



# Latest Early Pleistocene remains of *Lynx pardinus* (Carnivora, Felidae) from the Iberian Peninsula: Taxonomy and evolutionary implications

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## ABSTRACT

The Iberian lynx (*Lynx pardinus*) is a critically endangered felid that, during the last fifty years, has been subject to an intensive conservation program in an attempt to save it from extinction. This species is first recorded at ca. 1.7–1.6 Ma (late Villafranchian, late Early Pleistocene) in NE Iberian Peninsula, roughly coinciding with the large faunal turnover that occurred around the middle to late Villafranchian boundary. Here we describe the largest collection of *L. pardinus* remains available to date from the Iberian late Early Pleistocene (Epivillafranchian), including localities from the Vallparadís Section (Vallès-Penedès Basin, NE Iberian Peninsula) and Cueva Victoria (Cartagena, SE Iberian Peninsula). The morphology and biometry of the studied material attests to the widespread occurrence of *L. pardinus* in the Mediterranean coast of the Iberian Peninsula since the latest Early Pleistocene, i.e., about 0.5 million years earlier than it was generally accepted (i.e., at the beginning of the Middle Pleistocene). Based on the features observed in the large sample studied in this paper, we conclude that *Lynx spelaeus* is a junior synonym of *L. pardinus* and further propose to assign all the Epivillafranchian and younger fossil lynxes from SW Europe to the extant species *L. pardinus*. Due to the arrival of the Eurasian lynx (*Lynx lynx*) into Europe at the beginning of the Late Pleistocene, the attribution of specimens younger than MIS 5e to either this species or *L. pardinus* solely on morphological grounds has proven equivocal. Here we discuss the main diagnostic features of both species of European lynxes and further review their evolutionary history and paleobiogeography throughout the Pleistocene.

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## 1. Introduction

The Iberian lynx, *Lynx pardinus* (Temminck, 1827) (Carnivora, Felidae) is considered by the International Union for Conservation of Nature (IUCN) one of the most endangered living felids in the world (Rodríguez and Calzada, 2015). It is a Mediterranean species currently restricted to two disjunct regions of southwestern Spain, namely eastern Sierra Morena and the coastal plains west of the lower Guadalquivir (Rodríguez and Calzada, 2015). During the second half of the 20th century, this taxon was considered a local

variety or a “probable race” of the European lynx, *Lynx lynx* (Linnaeus, 1758), by many (Ellerman and Morrison-Scott, 1951; Honacki et al., 1982; Tumlison, 1987; Sokolov, 1988; Corbet and Hill, 1991), although not all (Werdelin, 1981; García-Perea et al., 1985), authors. However, the status of the Iberian lynx as a distinct species is currently undisputed (García-Perea, 1992; 1996), as supported by genetic (Beltrán et al., 1996; Johnson et al., 2004, 2006), morphological (Werdelin, 1981; García-Perea et al., 1985), and geographical and ecological (Sunquist and Sunquist, 2002; Nowak, 2005) evidence.

According to molecular phylogenetic studies (Bininda Emonds et al., 1999), the Iberian lynx would be the sister taxon of the clade comprising the Eurasian lynx and the Canadian lynx, *Lynx*

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*canadensis* Kerr, 1792 (Werdelin, 1981), whereas the North American bobcat, *Lynx rufus* (Schreber, 1777), would be the basal-most living species of the genus. All of these extant species of *Lynx* Kerr, 1792 are thought to have diverged from the extinct *Lynx issiodorensis* (Croizet and Jobert, 1828), an enduring Eurasian species recorded from the Early Pliocene to the latest Early Pleistocene (Werdelin, 1981). At least three subspecies of *L. issiodorensis* are currently considered taxonomically valid (Werdelin, 1981; Kurtén and Werdelin, 1984; Cipullo, 2010; Cherin et al., 2013): *L. i. issiodorensis* (Early Pliocene to latest Early Pleistocene from both Europe and Asia); *L. i. valdarnensis* Werdelin, 1981 (late Villafranchian from the Valdarno basin in the Northern Apennines, Italy); and *L. i. shansius* Teilhard de Chardin, 1945 (Early-Middle Pleistocene of Asia). There has been some controversy regarding the genus ascription of fossil European lynxes, following the inclusion of *L. issiodorensis* in genus *Caracal* (Schreber, 1776) by Morales et al. (2003). These authors further erected a new species, *Caracal depereti* Morales et al., 2003, based on the lynx material from the Early Pliocene of Layna (Soria, Northern Spain). However, this genus ascription has not been followed by subsequent authors (Garrido, 2008; Palombo et al., 2008; Cipullo, 2010; Cherin et al., 2013; Petrucci et al., 2013; among others), and in our opinion, based on dentognathic morphology, *C. depereti* is only a junior subjective synonym of *L. issiodorensis* (contra Morales et al., 2003).

The first extant species of *Lynx* to diverge was *L. rufus*, whose earliest fossil remains are dated to 2.4–2.5 Ma in Northern America (Werdelin, 1981). Successively, around 1.7–1.6 Ma, fossils ascribable to *L. pardinus* are recorded in the Mediterranean coastline of the NE Iberian Peninsula, attesting to the presence of the Iberian species already by the early late Villafranchian (Boscaini et al., 2015). By the Early-Middle Pleistocene, some Asian populations of *L. i. shansius* apparently gave rise to *L. lynx*, which later migrated into Europe during the early Late Pleistocene (Eemian interglacial period, MIS 5e; Werdelin, 1981; Kahlke, 1999). Most recently, in the last 0.2 Ma, *L. lynx* dispersed through the Bering Strait and originated *L. canadensis*, which pushed the distribution area of *L. rufus* toward more southern latitudes (Kahlke, 1999). Currently, there are only two European species of lynxes in Europe, *L. pardinus* and *L. lynx*, which have been recognized as distinct for more than two decades (Werdelin, 1981; García-Perea et al., 1985; Beltrán et al., 1996; Sunquist and Sunquist, 2002; Nowak, 2005).

The main morphological features that distinguish the Iberian from the European lynx are the following (García-Perea et al., 1985): the well marked interorbital convexity; the retention of a short sagittal crest, just behind the intersection of the temporal lines in adult individuals; the peculiar morphology of the pre-sphenoid bone; and the presence of a common cavity for the foramen lacerum posterius and the anterior condyloid foramen (respectively, synonyms of the jugular and the hypoglossal foramina; Gilbert, 1976). Furthermore, in extant *L. pardinus* the lower first molar frequently lacks the metaconid (83% of the individuals), although in some specimens it is slightly developed (as an inflection of the enamel; 14%) or even present as a distinct cusp (3%; García-Perea et al., 1985). To date, these distinctive morphological features have not been inspected in detail in the available fossil remains of this genus, which is required to discern the time and place of origin of the Iberian lynx, as well as its past geographic distribution. Consequently, there is some taxonomical confusion regarding the species assignment of late Early and Middle Pleistocene lynx remains from Southwestern Europe, which have been reported in the literature as either *L. pardinus* (e.g., Montoya et al., 1999, 2001a; Palombo and Valli, 2003; Palombo et al., 2008; Palombo, 2014; Boscaini et al., 2015), *L. pardinus spelaeus* (e.g., Kurtén and Granqvist, 1987; Lumley et al., 1988; Cardoso, 1996; García et al., 1997; García and Arsuaga, 1998, 1999), or *Lynx*

*spelaeus* (e.g., Bonifay, 1971; Testu, 2006; Ghezzi et al., 2014). Molecular studies have estimated the divergence date of the *L. pardinus* lineage at 1.53–1.69 Ma (Johnson et al., 2004) or 2.2 Ma (Bininda Emonds et al., 1999). These datings agree with the fossil record, as the oldest fossil remains of *L. pardinus* are recorded close to the middle-late Villafranchian boundary (ca. 1.7 Ma) in the Avenç Marcel cave (NE Iberian Peninsula; Boscaini et al., 2015). Soon thereafter, scanty lynx remains from other Iberian localities, such as Venta Micena (1.5 Ma) and Quibas (1.2 Ma), can be attributed to the same species (Moyà-Solà et al., 1981; Montoya et al., 1999, 2001a). More abundant lynx remains have been recovered during the last decade from the latest Early Pleistocene (Epivillafranchian, ca. 1.1–0.8 Ma) of the Iberian Peninsula. Here we describe and analyze the unpublished remains of *L. pardinus* from the Vallparadís section, together with the lynx remains from Cueva Victoria. The former had been previously reported as *Lynx* sp. (Alba et al., 2008; Madurell-Malapeira et al., 2010) or as *Lynx issiodorensis* by Madurell-Malapeira et al. (2014), but remained unpublished, whereas those from Cueva Victoria were recently attributed to *L. pardinus* (although not described or figured in detail) by Madurell-Malapeira et al. (2015). Based on this material, we discuss the morphological variability of the Iberian lynx in relation to the taxonomic uncertainties surrounding this species, and we also provide further details about the evolutionary history of this felid.

## 2. Geological and paleontological context

### 2.1. Vallparadís section

The Vallparadís composite section includes two sites: Cal Guardiola and Vallparadís Estació, respectively located in the western and eastern banks of the Torrent de Vallparadís, in the heart of the town of Terrassa (Catalonia, NE Spain; Fig. 1; Madurell-Malapeira et al., 2010). The Quaternary deposits of Cal Guardiola and Vallparadís Estació correspond to the Pleistocene alluvial fan system of Terrassa (Berástegui et al., 2000), which overlies a marked Miocene paleorelief. The sediments of the Cal Guardiola site consist of a 7 m-thick unit of massive conglomerates and gravels in a matrix-supported fabric. In the Vallparadís Estació site, there is a 14 m-thick sedimentary sequence, which is mainly composed of conglomerates and mudstones arranged in two units that are separated by an erosive angular unconformity (Madurell-Malapeira et al., 2010). Based on the faunal and floral assemblage (Berástegui et al., 2000; Postigo-Mijarra et al., 2007; Madurell-Malapeira et al., 2010, 2014; Minwer-Barakat et al., 2011), the paleoenvironment of the Vallparadís section has been interpreted as an open dry area characterized by warm temperatures, dominated by grassland and surrounded by a mixed deciduous forest. The Vallparadís section spans from the late Early Pleistocene to early Middle Pleistocene (between 1.2 and 0.6 Ma; Madurell-Malapeira et al., 2010). *Lynx* remains were recovered from layer CGRD3 of Cal Guardiola (ca. 1.2 Ma), and layers EVT12 (ca. 1.0 Ma), EVT10 (ca. 1.0 Ma) and EVT7 (ca. 0.86 Ma) of Vallparadís Estació.

