Systematic palaeontology (Vertebrate palaeontology)

The Iberian record of the puma-like cat *Puma pardoides* (Owen, 1846) (Carnivora, Felidae)

Le registre ibérique du Félidé semblable au puma Puma pardoides (Owen, 1846) (Carnivora, Felidae)

Joan Madurell-Malapeira [a,*], David M. Alba [a], Salvador Moyà-Solà [b], Josep Aurell-Garrido [a]

[a] *Institut Català de Paleontologia, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain*
[b] *ICREA at Unitat d'Antropologia Biològica (Department BABVE) and Institut Català de Paleontologia, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain*

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ABSTRACT

Fossil puma-like cats (*Puma pardoides*) are recorded from several Late Pliocene to Early Pleistocene Eurasian localities, but the interpretation of the phylogenetic relationships between them and the extant puma (*Puma concolor*) remains controversial. In the past, extinct puma-like cats have been classified into several genera and species, and a close relationship with both pumas (*Puma concolor*) and snow leopards (*Uncia uncia*) has been suggested. Here, we describe the fossil remains of puma-like cats from the Iberian Peninsula. These remains (from the localities of La Puebla de Valverde, Cueva Victoria and Vallparadís) cover the whole known chronological distribution of this species in Eurasia. Although there are dentognathic similarities with *U. uncia*, the Iberian remains of *P. pardoides* most closely resemble the extant *P. concolor*. It is concluded that *P. pardoides* is closely related to living pumas, which supports a likely Eurasian origin of the puma lineage.

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RÉSUMÉ

Les félidés fossiles semblables au puma (*Puma pardoides*) ont été enregistrés à partir de plusieurs sites eurasiatiques du Pliocène supérieur au Pléistocène inférieur, mais l'interprétation des relations phylogénétiques entre eux et le puma actuel (*Puma concolor*) est encore controversé. Dans le passé, les félidés disparus semblables au puma ont été classifiés dans plusieurs genres et espèces et un rapport proche a été suggéré avec les pumas (*Puma concolor*) et les léopards des neiges (*Uncia uncia*). Nous décrivons ici les restes fossiles des félidés semblables au puma de la Péninsule ibérique. Ces restes (aux sites de La Puebla de Valverde, Cueva Victoria et Vallparadís) couvrent toute la distribution chronologique connue de cette espèce à l'Eurasie. Bien qu'il y ait des ressemblances dentognathiques avec des *U. uncia*, les restes ibériques du *P. pardoides* ressemblent plus étroitement à ceux du *P. concolor* actuel. On conclut que le *P. pardoides* est étroitement rapporté aux pumas actuels, ce que corrobore une probable origine eurasiatique de la lignée du puma.

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  * Corresponding author.
  E-mail address: joan.madurell@icp.cat (J. Madurell-Malapeira).

1. Introduction

Pumas (also known as cougars or mountain lions) are classified into the species *Puma concolor* (Linnaeus, 1771), which is distributed though the American continent. Nonetheless, there are also puma-like fossil remains recorded throughout Eurasia (Hemmer et al., 2004), which following Hemmer (2001), we attribute to *Puma pardoides* (Owen, 1846) (Owen, 1846)—although in the past, they were generally attributed to *Panthera schaubi* Viret, 1954 (Viret, 1954), and even a new genus, *Viretailurus* Hemmer, 1964 (Hemmer, 1964), was erected on their basis. Unfortunately, these remains are very scarce, so that the anatomy of these middle-sized carnivores is poorly known and its phylogenetic status (and, by implication, taxonomic attribution) remains uncertain. Following Wilson and Reeder (Wilson and Reeder, 2005), we include the genus *Puma* Jardine, 1834 in the subfamily Felinae, although other authors include it into the Pantherinae (Wilson and Reeder, 2005).

In this article, we describe the unpublished dentognathic remains of *P. pardoides* from the Spanish Early Pleistocene sites of Cueva Victoria and Vallparadís, as well as the mandibular and postcranial remains from the Late Pliocene of La Puebla de Valverde (which had been previously mentioned, but not figured or described in detail (Kurtén and Crusafont-Pairó, 1977)). Besides providing a detailed comparison with extant pumas, we also compare this fossil material with extant snow leopards, *Uncia uncia* (Schreber, 1775), given the fact that similarities with this species have been noted in some puma-like fossil material from Saint-Vallier (Olive, 2006). Finally, the implications of Eurasian puma-like cats for the understanding of the origins of extant pumas are also discussed from a paleobiogeographic viewpoint.

