SYSTEMATIC POSITION OF A COMPLETE LION-LIKE CAT SKULL FROM THE EEMIAN OSSIFEROUS RUBBLE NEAR ZANDOBBIO (BERGAMO, NORTH ITALY)

FABIO BONA

Received: April 14, 2005; accepted: September 29, 2005

Key words: Zandobbio, Panthera leo spelaea, Eemian, mammals, carnassial tooth, skull.

Abstract. Morphologic and morphometric data of a lion-like cat skull found in the Zandobbio (Lombardy - Italy) Eemian ossiferous rubble and stored in the Civic Museum of Natural History "E. Caffi" of Bergamo are presented. The skull shows the typical lion morphology and its relatively small dimensions suggest that it belonged to a female individual. Carnassial tooth analysis underlines advanced lion characters already recognized in Italy during the Eemian. According to skull and teeth characters it is possible to ascribe the specimen to the group of Upper Pleistocene lion-like cats Panthera leo spelaea (Goldfuss, 1810). The presence of P. leo spelaea in the Quaternary deposit of Zandobbio has remarkable importance not only locally. In fact, besides being the first report of this great feline at Zandobbio, it is the second report from Lombardy and the oldest certain P. leo spelaea finding and the oldest complete P. leo spelaea skull known from Italy to date. The advanced P. leo spelaea characters were already present in Italy during the Eemian.

Riassunto. In questo lavoro vengono analizzati caratteri morfologici e morfometrici di un cranio completo, appartenente ad un grande felino, recuperato nella breccia ossifera Eemiana di Zandobbio (Lombardia - Italia). Il reperto è conservato presso il Museo Civico di Storia Naturale "E. Caffi" di Bergamo.

L'analisi svolta ha evidenziato come il cranio presenti la tipica morfologia leonina e, in base alle relativamente ridotte dimensioni assolute, si può attribuirne l'appartenenza ad un individuo femminile. L'approfondita analisi morfologica del quarto premolare presente evidenzia come già durante l'Eemiano siano presenti in Italia caratteri leonini considerati evoluti da molti autori. Prendendo atto dei dati ottenuti dall'analisi morfologica e morfometrica del cranio e della dentatura ed attenendosi ai dati genetici proposti da alcuni ricercatori è possibile attribuire il reperto studiato al gruppo di leoni presenti in Europa durante tutto il Pleistocene Superiore, *Panthera leo spelaea* (Goldfuss, 1810).

È interessante segnalare come la presenza di *P. leo spelaea* nei depositi quaternari di Zandobbio non rivesta solo un'importanza locale. Infatti, questa è la prima segnalazione in assoluto di questo grande felino a Zandobbio, la seconda per l'intera Lombardia e il più antico

resto di *P. leo spelaea* oggi conosciuto in Italia, rappresentando, sempre per l' Italia, anche il più antico cranio completo di *P. leo spelaea* sino ad ora recuperato.

Introduction

Morphologic and morphometric data of a lion-like cat skull collected towards the end of the 1970s and kept in the Civic Museum of Natural History "E. Caffi" of Bergamo are presented, and its systematic position is determined by comparison with populations of lion-like cats from other European sites. According to the discoverer, Claudio Signorelli, the skull comes from the "Grotta delle Ossa" of Zandobbio (Bg) (Fig. 1). Another topic of this work is to try to determine the first occurrence in Italy of some features, such as the morphology of the fourth upper premolar, considered "evolved" in lion-like cats by many authors (Schütt 1969; Sala 1990) and used to discriminate between the "fossilis" and "spelaea" groups.

We have reports of the presence of lion-like cats in Western Europe beginning from the middle Pleistocene, about 700.000 years ago, at Isernia la Pineta (Sala 1990).

The size of the European large cats was comparable to that of living African lions, except for the older specimens that had a larger body size.

Lion-like cats remains are quite frequent in several middle and upper Pleistocene European sites (e.g. Fabiani 1919; Schütt 1969; Schütt & Hemmer 1978; Sala 1980; Argant 1991; Gužvica 1998; Bon et al. 1991; Turner & Anton 1997), but they tend to be represented by a few bones or tooth fragments. Few skulls are as com-

¹ Dipartimento di Scienze della Terra "A. Desio", Università degli Studi di Milano, via Mangiagalli 34, 20133 Milano. E-mail: fabio.bona@unimi.it

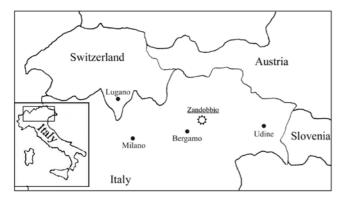


Fig. 1 - Geographical position of Zandobbio village.

plete as that of Zandobbio. For example, only a dozen such skulls are identified in France (Boule 1906; Argant 1998), and three in Italy, in addition to the skull described here. Currently, two of the latter are stored in the paleontological museum of the University of Padova (Piccoli et al. 1979) and one in the paleontological museum of the University of Bologna (Anelli 1954).

