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The tale of a short-tailed cat: new outstanding Late Pleistocene fossils of *Lynx pardinus* from southern Italy

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Abstract

The pardel lynx *Lynx pardinus* is today restricted to small populations living in southern Iberian Peninsula. However, this endangered species was widely spread throughout Iberia until historical times and is currently the subject of intense conservation programs. Paleontological data suggest that its past geographical range was much wider, including also southern France and northern Italy. Here, we report exceptionally preserved fossil remains of *L. pardinus* from the Late Pleistocene (about 40'000 years) of Ingarano (Italy), which represent the largest sample of fossil lynx currently known in Europe. This new evidence allows (1) to revise the taxonomy of European fossil lynxes, (2) to extend far southeast the paleobiogeographical distribution of *L. pardinus*, and (3) to offer new insights on the evolutionary history (e.g., relationships with other extinct and extant lynx species) and paleobiology (e.g., intraspecific variation, body mass) of this iconic European felid.

Keywords: Europe**,** Pleistocene, Carnivora, Felidae, Lynx, Evolution, Taxonomy, Paleobiogeography, Paleoecology

1. Introduction

With a geographical distribution limited to a few restricted areas of southwestern Iberian Peninsula (*Macdonald et al., 2010*), the pardel (or Iberian) lynx *Lynx pardinus* is considered one of the most threatened living felids by the International Union for Conservation of Nature (IUCN; ***Simón, 2012***; ***Simón et al., 2012***). Over the last decades many efforts have been made to better characterize the ecological and biological profile of this rare felid, mainly with the aim of developing conservation projects to increase population abundance and to expand its distribution. According to IUCN data, not more than 160 mature individuals exist today in southern Iberia (***Rodríguez and Calzada,***

2015). Currently, the pardel lynx is one of the best-known living felids, but despite this, its evolutionary history is still strongly debated among the specialists.

Since the mid-1970s, different scenarios on the evolution of genus *Lynx* have been proposed. ***Ficcarelli and Torre (1977)*** considered the Plio-Pleistocene *Lynx issiodorensis* as the ancestor of *L. pardinus*. This hypothesis was shared by ***Kurtén (1978)*** and partially revised by ***Werdelin (1981)***. The earliest records of *L. issiodorensis* date back to the Ruscinian European Land Mammal Age (ELMA), roughly corresponding to the early Pliocene (ca. 4 Ma). These records include scanty remains from Cuevas del Almanzora (Spain; ***Montoya et al., 2001a***), Layna (Spain; "*Caracal depereti*" in ***Morales et al., 2003***), Serrat d'en Vacquer (France; "*Caracal brevirostris*" in ***Depéret, 1890***), and Çalta (Turkey; ***Ginsburg, 1998***). *Lynx issiodorensis* then became a common element in terrestrial mammal assemblages during the Villafranchian ELMA, encompassing the late Pliocene and most of the Early Pleistocene (ca. 3.3-1.2 Ma). ***Werdelin (1981)*** divided *L. issiodorensis* into two chronologically distinct subspecies, namely *L. issiodorensis issiodorensis* (early-middle Villafranchian; ca. 3.3–2.1 Ma) forms and *L. issiodorensis valdarnensis* (late Villafranchian; ca. 2.1–1.2 Ma). The first includes, among others, the nearly complete skeleton from Les Etouaires (France; ***Kurtén, 1978***) and Saint Vallier (France; ***Viret, 1954***; ***Argant, 2004***); the second includes several well-preserved fossils from Italian sites such as Olivola, Upper Valdarno, and Pantalla (***Fabrini, 1896***; ***Del Campana, 1925***; ***Cherin et al., 2013***). The last occurrence of *L. issiodorensis* is from the Epivillafranchian site of Untermassfeld (Germany; ca. 1.0 Ma; ***Hemmer, 2001***). According to ***Werdelin (1981)***, *L. issiodorensis* has a pivotal role in lynx evolution, as it probably gave rise to both the lineages of *L. pardinus* in Europe and *Lynx lynx* in Asia in the Early Pleistocene. This is corroborated by molecular evidence, according to which the divergence between *L. pardinus* and *L. lynx* occurred between ca. 2.2 Ma (***Bininda-Emonds et al., 1999***) and 1.6 Ma (***Johnson et al., 2004***). The evolution of *L. lynx* from *L.*

issiodorensis in Asia probably involved *L. issiodorensis shansius* as an intermediate form (***Werdelin, 1981***; ***Kurtén and Werdelin, 1984***). The Eurasian lynx then reached Europe at the beginning of the Late Pleistocene (Eemian, MIS 5e; ***Werdelin, 1981***) and became a common element of the carnivore guild during the whole Last Glacial Period, especially in central and northern Europe (***Kahlke, 1999***; ***Sommer and Benecke, 2006***). On the other side, the long and gradual evolution from *L. issiodorensis* to *L. pardinus* involved the aforementioned intermediate subspecies *L. i. issiodorensis* and *L. i. valdarnensis*, followed by the Middle Pleistocene 'cave lynx' *L. pardinus spelaeus* (***Werdelin, 1981***). This anagenetic evolutionary trend characterized by a progressive reduction in body size and relative lengthening of the M_1 is accepted by several authors (***Kurtén and Granqvist, 1987***; ***García and Arsuaga, 1998***; ***Cherin et al., 2013***), although the taxonomic status of the 'cave lynx' is still debated. This taxon was established on fossil remains from Grotta del Principe (Ventimiglia, northwestern Italy) by ***Boule (1919)*** as "*Felis* (*Lynx*) *pardinus* race *spelaea*" mainly based on the strong craniodental similarity with the extant *L. pardinus*. However, the fossil form showed larger body size than the modern one.

The 'cave lynx' is reported from several Middle-Late Pleistocene sites of southwestern Europe, especially in southern France and northern Italy. In agreement with ***Werdelin's (1981)*** interpretation, many authors considered this taxon as a subspecies and probable ancestor of the modern *L. pardinus*, i.e., *L. pardinus spelaeus* (***Kurtén and Granqvist, 1987***; ***García-Perea, 1997***; ***Palombo et al., 2008***; ***Garrido and Arribas, 2008***; ***Rodríguez-Hidalgo et al., 2020; Fosse et al., 2020***). Conversely, other authors preferred to classify the 'cave lynx' as a distinct species, i.e., *Lynx spelaeus* (***Bonifay, 1971***; ***Ficcarelli and Torre, 1977; Arribas, 1994***; ***Rustioni et al., 1995***; ***Capasso Barbato et al., 1998***; ***Testu, 2006***; ***Ghezzo et al., 2015***).

The debate on the taxonomy and distribution of Quaternary lynxes in southwestern Europe has been enriched by recently described specimens. ***Boscaini et al. (2015)*** reported on a fragmentary cranium from the site of Avenc Marcel (Spain; 1.7–1.6 Ma) as the earliest fossil evidence of *L. pardinus* and they suggested an Early Pleistocene origin of this species from *L. issiodorensis*. ***Boscaini et al. (2016)*** analyzed the extensive collection of fossil lynx from the latest Early Pleistocene of Vallparadís Estació and Cueva Victoria (Iberian Peninsula) and the authors proposed to consider *L. spelaeus* as a junior subjective synonym of *L. pardinus*, since the two taxa do not show significant skeletal morphological differences other than the body size. The poor reliability of taxonomic identifications based on dimensional criteria, especially for Late Pleistocene material, was confirmed by the recent molecular study by ***Rodríguez-Varela et al. (2015)***. These authors analyzed the mtDNA of fossils from Arene Candide (Savona, northwestern Italy), which were previously attributed to *L. lynx* or *L.* cf. *spelaeus* based on their overall large dimensions (***Cassoli and Tagliacozzo, 1994a***). Molecular results allowed to refer some of the specimens to *L. lynx* and some to *L. pardinus*. Interestingly, some of the remains genetically attributed to the pardel lynx show dimensions relatively larger than the average values recorded for the 'cave lynx' (***Rodríguez-Varela et al., 2015***). The identification of *L. pardinus* in the latest Pleistocene (ca. 25–17 ka) deposits of Arene Candide represents the first direct evidence of the occurrence of this species in Italy, suggesting that its ancient distribution should exceed the Iberian Peninsula. However, taking into account the absence of diagnostic morphological differences between the pardel lynx and 'cave lynx', it has been proposed that Middle-Late Pleistocene samples from Mediterranean Europe originally referred to *Lynx* sp., *L. spelaeus*, or *L. pardinus spelaeus*, can be instead attributed to *L. pardinus* (***Boscaini et al., 2016***). For these reasons, unless otherwise stated, here we prefer using the terminology *L. pardinus sensu lato* (*s.l.*) to indicate extant and fossil pardel lynx, that is, including 'cave lynx'.

In this paper we report on the lynx remains from the Late Pleistocene site of Ingarano (Foggia, southeastern Italy), which represent the largest sample of fossil lynx in Europe, consisting of 415 remains including two almost complete crania. These remains were previously attributed to *L. lynx* mainly due to their large dimensions (***Capasso Barbato et al.,1992***; ***Petronio et al., 1996***; ***Petronio and Sardella, 1998***). More recently, ***Iurino et al. (2015)*** carried out a comparative study on a natural brain endocast from Ingarano, which was referred to *Lynx* sp. since the endocranial features did not show reliable interspecific differences. Here, we analyze the morphological and biometric features of the lynx craniodental material from Ingarano, we discuss its taxonomic attribution, as well as its paleoecological and paleobiogeographical implications.

2. Geological and paleontological framework

The Late Pleistocene fossiliferous site of Ingarano is located in the northwestern area of the Gargano promontory (270 m s.l.m.) close to the Gargano railway, nearby Apricena town (Foggia, southeastern Italy; ***Figure 1***). The Ingarano deposit is a karstic filling succession within the Jurassic-Cretaceous limestone of the “Calcare di Sannicandro” Formation. The stratigraphic succession was exposed by quarrying activities and is composed by five different layers, A–E from bottom to top (***Bedetti and Pavia, 2007***). Geochemical analysis of the phosphatic material from layer B with the ^{329}Th/^{234}U method provided dating of 40 ± 2 ka in agreement with the putative age of some Mousterian artifacts found between layers D-E (***Petronio et al., 1996***). Paleoecological and taphonomic studies confirmed that the Ingarano succession, at least from layers B to E (e.g., those bearing vertebrate remains), was deposited in a short time-span during MIS 3 (60–28 ka; ***Bedetti and Pavia, 2007***).

