Bollettino della Società Paleontologica Italiana, 52 (2), 2013, 103-111. Modena

New well-preserved material of *Lynx issiodorensis valdarnensis* (Felidae, Mammalia) from the Early Pleistocene of Pantalla (central Italy)

Marco Cherin, Dawid Adam Iurino & Raffaele Sardella

M. Cherin, Dipartimento di Scienze della Terra, Università degli Studi di Perugia, Piazza Università, I-06123 Perugia, Italy; marco.cherin@unipg.it
D.A. Iurino, Dipartimento di Scienze della Terra, "Sapienza" Università di Roma, Piazzale A. Moro 5, I-00185 Roma, Italy; IsIPU, Istituto Italiano di Paleontologia Umana, Via Aldrovandi 16/18, I-00197 Roma, Italy; dawid.iurino@uniroma1.it
R. Sardella, Dipartimento di Scienze della Terra, "Sapienza" Università di Roma, Piazzale A. Moro 5, I-00185 Roma, Italy; IsIPU, Istituto Italiano di Paleontologia Umana, Via Aldrovandi 16/18, I-00197 Roma, Italy; raffaele.sardella@uniroma1.it

KEY WORDS - Lynx issiodorensis valdarnensis*, Felidae, Late Villafranchian, Early Pleistocene, Pantalla, Italy.*

ABSTRACT - The rich mammal assemblage from Pantalla (Perugia, central Italy) represents an open window on the central Italy ecosystems during the early Late Villafranchian. The assemblage can be referred to the Olivola/Tasso Faunal Units and includes several cranial and postcranial remains of large herbivore and carnivore mammals in very good state of preservation. The fossil lynx from Pantalla is represented by a complete cranium, a right hemimandible, and a left calcaneus. The specimen can be referred to Lynx issiodorensis valdarnensis *Werdelin, 1981, in accordance with the early Late Villafranchian biochronology of the mammal assemblage. The material from Pantalla is the best preserved record of this subspecies in Italy, thus providing new, valuable morphologic and morphometric information on Early Pleistocene lynxes and, in general, on their evolutionary history.*

RIASSUNTO - [Nuovo materiale ben conservato di *Lynx issiodorensis valdarnensis* (Felidae, Mammalia) dal Pleistocene Inferiore di Pantalla (Italia centrale)] - *La ricca associazione a mammiferi di Pantalla (Perugia, Italia centrale) rappresenta una finestra aperta sugli ecosistemi presenti in Italia centrale durante la prima parte del Villafranchiano Superiore. Allo stato dell'arte, l'associazione può essere riferita alle Unità Faunistiche Olivola/Tasso. Essa include numerosi resti craniali e postcraniali di mammiferi in eccellente stato di conservazione, tra cui spiccano otto crani di carnivori e tre di erbivori pressoché completi. La lince fossile di Pantalla può essere riferita alla sottospecie* Lynx issiodorensis valdarnensis *Werdelin, 1981, che qui trova la sua segnalazione più meridionale. Tale determinazione sistematica concorda con le caratteristiche biocronologiche della fauna. Il materiale di Pantalla rappresenta il campione meglio conservato di questa sottospecie mai rinvenuto in Italia. Il suo studio ci ha consentito di ottenere un ampio ventaglio d'informazioni morfologiche e morfometriche che vanno a incrementare le nostre conoscenze sulle linci del Pleistocene Inferiore e, più in generale, sulla loro storia evolutiva.*

INTRODUCTION

The site of Pantalla is located about 30 km south of Perugia, in the southwestern branch of the Tiber Basin, a wide extensional continental basin that was filled mainly by clastic (lacustrine, palustrine, and fluvial) deposits since the Late Pliocene (Basilici, 1997). The basin extends from Sansepolcro to Terni and Spoleto describing an "upside-down Y" shape and splitting in a southeastern and a southwestern branch south of Perugia (Fig. 1). In particular, the southwestern branch corresponds to a well-defined half-graben filled with alluvial-lacustrine sequences and bounded westerly by the Amerini Mts-Narni Ridge and easterly by the Martani Mts. In the horsts the Mesozoic-Cenozoic Umbro-Marchean pelagic succession and the Miocene syn-orogenic flysch crop out. The main structural element of the basin is represented by the east-bounding Martana Fault, a N-S trending, west-dipping normal fault that abruptly separates the Plio-Pleistocene basin infill from the Martani Ridge. The fault likely exerted a strong control on local accommodation and sedimentation, at least up to Early Pleistocene time (Sardella et al., 2012, with references therein). As pointed out by Basilici (1997), at least the southwestern branch of the Tiber Basin has been characterized by a quite uniform depositional history, identifying four lithostratigraphic units, vertically exposed for about 450 m: the Fosso Bianco Formation is mainly constituted by silty clays deposited in a large lake system; the Ponte Naja Formation is probably partially heteropic with the uppermost part of the Fosso Bianco Formation, and is the result of the sedimentation activity of an alluvial fan on the lake margin; the Santa Maria di Ciciliano Formation is made up of silty clays and clayey silts deposited in alluvial plain environments, and sand bodies deposited in meandering fluvial channels; the Acquasparta Formation consists of continental carbonates deposited within shallow-lake and wetland environments. The Fosso Bianco Formation can be referred to the latest Pliocene-Early Pleistocene (magnetostratigraphic calibration in Abbazzi et al., 1997), while the other three units can be all dated to the Early Pleistocene in the light of their paleontological content (Abbazzi et al., 1997; Basilici, 1997; Girotti et al., 2003).