### 2.2. Cueva Victoria

The site of Cueva Victoria is situated in the San Ginés de la Jara hill, close to the town of La Unión (Cartagena, Southern Spain; Fig. 1; Gibert Clois et al., 2006; Gibert and Ferràndez-Cañadell, 2015). It is a karstic cavity excavated into the Triassic carbonated sediments of the Alpujarride complex (Emilia Unit; Ros and Llamusi, 2015). Remains of close to 100 species of vertebrates have been recovered from different places within this cavity, constituting one of the most diverse fossil faunas from the European late Early Pleistocene (Gibert Clois et al., 2006; Gibert and

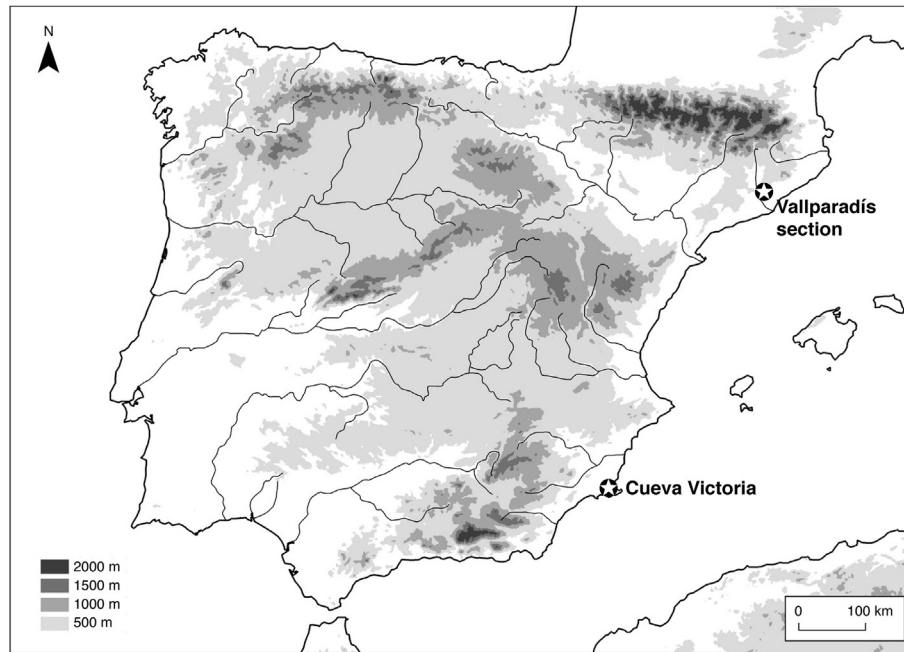


Fig. 1. Geographical location of Cueva Victoria and Vallparadís in the Iberian Peninsula.

Ferrández-Cañadell, 2015). The fossiliferous layers correspond to a massive conglomerate of big and heterogeneous carbonated pebbles, which is extremely rich in its upper part (Gibert Clois et al., 2006). The chronology of this association, based on magnetostratigraphy,  $^{230}\text{Th}/\text{U}$  dating of flowstones, and micromammal biostratigraphy, is constrained to 0.90–0.85 Ma (Martin, 2012; Budsky et al., 2015; Gibert and Scott, 2015). The faunal assemblage from Cueva Victoria has been also related to an open environment surrounded by forest and with warm temperatures (Blain, 2015).

### 3. Material and methods

#### 3.1. Studied remains and comparative sample

The remains from the Vallparadís section and Cueva Victoria are here described together, given their comparable (Epivillafranchian) age, their similar geographic provenance (eastern Iberian Peninsula, close to the Mediterranean coastline) and paleoenvironmental conditions (open habitat surrounded by forest and with warm temperatures), and their morphological and biometrical affinities (see next section).

The studied specimens from the Vallparadís section are housed in the ICP, whereas the specimens from Cueva Victoria are housed in the ICP, the MC and the IMEDEA (see abbreviations below). The comparative fossil sample includes unpublished material of *L. pardinus* from the Middle to Late Pleistocene (0.5–0.1 Ma) of the Iberian Peninsula (Turó del Moro, Cova del Toll, Cau d'en Borràs, Cova de l'Abreda, Cau del Duc, El Escarche, El Muscle), previously published remains of *L. i. valdarnensis* from the Early Pleistocene (ca. 2.0–1.4 Ma) of Italy (Olivola, Matassino, Upper Valdarno, Pantalla and Pirro Nord; Fabrini, 1896; Petrucci et al., 2013; Cherin et al., 2013) and Spain (Fonelas P-1; Garrido, 2008), and published material of *L. issiodorensis* ssp. indet. from the Epivillafranchian (ca. 1.0 Ma) of Germany (Untermassfeld; Hemmer, 2001). The comparative extant sample includes skulls of *L. pardinus* and *L. lynx* housed at the ICP and MZB. Additional comparative data for Pleistocene lynxes were taken from the literature (Boule, 1919;

Boule and Villeneuve, 1927; Bonifay, 1971; Pons-Moyà, 1985; Kurtén and Granqvist, 1987; García et al., 1997; García and Arsuaga, 1998, 1999; Montoya et al., 1999; Testu, 2006; Cipullo, 2010; Cherin et al., 2013; Ghezzi et al., 2014).

Measurements of the studied specimens were taken with a digital caliper to the nearest 0.1 mm.

#### 3.2. Abbreviations

##### 3.2.1. Locality abbreviations

EVT, Estació Vallparadís (Terrassa, Barcelona, Spain); CGR, Cal Guardiola (Terrassa, Barcelona, Spain); CV, Cueva Victoria (Cartagena, Spain).

##### 3.2.2. Institutional abbreviations

ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain); IMEDEA, Institut Mediterrani d'Estudis Avançats (Esporles, Mallorca, Spain); IGF, Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze (Italy); IPS, acronym of the ICP collections; IQW, Senckenberg Research Station of Quaternary Palaeontology (Weimar, Germany); MC, Museo Arqueológico Municipal de Cartagena (Spain); MZB, Museu de Ciències Naturals de Barcelona (Spain).

##### 3.2.3. Anatomical abbreviations

H, height; Hp4, height of the mandibular corpus at the level of p4; Hm1, height of the mandibular corpus at the level of m1; Hd, height of the mandibular corpus at the level of the diastema; Hr, height of the mandibular ramus; L, mesiodistal length; Ld, length of the diastema; Lm, length of the mandible; Lms, mesiodistal length of the metastyle; Lpa, mesiodistal length of the paracone; Lpad, mesiodistal length of the protoconid; Lprd, mesiodistal length of the protocone; Lpr, mesiodistal length of the protocone; Lps, mesiodistal length of the parastyle; Lsd, length of the dental series; W, buccolingual width.

#### 4. Systematic paleontology

Order Carnivora Bowdich, 1821.  
 Family Felidae Gray, 1821.  
 Subfamily Felinae Fischer von Waldheim, 1817.  
 Genus *Lynx* Kerr, 1792.  
*Lynx pardinus* (Temminck, 1827).  
 (Figs. 2–4).

##### 4.1. Referred material

###### 4.1.1. Vallparadís Section

Cal Guardiola (CGRD3): IPS84911, fragment of right C1. Vallparadís Estació (EVT12): IPS84922, fragment of left C1; IPS84913, right C1; IPS84920, right maxillary fragment with P3–P4 and alveoli of C1 and M1; IPS84916, left maxillary fragment with P3–P4 and C1 alveolus; IPS60461, left hemimandible with p3–m1 and c1 alveolus. Vallparadís Estació (EVT10): IPS84912, fragment of right C1; IPS84917, right maxillary fragment with P3–P4. Vallparadís Estació (EVT7): IPS84915, left maxillary fragment with C1 and P3–P4; IPS84914, right hemimandible with c1–m1.

###### 4.1.2. Cueva Victoria

IPS43408, left C1; MC (CV-2011-260), left C1; MC (CV-SMI-25), fragment of right C1; MC (CV-P-36), right P3; IPS43231, right maxillary fragment with P4 and distal fragment of P3; IPS43366, right P4; MC (CV-P-303), right P4 with fragmentary protocone; IMEDEA-33b, left P4 with fragmentary protocone; IMEDEA-C41b, distal fragment of right P4 with paracone and metastyle; IMEDEA-C9, right hemimandible with p3–m1 and alveoli of c1 and i3; MC (CV-MC-115), left hemimandible with p3–m1 and c1 alveolus; MC (CV-MC-253), left mandibular fragment with p3 and c1 alveolus; IMEDEA-C4, left hemimandible with m1 and alveoli of i3–p4; MC (CV-MC-1103), right mandibular fragment with m1; MC (CV-MC-275) mesial fragment of left dp3.

##### 4.2. Measurements

See Tables 1 and 2.

##### 4.3. Description

###### 4.3.1. Upper dentition

The upper canines are robust, with an elliptical cross-section and a double sulcation in buccal view, as it is typical of *Lynx* species (Fig. 2: A–B, C–D; Fig. 3: D–E). P3 is buccolingually compressed, with a high and rounded paracone, and normally without parastyle (the latter is present only in IPS84916 and IPS84920, which probably belong to a single individual; Fig. 3: G–I, J–L). The P3 metastyle is small and rounded, and a small distal cingulum is always observed. P4 has a small and mesiolingually-situated protocone and a slightly buccolingually-compressed parastyle, which is mesiodistally short relative to the paracone and metastyle. There is a distinct mesio Buccal ectoparastyle in IPS43366 (Fig. 2: K–M), which is incipient in IPS84915 (Fig. 3: D–F) and IMEDEA-33b (Fig. 2: Q–S), and absent from the remaining P4s. In all the specimens, the P4 paracone is always well developed and mesiodistally prominent relative to the metastyle, which is mesiodistally reduced and rounded on its distal side.

