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This is the **accepted version** of the journal article:

Cuccu, Andrea; Valenciano Vaquero, Alberto; Azanza, Beatriz; [et al.]. «A new lynx mandible from the Early Pleistocene of Spain (La Puebla de Valverde, Teruel) and a taxonomical multivariate approach of medium-sized felids». *Historical Biology*, (2022). DOI 10.1080/08912963.2021.2024181

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1 **A new lynx mandible from the Early Pleistocene of Spain (La Puebla de**  
2 **Valverde, Teruel) and a taxonomical multivariate approach of medium-sized**  
3 **felids**

4

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21

22 **ABSTRACT**

23 The fossil record of lynxes provides clear evidence of a large range across the  
24 North Hemisphere during the Pliocene and Pleistocene. However, their origin,  
25 systematics and evolutionary relationships are still fraught with difficulties and  
26 controversy. Here we report a complete hemimandible of a medium-sized felid  
27 from the Early Pleistocene (MN17, middle Villafranchian, 2.05 Ma) site of La  
28 Puebla de Valverde (Teruel, Spain). Based on comparative and multivariate  
29 analyses of the lower dentition of 458 individuals of medium-sized *Lynx*, *Caracal*  
30 and *Leptailurus*, we confidently ascribe the remains to *Lynx* aff. *issiodorensis*.  
31 Although the dental proportions are somewhat different from those of the Eurasian  
32 *L. issiodorensis* (smaller canines and more elongated p4/m1), *Lynx* aff.  
33 *issiodorensis* shows affinities with the Issoire lynx from the contemporaneous site  
34 of Saint Vallier (France), sharing a similar morphology of the mandible, reduced  
35 canines, and long m1. We further test the hypothesis of Morales et al. (2003) about  
36 the presence of the African/Asian *Caracal* in the European Plio/Pleistocene for *C.*  
37 *depereti* and *C. issiodorensis*, and discard the attribution of *L. issiodorensis* into  
38 *Caracal*. This mandible extends the record of the genus and contributes to update  
39 our understanding of the *Lynx* lineage and its variability within the European fossil  
40 record.

41

42 **KEYWORDS**

43 Quaternary, Villafranchian, Carnivora, Felidae, lynx, *Caracal*

44

45 **Introduction**

46 Despite lynxes were widely spread throughout Europe, Asia and North America  
47 during the Pliocene and Pleistocene, their origin is still far from being fully  
48 understood and a long-standing controversy exists over their evolutionary  
49 relationships (Sunquist and Sunquist, 2017). Within the family Felidae, some  
50 authors (Collier and O'Brien 1985; Janczewski et al. 1995) consider lynxes as more  
51 closely related to the genus *Panthera* Oken, 1816 (roaring cats), while some others  
52 point to a link with *Felis* Linnaeus, 1758 (Tumlison 1987)—a hypothesis that  
53 seems to be supported by the vocalizations of these felids (Peters 1987). From a  
54 molecular viewpoint, recent evidence shows that the divergence between *Panthera*  
55 and *Lynx* Kerr, 1792 is older than previously assumed (Johnson et al. 2006;  
56 Werdelin et al. 2010; Li et al. 2016), thus ranging from 11.5 to 10.8 Ma (Johnson  
57 2006; Li et al. 2016). The sister-group relationship of *Lynx* is even more  
58 controversial, as it separates from the clade that includes the domestic cat, the  
59 leopard cat, and the puma lineages at ca. 7.2 Ma (Johnson et al. 2006).  
60 Nevertheless, Li et al. (2016) consider the genus *Lynx* to split from its sister clade,  
61 which includes the Asian golden cat, the Bay cat (*Catopuma* Severtzov 1858) and  
62 the Marbled cat (*Pardofelis* Severtzov 1858), at 8 and 5.7 Ma. As such, it is evident  
63 that the relationships among extant *Lynx* and the remaining felids still remain open  
64 to debate. The same problem exists for lynx-sized felids from the Pliocene and  
65 Pleistocene of Eurasia (e.g., Croizet and Jobert 1828; Gervais 1852; Depéret 1890;  
66 Viret 1954; Kurtén and Crusafont 1977; Kurtén 1978; Werdelin 1981; Kurtén and  
67 Werdelin 1984; Soto and Morales 1985; Alcalá 1994; Alberdi et al. 1997; Arribas  
68 and Antón 1997; Montoya et al. 1999, 2001; Morales et al. 2003; Garrido 2008;  
69 Cherin et al. 2013; Madurell-Malapeira et al. 2015; Morales 2016; Boscaini et al.

70 2016; Lavrov et al. 2021; Mecozzi et al. 2021). These primitive forms, especially  
71 the earliest (Pliocene) ones, are very scarce, and there are few available  
72 dentognathic and postcranial remains. Because their dentitions are similar in size  
73 and morphology, their diagnostic traits are currently obscure.

74 The controversial Villafranchian *Felis issiodorensis* Croizet and Jobert, 1828 has  
75 been considered as the earliest *Lynx* (see Werdelin et al. 2010) and herein the  
76 ancestor of all living lynxes (Kurtén, 1978; Werdelin 1981). Its record in Eurasia  
77 through the Pliocene and Pleistocene is significantly diverse, with up to three  
78 subspecies being recognised: *L. i. issiodorensis* (Etouaires, type locality), *L. i.*  
79 *shansius* Teilhard, 1945, from localities in China and Mongolia (Kurtén and  
80 Werdelin 1984), and *L. i. valdarnensis* Werdelin, 1981 from localities in Italy,  
81 characterised by a smaller size and being the last subspecies of *L. issiodorensis*  
82 (e.g., Kurtén 1978; Werdelin 1981; Kurtén and Werdelin 1984; Cherin et al. 2013;  
83 Boscaini et al. 2015 and references therein). Despite this, the systematic position of  
84 *L. issiodorensis* at the genus level has been a recurring topic of debate. This is  
85 because it was first attributed to the genus *Felis* by Jobert and Croizet (1828), while  
86 it was reassigned to *Lynx* by Gervais (1852) (and subsequent authors; e.g., Kurtén  
87 and Crusafont 1977; Kurtén 1978; Werdelin 1981; Montoya et al. 1999, 2001, and  
88 attributed to *Caracal* Gray, 1843 by Depéret (1890). More recently, Morales et al.  
89 (2003) revalidated the hypothesis by Depéret (1890)—thereby emphasizing the  
90 complexity in the taxonomic attribution of these felids—including the oldest  
91 representatives of *L. issiodorensis* into *Caracal*, and more specifically erecting the  
92 species *Caracal depereti* Morales, Soria, Montoya, Pérez and Salesa, 2003.  
93 However, it is worth noting that such a hypothesis has not been further considered  
94 in the literature and *C. depereti* is still classified as *Lynx* by most authors (Garrido

95 2008; Cherin et al. 2013; Ghezzi et al. 2015; Boscaini et al. 2016; Terhune et al.  
96 2020; Mecozzi et al. 2021). Indeed, our understanding of the evolutionary history  
97 of the lynxes is limited by the controversial taxonomic attribution of the Early  
98 Pleistocene material from southern Europe. A controversy that originates from the  
99 limited number of diagnostic characters offered by the remains of these felids and  
100 the lack of a suitable morphological approach.

101 With the aim to improve our knowledge of *Lynx* history, systematics and  
102 palaeobiology, the present study describes and provides a taxonomic attribution for  
103 a new left hemimandible (MPZ 2020/470) of a medium-sized felid from La Puebla  
104 de Valverde (LPV) (Teruel, central Spain)—a key site for the European Plio-  
105 Pleistocene biochronology. We compare this hemimandible with felid remains from  
106 other Pliocene and Pleistocene sites from the Iberian Peninsula (Montoya et al.  
107 2001; Morales et al. 2003; Garrido 2008), southern Europe, and Asia (Kurtén 1978;  
108 Werdelin 1981; Kurtén and Werdelin 1984; Mecozzi et al. 2021). Additionally, we  
109 further test by using a multivariate analysis of lower dentognathic specimens of  
110 extinct felids, living lynxes and the African *Caracal caracal* (Schreber 1776) and  
111 *Leptailurus serval* (Schreber 1776) whether *L. issiodorensis* should be classified as  
112 *Lynx* or *Caracal*.

