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Earliest occurrence of *Puma pardoides* (Owen, 1846) (Carnivora, Felidae) at the Plio/Pleistocene transition in western Europe: New evidence from the Middle Villafranchian assemblage of Montopoli, Italy

Première occurrence du Puma pardoides (Owen, 1846) (Carnivora, Felidae) à la transition Plio/Pléistocène en Europe occidentale : une nouvelle preuve de l'assemblage du Villafranchien moyen de Montopoli, Italie

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ABSTRACT

The puma-like cat *Puma pardoides* (Owen, 1846) is reported from several Eurasian localities dated to the Late Pliocene–Early Pleistocene, but its Italian fossil record is really poor; in fact, the only possible occurrence comprises some fragmentary postcranial material from the Late Villafranchian locality of Pirro Nord (1.6–1.3 Ma). In the present paper, we describe an isolated left upper carnassial of a medium-sized felid belonging to the collection of fossil mammals from Montopoli (Tuscany, Italy), the type locality of the Middle Villafranchian Faunal Unit (~2.6 Ma). All the morphological and morphometric characters of the tooth are consistent with an attribution to *Puma pardoides* (Owen, 1846), which comes out as the second felid species from Montopoli together with *Acinonyx pardinensis* (Croizet et Jobert, 1828) and is, possibly with the specimens from Perrier–Étouaries, the earliest occurrence in western Europe.

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R É S U M É

Un félin semblable au puma *Puma pardoides* (Owen, 1846) est signalé dans plusieurs localités d'Eurasie du Pliocène supérieur au Pléistocène inférieur, mais ses archives fossiles sont très pauvres en Italie ; en fait, le seul signalement – douteux – concerne certains fragments postcrâniens dans la localité du Villafranchien supérieur de Pirro Nord (1,6 à 1,3 Ma). Dans le présent article, nous décrivons une carnassière supérieure gauche isolée appartenant à un félin de taille moyenne de la collection de mammifères fossiles de Montopoli (Toscane, Italie), localité type de l'unité faunique du Villafranchien moyen (~2,6 Ma). Tous les caractères morphologiques et morphométriques de la dent sont compatibles avec une attribution à *P. pardoides* (Owen, 1846), ce qui la fait apparaître comme la seconde espèce de félinidés

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de Montopoli avec *Acinonyx pardinensis* (Croizet et Jobert, 1828) ; elle en est, éventuellement avec les spécimens de Perrier-Étouaries, l'occurrence la plus précoce en Europe occidentale.

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1. Introduction

The felid tooth described in the present paper is stored in the Natural History Museum of Florence University and was examined by the senior author (M.C.) on the occasion of a review of cheetah-like cat fossil remains related to the description of new, still unpublished material of *Acinonyx pardinensis* from central Italy. Although the tooth is labeled as “*Acinonyx* sp.” in the museum catalog, its morphological and dimensional features clearly indicate that it cannot be referred to a cheetah, but to a puma.

The genus *Puma* Jardine, 1834 is represented today by the two species *Puma concolor* (Linnaeus, 1771) and the smaller *Puma yagouaroundi* (Lacépède, 1809) (Macdonald et al., 2010). *P. concolor* – commonly known as puma, cougar, or mountain lion – is a moderately large cat, with average weight of 53–72 kg for adult males and 34–48 kg for adult females (Macdonald et al., 2010); it shows an increasing trend in size from the Equator to the poles (Iriarte et al., 1991).

Pumas are distributed throughout the Americas, from Canada to Patagonia, and live in a wide variety of habitats, from tropical rainforests to semiarid scrublands, reflecting their great adaptability to a wide range of environmental conditions (Hornocker and Negri, 2010; Murphy and Macdonald, 2010). Prey ranges from mouse- to deer-sized animals, but prey size varies with latitude: in temperate areas this predator regularly preys on animals as large as or larger than itself, whereas in tropical regions prey normally weighs less than half the puma's weight. This difference reflects the relative availability of different-sized prey and possible competition with jaguars in the tropics (Macdonald et al., 2010).

