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The Late Villafranchian (Early Pleistocene) carnivores  
(Carnivora, Mammalia) from Pirro Nord (Italy)

by

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NAVARRO, LORENZO ROOK and RAFFAELE SARDELLA



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with 4 plates, 1 text-figure and 17 tables

## Zusammenfassung

Es werden die Carnivoren aus unterpleistozänen Faunenvergesellschaftungen aus Spaltenfüllungen der Umgebung zwischen Apricena un Poggio Imperiale (Gargano, Apulien, Italien) beschrieben. Das reiche Material wurde seit den 1980ern gesammelt und wird an verschiedenen Institutionen (Florenz, Rom Sapienza und der Universität Turin) aufbewahrt. Dreizehn verschiedene Taxa konnten identifiziert werden, am häufigsten der Canidae *Canis mosbachensis*, die Säbelzahnkatze *Homotherium latidens* und die Hyäne *Pachycrocuta brevirostris*. Die Pirro Nord Faunenvergesellschaftung ist sehr divers und liefert wertvolle Informationen bezüglich Evolution und Ökologie von unterpleistozänen Carnivoren.

**Schlüsselwörter:** Carnivora – Biochronologie – Dispersionevent – Spätes Villafranchium – Frühes Pleistozän – Italien

## Abstract

The carnivores from the Early Pleistocene faunal assemblage from fissure fillings in the area between Apricena and Poggio Imperiale (Gargano, Apulia, Italy) are herein described. The rich sample has been collected since 1980's and is stored in different institutions (Florence, Roma Sapienza and Turin universities). Fourteen different taxa have been identified, with the canid *Canis mosbachensis*, the sabertoothed-cat *Homotherium latidens* and the giant hyaena *Pachycrocuta brevirostris* most frequently recorded. The Pirro Nord faunal assemblage presented here is a diversified sample providing valuable information on the evolution and ecology of Early Pleistocene carnivores.

**Key words:** Carnivora – Biochronology – Dispersal Events – Late Villafranchian – Early Pleistocene – Italy

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## Introduction

Pirro Nord is a fossiliferous site located near Apricena (Foggia, Apulia, Southern Italy) on the northwest of the Gargano promontory. Early Pleistocene mammals from the silicoclastic sedimentary filling of a karst fissure network exposed in the surroundings of Apricena have been collected since the late 1960s (Pieri collection, University of Bari) and reported since the 1970s/1980s (FREUDENTHAL 1971, DE BEAUMONT 1979, DE GIULI & TORRE 1984, DE GIULI et al. 1987, ABBAZZI et al. 1996, ARZARELLO et al. 2007, ROOK 2013).

Pirro Nord fossil assemblage includes more than one hundred vertebrate species. This noticeable faunal assemblage has been assembled along almost 40 years of field investigations by different researchers systematically surveying the sandy-clayey fillings of the karst network developed along the contact between Mesozoic and Pliocene carbonatic successions (ABBAZZI et al. 1996). The Late Villafranchian elements of the mammal fauna suggest an Early Pleistocene age. The geomagnetic polarity of the sediments (NAPOLEONE et al. 2003, PAVIA et al., 2010) further suggests a chronology preceding the Jaramillo sub-magnetochrone.

The Pirro Nord assemblages are characterized by the occurrence of the vole *Allophaiomys* ex gr. *ruffoi* (MASINI et al. 1998) a species that is indicative of the Early Biharian (micro-) Mammal Age (SALA & MASINI 2007). The fossil assemblage is considered to be one of the youngest Italian faunas of the Late Villafranchian, and Cava Pirro has been designated as the type locality of the Pirro Faunal Unit (GLIOZZI et al. 1997, TORRE et al. 2001, ROOK & MARTÍNEZ-NAVARRO 2010).

The carnivore remains from Pirro Nord, although collected since late 1970s, have been only partially described. BEAUMONT (1979) provided a short description and illustrations of craniodental remains of felids, hyaenids and canids from the "Feist private collection" (Mr. Feist, a non professional palaeontologist from Mühlthal, Germany). One of us (RS) had the opportunity to examine casts of these specimens, stored at Geneva Palaeontological Museum (Switzerland).

MAZZA & RUSTIONI (1992) included Pirro Nord fossil remains in their study on Late Villafranchian Etruscan bear. Canids have been investigated by ROOK (1993, 1994) and ROOK & TORRE (1996), SARDELLA (1994, 1998) studied the sabre-toothed cats, while very recent discoveries allowed the

description of large mustelid *Pannonictis* (COLOMBERO et al. 2012).

In this paper we offer an updated overview of the Pirro Nord carnivore sample. The sample is outstanding, made up by 14 taxa, with almost all the Villafranchian carnivores documented.

According to the different "taphonomic context" (cfr. ABBAZZI et al. 1996), the preservation status of the specimens varies considerably. Some skeletal elements are perfectly preserved, in some cases still articulated, indicating sedimentary facies of very low energy, usually corresponding to burial settings into the karst cavities acting as natural traps. Other specimens are very poorly preserved (fractured, and in some case polished by water transport), when the fossils came from a sedimentary facies of high energy (such as sands or small conglomerates) corresponding to phases characterised by flooding of the karst system (ABBAZZI et al. 1996). Manganese encrustations can be recorded on the bones, which, in some cases, appear completely black.

Such scheme has been recently confirmed and developed after the taphonomical analyses, carried on the mammal fossil remains from the fissure P10 (PAVIA et al. 2012). The study reveals the presence of different status of preservation (e.g., different degree of abrasion or oxides coating) in the same Sedimentary Unit (SU), thus indicating the presence of reworked bones. However the absence of biochronological differences between and within the SU suggests that the reworking processes affected only sediments of minimal chronological differences, possibly already deposited within the same Villafranchian karst network.

The vertebrate assemblages found in the various fissures of the Pirro Nord palaeontological complex are well diversified, and they represent a relatively short time-span.

The fossil elements of the Pirro Nord FU indicate the presence of open dry environment with scattered patches of woodlands eventually along water courses or swamps, some of them with temporary characteristics, with a temperate to warm climate (PAVIA et al. 2012).

## Materials and Methods

In this paper have been considered fossils stored at different scientific institutions such as: the Natural History Museum (Geology and Paleontology section) of the University of Florence (IGF), the Earth Sciences

Department of the University of Florence (PN, DE and CAR), the Earth Sciences Department of Sapienza University of Rome (G), the Palaeontological Museum of the University of Turin (PU), the Pieri collection (Earth Sciences Department of the University of Bari), the "Feist collection" (casts at Geneva Paleontological Museum).

Comparisons are based on fossil and extant skeletal collections from the following institutions: Natural History Museum of the University of Florence, (Geology and Paleontology section, Zoological section "La Specola"), Earth Sciences Department of Sapienza-University of Rome, Istituto Italiano di Paleontologia Umana (Rome), Senckenberg Forschungstation für Quartärpaläontologie (Weimar), Museo De Prehistoria y Paleontología Josep Gibert in Orce (Granada), Naturhistorisches Museum (Basel), Geneva Palaeontological Museum.

Standard measurements of craniodental and postcranial anatomical elements have been taken with digital calliper following VON DEN DRIESTCH (1976).

The following taxa are identified:

Mustelidae

*Mustela* cf. *M. palerminea* PETENYI, 1864

*Meles meles* LINNAEUS, 1758

*Pannonictis nestii* (MARTELLI 1906)

Ursidae

*Ursus etruscus* CUVIER, 1823

Canidae

*Canis mosbachensis* SOERGEL, 1925

*Lycaon lycaonoides* (KRETZOI 1938)

*Vulpes alopecoides* FORSYTH MAJOR, 1877

Felidae

*Megantereon whitei* BROOM, 1937

*Homotherium latidens* (OWEN 1846)

*Lynx issiodorensis* ssp. (CROIZET & JOBERT 1828)

*Acinonyx pardinensis* CROIZET & JOBERT, 1828

*Panthera* ex gr. *toscana-gombaszoegensis*

*Puma pardoides* (OWEN 1846)

Hyaenidae

*Pachycrocuta brevirostris* (AYMARD 1846)

Mustelidae

*Mustela* cf. *M. palerminea* PETENYI, 1864

(Plate 1, Figs a1, a2, Table 1)

This species is represented by a small left mandible with a complete tooth-row (PU104625, Plate 1, Fig. a1) (PETRUCCI 2008). The lower profile is straight till the level of m1 talonid, and directs upward posteriorly. The mandible is high and relatively stout, with constant lateral thickness. The horizontal ramus is stronger than the vertical one. At p3 level, on the labial side, there are two mandibular foramina. The coronoid process is strongly developed and has triangular shape, with the conical upper point slightly separated. The condylar process is elongated laterally while it is slightly inclined downward lingually.

The second premolar is small, single rooted and rotated laterally. A similar structure can be seen in p3 (although this element has two roots), in both of the teeth the protoconid is oriented forward. The p4 has a different structure, with a high, sharp and well developed protoconid, located in central position. There is a cingulum, forming two accessory (respectively anterior and posterior) cuspets. The carnassial tooth is secodont, with three cusps: paraconid, protoconid in the trigonid region (metaconid lacking) and only one cusp (hypoconid) in the talonid (Plate 1, Fig. a2). The second molar is a rounded small cusp. It is single rooted and located very close to m1.

Significant morphological and morphometrical features of the mandible are the morphology of coronoid process and p4 and m1, as well as the dimensions of m1. All these features allow us to refer PU104625 to the lineage of ermine, although m1 size is slightly larger than those referred, in the available literature, to *Mustela palerminea* (BONIFAY 1971).

**Table 1.** Lower carnassial (m1) of *Mustela* from Pirro Nord compared with specimens from other Middle Pleistocene localities and extant species of the genus. Data come from BONIFAY (1971), GARCÍA & ARSUAGA (1999). See appendix for measurement explanation.

	PU 104625	<i>Mustela palerminea</i>				<i>M. praeglacialis</i>	<i>M. praenivalis</i>	<i>M. erminea</i>	<i>M. nivalis</i>
	Italy	France	Spain	Hungary	German	Hungary	Spain	Europe	France
	Pirro Nord	L'Escale-Lunel viel	Atapuerca		Erpfingen			extant	extant
m1L	5.34	4.7–5.0	4.8–5.0	4.4–5.5	4.6–5.3	5.5–6.0	3.8	5.1–6.24	4.04–4.34
m1AB	1.64	1.4–1.7	1.4–1.6	1.4–1.7	1.3–1.5	1.9	1.1	1.5–2.1	1.28–1.32
m1PB	1.54	1.1–1.3	1.3–1.6	1.4–1.8	1.3–1.8	1.6		1.8–2.1	

*Mustela palerminea* occurs in Europe in some late Early Pleistocene sites (Galerian faunal assemblages) like Betfia V, Romania (TERZEA 1996), Atapuerca TD6, Spain (GARCIA & ARSUAGA 1999) and also in some early Middle Pleistocene assemblages as Gombasek 1, Czech Republic (GARCIA & ARSUAGA 1999).

The left mandible from Pirro Nord represents an early specimen of the ermine evolutionary trend. For its morpho-dimensional features, and taking into account the scantiness of available comparative material, we prefer a cautious attribution for the Pirro Nord specimen PU104625 to *Mustela* cf. *M. palerminea*.

*Meles meles* LINNAEUS, 1758

(Plate 1, Fig. b, Tables 2, 3)

The Eurasian badgers in the Pirro Nord assemblage is represented by a mandibular fragment with m1 (PU 104151) (Plate 1, Fig. b), a left proximal femur (PU 104059), and a right distal radius (PU 106123) (PETRUCCI 2008).

The main diagnostic features have been recognized on the carnassial tooth, although the occlusal surface is worn. In the trigonid the cusps are very large: paraconid and protoconid have an elliptical section, while the metaconid, detached from the carnassial blade, is rounded. The talonid is developed, and proportionally as large as the trigonid. The cusps are developed, above all hypoconid and entoconid, and posteriorly a rounded raised edge along the margin, connect the hypoconulid and the entoconulid. For its sizes and morphology PU 104151 is fully comparable with the lower carnassial of the Pleistocene and living

*Meles meles* of Europe. Together with the recent finding of *M. meles* at Fuente Nueva 3 (Orce, Spain), dated ~1.3 Ma (MADURELL-MALAPEIRA et al. 2011b), the occurrence of Pirro Nord can be considered as the first occurrence of the species in Europe.