113

#### 114 **Geological and palaeontological setting**

115 The fossil locality of LPV (Figure 1a) is one of the most relevant middle  
116 Villafranchian localities. Earliest studies in the site were carried out by Crusafont et  
117 al. (1964), Gautier and Heintz (1974), Heintz and Aguirre, (1976) and Aguirre and  
118 Soto (1974, 1976). Later on, in 1998, more fossil assemblages were discovered,  
119 including the mandible MPZ 2020/470 herein described. The site is located in the

120 Sarrión-Mijares depression, also known as Cuenca de Mora de Rubielos (Sinusía et  
121 al. 2004; Rodrigo, 2011). The Neogene continental deposits unconformably lie over  
122 a Mesozoic bedrock and are divided into two Formations (Fms.): Sarrión and La  
123 Puebla de Valverde. The Sarrión Fm. includes sand-loam deposits with interspersed  
124 conglomerate levels; the faunal assemblage that it yielded correlates with the early  
125 Villafranchian (Adrover et al. 1978). The La Puebla de Valverde Fm. is 0-25  
126 meters thick it mostly consists of a thin layer of angular pebbles (Sinusía et al.  
127 2004).

128 LPV is a key site for the European Plio-Pleistocene biochronology (Sinusía et al.  
129 2004). It contains very well-preserved remains, with many of them still in  
130 anatomical connection (Sinusía et al. 2004). It provides a varied faunal assemblage  
131 (~22 taxa), including a cercopithecoid primate. The carnivoran assemblage (Soria  
132 and Aguirre 1976; Kurtén and Crusafont 1977; Antón et al. 2006; Madurell-  
133 Malapeira et al. 2010; Morales, 2016) includes hyaenids—*Pliocrocuta perrieri*  
134 (Croizet & Jobert 1828) and *Chasmaporthetes lunensis* (Del Campana 1914)—,  
135 ursids (*Ursus etruscus* Cuvier 1823), canids—*Vulpes alopecoides* (Del Campana  
136 1913), and *Nyctereutes vulpinus* Soria and Aguirre, 1976—, and a varied diversity  
137 of felids including sabretooth—*Megantereon cultridens* (Cuvier 1824) and  
138 *Homotherium latidens* (Owen 1846)—and non-sabretooth felids *Acinonyx*  
139 *pardinensis* (Croizet & Jobert 1828), *Puma pardoides* (Owen 1846), and a *Lynx*  
140 species formerly described as *L. issiodorensis* based on very fragmentary remains  
141 (Kurtén and Crusafont 1977). This faunal assemblage shares 16 species with the  
142 French locality of Saint Vallier, which is the reference locality for the MN17  
143 biozone. As such, LPV has been correlated to the middle Villafranchian (Sinusía et  
144 al. 2004; Azanza et al. 2016; Morales 2016). In addition, LPV is

145 magnetostratigraphically placed in the magnetochron C2r1r, whose lower boundary  
146 is placed at 2.128 Ma and the upper at 1.945 Ma (ATNTS2012, see Gradstein et al.  
147 2012), and its age is roughly 2.05 (Sinusía et al. 2004).

148

## 149 **Materials and methods**

### 150 *Institutional and locality abbreviations*

151 **IGF**: Istituto Geologia di Firenze, Florence, Italy; **IPS**: collection of the Institut  
152 Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de  
153 Barcelona, Spain; **LPV**: La Puebla de Valverde; **MCL**: Musée des Confluences  
154 de Lyon, France; **MCNUZ**: Museo de Ciencias Naturales de la Universidad de  
155 Zaragoza, Zaragoza, Spain; **MNHN**: Muséum national d'Histoire naturelle,  
156 Paris, France; **MPZ**: collection of the former Museo Paleontológico de la  
157 Universidad de Zaragoza; **MZUF**: Università di Firenze, Museo Zoologico "La  
158 Specola", Florence, Italy; **Pp**: collection of the locality of Serrat d'En Vaquer  
159 housed in Musée des Confluences, Lyon; **UCBL-FSL**: Université Claude  
160 Bernard Lyon 1 Lyon, France.

161

### 162 *Anatomical abbreviations*

163 **C**: lower canine; **c:cond**: lower canine to condyle; **H**: height; **i1**: first lower  
164 incise; **i2**: second lower incise; **i3**: third lower incise; **J**: jaw; **L**: length; **m1**:  
165 first lower molar; **p3**: third lower premolar; **p3m1**: lower cheek teeth row; **p4**:  
166 fourth lower premolar; **W**: width.

167

### 168 *Study material and comparative sample*



169 This study focuses on a complete left hemimandible (MPZ 2020/470) of an Early  
170 Pleistocene *Lynx* from LPV housed in the MCNUZ (Table 1). The specimen has  
171 been compared from metrical and morphological viewpoints with fossil remains  
172 and casts of *L. issiodorensis* from Upper Val d'Arno, Olivola (Late Villafranchian,  
173 Italy) and Saint Vallier (Middle Villafranchian, France) housed in the IGF, and  
174 with medium-sized extant caracal (*C. caracal*), Iberian lynx (*Lynx pardinus*  
175 Temminck 1827) and Eurasian lynx (*Lynx lynx* Linnaeus 1758) housed in the  
176 MZUF. Photographs and measurements of *Caracal depereti* from Serrat d'En  
177 Vaquer (Depéret 1890) were also taken from original material (PER-109 housed in  
178 MNHN and Pp64 housed in MCL) and casts (UCBL-FSL 41162 and UCBL-FSL  
179 41163 housed in UCBL-FSL). Photographs of *L. issiodorensis* from Etouaires  
180 (Kurtén 1978) and *L. i. shansius* from Asia (Kurtén and Werdelin, 1984) were also  
181 used as comparative material. Additional data used for statistical analysis were  
182 obtained from available literature (Viret 1954; Werdelin 1981; Alcalá 1994;  
183 Morales et al. 2003; Meachen-Samuels and Van Valkenburgh 2009a, 2011; Garrido  
184 2008; Boscaini et al. 2016; Mecozzi et al. 2021). Measurements (see Figure 1b)  
185 were taken with a digital sliding calliper to the nearest of 0.1 mm. All  
186 measurements are in millimetres.

187 The comparative sample consists of 458 and 231 adult specimens (for bivariate  
188 and multivariate analyses, respectively) of Pliocene and Pleistocene medium-sized  
189 *C. depereti*, and *L. issiodorensis*, as well as extant *C. caracal* and *Le. serval* (Table  
190 2). Our dataset primarily focused on data published by Werdelin (1981), although it  
191 has been significantly updated through more recent data (e.g., Soto and Morales  
192 1985; Alcalá 1994; Arribas and Antón 1997; Alberdi et al. 1997; Montoya et al.  
193 1999, 2001; Morales et al. 2003; Garrido 2008; Meachen-Samuels and Van

194 Valkenburgh 2011; Cherin et al. 2013; Madurell-Malapeira et al. 2015; Boscaini et  
195 al. 2016; Mecozzi et al. 2021).

196

197 *Statistical analyses*

198 The lower dentition of Pliocene and Pleistocene lynx-like felids is often incomplete  
199 or badly preserved, with very similar dental proportions and analogous  
200 morphologies among the group. This entails difficulties to accurate identifications  
201 of the fossils at the species level. The same occurs for extant *Lynx* spp.

202 Accordingly, as an innovative approach, this work focuses largely on morphometric  
203 analyses rather than classical morphological comparisons. Bivariate diagrams were  
204 used to detect possible dimensional differences between teeth of MPZ 2020/470  
205 and those of living and extinct lynxes, caracals and serval.

206 Principal Component Analyses (PCA) for assigning a taxonomic attribution to  
207 the fossil remains were performed using 8 variables of the lower dentition—which  
208 represent the most complete assemblage of measurements (cL, cW, p3L, p3W, p4L,  
209 p4W, m1L, and m1W) performed to date—. It is important to stress that lower  
210 teeth, and all mandibles in general, are the most common remains for  
211 Plio/Pleistocene lynxes, while maxillary bones are very scarce. The height of c, p3,  
212 p4 and m1 was not considered for analysis because the main cuspids of these  
213 elements are most exposed to wear and could mislead results. A first PCA was  
214 performed using the 8 raw variables on the lower dentition, and a second PCA was  
215 carried out using the Mosimann transformation (Mosimann and James 1979), a  
216 methodology that reduces the allometry caused by size differences (see  
217 Meachen-Samuels and Van Valkenburgh 2009a; Jović et al. 2014; Ercoli et al.  
218 2019; Valenciano & Baskin, in press). The PCA and the bivariate diagrams were

219 performed using the Palaeontological Statistics PAST statistical software package  
220 (Hammer et al. 2001).

221

## 222 **Systematic palaeontology**

223

224 Order Carnivora Bowdich, 1821

225 Family Felidae Fischer, 1817

226 Subfamily Felinae Fischer, 1817

227 Genus *Lynx* Kerr, 1792

228 *Lynx* aff. *issiodorensis*

229 (Figure 2; Table 1)

230 1977 *Lynx issiodorensis* Kurtén and Crusafont: 33.