Systematics of Lion-Like Cats

Two groups of lion-like cats are recognized at present by authors in Western Europe: the older "fossilis" group (middle Pleistocene), and the younger "spelaea" group (upper Pleistocene).

There is still an open discussion regarding the taxonomic rank of these two groups. Some authors consider the two groups as two different species, *P. fossilis* and *P. spelaea*, of the genus *Panthera* (Argant 1988; Baryshnikov & Boeskorov 2001; Sotnikova & Nikolskiy 2003), which includes tigers, leopards and lions.

According to others (Riedel 1982; Sala 1990; Schütt 1969), both groups belong to the same species of the living African and Asian lions *P. leo*, merely representing two different sub-species. Riedel (1982), who analyzed a large amount of bibliographic data and a specimen from Grotta Tilde, believes that the osteological differences between fossil and living lions are very small and that they mainly concern size, on average larger in fossil lion-like cats than in living *P. leo*.

According to Sotnikova & Nikolskiy (2003), *P. leo* differs from *P. spelaea* in some advanced features: a markedly more inflated and antero-laterally expanded bulla, more complex configuration of the zygomatic-maxillary suture, U-shaped frontal-maxillary suture, P³ with a more developed additional second cusp, upper carnassial with pre-parastyle and distinct cusp on the protocone bulge. Other features seem even more advanced, such as widened nasal bones and a reduced cup on the protocone bulge of P⁴.

Some authors believe that two distinct sub-species of lion lived in Europe during the upper Pleistocene.

Ballesio (1980) supports this point of view on the basis of bimodal size groupings in the large felid material from Jaurens, Corrèze, and other European sites. Turner (1984) and Kurten (1985) refute this idea and consider the bimodal distributions to be due to sexual dimorphism, as observed also in modern lions.

In a study of brain moulds of *P. leo*, *P. tigris* and *P. spelaea*, Groiss (1996) considers the "spelaea" group as a sub-species of *P. tigris*, the living tiger, on the basis of encephalic features.

On the contrary, according to Sotnikova & Ni-kolskiy (2003) *P. tigris* differs from *P. leo* and *P. spelaea* in many characters in cranial morphology.

Torre (1967) presents another interesting opinion on lion taxonomy. He notes that lions are very different from tigers and other similar species of the genus *Panthera*, because in *Panthera* the neurocranium is more developed than in the lion, as proved by the less efficient temporal muscle-mandible system in lions than in panthers (leopards, jaguars, tigers). Accordingly, he considers *Leo* (*leo*) a distinct genus.

DNA analysis carried out on two upper Pleistocene lion-like cat bones coming from Siegsdorf, (south eastern Bavaria) and Tischhofer cave (Kufstein in Tirol) suggest that Western European latest glacial lion-like cats are strictly linked to *P. leo*, of which they represent a subspecies (Burger et al. 2004).

History and faunal assemblage of Zandobbio

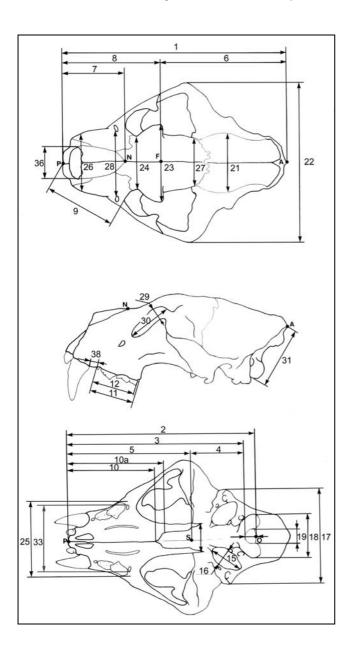
The faunal assemblage of the Zandobbio (Bergamo) ossiferous rubble has been known since Airaghi (1934). The paleontological material studied by Airaghi came from Barcella's "marmo bianco" quarry. It was during the exploitation of the quarry that some hollows covered by alabaster and with the bottom filled of "terre rosse" and rubble rich in mammal remains were discovered.

The bones recovered were described as poorly preserved, nearly always crushed, and strongly cemented in the rubble. The taxa determined by Airaghi are the following: *Hyaena crocuta spelaea* (recte *Crocuta crocuta spelaea*), *Vulpes vulpes*, *Bison priscus*, *Cervus elaphus* (Airaghi 1934).

The interest for this locality was emphasized by the almost complete and extensive study on the fauna that characterizes the cave deposit carried out by Vialli (1957). The author notes the presence of some "grotticelle", or natural cavities, containing deposits with angular rocks cemented in a stalagmitic crust.