In the last decades, several authors studied the abundant vertebrate fauna from Ingarano, which includes 41 taxa: Amphibians - *Rana* sp.; Reptiles - *Lacerta* sp.; Birds - *Circus aeroginosus*, *Buteo rufinus*, *Aquila chrysaëtos*, *Falco cherrug*, *Falco columbarius*, *Alectoris graeca*, *Perdix perdix*, *Columba livia*, *Otus scops*, *Nyctea scandiaca*, *Athene noctua*, *Pyrrhocorax graculus*, *Pyrrhocorax* sp., *Corvus corone*, *C. corone* vel *C. frugilegus*, *Corvus corax*; Mammals - *Erinaceus europaeus*, *Myotis blythi*, *Oryctolagus cuniculus*, *Lepus europaeus*, Arvicolidae indet., *Microtus* sp., *Microtus* ex gr. *arvalis/agrestis*, *Terricola savii*, *Apodemus sylvaticus*, *Eliomys quercinus*, *Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Mustela nivalis*, *Martes* sp., *Meles meles*, *Gulo gulo*, *Crocuta crocuta*, *Felis* sp., *Lynx lynx* (revised in this paper), *Panthera pardus*, *Equus hydruntinus*, *Cervus elaphus*, *Dama dama*, *Capreolus capreolus*, *Rupicapra* sp., *Bos primigenius* (***Capasso Barbato et al., 1992***; ***Petronio et al., 1996***; ***Petronio and Sardella, 1998***; ***Curcio et al., 2005***; ***Bedetti and Pavia, 2007***; ***Iurino, 2014***; ***Iurino et al., 2015***). An additional layer was identified by ***Petronio et al. (1996)***, including fossil remains attributed to *Panthera spelaea*, *Hippopotamus amphibius*, *Coelodonta antiquitatis*, *Stephanorhinus hemitoechus*, and *Palaeololoxodon antiquus*. This layer was composed by sandy clay in doubtful stratigraphic correlation with the infilling succession (***Petronio and Sardella, 1998***).

Figure 1

3. Materials and methods

The fossil material studied in this work were discovered in the 1990s by the research team of the Departments of Earth Sciences of Sapienza University of Rome and University of Turin during several geo-paleontological surveys at Ingarano. The collection counts 415 lynx remains represented by 346 postcranial and 68 craniodental remains housed in the PaleoFactory Laboratory of the Department of Earth Sciences of Sapienza University of Rome, except the skull MGPT-PU 135415, which is stored in the Museo di Geologia e Paleontologia of the University of Turin. In this paper, we focused on craniodental remains listed in ***Supplementary note 1***. All the specimens from Ingarano are marked with different alphanumeric codes: FG indicates the remains coming from the first geo-paleontological surveys (1989-90); specimens without field labels/numbers are indicated with ING-, INGND-, and M- and come from successive geo-paleontological surveys. The crania from Ingarano (MGPT-PU 135415, ING75), the cranium of *L. issiodorensis* from Pantalla (SABAP_UMB 337653) and a skull of extant *L. lynx* (MC 85) from the Museo Civico di Zoologia of Rome were acquired using a Philips Brilliance CT 64-channel scanner at M.G. Vannini Hospital (Rome). The slice thickness is 0.55 mm and interslice space is 0.27 mm. A cranium of extant *L. pardinus* (MNB 8865) and that of *L. issiodorensis* from Olivola (MNB Ol 1) were scanned at the Biomaterials Science Center of the University of Basel using the advanced microCT-system nanotom® m (phoenix x-ray, GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany); slice thickness and interslice space are both 66 µm. CT image processing was performed using Mimics 20.0, while the digital restoration process of the missing portions of the skulls was made with ZBrush 4R6. All the missing parts of the specimens were cloned and mirrored from those preserved, and their alignment and positioning were performed following the sagittal plane of the skull (***Cherin et al., 2018***; ***Iurino et al., 2020***). Finally, the reconstructed portions were highlighted using different colors (***Figures 3 and 10***).

Measurements were taken with a digital caliper to the nearest 0.1 mm, following ***Von den Driesch (1976)*** and ***Testu (2006)***. To build a comparative dataset, we used the available literature on late Pliocene-Pleistocene lynxes from several European sites (***Supplementary table 9***). We also collected morphological and biometric data on extant specimens of *L. pardinus* and *L. lynx*, as well as on fossil remains of *L. pardinus* from Cau d’en Borràs, Cau del Duc, Cova Toll, Cova Toixoneres, Cova de l’Arbreda, El Escarche, El Muscle, Turó del Moro (Spain), Monte Tignoso (Italy), and L’Escale (France); *L. issiodorensis* from Les Etouaires, Serrat d’en Vaquer, Saint Vallier (France),Olivola, Pantalla, Figline, Matassino, Poggio Rosso, and other Upper Valdarno localities (Italy), La Puebla de Valverde and Almanzora (Spain); *Lynx* sp. from Monte Argentario and Pirro Nord (Italy).

Biometric comparisons and statistical analysis were performed considering the length (L) and width (W) of the upper (P^4) and lower (M_1) carnassial. First, we used the Shapiro-Wilk test to check if the data were normally distributed. Given the negative results (P^4L, p-value < 0.01; M_1L, p-value < 0.01), non-parametric tests were preferred to evaluate differences in size between the Ingarano remains and the comparative sample. We carried out a Kruskall-Wallis test on each subsample for each variable, testing the null hypothesis that the samples originate from the same distribution. The alternative hypothesis is that they differ in at least one distribution. All statistical analyses were performed using the software R (***R Core Team, 2019***).

Body mass was estimated using the method by ***Van Valkenburgh (1990)***, who provided a series of predictive equations for several groups of carnivorans, based on different linear measurements. Among these, we tested the two equations for which we had more data available, namely the one based on the condylobasal length (CBL) and the one based on the length of the lower carnassial (M_1L), in their “Felidae only” version. By applying the two formulas to a control sample for which we had both linear measurements and body mass available (i.e., extant *L. pardinus* from Doñana, Spain; ***Beltrán and Delibes, 1993***), we verified that the CBL-based equation provided estimates very close to the actual average body mass (estimated body mass - females: 10.4 kg, males: 12.3 kg; actual body mass - females: 9.3 kg, males: 12.8 kg). The same equation was also tested on a sample of extant *L. lynx* from Croatia (***Gomerčić et al., 2010***) and we obtained a similar correspondence between estimated and actual values (estimated body mass - females: 17.0 kg, males: 21.0 kg; actual body mass - females: 18.4 kg, males: 21.9 kg). This confirmed ***Van Valkenburgh's (1990)*** claim that CBL is the most reliable proxy for estimating carnivoran body mass. Conversely, estimates based on M_1L resulted in body mass values 43 to 70% higher than actual average body mass for males and females, respectively.

The extraction of ancient DNA from Ingarano lynx specimens was attempted at the Archaeological Research Laboratory, University of Stockholm (Sweden), but it gave no results (***Supplementary note 4***).

4. Results

4.1. Description of the cranium and upper teeth

Ten cranial remains were recovered from Ingarano (***Supplementary note 1***), among which the specimens MGPT-PU 135415 and ING75 are the most complete (***Figures 2-3***). Measurements are reported in ***Table 1*** (see also ***Supplementary note 2-3, Supplementary figure 1*** and ***Supplementary tables 1-3***). Complete fusion of cranial sutures (where not obliterated by diagenesis) and eruption of permament dentition indicate that all remains belong to adult individuals.

Figure 2

In dorsal view, the studied specimens display laterally expanded frontals with well-developed triangular-shaped zygomatic processes, triangular nasals, and wide and semicircular zygomatic arches. The marked temporal ridges are lyre-shaped and converge posteriorly in a short sagittal crest, which in turn merges to a well-developed nuchal crest (***Figures 2-3***). In lateral view, the cranium is anteroposteriorly elongated with a rounded and domed dorsal profile. The orbits are large and rounded. The incisive line of the premaxillae is projected anteriorly, displaying a well-developed notch at the level of the I^3-C^1 diastema. In ventral view, the outline of the tympanic bullae appears elliptical and anteroposteriorly elongated. At the posteromedial corner of the tympanic bullae, the jugular and hypoglossal foramina are located into the same depression. In posterior view, the oval-shaped foramen magnum is slightly compressed dorsoventrally.

Figure 3

The upper teeth from Ingarano show a rather low overall morphological variation. The upper incisors are preserved in both the complete crania MGPT-PU 135415 and ING75; among them, the I^3 is the largest in size and it shows a marked cingulum. The C^1 is buccolingually compressed and smooth on the lingual side, whereas two longitudinal grooves are present on the buccal surface (***Figure 2***). The P^3 is buccolingually compressed, with a high and distally projected paracone, a small distal accessory cusp, and a marked distal cingulum. Four specimens (FG130, ING75, ING82, and ING86) possess an incipient mesiolingual accessory cusp, which is absent in the other remains. The P^4 shows a small protocone located mesiolingually. The parastyle is buccolingually compressed and mesiodistally shorter than the paracone and metastyle. The latter are well developed and separated by a deep grove, especially in the buccal side. Four remains, (FG101, FG130, ING82, and ING8) show a marked groove connecting the paracone and protocone. Only two remains (FG103 and ING76) exhibit a weak ectoparastyle. The three preserved M^1 (FG101, FG102, and ING75) are buccolingually expanded with two very small lingual and buccal cusps.

Table 1

4.2. Description of the mandible and lower teeth

Several complete or nearly complete hemimandibles as well as mandibular fragments, were discovered at Ingarano (***Figure 4***, ***Supplementary note 1***). Measurements are reported in ***Table 1*** (see also ***Supplementary table 4***). All remains belong to adult individuals.

Figure 4

The hemimandibles and lower teeth show a more marked variation in both size and shape than that observed for cranium and upper dentition remains. Indeed, a remarkable variation is observed for what concerns mandibular dimensions, number of the accessory cuspids, development of the cingula in the P_3 and P_4, and presence/absence of the metaconid in the M_1. Also, the mandibular mental foramina are variable in number and position. In particular, the majority of the specimens shows two mental foramina: one located posteriorly to the distal border of the C_1 and one ventral to the mid length of the P_3; several specimens possess a third foramen often placed at the level of the distal border of the P_3 (FG93, ING68, ING69, ING70, INGND318) or close to the distal border of the P_4 (INGND318, INGND868, INGND869). The anterior portion of the masseteric fossa generally reaches the level of the distal portion of the M_1 in lateral view, except for ING68, ING70, ING71, and ING72, in which it lies more posteriorly. The ventral border of the mandibular corpus is almost straight but anteriorly, in correspondence with the alveolus of the lower canine, it sharply bends dorsally. In medial view, the mandibular foramen opens near to the ventral border of the corpus and about halfway between the distal margin of the M_1 and the posterior end of the dentary. The ramus is high and inclined posterodorsally with an angle of ca. 45° with respect to the corpus long axis. The coronoid process is relatively long at its base and the angular process is also elongated and projects posteroventrally. In dorsal view, the mandibular condyle has a straight posterior border and is inclined in posterolateral direction.

No lower incisors are preserved. The C_1 is buccolingually compressed, smooth on the lingual side, and with a weak longitudinal groove on the buccal one. It is separated from the P_3 by a long diastema. The P_3 is buccolingually compressed and has a high and straight protoconid, a weak crest connecting the mesial cingulum to the protoconid, a weak distal accessory cuspid, and a marked distal cingulum; in addition, ten specimens (IN15NS, ING68, ING71, ING72, INGND144, INGND145, INGND312, INGND318, INGND373, and INGND870) show a small paraconid. The P_4 is also buccolingually narrow, with a high protoconid, which is however slightly projected distally. A paraconid, a distal accessory cuspid, and a distal cingulum are also recognizable in all specimens; in five specimens (ING63, ING68, ING69, INGND318, and INGND373) the distal cingulum is well developed and similar in size to the distal accessory cuspid, whereas in the other specimens (n=22) it is less prominent. The M_1 (***Figure 5***) has a protoconid that is similar in length, but higher than the paraconid. Generally, these cuspids are separated by a weakly marked incision, with the exception of ING61, ING63, ING68, ING72, INGND144, INGND319, INGND372, and INGND373, in which the incision is more pronounced. A distinct metaconid separated from the protoconid blade (***Boscaini et al., 2016***: Fig. 5A), is never observed in the Ingarano sample (n=27); a weak metaconid adjacent to the protoconid blade (***Boscaini et al., 2016***: Fig. 5B) is observed in FG107, FG108, ING70, ING73, ING79, INGND373, INGND868, and INGND869, whereas a small cuspulid-like enamel inflection (***Boscaini et al., 2016***: Fig. 5C) is observed in IN15NS, ING67, ING71, ING72, INGND145, and INGND319. However, the majority of the specimens (ING61, ING62, ING63, ING68, ING69, ING74, INGND144, INGND312, INGND369, INGND372, INGND867, INGND870, and MGPUTV135415) shows a completely smooth distal margin of the protoconid blade (***Boscaini et al., 2016***: Fig. 5D).