231

## 232 **Locality**

233 La Puebla de Valverde, Teruel, Spain.

234

## 235 **Age**

236 Early Pleistocene, MN17, Villafranchian. Magnetostratigraphically placed in the  
237 middle of the magnetochron C2r1r (2.128-1.945 Ma):  $2.05 \pm 0.095$  Ma (Sinusía et  
238 al. 2004; Gradstein et al. 2012).

239

## 240 **Referred material from La Puebla de Valverde**

241 IPS 27251, right m1, fragmented C, and fragmented mandible with c, both without  
242 catalogue number (Kurtén and Crusafont 1977).

243

244 **New material**

245 MPZ 2020/470, left hemimandible with i3, canine and p3-m1, including the most  
246 rostral part of the right hemimandible and the i1.

247

248 **Remarks**

249 The taxonomic status at the genus level of the Issoire felid has been controversial  
250 since the discovery of the first fossil remains. It was first attributed to *Felis* by  
251 Croizet and Jobert (1828) and then moved to *Lynx* and *Caracal* by Gervais (1852)  
252 and Depéret (1890), respectively. Although later authors (e.g., Kurtén and  
253 Crusafont 1977; Kurtén 1978; Werdelin 1981; Montoya et al. 1999, 2001) have  
254 also classified it as *Lynx*, Morales et al. (2003) rescued the hypothesis of Depéret  
255 (1890) and ascribed it into *Caracal* according to differences in the dental  
256 proportions and the postcranial skeleton. This hypothesis has not been followed,  
257 and most authors (e.g., Garrido 2008; Cherin et al. 2013; Ghezze et al. 2015;  
258 Boscaini et al. 2016) consider its attribution into *Lynx* as more suitable. Such a  
259 disagreement is mostly based on the highly convergent dentition of both genera,  
260 being felids with comparable dentition and lifestyles but occupying different  
261 ecosystems. Extant phylogenies based on molecular data (Bininda-Emonds et al.  
262 1999; Johnson et al. 2006; Li et al. 2016) point that both genera are significant  
263 different. According to Johnson et al. (2006), the *Caracal* lineage, which comprises  
264 *Caracal* and *Leptailurus* (serval), branches off at ca. 8.5 Ma and represents the  
265 sister group of a clade including the lineages of the ocelot, lynxes, puma, and small  
266 cats of the Old World (leopard cat and domestic cat). In addition, the genus *Lynx*,  
267 splitting off at ca. 7.2 Ma (Johnson et al. 2006), includes four species from Eurasia  
268 and North America, and conforms the sister group of the clade comprising the

269 lineages of the puma, and the small cats of the Old World. Werdelin et al. (2010,  
270 pag. 71) stated “an intriguing recent suggestion is that ‘*Felis*’ *issiodorensis*, a  
271 species generally referred to the genus *Lynx* (Werdelin 1981) should instead be  
272 referred to *Caracal* (Morales et al. 2003). This conclusion is based on the  
273 observation that the metric analyses of Werdelin (1981) showed that specimens  
274 identified as belonging to *L. issiodorensis* were more similar to specimens of  
275 *Caracal* than to specimens of *Lynx*. This possibility deserves further study, but it is  
276 well to remember that it is just as likely that the similarities between *Caracal* and *L.*  
277 *issiodorensis* are shared ancestral characters”. Thus, more complete remains of the  
278 whole skeleton of ‘*F*’ *issiodorensis*, and/or further molecular data would help  
279 clarify its adscription at the genus level.

280

### 281 **Description**

282 The hemimandible (Figure 2; Table 1) is well preserved, despite the dorsal part of  
283 the coronoid process and both the medial part of the articular and the angular  
284 processes are absent. It preserves part of the mandibular symphysis for the right  
285 hemimandible, including an embedded i1. The symphysis is relatively vertical and  
286 includes two mental foramina under the incisor alveoli in each hemimandible.  
287 There is a vertical sigmoid suture on the symphysis. The surface of the mandibular  
288 corpus is dissected by a few shallow fractures, caused by diagenetic processes. The  
289 horizontal ramus is low with a single mental foramen located under the p3 in the  
290 lateral (labial) side, and another one below the coronoid process in the medial  
291 (lingual) side. Ventrally, there is a scar for the *M. digastricus* on the most distal  
292 area. The ascending ramus and the coronoid process are heavily inclined  
293 backwards. The apex of the coronoid process slightly extends beyond the articular

294 process. In lateral view, there is a small and weak crest for the *M. masseter pars*  
295 *superficialis* which runs along the base of the masseteric fossa towards the angular  
296 process. The articular process is aligned with the dental cheek teeth row. The  
297 masseteric fossa is deep, and its rostral reaches the distal margin of the m1. The  
298 preserved teeth are the i3, c, p3, p4, and m1. The i3 is unicuspidal and  
299 buccolingually widened. Its cuspid is worn. The c is well developed, robust, with  
300 the typical feline groove over the buccodistal area. The c-p3 diastema is 8 mm long.  
301 The p3 is broken. Its main cuspid is missing. It has a partially preserved distal  
302 accessory cuspid. There is a small cingulid in the distolingual side of the tooth. The  
303 p4 is robust and elongated with both mesial and distal accessories cuspids, which  
304 are rounded and compressed buccolingually. The main cuspid and the distal ones  
305 are slightly worn. A robust distal cingulid is located in the distal area. The m1  
306 protoconid is slightly higher than the paraconid but of similar mesiodistal length.  
307 Both mesial and distal edges of the m1 are almost vertical in lateral view. The  
308 metaconid is absent and the talonid is barely visible as a non-significant convexity  
309 of the distolingual wall of the protoconid.

310

## 311 **Results**

### 312 ***Bivariate analysis***

313 MPZ 2020/470 shows (relatively) small dental dimensions if compared with other  
314 lynxes such as *L. lynx* or *L. issiodorensis*. The p3 of MPZ 2020/470 is plotted in the  
315 variability range of *Le. serval*, falling very close to the smallest species of *Lynx* (*L.*  
316 *pardinus* and *Lynx rufus* Schreber 1776) and the largest specimens of *C. caracal*  
317 (Figure 3a; Figure Supplemental 1). It also plots very close to the smallest  
318 specimens of *C. depereti* from Layna, whose larger specimens overlap with the

319 smallest specimens of *L. issiodorensis* represented by the subspecies *L. i.*  
320 *valdarnensis*. The p4 is comparable to that of *L. pardinus* and *Lynx canadensis*  
321 Kerr, 1792, as well as to the small *L. issiodorensis* from Asian localities, Val  
322 d'Arno and Saint Vallier (Figure 3b; Figure Supplemental 1). As in the p3 and p4,  
323 the m1 plots close to the variability range of small lynxes. It falls within extinct and  
324 extant *L. pardinus*, extant *L. canadensis*, and the smaller individuals of *L.*  
325 *issiodorensis*, and *C. depereti* from Layna (Figure 4; Figure Supplemental 2).  
326 *Caracal depereti* (UCBL-FSL 41162) from Serrat d'En Vaquer (Perpignan, France)  
327 and *L. issiodorensis* (MNHN 586) from the type locality display the most robust  
328 m1 among the whole sample. The m1 from LPV (IPS 27251) tentatively ascribed to  
329 *L. issiodorensis* by Kurtén and Crusafont (1977) is larger (L= 15.3 mm, W= 6.7  
330 mm) than the m1 of MPZ 2020/470. Most of the *L. issiodorensis* specimens have  
331 longer and wider lower carnassial than MPZ 2020/470 and overlap with the  
332 variability of extant *L. lynx* and extinct *L. pardinus*, whereas the specimen from the  
333 Vallparadís estació (IPS 60461) is the largest *L. pardinus* among the sample  
334 (Figures 3-4; Figures Supplemental 1-2).

