



The origin of the critically endangered Iberian lynx: Speciation, diet and adaptive changes



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ARTICLE INFO

Article history:

Received 18 February 2015

Received in revised form

30 June 2015

Accepted 1 July 2015

Available online xxx

Keywords:

Iberian lynx

Early Pleistocene

Iberian Peninsula

Felidae

Carnivora

ABSTRACT

A new cranial fossil attributable to the species *Lynx pardinus* (Temminck, 1827) attests to the presence of this felid in the late Early Pleistocene of the Iberian Peninsula. Certain diagnostic features, such as the confluence of the lacerum posterius and anterior condyloid foramina, and the long and lyre-shaped temporal ridges, allow this find to be established as the first occurrence of the Iberian lynx in Europe. The fossil described here was found in the Avenç Marcel cave (Vallirana, Barcelona, Spain) in association with many other Late Villafranchian faunal remains. The combined presence of the bovid genera *Capra* and *Soergelia*, and the rodent species *Mimomys medasensis* and *Mimomys tornensis*, allows the age of this deposit to be placed at about 1.6–1.7 Ma. Consequently, the appearance of *Lynx pardinus* is related here to the faunal turnover that occurred between the Middle and Late Villafranchian, considered to be one of the major changes in the European macromammal fauna. Such an early divergence is in accordance with the evolutionary split proposed by both the molecular data and with the glacial-interglacial dynamics that affected the European region during the Early Pleistocene. Under these circumstances, the Iberian lynx could have originated in isolation in the Iberian Peninsula (a recognized southern European refugium for several species), during one or more glacial episodes. In this time period, this species may also have developed a dependence on small-sized animal prey, such as the lagomorphs of the genus *Prolagus* and *Oryctolagus*, already widespread throughout the Iberian Peninsula by that point.

In the present work, several topics regarding the earliest evolutionary history of *Lynx pardinus* are discussed. Understanding the events that took place surrounding the origins of this lineage can shed new light on the future conservation of this extremely threatened felid.

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1. Introduction

The species *Lynx issiodorensis* (Croizet & Jobert, 1828), putative ancestor of all living *Lynx* species, originated in Africa during the Early Pliocene, ca. 4 Ma (Hendey, 1978 in Werdelin, 1981). Several finds in Europe, all Early Pliocene in age, subsequently attest to the sudden spread of this species from the Iberian Peninsula (Morales et al., 2003) to Eastern Europe (Ginsburg, 1998; Vislobokova et al., 2001; Spassov, 2003; Cipullo, 2010), where it persisted until the

Late Villafranchian (Kurtén, 1978; Werdelin, 1981; Argant, 2004; Lacombe et al., 2008; Palombo et al., 2008; Petrucci et al., 2013; amongst others). This long-lived species underwent some minor changes through time, the most evident being in its body size, as emphasized by Werdelin (1981), Montoya et al. (2001), and Cipullo (2010). The first species to split off was *Lynx rufus* (Schreber, 1777) around 2.4–2.5 Ma, dispersing into North America over the Bering Strait. A European population of *Lynx issiodorensis* also gave rise to *Lynx pardinus*: this speciation is supposed to have occurred around 1 Ma, corresponding with the Villafranchian-Galerian large mammal turnover (Palombo and Valli, 2003; Palombo et al., 2008). In Asia, *Lynx issiodorensis* gave rise to *Lynx lynx* (L., 1758), probably with *L. issiodorensis shansius* as an intermediate form (Werdelin,

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1981; Kurtén and Werdelin, 1984). *Lynx lynx* later dispersed in Europe during the Eemian period (MIS 5e) (Kahlke, 1999). In the last 200,000 years, Asian populations of the Eurasian lynx also spread into Northern America, giving rise to *Lynx canadensis* Kerr, 1792 (Werdelin, 1981) and displacing *Lynx rufus* into more southern geographic areas (Kahlke, 1999).