###### 4.3.2. Mandible

The corpus is low and robust, with a short diastema and one to four mental foramina (Fig. 4). The masseteric fossa is deep and reaches the level of the distal root of m1 in lateral view. The ramus and coronoid process are strongly inclined distally, IMEDEA-C9

(Fig. 4: A–C) more so than MC (CV-MC-115) (Fig. 4: D–F). The angular apophysis is robust and horizontally aligned toward its distal end. The condylar apophysis reaches the level of the tooth-row in lateral view.

###### 4.3.3. Lower dentition

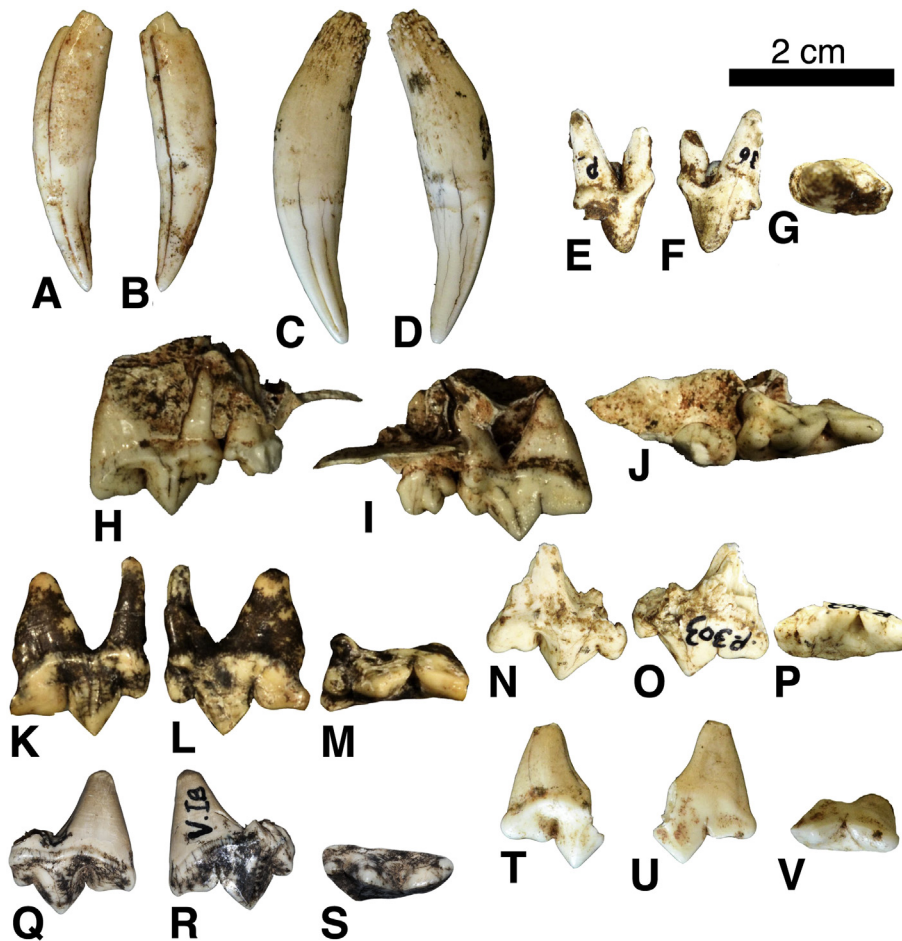
p3 is buccolingually compressed and almost symmetrical in lateral view. The protoconid is high. There is a paraconid, well developed in IMEDEA-C9 (Fig. 4: A–C) and IPS60461 (Fig. 4: S–U), moderately developed in MC (CV-MC-253) (Fig. 4: G–I) and extremely reduced in MC (CV-MC-115) (Fig. 4: D–F) and IPS84914 (Fig. 4: P–R). A small and rounded distal accessory cusp is present in all p3s, accompanied by an incipient distal cingulid. The p4s are robust, and more symmetrical in lateral view and less variable in shape than p3s. The protoconid is high. The paraconid is well developed and rounded. The posterior accessory cusp is slightly buccolingually compressed and buccodistally located. An incipient distal cingulid is present in all the four available p4s, even if more distinct in IPS60461 (Fig. 4: S–U) than in the remaining ones. The m1s display a protoconid that is slightly higher than, but of similar mesiodistal length to, the paraconid. There is a distinct metaconid only in MC (CV-MC-1103; Fig. 4: M–O); among the remaining specimens, this cusp is poorly developed in IMEDEA-C4, IPS60461 and IPS84914 (Fig. 4: J–L, P–R, S–U), merely represented by a small distal cuspule-shaped enamel inflection in MC (CV-MC-115) (Fig. 4: D–F), or even entirely absent in IMEDEA-C9 (Fig. 4: A–C).

##### 4.4. Comparisons and remarks

Among the described sample, all the cheek teeth are variable to some extent. This is interpreted as intraspecific variability, because it is not related to the provenance of the specimens, but observable in each sample separately. For example, P3 displays a distinct parastyle in two (IPS84916 and IPS84920) out of five specimens, although the former come from the same layer (EVT12) of Vallparadís section and, based on congruence in size and shape, they likely belong to a single individual. Similarly, one P4 from Cueva Victoria (IPS43366) out of the six studied upper carnassials has an ectoparastyle, which is extremely reduced or even absent in the remaining specimens from the other studied localities. Variability in P4 ectoparastyle development was already noted by Kurtén (1978) in specimens of *L. issiodorensis* from Les Etouaires (Late Pliocene, France). However, as noted by Kurtén (1978), this cusp is generally present in both *L. issiodorensis* and *L. lynx* and generally absent in *L. pardinus*. As remarked by Pons-Moyà (1985) in the first study of the lynx specimens from Cueva Victoria, these late Early Pleistocene remains likely represent an early stage of the *L. pardinus* lineage, so that variability in presence of the P4 ectoparastyle is to be expected.

The two complete mandibles from Cueva Victoria, IMEDEA-C9 (Fig. 4: A–C) and MC (CV-MC-115) (Fig. 4: D–F), are extremely similar in size, overall shape and dental morphology (see later). The only remarkable difference is the inclination of the ramus and the coronoid process, which is therefore attributed to intraspecific variability.

In the lower dentition, the p3 paraconid is well developed in two specimens, IMEDEA-C9 and IPS60461, but very reduced in the other two, MC (CV-MC-115) and IPS84914. However, the development of this cusp is extremely variable among both extinct and extant lynxes (Bonifay, 1971; Testu, 2006). The p4s are less variable in shape, being characterized by a sharp protoconid limited by almost symmetrical paraconid and distal accessory cusp. However, it is also noteworthy the variable development of the p4 distal cingulid among the studied sample, being poorly-developed in IPS60461, but lacking in the remaining ones. A prominent p4 distal



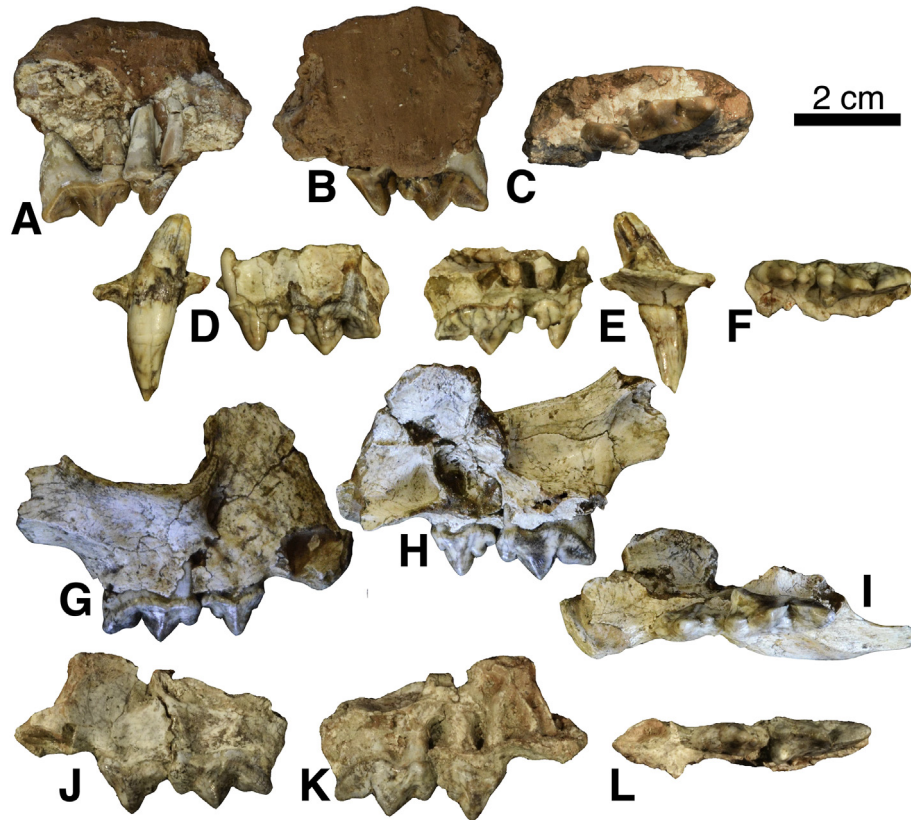
**Fig. 2.** Upper dentition of *Lynx pardinus* from Cueva Victoria. A–B: IPS43408, left C1, in labial (A) and lingual (B) views. C–D: MC (CV-2011-260), left C1, in labial (C) and lingual (D) views. E–G: MC (CV-P-36), right P3, in labial (E), lingual (F) and occlusal (G) views. H–J: IPS43231, right maxillary fragment with P4 and distal fragment of P3, in labial (H), lingual (I) and occlusal (J) views. K–M: IPS43366, right P4, in labial (K), lingual (L) and occlusal (M) views. N–P: MC (CV-P-303), right P4 with fragmentary protocone, in labial (N), lingual (O) and occlusal (P) views. Q–S: IMEDEA-33b, left P4 with fragmentary protocone, in labial (Q), lingual (R) and occlusal (S) views. T–V: IMEDEA-C41b, distal fragment of right P4 with paracone and metastyle, in labial (T), lingual (U) and occlusal (V) views.

cingulid has been considered diagnostic of *L. spelaeus* from the Middle Pleistocene of France (L'Escafe, Lunel Viel and Aragó Cave; Bonifay, 1971; Testu, 2006), purportedly justifying a distinct species status for these remains. Based on its documented high variability, as already noted by Bonifay (1971) and Testu (2006), we consider the development of the p4 distal cingulid of little taxonomic value.