During the Late Pliocene–Early Pleistocene, Eurasia was inhabited by the puma-like felid *Puma pardoides* (Owen, 1846) (Hemmer et al., 2004). Using skeletal and dental predictors of body mass in carnivores (Van Valkenburgh, 1990), it has been possible to estimate for *P. pardoides* a body size close to the extant *P. concolor* (Hemmer et al., 2004; Turner and Antón, 1997). The only complete cranium of this big cat has been found in the Middle Villafranchian locality of Saint-Vallier (Fig. 1) and described by Viret (1954) as *Panthera schaubi*. Later, Hemmer (1965) attributed the French specimen to the new genus *Viretailurus*, on the basis of differences from pantherine cats and similarities to the American puma. Sotnikova (1978) has been the first to refer the Saint-Vallier cranium to a real puma (*Felis (Puma) sp.*), together with some remains from central Asia. Finally, describing the Epivillafranchian remains from Untermaßfeld (Germany), Hemmer (2001) pointed out that all the Eurasian puma-like remains could be referred to the new combination *P. pardoides* (Owen, 1846), because the generic name *Viretailurus* Hemmer, 1965 and the specific name *schaubi* Viret, 1954 are junior synonyms of

Puma Jardine, 1834 and *pardoides* Owen, 1846, respectively.

Nevertheless, because fossil remains are scarce, the taxonomic attribution of these forms to the genus *Puma* has never been supported, either by the identification of any synapomorphy with the extant *Puma* spp., or by any strict phylogenetic analysis. In the present paper, we decided to

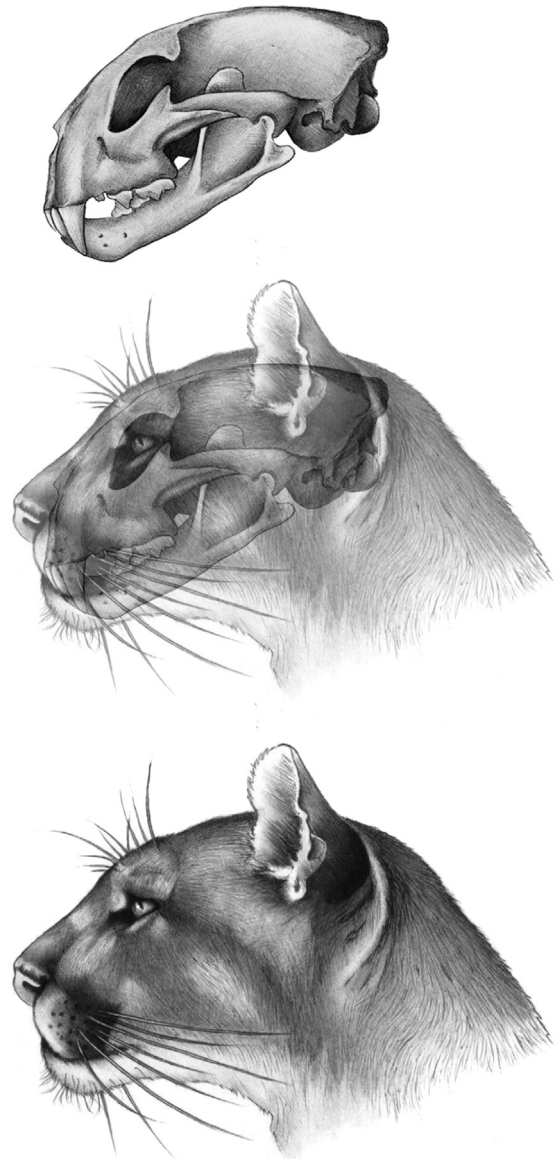


Fig. 1. Sequence of reconstruction of the head of *Puma pardoides*, based on the complete skull from Saint-Vallier, France. Artwork: Iurino D.A.
Fig. 1. Séquence de reconstruction de la tête de *Puma pardoides*, sur la base du crâne complet de Saint-Vallier, France. Dessin : Iurino D.A.

follow the most recent scientific literature in including the Eurasian Plio-Pleistocene puma-like cat remains within the species *P. pardoides*, but we are aware that further discoveries are needed for confirming, or not, the validity of this species.