Werdelin (1981) described the phylogenetic lineage *L. issiodorensis issiodorensis* - *L. i. valdarnensis* - *L. pardinus spelaeus* - *L. p. pardinus* as a long anagenetic evolutionary lineage, characterized by a decrease in size and a relative lengthening of the lower carnassial.

The evolutionary history of *Lynx pardinus* started in the early Middle Pleistocene with the largest representatives of the species and extends until today, with the few survivors clearly smaller in size.

Nowadays, the Iberian lynx is considered the most vulnerable felid species in the world (Beltrán et al., 1996; Nowell and Jackson, 1996; Ferreras, 2001; Millán et al., 2009; Rodríguez et al., 2011; amongst others), classified by the IUCN in the “critically endangered” category since 2002. The last-remaining specimens survive only in the southernmost portion of the Iberian Peninsula, under intensive conservation programs (Von Arx and Breitenmoser-Wursten, 2008). Even if some sign of recovery has been recently observed (Simón et al., 2012), the high level risk of extinction cannot be underestimated (Palomares et al., 2012).

Here we describe a new Late Villafranchian cranial fossil of *Lynx pardinus* and compare it with extinct and extant representatives of the genus *Lynx*, in order to shed light on the origins of the Iberian lynx.

2. Age and geological background

2.1. Geography, geology and historical background

The Avenç Marcel is a cave situated in the Garraf relief, on the West side of the Llobregat river (Fig. 1A) (Vallirana, Barcelona, Spain). The cave is part of an extensive complex of karst-related features, mostly located on the Pla del Marge del Moro plateau. Avenç Marcel, the main cavity in the area, is situated on the eastern edge of this small upland, mainly formed by calcareous-dolomitic materials (Asensio, 1993).

The majority of the fossil remains were recovered in the feature known as “Via dels ossos” (passage of the bones) which is supposed to have been connected to the original entrance of the cave (Fig. 1B) (Asensio, 1993). The material described here was found in the uppermost segment of this passage, in association with the original entrance of the cave. The fossil vertebrates were found by the Grup d'Investigacions Espeleològiques Sesrovires (GIREs) in 1991

(Asensio, 1993; Daura and Sanz, 2009) in three different facies: conglomerates of pebbles with largely indeterminate bone fragments; carbonate concretions bearing dental remains and large bones coming from the original entrance of the cave and transported by water; and fossil-bearing sand- and siltstones deposited in the floors of the widest chambers (Asensio, 1993).

2.2. Associated fauna and chronology

A preliminary faunal list was reported in Asensio (1993) and includes the following taxa: *Canis* sp., *Vulpes* sp., *Mammuthus* sp., *Stephanorhinus etruscus*, *Equus* sp., Cervidae indet., *Capra* sp., *Soergelia* sp., *Mimomys medasensis*, *Mimomys* aff. *tornensis*, *Apodemus* aff. *mystacinus*, and *Prolagus* cf. *calpensis*. The felid remains were initially classified as Felidae indet., *Megantereon* sp. and *Homotherium* sp. (Asensio, 1993), later as *Homotherium latidens*, *Megantereon* sp., and *Lynx issiodorensis* (Nebot and Hernández, 2008). In the last revision of the Avenç Marcel large mammal fauna, Madurell-Malapeira et al. (2014) provided an updated faunal list comprising *Homotherium latidens*, *Megantereon cultridens*, *Lynx issiodorensis*, *Canis* sp., *Vulpes* sp., Cervidae indet., Ovibovini indet. aff. *Soergelia* sp., *Capra* sp., *Equus* sp. and *Stephanorhinus hundsheimensis*.

The combined presence of the rodents *Mimomys medasensis* and *Mimomys tornensis* and the bovids of the genera *Capra* and *Soergelia*, allows the site to be placed immediately prior to the appearance of *Allophaiomys*, at around 1.5–1.6 Ma. The site has been dated to around 1.6–1.7 Ma, the late-Early Pleistocene (Asensio, 1993; Rook and Martínez-Navarro, 2010; Madurell-Malapeira et al., 2014) or slightly older according to Daura et al. (2014). The faunal association is also related to a warm-temperate climate and dry environments (Asensio, 1993).