2. Material and methods

The described sample: The material of *P. pardoides* described in this paper was recovered from the Spanish localities of La Puebla de Valverde (Teruel), Cueva Victoria (Murcia) and Vallparadís (Barcelona). This material is housed at the ICP, except for the Vallparadís remains, which are temporarily housed at the CRBMC.

Institutional abbreviations: ICP, Institut Català de Paleontologia, Universitat Autònoma de Barcelona (Cerdanyola del Vallès, Barcelona, Spain); CRBMC, Centre de Restauració de Béns Mobles de Catalunya (Valldoreix, Barcelona, Spain); MZB, Museu de Ciències Naturals de Barcelona (Spain).

Fossil collections abbreviations: EVT, Vallparadís (Terrassa, Barcelona, Spain); IPS, collections from the ICP (former Institut de Paleontologia M. Crusafont).

Dentognathic and poscranial abbreviations: DAPD, anteroposterior diameter at the distal epiphysis; DAPM, anteroposterior diameter at midshaft; DAPP, anteroposterior diameter at the proximal epiphysis; DDP, proximodistal length of the talus; DT, mediolateral width of the talus; DTD, mediolateral diameter at the distal epiphysis; DTM, mediolateral diameter at midshaft; DTP, mediolateral diameter at the proximal epiphysis; Hd, corpus height at the mandibular diastema; Hm1, corpus height below the first molar; Hp4, corpus height below the fourth premolar; L, mesiodistal length of the crown; Ld, mesiodistal length of the mandibular diastema; Lt, maximum proximodistal length in long bones; Lpa, paraconid mesiodistal length; Lpr, protoconid mesiodistal length; LSD, mesiodistal length from p3 to m1; W, buccolingual width of the crown.

3. Systematic palaeontology

Order Carnivora Bowdich, 1821
Family Felidae Fischer Von Waldheim, 1817
Subfamily Felinae Fischer Von Waldheim, 1817
Genus *Puma* Jardine, 1834
Species *Puma pardoides* (Owen, 1846)
Synonymy
Felis pardoides Owen (1846): original description of the species.
Panthera schaubi Viret (1954): original description of the species.
Viretailurus schaubi (Viret, 1954) in Hemmer (1964): original description of the genus.
Panthera schaubi Viret, 1954 in Kurtén (1976).
Felis (Puma) sp. in Sotnikova (1976).
Panthera cf. *schaubi* Viret, 1954 in Kurtén and Crusafont-Pairó (1977).
Panthera schaubi Viret, 1954 in Turner and Antón (1997).
Puma pardoides (Owen, 1846) in Hemmer (2001).
Felidae indet. (Puma size) in Petrucci (2008).
Referred specimens
La Puebla de Valverde: Left mandibular corpus with c1, dp3 alveolus, and broken dp4 and m1 (IPS36127). Distal segment of right humerus (IPS27272). Right fourth metacarpal (IPS27285a). Right femur (IPS27343). Distal epiphysis of right femur (IPS27347). Right tibia without proximal epiphysis (IPS27345). Left astragalus (IPS27285b). **Cueva Victoria**: Right mandibular corpus with c1, p3, p4 and m1 (IPS46144). Left p3 (IPS46145). **Vallparadís**: Partial left mandibular corpus with p4 and broken m1 (EVT4178).

Description and comparisons
Measurements: See Table 1 .
Mandible: See Fig. 1. The corpus is low and stoutly-build, as in *P. concolor*, *P. pardus* (Linnaeus, 1758) and *U. uncia* (Schreber, 1775). In lateral view, there are two large mental foramina (one below the distal margin of c1, the other one below the posterior root of the p3) and a smaller foramen just above the mesial one. This condition resembles that displayed by the Saint-Vallier material (E14 EFN1 1000-1001, cast) as well as extant *P. concolor* and *U. uncia*, whereas *P. pardus* usually displays only two foramina. Mandible from the Aragó Cave (cast IPS20039), attributed to *U. uncia* by Hemmer (Hemmer, 2003), also displays three mental foramina, although the distal one is more mesially situated. In the material from Cueva Victoria, the masseteric fossa reaches the level of the m1 protoconid, as in extant *P. concolor* and *U. uncia*. The mandibles from Saint-Vallier and the Aragó Cave display the same condition.