The Eurasian record of *P. pardoides* includes the following localities: Perrier-Étouaries (Hugueney et al., 1989), and Saint-Vallier (Argant, 2004; Viret, 1954), France; La Puebla de Valverde, Cueva Victoria, and Vallparadís, Spain (Madurell-Malapeira et al., 2010a); Red Craggs, Great Britain (Owen, 1846); Untermassfeld, Germany (Hemmer, 2001); Kvabebi, Georgia (Hemmer et al., 2004); probably Stránská Skála, Czech Republic (Hemmer, 2001); probably Varshets, Bulgaria (Spassov, 1997); Shamar, Mongolia and Berecovaya, Russia (Sotnikova, 1978). Other puma-like remains have been described from Tegelen, The Netherlands, by Hemmer (2001), but O'Regan and Turner (2004) later referred this material to *Panthera gombaszoegensis*. Similarly, the remains from Vallonnet, France (Moullé, 1992) could be attributed to *Panthera pardus* (Moullé et al., 2006). Recently, a well-preserved proximal part of left ulna from Pirro Nord, Italy has been attributed to *P. pardoides* by Petrucci et al. (2013).

Paleoenvironmental reconstructions of these different sites show important variability in land cover, with forests, woodlands, grasslands and transitional ranges (Hemmer et al., 2004). *P. pardoides* – like the closely-related extant *P. concolor* – was therefore characterized by a wide ecological tolerance, so does not provide detailed paleoenvironmental information.

P. pardoides seems to be present in Eurasia from the Late Pliocene (Kvabebi, Georgia and Shamar, Mongolia, more than 2.6 Ma, Hemmer et al., 2004) to the latest Early Pleistocene (Vallparadís, Spain, layer EVT7, ~0.83 Ma, Madurell-Malapeira et al., 2010b). The Montopoli local fauna has been correlated by Lindsay et al. (1980) to the base of the Matuyama magnetic chron (~2.6 Ma), approximately at the same age of Perrier-Étouaries, so the specimen described in the present work represents one of the earliest records of *P. pardoides*.

Institutional abbreviations – DSTR: Dipartimento di Scienze della Terra, Sapienza University of Rome; GSM: Georgian State Museum, Tbilisi; HNHM: Hungarian Natural History Museum, Budapest; IGF: Natural History Museum, Section of Geology and Paleontology, Florence University; MHNB: Natural History Museum, Basel; MHNL: Natural History Museum, Lyon; SBAU: Soprintendenza per i Beni Archeologici dell'Umbria, Italy; SPE: Natural History Museum, Section of Zoology “La Specola”, Florence University; UCBL: Collections UFR des sciences de la Terre, Université Claude-Bernard–Lyon-1.

2. Site and accompanying mammal fauna

The town of Montopoli Val d'Arno is located in Tuscany (central Italy), about 27 km east-southeast of Pisa and 40 km west-southwest of Florence. Most of the Montopoli collection comes from excavations made by Forsyth Major in 1880 and was found in gravelly sands alternating with marine littoral deposits. Continental mammal-bearing sands outcropped in at least two localities: “l'Uccellatoio”

hill and “Poggio di Montevectchio”, both located a few kilometers southeast of the town of Montopoli (De Giuli and Heintz, 1974). The felid tooth described in the present work probably comes from the former locality. Fossil mammals from Montopoli have been analyzed by several authors since their discovery (Azzaroli, 1977; Benvenuti et al., 1995; De Giuli and Heintz, 1974; Ficcarelli, 1984; Forsyth Major, 1885; Merla, 1949). According to published data the fauna is composed of the following taxa: *A. pardinensis*, *Nyctereutes megamastoides*, *Pliocrocuta perrieri*, *Mammuthus gromovi*, *Stephanorhinus jeanvireti*, *Stephanorhinus etruscus*, *Equus livenzovensis*, *Axis lyra*, *Croizetaceros ramosus*, *Eucladoceros falconeri*, *Procapreolus cusanus*, *Gazella borbonica*, *Leptobos stenometopon*.