Several Late Villafranchian - and possibly also Middle Villafranchian - mammal assemblages were recorded in the last decades from the Santa Maria di Ciciliano Formation: Capitone (Ambrosetti, 1972), Villa San Faustino, Colle Sant'Andrea, Colle Violino, Casale le Grotte (Ambrosetti et al., 1995; Sardella et al., 1995), Torre Picchio (Girotti et al., 2003), and Colle Sant'Umano (Petronio et al., 2002).

The site of Pantalla (Fig. 1) was discovered in 1994 and two paleontological excavations were carried out in 1995 by the Soprintendenza per i Beni Archeologici dell'Umbria, with the scientific and technical support of

ISSN 0375-7633 doi:10.4435/BSPI.2013.16

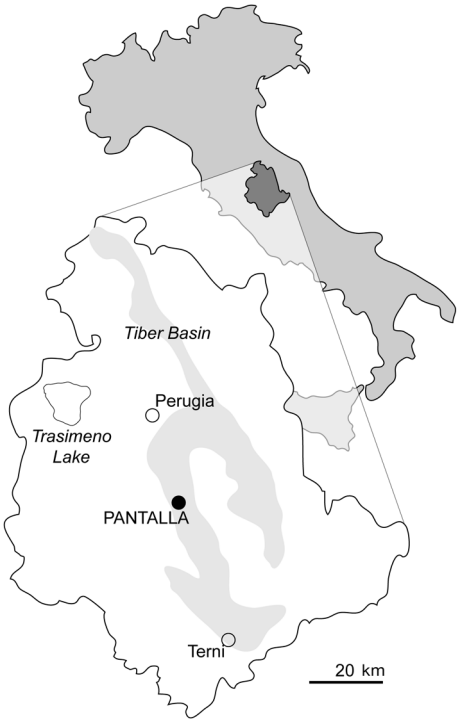


Fig. 1 - Location of the paleontological site of Pantalla (Italy). The Tiber Basin is highlighted in light grey along the middle part of Umbria.

the Dipartimento di Scienze della Terra, Università di Perugia. The Pantalla mammal fauna was recovered from a 15 m-thick stratigraphic succession referred to the Santa Maria di Ciciliano Formation. Mammal remains occurred within two different levels (Gentili et al., 1997): a) a silty sand level interpreted as a crevasse-splay deposit located in the middle part of the succession, where several carnivore and herbivore remains - especially skulls - were recovered from; b) a drained paleosol where vegetal remains (roots, leafs, and charcoal), terrestrial gastropods, and scanty fragmented postcranial bones of herbivore mammals were found. The absence of fluvial transport evidences and the "mosaic" pattern of the surface bone-cracking suggest a pedogenetic origin for the second accumulation. On the contrary, fossils from the first level were concentrated in a very small area (~2 m^2) and they were probably winnowed and accumulated by fluvial transport. The very good state of preservation, the homogeneous fossilization features of all the remains, and the absence of time- and space-averaging evidences suggest that the bones belong to an autochthonous thanatocoenose and can be considered coeval.

According to the preliminary study by Gentili et al. (1997) and the updated information from Cherin (2013) and Cherin et al. (2013), the following mammal species have been identified at Pantalla: *Apodemus* cf. *A. dominans* Kretzoi, 1959, *Canis etruscus* Forsyth Major, 1877, *Vulpes* sp., *Lynx issiodorensis* (Croizet & Jobert, 1828), *Acinonyx pardinensis* (Croizet & Jobert, 1828), *Lutra* sp., *Sus* cf. *S. strozzii* Forsyth Major, 1881, *Axis nestii* (Azzaroli, 1947), *Leptobos* aff. *L. furtivus* Duvernois & Guérin, 1989, *Equus* sp., *Mammuthus* cf. *M. meridionalis* (Nesti, 1825). From a biochronological point of view, the assemblage can be referred to the Olivola/Tasso Faunal Units (Gentili et al., 1997).

The goal of the present paper is the systematic description of the *Lynx issiodorensis* material - a cranium, a hemimandible, and a calcaneus - recovered from the first mammal-bearing level of Pantalla. These remains represent the best-preserved record of this species in Italy.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Family Felidae Fischer von Waldheim, 1817

Genus *Lynx* Kerr, 1792

Species *Lynx issiodorensis* (Croizet & Jobert, 1828)

Subspecies *Lynx issiodorensis valdarnensis* Werdelin, 1981
(Pl. 1, figs 1-3)

Type specimen - Skull MNHB Prr200 collected from the French locality of Étouaires (Perrier) and described by Croizet & Jobert (1828) as *Felis issiodorensis*.

Stratigraphic and geographic range - Early Pliocene to late Early Pleistocene of Eurasia and, possibly, Africa.

Material from Pantalla - SBAU 337653: cranium (Pl. 1, fig. 1); SBAU 167337: sand block containing a right hemimandible and two ribs (Pl. 1, fig. 2); SBAU 337636: left calcaneus (Pl. 1, fig. 3). The specimens belong to adult individuals. Morphometric data are reported in Tabs 1 and 2.