335

### 336 ***Multivariate analyses***

337 The first PCA (Figure 5, Table 3; Figure Supplemental 3) shows the taxa ordered  
338 along the first component (PC1, that explains the 91.784% of the total variance). It  
339 depicts the smallest specimens on the left (*L. rufus*, *Le. serval* and *C. caracal*) and  
340 the largest on the right (*L. lynx*, *L. issiodorensis* and *C. depereti* from Serrat d'En  
341 Vaquer), thus indicating that the PC1 is size-related. That is, due to the influence of  
342 size in the analysis, this PCA does not show taxonomic relationships among the  
343 taxa. On the contrary, the second PCA (Figure 6; Table 3; Figure Supplemental 4)

344 performed using the Mosimann transformation depicts taxa with no isometric  
345 effect, and clearly shows differences in the dental proportions among the groups.  
346 The first two components (Figure 6) account for the 66.18 % of the total variance  
347 (PC1=40.621%; PC2=25.564%). *Lynx pardinus* (extinct and extant), *L. canadensis*,  
348 *C. caracal*, and MPZ 2020/470 show positive scores and are separated from *L. lynx*  
349 and *L. issiodorensis* with negative scores along the PC1 (Figure 6). Factor loadings  
350 of PC1 indicate that the former taxa have larger p4 and m1, while *L. lynx*, and *L.*  
351 *issiodorensis* display larger and wider c. It is noteworthy to mention that specimens  
352 from Ingarano (Mecozzi et al. 2021) ascribed to *L. pardinus* fall closer to the  
353 Issoire lynx group rather than to extant and fossil Iberian lynx specimens, having a  
354 relatively more developed canine. The PC2 clearly separates *Le. serval* (with  
355 positive score, depicted by relatively long p3 and p4) from *L. pardinus* (with  
356 negative score, characterised by long m1 and, to a lesser extent, higher cL and cW).  
357 Also, *L. rufus* has intermediate values on both PCs. MPZ 2020/470 falls somewhat  
358 far from the Issoire lynx subspecies, which (almost) completely overlap each other.  
359 However, it is plotted close to *L. issiodorensis* from Saint Vallier, which has the  
360 most positive value in the PC1 among all *L. issiodorensis*. Also, *C. depereti* from  
361 Serrat d'En Vaquer is placed far from the variability range of *L. issiodorensis*,  
362 depicted by long and wide c.

363

## 364 **Discussion**

### 365 *Taxonomic attribution of the felid from LPV*

366 Although small to medium-sized felids are common from the Miocene onwards,  
367 they show a low diversity and abundance in the fossil record (Werdelin et al. 2010),  
368 being customarily reported during the Pliocene (Ruscinian) and specially through



369 the Pleistocene (Villafranchian). Among these later (non-Miocene) forms, it is  
370 important to underline the presence of the medium-sized lynx-like *Felis christoli*  
371 Gervais (1852) (Ficarelli and Torre 1975) from the Early Pliocene of Montpellier  
372 (MN14) (France) (Gervais 1852); *C. depereti* from the Early Pliocene of La Gloria  
373 4 and La Calera (MN14) (Spain) (Alcalá 1994; Morales 2016), Layna (MN15)  
374 (Spain) (Morales et al. 2003), and Serrat d'En Vaquer (MN15) (France) (Depéret  
375 1890); and *L. issiodorensis* from several Plio/Pleistocene localities of Eurasia  
376 (Kurtén 1978; Werdelin 1981; Kurtén and Werdelin 1984; Boscaini et al. 2016).  
377 All these felids are described upon very scarce material—except the Issoire felid  
378 from Etouaires and Saint Vallier—, and their intraspecific variability is far from  
379 being completely understood. This has prompted to a systematic debate at the genus  
380 level (i.e., *Lynx/Caracal*) that is difficult to resolve with the exclusive use of the  
381 dental morphology currently available.

382       The genus *Lynx* is among the most common carnivorans of the European Plio-  
383 Pleistocene faunal assemblages. So far, its early record in Europe refers to *L.*  
384 *issiodorensis* from the early Villafranchian (ca. 2.6 Ma) site of Etouaires (Kurtén  
385 1978), being common in the Villafranchian of western Europe and Asia (Werdelin  
386 1981). Additionally, this taxon is recorded in the Spanish Pliocene site of Cuevas  
387 de Almanzora (Montoya et al. 2001), as well as in MN16 Iberian localities of  
388 Piedrabuena, Villaroya and El Rincón-1 (Alberdi et al. 1997; Arribas and Antón  
389 1997; Morales 2016), and MN17 sites of Almenara, Fonelas P-1, and LPV (Kurtén  
390 and Crusafont 1977; Soto and Morales 1985; Garrido 2008). MPZ 2020/470 shares  
391 several traits with this species, such as a rectilinear symphysis, a long diastema  
392 between the lower canine and the p3, a well-developed mesial and distal accessory  
393 cuspids in the p4, a m1 without metaconid, a deep masseteric fossa, and a high

394 coronoid process backwardly tilted. These traits are also found in *L. issiodorensis*  
395 from the type locality of Etouaires (Kurtén 1978), and *C. depereti* from Serrat d'En  
396 Vaquer (Depéret 1890). Nevertheless, it differs from the former population in the  
397 absence of diastema between p3-p4, and in a less robust mandible with a slenderer  
398 mandibular corpus and a lesser mesiodistal width of the coronoid process, which is  
399 relatively more backward inclined. In this sense, the mandible and dentition  
400 resemble that of the small-sized *L. issiodorensis* from Saint Vallier (Viret, 1954).

401       Metrically, the teeth of MPZ 2020/470 (Figures 3-4) are smaller than those of *L.*  
402 *issiodorensis* and *L. lynx*, whereas they are closer to those of small extant lynxes  
403 such as the Iberian lynx (*L. pardinus*), the New-World lynxes (*L. rufus* and *L.*  
404 *canadensis*), and the smaller specimens of *C. depereti* from Layna described in  
405 Morales et al. (2003). PCA results based on Mosimann ordination (Figure 6)  
406 indicate differences in the dental proportions among the groups, which are instead  
407 difficult to detect through classical morphological comparisons. Our findings  
408 indicate that MPZ 2020/470 differs from most of the specimens of *L.*  
409 *issiodorensis*—including the specimens from the type locality and the more  
410 complete specimens from Cuevas de Almanzora (Montoya et al. 2011) and Fonelas  
411 P-1 (Garrido 2008)—by showing a relatively more elongated p4 and m1, more  
412 comparable to *L. pardinus*, and *L. canadensis*.

413       The left mandible of *L. issiodorensis* from Fonelas P-1 was previously described  
414 as *L. i. valdarnensis* by Garrido (2008). It is a very worn specimen with a broken  
415 m1 and a missing ascendant ramus which is located in our PCA between the  
416 population of *L. issiodorensis*—with the less negative scores in the PC1—and the  
417 more negative score of the PC1 of *L. pardinus*. This is in agreement with Garrido  
418 (2008), as it may represent an intermediate stage between the last populations of *L.*

419 *i. valdarnensis* and the first populations of the Early Pleistocene Iberian cave lynx  
420 (formerly named *Lynx pardinus spelaeus* or *Lynx spelaeus*, but recently  
421 synonymised with *L. pardinus* in Boscaini et al. 2016). LPV and Fonelas P-1 are  
422 nearly contemporaneous, being the former slightly older. The specimen from LPV  
423 lacks the metaconid and the talonid complex, and it has a relatively more elongated  
424 m1 and p4—showing more positive scores in the PC1—than the individual from  
425 Fonelas P-1 (Figure 6). MPZ 2020/470 falls close to *L. issiodorensis* (QSV 1132)  
426 from Saint Vallier (Figure 6), interpreted by Viret (1954) as a female on the basis  
427 of its small lower canine. It also shares a similar slender morphology of the  
428 mandibles with all the specimens from Saint Vallier. A second specimen from Saint  
429 Vallier (QSV 1131, a male according to Viret 1954) shows more developed  
430 canines, and falls in the PCA closer to the specimens from Etouaires (Figure 6).  
431 The felid from LPV has a relatively wider lower canine, a reduced p3, and a  
432 relatively longer p4, with a less developed distal accessory cuspid—but it is  
433 important to remark that the p3 is partially broken, so its entire width would be  
434 indeed similar to that of Saint Vallier. During the 1970's, *L. issiodorensis* was  
435 tentatively reported in LPV based on three isolated teeth, including the m1 IPS  
436 27251 (Kurtén and Crusafont 1977). Although the m1 of MPZ 2020/470 is smaller  
437 than the m1 IPS 27251 (Figure 4), both teeth are similar in morphology and share a  
438 simplified m1 with a talonid-metaconid complex absent. Accordingly, they can be  
439 therefore considered as belonging to the same species. Moreover, Mecozzi et al.  
440 (2021) quoted 3 m1s of *Lynx issiodorensis* from LPV, indicating that there are 2  
441 unpublished m1 which were not reported in Kurtén and Crusafont (1977).  
442 Unfortunately, and because these authors did not describe, figure, or provide  
443 catalogue number for the specimens, we cannot establish a comparison with MPZ

444 2020/470. Only the length of one m1 was provided (14.2 mm), which is  
445 intermediate between IPS 27251 and MPZ 2020/470. After removing the influence  
446 of allometry (Figure 6), the multivariate analysis of the lower dentition indicates  
447 that all specimens of *L. issiodorensis* (with the exception of one individual from  
448 Saint Vallier, Fonelas-1 and LPV) overlap. However, it is worth to mention that  
449 they are still placed close to the group of *L. issiodorensis*. Consequently, and due to  
450 strong similarities in the mandible and dentition with *L. issiodorensis* from Saint  
451 Vallier, in conjunction with the previously noted differences, and having in mind  
452 the scarce material from the site, we ascribed MPZ 2020/470 to *Lynx* aff.  
453 *issiodorensis*.

