

Lynx remains from the Pleistocene of Valdemino cave (Savona, Northwestern Italy), and the oldest occurrence of *Lynx spelaeus* (Carnivora, Felidae)

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Abstract Fossil lynxes are quite common in the Plio-Pleistocene mammal assemblages of Europe. Despite of this abundant record, the phylogeny of the genus Lynx and the relationships among the different recorded species are far from being resolved. The most controversial species of this group is Lynx pardinus spelaeus or Lynx spelaeus according to different scholars, recorded in the Middle and Late Pleistocene of France and Italy. Here, we describe unpublished remains of fossil lynxes from different layers of the Valdemino cave (Middle to Late Pleistocene, Savona, Italy). The reported evidence suggests that the lynx from Valdemino represents probably the most ancient well-documented material of L. spelaeus in Europe further reinforcing the idea of progressive size reduction and acquisition of more trenchant dentition in the European lineages of lynx (L. pardinus and L. spelaeus) during the Middle to Late Pleistocene.

Keywords Felinae · Lynx evolution · Middle and late pleistocene · Taxonomy · Morphology

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1 Introduction

Fossil remains ascribable to the genus Lynx are quite common in the Plio-Pleistocene sites of Europe, being a quite ubiquitous presence in the faunal lists of the related deposits (Werdelin 1981; Lorfèvre 2009; Cipullo 2010). However, many aspects of their evolutionary history remain unclear, starting from their own in-group phylogeny (Kurtén 1968, 1978; Werdelin 1981; Palombo et al. 2008; Boscaini 2014). This is ascribable to many causes, proposed in the past by many authors, namely: the scarcity of well-preserved fossils, the recent and quick divergence of the extant lineages (Johnson et al. 2004 and references therein), the extreme adaptability and "plasticity" of their body size, difficulties in defining reliable morphological diagnostic features (and observable in the fossil record) and dubious taxonomic attributions (Bonifay 1971; Olive 2006; Testu 2006; Palombo et al. 2008).

In recent times, a special attention has been directed on this group of felids, in the effort of clarifying these obscure points, specifically, in the last decade many studies on extant and fossil lynxes have been conducted on Southwestern European material (Testu 2006; Lorfèvre 2009; Cipullo 2010; Cherin et al. 2013; Boscaini 2014).

Part of this problem relies on the taxonomic attribution of several Middle and Late Pleistocene remains, mainly from caves in Southern France and Northern Italy and putatively belonging to the species *Lynx spelaeus* or *Lynx pardinus spelaeus*, surely the most controversial fossil species of the genus (Testu 2006; Palombo et al. 2008; Boscaini 2014).

The origin of the disagreement on the taxonomic attribution of this species must be tracked down in its first description by Boule (1919), when the author erected the subspecies *Felis* (*Lynx*) pardina race spelaea, now *Lynx* pardinus spelaeus. The specimens analyzed by Boule (1919) come from the Late Pleistocene Grotte du Prince and Grottes de Grimaldi (Grimaldi, North-West Italy) and immediately Boule notes typical intermediate characters between the living Lynx lynx and Lynx pardinus, stating that "il est difficile è identifier à l'une des espèces actuelles" (Boule and de Villeneuve 1927). A summary of the historical ambiguous attribution of these remains is available in Bonifay (1971). Nowadays, the divergent evolution between L. pardinus in Europe and L. lynx in Asia from the common ancestor L. issiodorensis is generally accepted by several authors; tempo and mode of extant European lynxes appearance are however a still open debate (cfr. Rodriguez et al. 2011; Cherin et al. 2013; and references therein). Even if the majority of the scientific community still considers L. spelaeus as a subspecies (and direct ancestor) of the living Iberian species with a some kind of anagenetic evolution beginning with the Villafranchian L. issiodorensis, throughout L. pardinus spelaeus and finishing in the living L. pardinus (Werdelin 1981; Kurtén and Granqvist 1987; García and Arsuaga 1998; among others), in other publications like Bonifay (1971), Testu (2006) and Lorfèvre (2009) a specific classification (L. spelaeus) of the cave lynx is preferred, considering that the last species is not in the phylogenetic lineage of extant L. pardinus.