Figure 5

4.3. Morphological comparisons

The crania from Ingarano display: (i) a short sagittal crest, (ii) long, well-separated, and lyre-shaped temporal ridges, and (iii) the confluence in the same cavity of the jugular and hypoglossal foramina, situated just behind the posteromedial border of the tympanic bulla. All these characters fit the morphology of extant and fossil *L. pardinus* (***Boule, 1919***; ***Boule and Villeneuve, 1927***; ***García-Perea et al., 1985***; ***García-Perea, 1996***; ***Boscaini et al., 2015***; ***Figure 6***). Conversely, this morphology contrasts with Early Pleistocene *L. issiodorensis* (***Viret, 1954***; ***Kurtén, 1978***; ***Cipullo, 2010***; ***Cherin et al., 2013***) (no Pliocene neurocrania of this species are available) and with extant and fossil *L. lynx* (***García-Perea et al., 1985***; ***García-Perea, 1996***; ***Cassoli and Tagliacozzo, 1994b***; ***Boscaini et al., 2015***), which are characterized by a longer and more marked sagittal crest and shorter temporal ridges. The jugular and hypoglossal foramina are separated by a septum in *L. lynx* (***Cassoli and Tagliacozzo, 1994b***; ***Larivière and Walton, 1997***; ***Boscaini et al., 2015***), whereas the condition observed in *L. issiodorensis* from Olivola and Pantalla (***Figure 6***) is similar to that of *L. pardinus* (i.e., confluent foramina). Unfortunately, it is not possible to evaluate this character in the other analyzed specimens of *L. issiodorensis* (Les Etouaires and Saint Vallier) due to preservation reasons (***Supplementary figure 2***).

As for the upper teeth, the P^4 of the Ingarano sample never shows a distinct ectoparastyle. According to **Kurtén (1978)** the ectoparastyle is generally present in *L. issiodorensis* and *L. lynx*.

Figure 6

Concerning lower dentition, a detached distal cingulum is visible in all P_3 (n=23) from Ingarano. Conversely, only 5 out of 27 specimens show a P_4 distal cingulum. A prominent P_4 distal cingulum was considered as characteristic for *'L. spelaeus'* from Middle Pleistocene French sites such as L'Escale, Lunel Viel, and Aragó Cave (**Bonifay, 1971**; **Testu, 2006**). However, the same authors recognized a certain variation in this character's development, which should be considered of little taxonomic value (**Boscaini et al., 2016**).

In the Ingarano sample, a distinct M_1 metaconid is absent in 19 out of 27 specimens (70.4%), whereas a weak metaconid adjacent to the protoconid blade is visible in the remaining M_1 (29.6%). A detached M_1 metaconid is observable in extant and fossil *L. lynx* (**Kurtén, 1963**; **Werdelin, 1987**), whereas it is totally absent or barely developed in extant *L. pardinus* (respectively, 83% and 14% of the 54 pardel lynx skulls analyzed by **García-Perea et al., 1985**). In fossil remains of *L. pardinus* from southwestern Europe, the M_1 metaconid shows a progressive trend of reduction from the late Early Pleistocene up to the extremely low percentages of presence observed in extant populations (**Bonifay, 1971**; **García-Perea et al., 1985**; **Testu, 2006**; **Boscaini et al., 2016**). In *L. issiodorensis*, the development of a well-defined M_1 metaconid shows an almost inverse chronological trend. This cuspid is absent in Ruscinian and Early Villafranchian forms, starts to occur in Middle Villafranchian forms, and is common in Late Villafranchian and Epivillafranchian forms (**Kurtén, 1963**; **Boscaini et al., 2016**; **Supplementary table 5**).

In sum, the morphology of craniodental remains from Ingarano more closely resembles *L. pardinus s.l.* than *L. lynx* and *L. issiodorensis*. In particular, the short sagittal crest, the lyre-shaped temporal ridges, the absence of P^4 ectoparastyle, and the absence of a distinct M_1 metaconid are characters clearly related to the pardel lynx. At the same time, particularly noteworthy is the fact that the Ingarano crania share with both *L. pardinus* and *L. issiodorensis* the anatomy of the jugular and hypoglossal foramina, which open in the same depression. This character is here described in *L. issiodorensis* for the first time.

4.4. Biometric comparisons

Comparative cranial measurements of European extant and fossil lynxes are reported in ***Supplementary table 6***. Extant *L. lynx* and *L. pardinus* are well distinguishable according to cranium size, with the first showing a total length normally exceeding 140 mm and the second rarely reaching this value in the available comparative samples. Late Pleistocene specimens of *L. lynx* are on average similar in size to *L. issiodorensis*, that is to say very large overall. However, when considering fossil remains of *L. pardinus* from the Pleistocene of southwestern Europe, the scenario becomes more complicated due to general overlapping in cranium size (***Supplementary table 6***). Indeed, most of the available fossils of *L. pardinus* show cranial dimensions closer to those of the Eurasian lynx. In particular, the two crania from Ingarano, MGPT-PU 135415 and especially ING75, are amongst the largest individuals in our comparative sample, with total lengths exceeding the average values of each sub-samples. On the contrary, the crania from Grotta del Principe and Grotte de l'Observatoire occupy an intermediate position, falling between the ranges of extant *L. lynx* and *L. pardinus* (***Supplementary table 6***). The same reasoning applies to the zygomatic width, although for this measurement the degree of dimensional overlapping between extant populations is much higher, thus preventing reliable taxonomic distinctions. Conversely, the length of the sagittal crest, which in turn reflects the development of temporal ridges, is of high taxonomic importance being significantly higher in *L. lynx* and *L. issiodorensis*, than in *L. pardinus*. The length of the sagittal crest of the specimens from Ingarano are close to the average length of the extant *L. pardinus* and to the few available lengths of fossil *L. pardinus* (***Supplementary table 6***).

Due to the relative scarcity of lynx well-preserved cranial findings in Europe, many of the comparative analyses conducted so far are based on measurements of teeth (e.g., ***Bonifay, 1971***; ***Ficcarelli and Torre, 1977***; ***Werdelin, 1981***; ***Testu, 2006***; ***Cipullo, 2010***; ***Ghezzo et al., 2015***), among which the P^4 and M_1 seem to be the most informative (***Supplementary figure 3)***. The length of the P^4 from Ingarano is undistinguishable from that of fossil *L. pardinus* (p.value > 0.01), smaller than those of *L. issioderensis* and *L. lynx* (p.value < 0.01), and larger than that of extant *L. pardinus* (p.value < 0.01). The range of the M_1 length of the Ingarano sample is very close to those of fossil *L. pardinus* and *L. issiodorensis* (p.value > 0.01), falling between the ranges of extant *L. pardinus* and *L. lynx* (***Supplementary table 7***).

To sum up, based on morphometric comparisons, the sample from Ingarano shows remarkably large cranial dimensions. On the contrary, dental measurements are more in line with the pardel lynx, and lower than those of *L. issiodorensis* and *L. lynx*.

5. Discussion

5.1. Taxonomy

The large lynx sample from Ingarano shows a distinctive craniodental morphology including: short sagittal crest, long and lyre-shaped temporal ridges, confluence of the hypoglossal and jugular foramina into the same cavity, absence of ectoparastyle in the P^4, and absence of a distinct metaconid in the M_1. These features are typical of *L. pardinus s.l.* (***Boule, 1919***; ***Boule and Villeneuve, 1927***; ***Van den Brink, 1971***; ***García-Perea et al., 1985***; ***García-Perea, 1996***; ***Larivière and Walton, 1997***; ***Boscaini et al., 2015, 2016***), and allow an unambiguous attribution of the studied craniodental material to this species. Opposite craniodental characters (i.e., long sagittal crest, separated hypoglossal and jugular foramina, presence of P^4 ectoparastyle, and presence of M_1 metaconid) are characteristics of *L. lynx* (***Kurtén, 1963***; ***García-Perea et al., 1985***; ***Tumlison, 1987***; ***Boscaini et al., 2015, 2016***). The more reliable criteria to separate *L. pardinus* from *L. issiodorensis* are currently represented by the P^4 length and the development of the sagittal crest and the consequent pattern of the temporal ridges (although the distance between the temporal ridges is subject to inter-individual variation in the extant pardel lynx being usually wider in juveniles and females, the general lyre-shaped pattern is very consistent in the species; ***García-Perea et al., 1985***). Moreover, *L. pardinus* and *L. issiodorensis* share the confluence of the hypoglossal and jugular foramina (***Figure 7***). Considering *L. issiodorensis* as the putative ancestor of *L. pardinus* (***Werdelin, 1981***), this can therefore be interpreted as a plesiomorphic character. This hypothesis is also supported by the fact that confluent foramina are also found in the bobcat *Lynx rufus* (***Larivière and Walton, 1997***), which is commonly considered the sister taxon to all the other extant lynxes (***Werdelin, 1981***; ***Bininda-Emonds et al., 1999***; ***Johnson et al., 2004, 2006***). On the contrary, the Canadian lynx *Lynx canadensis* shares with *L. lynx* the presence of a clear septum separating the two foramina (***Lavoie et al., 2019***). However, the phylogenetic relationships of *L. canadensis* are not clear, as it is considered as the sister taxon of *L. lynx* by some authors (***Werdelin, 1981***; ***Bininda-Emonds et al., 1999***), or as the sister taxon of the clade formed by *L. lynx* and *L. pardinus* by others (***Johnson et al., 2004, 2006***).