454 The Iberian lynx (*L. pardinus*) conforms an additional species of *Lynx* with a  
455 wide range in the Iberian and western European record during the Pleistocene  
456 (Boscaini et al. 2015). The so-called ‘cave lynx’ *Lynx spelaeus* (Boule, 1919) is a  
457 related form that occurred in southwestern Europe during the Middle-Late  
458 Pleistocene. It represents a close form to *L. pardinus* with larger body size (e.g.,  
459 Bonifay 1971; Mecozzi et al. 2021). There is no agreement about its taxonomic  
460 status, being a valid species for some authors (e.g., Bonifay 1971; Ghezzi et al.  
461 2015), and invalid species and *L. pardinus sensu lato* for others (e.g., Boscaini et al.  
462 2016, Mecozzi et al. 2021), or even a subspecies of the Iberian lynx *L. pardinus*  
463 *spelaeus* (e.g., Werdelin 1981; Fosse et al. 2021). Recent data (Boscaini et al. 2015)  
464 suggest that the oldest occurrence of *L. pardinus* is found in the late Early  
465 Pleistocene locality of Avenc Marcel cave (Spain), ca. 1.5-1.7 Ma. Most of the  
466 diagnostic features of extant *L. pardinus*—longer and narrower m1; reduced  
467 accessory distal margin on p4, confluence of the lacerum posterius and anterior  
468 condyloid foramina, long and lyre-shaped temporal ridges, and shorter sagittal crest

469 according to Bonifay (1971), Werdelin (1981), García-Perea et al. (1985), García-  
470 Perea (1996) and Boscaini et al. (2015)—, are observed in the cranium, so it is  
471 difficult to perform a direct comparison with MPZ 2020/470. The first PCA with  
472 untransformed variables (Figure 5) shows MPZ 2020/470 near the morphospace of  
473 *L. canadensis* and *L. pardinus* and more specifically closer to *L. pardinus*, formerly  
474 known as *Lynx spelaeus* (following Boscaini et al. 2016). However, when the  
475 allometric factor is removed (Figure 6), our results indicate that MPZ 2020/470  
476 differs from *L. pardinus* in having longer p4 and a relatively shorter m1. Also  
477 importantly, and following findings from our Mosimann transformation (Figure 6),  
478 *L. pardinus* from Ingarano differs from extant *L. pardinus* in having more  
479 developed canines and shorter m1, which could suggest a certain degree of  
480 differentiation between the fossil from this locality and the extant forms.

481 Another felid strongly linked to *L. issiodorensis* is *C. depereti*, a typical element  
482 of the Early Pliocene carnivore assemblages, customarily more limited to the  
483 Ruscinian of western Europe (and hence older than the earliest record of *L.*  
484 *issiodorensis*) (e.g., Werdelin 1981; Morales et al. 2003; Cipullo 2010; Morales  
485 2016). It was initially defined by Morales et al. (2003) from fossil remains from  
486 Layna and Serrat d’En Vaquer (MN15), though its earliest occurrence dates from  
487 La Gloria 4 and La Calera (MN14) (Alcalá 1994; Morales 2016). The absence of  
488 suitable skulls and mandibles of this form makes its systematic position  
489 controversial. A primitive subspecies of *L. issiodorensis*, (named as *L. issiodorensis*  
490 ssp.1) well distinguished from the other forms of *L. issiodorensis* has been  
491 proposed (Cipullo 2010). More recently, Boscaini et al. (2016) and Mecozzi et al.  
492 (2021) consider this taxon as a junior subjective synonym of *L. issiodorensis* based  
493 on its dentognathic morphology. However, there is no explanation for such a

494 conclusive statement. In our opinion, while the knowledge of this taxon is limited  
495 and its ascription to *Caracal/Lynx* is highly debatable, its validation at the species  
496 level is not questionable. Morales et al. (2003) distinguished *C. depereti* from *L.*  
497 *issiodorensis* on the basis of several postcranial and dentognathic traits, such a  
498 smaller size, slenderer P4, p3, and p4, and a greater width of the trochlea of the  
499 humerus and great development of the acromion of the scapula. The slender lower  
500 dentition of *C. depereti* including the lower carnassial is evident from our plots  
501 (Figures 3-4), except for the p4 and the m1 of some specimens (UCBL-FSL-41162  
502 and 41163) from Serrat d'En Vaquer. Only a single *C. depereti* specimen from  
503 Serrat d'En Vaquer with complete lower dentition was available to be included in  
504 multivariate analyses, but it clearly separates from the remaining *L. issiodorensis*,  
505 thus showing a quite short p4 and m1. This specimen, in addition to the  
506 morphological differences described previously, might confirm the validation as a  
507 distinct species. Nonetheless, one specimen precludes its attribution as either  
508 *Caracal* or *Lynx*, so we prefer to maintain its original determination until more  
509 complete material can be available. It is noteworthy that MPZ 2020/470 from LPV  
510 has similar proportions in the lower dentition to specimens from Layna (Figures 3-  
511 4), but it differs in several morphological traits, such as a p4 with shorter  
512 mesiodistal length of the main cuspid, including a more developed distal accessory  
513 cuspid, and a more reduced m1 talonid. Moreover, it also differs with UCBL-FSL  
514 41162 and 41163 in having a relatively slender m1 (Figure 4), a smaller length and  
515 width of the c, a shorter length of the p3 (Figure 6) and a more elongated m1 in  
516 relation to the lower dentition.

517 Finally, MPZ 2020/470 clearly differs from *F. christoli* from Montpellier  
518 (Gervais 1852; Ficarelli and Torre 1975) in having a slenderer mandibular corpus, a

519 relatively longer p4, and more derived m1 with an absent talonid. All these features  
520 discard its taxonomic assignation into this Early Pliocene taxon.

521

522 ***Caracal or Lynx: the use of multivariate analysis and Mosimann shape variables***  
523 ***to clarify and explain systematic affinity***

524 As previously explained, it exists a long-standing controversy over the systematic  
525 assignation of Plio/Pleistocene felids of intermediate size from Europe, and whether  
526 they belong to *Caracal* or *Lynx*. All the diagnostic traits to distinguish *Lynx* and  
527 *Caracal* are based on cranium and upper dentition (see Werdelin and Peigné 2010),  
528 with the consequent difficulty in differentiating these two forms based exclusively  
529 on mandibles and lower dentition. Whereas the hypothesis of Morales et al. (2003)  
530 that considers the genus as *Caracal* relies on upper and lower dentition (as well as  
531 in some postcranial traits), our Mosimann transformation fails to classify the Issoire  
532 lynx as *Caracal*, as all analysed specimens plot in the opposite corner of its  
533 morphospace (Figure 6 and Figure Supplemental 4). This transformation has been  
534 previously used for taxonomical purpose in felids and other taxa (e.g., Jojić et al.  
535 2014; Ercoli et al. 2019; Valenciano & Baskin, in press) and represents a powerful  
536 (although still very little explored) tool in systematic palaeontology. Individuals of  
537 *L. issiodorensis* (except MPZ 2020/470, one individual from Saint Vallier, and one  
538 individual of *L. i. shansius*) have negative values for the PC1, whereas specimens  
539 of *C. caracal* have positive values. This is probably due to the fact that *L.*  
540 *issiodorensis* has larger canines, while *C. caracal* has longer p4 and m1 compared  
541 with *L. issiodorensis*. In fact, the Issoire lynx is clearly different from the caracal  
542 group in both the bivariate and the multivariate analysis (Figures 3-4 and 6). It is  
543 therefore the first time that quantitative data to support the adscription of the Issoire

544 lynx into *Lynx* instead into *Caracal* are provided. Said this, the case of *C. depereti*  
545 deserves further analysis, and we cannot assume its ascription to *Lynx* due to the  
546 small sample of this species in all the fossil sites.