The mandibular robusticity (corpus height behind the m1 / mesiodistal length of the m1 $\times$ 100) displayed by the material from Cueva Victoria (150.8) matches the figures

Table 1
Dental and poscranial measurements (in mm) of the remains of *Puma pardoides* from Iberian sites of La Puebla de Valverde, Cueva Victoria and Vallparadís.
Tableau 1
Mesures dentaires et postcrâniennes (en mm) des restes de *Puma pardoides* provenant des sites ibériques de La Puebla de Valverde, Cueva Victoria et Vallparadís.

Site	Reference	c1		p3		p4		m1								
		L	W	L	W	L	W	L	W	Lpr	Lpa	Ld	LSD	Hp4	Hm1	Hd
Puebla Valverde	IPS36127	9.3	8.8					19.8	8.9	12.4	9.6					
Cueva Victoria	IPS46144	13.0	9.1	12.6	6.3	16.7	8.7	18.6	8.9	10.7	9.7	9.9	45.5	25.2	23.0	24.6
Cueva Victoria	IPS46145			12.5	6.8											
Vallparadís	EVT04178					15.6	7.8		8.0					20.2	23.2	

Site	Reference	Bone	Lt	DTP	DTM	DTD	DAPP	DAPM	DAPD	DT	DDP
Puebla Valverde	IPS27272	Humerus			15.9	41.4		19.2	24.8		
Puebla Valverde	IPS27343	Femur	271.0	–	23.9	48.5	31.9	20	47.1		
Puebla Valverde	IPS27345	Tibia		–	22.7	37.3	–	22.1	24.3		
Puebla Valverde	IPS27285	Astragalus								36.6	35.9
Puebla Valverde	IPS27285	Metacarpal IV	71.4	12.6	8.3	14.6	14.5	8.1	13.4		

for other material assigned to *P. pardoides* (150.1 and 148.9 in Saint-Vallier; and 153.9 in Untermassfeld (Hemmer, 2001)), which are higher than the mean value displayed by extant *P. concolor* (146.2; $n = 6$). Extant *U. uncia* (MZB collections, $n = 6$) and Pliocene *A. pardinensis* (IPS35087, IPS17147 and IPS17069) display even slender mandibles, with mean values of 139.9 and 135.6, respectively. On the contrary, the mandible from the Aragó Cave is stouter, with a value of 167.0 that best matches the range of 145–170 derived for fossil *P. pardus* ((Testu, 2006) and our own data).

Lower teeth: The two p3 from Cueva Victoria have a well-developed circular parastylid, which is more protruding than the distal accessory cuspid. This morphology resembles both *P. concolor* and *U. uncia*. In the material from Saint-Vallier, the parastylid is reduced and clearly less protruding than the distal cuspid. The material from the Aragó Cave displays a clearly reduced anterior accesory cuspid.
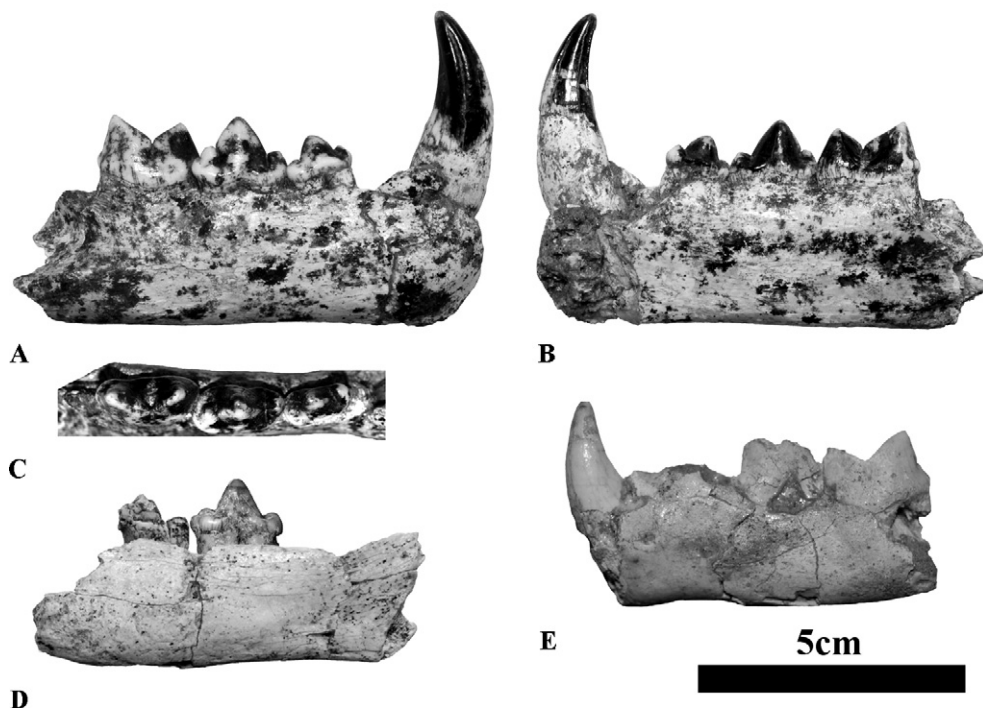