Figure 7

The occurrence of *L. pardinus* in the Late Pleistocene (MIS 3) of Ingarano offers some key cues for elucidating the natural history of this species in Europe. The taxonomic status of the pardel lynx has long been a subject of debate, until molecular studies (***Beltrán et al., 1996***) confirmed *L. pardinus* as a valid species. On the other hand, the so-called 'cave lynx' *L. spelaeus* (or *L. p. spelaeus*) from the Middle-Late Pleistocene of southwestern Europe, has been recently considered a junior synonym of *L. pardinus* (***Boscaini et al., 2016***). The latter authors illustrated how the morphological characters generally used to separate the two species are inconsistent. This is also supported by the results of molecular analyses (***Rodríguez-Varela et al. 2015***), according to which Late Pleistocene remains of "*L.* cf. *spelaeus*" from northwestern Italy were re-assigned to *L. pardinus* based on haplotype similarity. Conversely, many authors (***Werdelin, 1981***; ***Kurtén and Granqvist, 1987***; ***García-Perea, 1997***; ***Palombo et al., 2008***; ***Garrido and Arribas, 2008***; ***Rodríguez-Hidalgo et al., 2020***) in the last decades preferred to maintain a subspecific distinction (i.e., *L. p. spelaeus*) for Middle-Late Pleistocene pardel lynxes from southwestern Europe, following in some way the pioneering initial denomination (i.e., "*Felis* (*Lynx*) *pardinus* race *spelaea*") by ***Boule (1919)***. This taxonomic view is largely based on the allegedly larger dimensions of the fossil forms compared to the extant ones. In particular, according to the comprehensive study by ***Werdelin (1981)***, the sequence of chronosubspecies formed by *L. i. issiodorensis* (early-middle Villafranchian) - *L. i. valdarnensis* (late Villafranchian) - *L. p. spelaeus* (Middle-Late Pleistocene) - *L. p. pardinus* (recent), would represent a phylogenetic lineage, characterized by a progressive reduction in body size and an increase of relative length of M_1. However, the fossil record of European lynxes documented between ca. 1.6 and 0.6 Ma, which should include the *L. issiodorensis* - *L. pardinus* split, is mostly represented by isolated teeth and mandibles of unclear diagnostic value. Two remarkable exceptions at the limits of this range, that is, the neurocranium from the Avenc Marcel (1.7–1.6 Ma; ***Boscaini et al., 2015***) and the two crania from L'Escale (ca. 0.6 Ma; ***Bonifay, 1971***), are reliably referable to *L. pardinus.* The lack of cranial remains for more than 1 Ma has forced research over the past fifty years to focus on dental morphology, but despite many efforts, only some tooth measurements and the presence/absence of the P^4 ectoparastyle and the M_1 metaconid have been suggested as possible diagnostic traits (e.g., ***Bonifay, 1971***; ***Ficcarelli and Torre, 1977***; ***Werdelin, 1981***; ***Testu, 2006***; ***Cipullo, 2010***; ***Ghezzo et al., 2015***). However, the latter features show a marked interindividual variation when observable in large samples (***Boscaini et al., 2016***). The fossils from Ingarano represents an excellent example, given that, based only on the frequency of the aforementioned dental characters, it could equally be attributed to *L. pardinus* or *L. issiodorensis* (***Figure 7***; ***Supplementary table 5***). This confirms the inconsistency of tooth morphology, especially if considered alone and on small fossil samples, for taxonomic attributions of European Plio-Pleistocene lynx remains. Therefore, unless samples are large enough to evaluate the frequency of the aforementioned dental characters (e.g., Epivillafranchian *L. pardinus* from Vallparadís Estació and Cueva Victoria; ***Boscaini et al., 2016***), we suggest the use of the open nomenclature *Lynx* sp. for all European remains approximately comprised in the interval from 1.6 to 0.6 Ma, previously referred to *L. issiodorensis* or to 'cave lynx'. These include the records from Pirro Nord (Italy; ***Petrucci et al., 2013***), Monte Argentario (Italy; ***Cherin et al., 2018***), Valdemino (Italy; ***Ghezzo et al., 2015***), La Sartanette (France; ***Palombo and Valli, 2004***), Sainzelles (France; ***Palombo and Valli, 2004***), Le Vallonnet (France; ***Moullé et al., 2006***), Solehilac (France; ***Kurtén, 1957***), Sierra de Quibas (Spain; ***Montoya et al., 1999, 2001b***), Venta Micena (Spain; ***Moyà-Solà et al., 1981; Boscaini et al., 2016***), Untermassfeld (Germany; ***Hemmer, 2001***), Mauer (Germany; ***Voelcker, 1930***), Mosbach (Germany; ***Voelcker, 1930***), and Apollonia 1 (Greece; ***Koufos, 1992; Koufos and Kostopoulos, 1997***). Details are reported in ***Supplementary table 5***.

Additional information is provided by biometric analyses of upper and lower carnassials (***Figure 7***; ***Supplementary tables 3, 4, 6***). The lengths of the P^4 and M_1 show similar decreasing trends from Villafranchian *L. issiodorensis* (before 1.7 Ma) to later forms, that is, *Lynx* sp. (1.6–0.6 Ma) and *L. pardinus s.l.* (including the Ingarano sample; ***Supplementary figure 3***). This would support the hypothesis that dentognathic remains of *Lynx* sp. in the 1.6–0.6 Ma interval (see above) may be related to *L. pardinus*, but the absence of sufficiently complete crania encourages a cautious approach. The carnassials of the extant pardel lynx are usually smaller, whereas those of the Eurasian lynx are considerably larger, reaching and sometimes exceeding the size of some *L. issiodorensis* specimens (***Supplementary figure 3***). This trend indicates that the M_1 has undergone a slight decrease in length in the *L. issiodorensis* - *L. pardinus* lineage, rather than an increase as proposed by ***Werdelin (1981)***. Moreover, the larger size of the P^4 observed in *L. issiodorensis* does not seem to correspond to a relatively elongated cranium in this species, which is similar in length to specimens MGPT-PU 135415 and ING75 from Ingarano and to that of extant *L. lynx* (***Supplementary tables 1, 3, 6, 7***). This is also supported by our results on body mass estimates (see below), which evidence a substantial uniformity among European Pleistocene lynxes (***Supplementary table 8***).

In sum, in light of our results, we suggest a more parsimonious and simplified taxonomy for European fossil lynxes (***Supplementary table 9***). *Lynx issiodorensis* occurs in the interval between the Ruscinian and early late Villafranchian. The validity of the two subspecies *L. i. issiodorensis* and *L. i. valdarnensis*, which are only differentiated based on tooth dimensions (***Werdelin, 1981***), is questionable based on our data. In the early late Villafranchian (ca. 1.7–1.6 Ma), *L. pardinus* appears in western Mediterranean Europe (Avenc Mancel). The possible co-existence between *L. issiodorensis* and *L. pardinus* cannot be verified on the basis of available data. During the following period (i.e., latest Villafranchian to earliest Middle Pleistocene), with few exceptions (i.e., *L. pardinus* from

Vallparadís Estació and Cueva Victoria), an undeterminable form (*Lynx* sp.) probably related to *L. pardinus*, is found in Europe. The occurrence of *L. pardinus s.l.*, at least in southwestern Europe, is attested from the early Middle Pleistocene onwards.

5.2. Size variation in European fossil lynxes

The Ingarano sample, with its well-preserved cranial remains, allows to better explore the evolution of body size in European fossil lynxes, using condylobasal lengths as a proxy to estimate body mass following ***Van Valkenburgh (1990)*** (see Materials and methods). Of course, it is worth remembering that since the estimates are based on individual fossil specimens from different geographical and chronological contexts, our results do not presume to provide precise data, but only to reconstruct possible overall trends in the evolution of body size (and to compare these trends with what is suggested in the literature for fossil lynxes; see below). This is in agreement with the purpose with which the considered prediction equations were originally proposed (***Van Valkenburgh, 1990***).

Having ascertained that the Ingarano individuals are all adults as shown by the fully erupted permanent dentition and fusion of the cranial sutures (see Description), an aspect worth mentioning before discussing the data on body mass is sexual dimorphism. It has been proposed that sexual dimorphism may explain intraspecific differences in body size in some European Plio-Pleistocene felids (e.g., *Acinonyx pardinensis*, *Panthera gombaszoegensis;* ***Petrucci et al., 2013; Cherin et al., 2018***). However, as in extant taxa (***Macdonald et al., 2010***), the effect of sex on size is more pronounced in large felid species. As for extant *L. pardinus*, differences in cranial measurements between adult males and females are relatively low (e.g., mean condylobasal length is about 5% larger in males) and are reflected in a weight difference of about 27% between sexes (***Beltran and Delibes, 1993***). Similar if not smaller differences are found in extant *L. lynx* (e.g., mean condylobasal length about 6% larger in males, weight difference of about 16% between sexes; ***Wiig and Andersen, 1986; Červený and Koubek, 2000; Gomerčič et al., 2010***). In addition to these low average differences, the majority of cranial measurements show largely overlapping ranges of variation between males and females in both extant species, so much so that, at least for *L. pardinus*, distinguishing the sex of an individual on craniometric grounds is not reliable (***Beltran and Delibes, 1993***). Finally, ***Van Valkenburgh's (1990)*** prediction equation used in this paper, although originally obtained by regression starting from a mixed sample of males and females, does not allow for sex-differentiated estimates. For all these reasons, sexual dimorphism cannot be taken into consideration either for a priori sex separation of our samples on a biometric basis, or to speculate on the possible causes of differences in estimated body masses.

Figure 8 shows the estimates obtained from the Ingarano sample and other well-preserved crania available in the European Plio-Pleistocene fossil record. As for *L. issiodorensis*, what first stands out is the remarkable body mass (almost 35 kg) estimated for individual MNB Prr 200 from Les Etouaires (France; latest Pliocene, ca. 2.8 Ma; dating from ***Nomade et al., 2014***). Although the cranium is slightly crushed dorsoventrally (***Supplementary figure 2***), length measurements should be considered as reliable (***Kurtén, 1978***). This weight value is at least 10 kg higher than the maximum reached by males of the extant Eurasian lynx (***Heptner and Sludskii, 1992***; ***Gomerčić et al., 2010***), and is more similar to those recorded for larger felids (e.g., maximum body mass of female puma; ***Macdonald et al., 2010***). However, rare reports of extremely large individuals of *L. lynx* are present in the literature (32 kg in ***Ognev, 1935***; 38 kg in ***Kazlauskas and Matuzevicius, 1970***). On the other hand, the second individual from Les Etouaires (MNB Prr 411) for which it was possible to estimate the body mass (21.8 kg), is significantly smaller and very similar to MNB Ol 1 from Olivola (Early Pleistocene, ca. 2.1 Ma; dating from ***Napoleone et al., 2003***). It is worth mentioning that ***Werdelin (1981)*** referred some specimens from Olivola to *L. i. valdarnensis*, considered to be smaller than *L. i.*

issiodorensis (which includes the Les Etouaires material, among others) on the basis of dental measurements. The cranium SABAP_UMB 337653 from Pantalla (2.1–1.9 Ma; dating from **Cherin et al., 2019**) referred to *L. i. valdarnensis* based on morphological and biometric similarity with the samples from Olivola and Upper Valdarno (**Cherin et al., 2013**), retrieved a slightly lower body mass (19.7 kg). However, the individual DE 04 Liv II from Pirro Nord (1.6–1.3 Ma; **Arzarello et al., 2007**; **Lopez-García et al., 2015**), tentatively referred to *L. issiodorensis* (**Petrucci et al., 2013**) but here re-assigned to *Lynx* sp. due to the lack of clear craniodental characters, resulted as significantly larger (25.4 kg). In sum, with the exception of the extremely large-sized MNB Prr 200 from Les Etouaires, all other specimens of *L. issiodorensis* show estimated body masses falling in the upper part of the range of *L. lynx* (**Heptner and Sludskii, 1992**; **Gomerčić et al., 2010**). Similar values (19.3–22.9 kg) were also calculated for some Late Pleistocene individuals of the latter species (***Supplementary table 8***). This is in agreement with the reconstruction of the life appearance of *L. issiodorensis* by **Kurtén (1978)**, according to which this extinct felid would have been quite similar to the extant *L. lynx*, but with a relatively larger skull, slightly longer body (ca. 4%), and shorter limbs.