3. Material and methods

The tooth IGF 15358 from Montopoli (Fig. 2) is labeled as *Acinonyx* sp. in the current IGF catalog, although the identification “*Viretailurus schaubi*” was written with a pencil on the original paper catalog by an unknown past curator of the Museum. *Viretailurus schaubi* is an older synonym of *Puma pardoides*, according to Hemmer (2001). Tooth measurements were taken following Hemmer et al. (2004).

4. Description and comparison

The left upper carnassial IGF 15358 is in good state of preservation, although the two anterior roots are broken (Fig. 2).

In occlusal view, the tooth shows a peculiar T morphology (Argant, 2004), caused lingually by the advanced position of the protocone, and labially by the bulging of the antero-labial base of the parastyle, that does not form a true ectoparastyle. This feature seems to be less evident in the extant *P. concolor* (Fig. 3I), which is however characterized by strong morphological variability in its dentition (Hemmer et al., 2004).

The protocone is a well-developed cusp, slightly oriented frontwards and noticeably low-placed toward the root, as one can note in anterior view. The triangular pit formed by the parastyle, paracone, and protocone is quite deep, and a clear ridge runs from the paracone tip to the protocone. The parastyle is globular and much worn on the labial side. The indentation between the para- and metacone is deep and open.

All these morphological characters have been described for *P. pardoides* from various Eurasian sites (Argant, 2004; Hemmer, 1965; Hemmer et al., 2004; Viret, 1954).

It is evident that the tooth from Montopoli does not belong to a cheetah, *Acinonyx* sp., as indicated in the IGF catalog. In fact, the Villafranchian giant cheetah, *A. pardinensis*, is characterized by a larger and stronger carnassial, with a very reduced and posteriorly-placed protocone (Fig. 3H).

Morphometric values for IGF 15358 are very close to those of the holotype of “*Panthera*” *schaubi* from Saint-Vallier (Hemmer, 1965; Viret, 1954), but smaller than those of the other specimens from the same locality (Argant, 2004) and of *P. pardoides* from Kvabebi (Hemmer et al., 2004). Also the Recent puma, *P. concolor*, shows higher mean values for the upper carnassial (Table 1).