Fig. 1. Dentognathic remains of *Puma pardoides* from the Iberian sites. **A–C**, Right hemimandible IPS46144 from Cueva Victoria: **A**, buccal view; **B**, lingual view; **C**, occlusal view. **D**, Left hemimandible EVT4178 from Vallparadís, in lingual view. **E**, Left juvenile hemimandible IPS36127 from La Puebla de Valverde, in buccal view.
Fig. 1. Restes dentognathiques de *Puma pardoides* provenant de sites ibériques. **A–C**, Hémimandibule droite IPS46144 de Cueva Victoria : **A**, vue buccale ; **B**, vue linguale ; **C**, vue occlusale. **D**, Hémimandibule gauche EVT4178 de Vallparadís, en vue linguale. **E**, Hémimandibule juvénile gauche IPS36127 de La Puebla de Valverde, en vue buccale.

The p4 from Cueva Victoria and Vallparadís display a protruding and non-compressed anterior accessory cuspid. The protoconid is slender and symmetrical in buccal view. The distal accessory cuspid is protruding and slightly buccolingually compressed, and displays a well-developed distal cingulid. Extant *P. concolor* and the Untermassfeld material display the same features, while in the Saint-Vallier material, the distal accessory cuspid is slightly higher than the mesial one, and the protoconid is not entirely symmetrical but slightly inclined backwards. Extant *U. uncia* closely resembles the Iberian fossils, but differs regarding protoconid height, which is lower in the former. In the mandible from the Aragó Cave, the accessory cuspids are relatively small and the protoconid is asymmetric and slightly inclined backwards.

The m1 from La Puebla de Valverde and Cueva Victoria are stoutly-built, with a protoconid slightly longer and higher than the paraconid; both cuspids are vertically oriented. The same morphology is displayed by the Saint-Vallier material and extant *P. concolor*. This morphology also resembles the material from the Aragó Cave and extant *P. pardus*, although in these forms, the distal border of the protoconid is more vertical. On the contrary, the Untermassfeld material displays a slightly higher and shorter paraconid as compared to the protoconid. In *U. uncia*, the protoconid is slightly longer and higher than the paraconid, as in the Iberian fossil material, but in the former the base of the protoconid bears a small cuspid and, in some cases, even a lingual bulge between the two main cusps.

Postcranium: See Figs. 2 and 3. The humeral fragment IPS27272 displays a well-developed medial epicondyle, as in all extant large felids; the olecranon fossa is not particularly deep as compared to extant lynxes, pumas and jaguars; snow leopards have a shallower and wider fossa. The radial fossa is wide and low as in extant large felids (including *U. uncia*). The coronoid fossa is oval and deep as in extant *P. concolor* and *U. uncia*. The capitulum is slender and cylindrical.

The morphology of the fourth metacarpal IPS27285 (Fig. 2) closely resembles that of extant *P. concolor*, although in the latter the fourth metacarpal is slightly more slender, so that the former best matches *U. uncia* with regard to length and diaphyseal robusticity. Regarding the morphology of the proximal epiphysis, the articular surface for the third metacarpal is deeper, wider and more distally protruding than in extant pumas, thus more closely resembling snow leopards. The proximal articular surface is slightly convex and subdivided into two portions by a dorsopalmar smooth crest; this feature is also displayed by extant pumas, but only weakly developed in snow leopards, jaguars and leopards.