In the present work, this last vision is preferred: we consider *Lynx spelaeus* as the typical lynx species from the Galerian and Aurelian faunal assemblages of Southern France and Northern Italy, in accordance with Bonifay (1971), Testu (2006), Sala et al. (1992) and Rustioni et al. (1995). This specific attribution is preferred while the phylogenetic relationships with the extant species *Lynx pardinus* still remain undisclosed (Boscaini 2014).

Another obscure aspect of the evolutionary history of *Lynx spelaeus* is the evolutionary relationship with the other extant species *Lynx lynx* (Rustioni et al. 1995; Testu 2006). While it is generally accepted that the Eurasian lynx reaches Europe from Asia in the Eemian period (Middle–Late Pleistocene boundary) (Werdelin 1981), in the Italian Peninsula, it should be conducted a deep revision of the lynxes' fossil record of this time interval, to set accurately the arrival of this felid to the Alpine and Apennine ranges (Rustioni et al. 1995).

Here, we describe several *Lynx* specimens coming from the Middle and Late Pleistocene layers of the Valdemino cave (Savona, Northwestern Italy), further comparing the studied material with other Middle and Late Pleistocene lynxes to clarify the phylogenetic position of *Lynx spelaeus*.

1.1 Age and geological settings

The Valdemino cave is situated close the Borgio town (Savona Province, Northwestern Italy; WGS84: 44.1600,

8.3045; Fig. 1a). It is a touristic karst cavity part of a larger karst complex discovered in the 1950s (the largest room of the cave is named "Cranwell cavern" in honor of the RAF soldier that first entered in the inner part of the cave; Lamboglia 1955). In the early 1960s during the constructing works associated with the touristic guided tours, a vertical gallery was found which was filled with Pleistocene sediments (Fornasiero 1989). In accordance with Italian law regarding cultural heritage, the Valdemino cave in 1962 has been declared a site of paleontological and speleological importance, under responsibility of the local Soprintendenza Archeologica.

The gallery was firstly excavated at the end of the 1960s by E. Torgiorgi and C. Tozzi (University of Pisa). A brief note on the fauna (Tozzi 1969) also reported the occurrence of two discontinuous fossiliferous assemblages (called Upper and Lower Part), separated by a thick sterile layer. The excavation of the site was resumed by B. Sala (University of Ferrara) with two field surveys in 1989 and 1991 (Sala et al. 1992; Nocchi and Sala 1997a). These excavations allowed the recognition of several layers corresponding to the Upper Part (layers 20–23) and the Lower Part (layer 27) separated by a sterile complex (Fornasiero 1989; Nocchi and Sala 1997a; Fig. 1b).

The following species customarily attributed to Middle Galerian assemblages have been recognized in the Lower Part (layer 27) (Tozzi 1969; Sala et al. 1992; Sardella et al. 2006; Sala and Masini 2007): Microtus (Iberomys) breccensis, Apodemus sp., Allocricetus bursae, Miodes sp., Pliomys episcopalis, Microtus (Terricola) sp., Mammuthus armeniacus (=trogontherii), Stephanorhinus cf. kichbergensis, Cervidae indet., Sus scrofa, Bos primigenius, Macaca sylvanus, Ursus sp., Canis mosbachensis, Panthera pardus, Felis (Lynx) gr. spelaeus and Homotherium sp. Sala and Masini (2007) include the Lower Part of the Valdemino cave in the Isernia Faunal Unit (ca. 0.6 Ma) on the basis of the record of Allocricetus bursae, Pliomys episcoplais, small-sized Microtus brecciensis and Oryctolagus burgi. The inclusion of the layer 27 of the Valdemino cave in the Isernia Faunal Unit was supported by most of the scholars (see Palombo 2014 and references therein for discussion).

On the other side, in the Upper Part (layers 20–23), a typical Late Pleistocene mammal assemblage has been identified (Nocchi and Sala 1997b; Sardella et al. 2006; Sala and Masini 2007) with the presence of *Erinaceus europaeus*, *Myoxus glis*, *Arvicola terrestris*, *Microtus agrestis*, *Microtus (Terricola)* sp., *Apodemus* sp., *Oryctolagus burgi, Canis lupus*, *Vulpes vulpes*, *Sus scrofa*, *Mustela putorius*, *Panthera pardus*, *Crocuta crocuta spelaea*, *Cervus* sp., *Cervus elaphus*, and *Bos primigenius* (Nocchi and Sala 1997a, b).