The main cave, from which the material studied by Vialli's comes, is developed in the Liassic limestone at 370 meters on s.l. Vialli described the cavity as approximately 15 m long and 5 m wide, reachable by a

Fig. 2



- Measurements of the cranium of Panthera (modified by Argant 1998): l) Condylobasal length: aboral border of the occipital condyles Prosthion; 2) Total length: Akrokranion - Prosthion; 3) Basal length: Basion - Prosthion; 4) Basicranial axis: Basion - Synsphenion (= Intersphenoid suture); 5) Basifacial axis: Synsphenion - Prosthion; 6) Upper neurocranium length: Akrokranion - Frontal midpoint; 7) Viscerocranium length: Nasion - Prosthion; 8) Facial length: Frontal midpoint - Prosthion; 9) Lateral length of "snout": oral border of the orbit of one side Prosthion; 10) Median palatal length: Staphylion -Prosthion; l0a) Palatal length: the median point of intersection of the line joining the deepest indentations of the Choanae - Prosthion; 11) Length of the cheektooth row (measured along the alveoli on the buccal side); 12) Length of the premolar row (measured along the alveoli on the buccal side); 13) Length of P⁴. Taken from the buccal part of the cingulum; 14) Length of the carnassial alveolus. Not shown in Fig. 1; 15) Greatest diameter of the auditory bulla: from the most aborolateral point to the most oromedial point; 16) Least diameter of the auditory bulla: from the middle of the opening of the external acoustic meatus up to the most medial protrusion of the bulla on the apposite side of the bulla; 17) Greatest mastoid breadth = greatest breadth of occipital triangle: Otion -Otion; 18) Greatest breadth of the occipital condyles; 19) Greatest breadth of the foramen magnum; 20) Height of the foramen magnum: Basion - Opisthion; 21) Greatest neurocranium breadth = greatest breadth of braincase: Euryon - Euryon; 22) Zygomatic breadth: Zygion - Zygion; 23) Frontal breadth: Ectorbitale - Ectorbitale; 24) Least breadth between the orbits: Entorbitale - Entorbitale; 25) Greatest palatal breadth: measured across the outer borders of the alveoli; 26) Breadth at the canine alveoli; 27) Least breadth aboral of the supraorbital processes = breadth of the postorbital constriction; 28) Facial breadth between the infraorbital foramina (least distance); 29) Greatest inner length of the orbit: Ectorbitale - Entorbitale; 30) Greatest inner height of the orbit; 31) Height of the occipital triangle: Akrokranion - Basion; 32) Neurocranium capacity; capacity of braincase (cc); 33) Breadth between outer borders of M1 alveoli.

narrow vertical chimney. This cave was registered in 1981 (Paganoni & Zambelli 1981) with the acronym LoBG 1347 and it has been known as "Grotta delle ossa". The stratigraphy (Vialli 1957) consists of the following elements, from the top: 1- tawny mould, with rare pebbles and Holocene fauna; 2- "crostone travertinoso" dated to the Pluvial Wurmian, with rare red deer bones; 3- ossiferous rubble, chaotic disposition, thickness approximately 1.2 m. Faunal elements: elephant, rhinoceros and *Emys*; 4- calcareous alabaster; 5- bottom of the cavity.

The faunistic association described includes: Emys orbicularis, Ursus arctos fossilis (recte Ursus arctos), Ursus cf. spelaeus, Felis pardus (recte Panthera pardus), Sus scrofa, Bison priscus, Capreolus capreolus, Capreolus pygargus (recte Capreolus capreolus), Cervus elaphus, Dicerorhinus mercki (recte Stephanorhinus kirchbergensis), Elephas antiquus, Lepus cf. europaeus and the two taxa

determined by Airaghi (1934) *Hyaena crocuta spelaea* (recte *Crocuta crocuta spelaea*) and *Vulpes vulpes*. This association would indicate a rather warm climatic condition with winters warmer than today. The ancient elephant and Merck's rhinoceros association would indicate a probable Eemian age for the Zandobbio fauna.

The bones were recovered from the rubble layer: they are strongly fragmented and only the short ones were found complete. According to Vialli (1957), the paleontological material seems to have been transported inside the cave by water flows.

Both Airaghi (1934) and Vialli (1957) agree that the Zandobbio rubble finds are extremely fragmented and reworked, while MCSNB 5127, although composed of more fragments, is in a good state of preservation without traces of transport. In spite of its better preservation, it seems likely that MCSNB 5127 came from the "Grotta delle Ossa" as well, although it is not possible

to know its exact stratigraphic position. In light of this consideration it is likely that MCSNB 5127 came from a sheltered corner of the cave, probably located not far from Vialli's excavation. However, it is possible to connect with good approximation MCSNB 5127 to the faunal association described by Vialli (1957) for two main reasons: 1- morphologic and morphometric analyses indicate that MCSNB 5127 can be dated to the Eemian, and therefore belongs to the same temporal range as the fauna described; 2- in the quarry of the Zandobbio area there are no reported cavities with faunal remains more recent than those described by Vialli (1957), excluding the clearly Holocene "faunetta" described by Maviglia (1955).

The advanced state of fossilization of MCSNB 5127 excludes the possibility that the skull might belong to the Holocene fauna; based on present knowledge, it is very likely that MCSNB 5127 belongs to the described Eemian fauna (Vialli 1957).