547

#### 548 ***Palaeoevolutionary insights***

549 The resemblance among *L. aff. issiodorensis* from LPV, *L. issiodorensis* from Saint  
550 Vallier, and the Iberian lynx is clear. Overall, these forms exhibit slenderer  
551 mandibles and an elongation of the carnassial teeth (m1 and P4), which is more  
552 emphasised in living *L. pardinus* and *L. canadensis* (Figure 6). This may entail  
553 some remarkable evolutionary implications.

554 Previous studies on extant taxa demonstrated dietary specialization in medium-  
555 sized felids (Meachen-Samuels and Van Valkenburgh 2009b). Thus, *L. lynx* was  
556 interpreted as a large prey specialist due to its relatively robust canines, incisors,  
557 and wide muzzles, whereas *L. pardinus* and *L. serval* were classified as small prey  
558 specialists according to their smaller canines, narrower muzzles and slightly longer  
559 mandibles. These anatomic features provide *L. pardinus* and *L. serval* with a speed  
560 advantage when catching small and fast preys. Previous interpretations (Kurtén  
561 1978; Werdelin 1981) based on postcranial locomotor adaptation suggested a less  
562 remarkable specialisation for *L. issiodorensis* when compared to extant lynxes, and  
563 hence an adaptation to hunt medium-sized ungulates rather than lagomorphs, as  
564 seen today in *L. lynx*. More recent interpretations based on the postcranial skeleton  
565 and body mass inferences (Meloro 2011; Mecozzi et al. 2021) confirmed this view,  
566 and depicted *L. issiodorensis* as a form with a body mass similar to that of the  
567 larger individuals of *L. lynx* with a similar hunting strategy. Our findings lend  
568 support to this reconstruction of *L. issiodorensis* and provide data on a different



569 trend in *L. aff. issiodorensis* from LPV. According to our PCA results (Figure 6 and  
570 Figure Supplemental 4), all the analysed *L. issiodorensis* (except MPZ 2020/470,  
571 one specimen from Asia and one specimen from Saint Vallier) overlap with *L. lynx*,  
572 which is interpreted as a large prey specialist by Meachen-Samuels and Van  
573 Valkenburgh (2009b). MPZ 2020/470 differs from the rest of *L. issiodorensis* in  
574 having less developed canines and relatively elongated p4 and m1 (Figure 6 and  
575 Figure Supplemental 4), thus falling between the small prey specialist *L. pardinus*  
576 and the mixed prey specialist *L. canadensis*. This may indicate a similar dietary  
577 adaptation for *L. aff. issiodorensis* from LPV. These results agree with previous  
578 interpretation (Krofel et al. 2012; Viranta et al. 2021) which infer the switch in the  
579 diet from *L. issiodorensis* (large prey hunter) to forms of lynx with a relatively  
580 small body size and small prey specialists as a response to competition with  
581 sabertooth and pantherine felids, as well as to the probable pressure from  
582 scavengers. Therefore, the different dental proportions between *L. aff. issiodorensis*  
583 and *L. issiodorensis* from other contemporaneous localities in Europe (e.g., from  
584 Fonelas P-1, Val d'Arno, and Olivola) may suggest that the former probably  
585 underwent a change in its diet through smaller preys. More complete material of *L.*  
586 *aff. issiodorensis* from LPV including complete lower and upper dentition would  
587 indeed help to test this hypothesis.

588

## 589 **Conclusions**

590 We confidently confirm the record of *Lynx aff. issiodorensis* in the Early  
591 Pleistocene site of La Puebla de Valverde (Spain), based on metrical,  
592 morphological, and statistical analyses of a new mandible and lower dentition.  
593 This finding updates the systematic of the genus *Lynx* and extends its

594 geographical distribution in the European fossil record. MPZ 2020/470  
595 represents the smallest *L. issiodorensis* described to date, even when compared  
596 with ISP 27251 from the same locality which was tentatively ascribed to *L.*  
597 *issiodorensis* a few decades ago. As a novelty, we provide the first multivariate  
598 approach of the lower dentition of Plio/Pleistocene medium-sized felids from  
599 Europe and Asia, which also includes all extant species of lynx, and the African  
600 caracal and serval.

601 It is for the first time that we can provide quantitative data to contradict the  
602 attribution of *L. issiodorensis* to the genus *Caracal*, and support instead the view  
603 that the Plio-Pleistocene Issoire lynx should be attributed to *L. issiodorensis*.  
604 However, additional analyses comprising a wider sample size would be required  
605 to test the taxonomic attribution of the early Pliocene *C. depereti*. Finally, from a  
606 palaeobiological viewpoint, we interpret the lynx from LPV as a small/medium  
607 prey specialist, probably comparable to extant *L. pardinus* and *L. canadensis*.

608

### 609 **Acknowledgements**

610 We thank P. Agnelli (MZUF), E. Cioppi (IGF), and J. Robles (ICP) for granting  
611 access to comparative material under their care. We are also grateful to L. Werdelin  
612 (NRM) who kindly provided raw data for living lynxes, and J. Meachen (DMU) for  
613 sharing comparative data of *Caracal caracal* and *Leptailurus serval* from  
614 Meachen-Samuels and Van Valkenburgh (2011). We are indebted to P. Mazza  
615 (UNIFI) for valuable comments on fossil *Lynx*, J. Morales (MNCN) for  
616 measurements of extant *L. pardinus* and extinct *C. depereti*, E. Roberts (UCBL)  
617 and D. Berthet (MC Lyon) for pictures of *C. depereti*, J. Madurell-Malapeira (ICP)  
618 for pictures and provide the catalogue number of the m1 (IPS 27251) of *L.*

619 *issiodorensis* described in Kurtén and Crusafont (1977), L. Costeur (NMB) for  
620 pictures of *L. issiodorensis* from Etouaires; and Q. Jiangzou (Peking University) for  
621 pictures of *L. issiodorensis shansius* from China described in Kurtén and Werdelin  
622 (1984). The authors thank the Editor G. Dyke and two anonymous reviewers for  
623 their helpful criticism and comments on a previous version of the manuscript. This  
624 study was funded by the Government of Aragon (Group ref. E33\_20R), the Spanish  
625 Research Projects PGC2018-094122-B-100 and PID2020-116220GB-I00 (AEI/  
626 FEDER, UE), the Research Group UCM 910607, and the “Juan de la Cierva  
627 Formación” program (FJC2018-036669-I to A.V.) from the Spanish Ministry of  
628 Science, Innovation, and Universities.

629

### 630 **Disclosure statement**

631 No potential conflict of authors was reported by the authors.

632

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905

#### 906 **Figure captions**

907 **Figure 1.** Location of La Puebla de Valverde fossil site and measurements. A,  
908 Geographic and geological location of the site. Geological scheme modified from  
909 Cortés (1999). B: Diagram showing measurements on MPZ 2020/470. See the  
910 Material and Methods section for abbreviations.

911 **Figure 2.** Left hemimandible MPZ 2020/470 of *Lynx* aff. *issidorensis* from La  
912 Puebla de Valverde. A: buccal view. B: lingual view; C: occlusal view. Scale bar 2  
913 cm.

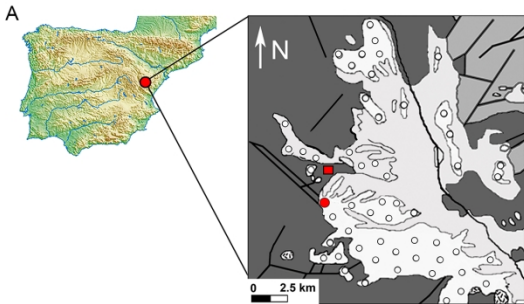
914 **Figure 3.** Bivariate plot of the length (L) and width (W) of the p3 and p4 of extant  
915 lynxes, caracal and selected Plio/Pleistocene felids of intermediate size (localities  
916 of *Lynx issidorensis* and *Lynx pardinus* s.l. are simplified). A: p3; B: p4.

917 **Figure 4.** Bivariate plot of the length (L) and width (W) of the m1 of extant lynxes,  
918 caracal and selected Plio/Pleistocene felids of intermediate size (localities of *Lynx*

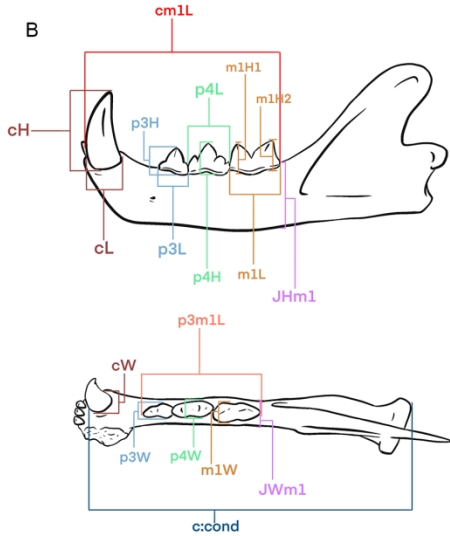
919 *issiodorensis* and *Lynx pardinus* s.l. are simplified).