Previously the Eurasian Badger was recorded in the Early Pleistocene site of Le Vallonnet (France) (MOULLÉ 1992). At Untermassfeld (Germany), a site chronologically correlatable with Le Vallonnet, WOLSAN (2001) reports the occurrence of *Meles hollitzeri* that he considered as a possible subspecies of *Meles meles*.

The systematic position of the Early Pleistocene badgers is actually matter of debate. Several species have been described for different fossils such as *Meles hollitzeri* (RABEDER 1976, WOLSAN 2001), *Meles dimitrius* (Migdonyan basin, Greece, KOUFOUS 1992) and *Meles atavus* (Püspöckfürdő, Romania, KOROS 1914).

According to some authors (KRETZOI 1938, WOLSAN 2001, BARYSHNIKOV et al. 2003, VILLANI et al. 2008, MADURELL-MALAPEIRA et al. 2009), on the basis of morphological and biometrical characteristics, all these species can be considered as subspecies of the highly polymorphic species *Meles meles*. The same interpretation is confirmed in a recent taxonomic revision of the European Plio-Pleistocene badger taxonomic status (MADURELL-MALAPEIRA et al. 2011a).

A number of traits make the badger from Pirro Nord very similar to the fossil Early Pleistocene badgers from Europe and the extant *Meles meles*: the trigonid and talonid similarly developed. On the contrary,

Table 2. Measurements of m1 for *Meles meles* from Pirro Nord for other specimens and from some Early Pleistocene localities, and extant species of the European *Meles*. Data from personal observations and from VIRET (1950), BONIFAY (1961), KOUFOUS (1992) and MOULLÉ (1992). See appendix for measurement explanation.

	PU 104151	<i>Meles thorali</i>	<i>M. dimitrius</i>	<i>M. atavus</i>	<i>M. hollitzeri</i>	<i>M. meles</i>	<i>M. meles</i>
	Italy	France	Greece	Romany	Germany	France	Italy
	Pirro Nord	St. Vallier	Migdonya		Untermassfeld	Le Vallonnet	extant
m1L	16.4	15.4–17.00	14.8–15.3	15.2	16.42	18.00 ca	15.4–17.4
m1B	7.0	6.9–7.5	6.3–7.2	6.9	7.11	7.9	7.2–8.2
m1TrL	8.8	9.4–10.0	8.3–8.5		9.03	8.6 ca	8.3–9.6

Table 3. Measurements of postcranial bones of *Meles meles* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	BP	DP	DH	DN	BSD	DSD	BD	DD
PU 104059	Turin DST	Femur	SX	25.9	11.75	11.65	6.5	8.3	7.6		
PU 106123	Turin DST	Radio	DX					4.7	6.85	15.5	10.9

*M. thorali* show a trigonid larger than talonid, showing a trenchant area more developed.

Taking into account the features observed in the specimens, and the comparison with Plio-Pleistocene and extant European badgers, we consider Pirro Nord specimen as the earliest *Meles meles* in Europe.

*Pannonictis nestii* (MARTELLI 1906)

A few specimens of *Pannonictis nestii* have been recently described (COLOMBERO et al. 2012) adding a new element to the very rich and diversified Pirro Nord vertebrate association (ARZARELLO et al. 2009). This is a very rare taxon in the Pirro Nord assemblage. The species has been previously reported, in the Italian fossil record, from the Early Pleistocene of Upper Valdarno in Tuscany (MARTELLI 1906, ROOK et al. 2013) and of Pietrafitta in Umbria (ROOK 1995). The Pirro Nord specimens represent the last occurrence of the taxon in Italy.

With regards to palaeoecological aspects, ROOK (1995) had hypothesized an aquatic adaptation and a life-style linked to humid habitats as it happens in extant *Ictonychinae* (a name that has nomenclatural priority on *Galictinae*; cfr. SATO et al. 2012). Nevertheless, GARCÍA & HOWELL (2008) did not find reliable evidence of an aquatic life-style in the cranial features. As a matter of fact, an adaptation to some kind

of wetlands could fit well with the inferred palaeoenvironment of Pirro Nord. Indeed, the occurrence of *Triturus* and *Emys* in the herpetofauna (DELFINO & BAILON 2000, DELFINO & ATZONI 2013), and of Anatidae and Charadriiformes among Aves (BEDETTI & PAVIA 2013) allows hypothesizing the presence of large water reservoirs.

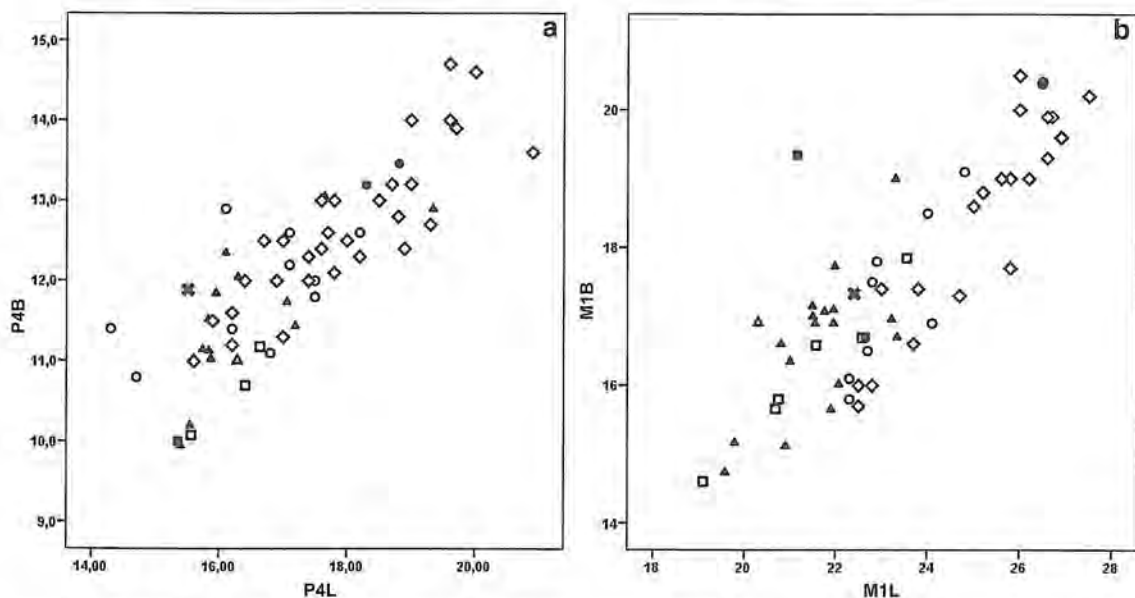
Ursidae

*Ursus etruscus* CUVIER, 1823

(Plate 1, Figs c–o, Text-fig. 1a–b, Tables 4, 5)

Bear remains are not abundant in the sample from Pirro Nord in the collections made field activities carried out from '70s to late '90s (cfr. MAZZA & RUSTIONI 1992). The collection assembled in the Turin Department Science in recent years increase the available sample of Pirro Nord fossil bear. On this ground, morphological and biometrical analysis of Pirro Nord remains, allow us to attribute them to *Ursus etruscus*.

Teeth are crucial elements for a proper attribution to this genus representatives: P4 (Plate 1, Fig. d) has a primitive shape, with a deuterocone variable in size but always smaller than paracone and metastyl. Deuterocone is positioned at the same level of metastyl and don't exceed the limit between this cusp and the paracone. In upper molars the structure of occlusal surface is simple and cusps don't show complex mor-



Explanation: \* Mt. Argentario; ○ Atapuerca TD; □ Pirro Nord; ▲ St. Vallier; ● Untermassfeld; ▲ Upper Valdarno; ◇ Le Vallonnet; ■ Venta Micena.

Text-fig. 1. Length (L) / Breadth (B) scattergram (mm) of the P4 (graph a) and M1 (graph b) of *Ursus etruscus* from Pirro Nord and other Early Pleistocene European bears.





Table 5. Measurements of *Ursus etruscus* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	GL	BP	DP	BSD	DSD	BD	DD
PU 104635	Turin DST	MT IV	SX	69.15	15.12	20.1	11.19	9.08	16.8	12.83
PU 104956	Turin DST	MT IV	SX	84.12	17.48	23.49	13.17	11.55	19.38	14.76
PU 106151	Turin DST	MT I	DX	54.12	19.12	19.36	9.38	8.45	16.51	11.4
PU 106152	Turin DST	MT II	DX	76.85	16.18	26.16	13.21	12.88	21.13	16.51
PU 106153	Turin DST	MT V	DX	74.15	21.21	18.88	9.98	9.28	16.55	13.38
PU 106105	Turin DST	MT I	SX	58.24	21.6	23.86	10.3	9.9	15.54	
PN 27	Florence DST	MT V	DX	88.85	25	23.8	13.2	12.35	22	17.4
DE 6.2	Florence DST	MT V	SX						21.45	16.5
PNR 6	Rome DST	MT I	SX	56.78	20.45	21.6	10.19	8.15	16.56	14.16
PNR 8	Rome DST	MT V	SX		22	23.18	11.35	11.28		
PNR 9	Rome DST	MT V	DX		22.37	19.58				
				GL	BP	DP	BSD	DSD	BD	DD
PU 104955	Turin DST	MC II	SX	65.49	11.41 <sub>ca</sub>	19.5	10.5	9.35	17.1	15.22
PU 104610	Turin DST	MC II	SX	72.72	14.34	23.49	13.45	12.23	19.43	17.18
PU 104744	Turin DST	MC V	DX	81.8	24.85	22.79	15.21	11.85	22.34	18.13
PU 106150	Turin DST	MC IV	SX	73.71 <sub>ca</sub>	16.17	24.97	12.79	10.86	21	17.15
PU 106061	Turin DST	MC IV	SX	68.08	14.61	22.5	11.85	9.53	19.05	16.32
PU 106060	Turin DST	MC III	DX	69.81	13.55	20.32	11.49	9.75	17.62	12.93
PU 104400	Turin DST	MC II	SX	64.46	12.3	18.28	10.55	8.93	17.4	14.35
DE 2D SSI 245	Florence DST	MC IV	DX	79.15	17.6	23.45	13.95	12.45		19.55
CAR 42	Florence DST	MC IV	DX	85	17.45	27	15.25	13.3	22.55	20.2
CAR 103	Florence DST	MC V	SX	80 <sub>ca</sub>	24.7 <sub>ca</sub>	27.75	15.8	12.25		18.7
PN 9 26.10.85	Florence DST	MC V	DX	76.25	23.1	24.5	15.95	11.95	22.95	18
PNR 7	Rome DST	MC V	DX	73.23	24.16	19.55	15.5	11.3	20.17	
DE 2D SI 85	Florence DST	Phalanx I		36.85	15.1	17.8				
CAR 43	Florence DST	Phalanx I		41.15	19.95	15.6				
PN 17 29.10.85	Florence DST	Phalanx I		39.1	18.2	16.5				
PNR 10	Roma-DST	Phalanx I		37.65	17.55	13.28				
PNR 11	Roma-DST	Phalanx I		34.67	14.77	12.82	13.83	9.49		
De 13.1 Liv, F 11.2.92	Firenze-DST	Phalanx II		29.65	16	14.3	12.7	9	13.85	
DE 12.1 4b 11.2.92	Florence DST	Phalanx II		26.55	16.1	13.75	11.4	8.2	10.85	
PNR 12	Rome DST	Phalanx II		33.31	18.01	17.25				
PNR 13	Rome DST	Phalanx II		25.48	15.75	13.03				
PNR 14	Rome DST	Phalanx II		26.54	14.46	12.17	11.76	9.32	13.37	
DE 2D SI 164	Florence DST	Phalanx III			12	19.75	13.35	9.35	15	

phology. M1 has a rectangular profile, parastyle and metastyle are relatively small. In M2 (Plate 1, Fig. c) the posterior extension of talon is detached from the body of the tooth by an abrupt step. This structure, common in all teeth of the specimen, shows a typical torsion.

Lower teeth are represented in a smaller amount in respect to the upper ones, but detectable features are unique comparable with other ursids. In the mandible, p4 (Plate 1, Fig. f) shows a simplified structure. The second molar cusps structure and disposition is very simple showing a primitive condition, as it is the

case for the upper molars. Third molar (Plate 1, Fig. g) tends to be rounded to oval, with a few and low cusps.

Postcranial bones (Plate 1, Figs h–o) are relatively slender. In the limb bones diaphyses are slender, on the contrary epiphyses, are relatively stout.