The greatest variability concerns the development of the m1 metaconid on the distal margin of the protoconid blade (Fig. 5). Among the six available lower carnassials, the metaconid is only distinct in a single specimen (Fig. 5A), whereas in three specimens it is poorly developed (Fig. 5B), and in the remaining two it is either only represented by a small cusplike enamel inflection (Fig. 5C) or lacking altogether (Fig. 5D). This variability in the development of the carnassial metaconid has been previously stressed for many fossil lynx samples (Boule, 1919; Viret, 1954; Kurtén, 1963; Bonifay, 1971), as well as for the extant *L. pardinus* (García-Perea et al., 1985). Among the Early Pliocene representatives of this lineage, attributed to a smaller form of *L. issiodorensis*, the carnassial metaconid is absent (Montoya et al., 2001b; Morales et al., 2003), like in the larger *L. issiodorensis* from the early Villafranchian (Late Pliocene) of Perrier and Les Etouaires (Kurtén, 1963, 1978). This cusp is not present with a substantial frequency until later in time, as shown by the material of *L. issiodorensis* from the middle Villafranchian (Early Pleistocene) of Saint Vallier and Pardines (Viret, 1954; Kurtén,

1963), although it does not become of common occurrence until the late Villafranchian (Fabrini, 1896; Kurtén, 1963; Hemmer, 2001; Petrucci et al., 2013). The constant presence of this cusp (types A and B of Fig. 5) has been recognized in the latest Early Pleistocene material of *L. issiodorensis valdarnensis* from the Upper Valdarno, accompanied by the presence of prominent and labially-directed distal cingulids in p3 and p4 (IGF 891; IGF 892; IGF 893; IGF 895; IGF 896; IGF 897; IGF 898; IGF 4396; IGF 12969; IGF 13894; IGF 13890; Fabrini, 1896). A distinct m1 metaconid associated to prominent distal cingulids in p3 and p4 is also present in the Epivillafranchian material from Untermassfeld [IQW 1994/24691 (Mei. 24220) and IQW 1980/16573 (Mei. 16094)], thus supporting the view (Hemmer, 2001) that these remains constitute the latest European occurrence of *L. issiodorensis*. In contrast, the progressive reduction of the accessory cusps in *L. pardinus* has been stressed by several authors (Kurtén, 1963; Bonifay, 1971; Testu, 2006). In this regard, the substantial differences between the Iberian material described here and that from the roughly coeval site of Untermassfeld discussed above support an attribution of the former to *L. pardinus*.

The dentognathic remains from Cueva Victoria and the Vallparadís section more closely resemble, both in morphology and in biometrical terms (Tables 1 and 2), the Middle Pleistocene material assigned by most authors to *L. pardinus spelaeus* (or sometimes



**Fig. 3.** Upper dentition of *Lynx pardinus* from the Vallparadis section. A–C: IPS84917, right maxillary fragment with P3–P4, in labial (A), lingual (B) and occlusal (C) views. D–F: IPS84915, left maxillary fragment with C1–P4 in labial (D), lingual (E) and occlusal (F) views. G–I, IPS84920, right maxillary fragment with P3–P4 and alveoli of C1 and M1, in labial (G), lingual (H) and occlusal (I) views. J–L: IPS84916, left maxillary fragment with P3–P4 and alveoli of C1, in labial (J), lingual (K) and occlusal (L) views.

distinguished as a separate species, *L. spelaeus*). In particular, the studied material displays a slender and shallower mandibular corpus than in *L. issiodorensis*. Instead, in both mandibular dimensions and proportions, the described material more closely resembles the Middle and Late Pleistocene remains attributed to *L. pardinus spelaeus* (see Bonifay, 1971; Testu, 2006). In fact, the dental measurements of all the studied Iberian remains fall within the metrical ranges for Middle Pleistocene sites (Aragó, Orgnac-3, Aldène, Lunel-Viel, Escale and Lazaret; see measurements in Testu, 2006).

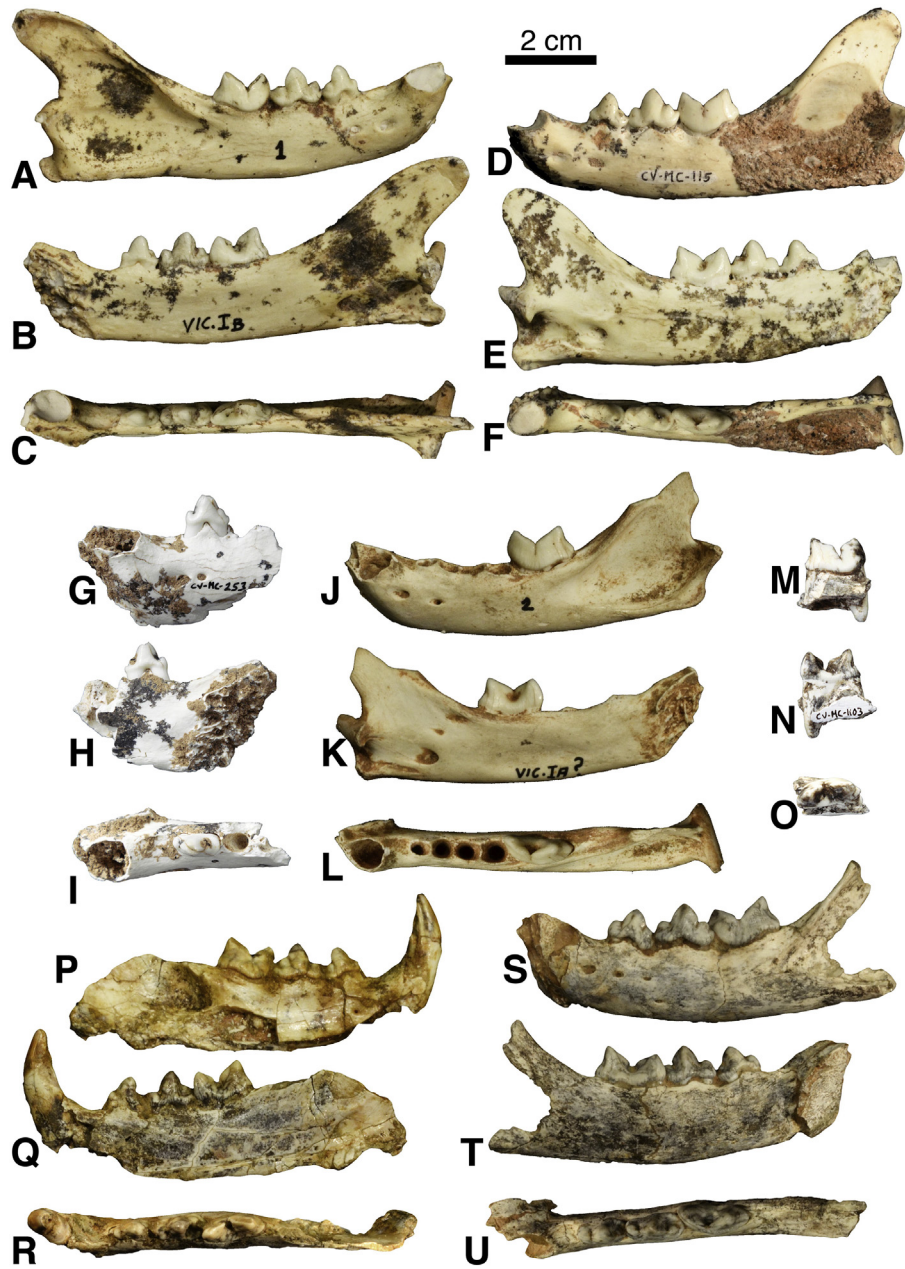
## 5. Discussion

### 5.1. Taxonomic attribution of the studied material

One of the main difficulties for deciphering the evolutionary history of European lynxes is the controversial taxonomic attribution of Middle to Late Pleistocene material from Southern Europe. This debate is as old as the description of the Late Pleistocene remains from the Grimaldi Cave by Boule (1919), because they show a panoply of mixed characteristics, reminiscent of both European extant species, *L. pardinus* and *L. lynx*. In particular, the cranial morphology of the Grimaldi Cave material most closely resembles that of *L. pardinus*, including the rounded and compact parietal region, the abrupt muzzle profile, the quite marked temporal constriction, the shallow depression at the midpoint of the frontal, the swollen cranial vault, and the long and parallel temporal ridges (Boule, 1919). The dentition in general also more closely resembles that of *L. pardinus*, with less elongated and sharper cheek teeth than in *L. lynx*, although the marked p4 distal cingulid more closely

resembles the condition of the latter, and tooth size is overall intermediate between the two species (Boule, 1919). It is also noteworthy that some m1 display a minuscule metaconid on the distal blade of the protoconid (Boule, 1919). Although this feature is characteristic of the late Villafranchian *L. issiodorensis* and the extant *L. lynx* (see Kurtén, 1963), in the extant *L. pardinus* it is also present in a low frequency (García-Perea et al., 1985). Boule (1919) attributed the material from the Grimaldi Cave to the same species as the Iberian lynx, given its overall closer similarities with this taxon, although given the above-mentioned distinctive features he distinguished the former as a distinct “race”, i.e., *Felis (Lynx) pardina* race *spelaea*.

