



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



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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,

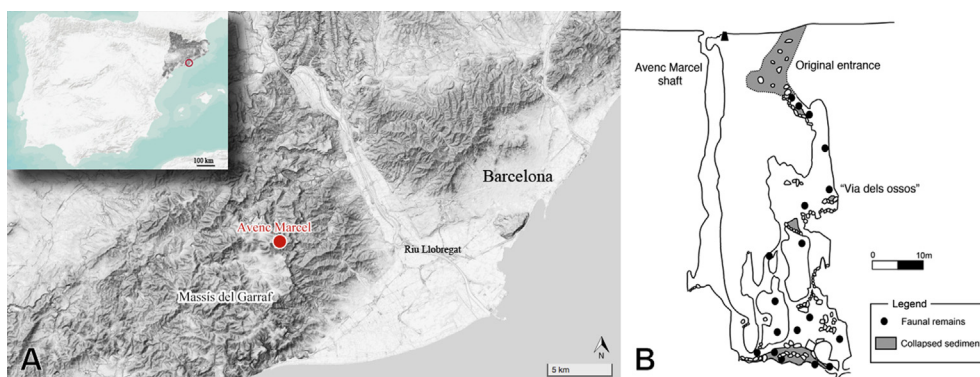


Fig. 1. The Avenç Marcel cave (Vallirana, Barcelona, Spain). A: Geographical setting. B: Cross-section. Modified from Daura et al. (2014).

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