3. Materials and methods

Institutional abbreviations: ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Cerdanyola del Vallès, Barcelona, Spain); IPS, collections from the ICP (former Institut de Paleontologia de Sabadell) (Barcelona, Spain); MZB, Museu de Ciències Naturals de Barcelona (Spain); IGF, Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze (Italy); SBAU, Soprintendenza per i Beni Archeologici dell'Umbria, Perugia (Italy).

The specimen described is housed in the Institut Català de Paleontologia Miquel Crusafont. The comparative sample includes the fossil specimens of *Lynx issiodorensis* from Pirro Nord (ca. 1.6–1.4 Ma; Italy; cranium IGF s.n.), Olivola (ca. 2.0 Ma; Italy; cranium IGF 4399), Étouaires (ca. 2.6 Ma; France; cranium IGF 12777,

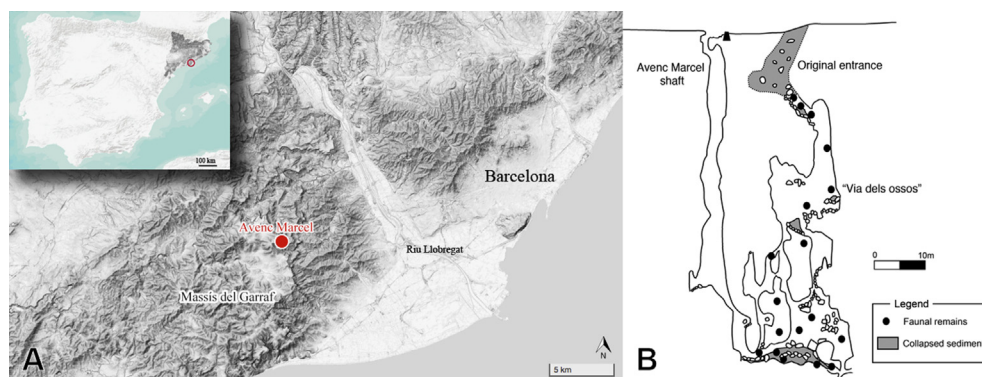


Fig. 1. The Avenç Marcel cave (Vallirana, Barcelona, Spain). A: Geographical setting. B: Cross-section. Modified from Daura et al. (2014).

cast), and *Lynx pardinus spelaeus* from L'Escaie (0.6 Ma; France; crania IGF 678V and IGF 679V, casts). The extant remains used for comparison belong to *Lynx pardinus* (skull IPS 82320), *Lynx lynx* (skull MZB 2010-1402). Additional comparative data for Pleistocene lynxes have been taken from the literature (Boule, 1919; Boule and Villeneuve, 1927; Bonifay, 1971; Testu, 2006; Cipullo, 2010; Cherin et al., 2013; Petrucci et al., 2013). Measurements of the studied specimens were taken with digital callipers to the nearest 0.1 mm.

4. Systematic palaeontology

Order: Carnivora Bowdich, 1821

Family: Felidae Gray, 1821

Subfamily: Felinae Fischer von Waldheim, 1817

Genus: *Lynx* Kerr, 1792

Lynx pardinus (Temminck, 1827)

(Figs. 2–3)

Referred material- IPS 4170, neurocranium. The specimen belongs to an adult individual.

Measurements- See Table 1.

Description- The cranium IPS 4170 preserves only the caudal part or neurocranium. It lacks the entire rostral part up to the level of the zygomatic processes of the frontal bones, which are broken at their base. In lateral view, it presents a high profile of the parietal roof, descending almost vertically in the occipital region. Consequently the cranium appears rounded and shortened. In dorsal view, the temporal lines are marked and almost parallel in the frontal and parietal region, connecting close to the caudal edge and giving rise to a very short sagittal crest (Fig. 2A). The resulting lyre-shaped surface, delimited by the temporal ridges, is only slightly narrower at the level of the coronal suture. The short sagittal crest is prolonged in the wide occipital bone. The foramen magnum is ovoidal in shape, being wider at its base. In ventral view, only a few features can be observed. Even if the auditory bulla is not preserved it can be noticed that the two foramina behind its margin, the

lacerum posterius and anterior condyloid, respectively synonyms of jugular and hypoglossal foramina (Gilbert, 1976), are confluent in the same cavity (Fig. 2B and Fig. 3E). The presphenoid, only partially visible, enlarges towards the rostral region of the cranium.