Until today, from the about 4.000 remains recovered from this cave, only very few taxa have been studied in





detail: the mandible of a macaque *Macaca sylvanus*, the almost complete skeleton of red deer *Cervus elaphus*, the leporid remains *Oryctolagus burgi*, and the vole *Microtus* (*Iberomys*) *breccensis* (Tozzi 1969; Nocchi and Sala 1997a, b; Davì 1994).

2 Materials and methods

The specimens described in this study are provisionally housed in the Dipartimento di Scienze della Terra of the University of Firenze (Italy). Soon after the publication of this study, the materials will be returned to the "Soprintendenza per i Beni Archeologici per la Liguria".

The comparative sample includes fossil remains of *Lynx issiodorensis valdarnensis* housed in the Museo di Storia Naturale (Geology and Paleontology Section) of the Firenze University, as well as specimens of *Lynx pardinus*, *L. issiodorensis issiodorensis*, *L. lynx*, *L. rufus* and *L. canadensis* housed in the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain) and Muséum national d'Histoire naturelle (Paris, France). Additional comparative data for Pleistocene *Lynx* are taken from the literature (Bonifay 1971; Testu 2006; Cipullo 2010). Measurements of the studied specimens were taken with a digital caliper to the nearest 0.1 mm.

2.1 Taphonomical remarks

The specimens from Valdemino are basically well preserved. Few remains are entire, mostly from the Lower Part. All the specimens from the Upper Part are partly encrusted by a strong thin reddish concretion. There are no signs of root etching, trampling, and abrasion or burning, but there are evidences of weathering, mostly for the bones from Upper Part.

The 22 *Lynx* remains are equally divided in the upper and lower layers, with a total MNI (Minimal Number of Individual) of four animals, two from each assemblage (MNI calculated on radius frequencies). Fig. 2 Maxillar specimens of *Lynx spelaeus* from the layer 27 of Valdemino cave. *Right* maxillar 015/01 with P3–P4 in a buccal, b occlusal and c lingual views. *Left* maxillar 015/02 with P3–P4 in d buccal, e occlusal and f lingual views



The complete dental eruption, the limited tooth wear, the maxillary sutures (zygomatic-maxillary almost visible; maxillary–premaxillary completely fused), allow to consider cranial elements as belonging to young adults, with an estimated age of death older than 8 months. According to Canadian *Lynx* postcranial growth pattern data (Tumlison 1987), joined epiphysis allows estimating age at death older than 32 months.

3 Systematic paleontology

Order Carnivora Bowdich, 1821 Family Felidae Gray, 1821 Genus *Lynx* Kerr, 1792 *Lynx spelaeus* (Boule 1919) Figures 2, 3, 4 and 5.

3.1 Referred specimens

015/01, right maxillar fragment with P3–P4; 015/02, left maxillar fragment with P3–P4; 015/00, occipital fragments; 015/07, left mandibular corpus with p4 and m1; 015/04, distal fragment of left humerus; 015/03, left radius; 008/01, proximal fragment of left radius; 015/05, right fifth meta-tarsal; 015/06, left forth metatarsal; 007/01, proximal phalanx; 008/02, caudal vertebra.



Fig. 3 Left hemi-mandibular corpus 015/07 of *Lynx spelaeus* from the layer 27 of Valdemino cave in **a** lingual, **b** occlusal and **c** buccal views

3.2 Stratigraphic position

Layer 27, Lower Part of the stratigraphic assemblage of Valdemino cave.



Fig. 4 Postcranial specimens of the genus Lynx from the Valdemino cave. Left radius of Lynx spelaeus (015/03) from layer 27 in **a** anterior and **b** posterior views. Distal fragment of right humerus of Lynx sp. (017/02) from the upper part in **c** anterior and **d** posterior views. Distal epiphysis of left humerus of Lynx spelaeus (015/04) from layer 27 in **e** anterior and **f** posterior views. The pictures in gray behind the studied specimens correspond to living Lynx lynx



Fig. 5 Metatarsals of lynxes from Valdemino cave. *Right* third metatarsal of *Lynx* sp (009/01) from the Upper Part in **a** proximal and **b** anterior and **c** posterior views. *Left* forth metatarsal of *Lynx* spelaeus (015/06) from the layer 27 in **d** proximal **e** anterior and **f** posterior views. Right fifth metatarsal of *Lynx* spelaeus (015/05) from layer 27 in **g** proximal, **h** anterior and **i** posterior views

3.3 Measurements

See Tables 1 and 2.