EXPLANATION OF PLATE 1

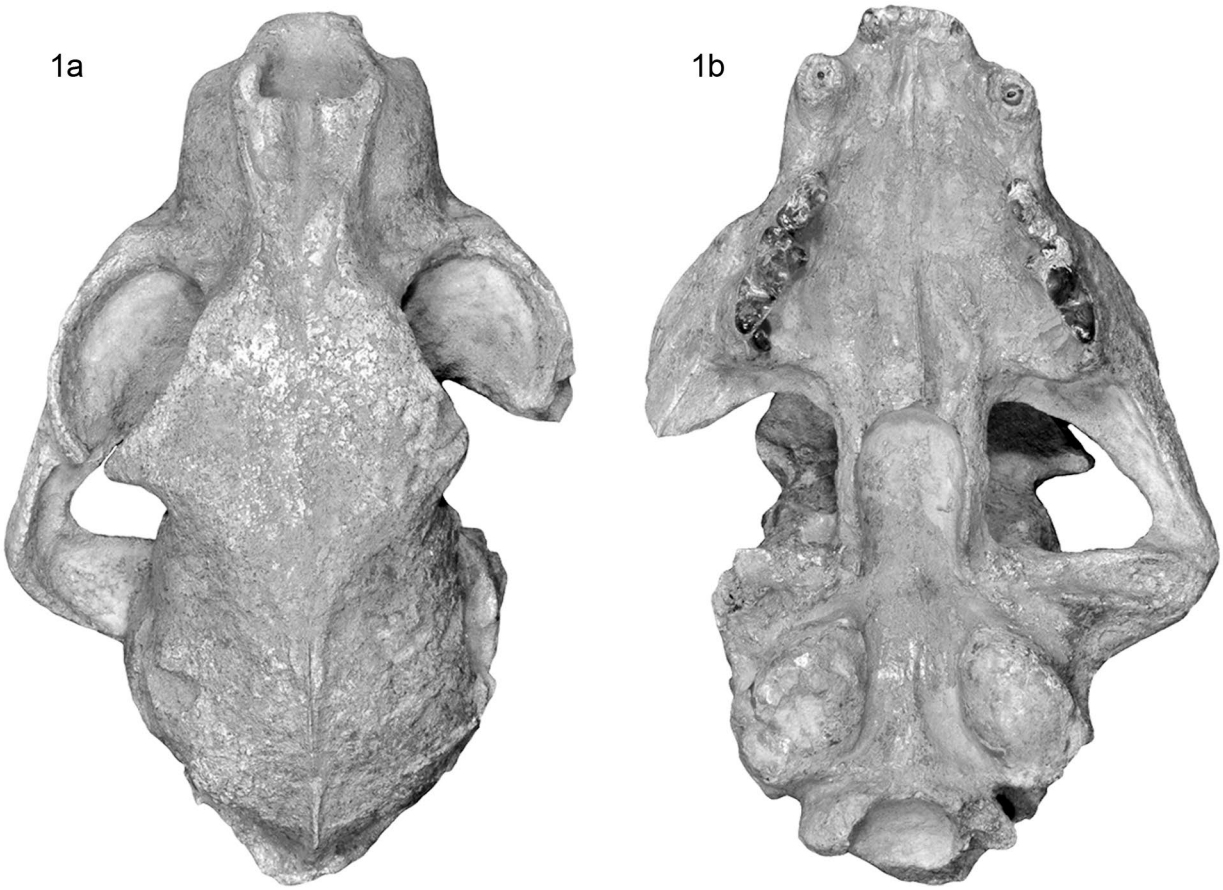
Lynx issiodorensis valdarnesis Werdelin, 1981 from Pantalla (Italy).

Fig. 1 - Cranium SBAU 337653 in dorsal (a), ventral (b), and left lateral (c) view.

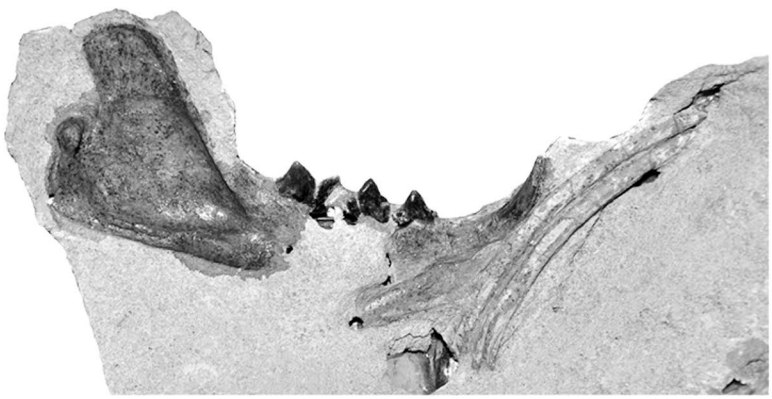
Fig. 2 - Right hemimandible SBAU 167337 in labial view.

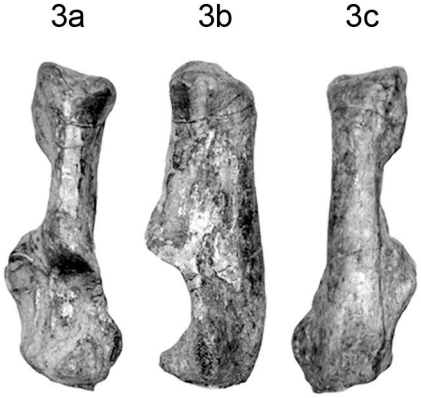
Fig. 3 - Left calcaneus SBAU 337636 in dorsal (a), medial (b), and ventral (c) view.

Scale bar = 30 mm.