Comparisons- Two of the features described: the separation of the temporal lines, which merge in the caudal part of the cranium, and the confluence in the same cavity of the lacerum posterius and anterior condyloid foramina, are clear characters of *Lynx pardinus* (Van den Brink, 1971; García-Perea et al., 1985; García-Perea, 1996; Larivière and Walton, 1997). The latter character is especially highly diagnostic, allowing one to distinguish reliably between the living Iberian and Eurasian lynxes (Larivière and Walton, 1997). Among the extant remains considered, these foramina are confluent in *Lynx pardinus* (e.g. IPS 82320; Fig. 3D) and separated in *Lynx lynx* (e.g. MZB 2010-1402; Fig. 3F). At the same time in IPS 82320 the temporal ridges are long and parallel, while in MZB 2010-1402 they are short and connected to a long sagittal crest (Fig. 3). These cranial features observed in IPS 4170 are replicated in the skulls of *Lynx pardinus spelaeus* from the Grimaldi cave (Boule, 1919) and L'Observatoire (Boule and Villeneuve, 1927). Furthermore, the Middle Pleistocene lynx remains from L'Escaie IGF 679V present the same pattern of the temporal ridges.

In contrast, this arrangement is never observed in *Lynx issiodorensis*, neither in the nominal taxon *L. i. issiodorensis* (e.g. the cranium IGF 2777 from Les Ètouaires, France) nor in the smaller-sized *L. i. valdarnensis* (IGF 4399 from Olivola and SBAU 337653 from Pantalla, Italy) (Viret, 1954; Kurtén, 1978; Cipullo, 2010; Cherin et al., 2013).

Regarding morphometric data, if the length of the sagittal crest in IPS 4170 is even shorter than in the extant *Lynx pardinus* (data in García-Perea, 1996), the width and the length of the temporal lines, depicting a clear lyre-shaped surface on the cranial roof, are higher than in extant specimens of *Lynx pardinus* (data in García-Perea et al., 1985). However, other measurements such as the mastoid and postorbital widths, are slightly out of the *Lynx pardinus* range,