Comparing Pirro Nord remains to *Ursus etruscus* from Upper Valdarno, Monte Argentario and Venta Micena (Spain), all morphologies typical of the Etruscan bear are easily recognizable. The simplified structures of teeth occlusal surfaces, together with a substantial slenderness of bones, allow us to attribute the bear of Pirro Nord to this species. Moreover, our bio-

metrical analysis on the upper carnassial teeth and the first molar, shows that also for what concern size and dimensions the teeth fall within the variability range of *Ursus etruscus* from Valdarno and Venta Micena, while is smaller than *Ursus rodei* (see next discussion) from Untermassfeld and *Ursus deningeri* from Le Valonnet (Text-fig. 1). Moreover, features of the upper teeth of *Ursus dolinensis*, such as the M1, include approximately squared angles and quite laterally compressed lingual cusps. *Ursus rodei* shares with *U. dolinensis* very similar cranio-dental morphological features, thus they have been considered synonymous (KAHLKE 2006). The teeth of *U. deningeri*, in particular the maxillary teeth, show a more complicated cusp structure, with additional cusps in the protocone of P4 and in the lingual cusps of M1 (MOULLÉ 1992).

The taxonomic interpretation of Pirro Nord bear has been interpreted in distinct ways according to different researcher. Initially, the remains were attributed to *Ursus etruscus* (DE GIULI et al. 1987). In later times, MAZZA & RUSTIONI (1992, 1994), revising the Pliocene record of Eurasian bears, emphasized that the bear from Pirro Nord does not entirely corresponds to the classical *U. etruscus*, but it would show features closer to *U. arctos*. These authors were thus suggesting referring the Pirro Nord bear to *Ursus* sp.

However, in our view, the fossil specimen studied by the latter authors (see the fossil list in MAZZA & RUSTIONI 1992) cannot provide a firm taxonomic attribution. The ursid larger sample recently discovered from Pirro Nord site (PETRUCCI 2008), provides a better ground for a taxonomic attribution of the Pirro Nord bear.

The Pirro Nord fossils have been compared with Early Pleistocene bears from other Italian and European localities.

Nowadays different species of genus *Ursus* are reported in the fossil record. In particular the Late Villafranchian – Early Galerian forms show intermediate features between “Etruscan bears”, the “deningeroid-spelaeoid” and the “arctoid” forms (MAZZA & RUSTIONI 1992, GARCÍA & ARSUAGA 2001, ARGANT 2006, KAHLKE 2006, OLIVE 2006, PALOMBO et al. 2007). The species are: *Ursus etruscus* (MAZZA & RUSTIONI 1992, 1994), *Ursus deningeri* (MOULLÉ 1992), *Ursus dolinensis* (GARCIA & ARSUAGA 2001), *Ursus rodei* (MUSIL 2001), and the discussion on their status and evolutionary relationships can be summarised:

- 1) The first occurrence of *Ursus etruscus* is recorded in the Olivola F. U., latest Pliocene (MAZZA & RUSTIONI 1992, GLIOZZI et al. 1997), and become a common species in Europe during the Early Pleis-

Table 6. Measurements of *Vulpes alopecoides* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	CL	CB	P4L	P4B	M1L	M1B	M2B		
PN 30	Rome DST	Maxilla with P4, M1 and M2	DX			10,49	4,34	7,35	9,27	5,1		
PU 104618	Turin DST	Maxilla with P4	DX			11,27	5,59					
PU 104805	Turin DST	P4	SX			11,34	5,03					
PU 104661	Turin DST	C	SX	4,89	3,21							
				Lm1	Bm1	m1TrL						
PU 104721	Turin DST	m1	DX	13,1	5,27	8,4						
PU 106227	Turin DST	Mandible with m1	DX	12,4	5,16	7,93						
				AdL	H	BFcr	BFed					
PU 104617	Turin DST	Axis		24,2	19	15,61	8,88					
				GL	GB	SBT						
PU 104189	Turin DST	Calcaneus	DX	27,2	12	4,58						
				GL	BP	DP	DH	DN	BSD	DSD	BD	DD
PU 104873	Turin DST	Humerus	SX	92,2	13,39	18,29			6,06	6,58	15,61	11,3
PU 106063	Turin DST	Humerus	DX	92,1	13,39	18,49			6,58	6,4	15,44	11,7
PU 104455	Turin DST	Humerus	SX									
PU 104384	Turin DST	Radius	SX		10,47	6,28			7,57	3,59		
PU 104849	Turin DST	Femur	DX		9,24	10,32	10,31	6,21				
PU 106055	Turin DST	Radio	DX		9,51	5,79			7,09	3,55		
PU 104619	Turin DST	MC V	DX	29,3	5,25	4,67			3,68	2,73	4,71	4,22

tocene. MAZZA & RUSTIONI (1994) consider the Etruscan bear as a species without descents, with – probably – its last occurrence at the transition Late Villafranchian – Early Galerian. Successive arctoid and speleoid forms would have been derived from a Late Pliocene bear group, *U. aff. U. etruscus*.

- 2) Other authors (PETRONIO et al. 2003, OLIVE 2006) consider that *U. etruscus*, *U. deningeri* and, later, *U. spelaeus* were forming the speleoid lineage. *U. arctos* would derive by an Asian arctoid group and occurred in Europe in the second half of Middle Pleistocene (PETRONIO et al. 2003) or by divergence in the Early Pleistocene from the speleoid lineage (OLIVE 2006).
- 3) On the contrary, ARGANT (2006) supposes a divergence of the speleoid and arctoid lineages from the latest mosaic forms of *Ursus etruscus* at the latest Early Pleistocene. These forms are respectively *U. rodei* (MUSIL 2001) and *U. dolinensis* (GARCIA & ARSUAGA 2001). ARGANT supposes also that *Ursus dolinensis* is at basal stem of the speleoid lineage, in according with the authors of this specie (GARCIA & ARSUAGA 2001), and *Ursus rodei* would be one of the first represents of the arctoid lineage.
- 4) KAHLKE (2006), on the contrary, retains the two as being the same species (*U. rodei* = *U. dolinensis*), while OLIVE (2006) hypothesizes that are in synonymy of *Ursus arctos*. At the same time of Untermassfeld and Atapuerca TD 6, at Le Vallonet site, we record the occurrence of the first represent of *Ursus deningeri* (MOULLÉ 1992, MOULLÉ et al. 2006).

In the Late Villafranchian faunal assemblages of the Italian Peninsula, the occurrence of *Ursus etruscus* has been recognized at Olivola, Upper Valdarno, Monte Argentario (PETRUCCI & SARDELLA 2009) and in the latest Villafranchian site of Pietrafitta (MAZZA & RUSTIONI 1994). The Italian Etruscan bears clearly represent a definite group closer to St. Vallier and Venta Micena *Ursus etruscus*, and are morphologically and morphometrically distinguished from *Ursus dolinensis* from Atapuerca, *U. deningeri* from Vallonet and *U. rodei/U. dolinensis* from Untermassfeld.

As a matter of fact, the analysis of the bear material from Pirro Nord evidences strong affinities with the Early Pleistocene Italian sample and does not present the high variability degree occurring in other late Early Pleistocene European sample.

This interpretation of the Pirro Nord bear sample provides evidence that Etruscan bears continued to characterize the Latest Villafranchian mammal faunal assemblages of Italy.

#### Canidae

##### *Vulpes alopecoides* FORSYTH MAJOR, 1877

(Plate 2, Figs a, b, Table 6)

Fox remains from Pirro Nord are represented by a number of lower teeth and mandible fragments as well as upper dental ad maxillary remains. These show features typical of *Vulpes alopecoides* as results by comparison with the ones from the type locality (Upper Valdarno, FORSYTH MAJOR 1877) and Apollonia site (Greece, KOUFOUS 1992). In the maxilla (Plate 2, Fig. a) upper carnassial tooth, the protocone is positioned forward and the anterior cusp is well developed. In the first molar, paracone and metacone have the same breadth, the paraconule the protocone and the metaconule are lower than the first two, and all together surround a deep talon basin. Internally, a developed edge encloses a second less deep basin. The second molar shows similar feature, with the reduction of the metacone and the metaconule respecting the other cusps. In the lower carnassial tooth (Plate 2, Fig b), the protoconid is placed posteriorly, and a vertical posterior edge defines the trigonid. The talonid is much lower than the trigonid.

*Vulpes alopecoides* from Pirro Nord is smaller than *V. praeglacialis*, the fox of the latest Early Pleistocene from l'Escale (BONIFAY 1971) and Venta Micena (MARTINEZ-NAVARRO 1992), and is comparable with the same specie from St. Vallier (France, ARGANT 2004), Upper Valdarno (Italy, BONIFAY 1971), Villaroya and Puebla de Valverde (Spain, KURTÉN & CRUSAFONT 1977) and Apollonia (Greece, KOUFOUS 1992). This condition is visible especially in the carnassial teeth. Moreover, in the p3 a typical small accessory cusp is present, absent in *V. praeglacialis* (GARCIA & ARSUAGA 1997).

*Vulpes alopecoides* is a rare taxon in the European Late Pliocene – Early Pleistocene fossil record. It has been recorded for the first time in St. Vallier (ARGANT 2004) and occurred in the Early Pleistocene sites mentioned above. Phyletic relationships between this species and *V. praeglacialis* are unclear (ARGANT 2004), as well as the relationship between them and *Vulpes vulpes* and *Alopex lagopus*.

Table 7. Measurements of cranial and mandible remains of *Canis mosbachensis* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	I3L	I3B	CH	CHc	CL	CB	LP2	BP2	LP3	BP3	P4L	P4B	M1L	M1B	M2L	M2B
PU 104451	Turin DST	I3	SX	5.74	4.42														
PU 104452	Turin DST	C	SX					9.43	5.05										
PU 104683	Turin DST	C	DX			34.11	16.64	8.71	5.04										
PU 104577	Turin DST	C	SX					8.58	4.96										
DE12-1	Florence DST	Maxilla with P4, M1 and M2	DX											21.3	9.7	13.9	17	7.8	11
DE s.n.	Florence DST	Maxilla with P2, P3, P4, M1 and M2	DX							11.3	4.4	13.5	4.9	21.4	10.2	13.9	16.2	7.8	10.8
PU 104450	Turin DST	Maxilla with P4, M1	DX											18.66	9.3	13.28	15.38		
PN 27	Florence DST	P2	SX							11.1	5.4								
PU 104726	Turin DST	P2	SX							10.27	4.48								
PU 104773	Turin DST	P2	DX							12.14	4.88								
PU 104725	Turin DST	P3	DX									13.41	5.35						
PU 104684	Turin DST	P3	DX									10.94	5.13						
PU 104679	Turin DST	P4	SX											19.24	10.13				
PU 104681	Turin DST	P4	DX																
PN 23	Florence DST	P4	DX											25.1	11.5				
PU 104894	Turin DST	M1	DX													13.02	15.32		
PU 104727	Turin DST	M1	DX													13.37	16.56		
PN2	Florence DST	M1	DX													11.7	15.5		
PP 187	Florence DST	M1	SX													12.7	14		
				cHC	cL	cB	Lp1	Bp1	Lp2	Bp2	Lp3	Bp3	Lp4	Bp4	m1L	m1B	m1TrL	m2L	m2B
PU 104778	Turin DST	c	DX		10.34	7.43													
PU 104530	Turin DST	c	DX		7.26	4.48													
PU 104730	Turin DST	p1	SX				5.56	3.96											
PU 104723	Turin DST	p4	SX										14.9	7.17					
PU 104724	Turin DST	p4	DX										13.45	6.26					
PN 24	Florence DST	m1	SX												23.5	9	17		
PU 104680	Turin DST	m1	DX													9.13	15.26		
PU 104704	Turin DST	m1	SX																
PP 203	Florence DST	m2	DX															9.9	7.5
PU 104678	Turin DST	Mandible	SX	16.91	10.6	6.86			11.22	4.95	11.99	5.42	14.3	6.82	24.34	9.89	15.62	10.68	7.31
PU 104658	Turin DST	Mandible	SX						9.31	4.3	10.75	4.51	12.22	5.59	20.49	8.52	13.26		
PU 104001	Turin DST	Mandible	DX						10.41	4.84	11.8	5.24	14.54	6.67	24.65	9.39	16.5	11.09	7.39
PU 106435	Turin DST	Mandible	DX								11.14	4.54			23.06	8.86	15.14	10.2	6.81
PU 104787	Turin DST	Mandible	DX						9.28	3.75	10.17	4.07	11.96	5.11					
PU 106207	Turin DST	Mandible fragment	SX															9.51	6.14
PU 106028	Turin DST	Mandible fragment	SX						10.14	5	11.57	5.13			22.44	9.18	15.48	10.08	7.07
PU 104294	Turin DST	Mandible fragment	SX																
PU 104659	Turin DST	Mandible fragment	SX																
PU 104398	Turin DST	Mandible fragment	DX															9.5	6.91
PU 106032	Turin DST	Mandible fragment	DX															10.09	6.52
PU 106103	Turin DST	Mandible fragment	SX																
PU 106232	Turin DST	Mandible fragment	SX																