Systematic Palaentology

Order **Carnivora** Bowdich, 1821 Family Felidae (Gray, 1821) Subfamily Felinae Simpson, 1945 Genus *Panthera* Oken, 1816

Panthera leo spelaea (Goldfuss, 1810)

Material. The material studied is an almost complete skull of a lion-like cat, lacking the lower jaw, the two canines and a few other teeth. The material is kept in the Museo Civico di Storia Naturale "E. Caffi" of Bergamo (MCSNB 5127).

Metric analysis was carried out according to Driesch (1976), with the accuracy of 0.1 mm (Fig. 2, 3). For the metric comparative analysis of the skull and teeth data present in the literature were used, mainly Anelli (1954), Argant (1991), Boule (1906), Fabiani (1919), Gužvica (1998), Koby (1946), Leonardi (1935), Piccoli et al. (1979), Sala (1990), Schütt (1969), Schütt & Hemmer (1978). For extant lions, measurements were taken by the author on specimens stored in the Museo Civico di Storia Naturale of Milano (MCSNM 4308, MCSNM 4310 and MCSNM 6384).

Description

Skull Morphology. MCSNB 5127 shows a short muzzle, great extension of the temporal and orbital fossae and wide zygomatic arches. These features are typical of large panthers (Argant 1998). Moreover, the splanchnocranium is convex with respect to the ectorbital protuberances. The neurocranium shows a straight profile letting down posteriorly. The acrocranium projection extends posteriorly to the occipital condyles. The cranial sutures are easy visible and the sagittal crest is very marked. Both lateral profiles (Pl. 1 - B, C) lack

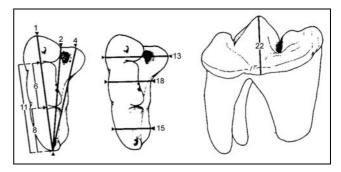


Fig. 3 - Measurements of the fossils lions upper carnassial (P⁴) tooth (modified by Sala 1990): 1) Total length of the P⁴; 2) Length of P⁴ measured from the anterior recess; 3) 2 x 100/1; 4) Length of P⁴ measured from the deuterocone; 5) 4 x 100/1; 6) Length of paracone; 7) 6 x 100/1; 8) Length of the metacono; 9) 8 x 100/1; 10) 8 x 100/6; 11) Length of the paracone + metacono; 12) 11 x 100/1; 13) breadth across the deuterocone; 14) 13 x 100/1; 15) Greatest posterior breadth; 16) 15 x 100/1; 17) 15 x 100/13; 18) breadth in the back of deuterocone; 19) 18 x 100/1; 20) 18 x 100/

the bone portion between frontal and sphenoid forming the orbital septum. Other small gaps are present as well. Many bone fragments are missing on the left side after the ectorbital, in the point of maximum opening between the parietal and the temporal bones, and in the posterior part of the parietal bone. On the right side a small bone fragment is missing posterior to the ectorbital bone and a large one along the squamosal suture.

The ventral portion of the skull is well preserved (Pl. 1 - D), with only two small gaps. The first of these is on the right maxillary bone near the third premolar and the second is on the posterior portion of the palatal bone. The auditory bullae are well preserved, except for a small hole on the left one. They are antero-posteriorly lengthened and latero-mesially narrow.

Dentition. Only the following teeth are present: right I², I³, P³, left I³, P³, P⁴. The alveoli of missing teeth are well preserved. The canine alveoli are slightly fractured laterally. The state of wear of the teeth is not advanced, in particular the incisors show wear only on the main cusp; in the right I² the wear forms a half-moon shape under which it is possible to observe the dentine; in the same tooth the small external cusp is slightly worn. Both I³ show the dentine on the main cusp. Both P³ are slightly worn on the protocone, while P⁴ shows the wear on the paracone and a small fracture in the lingual part of the tooth metacone.

Morphologic and Morphometric skull analysis

Morphologic analysis of MCSNB 5127 shows the following peculiarities: 1- the line connecting the frontal apophyses of the maxillary is placed posterior to the Nasion (Pl. 1 - A); 2- the nasal bones are flat and weakly