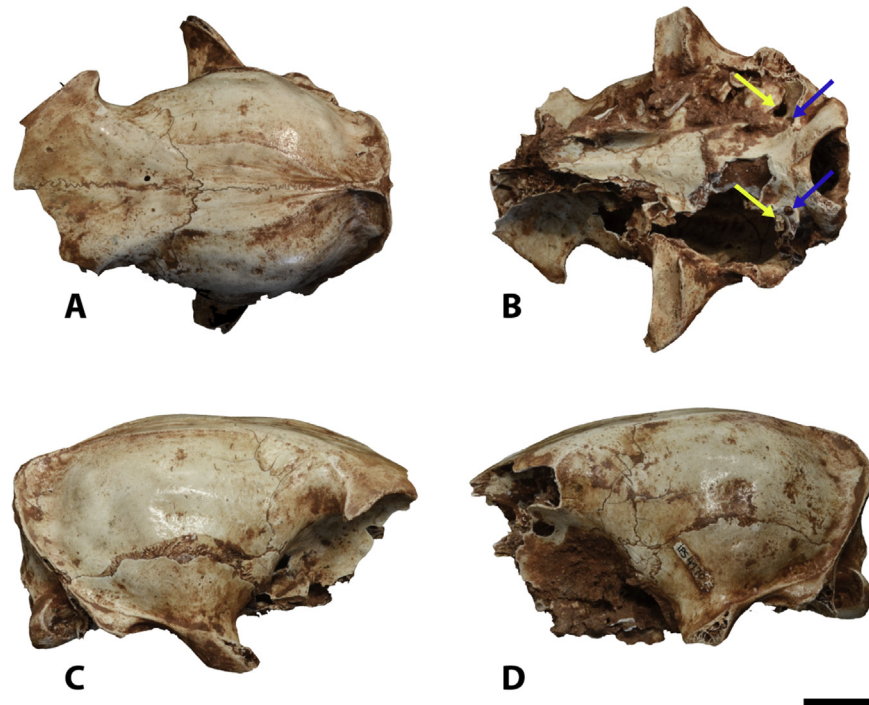


Fig. 2. IPS 4170, neurocranium. A: dorsal view; B: ventral view; C: right lateral view; D: left lateral view. Yellow arrows indicate the lacerum posterius (or jugular) foramina; blue arrows indicate the anterior condyloid (or hypoglossal) foramina. Scale bar length: 2 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

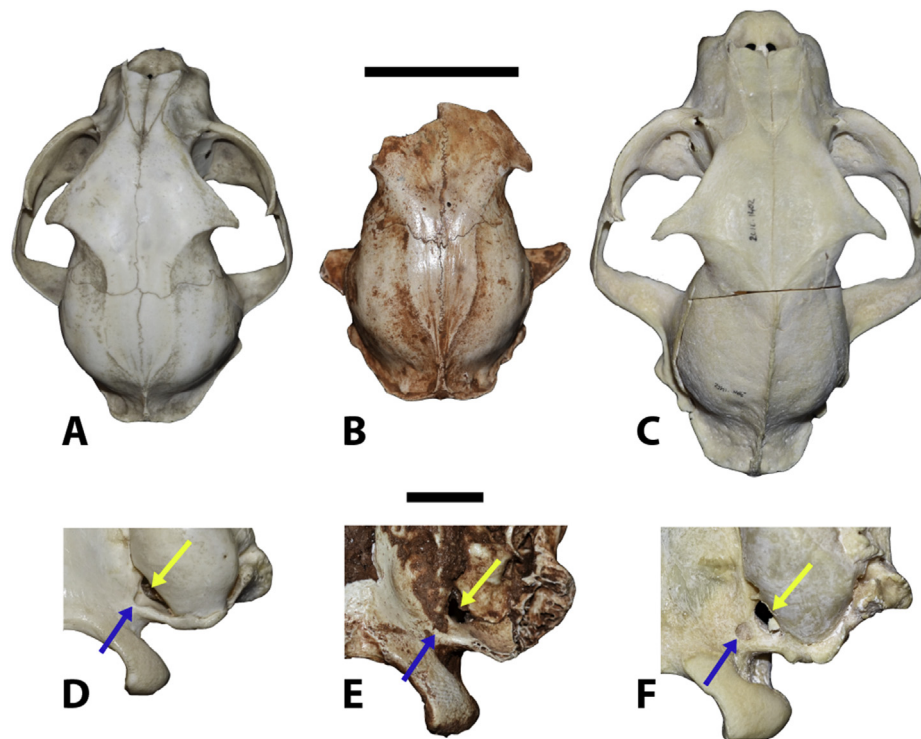


Fig. 3. Upper series (A–B–C): *Lynx* crania in dorsal view. A: extant *Lynx pardinus* (IPS 82320); B: *Lynx pardinus* from Avenç Marcel (IPS 4170); C: extant *Lynx lynx* (MZB 2010-1402). Scale bar length: 5 cm. Lower series (D–E–F): details of the auditory region. D: extant *Lynx pardinus* (IPS 82320); E: *Lynx pardinus* from Avenç Marcel (IPS 4170); F: extant *Lynx lynx* (MZB 2010-1402). Yellow arrows indicate the lacerum posterius (or jugular) foramina; blue arrows indicate the anterior condyloid (or hypoglossal) foramina. Scale bar length: 1 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
IPS 4170. Cranial measurements (mm) of *Lynx pardinus* from Avenç Marcel cave.

