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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.

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 though 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 presphenoid 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; Ghezzo 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 Avenc 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 Clols 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 Llamusí, 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 Clols et al., 2006; Gibert and