3.4 Description

3.4.1 Dentognathic remains

Two maxillar fragments were recovered from layer 27 (015/01 and 015/02), probably corresponding to the same individual (Fig. 2). Both specimens preserve the alveoli of I2 and I3, C1 and P3–P4. P3 displays high and sharp (buccal-lingually compressed) paracone, well-developed metastyle with a slightly developed distal cingulum. The protocone on P4 is proportionally small and diagonally oriented with respect to the mesial plane. No trace of ectoparastyle was observed on the well-developed parastyle. Paracone and metacone are sharp (buccal-lingually compressed); both cusps are more or less of the same mesiodistal length.

A left mandibular corpus (015/07) was recovered from layer 27 (Fig. 3). The corpus preserves c1, p4-m1 and the alveoli of p3; the latter is slender with a short diastema and a slightly concave ventral profile. p4 has a symmetrical protoconid in lateral view with two well-developed accessory cusps (mesial and distal) and a marked distal cingulum. p4 and m1 as in the upper premolars are buccolingually compressed post-canine elements. m1 bears two cusps, paraconid and protoconid, without any trace of talonid or metaconid.

3.4.2 Postcranial remains

One distal fragment of left humerus was recovered from the lower layers (015/04). The morphology of the distal epiphysis, with supracondylar foramen, reduced epicondyles and a deep articular surface is characteristic of the genus *Lynx* (Fig. 4e, f). The complete left radius (015/ 03) displays an anteroposteriorly flattened diaphysis, with a proximodistally enlarged radial tuberosity and reduced insertions for *m. brachioradialis* and *m. pronator quadratus* and a reduced articular surface for the distal ulnar facet (Fig. 4a, b). The forth (007/01) and fifth metatarsals (015/05) show slender rectilinear diaphysis with a slightly dorsopalmar torsion (Fig. 5d–i). The articular facet for the unciform in the proximal epiphysis of the forth metacarpal displays a slightly convex morphology. *Lynx* sp. Figures 4 and 5.

3.5 Referred specimens

017/05, left maxillar fragment with P3–P4; 017/07, left C1; 017/08, left c1; 017/01, distal fragment of right humerus; 017/02, distal fragment of right humerus; 013/01, proximal fragment of right radius; 008/03, fragment of left radius; 017/06, proximal fragment of right ulna; 017/04, proximal fragment of right femur; 009/01, right third metatarsal.

3.6 Stratigraphic position

Upper Part of the stratigraphic assemblage of Valdemino cave.

3.7 Measurements

See Tables 1 and 2.

L mesiodistal length,

Table 1Measurements (inmm) of the upper and lowerdentition of Lynx spelaeus andLynx sp. from Valdemino cave

W labiolingual breadth, *H* crown height, *Lproto* mesiodistal length of P4 protocone, *Lpara* mesiodistal length of P4 paracone, *Lmeta* mesiodistal length of P4 metastyle, *Lproto* mesiodistal length of m1 protoconid, *Lpara* mesiodistal length of m1 paraconid

3.8 Description

3.8.1 Dentognathic remains

A left maxillar fragment was recovered from the upper layers (017/06), it preserves P3 and P4 showing the same morphology of the previously described specimens only with an appreciable small ectoparastyle on the P4.

3.8.2 Postcranial remains

Two distal fragments of humerus were recovered from the upper layers (017/01 and 017/02), these specimens display in general the same morphology but larger biometrical dimensions when compared with the specimens from the lower layers (015/03) (Fig. 4). The radius (008/03) is a medial fragment of diaphysis with a flatted anterior surface and posteriorly convex. The proximal fragment of ulna (017/06) only conserves the olecranon process and fossae, being only observable a curved anconeus process.