Based exclusively on the original description, the name erected by Boule (1919) should be considered infrasubspecific, even if published before 1961, because he denoted it as a “race” instead of “variety” or “form” (ICZN, 1999: Article 45.6.4). However, the name is currently available as a species-group taxon (ICZN, 1999: Article 45.6.4), because it was adopted as the valid name of a species before 1985 (i.e., Bonifay, 1971). The name has been subsequently used by several authors, either as a distinct species or subspecies, for material from the late Early and Middle Pleistocene of France (L’Escale, Aragó, Lunel-Viel and Orgnac) and Spain (Cueva Victoria, Sima de los Huesos, Trincherá Galería). For example, Testu (2006) distinguished it at the species rank in order to emphasize its dental similarities with *L. lynx*. Other authors have considered that the Middle Pleistocene material should be only distinguished as a subspecies of *L. pardinus*, given its close morphological similarities coupled with a larger size (Kurtén and Granqvist, 1987; Lumley et al., 1988; Wolsan, 1993; Cardoso, 1996; García et al., 1997; García and Arsuaga, 1998, 1999; Olive, 2006). However, the



**Fig. 4.** Lower dentition of *Lynx pardinus* from Cueva Victoria (A–O) and the Vallparadis section (P–U). A–C: IMEDEA-C9, right hemimandible with p3–m1 and alveoli of c1 and i3, in labial (A), lingual (B) and occlusal (C) views. D–F: MC (CV-MC-115), left hemimandible with p3–m1 and c1 alveolus, in labial (D), lingual (E) and occlusal (F) views. G–I, MC (CV-MC-253), left mandibular fragment with p3 and c1 alveolus, in labial (G), lingual (H) and occlusal (I) views. J–L, IMEDEA-C4, left hemimandible with m1 and alveoli of i3–p4, in labial (J), lingual (K) and occlusal (L) views. M–O: MC (CV-MC-1103), right mandibular fragment with m1, in labial (M), lingual (N) and occlusal (O) views. P–R, IPS84914, right hemimandible with c1–m1, in labial (P), lingual (Q) and occlusal (R) views. S–U, IPS60461, left hemimandible with p3–m1 and c1 alveolus, in labial (S), lingual (T) and occlusal (U) views.

taxonomic validity of this taxon, either as a distinct species or subspecies, is far from clear (Bonifay, 1971; Ficcarelli and Torre, 1977; Hemmer, 2004; Moigne et al., 2006; Moullé et al., 2006; Testu, 2006). Thus, other scholars have simply referred the Early and Middle Pleistocene lynx material from Spain and France to *L. pardinus* (without subspecies designation), in considering that the minor morphological differences and the larger size do not justify a taxonomic distinction (Kurtén, 1968; Montoya et al., 1999, 2001a; Guérin and Patou-Mathis, 1996; Palombo and Valli, 2003; Palombo et al., 2008; Palombo, 2014; Boscaini et al., 2015). Based on the diagnostic morphological features of the extant Iberian lynx (Van den Brink, 1971; García-Perea et al., 1985; García-Perea, 1992,

1996; Beltrán and Delibes, 1993; Larivière and Walton, 1997), we concur with the latter opinion, and thereby conclude that *Lynx spelaeus* is best considered a junior subjective synonym of *L. pardinus*. We therefore propose to assign all the Epivillafranchian and younger fossil lynxes from southwestern Europe to the extant species *L. pardinus* with no distinction at the subspecies rank. This is justified by the fact that these samples already display the main diagnostic features of the Iberian lynx, as further discussed below in greater detail.

One of the most conspicuous diagnostic features of *L. pardinus* displayed by the Middle Pleistocene material is the presence of long temporal ridges that conform a lyre-shaped surface on the cranial

**Table 1**Measurements (in mm) of the upper dentition of *Lynx pardinus* from Cueva Victoria and Vallparadís section. For measurement abbreviations, see the main text.

Site	Catalog no.	Side	C			P3		P4								
			L	W	H	L	W	L	W	Lpr	Lps	Lpa	Lms			
Cueva Victoria	IPS43408	Left	8.0	6.3	17.3											
Cueva Victoria	MC (CV-2011-260)	Left	8.4	6.9	21.2											
Cueva Victoria	MC (CV-SMI-25)	Right	10.5	7.0												
Cueva Victoria	MC (CV-P-36)	Right						10.6	5.1							
Cueva Victoria	IPS43231	Right							5.1	16.1	8.2	4.4	3.7	7.0	6.9	
Cueva Victoria	IPS43366	Right								18.1	9.1	3.8	4.3	7.4	7.0	
Cueva Victoria	MC (CV-P-303)	Right								16.8			3.5	7.6	6.7	
Cueva Victoria	IMEDEA-33b	Left								15.9			3.6	6.6	6.6	
Cueva Victoria	IMEDEA-41b	Right												6.5	6.7	
Cal Guardiola (CGRD3)	IPS84911	Right	7.7	6.3												
Vallparadís Estació (EVT10)	IPS84912	Right	8.8	6.2												
Vallparadís Estació (EVT12)	IPS84922	Left	8.1	5.8												
Vallparadís Estació (EVT12)	IPS84913	Right	8.5	6.8	16.6											
Vallparadís Estació (EVT7)	IPS84915	Left	8.7	6.5				10.8	5.9	17.2	8.1	3.2	3.6	7.1	6.5	
Vallparadís Estació (EVT10)	IPS84917	Right						11.3	5.4	17.4	7.9	3.4	4.0	6.9	7.0	
Vallparadís Estació (EVT12)	IPS84920	Right						12.4	5.7	19.1	8.8	3.9	4.5	7.5	7.6	
Vallparadís Estació (EVT12)	IPS84916	Left						12.7	5.7	19.1	8.9	4.1	4.6	7.7	7.9	

**Table 2**Measurements (in mm) of the lower dentition and mandible of *Lynx pardinus* from Cueva Victoria and Vallparadís Estació. For measurement abbreviations, see the main text.

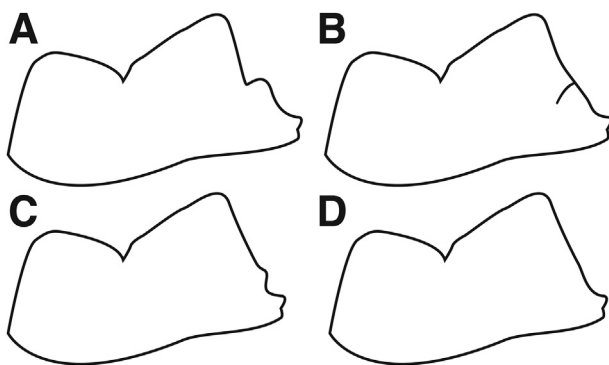
Site	Ref.	Side	c1			p3		p4		m1				Mandible						
			L	W	H	L	W	L	W	L	W	Lpad	Lprd	Ld	Lm	Lds	Hp4	Hm1	Hd	Hr
Cueva Victoria	IMEDEA-C9	Right				8.3	4.1	12.4	5.3	13.2	5.7	6.4	7.7	10.8	97.2	32.4	18.4	16.6	16.8	39.8
Cueva Victoria	MC (CV-MC-115)	Left				8.5	4.6	10.6	5.3	12.9	5.8	6.8	8.0	9.6	86.8	32.9	16.5	15.6	14.8	38.0
Cueva Victoria	MC (CV-MC-253)	Left				9.3	4.6	v						10.6					19.3	
Cueva Victoria	IMEDEA-C4	Left								14.6	5.7	7.4	8.9	5.7		33.4	15.5	14.5	15.3	
Cueva Victoria	MC (CV-MC-1103)	Right								13.1	5.8	5.4	6.4							
Vallparadís Estació (EVT7)	IPS84914	Right	8.5	7.1		9.3	4.4	11.4	5.3	13.3	5.6	6.6	7.7	8.3		32.2				
Vallparadís Estació (EVT12)	IPS60461	Left				10.4	4.9	12.8	5.8	15.6	6.5	7.7	9.0	6.2		37.4	17.4	16	15.7	

roof and distally join each other into a very short sagittal crest. This morphology is characteristic of young specimens of both *L. pardinus* and *L. lynx*, but among adults it only persists in the Iberian species (being displayed by all specimens; [García-Perea et al., 1985](#); [García-Perea, 1996](#)). In contrast, adults of *L. lynx* invariably display a long and prominent sagittal crest, which allows to easily discriminate between the two extant European species based on cranial morphology ([García-Perea et al., 1985](#)). This feature also distinguishes *L. pardinus* from its purported ancestor, the extinct *L. issiodorensis*, including not only the nominotypical subspecies, but also the smaller *L. i. valdarnensis*. The fact that *L. issiodorensis*

displays the same morphology as *L. lynx* ([Viret, 1954](#); [Kurtén, 1978](#); [Cipullo, 2010](#); [Cherin et al., 2013](#)) evidences that the condition of *L. pardinus* is derived. The typical pattern of *L. pardinus* is first recorded by a neurocranium (IPS4170) from Avenc Marcel (NE Iberian Peninsula, 1.7–1.6 Ma; [Boscaini et al., 2015](#)), and subsequently displayed by the French material from the Middle Pleistocene of L'Escaie (IGF679V, cast of H-7622; [Bonifay, 1971](#)) and from the Late Pleistocene of Grimaldi and Observatoire ([Boule, 1919](#); [Boule and Villeneuve, 1927](#)).

Another important diagnostic feature refers to the confluence in *L. pardinus* of the foramen lacerum posterium and the anterior condyloid foramen into a single depression, just behind the auditory bulla, whereas in *L. lynx* these foramina are separated ([Van den Brink, 1971](#); [García-Perea et al., 1985](#); [Larivière and Walton, 1997](#)). This feature is more useful to ascribe extant specimens to either species, because it is seldom preserved in fossil specimens due to the fragility of this anatomical region. However, this feature can be observed in the remains from both Observatoire and Avenc Marcel ([Boule and Villeneuve, 1927](#); [Boscaini et al., 2015](#)), in which the two foramina are confluent, as in extant *L. pardinus*. Other features, such as the degree of interorbital convexity, the shape of the presphenoid, and the development of the metaconid in the lower carnassial, are less diagnostic when taken alone, although they remain useful when combined with other features ([García-Perea et al., 1985](#)).

Interorbital convexity and presphenoid shape are only seldom preserved in fossil remains, but the development of the m1 metaconid can be readily ascertained in many fossil samples, which explains why this feature has been widely discussed in the literature (e.g., [Kurtén, 1963](#); [Bonifay, 1971](#); [Montoya et al., 2001b](#); [Morales et al., 2003](#); [Testu, 2006](#); [Garrido, 2008](#); [Cipullo, 2010](#)).



**Fig. 5.** Schematic depiction of the variability in m1 metaconid observed within the sample of *Lynx pardinus* described here. A: metaconid well distinct; B: metaconid present but poorly-developed; C: metaconid lacking except for a cuspid-like enamel inflection on the protoconid blade; D: metaconid completely absent. Crowns are depicted in lingual view, with mesial toward the left.