920 **Figure 5.** Principal Component Analysis of 8 linear measurements for the lower  
921 dentition based on raw variables (localities of *Lynx issiodorensis* are simplified).

922 **Figure 6.** Principal Component Analysis of 8 linear measurements (Mosimann  
923 variables) for the lower dentition (localities of *Lynx issiodorensis* are simplified).



- La Puebla de Valverde village
- LPV (fossil site)
- Plio/Pleistocene
- Miocene
- Cretaceous
- Jurassic
- Triassic





A



B

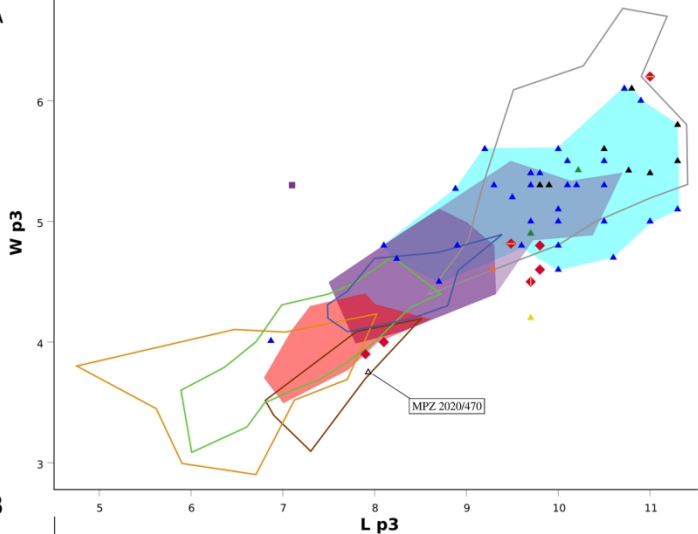


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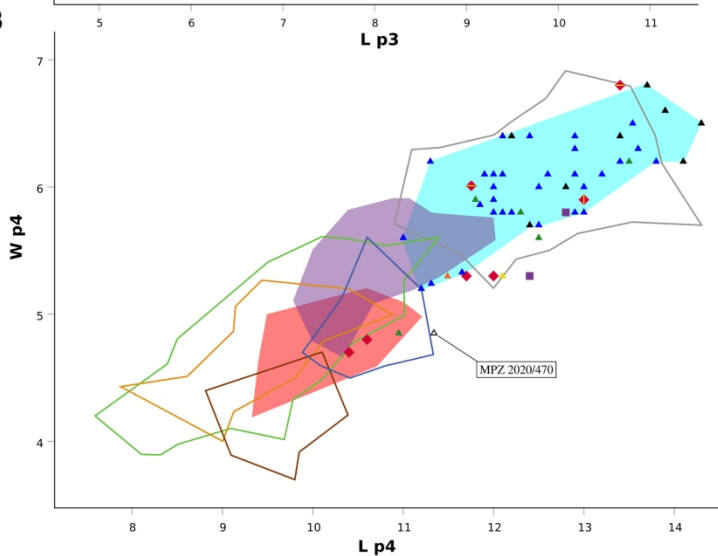
C



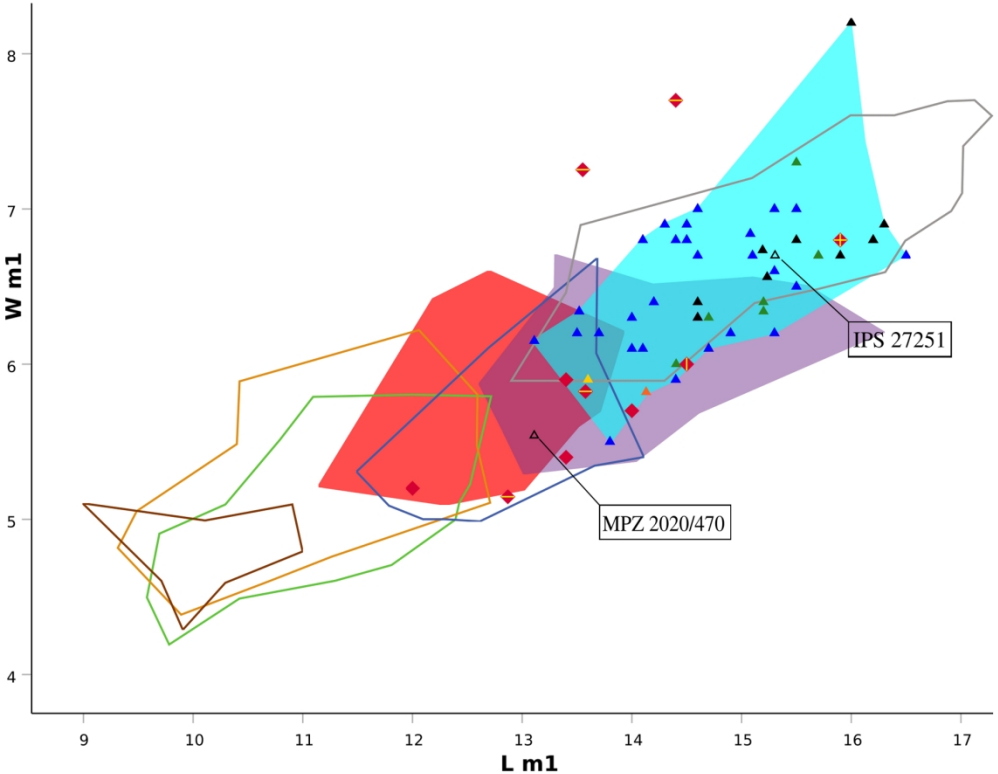
A



B



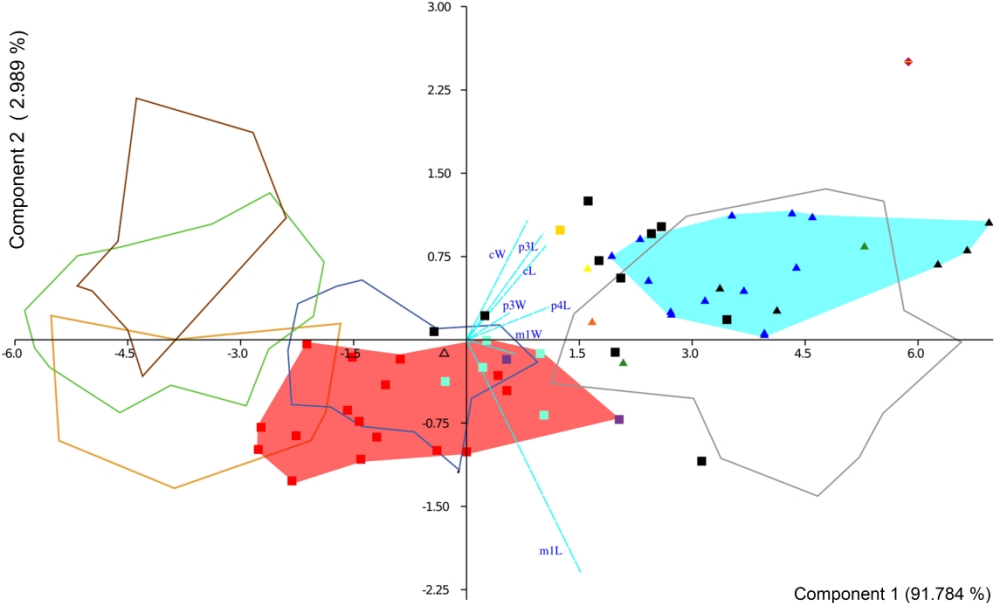
- ◆— *Caracal caracal*
- ◆ *Caracal depereti* (Layna)
- ◆ *Caracal depereti* (La Calera)
- ◆ *Caracal depereti* (Serrat d'En Vaquer)
- ▲ *Lynx issiodorensis* (Perrier-Étouaires)
- ▲ *Lynx issiodorensis* ssp.
- ▲ *Lynx issiodorensis* (Cuevas de Almanzora)
- △ MPZ 2020/470
- ▲ *Lynx aff. issiodorensis* (LPV)
- ▲ *Lynx issiodorensis* (Saint Vallier)
- ▲ *Lynx issiodorensis* (Fonelas P-1)
- ◆— *Leptailurus serval*
- ◆— *Lynx canadensis*
- *Lynx lynx*
- *Lynx pardinus* (extant)
- *Lynx pardinus* (fossil)
- ◆— *Lynx rufus*