The partial femur (IPS27343) from La Puebla de Valverde (Fig. 3; 271 mm) is clearly longer than those of snow leopards (231.1–235.5, n = 6) and also slightly longer than the maximum length of jaguars (229.8–265.5 mm, n = 8; (Christiansen and Adolfssen, 2007)). Therefore IPS27343 only overlaps with the range reported for extant pumas (226.3–274.3 mm, n = 6; (Christiansen and Adolfssen, 2007)), although being included within the upper range of the latter. Among the three other femora of *P. pardoides* previously reported, that from Étouaires (France) displays a comparable length of 274 mm (Kurtén and Crusafont-Pairó, 1977), whereas those from Saint-Vallier (Viret, 1954) and Untermassfeld (Hemmer, 2001) are considerably shorter (209 and 202 mm, respectively), under the minimum values for extant pumas. Regarding femoral proportions, extant jaguars, pumas and snow leopards mainly differ in diaphyseal robusticity, which is clearly higher in *P. onca* (Linnaeus, 1758) and *U. uncia* (Schreber, 1775). Thus, the ratio between the minimum circumference of the femoral diaphysis and articular length is higher in the specimen from La Puebla de Valverde (0.271) as compared to extant *P. concolor* (0.234 ± 0.006) and extant *P. onca* (0.263 ± 0.006). The ratio for the material described in this paper matches the figures for both *P. leo* (Linnaeus, 1758) (0.271 ± 0.004) and *U. uncia* (0.274 ± 0.01) (Christiansen and Adolfssen, 2007).

With regard to femoral morphology, like in extant pumas, the gluteal tuberosity is only slightly marked. Similarly, the supracondylar tuberosities are only insinuated in IPS27243, as in extant pumas and snow leopards, whereas they are well-developed and more distally placed in extant jaguars, lions and leopards.

A right tibia with broken proximal epiphysis is also available from La Puebla de Valverde (Fig. 3). The estimated length of this bone is ca. 240 mm, which agrees with both femoral length and the length of tibiae from *P. concolor* and *U. uncia*. Regarding tibial morphology, the diaphysis is straight and stout, as in snow leopards, thus contrasting with the more slender morphology of *P. concolor*. The
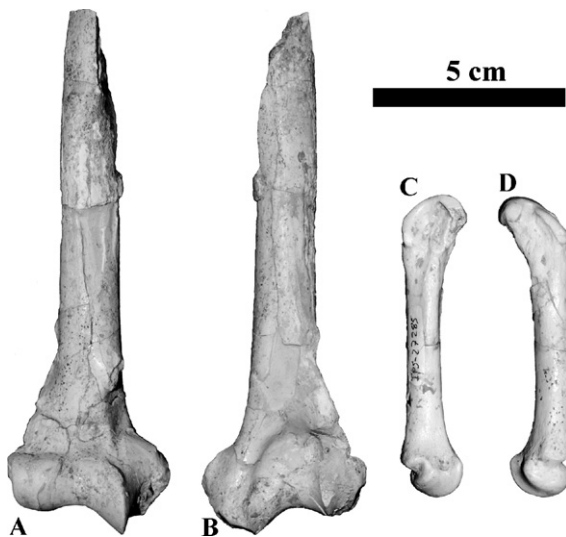

Fig. 2. Forelimb remains of *Puma pardoides* from La Puebla de Valverde. **A–B**, Right humerus IPS27272: **A**, anterior view; **B**, posterior view. **C–D**, Right fourth metacarpal IPS27285a: **C**, medial view; **D**, lateral view.

Fig. 2. Restes de l'extrémité antérieure du *Puma pardoides* de La Puebla de Valverde. **A–B**, Humérus droit IPS27272 : **A**, vue antérieure ; **B**, vue postérieure. **C–D**, Quatrième métacarpien droit IPS27285a : **C**, vue médiale ; **D**, vue latérale.

Fig. 3. Hind limb remains of several felids. **A–D**, Right femur of *Puma pardoides* from La Puebla de Valderde IPS27343: **A**, anterior view; **B**, posterior view. **C–D**, Right tibia of *Puma pardoides* from La Puebla de Valverde IPS27345: **C**, anterior view; **D**, posterior view. **E–F**, Left astragalus of *Acinonyx pardinensis* from La Puebla de Valverde: **E**, upper view; **F**, lower view. **G–H**, Left astragalus of extant *Panthera onca* MZB 2003-1166: **G**, upper view; **H**, lower view. **I–J**, Left astragalus of *Puma pardoides* from La Puebla de Valverde IPS27285b: **I**, upper view; **J**, lower view. **K–L**, Left astragalus of extant *Puma concolor* MZB 93-0140: **K**, upper view; **L**, lower view.