Figure 8

Body mass data on *L. pardinus s.l.* are noteworthy for the purposes of this study. The estimates for the two better preserved crania from the early Middle Pleistocene of L'Escale (France; **Bonifay, 1971**) are higher than those from the late Middle(?)-Late Pleistocene of Grotte de l'Observatoire (Monaco; **Boule and Villeneuve, 1927**) and Late Pleistocene of Grotta del Principe (Italy; **Boule, 1919**). These results alone, although based on a limited number of crania, seem to disprove the statement that the Middle-Late Pleistocene 'cave lynx' underwent a further progressive reduction in size along the evolutionary lineage that led to the pardel lynx (**Werdelin, 1981**). In addition to this, the two complete crania from Ingarano (MGPT-PU 135415 and ING75) resulted in remarkably high body mass estimates (23.7 and 25 kg, respectively). The relatively recent (ca. 40 ka) Ingarano individuals are therefore the largest ever reported for *L. pardinus s.l.*

Kurtén and Granqvist (**1987**: 42) defined the Middle-Late Pleistocene *L. pardinus* as "plastic in size". These geographical and chronological body mass variations indicate that this species has not actually experienced a progressive reduction in size, thus supporting the inconsistency of the fossil (chrono)subspecies *L. p. spelaeus,* as proposed by **Boscaini et al.** (**2016**) on morphological grounds.

Once recognized the body mass variation in the fossil record of *L. pardinus*, it remains to be clarified how this relates with the populations living today in southwestern Spain. The average body mass of the extant pardel lynx ranges between ca. 9 kg (females) and 13 kg (males; **Beltrán and Delibes, 1993**). These values are much closer to those of Nearctic species, that is, *L. rufus* (ca. 7/10 kg in females/males; **Banfield, 1987**) and *L. canadensis* (ca. 9/11 kg in females/males; **Sunquist and Sunquist, 2002**), than to those of *L. lynx* (ca. 17/20 kg in females/males; **Heptner and Sludskii, 1992**). However, according to studies on conservation (**Simón, 2012**, and references therein) and molecular biology (**Johnson et al., 2004**), *L. pardinus* suffered a recent strong demographic contraction (which however would not appear to be associated with a substantial reduction in genetic variation, at least in the last 50 ka; **Rodríguez et al. [2011]**). The dramatic historical decline of pardel lynx populations prevents us to consider the few survivors as a reliable representation of the species' dimensional variation at the geological time scale. At the state of the art, we can only point out that the body mass estimates obtained for some fossil individuals, namely those from Grotte de l'Observatoire and Grotta del Principe (**Figure 8**), are close to the maximum values recorded for extant males from southern Spain (ca. 14.5 kg; **Beltrán and Delibes, 1993**).

5.3. Paleoecology

Whether the body size variations observed in European fossil lynxes are related to paleoclimatic factors, such as glacial/interglacial dynamics and/or latitude-driven factors, is still unclear. Actually, the majority of the lynx remains from Ingarano (including the aforementioned crania) come from the lower part of the stratigraphic succession (***Petronio and Sardella, 1998***), which is correlated to a cold phase during MIS 3 (***Bedetti and Pavia, 2007***). However, recent works conducted on other large mammal taxa from the same region, suggest a cautious approach in recognizing correlations between Middle-Late Pleistocene climatic fluctuations and body size in such a peripheral Mediterranean area (cf. ***Sardella et al. [2014]*** for *Canis lupus* and ***Iannucci et al. [2020]*** for *Sus scrofa*).

The extant pardel lynx also shares with North American lynx species some ecological adaptations, among which the feeding preference upon lagomorphs. The European rabbit *Oryctolagus cuniculus* and the snowshoe hare *Lepus americanus* account respectively for 80–99% (***Ferreras et al., 2010***) and 60–97% (***Sunquist and Sunquist, 2002***) of the diet of *L. pardinus* and *L. canadensis*, and also *L. rufus* preys primarily on lagomorphs (***Sunquist and Sunquist, 2002***). These diet preferences strongly influence the pardel lynx's habitat selection, as the species is only found today in Mediterranean shrublands with scrub-pasture ecotones and dense rabbit populations (***Palomares et al., 2000***; ***Palomares, 2001***). Unfortunately, the available data do not allow obtaining clear information on the paleoecology of Pleistocene *L. pardinus*. Some anatomical features such as the very short sagittal crest and slender dentition, were interpreted as indicators of a diet based on small prey, throughout the history of *L. pardinus s.l.* (***Werdelin, 1981***; ***García-Perea, 1996***; ***Boscaini et al., 2015***). Some data even seem to suggest a close correlation between the evolution of the pardel lynx and that of the European rabbit (***Kurtén, 1968***), whose geographical distributions followed the same contraction dynamics according to Pleistocene glacial-interglacial oscillations (***Lopez-Martinez, 2008***; ***Ferreras et al., 2010***). Moreover, recent taphonomic analysis carried out on Late Pleistocene (MIS 3) fossils from Cova del Gegant (Spain) pointed out a biogenic origin of the paleontological accumulation of layer IIIa, characterized by the very abundant occurrence of lynx and rabbit remains and interpreted as a *L. pardinus* den (***Rodríguez-Hidalgo et al., 2020***). However, we cannot currently confirm if the pardel lynx has always been a specialized rabbit hunter, or if it also relied on larger prey in the past, as the large body mass that we estimated for some fossil individuals would seem to suggest.

Similarly, we do not have a clear picture of the habitat preferences of extinct populations of *L. pardinus*, due to the lack of paleoecological information on the sites from which it has been reported. The few available data on Ingarano comes from the analysis of the fossil bird assemblage, which suggests a paleoenvironment dominated by open areas, with secondary presence of wetlands and woods (***Bedetti and Pavia, 2007***). This reconstruction only partially fits the aforementioned restricted Mediterranean habitat of the extant pardel lynx. Based solely on the geological contexts in which fossil remains of *L. pardinus* have been found, largely represented by caves and other karst cavities, we can speculate that the species has always maintained the need to occupy areas with the presence of natural cavities, used as natal dens (***Fernández et al., 2002, 2006***; ***Rodríguez-Hidalgo et al., 2020***). In general, also taking into account the much wider geographical distribution, it is reasonable to think that, at least outside the Iberian Peninsula, the species had more diversified food and habitat preferences in the Pleistocene than today.

5.4. Paleobiogeography

According to the available data, the first appearance of *L. pardinus* in Europe is rooted in the Early Pleistocene. The record from Avenc Mancel (1.7–1.6 Ma; ***Boscaini et***

al., 2015) suggests that the origin of this species may be part of the important faunal turnover occurred at the Gelasian-Calabrian boundary (***Sardella et al., 2018***). The glacial pulse recorded around 1.8 Ma (MIS 64-62) could have played a key role in the separation of populations of *L. issiodorensis*, triggering the speciation of *L. pardinus* (***Boscaini et al., 2015***). Unfortunately, as stated above, the characters useful for a reliable attribution of fossils to *L. issiodorensis* or *L. pardinus* are only found in well-preserved cranial remains, whereas dental morphology can be considered only if analyzed in large samples. For these reasons, most European records from the latest Villafranchian-Epivillafranchian should be prudentially referred to *Lynx* sp. (***Figure 9*****;** **Supplementary tables 5, 9**). Due to this uncertainty, it is currently hard to evaluate the impact on lynx evolution of another crucial turnover, that is, the Early-Middle Pleistocene Transition (EMPT), also known as the “Mid-Pleistocene Revolution” (ca. 1.2–0.4 Ma; ***Head and Gibbard, 2005***). During this interval, global-scale climatic changes strongly affected the faunal and floral composition of European ecosystems also in Mediterranean areas (***Kahlke et al., 2011***; ***Magri and Palombo, 2013***; ***Strani et al., 2019***; ***Cherin et al., 2020***), although in a more mitigated way if compared to higher latitudes (***Head and Gibbard, 2015***). However, starting from ca. 0.6 Ma, i.e, from the L'Escale record (***Bonifay, 1971***), *L. pardinus s.l.* is undoubtedly recognized in southwestern Europe (Iberian Peninsula, southern France, and Italy; ***Figure 9***). If new discoveries from Untermassfeld (Germany, ca. 1.0 Ma) confirm the presence of *L. issiodorensis* at the site (***Hemmer, 2001***), an interesting latitudinal separation between the last representatives of this species in central Europe and *L. pardinus* in Mediterranean areas during the EMPT would be expected.

To date, the outstanding sample from Ingarano represents the southernmost record of the species in Italy and the easternmost in Europe (***Figure 9***). The lynx fossil record along the eastern coast of the Adriatic Sea is still fragmentary. Middle-Late Pleistocene lynx remains were reported from several caves in Slovenia and Croatia (***Miracle, 1991,***

1995), but nevertheless these historical reports of *L. pardinus* (e.g., Veternica cave) were recently denied (***Miracle et al., 2010***). Although these coastal areas presumably showed paleoecological conditions favorable to the presence of the pardel lynx, new discoveries and a reappraisal of preexisting collections are needed to confirm the possible occurrence of the species.

Figure 9

One of the main issues affecting the reconstruction of the paleobiogeographical history of *L. pardinus* in Europe is the co-occurrence with *L. lynx*. This species spreads in Europe at the beginning of the Late Pleistocene (MIS 5e) and it is recorded together with *L. pardinus* in some Mediterranean localities, e.g., Grotte de l'Observatoire layers A-F (***Boule and Villeneuve, 1927***), Grotte de Cotencher (***Dubois and Stehlin, 1933***), and Arene Candide cave (***Rodríguez-Varela et al., 2015***). However, the size-based classifications performed in the past have probably contributed to overestimate the presence of *L. lynx* in the Late Pleistocene of southern Europe, as it is the case for Ingarano. Molecular data indicate that the Eurasian lynx was spread in the Mediterranean area during the Last Glacial Period (MIS 2) (e.g., Grotta della Madonna, Arene Candide, and Rascaño; ***Rodríguez-Varela et al., 2015, 2016***) (***Supplementary table 8***). Moreover, *L. lynx* is mainly documented from isolated postcranial remains until the Last Glacial stage, and only a few exceptionally preserved crania were found (e.g., the layers A-F of Grotte de l'Observatoire, ***Boule and Villenueve, 1927***; Col d'Aran, ***de Beaufort, 1965***; Rèseau de Cèbèri, ***Clot & Besson, 1974***; Arene Candide, ***Cassoli and Tagliacozzo, 1994a***). Similarly to what recognized from 1.7 Ma to 0.6 Ma, the early Late Pleistocene (MIS 5 to MIS 3) is characterized by the lack of cranial remains clearly ascribable to *L. lynx*, therefore, the earliest occurrence of this species during the MIS 5e cannot be confirmed.

The high ecological plasticity of the Eurasian lynx probably favored the replacement of *L. pardinus* in most the continent, with the exception of the Iberian Peninsula (***Rodríguez-Varela et al., 2015***), which probably acted as a refugium for the latter species. As a matter of fact, *L. lynx* is reported from the latest Pleistocene until historical times in northern Spain (***Ferreras et al., 2010***; ***Clavero and Delibes, 2013***; ***Rodríguez-Varela et al., 2016***). Nevertheless, several authors reported the presence of *L. pardinus* in French Bronze Age deposits (***Gagniere, 1926; Vigne, 1996; Vigne and Pascal, 2003***) thus suggesting that the contraction of its geographical range has occurred in recent times, and was probably further driven by human pressure. A similar decline has been documented for the Eurasian lynx in the Italian Peninsula, where human impact led to the complete eradication of Apennine populations in 1850 and Alpine ones in 1920 (***Bologna and Mingozzi, 2003***).