1a
1b


1c


2


3a
3b
3c

Cranium	SBAU 337653		I^3	dx	sx
Total length (Akrokranion-Prosthion)	147.0		Length	4.5	-
Condylobasal length	140.0		Breadth	4.4	-
Basal length	127.3		C^{max}	dx	sx
Neurocranium length (Akrokranion-Frontal midpoint)	80.0		Length	9.0	-
Facial length (Frontal midpoint-Prosthion)	75.0		Breadth	7.1	6.7
Viscerocranium length (Nasion-Prosthion)	-		P^3	dx	sx
Basicranial axis (Basion-Synsphenion)	41.0		Length	11.8	11.7
Basifacial axis (Synsphenion-Prosthion)	87.0		Max breadth	5.5	5.1
Median palatal length (Staphylion-Prosthion)	64.1		Anterior breadth	4.6	4.7
Zygomatic breadth	~102		Paracone length	6.6	6.5
Neurocranium breadth	62.3		Paracone height	8.1	8.3
Breadth at the canine alveoli	40.4		P^4	dx	sx
Max palatal breadth (at the P^4 alveoli)	61.4		Length	18.3	18.0
Frontal breadth (Ectorbitale-Ectorbitale)	59+		Length at the protocone	17.1	17.8
Min breadth across orbits (Entorbitale-Entorbitale)	31.3		Max breadth	8.8	8.6
Breadth postorbital constriction	43.6		Breadth behind to protocone	6.5	6.4
Mastoid breadth	58.3		Max posterior breadth	5.7	6.1
Breadth of the occipital condyles	34.8		Paracone length	7.5	7.0
Breadth of the foramen magnum	18.3		Metacone length	7.5	6.6
Max diameter of the tympanic bulla	21.4		Paracone + Metacone length	14.4	14.0
Min diameter of the tympanic bulla	17.0		Paracone height	9.9	9.6
I^2	dx	sx	M^1	dx	sx
Length	2.9	-	Length	3.3	-
Breadth	2.7	-	Breadth	5.8	-

Tab. 1 - Cranial measurements (mm) of *Lynx issiodorensis valdarnesis* from Pantalla (Italy).

Mandible	SBAU 167337		
Length at the condyloid process	~98		
Length at the coromoid process	~97	P_4	
Max height	45.7	Length	11.0
Height behind the canine	-	Max breadth	-
Height behind M_1	20.0	Anterior breadth	-
Breadth at P_4	-	Paraconid length	5.4
Length of the diastema	10.8	Paraconid height	~7.5
Cheek teeth length (alveolar)	35.2		
C_{mand}		M_1	
Length	-	Length	~14.5
Breadth	-	Max breadth	-
Crown height	19.5	Protoconid length	~7
P_3		Protoconid height	-
Length	9.4	Paraconid length	7.3
Max breadth	-	Paraconid height	8.0
Anterior breadth	-	Height at the central notch	5.6
Paraconid length	5.0		
Paraconid height	6.4		

Tab. 2 - Mandibular measurements (mm) of *Lynx issiodorensis valdarnesis* from Pantalla (Italy).

Cranium	Étouaires				Pantalla	Olivola
	MNHB Prr 200	MNHB Prr 201	MNHB Prr 411	MNHB Prr 8	SBAU 337653	IGF 4399
Total length (Akrokranion-Prosthion)	-	-	-	-	147.0	148.0
Condylobasal length	168.0	-	-	-	140.0	-
Basal length	158.0	-	-	-	127.3	-
Neurocranium length (Akrokranion-Frontal midpoint)	-	-	-	-	80.0	76.0
Facial length (Frontal midpoint-Prosthion)	-	-	-	-	75.0	53.0
Viscerocranium length (Nasion-Prosthion)	-	-	-	-	-	81.0
Basicranial axis (Basion-Synsphenion)	-	-	-	-	41.0	-
Basifacial axis (Synsphenion-Prosthion)	-	-	-	-	87.0	-
Median palatal length (Staphylion-Prosthion)	82.0	78.0	-	-	64.1	-
Zygomatic breadth	120.0	-	-	-	~102	-
Neurocranium breadth	-	-	-	-	62.3	-
Breadth at the canine alveoli	47,0	47.0	-	-	40.4	41.0
Max palatal breadth (at the P4 alveoli)	-	67.0	-	-	61.4	63.0
Frontal breadth (Ectorbitale-Ectorbitale)	~73	-	-	-	59+	-
Min breadth across orbits (Entorbitale-Entorbitale)	~36	-	-	-	31.3	34.0
Breadth postorbital constriction	~41	-	-	-	43.6	41.0
Mastoid breadth	68.0	-	-	-	58.3	-
Breadth of the occipital condyles	38.8	-	-	-	34.8	-
Breadth of the foramen magnum	-	-	-	-	18.3	-
Max diameter of the tympanic bulla	-	-	-	-	21.4	-
Min diameter of the tympanic bulla	-	-	-	-	17.0	-
C^{max}						
Length	10.5	10.2	9.1	10.0	9.0	-
Breadth	7.8	8.4	7.1	-	7.1	-
P^3						
Length	14.0	13.6	13.0	-	11.8	-
Max breadth	6.5	6.4	6.2	-	5.5	-
P^4						
Length	20.4	20.5	19.6	19.9	18.3	18.0
Max breadth	9.6	9.6	8.9	10.3	8.8	8.4
Max posterior breadth	6.5	6.4	6.8	6.4	5.7	-
M^1						
Breadth	7.4	7.6	7.8	7.4	5.8	-

Tab. 3 - Comparative craniodental measurements (mm) of *Lynx issiodorensis* from Étouaires (data from Kurtén, 1978), Olivola, and Pantalla. Sites are arranged in chronological order (the oldest one on the left).