Fig. 3. Restes de l'extrémité postérieure de plusieurs félidés. **A–D**, Fémur droit du *Puma pardoides* de La Puebla de Valderde IPS27343 : **A**, vue antérieure ; **B**, vue postérieure. **C–D**, Tibia droit du *Puma pardoides* de La Puebla de Valverde IPS27345 : **C**, vue antérieure ; **D**, vue postérieure. **E–F**, Astragale droit de l'*Acinonyx pardinensis* de La Puebla de Valverde : **E**, vue supérieure; **F**, vue inférieure. **G–H**, Astragale gauche de l'actuelle *Panthera onca* MZB 2003-1166 : **G**, vue supérieure ; **H**, vue inférieure. **I–J**, Astragale gauche du *Puma pardoides* de La Puebla de Valverde IPS27285b : **I**, vue supérieure ; **J**, vue inférieure. **K–L**, Astragale gauche de l'actuel *Puma concolor* MZB 93-0140 : **K**, vue supérieure ; **L**, vue inférieure.

medial malleolus is relatively larger anteroposteriorly than in extant pumas and ounces, which display a slender and shorter malleolus. The lateral malleolus is wide, as in other large felids.

Finally, a left astragalus from La Puebla de Valverde (Fig. 3) is available. It displays the proximal segment of the plantar medial facet constricted by the medial expansion of the tarsal sinus; this feature is also displayed by *P. concolor*, *U. uncia*, *Lynx issiodorensis* (Croizet and Jobert, 1828), *A. pardinensis* (Croizet et Jobert, 1828), *P. pardus* and *P. leo*, whereas it is never present in *P. onca*.

The palmar lateral facet is mediolaterally constricted in *P. concolor*, whereas in IPS27285 this constriction is less marked and the facet is relatively wider than in the former species and other living large felids (including snow leopards). Close to the neck, in front of the ventral medial facet, the studied specimen displays a deep notch; this notch is shallower or even absent in jaguars, while it is deeper and oval in pumas, snow leopards, cheetahs and lynxes. In dorsal view, the neck of the studied specimen is relatively long, as in pumas and snow leopards.

4. Discussion

4.1. Taxonomic remarks

Until recently, Eurasian puma-like fossil remains were still attributed to *P. schaubi* (Turner and Antón, 1997), which was originally described on the basis of material Saint-Vallier (France; ca. 2.1 Ma) (Viret, 1954). Soon later, however, Hemmer (1964) showed that this material was clearly not pantherine, but displayed many shared features with the American puma, and on this basis erected the genus *Viretailurus*. Further similarities in dental dimensions and the position of mental foramina between this species and fossil American pumas were remarked by Kurtén (1976), while Sotnikova (1976) similarly noted that the material from Central Asia attributed to *Felis (Puma)* sp. also displayed similarities with this European species. It was not until the paper by Kurtén and Crusafont-Pairó (1977), describing the carnivore remains from La Puebla de Valverde, that the similarities between the above-mentioned species and *Felis pardoides* Owen (1846), originally described from the English Red Crags, were noticed. Most recently, Hemmer (2001) described the puma-like remains from the Epivillafranchian of Untermassfeld, and concluded that *Viretailurus* Hemmer, 1964 and *Panthera schaubi* Viret, 1954 were junior subjective synonyms of *Puma* Jardine, 1834 and *Puma pardoides* (Owen, 1846), respectively.

4.2. The Eurasian record of puma-like cats

In the Iberian Peninsula, *P. pardoides* is first recorded at the MN17 locality of La Puebla de Valverde (Kurtén and Crusafont-Pairó, 1977), on the basis of the remains described in this paper. *P. pardoides* is also recorded in the Early Pleistocene site of Cueva Victoria (ca. 1.1 Ma, according to (Blain et al., 2008) and references therein). Finally, as shown in this paper, *P. pardoides* is also recorded from the late Early Pleistocene site of Vallparadís in Terrassa (Barcelona, Spain; (Alba et al., 2008)). An estimated age of more than 0.8 Ma has been proposed for this locality (Alba et al., 2008), so that it might represent the youngest citation of this species from the Iberian Peninsula. *P. pardoides* had not yet been recognized from the Vallparadís assemblage when the preliminary faunal list from this locality was published (Alba et al., 2008).