N°	MCSNB 5127	Pocala 25260	Pocala 25262	Pocala (1929 univ. Bologna)^	AZE.K.13.29*	Gailenrenth^	Herm ^o	Cajarc°	Vence ^o	MCSNM 4310 Panthera leo leo	MCSNM 6384 (female) Panthera leo leo	MCSNM 4308 Panthera leo leo	
1	324,2	370	311		417,4			393	354	356,5	290,3	371,3	
2	295,6	354	311	360	368,6	362	350	350	320	320,8	259,3		
3	281,0	330	264,9	337	347,7					304,3	241,6	309,2	
4					106,4					142,4	130	140,8	
5					247,5					161,6	141,3	169,6	
6	160,9				207,9								
7	140,9				172,6					174,9	138,9	181,6	
8	185,9				233,8					170,3	140,3	173,3	
9	128,3				162,5					206,9	171,9	215,8	
10		175 *	161		181,0					143,5	120,4	147,5	
10a	159,4		J.								9		
11	73,6	67	66,7		89,3 - 86,3					78,5	70,8	75,5	
12	71,1				84,2 - 84,9					74,6	68	72,5	
13	36,3	37	34			41		37	39	36,3	33,3	35,9	
14	36,2									35,7	32,5	37	
15	46,7				54,0 - 51,0					47,1	46,3	54,7	
16	28,3				34,0 - 34,4					28,4	30,5	32,7	
17	130,1	147,4	119		162,5					136	113,9	144,9	
18	60,1				74,0					67,1	57,5		
19	27,4	33	27,6		32,6					32,8	26,9	29	
20	24,4	30	23		27,0					19,5	19	18,1	
21	93,9 *				111,3					108,6	92,9	113,3	
22	225,1	264	225	253	283,4	276	245	265	241	234,6	201,6	254,2	
23	100 *	107 *	95,5	102*	133,9					108,9	99,1	125,3	
24	71,5				93,0			70,0	100,0	72,4	59,9	78,2	
25	135,1	141	108		143,3					127,6	121,1	105,3	
26		104	88							53,7	48,3	52,2	
27	62,6				95,3					59,7	64	67,1	
28	96,7	99	67		121,2					95,1	84	96,4	
29	60,7	72	59		79,5 - 80,5					69,1	63,7	74,1	
30	47,2	57	46,5		54,0 - 45,3					48,9	46,2	48,1	
31	100,2		,.		126,5					105,8	85,8	104,2	
32	,=									,.	00,0	,2	
33	118,8	124,5	101							132,3	121,8	118,4	

Tab. 1 - Data of lions skulls taken as described in fig. 1 (in mm). [* Argant (1998); ° Boule (1906); ^ Anelli (1954)].

convex towards the frontal end; 3- the opening of the nasal fossae is relatively wide, with a regular increase from ventral to dorsal (Pl. 1 - E); 4- the frontal bones produce a large and flat inter-orbital space: this feature contributes to confer a wide and flat aspect to the forehead both transversally and antero-posteriorly.

Comparisons of MCSNB 5127 dimensions with data found in the literature (Boule 1906; Argant 1998; Piccoli et al. 1979; Anelli 1954), clearly show that the skull belonged to a lion of small size (Tab. 1; Fig. 4).

Differences in size due to pronounced sexual dimorphism is a characteristic of large felines in general, and the lion is no exception (Kurten 1985). In fact, specimens more than 2 years old may be readily sexed on the basis of skull and canine tooth measurements (Smuts et al. 1978). Sexual dimorphism in Pleistocene

European lions has been noted by many authors and Turner (1984) demonstrated this based on morphometric features of canines and first lower molars. Turner's study shows that, as in extant lions, females are smaller than males. So, due to its small dimensions, MCSNB 5127 could be interpreted as belonging to a female (Fig. 4).

The auditory bullae are well developed, and the greater diameter, measured from the most aborolateral point to the most oromedial point, and the smaller diameter, measured from the middle of the opening of the external acoustic meatus to the medialmost protrusion of the bulla on the opposite side of the bulla, shows a ratio of 1.65.

MCSNM 4308 and MCSNM 4310 show similar values, 1.67 and 1.66 respectively, whereas Aze (1.56) and MCSNM 6384 (1.52) have lower values.

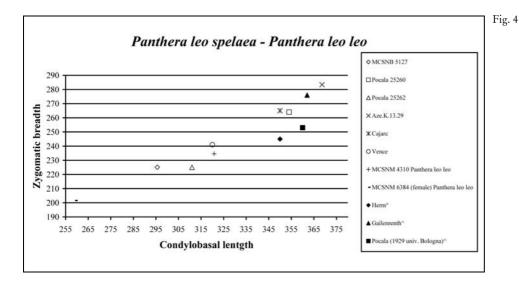


 Diagram (condylobasal length vs zygomatic breadth) underlines a clear samples division in two dimensional groups easily interpreted as sexual dimorphism. MCSNB 5127 falls in the female group (measurements expressed in mm).

		MD	VLM	HC
MCSNC 5127	S	24,1	13,6	11,8
MCSNC 3127	D	24,2	13,7	12,4
AZE.K.13-29°	S	29,3	13,1	17
AZE.K.13-29°	D	30,6	13,6	15
Panthera leo MCSNM 4310	S	24,5	12,7	13,1
Panthera leo MCSNM 6384	S	23	10,9	13,5
Panthera leo MCSNM 4308	S	27,7	13,8	15,3
	n	3	3	1
Panthera leo fossilis ³	min- max	23,8-29,3	14,5-19,2	17,2
	M	26,7	16	
	n	8	8	3
Panthera leo spelaea ³	min- max	25,4-28,6	13,5-16,8	15-16
	M	26,5	14,5	11,8 12,4 17 15 13,1 13,5 15,3 1 17,2
Panthera leo spelaea (Pocala Ind. I)"		28	13	
Panthera leo spelaea (St- Brais I)'		24,8	12,9	13
Panthera leo spelaea (Pocala 25260)"		28	12	
Panthera leo spelaea (Pocala 25262)"		24	11	
Panthera leo spelaea (Pocala)•		27,3	14,5	12,5

Tab. 2 - Data of lions P³ (in mm). (° Argant (1988); ³ Schütt (1969); " Leonardi (1935); ' Koby (1946); Piccoli et alii (1979); • Fabbiani (1919); MD= mesiodistal diameter; VLM= vestibulo-lingual mesial diameter; HC= crown heigth).