Comparative material - Lynx issiodorensis: Olivola (mandible IGF 4396, cranium IGF 4399); Upper Valdarno (cranial fragments IGF 500V, right hemimandible IGF 891, right hemimandible IGF 892, fragmented maxillae and mandible IGF 893, mandible IGF 894, left hemimandible IGF 895, right hemimandible IGF 896, left maxilla IGF 897, right hemimandible IGF 898, fragmented mandible IGF 12969, incomplete cranium IGF 13890, canine IGF 13893, left maxilla IGF 13894, left hemimandible IGF 13895, right calcaneus IGF 13888, right calcaneus IGF 13902); Selvella (mandible IGF 14151); Garfagnana (left maxilla and right hemimandible IGF 1445V); Étouaires,

	Etouaires (n=11)	St.Vallier (n= 5)	SBAU 167337	Up.Valdarno (n=7)	Untermassfeld (n=3)
P_3 length	10.6	10.4	9.4	9.3	8.4
P_4 length	13.7	12.9	11.0	11.9	11.4
M_1 length	15.5	15.2	~14.5	14.1	13.4+

Tab. 4 - Length (mm) of the lower teeth of *Lynx issiodorensis valdarnensis* from Pantalla compared to the average values (sample size in brackets) from other European sites. Data for Étouaires and Saint Vallier are from Kurtén (1978); Upper Valdarno: Ficcarelli & Torre (1977); Untermassfeld: Hemmer (2001). Sites are arranged in chronological order (the oldest one on the left).

France (cranium IGF 12777, cast). *Lynx lynx*: skull SPE 2134; skull MCZR ost85; skull MCZR ost305; skull MCZR ost249; skull MCZR ostPR8.

Morphometric data published by Viret (1954), Ficcarelli & Torre (1977), Kurtén (1978), and Cipullo (2010) were also considered for comparisons. Morphometric measurements were collected following Driesch (1976).

Institutional abbreviations - IGF: Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze; MCZR: Museo Civico di Zoologia, Roma; MNHB: Muséum d'Histoire Naturelle, Basel; SBAU: Soprintendenza per i Beni Archeologici dell'Umbria, Perugia; SPE: Museo di Storia Naturale, Sezione di Geologia "La Specola", Università di Firenze.

Description and comparisons -

Cranium - The cranium SBAU 337653 is in very good state of preservation, although the right zygomatic arch and both canines are broken. In addition, the specimen shows a diagenetic dorso-ventral compression. For this reason, in lateral view the cranium is flattened if compared with less-deformed fossil specimens (e.g., MNHB QSV1133, figured by Viret, 1954) or extant lynxes.

In dorsal view, the neurocranium appears quite narrow. The relative breadth of the zygomatic arches (respect to the total length) is lower than the extant *L. lynx*, while the snout is relatively longer. Nasal bones - that are slightly crushed into the nasal cavities - are markedly laterally enlarged in the anterior portion.

Even if incomplete, the sagittal and nuchal crests are not particularly tall, as in *L. issiodorensis* from Sain Vallier (MNHB QSV1133). Similarly to extant lynxes, tympanic bullae are very large and rounded. The palate is large and flat. All the above morphologic features have been described by Viret (1954), Kurtén (1978), and Werdelin (1981) for *L. issiodorensis*.

From a morphometric point of view, the cranium is slightly larger than the specimen from Saint Vallier (MNHB QSV1133), very similar to the one from Olivola (IGF 4399), and smaller than the one from Étouaires (MNHB Prr200) (Tab. 3).

Upper teeth - Only right I^2 and I^3 are preserved, and both canines are broken at the crown base. P^2 is absent on both sides. This has been considered as a peculiar character of lynxes by some authors (e.g., Teilhard de Chardin & Leroy, 1945), but Werdelin (1981) has pointed out that P^2 is present in a number of fossil specimens.

P^3 is characterized by a high-crowned, pointed paracone. The protocone is absent, while the hypocone is well developed and rounded. A posterior cingulum is visible.

The upper carnassial is dominated by a strong paracone, which is as tall as the one of P^3. In occlusal view, the protocone is placed anteriorly and elongated lingually, but is quite slender on the whole. A small ectoparastyle is present on the antero-labial angle of the P^4, as recognized by Kurtén (1978) for *L. issiodorensis*.

M^1 is preserved only on the right side. It has an elliptical occlusal outline, and is very small and lingually-placed.

Once again, morphometric values of the upper dentition are very close to *L. issiodorensis* from Olivola (IGF 4399), and smaller than the specimens from Étouaires (Tab. 3).

Mandible - The right hemimandible SBAU 167337 is partially embedded in a sand block, together with two slender ribs, and is therefore visible only on the labial side. In addition, the mandibular branch is broken in the middle part, so it was left in the block for not endangering its integrity. As a consequence, it was possible to take just few morphometric data (Tab. 2).

As previously described for *L. issiodorensis* from Étouaires by Kurtén (1978), the mandible is more massive but with smaller teeth than the extant *L. lynx*. The coronoid process is high and posteriorly-oriented, while the angular process is small. The masseteric fossa is very wide, suggesting the presence of strong jaw muscles. Even if the ventral part of the hemimandible is partially covered by the sediment, the ventral outline seems to be quite flat.

Lower teeth - The lower canine is high and curved. A long diastema separates the canine from the P_3. The protoconid of P_3, P_4, and M_1 and the paraconid of M_1 form an aligned sequence of very pointed cusps of about the same height. The P_3 has a quite indistinct paraconid and a little hypoconid, while in the P_4 these two cusps are more developed. Lower teeth dimensionally resemble the *L. issiodorensis* specimens from Upper Valdarno, while they are larger than the lynx from Untermassfeld and smaller than the specimens from French localities (Tab. 4).

Calcaneus - The left calcaneus SBAU 337636 is virtually complete, since only the lateral tip of the sustentaculum tali is broken. The calcaneus has a length of 55.2 mm and a maximum antero-posterior breadth of 19.7 mm. The articular area for the talus is strongly concave, describing a "C" shape in medial view. It is mainly due to the presence of a little swelling on the antero-ventral angle of the articular surface. In posterior view, the calcaneus body is separated from the sustentaculum tali by a deep longitudinal furrow. All the morphometric and morphologic features strongly resemble the calcanei of *L. issiodorensis* from Upper Valdarno (IGF 13888 and IGF 13902).