Table 8. Measurements of postcranial remains of *Canis mosbachensis* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	GL	GB	GBT	ANW	AHW					
PU 106029	Turin DST	Astragalus	DX	26.13	21.54	14.48	10.27	14.1					
				GL	BP	DP	BSD	DSD	BD	DD	HT		
PU 104354	Turin DST	Humerus	SX				10.72	11.53	27.02	20.07	15.29		
PU 104641	Turin DST	Humerus	DX				10.9	12.51					
PU 106252	Turin DST	Radius	DX						19.87	11.24			
PU 106164	Turin DST	Radius	DX		14.81	10.23	11.38	5.29					
PU 104850	Turin DST	Tibia	SX				11.36	11.02	21.83	15.25			
PU 106100	Turin DST	Tibia	SX				12.48	12.5	23.31	15.95			
PU 104777	Turin DST	MC II	DX	50.59	5.67	9.16	5.71	4.73	8.04	6.98			
PU 106154	Turin DST	MC III	SX	62.47	10.85	7.49	5.69	4.54	7.96	8.42			
PU 104735	Turin DST	MC III	SX		8.72	7.6							
PU 104106	Turin DST	MC IV	DX		10.61	8.53							
PU 104734	Turin DST	MC IV	SX	56.21	10.04	9.72	5.77	5.47	8.47	8.51			
PU 104736	Turin DST	MT III	SX	71.1	7.99	12.78	6.37	5.78	7.92	8.72			
PU 104799	Turin DST	MT III	SX	65.86	8.05	12.03	6.38	4.64	7.94	8.35			
PU 104606	Turin DST	Phalanx I		22.01	8.08	7.44	4.97	5.26	6.39	5.42			
PU 104512	Turin DST	Phalanx I		26.82	10.06	8.98	6.64	5.99					

Table 9. Measurements of *Lycyon lycanoides* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	I3L	I3B	CH	CHc	CL	CB	P4L	P4B	MIL	MIB	M2L	M2B		
DE 11-1 s.n	Florence DST	Maxilla fragment with P4 and M2	SX							26.1	12.9			9.4	12.1		
PU 104682	Turin DST	I3	DX	9.45	7.02												
PU 106140	Turin DST	I3	SX	9.72	6.99												
PU 104753	Turin DST	C	DX			48.72	22.7	12.4	7.89								
PP 186	Florence DST	P4	DX							25.3	11.5	17.7	18.6				
PN 23	Florence DST	P4	DX							25.2							
PN 2c s.n	Florence DST	M1	DX									14.3	16.7				
PN 2e s.n	Florence DST	M1	SX									16.7	16.7				
PN 2c s.n	Florence DST	M2	SX											8.5	10.8		
PN 22	Florence DST	Mandible fragment with p2 and p3	SX	i3L	i3B	cH	cHC	cL	cB	p2L	p2B	p3L	p4L	p4B	M2L	M2B	
PU 104754	Turin DST	c	DX			55.76	26.04	14.76	9.55	13.3	6.00	14					
PU 104703	Turin DST	c	SX				24.99	14.04	9.41								
PU 105413	Turin DST	i3	DX	6.43	4.77												
PN 25	Florence DST	p4	DX										16.5	7.3			
PN 35	Rome DST	m1	DX												27.91	10.54	
PN (4)	Florence DST	m2	SX													16.9	
PU 104685	Turin DST	Adias		AdL	H	BFer	BFed										7.5
				20.39	31.91	44.55	38.64										
PU 104954	Turin DST	Pelvis	DX	GL	LA	SH											
					34.96	28.5											
PU 106116	Turin DST	Calcaneus	DX	GL	GB	GBT	SBT	ANW	AHW	H							
				60.65	28.01		10.84										
PU 104648	Turin DST	Astragalus	SX	34.46	28.72	19.88		16.15	19.15								
PU 104080	Turin DST	Scaphoid	DX	24.83	18.12												
				GL	BP	DP	DH	DN	BSD	DSD	BD	DD	HT				
PU 104004	Turin DST	Humerus	DX						15.76	17.93	39.91	30.91	21.93				
PU 104513	Turin DST	Femur	SX					14.31									
PN 17	Rome DST	Tibia	SX	203.14	42.01	44.56			15.97	16.11	26.66	18.25					
PU 104756	Turin DST	MC I	DX	27.74	6.26	7.89			4.08	5.3	7.28	5.54					
PN 7	Rome DST	MC II	SX	73.51	10.97	14.84			9.84	8.91	13.16	11.73					
PU 106112	Turin DST	MC II	SX	78.3					8.56	8.43	13.82	12.04					
PN 8	Rome DST	MC III	SX	86.17	11.92	14.88			9.53	8.79	11.92	13.23					
PN 9	Rome DST	MC IV	SX	86.89	9.6	14.42			8.71	7.78	11.36	12.95					
PN 10	Rome DST	MC V	SX	71.34	14.69	14.34			8.88	8.36	13	11.74					
PU 106155	Turin DST	MTV	SX	91.38	17.12	11.67			7.8	8.98	11.75	12.33					
PU 104517	Turin DST	Phalanx I		37.88	14.46	15.48			9.21	9.67	13.09	8.75					
PU 104391	Turin DST	Phalanx I		32.28	12.78	11.54			7.21	8.31	9.58	8.32					

*Canis mosbachensis* SOERGEL, 1925

(Plate 2, Figs c–h, Tables 7, 8)

The small wolf remains from Pirro Nord (mostly from Earth Sciences Department of the University of Florence collections) have been described and figured by ROOK (1993) and ROOK & TORRE (1996). These authors referred the material to *Canis* aff. *C. arnensis* and discussed the problem of small wolves in the Mediterranean area during the late Early Pleistocene and earliest Middle Pleistocene (the transition Late Villafranchian – Early Galerian).

As a matter of fact, the fossil record of Early Pleistocene dogs is a matter of debate. While in the base of the Late Villafranchian (~1.7–2.0 Ma) two species are distributed in Europe (the larger, wolf-like, *Canis etruscus* and the smaller, coyote-like, *Canis arnensis*), in most of the Late Villafranchian and the base of the Middle Pleistocene record only the occurrence of a small wolf is recorded. The evolutionary relationships among these canids have not been solved yet.

The Mosbach wolf, described as *Canis mosbachensis* by SOERGEL in 1925, was considered as a subspecies of *Canis lupus* by THENIUS (1954) and then synonymised with *Canis etruscus* and *Canis arnensis* by BONIFAY (1971). Such an interpretation has been contended by TORRE (1974), who demonstrated that *Canis mosbachensis* is much closer to the extant wolf than to the Late Villafranchian species. One of the characteristics of this species is the occurrence of a lower carnassial paraconid higher than premolars, in particular p4 (TORRE 1974, ROOK & TORRE 1996, GARCIA & ARSUAGA 1999).

The modern wolf is commonly thought to be derived from the evolutionary lineage *C. etruscus* – *C. mosbachensis* – *C. lupus* (TORRE 1967, MUSIL 1972, SOTNIKOVA 1989, 2001, ARGANT 1991, SOTNIKOVA & ROOK 2010). On the basis of the reversal size trend in this evolutionary lineage, a different point of view was proposed by ROOK & TORRE (1996). In their description of the Pirro Nord specimens these authors suggested the possibility that the latest Villafranchian – earliest Galerian medium-sized dogs from the Mediterranean area were not connected with the *C. etruscus* – *C. mosbachensis* clade, but instead continued the phylogenetic line of the coyote-like *C. arnensis*. Although this hypothesis has been criticised by some authors (MARTÍNEZ-NAVARRO 2002, 2009, GARCIA & ARSUAGA 1999, MOULLÉ et al. 2006a), the evolutionary scenario described in ROOK & TORRE (1996)

is supported by others (BARYSHNIKOV & TSONKALA 2010, MELORO & ROOK in progress).

The revision of the outstanding canid fossil sample from the sites of Untermassfeld in Germany and 'Ubeidiya in Israel, allowed SOTNIKOVA (2001) and MARTÍNEZ-NAVARRO (2009), respectively, to explore some of these aspects and to suggest the occurrence in the latest Villafranchian assemblages, of the primitive stages of the Middle Pleistocene *C. mosbachensis*.

In the Turin Paleontological Museum is housed a large *Canis* sample from Pirro Nord including isolated teeth, mandibles, and different elements of the skeleton. At least 9 individuals are represented. These new specimens show some important evidence. Mandibles are different in thickness and in sturdiness of the horizontal branch. Such features can be related to sexual dimorphism, confirming the observations due to SOTNIKOVA (2001) on the Untermassfeld remains. Moreover, some anatomical differences of teeth (see below), and in general a smaller size of postcranial bones, could demonstrate a very large variability of this species. In addition a taxonomic attribution is grounded on the lower carnassial morphology. In fact, in m1, hypoconid and entoconid are small and united by a crest that divides the talonid basin. This morphology occurs in the small wolf from Venta Micena, initially considered as *Canis etruscus* (MARTÍNEZ-NAVARRO 1992), *Canis* aff. *C. arnensis* (ROOK & TORRE 1996), and successively as *C. mosbachensis* (MARTÍNEZ-NAVARRO et al. 2003).

Remains from Pirro Nord compared with the small wolf from Untermassfeld, 'Ubeidiya, Venta Micena, Fuente Nueva 3, and Barranco León, show similar features. In the maxillar teeth, P3 has a single posterior cusplet instead of two and in the carnassial tooth, the protocone forms a right angle with the paracone. In the mandible, the paraconid of carnassial tooth is higher than protoconid of p4.

Such evidences would incline us to refer the wolf from Pirro Nord to *Canis mosbachensis*, while one of the authors (LR) would favour an attribution of the Pirro Nord small wolf to *Canis* aff. *C. arnensis* (original view expressed in ROOK & TORRE 1996), supported by an ongoing morphometrical revision of extant and Plio-Pleistocene European canini (MELORO & ROOK in progress).

*Lycaon lycaonoides* (KRETZOI 1938)

(Plate 2, Figs i–l, Table 9)

The wild dog from Pirro Nord is represented by a few but significant remains. The specimens of this large-sized canid from Pirro Nord recovered in the early investigations from the late '70s to the late '90s (Florence and Rome collections) have been described by ROOK (1993, 1994). The material was originally attributed to *Canis (Xenocyon) ex. gr. falconeri* (ROOK 1994). Later on, in a revision of the African hunting dog evolution (MARTÍNEZ-NAVARRO & ROOK 2003), the Old World representatives of *Canis (Xenocyon)* have been synonymised within the genus *Lycaon*.

Noticeable within the new sample is the occurrence of a first right metacarpal (ROOK 1994, MARTÍNEZ-NAVARRO & ROOK 2003) and a right mandibular carnassial tooth.

In the present days however, there is not a consensus on the taxonomic position of this large-sized canid, and some authors prefer to maintain the use of the genus *Xenocyon* (SOTNIKOVA 2001, MOULLÉ et al. 2005, ÉCHASSOUX et al. 2008, HARTSTONE-ROSE et al. 2010) instead to use the genus *Lycaon* as suggested by MARTÍNEZ-NAVARRO & ROOK (2003).

In the opinion of MARTÍNEZ-NAVARRO & ROOK (2003) *Lycaon lycaonoides* would represent the Eurasian Early Pleistocene species of large canid, intermediate between Eurasian Late Pliocene *L. falconeri* and the African extant *L. pictus*. The evolution of this lineage is characterized by the transition from a more generalised dental condition, with large chewing surface in molars, into a condition of hypercarnivory, in which molars become smaller and trenchant.