Dental analysis

The third premolars have a small anterior accessory cusp connected mesially by a small ridge to the main cusp. Distally to the main cusp there is a posterior accessory cusp which has a basal cingulum on its lingual side.

The third premolars of MCSNB 5127 are on average smaller than third premolars of *P. leo fossilis* and *P. leo spelaea* (Schütt 1969), but they fall in the range of *P. leo* (Tab. 2). Third premolars of St-Brais I [erroneously determined as second premolars by Koby (1946)] and Pocala 25262 (Piccoli et al. 1979) show comparable measurements (Tab. 2). The small size of the third pre-

molars may support the attribution of MCSNB 5127 to a female individual.

The fourth upper left premolar is the only preserved carnassial tooth. Also in this case, measurements of MCSNB 5127 were compared with data from the literature (Schütt 1969; Piccoli et al. 1979; Sala 1990; Gužvica 1998; Argant 1998). All data are shown in Tab. 3.

The main observations concern the metacone/paracone relationship. Many researchers (Schütt 1969; Sala 1990) consider this feature important in separating middle and upper Pleistocene lion-like cats. The MCSNB 5127 fourth premolar has a metacone/paracone ratio (107.6) that is very similar to that of the typical lion-like cats of the upper Pleistocene, where the metacone is more developed than the paracone (Tab. 3).

In particular, the carnassial of MCSNB 5127 shares this feature with other specimens such as Broion 228 (105.1), Broion 226 (117.4), Pocala 25250 (105.6), Pocala 25262 (106.1), Vindija 318/car (112.2), Velica pecina 143/car "K"(104.4) and Cannita (106.2), while Isernia (96.6) and Veternica 600/car "f"(91) have a different ratio, with the paracone more developed than the metacone.

According to Sala (1990) and Schütt (1968), the opposite dimensional relationship would be typical of the lower and medium Pleistocene lions. According to these authors, the rather sinuous aspect of the tooth profile of MCSNB 5127 in occlusal view is another typical feature of upper Pleistocene lions. On the other hand, they believe that a rectilinear profile is typical of the geologically older lion-like cats (Fig. 5).

The tooth total length is not a useful character for distinguishing the primitive from the advanced form of lion (Sala 1990). The MCSNB 5127 carnassial tooth shows rather small absolute dimensions related, as just discussed, to its sexual attribution (Tab. 3).