DISCUSSION

At the state of the art the taxonomic status of *Lynx issiodorensis* has not been fully clarified. The evolutionary history of Pleistocene European lynxes proposed by Werdelin (1981) - with the gradual passage from *L. issiodorensis issiodorensis* to *L. pardinus pardinus* through *L. issiodorensis valdarnensis* and *L. pardinus spelaeus* - has been slightly modified by Cipullo (2010) with the recognition of two new, still unnamed subspecies: a) *L. issiodorensis* ssp. 1 represents the most archaic subspecies, found at Layna (Spain), Serrat d'En Vaquer (France), and Câlta (Turkey). The evolutionary relationships between *L. issiodorensis* ssp. 1 and the successive - and larger - *L. issiodorensis issiodorensis* are not fully clear. b) The second new subspecies, *L. issiodorensis* ssp. 2, from Pirro Nord (Italy), Monte Argentario (Italy), and Untermassfeld (Germany), seems to fit better with the progressive body

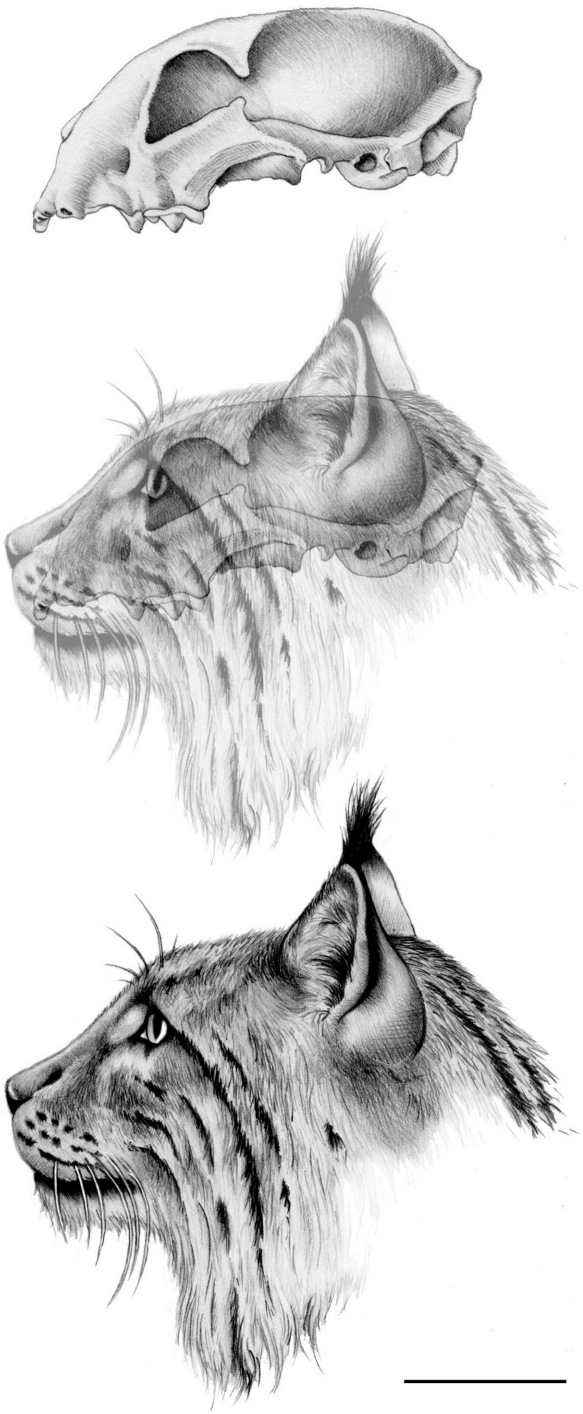


Fig. 2 - Sequence of reconstruction of the head of *Lynx issiodorensis*, based on the material from Pantalla (Italy). Scale bar represents 50 mm. Artwork: D.A. Iurino.

size reduction recognized by Werdelin (1981) in the above lineage. According to the data collected until now, it seems that the above subspecies are well chronologically separated and describe a sequential evolutionary pattern leading to the extant Iberian lynx *L. pardinus* (Werdelin, 1981; Cipullo, 2010). *L. issiodorensis* ssp. 1 (whose taxonomic status and evolutionary relationships have to be more carefully investigated) is probably limited to the Ruscinian (i.e., Pliocene), while the following *L. issiodorensis issiodorensis* characterized the Early-Middle Villafranchian. *L. issiodorensis valdarnensis* is limited to the early Late Villafranchian (Olivola and Tasso FUs) and *L. issiodorensis* ssp. 2 to the latest Villafranchian and Epivillafranchian. As a consequence, the *L. issiodorensis* forms should be regarded as chronosubspecies.

In this framework, the material from the site of Pantalla provides new useful data for explaining the evolutionary history of fossil lynxes. In the light of the supposed age of the Pantalla assemblage (Olivola/Tasso FUs), the lynx material should be referred to the chronosubspecies *L. issiodorensis valdarnensis*. This hypothesis is fully supported by the biometric data collected on the Pantalla specimens, which fits very well with the *L. issiodorensis valdarnensis* material from Upper Valdarno and Olivola (see Tabs 3 and 4).