Such an evolutionary trend in the reduction of the m1 entoconid, and later on its disappearance, and the increase in size of the hypoconid, is associated

with the reduction of the m2 and the m3, and the reduction of basin, on the upper molars, between the protocone and the hypocone, and the increase of the upper molars trigonid basin. Another characteristic of this lineage would be the absence of metacarpal I, missing the articular surface on metacarpal II, and the consequent condition of tetradactyly in forelimbs showed in Early Pleistocene postcranial skeletal remains, a characteristic feature of the extant wild dog, unique among canids (MARTÍNEZ-NAVARRO & ROOK 2003).

MOULLÉ et al. (2006b) considered findings of the later Early Pleistocene from Europe as belonging to species *Xenocyon lycaonoides*, and ÉCHASSOUX et al. (2008) also ascribed the findings from the late Early Pleistocene of Yunxian (China) to *Xenocyon dubius*. In their opinion these species have a high intraspecific variability. Moreover, the absence of MC1 is questioned because of the presence of this metacarpal in an Asian form (MOULLÉ et al. 2006a, ÉCHASSOUX et al. 2008). Some populations show characteristic similar to genus *Lycaon*, but they think that in other cases some features are similar to genus *Cuon*. This situation would mean that from the genus *Xenocyon* derived both *Lycaon* and *Cuon*, the first one in Africa and the second in Asia.

OLIVE (2006) considers the same hypothesis and points out that the nasal bones don't reach the frontomaxillary suture, a plesiomorphic character in the *Xenocyon/Lycaon/Cuon* group.

In a recent paper by HARTSTONE-ROSE et al. (2010), a nice specimen from Early Pleistocene (1.9–1.0 Ma) South African sites is described as representing a putative ancestor of the wild dog. This canid (*Lycaon sekowei*) is large and robust. Its dentition is characterised by morphologies unique to *Lycaon* among living canids as, for example, the presence of the ante-

Table 10. Measurements of *Lynx issiodorensis* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	P4L	P4B							
s.n.	Florence DST	P4		20.1	9							
				cH	cHC	cL	cB	p3L	p3B	p4L	m1L	LD
s.n.	Florence DST	p3						9.5				
s.n.	Florence DST	p4								12		
s.n.	Florence DST	m1									14.4	
PU 104731	Turin DST	c	DX	34.86	16.19	7.54	5.87					
PU 106052	Turin DST	mandible portion with p3	DX					8.31	4.19			8.36
				SDO	DPA	BPC	HO	HGIS	DGIS			
PU 104644	Turin DST	Ulna	SX	19.07	22.62	13.39	21.85	17.96	14.42			

rior accessory cusp in the p4, or the reduction of the bucco-lingual diameter and the presence of a deep central basin in the M1, but its post-cranial morphology do not shows the presence of a well known autapomorphy of *L. pictus*, the tetradactyl manus, the Paratype skeleton from Gladysvale includes, in fact, a large first metacarpal. Thus, the anatomy of this new early member of the *Lycaon* branch suggests that, contrary to previous hypotheses, dietary specialization appears to have preceded cursorial hunting in the evolution of the *Lycaon* lineage. Similar anatomic characteristics on the dentition are present on the specimens ascribed to *Lycaon lycaonoides* from the site of Venta Micena (MARTÍNEZ-NAVARRO 1992), but also, as it has been reported above, the occurrence of a metacarpal I is known on the individuals ascribed to *Xenocyon dubius* from Yunxian (ÉCHASSOUX et al. 2008), showing that no important anatomical differences are found among these Eurasian large canids and the specimens ascribed to *Lycaon sekowei*.

The recent fossil collection from Pirro Nord housed in the Turin Paleontological Museum, allowed us to increase the available sample of this large dog with some useful elements. In fact we had the opportunity to identify a metacarpal I (Plate 2, Fig. j) and a mandibular carnassial tooth (Plate 2, Fig. i). The iden-

tification of MCI is important because it attests the occurrence of this anatomical element, despite the absence of the articular surface in MCII as was already documented (ROOK 1994). We cannot rule out that such features could be variable in the population and that *Lycaon* from Pirro Nord may have been highly polymorphic with individuals maintaining a reduced MCI, with other ones still maintaining it.

In the case of the lower carnassial, we note that the talonid is formed by a large hypoconid, slightly moved to the centre of the talonid basin, and a very small entoconid. The structure is then complicated by the presence of small cusplets. This condition is very similar to what can be observed in forms from Late Villafranchian - Early Galerian.

The comparison of other postcranial elements shows a body size slightly smaller than the wild dog ones from Untermassfeld, Le Vallonet and Venta Micena, but a strong similarity with forms from these sites. The debate about Early Pleistocene *lycaon*-like dogs, and its implication on the taxonomy and evolution of *Xenocyon/Lycaon/Cuon* group, is still in progress.

In our view, we can confirm the attribution of the Pirro Nord wild dog to the species *Lycaon lycaonoides*, on the basis of anatomical evidences in the teeth. The

Table 11. Measurements of *Megantereon whitei* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	CL	CB	LP3	BP3	P4L	P4BM	P4B						
G1	Rome DST	Maxillar portion with C. P3 and P4	DX	28.7	16.5	11	5.2	27								
PU 104369	Turin DST	C		24.75	11.8											
PU 104691	Turin DST	C		25.65	12.65											
PU 104754	Turin DST	P4	SX					30	9.1	13.65						
				Lp4	Bp4											
PU 104616	Turin DST	p4	SX	16.15	7.45											
PU 104616	Turin DST	p4	SX	15.9	7.3											
				GB	GL	H	BP	DP	BSD	DSD	BD	DD				
PU 104315	Turin DST	Tibia	DX		249.4		54.5	59.74	22.87	26.07						
G3	Rome DST	Scapholunar	SX	29.43	29.9	20.07										
G5	Rome DST	Trapezoid	SX	18.1	16.15	11.04										
G6	Rome DST	Trapezium	SX	11.54	22.39	19.21										
G9	Rome DST	Magnum	SX	12.25	18.16	12.98										
G 12	Rome DST	MC II	SX		75		18	21	11.5	11	18	14				
G 13	Rome DST	a	SX		81.5		20	20	12.8	10	18.5	16				
G 14	Rome DST	MC IV	SX		77		15	17.5	10.5	10.2	16.5	15.5				
G 15	Rome DST	MC V	SX		65		16.8	16.5	11	10	16	13.8				
G4	Rome DST	Phalanx 1-I	SX		27.39		17.84	12.23	13.93	9.2	15.75	9.4				
G 16	Rome DST	Phalanx 1-II	SX		39.6		17.05	14.82	12.4	10.19	12.83	9.87				
G 17	Rome DST	Phalanx 1-III	SX		39.8		15.89	13.05	10.97	8.74	11.73	8.82				
G 18	Rome DST	Phalanx 1-IV	SX		34.19		15.32	12.64	8.77	9.25	11.04	8.79				
G 91	Rome DST	Phalanx 2-III	SX		18.42		10.32	9.54	8.18	6.01	10.09	7.42				
G 92	Rome DST	Phalanx 2-IV	SX		19.32		11.78	10.84	8.41	5.58	10.3	7.75				



presence of MCI and at the same time the absence of articular surface for this metacarpal in MCII, would demonstrates a non functionality of the first metacarpal, a condition versus the modern tetradactily of extant *Lycaon pictus*.

#### Felidae

*Lynx issiodorensis* ssp. (CROIZET & JOBERT 1828)

(Plate 4, Figs a, b, Table 10)

Fossils referable to *Lynx* are stored in different collections. The most complete specimen is a partial skull with mandible housed in the Florence Earth Sciences Department. In addition a single part of a mandible with p3 and an ulna (Turin, Plate 4, Fig. a), a fragmentary scapula and ulna (Sapienza) have been collected. The partial skull (Plate 4, Fig. b) includes the zygomatic, part of the temporal, the right upper canine and jugal teeth. The articulated mandible can be partially studied and includes the lower canine and jugal teeth. The partial mandibula with p3 (Turin collection) is smaller than the fossil stored in Florence and is closer to *Lynx pardinus spelaeus*.

In general, the Pirro Nord *Lynx* size falls within the range of the late Villafranchian subspecies. The relative proportions of the jugal teeth are similar to those of the Early Galerian (Epivillafranchian) *Lynx* from Untermassfeld (*Lynx issiodorensis* ssp. aff. *spelaeus* in HEMMER 2001), thus the *Lynx* from Pirro Nord can provisionally be referred to *Lynx issiodorensis* ssp. to be considered as an advanced form of the Issoire *Lynx* transitional to the galerian *Lynx pardinus spelaeus*. WERDELIN (1981) pointed out the evolutionary trends in the *Lynx* lineage. It includes the

Larger Early Villafranchian *Lynx issiodorensis issiodorensis*, the Late Villafranchian *Lynx issiodorensis valdarnensis*, the Galerian *Lynx pardinus spelaeus* and, finally, the living, highly endangered, *Lynx pardinus pardinus*.

*Megantereon whitei* BROOM, 1937

(Plate 3, Figs a–d, Table 11)

The occurrence of *Megantereon* is testified by cranio-dental remains referable to at least three adult individuals and a juvenile one. In addition, a distal part of a humerus, elements of a left hand (Plate 3, Fig. d) and a single IV metatarsal have been recorded. SARDELLA (1998) referred part of this material to *Megantereon* ex gr. *cultridens* (advanced form). Further analysis and comparison to other fossils led to follow the taxonomy suggested by MARTÍNEZ-NAVARRO & PALM-QVIST (1995) and the Pirro Nord dirk-toothed cat is referred to the African species *Megantereon whitei*.

In particular, the specimen G1 (Plate 3, Fig. a) (maxilla with incisors, C, P3 and P4, and part of the zygomatic process) is characterised by a very developed upper canine, stronger than any other European specimen. Such features are confirmed in the fossils stored in Turin University. An isolated uncrenulated upper canine is very elongated antero-posteriorly, much more than specimen from Upper Valdarno and Sénéze. Upper carnassial teeth (Plate 3, Fig. b) and p4 (Plate 3, Fig. c) show features close to those of the African dirk-toothed cat. In P4, preparastyle is absent and protocone is reduced.

The humerus is much stouter and stronger in *Megantereon* than in *Panthera*, which is confirmed by

Table 12. Measurements of *Homotherium latidens* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	P4L	P4B						
G 21	Rome DST	P4	SX	39.31	13.11						
				GL	BP	DP	BSD	DSD	BD	DD	
G 26	Rome DST	Humerus	DX	337.6	60.68	82.83	26.4	39.1	72.75	46.93	
G 32	Rome DST	Radio	SX	307	36.19	26.73	30.28	19.4	52.42	34.15	
G 41	Rome DST	MC II	SX	98.9	22.91	26.47	13.94	14.96	19.38	19.17	
G 42	Rome DST	MC III	SX		18.91	23.83	16.11	12.33			
G 43	Rome DST	MC IV	SX	109.2	16.99	24.15	14.35	10.8	19.73	20.23	
G 44	Rome DST	MC V	SX	93.02	20.95	23.4	11.14	13.62	20.49	19.5	
G 81	Rome DST	MT II	DX	98.29	21.82		13.61	14.22	19.36	20.03	
G 82	Rome DST	MT III	DX	110.7	21.22	30.29	17.03	14.68	20.36	21	
G 83	Rome DST	MT IV	DX	110.1	17.28	30.06	14.93	12.92	18.85	19.56	
G 84	Rome DST	MT V	DX	98.7	17.47	18.38	12.52	10.83	17.16	17.85	

the Pirro Nord specimen (SARDELLA 1998, SARDELLA et al. 2008). An almost complete left manus, including scapholunar, carpal bones, I and II phalanges have been recorded and partially described (SARDELLA 1998). Comparison with the manus of *M. cultridens* from Sènèze and *M. whitei* from Monte Argentario reveals great similarities (SARDELLA et al. 2008). Metacarpals have strong diaphyses and quite long first phalanges, similar to those of extant felids. Such features of the forelimb of *Megantereon* are closely related to ambush behaviour (PALMQVIST et al. 2007, SARDELLA et al. 2008).