The unreliability of size-based criteria for the taxonomic recognition of European fossil lynxes confirmed in this work opens many questions on the paleobiogeography of *L. pardinus* and *L. lynx*, especially in the Late Pleistocene. Some answers may come in the future from genetic analyses, which have proved useful in differentiating the two species (***Rodríguez-Varela et al., 2015, 2016***), as well as from the discovery of sufficiently complete cranial material, such as those from Ingarano (***Figure 10***).

Figure 10

Acknowledgments

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Additional files

Supplementary information

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Figure captions

Figure 1. Location of the paleontological site of Ingarano (Foggia, Italy).

Figure 2. Crania of *Lynx pardinus* from Ingarano (Italy). MGPT-PU 135415 (A1-A3), ING75 (B1-B3), ING76 (C1-C3), M693 (D1-D3). Crania figured in dorsal (1), ventral (2) and lateral (3) views. Scale bar 3 cm.

Figure 3. 3D model of the complete skull of *Lynx pardinus* MGPT-PU 135415 from Ingarano (Italy), in anterior (A), posterior (B), right lateral (C) and left lateral (D) views.

Figure 4. Hemimandibles of *Lynx pardinus* from Ingarano (Italy). Hemimandibles associated with the cranium MGPT-PU 135415 (A1-A4) figured in labial (1, 3) and buccal

(2, 4) views. Right hemimandibles: ING68 (B1-B2), ING69 (C1-C2), INGND870 (D1-D2), IN15NS (E1-E2), INGND869 (F1-F2), ING72 (G1-G2), ING73 (H1-H2). Left hemimandibles: INGND312 (I1-I2), ING61 (J1-J2), INGND868 (K1-K2), INGND455 (L1-L2), INGND144 (M1-M2). Hemimandibles figured in lingual (1) and buccal (2) views. Scale bar 3 cm.

Figure 5. First lower molars (M_1) of *Lynx pardinus* from Ingarano (Italy). Right M_1: ING68 (A1-A2), ING69 (B1-B2), INGND870 (C1-C2), IN15NS (D1-D2), INGND869 (E1-E2), ING72 (F1-F2), ING73 (G1-G2), MGPUTV35415 (H1-H2), ING63 (I1-I2), ING70 (J1-J2), ING79 (K1-K2), INGND369 (L1-L2), INGND372 (M1-M2), INGNDF318 (N1-N2). Left M_1: INGND312 (O1-O2), ING61 (P1-P2), INGND868 (Q1-Q2); INGND319 (R1-R2), INGND867 (S1-S2), INGND145 (T1-T2), ING62 (U1-U2), INGND144 (V1-V2), INGND373 (W1-W2), ING71 (X1-X2), FG107 (Y1-Y2), MGPT-PU V35415 (Z1-Z2), FG109 (AA1-AA2). Teeth figured in lingual (1) and buccal (2) views. Scale bar 1 cm.

Figure 6. Comparative cranial morphology of *Lynx pardinus* from Ingarano (MGPT-PU 135415, A1-A3; ING75, B1-B3; M693, C1-C2); *L. pardinus* from Grotta del Principe (D1-D2); *L. pardinus* from Grotte de l'Observatoire (E1-E3); extant *L. pardinus* MNB 8865 (F1-F3); extant *Lynx lynx* MC 85 (G1-G3); *Lynx issiodorensis* SABAP_UMB 337653 from Pantalla (H1-H3); *L. issiodorensis* MNB OI 1 from Olivola (I1-I3). The white arrows indicate the temporal ridges, the black arrows indicate the sagittal crest, and the zoom-boxes show the arrangement of the jugular and hypoglossal foramina. The crania are normalized.

Figure 7. Schematic representation of the diagnostic characters of *Lynx issiodorensis*, extant *Lynx lynx*, *Lynx pardinus* from Ingarano (as a representative of fossil *L. pardinus*), and extant *L. pardinus*. A, Length of carnassial teeth; B, Frequency of diagnostic characters of carnassial teeth in the analyzed samples; C, Shape of the temporal ridges and sagittal crest; D, Average body mass; E, Arrangement of the jugular and hypoglossal foramina.

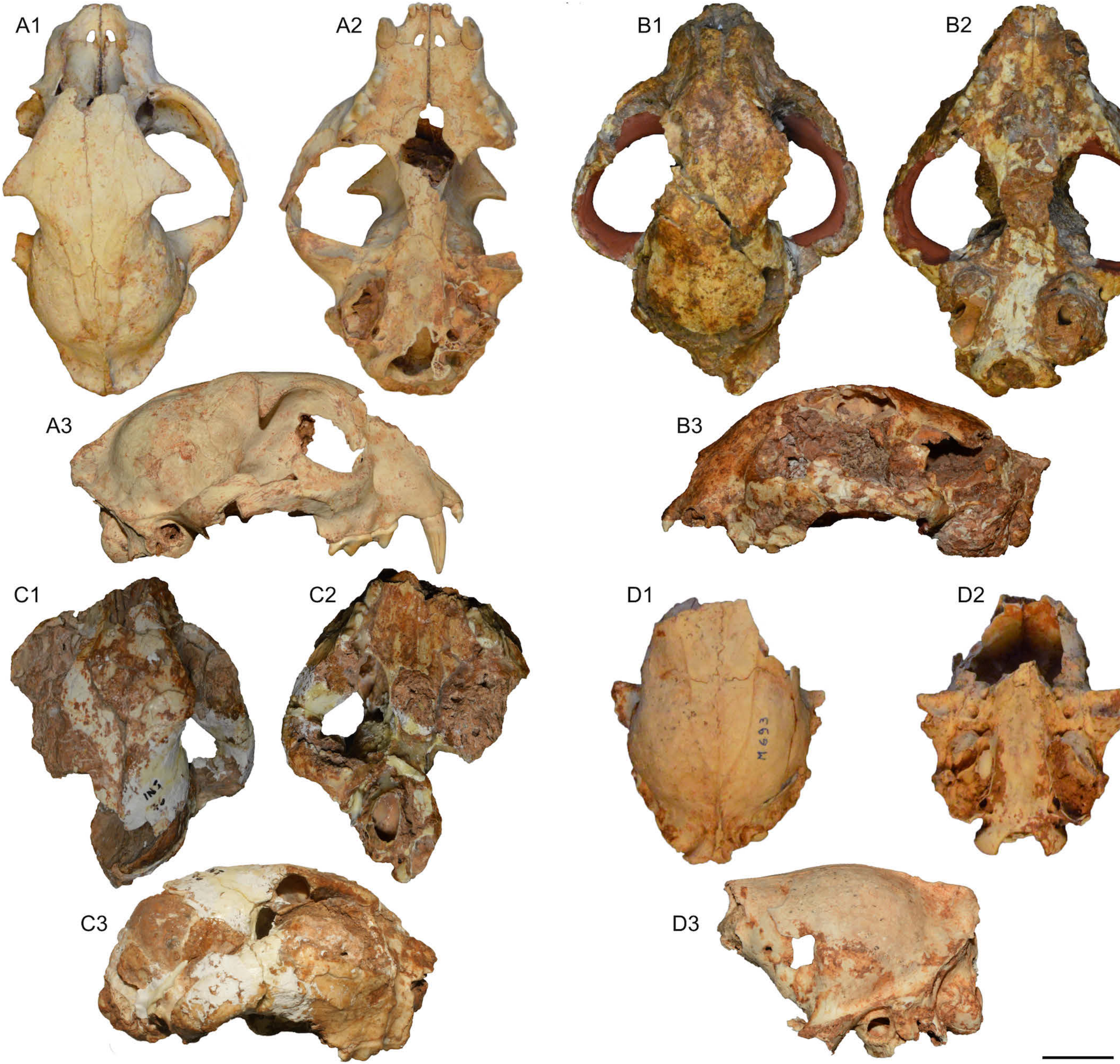
Figure 8. Estimated body masses (kg) for *Lynx issiodorensis*, *Lynx* sp., *Lynx pardinus s.l.*, and *Lynx lynx* from various Plio-Pleistocene sites of Europe. Estimates are based on condylobasal length, following ***Van Valkenburgh (1990)***. The body mass range for extant species is shown on the right. Details are in ***Supplementary table 8***.