The complexity of the Italian Late Villafranchian carnivore guild is well represented at Pantalla, where the medium-sized *Lynx issiodorensis* (Fig. 2) probably competed with two other predators - the larger *Acinonyx pardinensis* and the smaller *Canis etruscus* - for the exploitation of trophic resources (the other two carnivores from Pantalla, *Vulpes* sp. and *Lutra* sp., are not considered here because they both occupied different ecological niches). The taphonomy of the Pantalla assemblage (see above) clearly indicates that the three carnivore species occupied the same geographical area in the same period. A similar ecological framework - with the sympatry of a medium-sized cat, a large-sized one, and a medium-sized dog - does not find any correspondence in the Present-day European ecosystems, but can be observed in other geographic areas. For instance, Andheria et al. (2007) have reported the case of the Bandipur Tiger Reserve in India, where three medium/large predators - the tiger *Panthera tigris* (Linnaeus, 1758), the leopard *Panthera pardus* (Linnaeus, 1758), and the dhole *Cuon alpinus* (Pallas, 1811) - show a strong overlapping in their ecological niches, since their diet is based for the 88-97% (in biomass) on the same three ungulate species. A similar situation can be also observed in North America, where the co-occurrence of the cougar *Puma concolor* (Linnaeus, 1771), the bobcat *Lynx rufus* (Schreber, 1778), and the coyote *Canis latrans* Say, 1823 represents a valuable example of both exploitative competition and intra-guild predation (between 12 and 62% of bobcats are killed by the other two species in some areas) (Macdonald et al., 2010).

The structure of the carnivore assemblage from Pantalla opens an interesting window on the early Late Villafranchian ecosystems of Italy. This time span is widely considered as a turning point in biochronology (cfr. Sardella et al., 1998), since it is characterized by an important dispersal phase from Asia occurred approximately 1.9-1.7 Ma ago. In this period, medium-sized canids, *Panthera gombaszoegensis* (Kretzoi, 1938) and *Pachycrocuta brevirostris* (Aymard, 1846) spread into Europe, causing a strong increase in the complexity of the large carnivore guild.

ACKNOWLEDGEMENTS

We are indebted to M.C. De Angelis (Soprintendenza per i Beni Archeologici dell'Umbria), who entrusted the first author (MC) with the study of the mammal collection from Pantalla. We

are grateful to E. Cioppi (Università di Firenze), R. Carlini (Museo Civico di Zoologia di Roma), P. Agnelli (Università di Firenze), and all the staff of the "Palazzone", Perugia (Soprintendenza per i Beni Archeologici dell'Umbria), for the access to museum collections and for their precious technical support. We would like to thank Joan Madurell and an anonymous reviewer for their valuable comments on the manuscript.

REFERENCES

Abbazzi L., Albianelli A., Ambrosetti P., Argenti P., Basilici G., Gentili S., Masini F. & Pontini M.R. (1997). Paleontological and sedimentological records in Pliocene distal alluvial fan deposit at Cava Toppetti (Todi, Central Italy). *Bollettino della Società Paleontologica Italiana*, 36: 5-22.

Ambrosetti P. (1972). Lo scheletro di *Dicerorhinus etruscus* (Falc.) di Capitone (Umbria meridionale). *Geologica Romana*, 11: 177-198.

Ambrosetti P., Basilici G., Capasso Barbato L., Carboni G., Di Stefano G., Esu D., Gliozzi E., Petronio C., Sardella R. & Squazzini E. (1995). Il Pleistocene inferiore nel ramo Sud-Occidentale del Bacino Tiberino (Umbria): aspetti litostratigrafici e biostratigrafici. *Il Quaternario*, 8: 19-36.

Andheria A.P., Karanth K.U. & Kumar N.S. (2007). Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology*, 273: 169-175.

Aymard A. (1846). Communication sur le gisement de Sainzelles. *Annales de la Société d'Agriculture, Science, et Arts Commerce du Puy*, 13: 153-155.

Azzaroli A. (1947). I cervi fossili della Toscana con particolare riguardo alle specie villafranchiane. *Palaeontographia Italica*, 43: 45-82.

Basilici G. (1997). Sedimentary facies in an extensional and deep-lacustrine depositional system: the Pliocene Tiberino Basin, Central Italy. *Sedimentary Geology*, 109: 73-94.

Bowdich T.E. (1821). An Analysis of the Natural Classification of Mammalia for the Use of Students and Travellers. 115 pp. J. Smith, Paris.

Cherin M. (2013). Systematic, paleoecological and biochronological study of some Quaternary mammal faunas from central Umbria (Italy). 175 pp. PhD thesis, Università di Perugia, Italy.

Cherin M., Bertè D.F., Rook L. & Sardella R. (2013). Re-defining *Canis etruscus* (Canidae, Mammalia): A new look into the evolutionary history of Early Pleistocene dogs resulting from the outstanding fossil record from Pantalla (Perugia, central Italy). *Journal of Mammalian Evolution*, DOI 10.1007/s10914-013-9227-4.

Cipullo A. (2010). L'evoluzione del genere *Lynx* dal Pliocene al Pleistocene Medio nell'area mediterranea. 118 pp. PhD thesis, Università di Modena-Bologna-Roma, Italy.

Croizet J.B. & Jobert A. (1828). Recherches sur les ossemens fossils du Département du Puy-de-Dôme. Thibaut-Landriot, Paris: 1-224.

Driesch A. von den (1976). A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletins*, 1: 1-137.

Duvernois M.P. & Guérin C. (1989). Les Bovidae (Mammalia, Artiodactyla) du Villafranchien supérieur d'Europe Occidentale. *Géobios*, 22: 339-379.

Ficcarelli E. & Torre D. (1977). Phyletic relationships between *Lynx* gr. *issiodorensis* and *Lynx pardina*. *Bollettino della Società Paleontologica Italiana*, 16: 197-202.