Outside of the Iberian Peninsula, *P. pardoides* is recorded from the MN16b of Perrier-Étouaires (Hugueney et al., 1989) and the MN17 of Saint-Vallier (Vislobokova et al., 1993; Argant, 2004) in France; the MN16b or MN17 locality of Newborn, Red Crags in Great Britain (Owen, 1846; Hemmer et al., 2004); Untermassfeld (above the base of the Jaramillo chron, ca. 1 Ma) in Germany (Hemmer, 2001); probably Stránská skála (late Early Pleistocene) in the Czech Republic (Hemmer, 2001); possibly from the MN17 locality of Varshets in Bulgaria (Spassov, 2000); the MN16 site of Kvabebi in Georgia (Hemmer et al., 2004); and the Early Villafranchian localities of Shamar and Beregovaya in Mongolia (Sotnikova, 1976), which respectively correspond to the MN16a and MN16b (Vislobokova et al., 1993). Additional puma-like fossil remains have been

described from the localities of Vallonnet (Jaramillo chron, ca. 1 Ma) (Moullé, 1992) in France and Tegelen (MN17) in The Netherlands (Hemmer, 2001), although their attribution to *P. pardoides* remains doubtful (Moullé et al., 2006; O'Regan and Turner, 2004). Recently, Petrucci (Petrucci, 2008) has noted that an ulna and a fifth metacarpal from the Early Pleistocene locality of Pirro Nord in Italy resemble puma-like cats in both size and morphology, although he formally attributes them to "Felidae indet. (*Puma* size)".

4.3. Attribution of the Iberian material

The Iberian specimens of *P. pardoides* from La Puebla de Valverde, Cueva Victoria and Vallparadís display many dentognathic similarities to the extant *P. concolor*; these include: (1) the location of the three mental foramina; (2) the position of the masseteric fossa, reaching the level of the m1 protoconid; (3) p3 with a well-developed anterior accessory cusp, more protruding than the posterior cusp; (4) p4 with symmetrical protoconid (in lateral view), and well-developed and similarly-sized accessory cusps; and (5) m1 with a protoconid slightly larger and higher than the paraconid, and quite vertically oriented. With regard to the postcranial material, the Iberian fossil remains are almost entirely comparable to extant pumas on morphological grounds, except for a general greater robusticity and a slightly larger size (near the maximum values of the extant species).

The Iberian remains described in this paper also display several similarities to extant *U. uncia*: (1) stoutly-built lower mandibular corpus; (2) number and position of the mental foramina; (3) masseteric fossa reaching the level of the m1 protoconid, in lateral view; (4) p3 with a well-developed, circular parastylid that is more protruding than the posterior accessory cuspid; and (5) p4 with a symmetrical protoconid in lateral view and with two well-developed and similarly-sized accessory cuspids. Nevertheless, the Iberian remains further differ from *U. uncia* by several other features, namely: (1) m1 protoconid slightly larger and more protruding than the paraconid, with a small cuspid at the base of the protoconid and, in some cases, a lingual bulge between the two main cuspids; (2) lower values of the mandibular robusticity index; and (3) relatively short and robust femur.

Additional comparisons with Early Pliocene European felids, such as the machairodont *Dinofelis* Zdansky, 1924, would be interesting, especially given some poscranial similarities—*Dinofelis* displays a forelimb morphology convergent with that of pantherines (Werdelin and Lewis, 2001). Unfortunately, the scarce European remains of this genus (Werdelin and Lewis, 2001) prevent a correct comparison with the material of *P. pardoides* reported here.

To sum up, the Iberian fossil remains described in this paper display many similarities to the extant *P. concolor* and the fossil *P. pardoides* from Saint-Vallier, while they can be distinguished from *U. uncia* on both dental and postcranial grounds. As such, we attribute the puma-like remains described in this paper to *P. pardoides*, albeit noting that, to some regards, the dental remains from Cueva Victoria

and Vallparadís more closely resemble extant pumas than *P. pardoides* from Saint-Vallier and La Puebla de Valverde.