The m1 metaconid is almost lacking in the earliest Pliocene specimens of *L. issiodorensis* from southern Europe (Montoya et al., 2001b; Morales et al., 2003; Cipullo, 2010) and in the larger-sized specimens of *L. issiodorensis* from the early Villafranchian of France (Kurtén, 1963, 1978). The m1 metaconid is more frequently displayed in specimens of *L. issiodorensis* from the middle Villafranchian (Viret, 1954; Kurtén, 1963), until it becomes fixed in this taxon by the late Villafranchian and Epivillafranchian (Fabrini, 1896; Kurtén, 1963; Hemmer, 2001; Petrucci et al., 2013). It is uncertain whether this is merely the result of in situ evolution of these populations in Europe, or the result of recurrent dispersal events of lynx populations from Asia into Europe; the scarcity of the fossil record of lynxes in Asia (Testu, 2006) precludes testing among these two alternatives. In any case, among European extant lynxes, in *L. pardinus* the m1 metaconid is only present in 3% of the specimens (García-Perea et al., 1985), whereas in *L. lynx* it is present in 100% of the individuals (Kurtén, 1963). Since the Middle Pleistocene, in *L. pardinus* the m1 metaconid was progressively reduced in parallel to the acquisition of a more cutting and smaller dentition, including the complete loss of the P4 ectoparasyle and the reduction of the p4 distal cingulid (Bonifay, 1971; Werdelin, 1981).

Overall, the lynx remains from the Middle Pleistocene of Southern Europe discussed above possess several features indicating very close affinities with the extant Iberian lynx. This shows that there is no solid morphological basis for assigning these remains to a purportedly distinct taxon, either at the species (*L. spelaeus*) or subspecies (*L. pardinus spelaeus*) rank. The same holds for the latest Early Pleistocene sample described in this paper, in which the features classically taken as distinctive of *L. spelaeus* (such as the development of the p4 distal cingulid and m1 metaconid) are extremely variable and, hence, of poor taxonomic value. Our contention that *L. spelaeus* is a junior synonym of *L. pardinus* is further reinforced by ancient DNA analyses of lynx samples from the Late Pleistocene of Northwestern Italy and the Holocene of Southern France, which show that *L. pardinus* was distributed outside the Iberian Peninsula (overlapping with *L. lynx*) in the recent past (Rodríguez-Varela et al., 2015). Particularly interesting are some samples from the Late Pleistocene of Italy (Arene Candide), previously attributed to *L. cf. spelaeus* on a morphological basis (including a larger body size; Cassoli and Tagliacozzo, 1994), but assigned to *L. pardinus* (without evidence of subspecies differentiation) on molecular grounds (Rodríguez-Varela et al., 2015). On this basis, Rodríguez-Varela et al. (2015) stressed the difficulties in determining the taxonomic affinities of Middle to Late Pleistocene lynx remains from southern Europe solely on the basis of metrical differences. Intraspecific variation in overall body size in *L. pardinus* was already recognized by Kurtén and Granqvist (1987) in the description of some remains from the Late Pleistocene of France. These authors referred to the fossil Iberian lynx as a “plastic” taxon, whose body size not only changed through time (Werdelin, 1981), but also showed a geographical cline, with roughly coeval specimens from the Iberian Peninsula being significantly smaller than the French ones (although still larger than the extant specimens).

## 5.2. Evolutionary history and paleobiogeography of European lynxes

Based on the currently available European record of the genus *Lynx*, the extant Iberian endemic *L. pardinus* appears much older than previously recognized, being first recorded by the early late Villafranchian in Northeastern Iberian Peninsula (ca. 1.7–1.6 Ma; Boscaini et al., 2015), and subsequently represented in slightly younger late Villafranchian localities from both Southern (Venta Micena and Quibas, ca. 1.5–1.2 Ma; Moyà-Solà et al., 1981; Montoya et al., 1999, 2001a) and Northern (Trincheria Dolina, MIS 19–21, ca.

0.9–0.8 Ma; García and Arsuaga, 1999) Iberia. As discussed above, *Lynx pardinus* is morphologically more derived than the Eurasian lynx (Kurtén, 1968; Werdelin, 1981) and probably originated from an autochthonous population of *L. issiodorensis* (Hemmer, 1979, 2001). In the Iberian Peninsula, the latter is recorded from the Ruscinian to the early–middle Villafranchian (Montoya et al., 2001b; Morales et al., 2003; Garrido, 2008; Cipullo, 2010). The earliest representatives of *L. issiodorensis* are smaller and display a lower occurrence of the m1 metaconid than later representatives of the same species (Kurtén, 1963; Montoya et al., 2001b; Morales et al., 2003; Cipullo, 2010), and thus represent a plausible starting point from which the Iberian lineage might have diverged.

The fossil remains described in this paper represent the largest sample of Early Pleistocene *Lynx pardinus* available to date, attesting to the continuous presence of the Iberian lynx in the Mediterranean coastal margin of the Iberian Peninsula until 1.0 Ma. By that time, the existence of a lowland corridor for fauna and flora has been recognized during interglacial phases (Jalut et al., 2000; González-Sampériz et al., 2005; O’Regan, 2008). It is thus conceivable that the Iberian lynx extended its geographical range outside the Iberian Peninsula approximately by this time. This is further supported by the fact that the lynx remains from late Villafranchian and Epivillafranchian localities of southern France (such as Sartanette, Sainzelles and Vallonnet) have been attributed to *L. pardinus* on biometrical grounds (Lumley et al., 1988; Palombo and Valli, 2003; Palombo, 2014; Moullé et al., 2006). Unfortunately, discrete diagnostic traits of the Iberian lynx cannot be ascertained among these samples due to preservational reasons. After the Early–Middle Pleistocene transition (ca. 1.2–0.6 Ma), *L. pardinus* reached its maximum geographical extension during the Middle and Late Pleistocene, being recorded not only in the Iberian Peninsula (García et al., 1997; García and Arsuaga, 1998), but also in Southern France (Bonifay, 1971; Testu, 2006) and Northwestern Italy (Ghezzi et al., 2014; Rodríguez-Varela et al., 2015). In fact, from 0.6 to 0.5 Ma onward, *L. pardinus* becomes one of the constant elements of the fossil faunal assemblages from Southern Europe (Palombo and Valli, 2003; Palombo et al., 2008; Palombo, 2014), persisting in Southern France until the Holocene (Vigne, 1996; Vigne and Pascal, 2003; Rodríguez-Varela et al., 2015).

With regard to *L. lynx*, it is very similar in morphological features, body size, and probably diet as well to the extinct *L. issiodorensis*, as previously stressed by several authors (Dubois and Stehlin, 1933; Kurtén, 1958, 1963, 1978; Crusafont-Pairó and Reguant, 1970; Bonifay, 1971; Kurtén and Werdelin, 1984; Agustí and Antón, 2002). These two species resemble each other (and differ from *L. pardinus*) in the possession of a long sagittal crest, an elongated skull with depressed frontal bones, a stouter dentition with robust premolars and molars, and an invariably presence of metaconid in the m1 (Boule, 1919; Kurtén, 1963; Bonifay, 1971; Testu, 2006). In fact, morphologically these species only differ in body proportions (Kurtén, 1978) and in the reinforcement of a crushing dentition in *L. lynx*, due to the frequent reacquisition (with high and stable frequencies in many populations) of the m2 (Kurtén, 1963; Werdelin, 1987). The Eurasian lynx apparently originated in Asia during the Villafranchian, from a local population of *L. issiodorensis shansius*, but did not subsequently disperse into Europe until the early Late Pleistocene (Werdelin, 1981; Kurtén and Werdelin, 1984; Kahlke, 1999). As a result, during the Late Pleistocene the two extant European species became sympatric (their geographic distribution overlapped; Kurtén, 1968; Rodríguez-Varela et al., 2015), so that it is common to find both species within the same locality (Boule, 1919; Boule and Villeneuve, 1927; Dubois and Stehlin, 1933; Rodríguez-Varela et al., 2015). The geographic distribution of the *L. lynx* reached the Iberian Peninsula (although only up to the Pyrenees) and the northernmost Atlantic

coast (Altuna, 1980; Sommer and Benecke, 2006; Rodríguez-Varela et al., 2016) at about the Pleistocene–Holocene boundary. Since a few centuries ago, *L. pardinus* is the only lynx species recorded in the Iberian Peninsula, whereas *L. lynx* survives, with a fragmentary geographic distribution, in several areas of Europe (Sommer and Benecke, 2006; Rodríguez-Varela et al., 2016).

## 6. Conclusions

The lynx remains from the late Early Pleistocene of the Vallparadís section and Cueva Victoria described in this paper are attributed to the extant species *L. pardinus* on the basis of several morphological features that enable the distinction of this species from both the extant *L. lynx* and their putative extinct common ancestor, *L. issiodorensis*. These features include the sharp and cutting dentition, as well as the low frequency of a well-developed m1 metaconid and accessory cusp(-ids) in the upper and lower cheek teeth. Additionally, the studied sample shows the main dentognathic characters classically considered diagnostic of *L. spelaeus* (such as the development of the p4 distal cingulid and m1 metaconid), which are extremely variable and, consequently, they lack taxonomic value. Based on the comparison of the described specimens and other Early Pleistocene samples of *L. pardinus* with Middle Pleistocene to extant lynx samples from Europe, and in accordance with the latest molecular studies, we concur with some previous authors that *L. spelaeus* must be considered a junior synonym of *L. pardinus*, and that there is no valid criterion for distinguishing the former taxon even at the subspecies rank. Therefore, we include into the hypodigm of *L. pardinus* all lynx specimens recovered in Southwestern Europe from the Epivillafranchian (latest Early Pleistocene) to at least the early Late Pleistocene, when *L. lynx* reached Western Europe.

The sample described here represents the largest available sample of Early Pleistocene *L. pardinus*, following its earliest occurrence in the late Villafranchian of Avenc Marcel, and thus attests to the widespread occurrence of this species along the Mediterranean coast of the Iberian Peninsula by the latest Early Pleistocene. The record of this taxon in roughly coeval sites from Northern Iberian Peninsula and on the Eastern side of the Pyrenees suggests that *L. pardinus* first dispersed out of Iberia before the faunal turnover that took place in the Middle Pleistocene. However, this species only became a widely distributed faunal element throughout Southwestern Europe after the 'Early–Middle Pleistocene Transition', until it became restricted to Iberia again in very recent times. Discriminating between the two extant European lynx species, exclusively on the basis of discrete morphological traits and/or biometrical criteria, is very difficult in the case of Late Pleistocene and Holocene remains, because both species are often recovered within the same locality. Only the pattern depicted by the temporal ridges and the confluence of the jugular and hypoglossal foramina are reliable criteria, and ancient DNA analyses are recommendable whenever possible. In contrast, relying on body size alone may easily lead to misidentifications.