Cranium measurement	Length (mm)
Length of the sagittal crest (Akrokranium to junction of the two lineae temporales)	12.5
Distance between the lineae temporales (at the level of the coronal suture)	20.9
Length of the lineae temporales (Frontal midpoint to junction of the two lineae temporales)	63.7
Greatest neurocranium breadth (Euryon – Euryon)	63.5
Upper neurocranium length (Akrokranium – Frontal midpoint)	76.2
Basicranial axis (Basion – Synsphenion)	42.3
Breadth of the postorbital constriction	40.9
Frontal breadth (Ectorbitale – Ectorbitale)	60.0
Height of the foramen magnum (Basion – Opisthion)	18.8
Greatest breadth of the foramen magnum	20.1
Greatest breadth of occipital condyles	35.7
Height of the occipital triangle (Akrokranium – Basion)	43.0
Greatest mastoid breadth (Otion – Otion)	61.3

being comparable with the cranium of *Lynx issiodorensis valdarensis* from Pantalla and Olivola (Cherin et al., 2013) and suggesting that this specimen could represent one of the earliest forms of *Lynx pardinus*.

The larger size of the first representatives of the *Lynx pardinus* lineage is well documented in the literature (Boule, 1919; Boule and Villeneuve, 1927; Kurtén, 1968; Bonifay, 1971; Werdelin, 1981; Testu, 2006).

5. Discussion

5.1. Biomechanical inferences

As suggested by García-Perea (1996), the marked reduction of the length and height of the sagittal crest in *Lynx pardinus*, could be related to a lower development of the temporalis, the strongest and largest muscle of the head, related with mastication (Miller et al.,

1964; De Iuliis and Pulerà, 2006). This bipennate muscle inserts on the mandible, originating from the temporal fossa, an area situated on the caudal cranial roof, bounded anteriorly by the orbital ligament and the external frontal crest, laterally by the zygomatic arch, caudally by the dorsal nuchal crest and medially by the external sagittal crest or temporal line (Miller et al., 1964; Evans and de Lahunta, 2013). A reduced extension of the temporal fossa indicates the presence of a smaller temporalis, which could be related to a decrease in its strength and an adaptation towards predation upon small-sized animals such as like lagomorphs, rodents and birds. These are the favorite prey of the extant Iberian lynx, constituting almost the totality of its diet (Hemmer, 1984; Sunquist and Sunquist, 2002; Nowak, 2005). Amongst these, the lagomorph *Oryctolagus cuniculus* predominates, allowing *Lynx pardinus* to be considered as a super-specialist predator (Ferrer and Negro, 2004).

The same shape of the temporal ridges and sagittal crest is also usually observed in the other two small-sized lynx species, *Lynx*

rufus and *Lynx canadensis* (García-Perea, 1996), whose diets are largely dominated by prey with a reduced body mass (approximately 1–2 kg) (Sunquist and Sunquist, 2002; Hemmer, 2004; Nowak, 2005).

Werdelin (1981) suggested that the evolution of smaller-sized lynx species during the Pleistocene (*L. issiodorensis valdarnensis* and *L. pardinus*) was a response to competition with larger felids (respectively *Puma pardoides* [Owen, 1846] and *Lynx lynx*) that preyed on larger animals. For these “Mediterranean” felids, the adopted strategy was to feed on smaller animals, also evolving a more slender dentition when compared with the stouter one in *L. issiodorensis* and *L. lynx* (Werdelin, 1981; Testu, 2006). The reduction of the length of the sagittal crest is not observed in either *L. issiodorensis* or in *L. lynx* (García-Perea, 1996), suggesting that they fed preferentially on large animals, about the size of a red deer (Werdelin, 1981; Hemmer, 2004).

5.2. Previous remains

The discovery of the neurocranium IPS 4170 with such diagnostic features allows the presence of *Lynx pardinus* to be firmly established in the Late Villafranchian of the Northeastern Iberian Peninsula and, to date, this represents the earliest occurrence of this taxon.