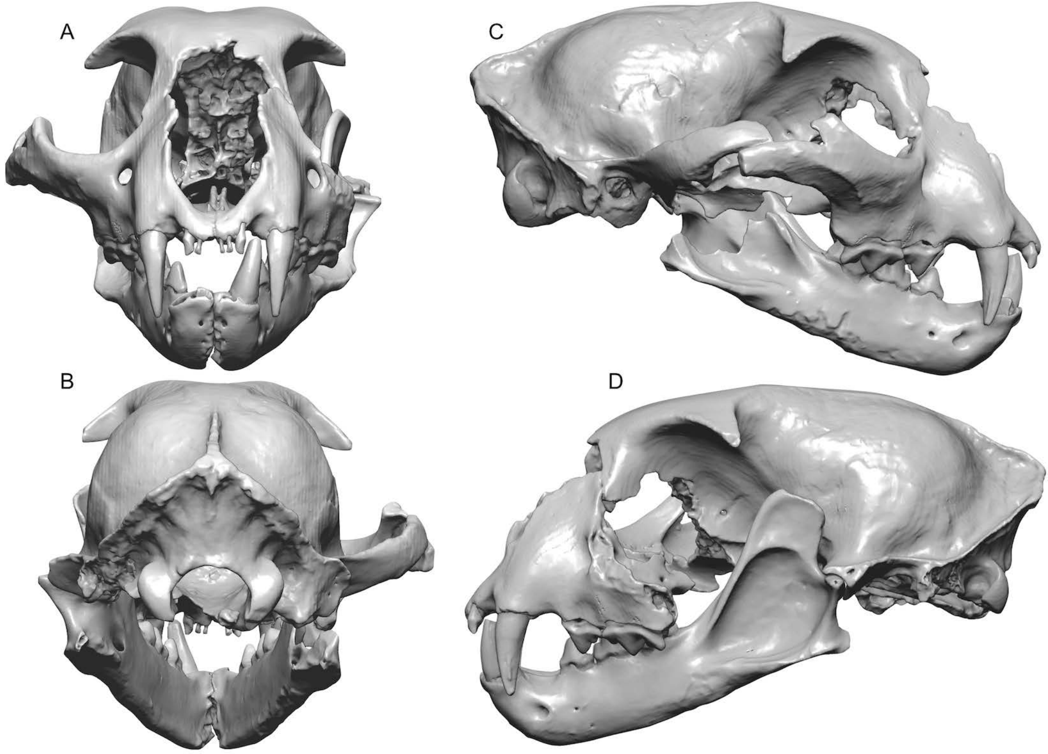
Figure 9. Map of the Plio-Pleistocene records of European lynxes. Early Pliocene: 1 Almanzora, 2 La Gloria 4, 3 La Calera; Late Pliocene: 4 Serrat d'en Vaquer, 5 Les Etouaires, 6 La Côte d'Ardé, 7 Pardines, 8 Garfagnana, 9 Layna, 10 Çalta; Early Pleistocene: 11 Olteţ River Valley, 12 La Puebla de Valverde, 13 Fonelas P-1, 14 Villarroya, 15 Saint Vallier, 16 Olivola, 17 Pantalla, 18 Upper Valdarno, 19 Figline, 20 Matassino, 21 Pirro Nord, 22 Untermassfeld, 23 Apollonia, 24 Tourkovounia, 25 Argentario, 26 Avenc Marcel, 27 Sierra de Quibas, 28 Cueva Victoria, 29 Cal Guardiola, 30 Vallparadís Estació, 31 Vallonnet, 32 Somssich Hill, 33 Ubeidiya, 34 Venta Micena, 35 Trinchera Dolina 6, 36 Sainzelles, 37 Soleilhac, 38 Grotte de la Sartenette; Middle Pleistocene: 39 Trinchera Galeria, 40 Sima de Los Huesos, 41 Aldene - Lower levels, 42 Caune de l'Arago, 43 L'Escale, 44 Lazaret, 45 Lunel-Viel, 46 Mosbach, 47 Mauer, 48 Ponte Molle, 49 Valdemino - lower levels, 50 Villacastín; Late Pleistocene: 51 Abri Cornille, 52 Aldene - upper level, 53 Baume-Longue, 54 Campfiel, 55 Grotte Balauzìere, 56 Grotte de l'Observatoire, 57 Grotta de Reihac, 58 Grotte Vaufrey, 59 Hortus, 60 La Crouzade, 61 La Salpetriére, 62 Moula Guercy-Baume, 63 Orgnac 3, 64 Portel Ouest, 65 Puech-Margal, 66 Grotta del Principe, 67 Grotta della Masseria del Monte, 68 Monte Tignoso, 69 Valle Radice, 70 Abric Romaní, 71 Almada, 72 Cau d'en Borràs, 73 Cau del Duc, 74 Cova de l'Arbreda, 75 Cova Negra, 76 Cova Toll, 77 Cova Toixoneres, 78 Cueva de Chaves, 79 Cueva del Puerto, 80 Devil's Tower, 81 El Escarche, 82 El Muscle, 83 Ermittia, 84 Erralla, 85 Gorham's Cave, 86 Pena de Estebanvela, 87 Turó del Moro, 88 Windmill Hill, 89 Alargo do Casais, 90 Caldeirao, 91 Casa do Moira, 92 Columbeira, 93 Escoural, 94 Furinha, 95 Prado des Salemas, 96 Arene Candide, 97 Buca della Iena, 98 Grotta della Madonna, 99 Grotta delle Striare, 100 Grotta dei Colombi, 101 Grotta di Equi, 102 Grotta Polesini, 103 Grotta Sant'Agostino, 104 Grotta Tina di Camerota, 105 Melpignano, 106 Riparo Fumane, 107 San Sidero, 108 Col d'Aran, 109 Groutte de Pène, 110 Mostayous, 111 Réseau du Cébéri, 112 Willendorf, 113 Beeston Tor, 114 Lynx Cave, 115 Neale's Cave, 116 Sewell's Cave, 117 Cueva de Los Casares, 118 Pagolusieta, 119 Cueva de Santimamine, 120 Kostenki 21, 121 Grotte du Bourrouilla, 122 Valdemino - upper level, 123 Ingarano.

Figure 10. Reconstruction sequence of the head appearance of *Lynx pardinus* MGPT-PU 135415 from Ingarano (Italy). Artwork by D.A. Iurino.

Table 1. Measurements of the Ingarano sample (see also ***Supplementary tables 1-3***).


Ingarano
Foggia
APULIA
N
40 km


A1
A2
B1
B2
A3
B3
C1
C2
D1
D2
M693
C3
D3


A
B
C
D


A1
A2
A3
A4
B1
B2
C1
C2
ING69
D1
D2
E1
E2
IN15NS
F1
F2
G1
G2
H1
ING73
H2
I1
I2
J1
J2
ING61
K1
K2
L1
L2
M1
M2


A1
A2
B1
B2
C1
C2
D1
D2
E1
E2
F1
F2
G1
G2
H1
H2
I1
I2
J1
J2
K1
K2
L1
L2
M1
M2
N1
N2
O1
O2
P1
P2
Q1
Q2
R1
R2
S1
S2
T1
T2
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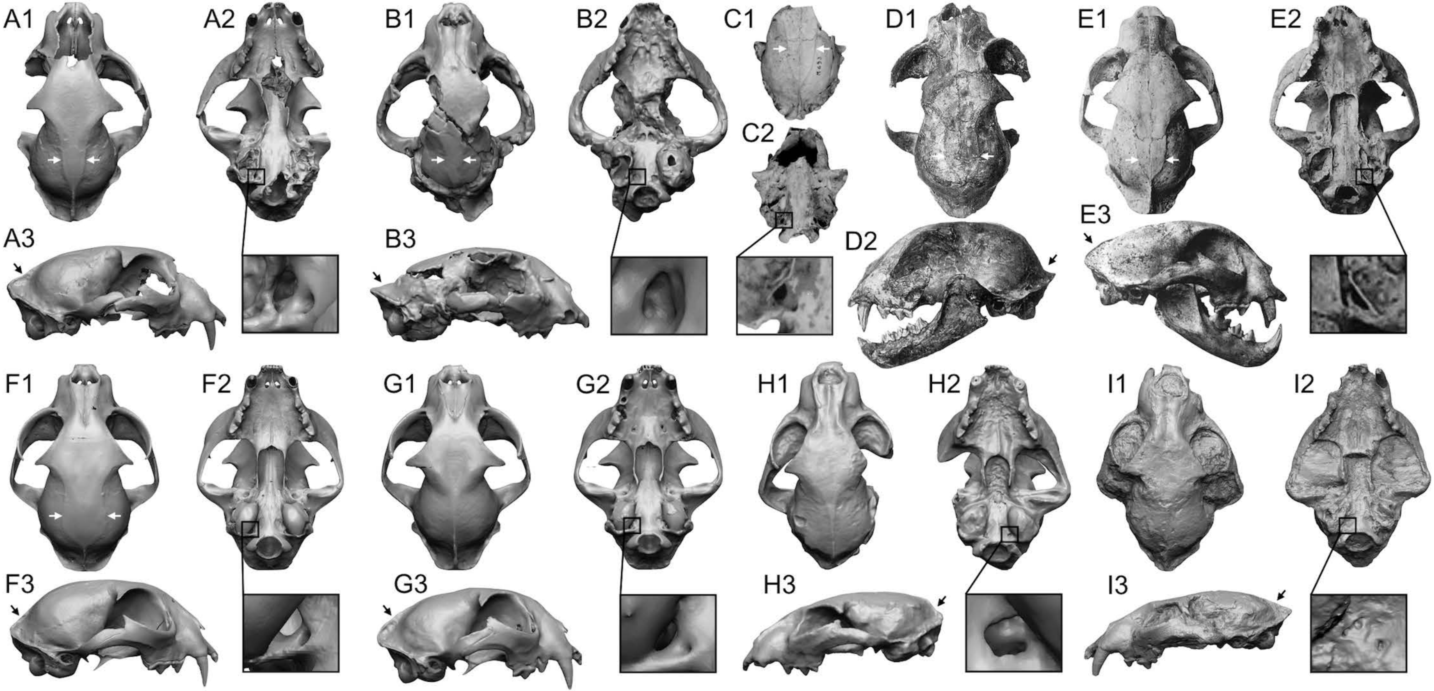
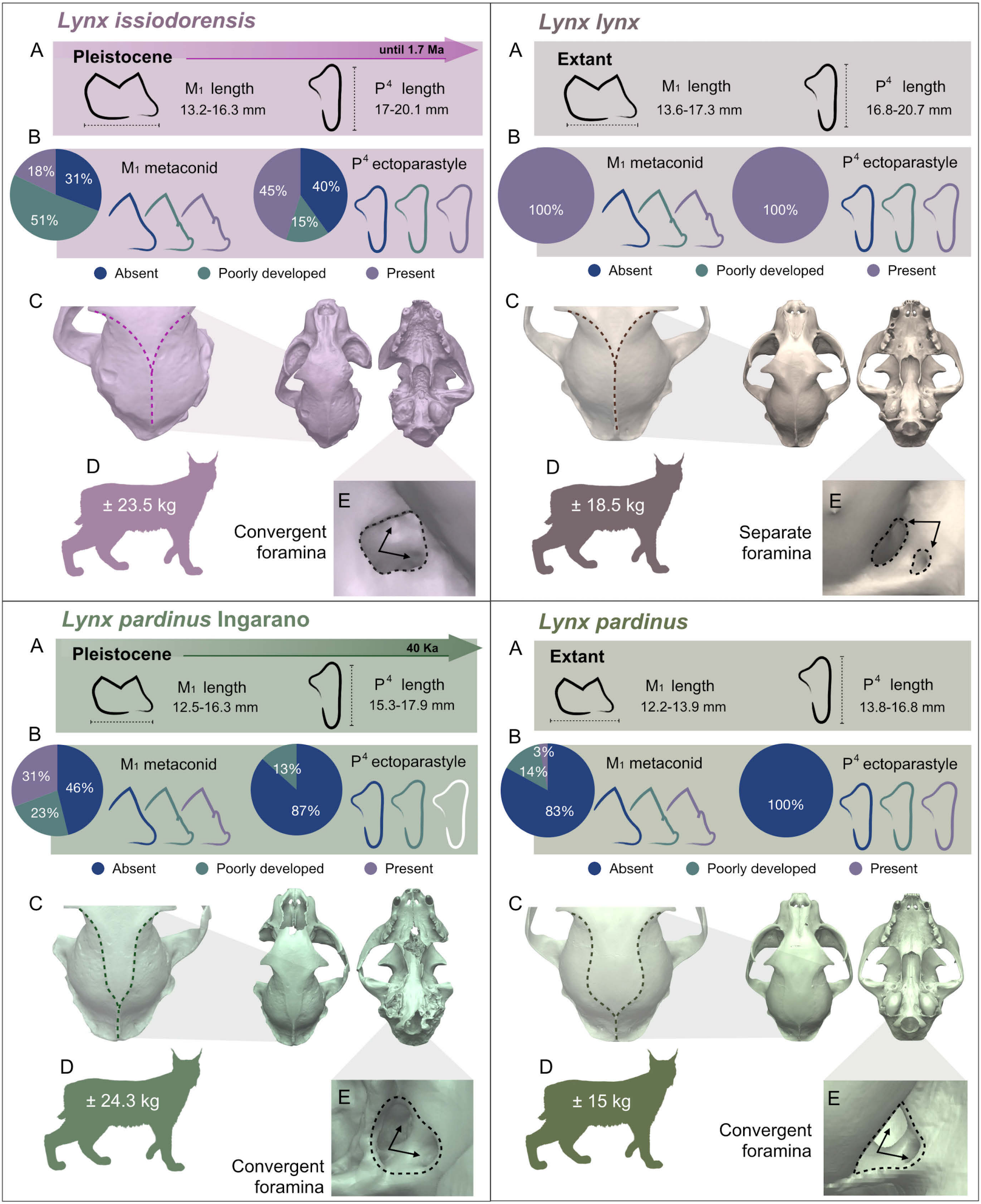
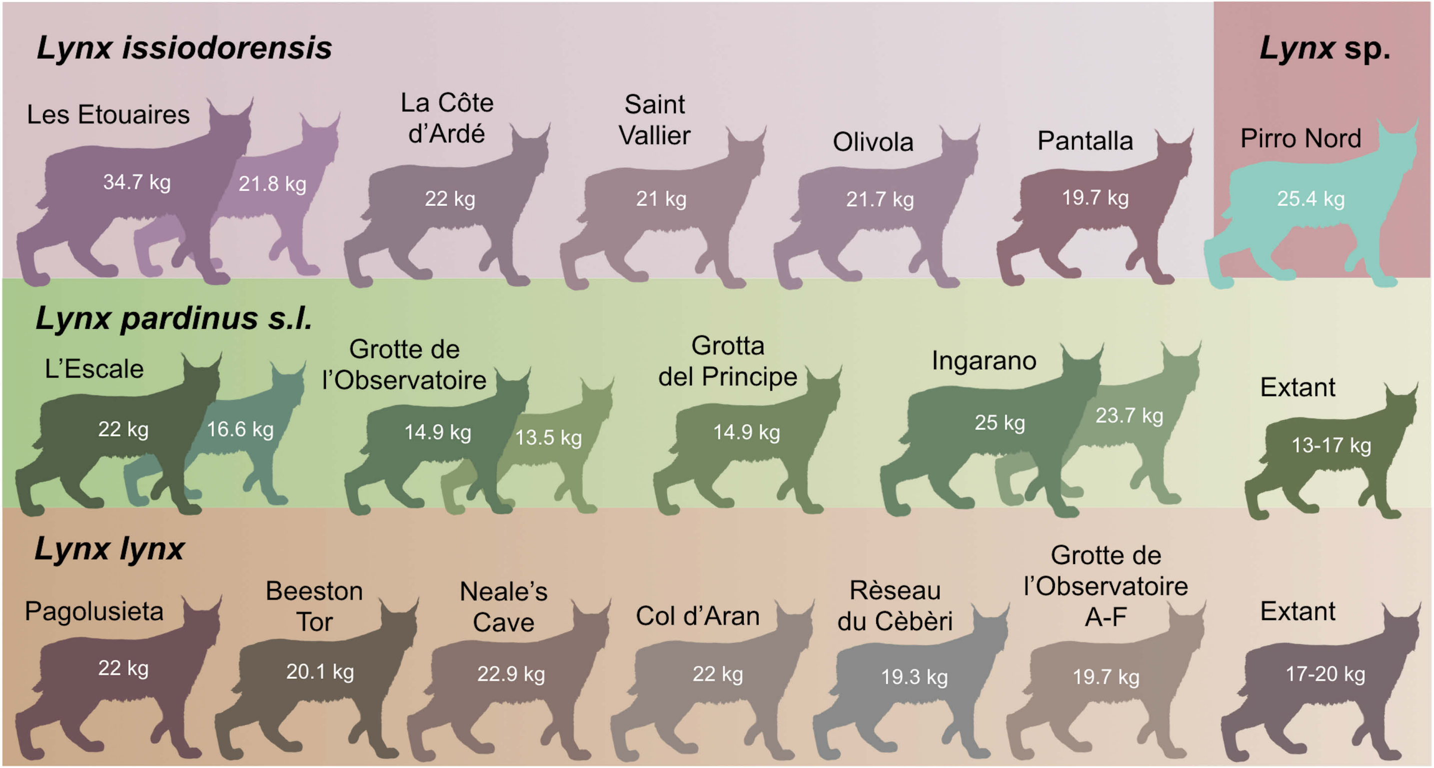
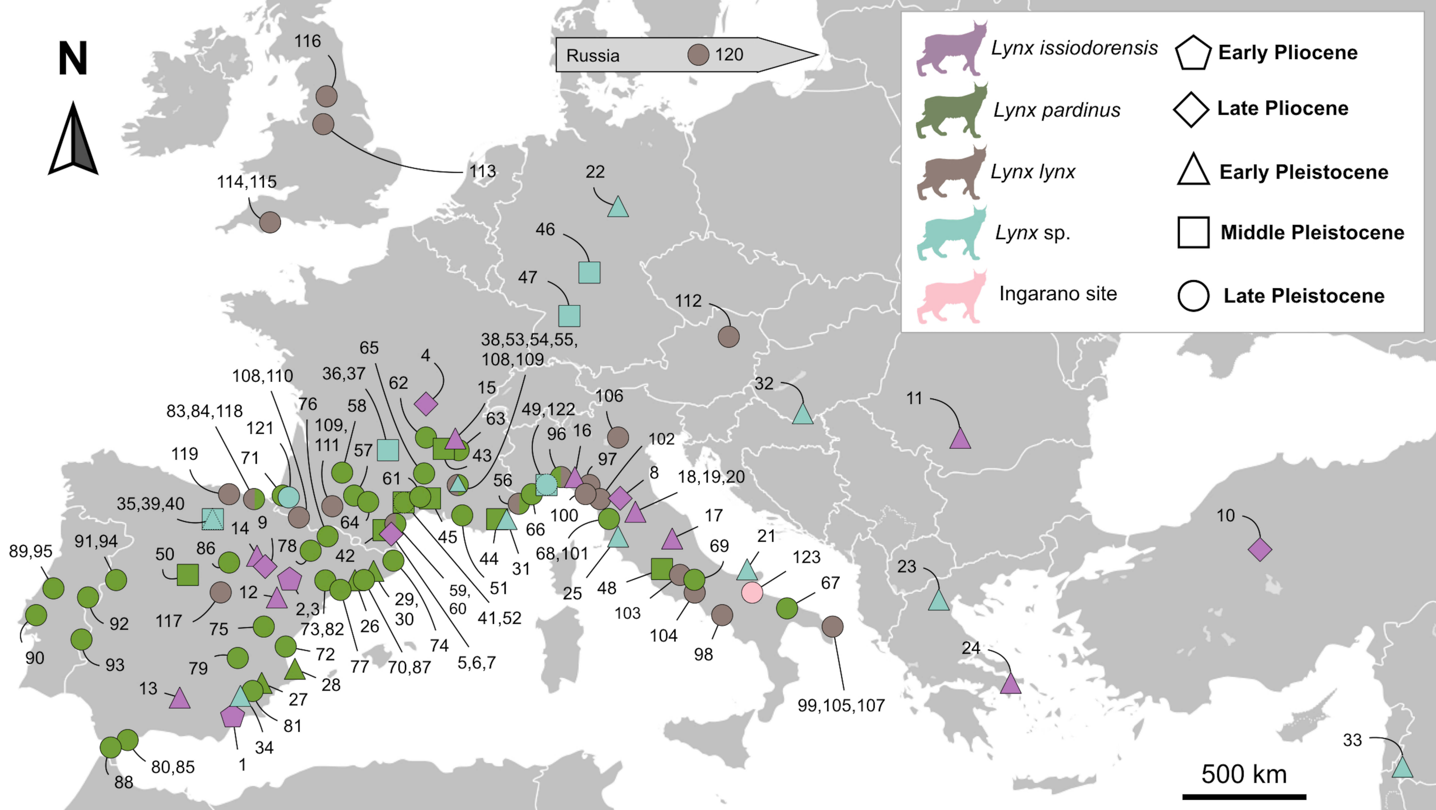
V1
V2
W1
W2
X1
X2
Y1
Y2
Z1
Z2
AA1
AA2