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## References

- Agustí, J., Antón, M., 2002. Mammoths, Sabertooths, and Hominids: 65 million Years of mammalian evolution in Europe. Columbia University Press, New York.
- Alba, D.M., Aurell, J., Madurell-Malapeira, J., Gómez, M., Moyà-Solà, S., Berástegui, X., 2008. Paleontología i geologia del jaciment del Pleistocè inferior de Vallparadís (Terrassa, Vallès Occidental). Trib. Arqueol. 2007, 29–44.
- Altuna, J., 1980. Hallazgo de un lince nórdico (*Lynx lynx* L. Mammalia) en la sima de Pagolusieta, Gorbea (Vizcaya). Munibe 32, 317–322.
- Beltrán, J.F., Delibes, M., 1993. Physical characteristics of Iberian lynxes (*Lynx pardinus*) from Doñana, southwestern Spain. J. Mammal. 74, 852–862.
- Beltrán, J.F., Rice, J.E., Honeycutt, R.L., 1996. Taxonomy of the Iberian lynx. Nature 379, 407–408.
- Berástegui, X., Moyà-Solà, S., Casanovas, S., 2000. El jaciment paleontològic de Cal Guardiola: Una finestra oberta al Pliocè inferior de Catalunya: Contextualització geològica. Trib. Arqueol. 1997–1998, 255–278.
- Bininda Emonds, O.R.P., Gittleman, J.L., Purvis, A., 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). Biol. Rev. 74, 143–175.
- Blain, H.A., 2015. Anfíbios y escamosos de Cueva Victoria. Mastia 11–13. In: Gibert, L., Ferrández-Cañadell, C. (Eds.), Geología y paleontología de Cueva Victoria. Ayuntamiento de Cartagena, Cartagena, pp. 175–189.
- Bonifay, M.-F., 1971. Carnivores quaternaires du Sud-Est de la France. Mém. Mus. Natl. Hist. Nat. Paris C 21, 1–377.
- Boscaini, A., Madurell-Malapeira, J., Llenas, M., Martínez-Navarro, B., 2015. The origin of the critically endangered Iberian lynx: Speciation, diet and adaptive changes. Quat. Sci. Rev. 123, 247–253.
- Boule, M., 1919. Géologie et Paléontologie. In: Les Grottes de Grimaldi (Baousserousse), vol. 1. Imprimerie de Monaco, Monaco, pp. 237–362.
- Boule, M., Villeneuve, L. de, 1927. La grotte de l'Observatoire à Monaco. Arch. Inst. Paléontol. Hum. 1, 1–113.
- Budsky, A., Scholz, D., Gibert, L., Mertz-kraus, R., 2015. <sup>230</sup>Th/U-dating of the Cueva Victoria flowstone sequence: preliminary results and paleoclimatic implications. Mastia 11–13. In: Gibert, L., Ferrández-Cañadell, C. (Eds.), Geología y paleontología de Cueva Victoria. Ayuntamiento de Cartagena, Cartagena, pp. 101–110.
- Cardoso, J.L., 1996. Les grands Mammifères du Pléistocène supérieur du Portugal. Essai de synthèse. Geobios 29, 235–250.
- Cassoli, P.F., Tagliacozzo, A., 1994. I macromammiferi dei livelli tardopleistoceni delle Arene Candide (Savona, Italia): considerazioni paleontologiche e archeozoologiche. Quat. Nova 4, 101–262.
- Cherin, M., Iurino, D.A., Sardella, R., 2013. New well-preserved material of *Lynx issiodorensis* (Felidae, Mammalia) from the Early Pleistocene of Pantalla (central Italy). Boll. Soc. Paleontol. Ital. 54, 103–111.
- Cipullo, A., 2010. L'evoluzione del genere *Lynx* dal Pliocene al Pleistocene medio nell'area mediterranea. Unpublished Ph.D. dissertation. Università di Modena-Bologna-Roma.
- Corbet, G.B., Hill, J.E., 1991. A World List of Mammalian Species, third ed. Natural History Museum Publications - Oxford University Press, London.
- Crusafont-Pairó, M., Reguant, S., 1970. The nomenclature of intermediate forms. Syst. Biol. 19, 254–257.
- Dubois, A., Stehlin, H.G., 1933. La Grotte de Cotencher, station moustérienne. Birkhäuser, Basel.
- Ellerman, J.R., Morrison-Scott, T.C.S., 1951. Checklist of Palaearctic and Indian Mammals, 1758 to 1946. British Museum (Natural History), London.
- Fabrini, E., 1896. La lince del Pliocene italiano. Palaeontogr. Ital. 2, 1–24.
- Ficcarelli, G., Torre, D., 1977. Phyletic relationships between *Lynx* group *issiodorensis* and *Lynx pardina*. Boll. Soc. Paleontol. Ital. 16, 197–202.
- García, N., Arsuaga, J.-L., 1998. The carnivore remains from the hominid-bearing Trinchera-Galería, Sierra de Atapuerca, Middle Pleistocene site (Spain). Geobios 31, 659–674.
- García, N., Arsuaga, J.L., 1999. Carnivores from the Early Pleistocene hominid-bearing Trinchera Dolina 6 (Sierra de Atapuerca, Spain). J. Hum. Evol. 37, 415–430.
- García, N., Arsuaga, J.L., Torres, T., 1997. The carnivore remains from the Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain). J. Hum. Evol. 33, 155–174.
- García-Perea, R., 1992. New data on the systematics of lynxes. Cat News 16, 15–16.
- García-Perea, R., 1996. Patterns of postnatal development in skulls of lynxes, genus *Lynx* (Mammalia: Carnivora). J. Morphol. 229, 241–254.
- García-Perea, R., Gisbert, J., Fernando, P., 1985. Review of the biometrical and morphological features of the skull of the Iberian lynx, *Lynx pardina* (Temminck, 1824). Säugetierkundl. Mittl. 32, 249–259.
- Garrido, G., 2008. Lince y guepardos (Felidae, Carnivora, Mammalia) en el Plioceno superior terminal de Fonelas P-1 (Cuenca de Guadix, Granada). In: Arribas, A. (Ed.), Vertebrados del Plioceno Superior Terminal en el Suroeste de Europa: Foneals P-1 y el Proyecto Fonelas. Cuadernos del Museo Geominero, vol. 10, pp. 231–249.
- Ghezzi, E., Boscaini, A., Madurell-Malapeira, J., Rook, L., 2014. Lynx remains from the Pleistocene of valdemino cave (Savona, northwestern Italy), and the oldest occurrence of *Lynx spelaeus* (Carnivora, Felidae). Rendiconti Lincei 26, 87–95.
- Gibert Cols, J., Gibert Beotas, L., Fernández Canyadell, C., Róbot, F., Iglesias, A., Gibert Beotas, P., 2006. Cueva Victoria: geología, paleontología, restos humanos y edades. Memorias Arqueol. Región Murcia 14, 37–62.