TURNER (1987) considered the differences recorded into the Eurasian and African sample of *Megantereon* as due to sexual dimorphism, comparing the data to those of the living leopard. Other authors claimed a convergent evolution of the European samples of *Megantereon cultridens* with the African *Megantereon whitei*, due to the paleoclimatic and paleoenvironmental conditions prevalent at the end of Pliocene. They named this form *M. cultridens adroveri* (PONS MOYA 1987, HEMMER 2001). SARDELLA (1998) suggested the use of open taxonomy including the Early Pleistocene European specimens in *Megantereon* ex gr. *cultridens* (advanced form). MARTÍNEZ-NAVARRO & PALMQVIST (1995, 1996) suggested that the Early Pleistocene European *Megantereon* represent a dispersal of the African form *M. whitei* that replaced *M. cultridens* at the Plio-Pleistocene transition. Recently PALMQVIST et al. (2007) support this hypothesis taking into account new data. A different interpretation of the Old World *Megantereon* fossil remains is offered by LEWIS & WERDELIN (2010) who refer the late Eurasian *Megantereon* to *Megantereon adroveri*.

*Homotherium latidens* (OWEN 1846)

(Plate 3, Figs e–j, Table 12)

This large sabertoothed cat is probably the best represented carnivore at Pirro Nord. At least seven individuals occur in the different collections. A partial complete skeleton of one individual (skull and mandible, limb bones), mandibles and isolated limb bones are housed at Florence University collection. Turin collection includes a juvenile mandible with both milk and adult dentition (Plate 3, Fig. f). Sapienza collection includes two fragmentary skulls (one braincase and a muzzle, but coming from different fissures), a mandible (poorly preserved), isolated teeth, several limb bones, many metapodials and phalanges (an almost complete manus and pes) (Plate 3, Figs g, h). The humerus is the most frequent skeletal element (three complete bones and four partial ones) (Plate 3, Fig. i) showing a substantial size uniformity, within the range of the Early Pleistocene *Homotherium latidens*. Interestingly a wider variability can be observed in the metatarsal bones, with robust or very slender diaphyses.

The sample from Pirro Nord includes juvenile, adult and aged specimens (occurrence of heavily worn jugal teeth). P3 and p4 were reduced (p3 very reduced), P4 has no trace of preparastyle, with an extremely reduced protocone. The postcranial elements confirm the reconstruction of *Homotherium latidens* as a powerful lion size and long-legged predator, with a relatively fast run and lesser abilities in climbing in respect to pantherine cats (GALOBART et al. 2003).

*Homotherium latidens* is quite well represented in the Early Pleistocene European faunal assemblages, and is still present, even if rare, in the Middle Pleistocene. Radiometrical data on a mandible from the North Sea provide evidences of a surviving till the Late Pleistocene (REUMER et al. 2003).

Table 13. Measurements of *Acinonyx pardinensis* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	SDO	DPA	BPC	HO	HGIS	DGIS	BSD	DSD
G 104	Rome DST	Ulna	DX	42.25	49.21	34.14	44.86	31.86	31.4	16.57	22
				GL	BP	DP	BSD	DSD	BD	DD	
PU 104234	Turin DST	MT IV	SX	95.96	17.52	22.04	12.15	10.74	15.9	15.52	

Table 14. Measurements of *Panthera gombaszoegensis* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	P3L	P3B	P4L	P4B
PN 31	Rome DST	Maxillar portion with P3 and P4	SX	18.5	9.26	27.13	13.86

*Acinonyx pardinensis* CROIZET & JOBERT, 1828

(Plate 4, Figs d, e, Table 13)

The occurrence of the cheetah is testified by a large left ulna, belonging to a felid of the size of a lion, housed in the Sapienza collection (Plate 4, Fig. e) and a IV metatarsal (PU 104234, Plate 4, Fig. d) stored in Turin collection. The ulna general morphology is similar to that of *Panthera*, but the diaphysis is more slender and curved, much more than what observed in *Homootherium*.

The comparison with the analogue IV metatarsal in the sample from Untermassfeld, show the same morphology, although the articular surfaces of PU 104234 are less developed. Such differences in size could indicate evidence of sexual dimorphism in *Acinonyx pardinensis*.

The cheetah characterizes the Villafranchian faunal assemblages of Europe, with individuals considerably larger than the living species (up to 60 kg) (TURNER & ANTÓN 1997). *Acinonyx pardinensis* probably shared with the living *Acinonyx jubatus* the hunting strategy, running even faster than the living relatives (TURNER & ANTÓN 1997). Similarly to the modern cheetah, *Acinonyx pardinensis* could be mainly a solitary animal, and this can explain why the number of known specimens is relatively small. The most complete material comes from the Late Pliocene locality of Saint-Vallier (France) and the late Early Pleistocene site of Untermassfeld (Germany) (TURNER & ANTÓN 1997, HEMMER 2001). The giant cheetah survived until the Middle Pleistocene (Mosbach, Germany) (TURNER & ANTÓN 1997). The occurrence of *Acinonyx pardinensis* at Pirro Nord can be considered as the latest occurrence of this felid in Italy.

*Panthera ex gr. toscana-gombaszoegensis*

(Plate 4, Fig. c, Table 14)

The occurrence of a large pantherine cat has been illustrated by BEAUMONT (1979) on the basis of a skull lacking the facial area. A cast of this specimen was studied at the Paleontological Museum of Geneva by one of us (RS). In addition a left maxillary bone with jugal teeth (Plate 4, Fig. c) stored at Sapienza University has been considered. P3 is much more developed (if compared to P4) than what can be observed in machairodontine cats, its main cusp is strong, and inclined backward. The protocone of the upper carnassial is located besides the parastyle.

The systematics of this large felid has been recently focused by HEMMER (2001), HEMMER et al. (2001), O'REGAN & TURNER (2004). HEMMER et al. (2001) described the fossil specimens from Untermassfeld (Germany) and Akhalkalaki (Georgia) and refer the Late Villafranchian and Galerian fossil remains of this pantherine cat to the European chronosubspecies of the jaguar *Panthera onca* (*Panthera onca toscana* for the Late Villafranchian specimens and *Panthera onca gombaszoegensis* for the Galerian ones). Such taxa could be distinguished for the relative dimensions of p3 and for the inclination and the extension of the mandible at the c-p3 diastema. We prefer to include the Eurasian jaguar specimens in the *Panthera ex gr. toscana-gombaszoegensis*. During the Early Pleistocene, the jaguar is not very frequent in the Western Europe, and became extinct at the beginning of the Middle Pleistocene. The European jaguar has been recorded in Europe in the Late Pliocene localities of Tegelen (The Netherlands) (O'REGAN & TURNER 2004) and Slivnitza (Bulgaria) (SPASSOV

Table 15. Measurements of the fifth metacarpal of the Felide indet., *Puma-size* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	BP	DP	BSD	DSD
PU 106067	Turin DST	MC V	DX	14.9	13.85	8.75	8.1

Table 16. Comparison between the ulna of *Puma pardoides* from Pirro Nord, *P. pardoides* from Untermassfeld and extant *Panthera pardus* (MHNP: Muséum national d'Histoire Naturelle de Paris). See appendix for measurement explanation.

	Provenance	Element	Side	Species	SDO	DPA	BPC	HO	HGIS	DGIS
PU 104225	Pirro Nord	Ulna	SX	<i>Puma pardoides</i>	26.77	31.2	29.7	26.93	21.75	20.93
IQW 1995/25335 (Mei. 24864)	Untermassfeld	Ulna	DX	<i>Puma pardoides</i>	24.73	31.19	25.01	28.88	19.95	20.49
1910-72	MHNP	Ulna	SX	<i>Panthera pardus</i>	32.67	33.67	28.19	33.19	25.14	21.85

2003). The first occurrence of *Panthera gombaszoegensis-toscana* has been considered by AZZAROLI (1977) as one of the main bioevents of the beginning of the Pleistocene (Late Villafranchian, Olivola F.U.). At present, Olivola F.U. is referred to the latest Pliocene (GLIOZZI et al. 1997). In Italy this felid occurs in the Late Villafranchian and the Early Galerian faunal assemblages (GLIOZZI et al. 1997): Upper Valdarno and Val di Chiana (Tuscany), in different localities in the Tiber River basin and at Pietrafitta and Monte Peglia (Umbria), and Slivia (Friuli Venezia Giulia) (SARDELLA 2006, and references therein).

*Puma pardoides*

(Plate 4, Figs f, g, Tables 15, 16)

The left ulna PU 104225 (Tables 15 and 16, Plate 4, Fig. f) is constituted by a proximal part, quite well preserved. Olecranus is located in a lower position than in other large felids and the tuberosity presents a smooth surface with prominent edges in the posterior side. The articular trochlear surface is wide and convex. The external edges are rounded and the internal

ones are marked. The articular surface with the radius is high and wide, and a vertical slender protuberance is present laterally. In the internal side, there is a trapezoidal protuberance.

The comparison with the ulna of *Puma pardoides* from Untermassfeld, shows general similarities, but also some differences. In particular, the articular surface of the olecranus is much more inclined in the Pirro Nord specimen, with the olecranus profile more rounded in shape. We have compared PU 104225 with the analogue bone of *Panthera gombaszoegensis* from Untermassfeld and extant *P. pardus*. Significant differences in the morphology of the articular surface with the humerus, and in the posterior edge, suggest that Pirro Nord specimen cannot be referred to *Panthera* and in particular, to *P. pardus*.

In Europe, *Puma pardoides* is recorded from the Early Pliocene (Villaroya, Spain, MN16a) (KURTÉN & CRUSAFONT PAIRÒ 1977) to the end of Early Pleistocene (Untermassfeld, Germany) (HEMMER 2001). In Western Mediterranean this can be considered as a quite rare species. Its occurrence at Le Vallon-

Table 17. Measurements of *Pachycrocuta brevirostris* from Pirro Nord. See appendix for measurement explanation.

Catalogue Number	Collection	Anatomic element	Side	I3H	I3He	I3L	I3B	LP1	BP1	LP3	BP3			
PN 32	Rome DST	I3	DX	52	26.46	15.86	11.97							
PU 104505	Turin DST	I3	SX		24.29	17.7	15.19							
PU 104764	Turin DST	I3	DX		23.78	15.76	12.27							
PU 104774	Turin DST	P1	DX					8.82	7.5					
PU 104746	Turin DST	P3	SX							21.47	14.68			
PU 104707	Turin DST	P3	DX							21.02	14.57			
				cL	cB	Lp3	Bp3	Lp4	Bp4	Lm1	Bm1	mITL		
G 106	Rome DST	Mandible with p4 and m1	DX					27.66	18.09	29.42	15.58	24.44		
PU 104814	Turin DST	mandibola con p3,p4	DX			24.63	16.61	27.91	15.11					
PU 104752	Turin DST	canino	SX	20	17.68									
PU 104663	Turin DST	canino	DX	20	16.44									
PU 104786	Turin DST	canino	SX	20	15.23									
PU 104516	Turin DST	p3	DX			25.03	17.16							
PU 104708	Turin DST	p3	SX			24.57	18.38							
PU 104488	Turin DST	p4	DX					27.7	18.3					
PU 104701	Turin DST	m1	DX							31.71	16.32	25.56		
PU 106144	Turin DST	m1	SX							29.05	15.14	21.95		
				AdL	H	BFer	BPacd							
PU 104677	Turin DST	Epistrofeo		89	69.42	61.5	64.11							
				SDO	DPA	BPC	HO	HGIS	DGIS	BSD	DSD	BD	DD	HT
PU 104003	Turin DST	Omero	DX	46	51.05	35.16	35.69	41.62	32.68	22.72	28.41	65.42	49.54	37.29
PU 104515	Turin DST	Omero	DX							23.21	29.98	67.34	53	37.27
G 116	Rome DST	Ulna	DX	48.20	51.02	36.27	34.88	36.7	32.69	18.45	24.51			
PU 106024	Turin DST	Ulna	SX	42	49.4	35.79	37.93	35.38	31.16	25.46	20.48	29.83	29.62	

net (France) has been debated and some authors refer the French fossils (two lower carnassials) to *Panthera pardus* (MOULLÉ 1992, TURNER 1995, HEMMER et al. 2004, MOULLÉ et al. 2005, 2006b). Recently, MADURELL et al. (2010) describe the specimen belonging to *P. pardoides* from Spanish localities, contributing to enlarge the knowledge on this felid. On the basis of the new fossils and the comparison with several extant specimens, we can attribute the ulna to *Puma pardoides*, confirming its occurrence in the Late Villafranchian faunas of the Italian Peninsula.