A1
A2
A3
B1
B2
B3
C1
C2
D1
D2
E1
E2
E3
F1
F2
F3
G1
G2
G3
H1
H2
H3
I1
I2
I3


Lynx issiodorensis
A
Pleistocene
until 1.7 Ma
M1 length
13.2-16.3 mm
P4 length
17-20.1 mm
B
18%
31%
51%
M1 metaconid
45%
40%
15%
P4 ectoparastyle
Absent
Poorly developed
Present
C
D
± 23.5 kg
E
Convergent foramina
Lynx lynx
A
Extant
M1 length
13.6-17.3 mm
P4 length
16.8-20.7 mm
B
M1 metaconid
100%
P4 ectoparastyle
100%
Absent
Poorly developed
Present
C
D
± 18.5 kg
E
Separate foramina
Lynx pardinus Ingarano
A
Pleistocene
40 Ka
M1 length
12.5-16.3 mm
P4 length
15.3-17.9 mm
B
31%
46%
23%
M1 metaconid
13%
87%
P4 ectoparastyle
Absent
Poorly developed
Present
C
D
± 24.3 kg
E
Convergent foramina
Lynx pardinus
A
Extant
M1 length
12.2-13.9 mm
P4 length
13.8-16.8 mm
B
3%
14%
83%
M1 metaconid
100%
P4 ectoparastyle
Absent
Poorly developed
Present
C
D
± 15 kg
E
Convergent foramina


Lynx issiodorensis
Les Etouaires
34.7 kg
21.8 kg
La Côte d'Ardé
22 kg
Saint Vallier
21 kg
Olivola
21.7 kg
Pantalla
19.7 kg
Lynx sp.
Pirro Nord
25.4 kg
Lynx pardinus s.l.
L'Escale
22 kg
16.6 kg
Grotte de l'Observatoire
14.9 kg
13.5 kg
Grotta del Principe
14.9 kg
Ingarano
25 kg
23.7 kg
Extant
13-17 kg
Lynx lynx
Pagolusieta
22 kg
Beeston Tor
20.1 kg
Neale's Cave
22.9 kg
Col d'Aran
22 kg
Rèseau du Cèbèri
19.3 kg
Grotte de l'Observatoire A-F
19.7 kg
Extant
17-20 kg


N
Russia
120
Lynx issiodorensis
Lynx pardinus
Lynx lynx
Lynx sp.
Ingarano site
Early Pliocene
Late Pliocene
Early Pleistocene
Middle Pleistocene
Late Pleistocene
500 km
116
113
114,115
22
46
47
112
32
11
10
23
24
33
4
65
62
15
63
43
38,53,54,55,
108,109
36,37
58
57
61
109,
111
76
108,110
121
83,84,118
71
119
35,39,40
9
14
86
78
50
12
2,3
117
75
73,82
42
64
45
59,
60
51
41,52
44
31
56
66
49,122
96
16
97
102
100
68,101
8
18,19,20
17
25
48
103
104
98
69
21
123
67
99,105,107
26
29,
30
74
5,6,7
77
70,87
72
28
27
81
34
1
13
79
89,95
91,94
92
90
93
80,85
88
106


2020

Cranial measurements (mm)	**Number of specimens**	**Mean**	**Min-Max**
Total length	2	160.5	157.6 - 163.4
Condylobasal length	2	149.8	148.6 - 151.1
Basal length	2	133.1	131.4 – 134.9
Length of the sagittal crest (Akrokranion to junction of the two linae temporalis)	2	26.9	25.6 – 28.2
Distance between the linae temporalis (at the level of the coronal suture)	2	18.5	16.8 – 20.3
Length of the temporal ridges (Frontal midpoint to junction of the two temporal ridges)	1	67.6	
Zygomatic breadth	1	117.2	
Greatest neurocranium breadth	3	61.7	60.3 – 62.7
Breadth of the postorbital constriction	1	40.3	
Greatest mastoid breadth	2	60.4	59.7 – 61.2
P^4 length	15	16	15.5 – 17.9
Mandible measurements (mm)			
Total length	4	96.3	77.0 – 111.4
Length of the cheektooth row (P_3 – M_1)	20	34	30.9 – 37.8
M_1 length	26	14	12.6 – 16.3