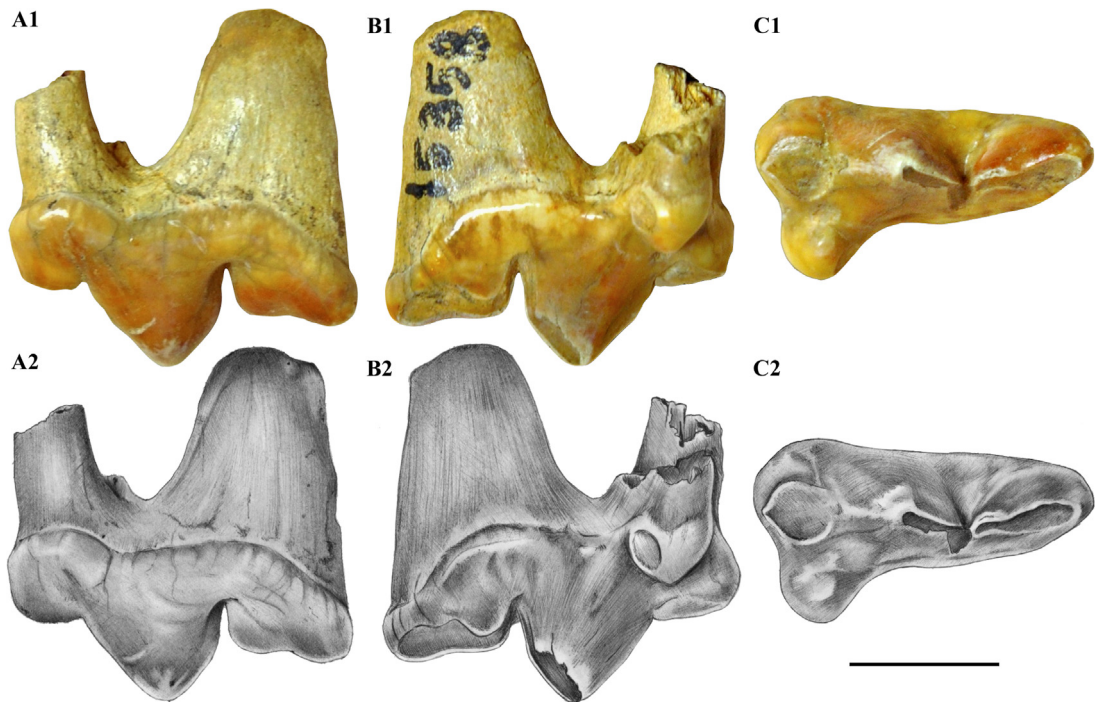


Fig. 2. Left upper carnassial of *Puma pardoides* (IGF 15358) from Montopoli (Italy). A1–2: labial view; B1–2: lingual view; C1–2: occlusal view. Photographs (A1–C1): Cherin M.; artwork (A2–C2): Iurino D.A. Scale bar: 1 cm.

Fig. 2. Carnassière supérieure gauche de *Puma pardoides* (IGF 15358) de Montopoli (Italie). A1–2: vue labiale; B1–2: vue linguale; C1–2: vue occlusale. Photos (A1–C1): Cherin M.; dessins (A2–C2): Iurino D.A. Échelle graphique: 1 cm.

More detailed comparisons are needed for *Lynx issiodorensis*. In fact, although this species is not reported at Montopoli, it was undoubtedly present in Europe at the beginning of the Middle Villafranchian (Werdelin, 1981). In addition, as Kurtén highlighted (1978), the overall morphology of the Issoire lynx was more “generalized” than extant lynxes, thus resembling a puma in some respects (larger head, longer neck, shorter limbs, and heavier body). Nevertheless, dental differences between *L. issiodorensis* and *P. pardoides* seem to be quite definite, as Viret (1954) stressed in describing the fossils from Saint-Vallier, where both species have been reported. Although the two felids are dimensionally similar, the upper carnassial of *P. pardoides* is on average slightly larger than that of *L. issiodorensis* (Table 1). The main morphological differences lie in the following characters (for a graphic comparison, see Fig. 3A–C for *P. pardoides* and Fig. 3D–F for *L. issiodorensis*): *P. pardoides* has a stouter upper carnassial on the whole, with a *Panthera*-like, massive, lingually-projected protocone. The parastyle is stout and globular as well. In addition, *L. issiodorensis* normally shows a well-developed ectoparastyle (more prominent than in the living lynx; Kurtén, 1978), which gives a sharp appearance to the antero-labial angle of the tooth (black arrows in Fig. 3D–F). On the contrary, the parastyle does not bulge labially (T-shaped occlusal outline of *P. pardoides*). The P4 protocone of *L. issiodorensis* is more slender than in *P. pardoides*; furthermore, its posterior margin strongly recedes in occlusal view (grey arrows in Fig. 3D–F), whereas in *P. pardoides* the protocone is more clearly isolated from

the lingual wall of the tooth, coming off with a sharper angle.

The length and maximum breadth of the examined tooth are close to the smaller values for the extant leopard, *P. pardus* (Table 1), but the latter normally shows a stronger and stouter carnassial, with the absence of the typical T-shaped occlusal morphology (Fig. 3G), as in *L. issiodorensis*.