A fifth right metacarpal (PU 106067 MC V, Plate 4, Fig. g, Table 15) and a left ulna can be referred to a medium sized cat, but a more detailed taxonomic attribution cannot be provided. The fifth right metacarpal (Plate 4, Fig. g), is well preserved, but lacking the distal epiphysis. Morphologies of the proximal epiphysis, as the triangle on the anterior surface, or the vertical prominence on the internal surface, are typical felid features.

After the comparison with *M. cultridens* from Sènze, *Acinonyx pardinensis* from Untermassfeld, and *Lynx* we can exclude the attribution of this fossil to these genera. Its general morphology recalls that of *Panthera*, but PU 106067 is clearly smaller than *Panthera gombaszoegensis*. An attribution to *Puma pardoides* (HEMMER 2001), cannot be ruled out, albeit with a high degree of uncertainty.

#### Hyaenidae

##### *Pachycrocuta brevirostris* (AYMARD 1846)

(Plate 4, Figs h–k, Table 17)

The giant short faced hyaena is well represented with isolated teeth, skull fragments, two partial left mandibles (Sapienza collection), and elements of the postcranial skeleton. Among them, the ulna is the best represented bone. In the Sapienza collection at least two individuals are present. The mandibles are massive (Plate 4, Fig. k), comparable to the largest specimens of the species, with strong canines and powerfully build jugal teeth. The p2, p3 and p4 have strong conical main cusps. The m1 length is reduced and this tooth is larger compared to that of *Crocuta*, in which is proportionally much longer than p3 and p4.

In the ulna (Plate 4, Fig. i) the diaphysis is massive, mainly in the distal portion, and has broad muscle insertion areas. Interestingly, in the Sapienza sample, together with very large individuals (the size of a lion) also smaller individuals occur. This could be considered as evidence of sexual dimorphism in *Pachy-*

*crocuta brevirostris*, more marked than in *Crocuta crocuta*.

Some coprolites have been collected (Plate 4, Fig. h) referables to hyaenas. Some of them have been studied to check the presence of pollens, but unfortunately such analyses do not provide the expected results.

*Pachycrocuta brevirostris* is a very large hyaena (more than 100 kg estimated body mass) (WERDELIN 1999, PALMQVIST et al. 2011). The dispersal of this species in Europe has great biochronological significance. The genus appeared in Africa about 3.5 Ma ago (South Turkwell, Kenya) (WERDELIN & LEWIS 2000). Its occurrence is testified in Western Europe from the Late Pliocene at Olivola (Italy) and Fonelas 1 (ARRIBAS et al. 2004, TURNER & ANTON 1996, SARDELLA & PALOMBO 2007). In many Late Villafranchian faunal assemblages such as Poggio Rosso–Upper Valdarno, Venta Micena and Fuente Nueva 3 (Spain) and Untermassfeld (Germany) the giant hyaena had an important role in bone accumulation (ARRIBAS & PALMQVIST 1998, PALMQVIST & ARIBAS 2001, MAZZA et al. 2004, KAHLKE 2006, ESPIGARES 2010, PALMQVIST et al. 2011). This large powerful scavenger characterized most of the Early Pleistocene local faunas, and became extinct during the early Middle Galerian possibly because of competition with the newcomer *Crocuta crocuta*.

#### Final Remarks

The carnivores of Pirro Nord faunal assemblage constitutes a very diversified sample, one of the most complete in Europe, with fourteen species identified. In many cases part of articulated skeletons provides valuable information on the anatomy of species still poorly known, and taxonomy is based mainly on cranio-dental features. The analysis of the articulated limb bones of *Lycaon lycaonoides* or *Megantereon whitei*, among the others, provides information improving our knowledge on their locomotion, palaeoecology, and phyletic relationships. In addition, new diagnostic elements are described allowing a better define diagnosis for different species. The discovery of MCI referable to *Lycaon lycaonoides*, e.g., is important for this purpose. It attests the presence of a very important anatomical element in the wild dogs' evolutionary trend toward modern *Lycaon pictus*, the only living canid with four digits in the forelimb. Thus *Lycaon* from Pirro Nord may have been highly polymorphic with individuals maintaining a reduced MCI, while other ones still maintaining it.

In addition, at Pirro Nord have been unearthed also rare taxa such as *Mustela* and the *Puma*-size felid. The occurrence of *Acinonyx pardinensis*, *Homotherium latidens* and *Lycaon lycaonoides* can be related to the predominance of open habitats, where *Pachycrocuta brevirostris* could have had a crucial role in accumulating carcasses.

The Pirro Nord carnivore guild includes also data of biochronological interest, such as the earliest occurrence of *Meles* and *Mustela* and the latest occurrence of *Megantereon* and *Acinonyx* in Italy.

There is quite an agreement in the literature on the fact that ecological structure of the carnivore community remained stable during the Late Villafranchian. Carnivore guilds over time do not much reveal the influence of climate change over the community structure (TURNER 1992, 1995, TORRE et al. 2001, PALOMBO et al. 2007, CROITOR & BRUGAL 2010). Important structural changes started during the latest Early Pleistocene and at the Early-to-Middle Pleistocene Transition. These changes are especially marked by extinction of solitary hypercarnivores and increasing of collective hunters' importance with broad range of diet specialization and omnivorous species. Moreover, it is at this time that carnivores are important elements of the dispersal events from Africa to Europe that took place at about 1.8 Ma in the Early Pleistocene (the Plio-Pleistocene transition, prior to the formal recognition – June 2009 – of Quaternary as a Period/System, and the redesignation of the base of the Pleistocene Series/Epoch in the 2.59 Ma GSSP of the Gelasian Stage), with *Pachycrocuta brevirostris*, *Panthera* ex gr. *toscana-gombaszoegensis* and *Megantereon whitei*. In particular, the dispersal of *M. whitei* into Europe occurred concurrently with other African species through the principal path of dispersal between Africa and Eurasia: the Levantine Corridor (MARTÍNEZ-NAVARRO 2004, 2010, O'REGAN et al. 2006, TURNER & O'REGAN 2005). The influence of forms of African origin in the Early Pleistocene of the Levant is evident, as at the 'Ubeidiya site (Israel) (TCHERNOV 1986, MARTÍNEZ-NAVARRO et al. 2009, 2010). In this locality, *Megantereon* cf. *whitei*, and *Crocuta crocuta* are documented together with (among others) *Homo*, *Theropithecus* sp., *Hippopotamus gorgops*, *Kolpochoerus olduvaiensis*, and *Bos oldowayensis*. However, only few of these African species expanded their range into northernmost regions of Eurasia. This group is composed together with *M. whitei* by *T. oswaldi*, *Hippopotamus antiquus* and, ob-

viously, *Homo* and is partially documented at Pirro Nord (ROOK et al. 2004, ROOK & MARTÍNEZ-NAVARRO 2013, ARZARELLO et al. 2007, 2009). This assemblage has been in part found in Western Europe, in Spain (Venta Micena, Fuente Nueva-3, Barranco León-5, Cueva Victoria and Incarcál), France (Sainzelles), Italy (Monte Argentario), Germany (Untermassfeld), Greece (Apollonia and Ravin de Voulgarakis).

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## Appendix

### Cranial measurements

I3H	I3 height
I3Hc	I3 crown height
I3L	I3 length
I3B	I3 breadth
CH	Canine height
CHc	Canine crown height

CL	Canine length	Ulna	
CB	Canine breadth	GL	Greatest length
(tooth) L, B	Respectively length and breadth of indicated tooth	SDO	Olecranic lowest depth
<b>Mandible measurements</b>		DPA	Olecranic maximum depth
L, B	Respectively length and breadth of indicated tooth	BPC	Proximal articular surface breadth
cH	Canine height	HO	Olecranic height
cHC	Canine crown height	HGIS	Proximal articular surface height
m1TrL	M1 trigonid length	DGIS	Ulna depth at the middle point of the proximal articular surface
AB, PB	Respectively anterior and posterior breadth of indicated tooth	DD	Distal epiphysis depth
<b>Atlas</b>		<b>Femur</b>	
AdL	Middle dorsal bow length	GL	Greatest length
BFcr	Cranial articular surfaces breadth	BP	Proximal epiphysis breadth
H	Total highness	DP	Proximal epiphysis depth
BFcd	Caudal articular surfaces breadth	DH	Femur head depth
<b>Axis</b>		DN	Neck of the articular surface depth
BFcr	Cranial articular surfaces breadth	BSD	Diaphysis breadth
H	Total highness	DSD	Diaphysis depth.
<b>Cervical, thoracic, lumbar and caudal vertebrae</b>		BD	Distal epiphysis breadth
PL	Body vertebrae length	DD	Distal epiphysis depth
BPacr	Cranial articular processes length	BTr	Troclea breadth
BPacd	Caudal articular processes length	HT	Troclea height
BFcr	Cranial articular surface breadth	<b>Tibia/Fibula</b>	
BFcd	Caudal articular surface breadth	GL	Greatest length
Hcr	Cranial articular surface height	BP	Proximal epiphysis breadth
Hcd	Caudal articular surface height	DP	Proximal epiphysis depth
BPtr	Transversal process length	BSD	Diaphysis breadth
H	Total height	DSD	Diaphysis depth
<b>Scapula</b>		BD	Distal epiphysis breadth
GLP	Articular process greatest length	DD	Distal epiphysis depth
LG	Glenoid cavity length	<b>Calcaneus</b>	
BG	Glenoid cavity height	GL	Greatest length
SLC	Neck scapula lowest length	GB	Greatest breadth
<b>Pelvis</b>		SBT	Lowest breadth
GL	Total length.	<b>Astragalus</b>	
LA	Acetabulum length	GL	Greatest length.
SH	Iliac ramus lowest height	GB	Greatest breadth.
<b>Humerus</b>		GBT	Troclea greatest length.
GL	Greatest length	ANW	Neck width.
BP	Proximal epiphysis breadth	AHW	Head width.
DP	Proximal epiphysis depth	<b>Other carpal and Tarsal bones</b>	
BSD	Diaphysis breadth	GL	Greatest length.
DSD	Diaphysis depth	GB	Greatest breadth.
BD	Distal epiphysis breadth	H	Greatest highness.
DD	Distal epiphysis depth	<b>Metacarpal and Metatarsal bones, and first and second phalanges</b>	
HT	Troclea height	GL	Greatest length.
<b>Radius</b>		BP	Proximal epiphysis breadth.
GL	Greatest length	DP	Proximal epiphysis depth.
BP	Proximal epiphysis breadth	BSD	Diaphysis breadth.
DP	Proximal epiphysis depth	DSD	Diaphysis depth.
BSD	Diaphysis breadth	BD	Distal epiphysis breadth.
DSD	Diaphysis depth	DD	Distal epiphysis depth.
BD	Distal epiphysis breadth	<b>Third phalanx</b>	
DD	Distal epiphysis depth	BP	Proximal breadth
		DP	Proximal depth.