Previously, the oldest Iberian lynx fossils were the dubious remains from Venta Micena (Orce, Southern Spain) (Moyà-Solà et al., 1981) and Sierra de Quibas (Murcia, Southern Spain) (Montoya et al., 1999). In Venta Micena (ca. 1.5 ± 0.1 Ma), the material consists of just two dental remains of small size, suggesting the presence of an ancestral form of *Lynx pardinus* (Moyà-Solà et al., 1981). In Sierra de Quibas, dental fragments have been found, the dimensions of which fall into the *Lynx pardinus* range, together with a fifth metacarpal slightly larger than modern specimens. For these reasons, previous authors have suggested that *Lynx pardinus* in the Iberian Peninsula from 1.2 Ma was closely comparable with its living representatives although a little larger in size (Montoya et al., 1999). The new findings push back the origin of this species to close to the top of the Olduvai normal subchron. Other *Lynx pardinus* remains from late Early and Middle Pleistocene sites in the Iberian Peninsula have been described in Pons-Moyà (1983), García et al. (1997), García and Arsuaga (1998, 1999).

5.3. An expected find

The suggested age of the first remains of *Lynx pardinus* is consistent with the divergence timing provided by molecular analyses. The supposed split of the Iberian lynx was suggested to occur between 1.53 and 1.68 Ma by Johnson et al. (2004), and at 2.2 Ma by Bininda-Emonds et al. (1999). Furthermore, recent molecular studies have confirmed that there was no genetic drift in *Lynx pardinus* during recent times (historical or at the Late Pleistocene/Holocene transition) (Rodríguez et al., 2011). The long-term low mtDNA diversity could be the result of postglacial founder events (Rodríguez et al., 2011). The hypothesis of the origin of *Lynx pardinus* in the Iberian Peninsula was previously proposed by Hemmer (1979, 2001), Ferrer and Negro (2004) and Johnson et al. (2004), who suggested that the isolation of an Iberian population was caused by one or more glacial events.

5.4. Speciation, diet and adaptive changes

A good candidate for the separation of the European lynx populations is the glacial pulse at 1.8 Ma (MIS 64–63–62), also being the midpoint of the range established by the molecular studies. This pulse is already known as the point of separation between the

Middle and Late Villafranchian and marked the previous boundary between the Pliocene and the Pleistocene. Additionally, the beginning of the Late Villafranchian (MIS 63) represents a major faunal renewal, which involved the extinction of several species (mostly herbivores) as well as the arrival of several new forms of Asian and African origin. Several taxa with a long record during the Villafranchian, such as *Stephanorhinus etruscus*, *Equus stenonis*, *Leptobos*, *Gazellospira*, *Gazella*, *Cervus philisi*, *Arvernoceros ardei* and *Croizetoceros ramosus*, vanished from the Iberian Peninsula and the rest of Europe around the Middle-Late Villafranchian boundary. These were replaced by new incoming taxa, most of them of Asian origin, namely *Stephanorhinus hundsheimensis*, *Equus altidens*, *Praemegaceros verticornis*, *Bison*, *Hemibos*, *Hemitragus* and *Soergelia minor*. Regarding the carnivores, several Middle Villafranchian species did not survive the transition into the Late Villafranchian and its associated climatic shifts, including *Megantereon cultridens*, *Pliocrocuta perrieri*, *Chasmaportetes lunensis*, *Lycaon falconeri*, *Nyctereutes megamastoides* and *Meles thoralis*, which were replaced by other forms mainly of African origin, such as *Megantereon whitei*, *Panthera gombaszoegensis* and *Pachycrocuta brevirostris*, but also of Asian origin, such as *Lycaon lycaonoides* and *Meles meles atavus* (Palombo, 2010; Rook and Martínez-Navarro, 2010; Madurell-Malapeira et al., 2014; and references therein).

In contrast, the role of the Iberian Peninsula as a climatic refugium during Quaternary glaciations is supported by several data. *Chorthippus parallelus*, *Ursus arctos*, *Alnus glutinosa*, *Arvicola terrestris*, *Fagus sylvatica*, *Sorex araneus* are just some of the species that found refuge over the southern side of the Pyrenees (Hewitt, 1999). Some of them remained in the Peninsula during the warmer conditions of the interglacial phases, whereas others spread out again through Central and Northern Europe during temperate-climate episodes (Hewitt, 1999). In recent times, the refugial role played by the Iberian Peninsula has also been proved for the European rabbit (*Oryctolagus cuniculus*), the main prey of *Lynx pardinus*, constituting 75%–93% of its diet according to Sunquist and Sunquist (2002) and up to 99% according to Fedriani et al. (1999).