Panthera leo MCSNM 4310		36,20	34,30	94,75	34,80	96,13	14,90	41,16	12,80	35,36	85,91	28,00	77,35	17,70	48,90	12,00	33,15	67,80	13,60	37,57	76,84	29,06	20,20	55,80	/	/
Panthera leo Panthera leo Panthera leo MCSNM MCSNM MCSNM 4308 6384 4310		33,50	31,50	94,03	32,40	96,72	12,10	36,12	12,70	37,91	104,96	25,10	74,93	16,40	48,96	10,00	29,85	86,09	12,60	37,61	76,83	126,00	18,50	55,22	3,60	10,75
Panthera leo MCSNM 4308		36,30	34,00	93,66	35,80	98,62	13,90	38,29	13,10	36,09	94,24	26,70	73,55	18,60	51,24	11,40	31,40	69'18	15,20	41,87	81,72	133,33	20,80	57,30	5,20	14,33
laea ³	M	39,3	37,9	5'96	38,7	9,86	15,3	38,9	15,6	39,6	6,101	29,6	75,5	9,61	6,64	14,9	38		14,2	36						
Panthera leo spelaea³	min-max	35,5-41,4	34,8-41,2	94,8-99,5	35,7-41,6	95,5-100,5	14,0-16,9	36,8-40,8	14-16,9	37,5-41,7	96,7-112	27-32,1	73-77,9	18-21,4	46-53	13,7-16,4	34-41,5		12,9-15,1	33-38,4						
Pan	u	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6		6	6						
ssilis ³	M	39,9	37,8	96,5	40,1	99,4	15,4	38,7	15,2	37,2	95,3	29,8	74	19,6	50,5	15,3	38,8		14,8	37,1						
Panthera leo fossilis ³	min-max	36,4 - 45,1	35,5 - 42,6	95,7 - 97,5	36,4 - 44,9	98,7-100,0	14-17,5	37-40,1	13,8-16,8	35,9-39,5	95-98	27,3-32,7	72,5-76	18,3-21,7	48,8-51,8	14-17,3	37,7-39,5	0 5	13-17,8	36-40						
	п	9	4	4	5	5	9	9	9	5	5	5	5	4	4	9	5		9	9						
Panthera leo fossilis	Iscillia	39,4	36,5	6'06	37,7	95,6	15,0	38,1	14,5	36,8	9,96	28,9	73,3	20,8	52,7	14,3	36,2	68,7	14,0	35,5	67,3	0,86	19,5	49,4	7,1	18,0
Pointe de bois G		43,6	42,2	8,96	42,0	6,96	15,6	35,8	16,3	37,4	104,5	31,7	72,7	22,6	51,8	17,6	40,4	6,77	16,5	37,8	73,0	93,8				
13-29°	D	41,3	40,0	8,96	40,9	0,66	15,5	37,5	15,7	38,0	101,2	31,6	76,5	22,8	55,2	17,7	42,8	77,6	15,8	38,2	69,3	89,3				
AZE.K.13-29°	S	41,3	40,0	8'96	40,8	98,7	15,7	38,0	15,5	37,5	98,7	31,3	75,7	23,0	55,6	17,6	42,6	76,5	16,1	38,9	70,0	5,16				
143/car "K" Velica pecina¹		36,3	34,6	95,3	35,1	2'96	13,5	37,2	14,1	38'8	104,4	27,2	74,9	17,2	47,4	13,4	36,9	9,11	32,0							
318/car 600/car "f" Vindija¹ Veternica¹		41,5					16,7	40,2	15,2	36,6	91,0			19,4	46,7	17,0	41,0									
318/car Vindija¹		39.7	36,4	7.16			13,9	35,0	15,6	39,3	112,2	29,3	73,8			13,9	35,0		14,1	35,5		101,4				
317/car "H" Vindija¹		42,3	39,8	94,1	42,1	5,66	16,5	39,0	9,91	39,2	9,001	31,3	74,0	21,3	50,4	16,2	38,3	76,1	15,0	35,5	70,4	97,6				
Cannita *		37,8	35,1	92,8	36,2	8,56	14,5	38,3	15,4	40,7	106,2	29,7	9,87	18,8	49,7	13,0	34,4	1,69	12,5	33,1	66,5	1,96	9,81	49,2	4,8	12,7
25251 25250 25262 Pocala 2 Pocala 2		33,7	31,4	93,1	32,6	2.96	13,0	38,6	13,8	40,9	100,1	25,7	76,3	17,3	51,3	11,4	33,8	62,9	11,3	33,5	65,3	1,66	14,2	42,1		
25250 Pocala 2		37,5	35,3	94,1	36,0	0,96	14,2	37,9	15,0	40,0	9,501	29,0	77,3	21,0	999	15,0	40,0	71,4	14,5	38,7	0,69	2'96	17,5	46,7		
25251 Pocala ²		37,5	35,3		37,3		15,6		>14			30,0		21,0		15,0			14,6				18,0			
226 IGPC83 Broion* Pocala 2		38,4	35,0	91,1	36,4	8,46	14,6	38,0	14,7	38,3	100,7	28,2	73,4	21,2	55,2	14,9	38,8	70,3	15,0	39,1	70,7	9,001	19,7	51,3		
226 Broion*		41.1	38,6	93,3	40,1	9.76	14,4	35,0	6,91	41,1	117,4	30,0	73,0	22,0	53,5	15,9	38,7	72,3	14,7	35,8	8,99	92,4	19,0	46,2		
228 Broion*		41,7	38,9	93,3	40,0	6'56	15,8	37,9	9'91	39,8	105,1	31.5	75,5	22,1	53,0	16,0	38,4	72,4	13,9	33,3	67.9	6'98	21,0	50,3		
N° MCSNC 5127		36,6	34,4	93,9	34,5	94,3	13,2	36,1	14,2	38,8	9,701	27,0	73,8	17,0	46,4								15,5	42,3		
ž		-	2	3	4	5	9	7	8	6	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25

Tab. 3 - Data of lions P⁴ taken as described in fig. 2 (in mm). [* Sala (1990); ° Argant (1988); ¹ Gužvica (1998); ² Piccoli et al (1979); ³ Schütt (1969)].