5. Discussion

The Montopoli Faunal Unit is the earliest unit of the Middle Villafranchian (Rook and Martínez-Navarro, 2010). This large mammal assemblage provides a clear indication of the strong environmental change that occurred at the beginning of the Pleistocene, with the disappearance of some of the taxa with subtropical affinities that still characterize the previous Early Villafranchian Triversa FU, as well as the dispersal of herbivores such as a primitive species of the genus *Mammuthus*, the monodactyl horse (*Equus* cf. *livenzovensis*) (the so-called “elephant-*Equus* event” of Azzaroli, 1977), the large deer *Eucladoceros tegulensis*, and the bovid *Gazella borbonica*. The Montopoli FU – corresponding to the MN16b unit in the European MN-system of Mein (1975) – was originally included in the Early Villafranchian (Azzaroli, 1977; Gliozzi et al., 1997), but the clear importance of the faunal turnover observable at the transition from the Triversa FU to the Montopoli FU suggested considering the latter as the basal FU of the Middle Villafranchian (Rook and Martínez-Navarro, 2010).

Table 1

Dental measurements (in mm) of *Puma pardoides* from Montopoli, Saint-Vallier (data from Argant, 2004; Hemmer et al., 2004), and Kvabebi (data from Hemmer et al., 2004), compared to *Puma concolor*, *Panthera pardus*, and *Lynx issiodorensis*.

Tableau 1

Mesures dentaires (en mm) de *Puma pardoides* de Montopoli, Saint-Vallier (données de Argant, 2004; Hemmer et al., 2004) et Kvabebi (données de Hemmer et al., 2004), par rapport à *Puma concolor*, *Panthera pardus* et *Lynx issiodorensis*.

		TL	MaxB	BlaB	ParL	MetL
<i>Puma pardoides</i>						
Montopoli						
IGF 15358	sx	20.0	11.2	7.2	7.4	7.1
Saint-Vallier						
MHNL QSV.136	dx	21.0	11.6	7.5	8.4	8.1
MHNL QSV.136	sx	20.0	11.4	7.5	8.7	7.4
MHNL SV.97.020	sx	23.2	13.2	–	9.6	8.9
MHNB StV.273	dx	23.2	11.3	8.2	9.8	9.1
MHNB StV.273	?	22.7	11.2	–	–	–
Kvabebi						
GSM K-243	dx	21.5	13.0	8.7	9.8	7.6
GSM K-244	sx	–	12.8	–	9.8	–
<i>Puma concolor</i>						
Schmid, 1940 (n = 8)		24.0	11.9	8.6	9.6	10.2
Young and Goldman, 1946 (n = 127)		22.4	11.3	–	–	–
HNHM (n = 3)		21.3	11.4	–	–	–
Werdelin (n = 21)*		23.8	11.8	8.9	9.7	9.5
<i>Panthera pardus</i>						
Schmid, 1940 (n = 156)		24.2	12.2	–	–	–
HNHM and SPE (n = 17)		23.5	12.1	–	–	–
Werdelin (n = 31)*		25.1	12.9	8.6	10.1	9.9
<i>Lynx issiodorensis</i>						
Perrier-Étouaries						
MHNB Prr200		20.4	9.6	6.5	8.2	8.7
MHNB Prr201		20.5	9.6	6.4	8.7	8.7
MHNB Prr411		19.6	8.9	6.8	8.2	8.2
MHNB Prr8		19.9	10.3	6.4	8.5	7.6
IGF 12777		19.9	9.6	7.0	8.0	8.0
MNHN 583*		20.5	9.8	6.9	8.0	8.0
Saint-Vallier						
MHNB StV.767*		20.6	11.1	6.7	8.7	8.3
MHNL QSV...*		19.4	9.4	6.3	8.0	7.2
Pantalla						
SBAU 337624		18.2	8.7	6.3	7.3	7.3
Olivola						
IGF 4399		18.0	8.4	–	7.1	–
Upper Valdarno						
IGF 13890		17.2	7.3	5.5	6.7	5.8
IGF 13894		16.9	7.8	–	–	–
IGF 893		17.7	8.7	5.7	7.4	6.9
Garfagnana						
IGF 1445V		18.0	8.6	–	–	–
Pirro Nord						
DSTR...		20.1	9.0	6.9	7.5	7.2

TL: total length; MaxB: breadth at the protocone (maximum breadth); BlaB: blade (paracone + metacone) length; ParL: paracone length; MetL: metacone length. For average data, sample size is indicated in brackets. Values indicated by an asterisk were kindly provided by Lars Werdelin.