Fisher von Waldheim G. (1817). Adversaria Zoologica. *Mémoires de la Société Impériale des naturalistes de Moscou*, 5: 368-428.

Forsyth Major C.I. (1877). Considerazioni sulla fauna dei Mammiferi pliocenici e postpliocenici della Toscana. III. Cani fossili del Val d'Arno superiore e della Valle dell'Era. *Memorie della Società Toscana di Scienze Naturali,* 3: 207-227.

Forsyth Major C.I. (1881). Studi sugli avanzi pliocenici del genere *Sus*. *Atti della Società Toscana di Scienze Naturali, Processi Verbali*, 2: 227.

Gentili S., Ambrosetti P. & Argenti P. (1997). Large carnivores and other mammal fossils from the early alluvial plain of the Tiberino Basin (Pantalla, Central Italy). Preliminary reports. *Bollettino della Società Paleontologica Italiana*, 36: 233-240.

Girotti O., Capasso Barbato L., Esu D., Gliozzi E., Kotsakis T., Martinetto E., Petronio C., Sardella R. & Squazzini E. (2003). The section of Torre Picchio (Terni, Umbria, Central Italy): a Villafranchian site rich in Vertebrates, Molluscs, Ostracods and Plants. *Rivista Italiana di Paleontologia e Stratigrafia*, 109: 77-98.

Hemmer H. (2001). Die Feliden aus dem Epivillafranchium von Untermassfeld. *In* Kahlke R.D. (ed.), Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), Teil 3. Habelt Verlag, Bonn: 699-782.

Kerr R. (1792). The Animal Kingdom, or Zoological System, of the Celebrated Sir Charles Linnaeus. Class I. Mammalia. 644 pp. A. Strahan & T. Cadell, London and W. Creech, Edinburgh.

Kretzoi M. (1938). Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna (Ein Beitrag zur Stratigraphie des Altquartärs). *Annales Musei Nationalis Hungarici, Pars Mineralogica, Geologica, Palaeontologica*, 31: 88-157.

Kretzoi M. (1959). Insectivoren, nagetiere und lagomorphen der jüngstpliozänen fauna von Csarnóta im Villányer Gebirge (Südungarn). *Vertebrata Hungarica,* 1: 237-246.

Kurtén B. (1978). The lynx from Etouaries, *Lynx issiodorensis* (Croizet & Jobert), late Pliocene. *Annales Zoologici Fennici*, 15: 314-322.

Linnaeus C. (1758). Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonimys, Locis. Tomus I. 338 pp. Laurentius Salvus, Stockholm.

Linnaeus C. (1771). Mantissa plantarum altera generum editionis VI et specierum editionis II. 588 pp. Laurentius Salvius, Stockholm.

Macdonald D.W., Loveridge A.J. & Nowell K. (2010). Dramatis personae: an introduction to wild felids. *In* Macdonald D.W. & Loveridge A.J. (eds), Biology and conservation of wild felids. Oxford University Press, New York: 3-58.

Nesti F. (1825). Sulla nuova specie di elefante fossile del Valdarno all'Illustrissimo Sig. Dott. Prof. Ottaviano Targioni Tozzetti (Lettere sopra alcune ossa fossili del Valdarno non per anco descritte). *Nuovo Giornale di Lettere*, 11: 195-216.

Pallas P.S. (1811). Zoographia Rosso-Asiatica. Tomus Primus. 568 pp. Petropoli.

Petronio C., Argenti P., Caloi L., Esu D., Girotti O. & Sardella R. (2002). Updating Villafranchian molluscs and mammal faunas of Umbria and Latium (Central Italy). *Geologica Romana*, 136: 311-334.

Sardella R., Abbazzi L., Argenti P., Azzaroli A., Caloi L., Capasso Barbato L., Di Stefano G., Ficcarelli G., Gliozzi E., Kotsakis T., Masini F., Mazza P., Mezzabotta C., Palombo M.R., Petronio C., Rook L., Sala B. & Torre D. (1998). Mammal faunal turnover in Italy from the Middle Pliocene to the Holocene. *Mededelingen Nederlands Instituut voor Toegepaste Geoweteschappen TNO*, 60: 499-512.

Sardella R., Di Stefano G. & Petronio C. (1995). The Villafranchian mammal faunas from the Tiber River Basin (Umbria, Central Italy). *Il Quaternario*, 8: 509-514.

Sardella R., Squazzini E. & Mancini M. (2012). The late Villafranchian faunal assemblages from southern Umbria (central Italy): an useful tool for reconstructiong intramontane basin infill evolution. *Rendiconti Online della Società Geologica Italiana*, 21: 1245-1248.

Say T. (1823). Account from an expedition from Pittsburgh to the Rocky Mountains performed in the years 1819 and '20, by order of the Hon. J.C. Calhoun, sec'y of war: under the command of Major Stephen J. Long. From the notes of Major Long, Mr. T. Say, and other gentlemen of the exploring party. Comp. by Edwin James, botanist and geologist for the expedition. Vol. 1. 172 pp. H.C. Carey & I. Lea, Philadelphia.

Schreber J.C.D. von (1778). Die Saugthiere in Abbildungen nach der Natur mit Beschreibungen. Dritter Theil. 309 pp. Erlangen, Germany.

Teilhard de Chardin P. & Leroy P. (1945). Les Félidés de Chine. *Publications of the Institute of Geobiology of Peking*, 11: 1-58.

Viret M.J. (1954). Le loess a bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 4: 1-195.

Werdelin L. (1981). The evolution of lynxes. *Annales Zoologici Fennici*, 18: 37-71.

Manuscript received 11 November 2012
Revised manuscript accepted 21 June 2013
Published online 30 October 2013
Editor Marco Balini