- *Caracal caracal*
- ◆ *Caracal depereti* (Layna)
- ◆ *Caracal depereti* (La Calera)
- ◆ *Caracal depereti* (Serrat d'En Vaquer)
- ◆ *Caracal depereti* (La Gloria)
- ▲ *Lynx issiodorensis issiodorensis* (Perrier-Étouaires)

- ▲ *Lynx issiodorensis* ssp.
- ▲ *Lynx issiodorensis* (Cuevas de Almanzora)
- △ *Lynx aff. issiodorensis* (LPV)
- ▲ *Lynx issiodorensis* (Saint Vallier)
- ▲ *Lynx issiodorensis* (Fonelas P-1)

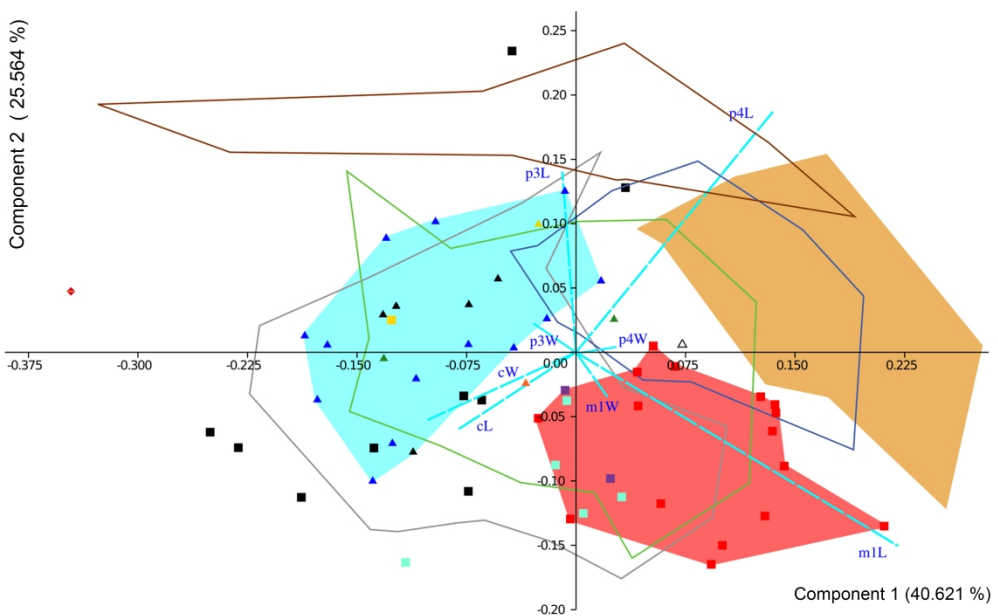
- *Leptailurus serval*
- *Lynx canadensis*
- *Lynx lynx*
- *Lynx pardinus* (extant)
- *Lynx pardinus* (fossil)
- *Lynx rufus*



- *Caracal caracal*
- ◆ *Caracal depereti* (Serrat d'En Vaquer)
- ▲ *Lynx issiodorensis issiodorensis* (Perrier-Étouaires)
- ▲ *Lynx issiodorensis ssp.*
- ▲ *Lynx issiodorensis* (Cuevas de Almanzora)

- △ *Lynx aff. issiodorensis* (LPV)
- ▲ *Lynx issiodorensis* (Saint Vallier)
- ▲ *Lynx issiodorensis* (Fonelas P-1)
- *Lynx rufus*
- *Lynx lynx*
- *Lynx canadensis*

- *Lynx pardinus* (extant)
- *Lynx pardinus* (fossil)
- *Lynx pardinus* (fossil, Gibraltar)
- *Lynx pardinus* (fossil, Vallparadis Estaciò)
- *Lynx pardinus* (fossil, Ingarano)
- *Leptailurus serval*



- *Caracal caracal*
- ◆ *Caracal depereti* (Serrat d'En Vaquer)
- ▲ *Lynx issiodorensis issiodorensis* (Perrier-Étouaires)
- ▲ *Lynx issiodorensis ssp.*
- ▲ *Lynx issiodorensis* (Cuevas de Almanzora)

- △ *Lynx aff. issiodorensis* (LPV)
- ▲ *Lynx issiodorensis* (Saint Vallier)
- ▲ *Lynx issiodorensis* (Fonelas P-1)
- *Lynx rufus*
- *Lynx lynx*
- *Lynx canadensis*

- *Lynx pardinus* (extant)
- *Lynx pardinus* (fossil)
- *Lynx pardinus* (fossil, Gibraltar)
- *Lynx pardinus* (fossil, Vallparadis Estaciò)
- *Lynx pardinus* (fossil, Ingarano)
- *Leptailurus serval*

**Table 1.** Measurements of *Lynx aff. Isslodorensis* from La Puebla de Valverde.

<b>cL</b>	<b>cW</b>	<b>cH</b>	<b>p3L</b>	<b>p3W</b>	<b>p3H</b>
7.6	6.1	13.5	7.9	3.7	
<b>p4L</b>	<b>p4W</b>	<b>p4H</b>	<b>m1L</b>	<b>m1W</b>	<b>m1H1</b>
11.3	4.8	7.0	13.1	5.5	
<b>m1H2</b>	<b>JHm1</b>	<b>JWm1</b>	<b>CM1L</b>	<b>p3m1L</b>	<b>c:cond</b>
7.5	15.6	8.2	48.0	32.1	89.5

In bold measurements used for statistical analysis. Abbreviations: **c:cond** – lower canine to condyle length; **cL** – lower canine length; **cH** – lower canine height; **cW** – lower canine width; **cm1L** – lower canine to lower molar length; **JHm1** – height of the mandibular corpus at the distal side of the lower molar; **JWm1** – width of the mandibular corpus at the distal side of the lower molar; **m1L** – lower molar length; **m1H1** – lower molar paracond height; **m1H2** – lower molar protocond height; **m1W** – lower molar width; **p3L** – third lower premolar length; **p3H** – third lower premolar height; **p3W** – third lower premolar width; **p3m1L** – lower teeth row length; **p4L** – fourth lower premolar length; **p4H** – fourth lower premolar height; **p4W** – fourth lower premolar.

**Table 2.** Comparative sample of study for analyses described in this work.

## Lower dentition

Species	Bivariate N	Multivariate N
<i>Caracal caracal</i>	14	9
<i>Caracal depereti</i>	12	1
<i>Leptailurus serval</i>	9	9
<i>Lynx issiodorensis</i>	52	23
<i>Lynx canadensis</i>	53	46
<i>Lynx lynx</i>	111	56
<i>Lynx pardinus</i>	80	34
<i>Lynx rufus</i>	127	53
Total	458	231

*Lynx pardinus* is composed by 20 extant and 60 extinct specimens in the bivariate analysis; 16 extant and 18 extinct specimens in the lower for the multivariate analysis. Abbreviations: N – number of individuals.

**Table 3.** Principal Component Analysis and Mosimann shape variables for the lower dentition. Percentages of variance and factor loadings of the linear variables obtained from the PCA and Mosimann transformation. Abbreviations:  $\lambda$  – Eigenvalues; **cL** – lower canine length; **cW** – lower canine width; **m1L** – lower molar length; **m1W** – lower molar width; **p3L** – third lower premolar length; **p3W** – third lower premolar width; **p4L** – fourth lower premolar length; **p4W** – fourth lower premolar width; % **Tot. var.** – percentage of total variance.

PCA (raw data)	PCA (Mosimann transformation)					
	1	2	1	2	3	4
$\lambda$	12.3168	0.401166	0.0107166	0.006574436	0.00330453	0.00261751
% Tot. var.	91.784	2.9895	40.621	25.564	12.526	9.9215
<b>cL</b>	0.38875	0.33193	-0.2792	-0.16567	0.19134	0.46102
<b>cW</b>	0.30507	0.44572	-0.39793	-0.18835	0.086551	0.46294
<b>p3L</b>	0.37502	0.32092	-0.017419	0.44422	0.75565	-0.28824
<b>p3W</b>	0.21014	0.087666	-0.074348	0.019318	-0.09219	-0.37744
<b>p4L</b>	0.40024	0.053371	0.5055	0.61695	-0.1899	0.51587
<b>p4W</b>	0.20273	0.058538	0.033337	0.0034453	-0.32554	-0.14927
<b>m1L</b>	0.55976	-0.75541	0.70115	-0.59228	0.3355	0.067015
<b>m1W</b>	0.23745	-0.059657	0.098044	-0.089122	-0.34899	-0.23389