TL: longueur totale; MaxB: largeur au protocône (largeur maximale); BlaB: longueur lame (paracône + métacône); ParL: longueur paracône; MetL: longueur métacône. Pour les données moyennes, la taille de l'échantillon est indiquée entre parenthèses. Les valeurs marquées d'un astérisque ont été aimablement fournies par Lars Werdelin.

The Montopoli large mammal assemblage and the related Faunal Unit occur at the Gauss/Matuyama boundary (~2.6 Ma) (Lindsay et al., 1980). Therefore the Early/Middle Villafranchian transition corresponds to the newly redefined Plio/Pleistocene boundary, lowered to the Global Stratotype Section and Point (GSSP) of the Gelasian Stage at Monte San Nicola, Sicily (Gibbard et al., 2010; Rio et al., 1994).

Puma-like cats – which probably represent the most poorly known carnivores within the European Pleistocene faunas – spread into western Europe at the beginning

of the Pleistocene and their diffusion can be considered one of the bioevents that characterized the Early/Middle Villafranchian faunal turnover (Hemmer et al., 2004). As suggested by several authors (Hemmer et al., 2004; Madurell-Malapeira et al., 2010a; Salles, 1992; Spassov, 2011; Van Valkenburgh et al., 1990), the puma is closely related to the cheetah and the snow leopard (although recent genetic analyses (Johnson et al., 2006) seem to put the close affinities between the snow leopard and the *Puma-Acinonyx* clade up for discussion). At present, the incompleteness of the fossil record cannot provide clear

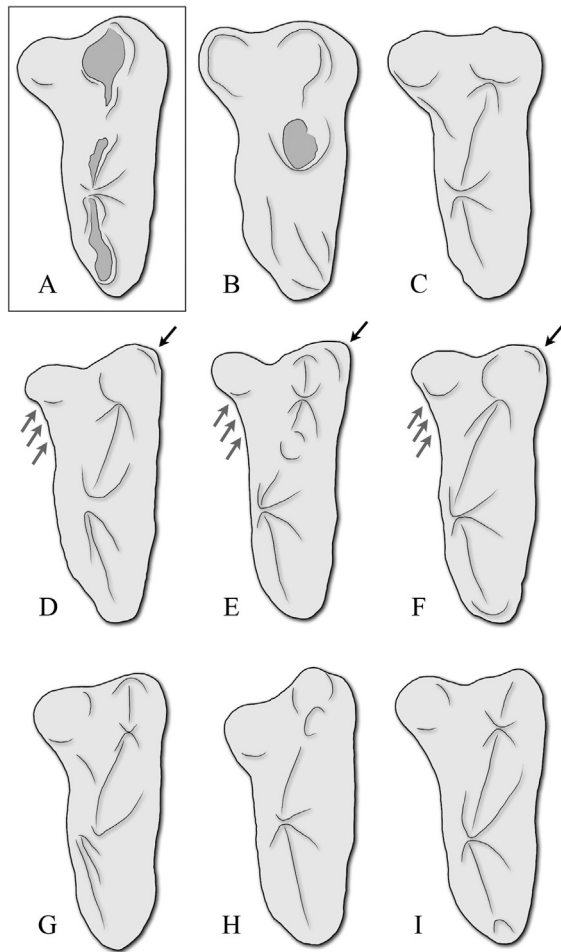


Fig. 3. Upper carnassial of selected fossil and living felids in occlusal view. A. *Puma pardoides* from Montopoli (IGF 15358). B. *P. pardoides* from Saint-Vallier (cast IGF 13511). C. *P. pardoides* from Saint-Vallier (UCBL SV.97.020). D. *Lynx issiodorensis* from Perrier-Étouaries (cast IGF 12777). E. *L. issiodorensis* from Upper Valdarno (IGF 13894). F. *L. issiodorensis* from Saint-Vallier (cast IGF 15072). G. *Panthera pardus* (HNHM 65.52.1). H. *Acinonyx pardinensis* from Montopoli (IGF 12477). I. *Puma concolor* (HNHM 66.269.1). The black arrows indicate the ectoparastyle in *L. issiodorensis*. The grey arrows indicate the typical profile of the protocone in *L. issiodorensis*. Drawings are not to scale.