4.4. Paleobiogeographic implications

The evolutionary origins of the puma lineage are far from being definitively settled. It has been previously argued that the cheetah-like cat lineage of *Miracinonyx* Adams, 1979 and the puma lineage might have shared a last common ancestor in the Middle to Late Pliocene of America (Johnson et al., 2006), thus implying an American origin of the genus *Puma*. However, this is not supported by paleontological evidence, because the fossil record of *P. concolor* in the American continent begins at around 400 ka (Van Valkenburgh et al., 1990). On the contrary, the presence of puma-like cats in Eurasia deserves further consideration regarding the origins of American pumas from a phylogenetic and biogeographic viewpoint.

The puma-like cat *P. pardoides* is recorded from western Europe to central Asia from the MN16 until the MN17, and hereafter this taxon is not recorded (with the possible exception of the scarce remains from Pirro Nord) until above the base of the Jaramillo chron in Untermassfeld and several other sites. The chronology of *P. pardoides* in the Iberian Peninsula also ranges from the Late Pliocene to the latest Early Pleistocene, thus coinciding with the range of the species elsewhere in Eurasia. The disappearance of *P. pardoides* from the Eurasian fossil record occurs at the Early/Middle Pleistocene boundary, coinciding with the arrival of leopards into this continent, which became a common element from the late Middle to the Late Pleistocene (Palombo et al., 2008). This suggests that, if the Eurasian *P. pardoides* and the extant *P. concolor* are indeed closely related, the former must have dispersed across the Bering Strait during the Middle Pleistocene, before its first record in the American continent (Van Valkenburgh et al., 1990). Given the 400 kyr gap between the last European record of puma-like cats and their first American record, it may be hypothesized that pumas inhabited northern Asia during the early Middle Pleistocene, before dispersing into America. A revision of the Asian fossil material would be required in order to decipher whether puma-like remains have been incorrectly determined due to their similarities with leopards and snow leopards.

Unfortunately, this issue is further complicated by the uncertainties surrounding the origin of the snow leopard, *U. uncia*. Its fossil record is very scarce, and only a few citations from the Late Pleistocene Altai Caves are probably correct (Hemmer, 1972). The recent assignment by Hemmer (2003) of a mandible from the Middle Pleistocene Aragó Cave to *Uncia uncia* was disputed by Testu (2006), who assigned it to *Panthera* sp. On the other hand, Olive (2006) noted the presence of derived features of *U. uncia* in the puma-like cranium QSV 136 from Saint-Vallier. The presence of these exclusive snow leopard characters in the Saint-Vallier cranium further implies that puma-like Eurasian cats might be also closely related to the former. Studies of molecular phylogeny are not conclusive to this regard. It has been recently concluded that *U. uncia* and *P. leo* may be sister taxa (Wei et al., 2008), but other analyses have alternatively concluded that the former is a stem member of the *Panthera* clade (Johnson et al., 2006), that it is a close relative of *P. tigris* (Linnaeus, 1758) (Jae-Heup et al., 2001), or that it is the sister taxon of *P. pardus* (Yu and Zhang, 2005). Most of these studies also support a close relationship between *P. concolor* and *Acinonyx pardinensis* with the exclusion of the snow leopard (Johnson et al., 2006), thus further complicating the phylogenetic interpretation of Eurasian puma-like cats that share morphological features with both extant pumas and snow leopards.

5. Conclusions

The Iberian record of the enigmatic, Eurasian felid *Puma pardoides* includes in the localities of La Puebla de Valverde (MN17), Cueva Victoria (base of the Jaramillo subchron) and Vallparadís (below the Brunhes-Matuyama boundary). The Iberian specimens share many dentognathic features with those from Saint-Vallier (France), and further closely resemble the extant *Puma concolor*, even though the fossil specimens are clearly more robust both cranially and poscranially, and closer in size to the maximum figures of the extant species. Although the material described in this paper shares cranial and poscranial features with the snow leopard (*Uncia uncia*), it can be distinguished from the latter on the basis of significant dentognathic characters. Despite some recent claims on the phylogenetic significance of these similarities between the Old World puma-like cats and snow leopards, the lack of fossil remains from the latter preclude an accurate deciphering of their affinities. On the other hand, the puma-like fossil remains described in this paper significantly contribute to our understanding of the evolutionary history of the puma lineage. In particular, they confirm that Eurasian puma-like cats (*Puma pardoides*) are indeed closely related to American pumas (*Puma concolor*), further showing that Eurasian pumas are recorded from the Late Pliocene until the latest Early Pleistocene. Overall, from a paleobiogeographic viewpoint, this is consistent with the puma lineage having originated in Eurasia.

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