- Gibert, L., Ferràndez-Cañadell, C. (Eds.), 2015. Geología y paleontología de Cueva Victoria. Mastia, vols. 11–13.
- Gibert, L., Scott, G., 2015. Edad del yacimiento de Cueva Victoria y su relación con otros yacimientos de la Península Ibérica. Mastia 11–13. In: Gibert, L., Ferràndez-Cañadell, C. (Eds.) Geología y paleontología de Cueva Victoria. Ayuntamiento de Cartagena, Cartagena, pp. 85–100.
- Gilbert, S.G., 1976. Pictorial Anatomy of the Cat. University of Toronto Press, Toronto.
- González-Sampériz, P., Valero-Garcés, B.L., Carrión, J.S., Peña-Monné, J.L., García-Ruiz, J.M., Martí-Bono, C., 2005. Glacial and lateglacial vegetation in North-eastern Spain: new data and a review. *Quat. Int.* 140, 4–20.
- Guérin, C., Patou-Mathis, M., 1996. Les Grands Mammifères Plio-pléistocènes d'Europe. Masson, Paris.
- Hemmer, H., 1979. Fossil history of living Felidae. *Carnivore* 2, 58–61.
- Hemmer, H., 2001. Die Feliden aus dem Epivillafranchium von Untermaßfeld. Teil 3. In: Kahlke, R.D. (Ed.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Monographien des Römisch-Germanischen Zentralmuseums Mainz 40, pp. 699–782.
- Hemmer, H., 2004. Notes on the ecological role of European cats (Mammalia: Felidae) of the last two million years. In: Baquedano, E., Rubio Jara, S. (Eds.), Zona Arqueológica 4. Miscelánea en homenaje a Emiliano Aguirre, vol. II. Paleontología. Museo Arqueológico Regional, Alcalá de Henares, pp. 214–232.
- Honacki, J.H., Kinman, K.E., Koeppl, J.W., 1982. Mammal Species of the World. A Taxonomic and Geographic Reference. Allen Press and The Association of Systematics Collections, Lawrence, Kansas.
- International Commission on Zoological Nomenclature (ICZN), 1999. International Code of Zoological Nomenclature, fourth ed. The International Trust for Zoological Nomenclature, London.
- Jalut, G., Amat, A.E., Bonnet, L., Gauquelin, T., Fontugne, M., 2000. Holocene climatic changes in the Western Mediterranean, from south-east France to south-east Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 160, 255–290.
- Johnson, W.E., Godoy, J.A., Palomares, F., Delibes, M., Fernandes, M., Revilla, E., O'Brien, S.J., 2004. Phylogenetic and phylogeographic analysis of Iberian lynx populations. *J. Hered.* 95, 19–28.
- Johnson, W.E., Eizirik, E., Pecon-Slattery, J., Murphy, W.J., Antunes, A., Teeling, E., O'Brien, S.J., 2006. The late Miocene radiation of modern Felidae: a genetic assessment. *Science* 311, 73–77.
- Kahlke, R.D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene *Mammuthus-Coelodonta* Faunal Complex in Eurasia (Large Mammals). Fenske Companies, Rapid City.
- Kurtén, B., 1958. A differentiation index and a new measure of evolutionary rates. *Evolution* 12, 146–157.
- Kurtén, B., 1963. Return of a lost structure in the evolution of the felid dentition. *Soc. Sci. Fenn. Comment. Biol.* 26, 3–11.
- Kurtén, B., 1968. Pleistocene Mammals of Europe. Aldine, Chicago.
- Kurtén, B., 1978. The Lynx from Etouaires, *Lynx issiodorensis* (Croizet & Jobert), late Pliocene. *Ann. Zool. Fenn.* 15, 314–322.
- Kurtén, B., Granqvist, E., 1987. Fossil pardel lynx (*Lynx pardina spelaea* Boule) from a cave in southern France. *Ann. Zool. Fenn.* 24, 39–43.
- Kurtén, B., Werdelin, L., 1984. The relationships of *Lynx shansius* Teilhard. *Ann. Zool. Fenn.* 21, 129–133.
- Larivière, S., Walton, L.R., 1997. *Lynx rufus*. *Mamm. Species*, 563, pp. 1–8.
- Lumley, H. de, Kahlke, H.D., Moigne, A.M., Moullé, P.E., 1988. Les faunes de grands mammifères de la grotte du Vallonet, Roquebrune-Cap-Martin, Alpes-Maritimes. *L'Anthropologie* 92, 465–495.
- Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., Berástegui, X., 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest villafranchian faunas of Europe. *Quat. Sci. Rev.* 29, 3972–3982.
- Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Alba, D.M., Aurell-Garrido, J.A., 2014. Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events. *J. Iber. Geol.* 40, 167–178.
- Madurell-Malapeira, J., Morales, J., Vinuesa, V., Boscaini, A., 2015. Úrsidos, hiénidos y félidos del Pleistoceno inferior de Cueva Victoria (Cartagena, Murcia). *Mastia* 11–13, 401–432.
- Martin, R.A., 2012. *Victoriamys*, a new generic name for Chaline's vole from the Pleistocene of Western Europe. *Geobios* 45, 445–450.
- Minwer-Barakat, R., Madurell-Malapeira, J., Alba, D.M., Aurell-Garrido, J., De Estaban-Trivigno, S., Moyà-Solà, S., 2011. Pleistocene rodents from the Torrent de Vallparadís section (Terrassa, northeastern Spain) and biochronological implications. *J. Vert. Paleontol.* 31, 849–865.
- Moigne, A.M., Palombo, M.R., Belda, V., Heriech-Briki, D., Kacimi, S., Lacombat, F., Lumley, M.-A. de, Moutoussamy, J., Rivals, F., Quilès, J., Testu, A., 2006. Les faunes de grands mammifères de la Caune de l'Arago (Tautavel) dans le cadre biochronologique des faunes du Pléistocène moyen italien. *L'Anthropologie* 110, 788–831.
- Montoya, P., Alberdi, M.T., Blázquez, A.M., Barbadillo, L.J., Fumanal, M.P., Van der Made, J., Marín, J.M., Molina, A., Morales, J., Murelaga, X., Peñalver, E., Robles, F., Bustos, A.R., Sánchez, A., Sanchiz, B., Soria, D., Szyndlar, Z., 1999. La fauna del Pleistoceno inferior de la Sierra de Quibas (Abanilla, Murcia). *Estud. Geol.* 55, 127–162.
- 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., 2001a. Une faune très diversifiée du Pléistocène inférieur de la Sierra de Quibas (province du Murcia, Espagne). *C. R. Acad. Sci. Paris* 332, 387–393.
- Montoya, P., Morales, J., Sendra, J., 2001b. Una mandíbula de *Lynx issiodorensis* (Croizet y Jobert, 1828) (Carnivora, Mammalia) en el Plioceno inferior de Cuevas de Almanzora (Almería, España). *Rev. Esp. Paleontol.* núm. ext. 125–131.
- Morales, J., Soria, D., Montoya, P., Pérez, B., Salesa, M.J., 2003. Caracal depereti nov. sp. y Felis aff. silvestris (Felidae, Mammalia) del Pleistoceno Inferior de Layna (Soria, España). *Estud. Geol.* 59, 229–247.
- Moullé, P.E., Lacombat, F., Echassoux, A., 2006. Apport des grands mammifères de la grotte du Vallonet (Roquebrune-Cap-Martin, Alpes-Maritimes, France) à la connaissance du cadre biochronologique de la seconde moitié du Pléistocène inférieur d'Europe. *L'Anthropologie* 110, 837–849.
- Moyà-Solà, S., Agustí, J., Gibert, J., Pons-Moyà, J., 1981. El yacimiento cuaternario de Venta Micena (España) y su importancia dentro de las asociaciones faunísticas del Pleistoceno inferior europeo. *Paleontol. i Evol.* 16, 39–53.
- Nowak, R.M., 2005. Walker's Carnivores of the World. The Johns Hopkins University Press, Baltimore.
- O'Regan, H.J., 2008. The Iberian Peninsula – corridor or cul-de-sac? Mammalian faunal change and possible routes of dispersal in the last 2 million years. *Quat. Sci. Rev.* 27, 2136–2144.
- Olive, F., 2006. Évolution des grands Carnivores au Plio Pléistocène en Afrique et en Europe occidentale. *L'Anthropologie* 110, 850–869.
- Palombo, M.R., 2014. Deconstructing mammal dispersals and faunal dynamics in SW Europe during the Quaternary. *Quat. Sci. Rev.* 96, 50–71.
- Palombo, M.R., Sardella, R., Novelli, M., 2008. Carnivora dispersal in western Mediterranean during the last 2.6 Ma. *Quat. Int.* 179, 176–189.
- Palombo, M.R., Valli, A.M.F., 2003. Remarks on the biochronology of mammalian faunal complexes from the Pliocene to the Middle Pleistocene in France. *Geol. Romana* 37, 145–163.
- Petrucci, M., Cipullo, A., Martínez-Navarro, B., Rook, L., 2013. The late villafranchian (Early Pleistocene) carnivores (Carnivora, Mammalia) from Piro Nord (Italy). *Paleontogr. Abt. A* 298, 113–145.
- Pons-Moyà, J., 1985. Presencia de *Lynx spelaea* (Fissipeda, Mammalia) en el Pleistoceno inferior de la Península Ibérica. *Paleontol. i Evolució* 18, 39–42.
- Postigo Mijarra, J.M., Burjachs, F., Gómez Manzanque, F., Morla, C., 2007. A palaeoecological interpretation of the lower-middle Pleistocene Cal Guardiola site (Terrassa, Barcelona, NE Spain) from the comparative study of wood and pollen samples. *Rev. Palaeobot. Palynol.* 146, 247–264.
- Rodríguez, A., Calzada, J., 2015. *Lynx pardinus*. The IUCN Red List of Threatened Species 2015: e.T12520A50655794. <http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T12520A50655794.en>. Downloaded on 1 October 2015.
- Rodríguez-Varela, R., Tagliacozzo, A., Ureña, I., García, N., Crégut-Bonnoure, E., Mannino, M.A., Arsuaga, J.L., Valdiosera, C., 2015. Ancient DNA evidence of Iberian lynx palaeoendemism. *Quat. Sci. Rev.* 112, 172–180.
- Rodríguez-Varela, R., García, N., Nores, C., Álvarez-Lao, D., Barnett, R., Arsuaga, J.L., Valdiosera, C., 2016. Ancient DNA reveals past existence of Eurasian lynx in Spain. *J. Zool.* 298, 94–102.
- Ros, A., Llamusi, J. L., 2015. Reconstrucción y génesis del karst de Cueva Victoria. Mastia 11–13. In: Gibert L., Ferràndez-Cañadell, C. (Eds.), Geología y paleontología de Cueva Victoria. Ayuntamiento de Cartagena, Cartagena, pp. 111–125.
- Sokolov, W.E., 1988. Dictionary of animal names in five languages. Mammals. Russky Yazyk Publishers, Moscow.
- Sommer, R.S., Benecke, N., 2006. Late Pleistocene and Holocene development of the felid fauna (Felidae) of Europe: a review. *J. Zool.* 269, 7–19.
- Sunquist, M., Sunquist, F., 2002. Wild Cats of the World. Chicago University Press, Chicago.
- Testu, A., 2006. Étude paléontologique et biostratigraphique des Felidae et Hyacnidae pléistocènes de l'Europe méditerranéenne. Ph.D. dissertation. Université de Perpignan.
- Tumilson, R., 1987. *Felis lynx* linnaeus, 1758. *Mamm. Species* 269, 1–8.
- Van den Brink, F.H., 1971. Le lynx pardelle en France. *Bull. la Société d'Étude Sci. Nat. Nîmes* 51, 109–117.
- Vigne, J.D., 1996. La faune des vertébrés. In: Gasco, J. (Ed.), Le Laouret et la Montagne d'Alaric à la Fin de l'Âge du Bronze. Un Hameau Abandonné entre Floure et Monze (Aude). Centre d'Anthropologie, Toulouse, pp. 197–239.
- Vigne, J.D., Pascal, M., 2003. Le Lynx pardelle (Temnick, 1827). In: Pascal, M., Lorgeac, O., Vigne, J.D., Keith, P., Clergeau, P. (Eds.), Évolution de la Faune de Vertébrés en France Métropolitaine depuis le Début de l'Holocène. Invasions et Extinctions. Museum National d'Histoire Naturelle de Paris, Paris, pp. 87–89.
- Viret, J., 1954. Le loess a bancs durcis de Saint-Vallier (Drome) et sa faune de mammifères villafranchiens. *Nouv. Arch. Mus. Hist. Nat. Lyon* 4, 1–200.
- Werdelin, L., 1981. The evolution of lynxes. *Ann. Zool. Fenn.* 18, 37–71.
- Werdelin, L., 1987. Supernumerary teeth in *Lynx lynx* and the irreversibility of evolution. *J. Zoology* 211, 259–266.
- Wolsan, M., 1993. Evolution des carnivores quaternaires en Europe centrale dans leur contexte stratigraphique et paleoclimatique. *L'Anthropologie* 97, 203–222.