Fig. 3. Carnassière supérieure de félinés fossiles et vivants en vue occlusale. A. *Puma pardoides* de Montopoli (IGF 15358). B. *P. pardoides* de Saint-Vallier (coulée IGF 13511). C. *P. pardoides* de Saint-Vallier (UCBL SV.97.020). D. *Lynx issiodorensis* de Perrier-Étouaries (coulée IGF 12777). E. *L. issiodorensis* de Valdarno Supérieur (IGF 13894). F. *L. issiodorensis* de Saint-Vallier (coulée IGF 15072). G. *Panthera pardus* (HNHM 65.52.1). H. *Acinonyx pardinensis* de Montopoli (IGF 12477). I. *Puma concolor* (HNHM 66.269.1). Les flèches noires indiquent la ectoparastyle dans *L. issiodorensis*. Les flèches grises indiquent le profil type de l'protocône dans *L. issiodorensis*. Les dessins ne sont pas à l'échelle.

information on the origin and systematics of these small-headed large cats, which are normally distinguished only on the basis of craniodental features.

The Early and Middle Villafranchian European mammal assemblages are characterized by the occurrence of different large felids such as two machairodontine cats (*Homotherium* and *Megantereon*), the giant cheetah *A. pardinensis*, and *L. issiodorensis*, besides *P. pardoides*.

During the Late Villafranchian, the Eurasian jaguar *Panthera gombaszoegnesis* also spread into Europe, together with the giant hyaena *Pachycrocuta brevirostris* (“*Pachycrocuta brevirostris* event” of Martínez-Navarro, 2010) and the first wolf/jackal-sized dogs of the genus *Canis* (“wolf event” of Azzaroli, 1983) (Palombo et al., 2008). In the present paper, we confirm that *P. pardoides* was present in western Europe at least from the Plio/Pleistocene transition (while its first occurrence in eastern Europe – Kvabebi, Georgia – and Asia – Shamar, Mongolia – is probably slightly older; Hemmer et al., 2004). Therefore, keeping in mind that its youngest record is at Vallparadís, Spain, around the latest Early Pleistocene (Madurell-Malapeira et al., 2010b), we can conclude that this species was present in Europe for at least 2 Ma. Probably, the presumed high ecological adaptability of *P. pardoides* – inferred from the very different paleoecological features of the sites where this species has been found, as well as from the ecological data for the closely-related extant *P. concolor* – allowed this big cat to find space in the complex framework of the Early Pleistocene carnivore guild. It is not accidental that the disappearance of *P. pardoides* from the Eurasian fossil record at the end of the Early Pleistocene coincides with the arrival of an other ecologically flexible large cat, the leopard *P. pardus* (probably first recorded in the Vallonnet Cave at about 1.0 Ma, Moullé et al., 2006), which probably replaced the Eurasian puma occupying the same ecological niche. Unfortunately, even in this case the scantiness and ambiguity of the fossil record make the definition of this ecological “transition” unclear.

6. Conclusions

The occurrence of *P. pardoides* in the Montopoli assemblage is here documented thanks to the description of a left upper carnassial stored at the IGF. This fossil therefore can be considered as the earliest evidence of this species in Italy at the Plio/Pleistocene transition, when this felid spread into western Europe possibly from Asia. The Montopoli Faunal Unit, now referred to the Middle Villafranchian (Rook and Martínez-Navarro, 2010), can be related to an important faunal change driven by the climate change at the beginning of the Pleistocene, with the dispersal and diffusion of elephantids, gazelles, antelopes, and monodactyl horses. The puma-like cat *P. pardoides* was one of the top predators, together with the giant cheetah, machairodontine cats, and – later on – pantherine cats, that characterized the western Europe terrestrial ecosystems for hundreds of thousands of years. This felid became extinct at the end of the Early Pleistocene, when lions and leopards spread widely into Europe.

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