## Explanation of plates

### Plate 1

*Mustela cf. M. palerminea*

a: left mandible PU 104625, a1 labial view, a2 occlusal view

*Meles meles*

b: mandibular fragment with m1 PU 104151

*Ursus etruscus*

c: right M2 PU 104091

d: left P4 PU 104655

e: left upper canine PU 104750

f: left p4 PU 104893

g: left m3 PU 106128

h: right humerus, PN 3

i: right ulna, PN 15

l: right calcaneus PU 104650

m: right astragalus PU 106625

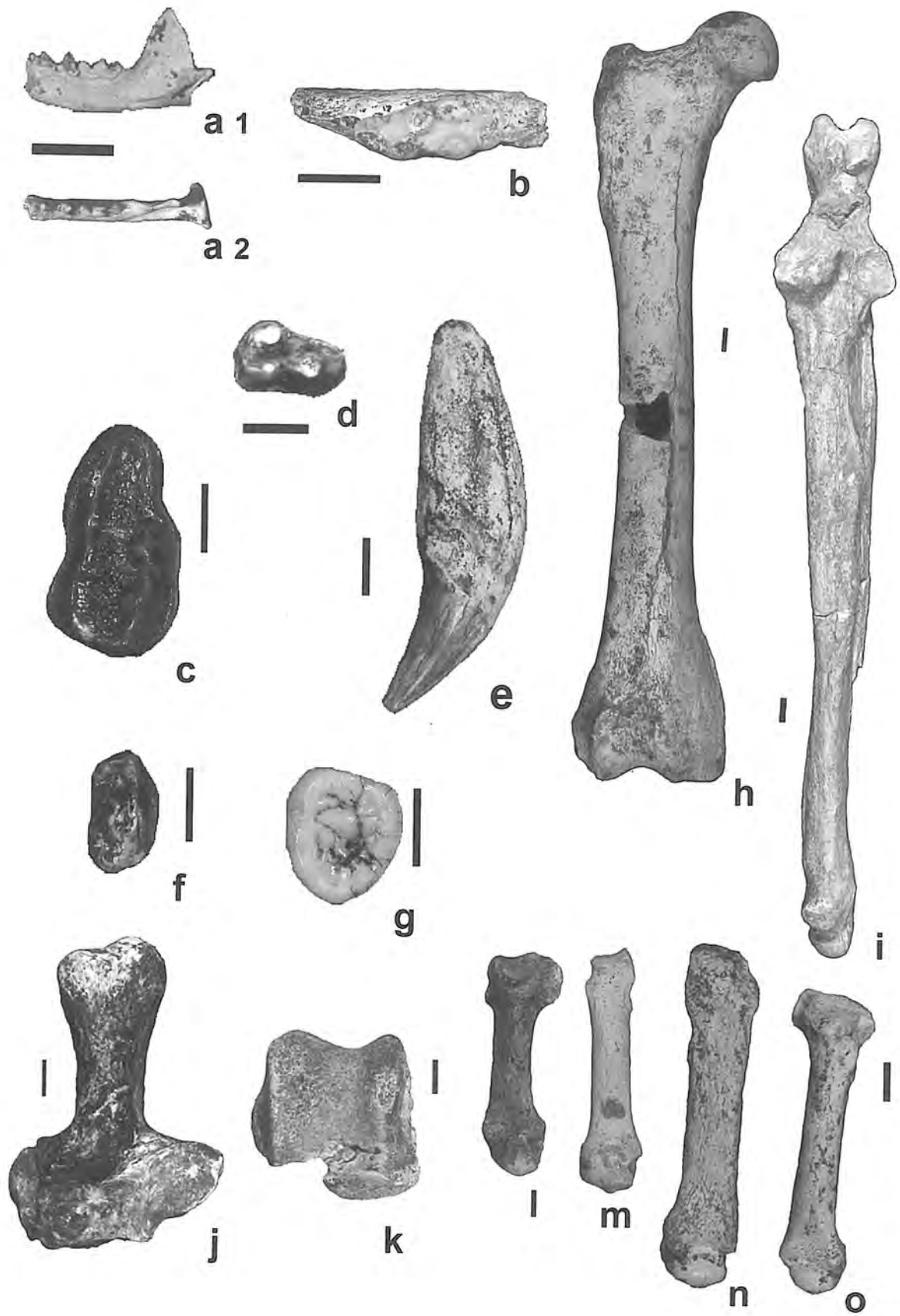
n: left MT I PU 106151

o: right MT II PU 106111

p: left MT IV PU 104635

q: right MT V PU 106153

Scale bar 1 cm.



**Plate 2**

*Vulpes alopecoides*

- a: right maxillar portion with P4, M1, M2, PN 30
- b: right mandible portion with m1 PU 106227

*Canis mosbachensis*

- c: left mandible PU 104678
- d: right MC II, PU 104777
- e: left MC III, PU 106154
- f: right MC V Sx, PU 104734
- g: left MT III, PU 104799
- h: right maxillar ramus portion with P4, M1, PU 104450

*Lycaon lycaonoides*

- i: right m1, PN 35
- j: right MC1 PU 104756
- k: left MC II, III, IV, V of the same hand, PN 7-10
- l: left tibia PN 17

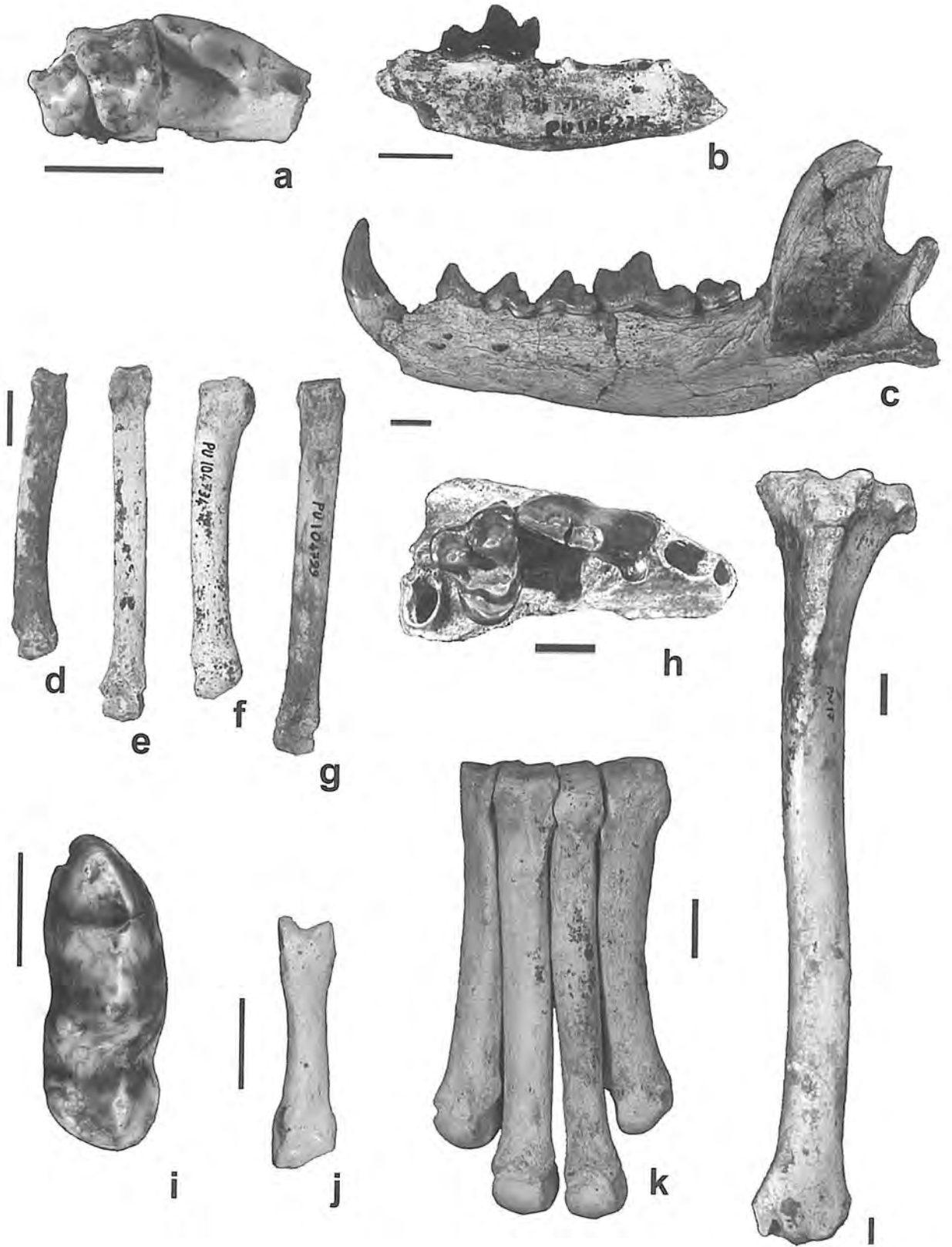


Plate 3

*Megantereon witbei*

- a: left maxillar bone with canine, P3 and P4, G1
- b: right P4 PU 106754
- c: left p4 PU 104616
- d: right hand G 3,4,5,6,9,12,13,14,15,16,17,18,91,92

*Homotherium latidens*

- e: left P4, G21
- f: right juvenile mandible with teeth and (f1) adult teeth: from the right side i1, i2, i3, c, p4 e m1, PU 104875 a, b, c, d, e, f
- g: left MC II, III, IV, V of the same hand, G41, 42, 43, 44
- h: right MT II, III, IV, V from the same feet, G 81, 82, 83, 84
- i: right humerus, G 26
- j: left radius, G 32



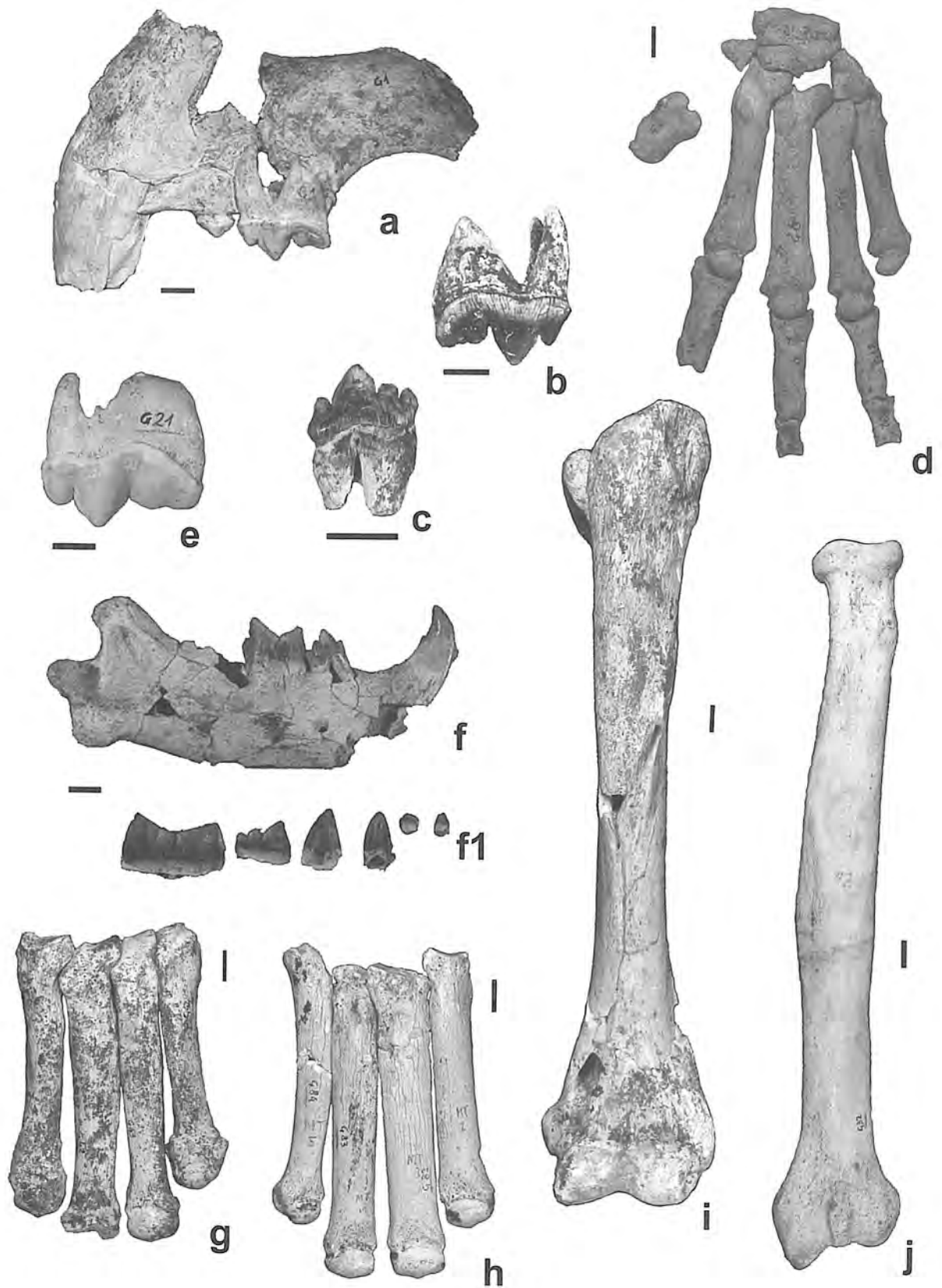


Plate 4

*Lynx issiodorensis*

a: left ulna PU 104644

b: skull, right side view, s.n.

*Panthera ex gr. toscana-gombaszoegensis*

c: left maxillar portion with P3 and P4, PN 31

*Acinonyx pardinensis*

d: right ulna

e: left MT IV PU 104234

*Puma pardoides*

f: left ulna PU 104225

Felidae indet

g: right MC V PU106067

*Pachycrocuta brevirostris*

h: coprolites

i: right ulna, G116

j: right I3, PN 32

k: right mandibular portion with p4 and m1

