr>.
- Yravedra Sainz de Los Terreros, J. (2005-2006): Aprovechamiento cárnico de lince (*Lynx pardina*) durante el Pleistoceno superior en el interior de la Península Ibérica. *Munibe* 57, 303-311.