Species	Record no.	Lat	C1		Р3		P4				
			L	W	L	W	L	W	Lproto	Lpara	Lmeta
L. spelaeus	015/01	R	9.0	7.6	10.1	5.2	16.1	7.0	2.8	6.7	6.8
L. spelaeus	015/02	L	9.0	7.3	10.3	5.2	16.1	7.2	3.2	6.7	7.3
Lynx sp.	017/05	L	8.9	6.7	11.6	6.0	17.1	8.9	3.5	7.2	7.4
Lynx sp.	017/07	L	8.1	6.3							
Species	Record no.	Lat	c 1			p4		m1			
			L	W	Н	L	W	L	W	Lprotd	Lpard
L. spelaeus	017/07	L	7.9	6.54		10.5	5.1	13.1	5.4	7.5	6.6
Lynx sp.	017/08	L	7.6	5.9	18.1						

 Table 2 Measurements (in mm) of the postcranial remains of Lynx spelaeus and Lynx sp. from Valdemino cave

Species	Element	Catalog no.	L	PMLD	MMLD	DMLD	PDPD	MDPD	DDPD
L. spelaeus	Humerus	015/04				29.5			19.5
Lynx sp.	Humerus	017/02				31.6			19.7
Lynx sp.	Humerus	017/01			12			14.3	
L. spelaeus	Radius	015/03	141.6	11.2	18.3	17.0	7.9	5	10.4
Lynx sp.	Radius	013/01		13.0			9.4		
L. spelaeus	Radius	008/01		11.3			8.0		
Lynx sp.	Femur	014/04		36.9			16.3		
Lynx sp.	III Mtt	009/01	69.1	9.4	6.4	8.5	11.5	5	7.9
L. spelaeus	IV Mtt	015/06	75.9	7.2	5.7	7.6	11.0	5.2	8.4
L. spelaeus	V Mtt	015/05	74.1	9.8	5	8.2	7.3	4.6	7.8

L proximodistal length, PMLD proximal mediolateral width, MMLD mediolateral width at midshaft, DMLD distal mediolateral width, PDPD proximal dorsopalmar height, MDPD dorsopalmar width at midshaft, DDPD distal dorsopalmar height

The proximal femur fragment (017/04) displays a rounded and slightly flattened head without *fovea capitis* and a proportionally reduced *m. vastus lateralis* when compared with *L. lynx*. The third metatarsal (009/01) displays a slender, rectilinear and slightly dorsopalmary torsioned diaphysis (Fig. 5a–c).

4 Discussion

4.1 Taxonomic attribution

4.1.1 Lower Part specimens

The material from the Lower Part (Layer 27) described above, is consistent both in features and measurements, with the fossil lynx material coming from the Middle and Late Pleistocene French localities of L'Escale, Lunel-Viel and Aragó Cave and attributed to the species Lynx spelaeus (Bonifay 1971; Olive 2006; Testu 2006; Palombo et al. 2008). Some evident features, mainly in the lower dentition, allow a comparison with these Pleistocene lynxes. The main common characteristic is the presence of a small but detached cingulum in the distal margin of p4 (Bonifay 1971; Testu 2006). This distinctive character is also present in the species Lynx issiodorensis, its putative ancestor, and less marked (or even absent) in extant Lynx pardinus. However, the material from the Valdemino cave slightly disagrees with the other Galerian remains in another feature: the corpus fragment 015/07 completely lacks the metaconid in the distal margin of m1. The presence/absence of the metaconid is a variable feature, whose "unfixed" occurrence has already been stressed by Viret (1954), Kurtén (1963), Bonifay (1971) and Testu (2006). Many authors evaluate this feature in percentages among the available sample: while it is almost ubiquitous in the latest Villafranchian lynxes (i.e., Lynx issiodorensis valdarnensis) (Garrido 2008) and very rare in extant Lynx pardinus (García-Perea et al. 1985). The Galerian-Aurelian lynxes show a gradual decreasing of this structure through time. In L'Escale, it is present in 7 over 8 lower carnassials, in Lunel-Viel 2 over 4 and in the Grimaldi cave 3 over 7 (Bonifay 1971). Also the material from the Aragó Cave, Orgnac 3, Portel-Ouest, Hortus, La Crouzade and Aldène presents similar proportions (Testu 2006). In the past Bonifay (1971) and Testu (2006) suggested that the gradual decreasing of this feature is related with the achievement of a progressively more cutting/trenchant dentition. The studied specimens are too scanty to allow any kind of conjecture; in any case, it is remarkable the complete lack of this structure in sediments of this age. This does not affect the taxonomic attribution, given that also in L'Escale, 1 over 8 lower carnassials of Lynx spelaeus completely lacks the metaconid.