The genus *Oryctolagus* originated in the Iberian Peninsula around 3.5 Ma and since then, it has been a constant element of the Iberian Quaternary fauna (Lopez-Martínez, 2008).

In the Early Pleistocene, the European rabbit found refuge in two areas: southern Spain and southeastern France, giving rise to different subspecies. The divergence time of the two lineages is estimated at approximately 2 Ma, or at the Middle-Late Villafranchian transition (Biju-Duval et al., 1991), coinciding with the putative split of *Lynx pardinus* from *Lynx issiodorensis*.

This lagomorph survived in the Iberian Peninsula in two separated localities: the Mediterranean coast and in the southernmost area of Spain, close to the Gibraltar Strait, giving rise to two different haplotypes (Branco et al., 2002). In these regions, the European rabbit was able to maintain large populations throughout the Quaternary glaciations, until today (Biju-Duval et al., 1991; Branco et al., 2002).

The dependence on rabbits as a way to explain the evolution of the Iberian lynx was initially introduced by Kurtén (1968) and recently confirmed by Ferreras et al. (2010), who recognized that the geographic distributions of *Lynx pardinus* and *Oryctolagus cuniculus* follow the same contraction dynamics in accordance with the Pleistocene glacial-interglacial pulses (Rodríguez and Delibes, 2002; Lopez-Martínez, 2008; Ferreras et al., 2010). Given such a close prey–predator relationship, the decreasing size in the genus *Oryctolagus* (Rogers et al., 1994) may also be related with the decreasing size in the Iberian lynx.

The morphological characteristics that distinguish *Lynx pardinus*, such as the longer and narrower m1 (Werdelin, 1981), reduced

accessory distal margin on p4 (Bonifay, 1971) and the shorter sagittal crest with respect to *L. issiodorensis* (García-Perea et al., 1985; García-Perea, 1996) can therefore be seen as the result of selection towards extremely specialized feeding habits (Bonifay, 1971; Testu, 2006).

6. Conclusions

The evidence reported here attests to the presence of *Lynx pardinus* at 1.6–1.7 Ma in the Iberian Peninsula, significantly earlier than its currently accepted appearance at the Epivillafranchian turnover (ca. 1 Ma). According to our data, the appearance of the Iberian lynx occurred around the Middle-Late Villafranchian faunal turnover, with *Lynx pardinus* evolving in the Iberian Peninsula from a population of *Lynx issiodorensis* that was isolated during one or more consecutive glacial pulses (following Hemmer, 1979, 2001). The timing of this divergence is also in accordance with the molecular data proposed by Johnson et al. (2004) and Bininda-Emonds et al. (1999).

Since its first appearance, the Iberian lynx shows highly diagnostic features and a peculiar sagittal crest morphology, suggesting an early dependence on small-sized animal prey, such as the rabbit genus *Oryctolagus*, already abundant at this time across the whole Iberian Peninsula.

Acknowledgments

This work has been supported by the Spanish Ministry of Economy and Competitiveness CGL2010-15326/BTE, CGL2011-28681, Generalitat de Catalunya GENCAT 2014 SGR 901 and 2009 SGR 754 GRC. We sincerely thank M. Nebot, R. Sardella, D. A. Iurino, M. R. Palombo, E. Cioppi, L. Rook, R. D. Kahlke, L. Costeur, F. Vigouroux, J. Quesada, A. R. Gómez-Cano, V. Vicedo and J. F. Beltrán for providing suggestions, information and access to the collections under their care. This paper greatly benefited from the careful reading and thoughtful comments by the Editor D. Schreve and the reviewers M. Cherin and M. J. Salesa.

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