Fig. 6 Dental proportions of the cheek teeth in different living and extinct species of the genus *Lynx* compared with the specimens from Valdemino cave. Hand-drawn polygons link the most extreme values of each forms, to ease visualization of metrical differences among them, *black polygons* represent the small-sized lynx species and the *gray polygons* the large-sized. **a** P4 and **b** m1

Also the presence/absence of the ectoparastyle on P4 seems to be another variable character with scanty diagnostic value, being absent on Lower Part layer specimens (015/01 and 015/02) and present on the only recovered maxilla from the Upper Part layers (017/06). Even if it tends to be more common in large-sized lynxes *L. issiodorensis* and *L. lynx* (Kurtén 1978), it can occur with some low percentages also in *Lynx rufus* and *Lynx canadensis* (Boscaini 2014).

When looking at measurements, it appears that they are consistent with the range established for *Lynx spelaeus*, more precisely with the smallest representatives of the interval. They are also smaller in size than the Villafranchian *Lynx* *issiodorensis* and the extant *Lynx lynx*, but sensibly larger than extant *Lynx pardinus* (Fig. 6).

4.1.2 Upper part specimens

The material recovered from the Upper Part layers is indeed more difficult to determine, as it lacks the main dentognatic diagnostic features. As we said above the presence of ectoparastyle in the P4 of the 017/06 maxilla is a taxonomic character without diagnostic value. Concerning measurements from both dentognathic and postcranial specimens, these fossils appear larger than the lower layers ones but of surely smaller size than in the extant *Lynx lynx*. For this reason, they have been parsimoniously classified as *Lynx* sp.

4.2 Evolutionary implications

According to the provided data, the lynx remains from the Lower Part layer of Valdemino cave can be one of the earliest occurrences of L. spelaeus in the fossil record, for sure the most ancient recovered in the Italian Peninsula (Sardella et al. 2006) and probably the best preserved one. The Valdemino deposits are slightly older than the ones of the French localities of L'Escale (ca. 0.6-0.5 Ma; Bonifay 1971) and Aragó Cave (ca. 0.55 Ma; MIS14; Moigne et al. 2006), the oldest well-known records of this species. Older deposits with putatively remains of Lynx spelaeus are La Sartanette and Le Vallonnet, again in France, respectively, 1.3 and 1.0 Ma in age. Anyway these lynxes are only known by scanty, not diagnostic, or unpublished remains (Palombo and Valli 2003; Moulle 1992). For the last reasons, the record of Lynx spelaeus from the Lower Part of Valdemino cave can be considered, to date, the most ancient well-documented material of this species.

The obtained results show that the small size and the absence of m1 metaconid (derived features in the *Lynx* genus) were already present at least at 0.6 Ma, accordingly with the tendency pointed by many authors of progressive size reduction, gradual loss of m1 metaconid and acquisition of trenchant dentition throughout the Pleistocene in the *Lynx* genus (Bonifay 1971; Testu 2006; Cipullo 2010).

The Valdemino *Lynx* record offers new evidences on *Lynx* evolutive trends. The slender cranio-dental features of Valdemino older remains (Lower Part, layer 27) are consistent with specific characters of *L. spelaeus*, and the postcranial features also retrace the skull characters with slender fore- and hindlimbs. Taking into account the evolutionary trend of *L. pardinus* in Spain (and the similar latitudinal range), we could infer that circum-Mediterranean populations may represent the result of a genetic bottleneck or allopatric effect (as demonstrated for the Iberian species by Rodriguez et al. 2011), and convergent

evolution to a smaller size with trenchant teeth under similar geographic barriers and climatic variability throughout the Middle–Late Galerian and Aurelian Mammal Ages.

5 Conclusions

The lynx specimens from the Valdemino cave described in this paper, specially the studied fossils from the layer 27, share several morphologic characters with the typical material ascribed to the species *Lynx spelaeus* (Bonifay 1971; Testu 2006), namely: small size as compared with the living *Lynx lynx*, presence of well-developed cingulum on p4 and normally absence of ectoparastyle in P4. According to the former evidence, the described lynx material from Valdemino layer 27 (Isernia Faunal Unit, Middle Galerian) can be considered the earliest well-documented and preserved occurrence of this taxon close to the Early–Middle Pleistocene boundary.

The obtained results also reinforce the idea of a progressive size reduction and gradual acquisition of trenchant dentition in the European lineages (*L. pardinus* and *L. spelaeus*) of the genus *Lynx*.

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