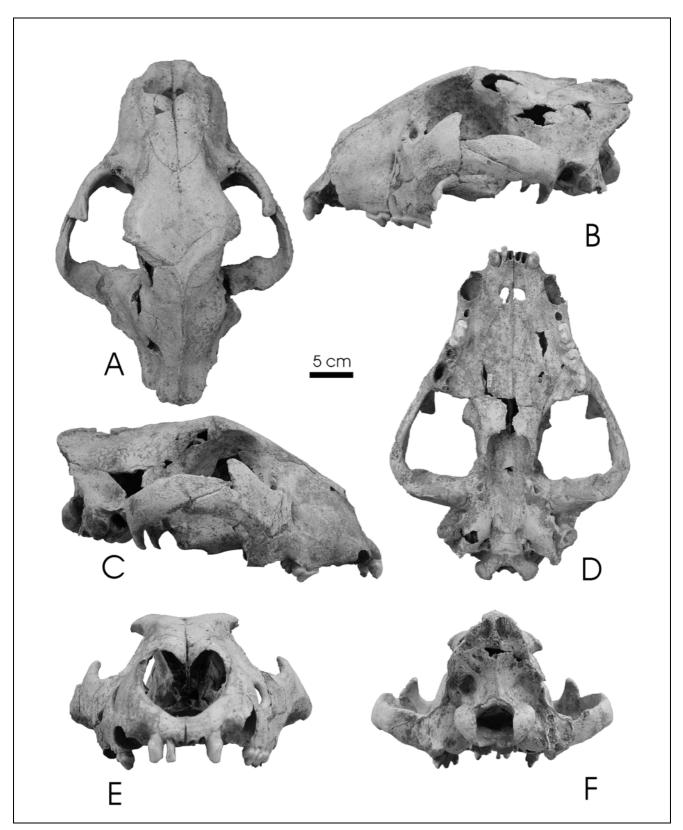


PLATE 1

Panthera leo spelaea (Goldfuss, 1810) MCSNB 5127: A- Dorsal view; B- left side; C- right side; D- Ventral view; E- anterior view; F- posterior view.



Fig. 5 - Panthera leo spelaea (Goldfuss, 1810) MCSNB 5127: left fourth upper premolar: occlusal view (total length: 36.6 mm).

Conclusions

The analysis of the morphometric and morphologic features of MCSNB 5127 and the peculiarity of its left carnassial tooth supported the attribution of MCSNB 5127 to *P. leo spelaea* (Goldfuss 1810), the subspecies of lion-like cats present in Europe during the Upper Pleistocene (Schütt 1969).

The relatively small dimensions suggest that the specimen probably belonged to a female lion.

In this paper MCSNB 5127 was attributed to *P. leo spelaea* (Goldfuss, 1810) because the data were insufficient to discuss the phylogenetic position of the lion-like cat or the cave lion. This hypothesis seems to be preferred among scholars also in light of the genetic work of Burgher et al. (2004).

It is important to stress that the presence of *P. leo spelaea* in the Quaternary deposit of Zandobbio is important not only locally. In fact, this is the first report of this great feline at Zandobbio, the second report for Lombardy (Arduini et al. 2001), and the oldest certain

find of *P. leo spelaea* and the oldest complete skull of *P. leo spelaea* known from Italy to date. So it is possible to conclude that advanced *P. leo spelaea* characters were already present in Italy during the Eemian.

Acknowledgements. I am very indebted to Dr. A. Paganoni (Museo di Storia Naturale "E. Caffi" of Bergamo) for giving me the possibility to study this specimen and for her helpfulness.

I am grateful to Dr. F. Confortini and M. Malzanni for their help in the Museo di Storia Naturale of Bergamo, to Prof. B. Sala (Ferrara) and Dr. R. Sardella (Roma) for helpful suggestions on an earlier version of the manuscript, and to Dr. G. Bardelli (Museo Civico di Storia Naturale of Milano) for assistance in the location of modern lion specimens. I thank Dr. L. Werdelin (Stockolm) and Dr. A. Turner (Liverpool) for the critical reading of the manuscript and fruitful suggestions. A special thanks to Dr. C. Lombardo for her advice. English revision by Elisabetta Fois.

REFERENCES

- Airaghi C. (1934) Mammiferi del Quaternario di Zandobbio presso Trescore Balneario (prov. di Bergamo). *Natura*, 25: 63-67, Milano.
- Anelli F. (1954) Contributo alla conoscenza della fauna diluviale della Caverna Pocala di Aurisina (Trieste). *Mem. Serv. Descr. Carta Geol. Italia*, 11: 1-57, Roma.
- Arduini P., Krieger C., Rossi M. & Santi G. (2001) Un femore di *Pantera leo spelaea* dalla Grotta del Buco dell'Orso (Laglio, Lombardia, Italia settentrionale). *Geol. Insubr.*, 6/1: 23-28, Lugano.
- Argant A. (1991) Carnivores quaternaires de Bourgogne. Docum. Lab. Géol. Lyon, 115: 1-301, Lyon.
- Argant A. (1998) Etude de l'exemplaire de *Panthera spelaea* (Goldfuss, 1810) (Mammalia, Carnivora, Felidae) du gisement Pleistocene moyen recent de la grotte d'Aze (Saone et Loire). *Rev. Pal.*, 7: 449-466, Genève.
- Baryshnikov G.F. & Boeskorov G. (2001) The Pleistocene lion-like cat, *Panthera spelaea* (Carnivora, Felidae) from Yakutia, Russia. *Cranium*, 18 (1): 7-24, Culemborg.
- Bon M., Piccoli G. & Sala B. (1991) I giacimenti quaternari di vertebrati fossili nell'Italia nord-orientale. *Mem. Sci. Geol.*, 54: 51-63, Padova.
- Boule M. (1906) Les grands chats des cavernes. *Ann. Palaontol.*, I: 69-95, Paris.
- Burgher J., Rosendahl W., Loreille O., Hemmer H., Eriksson T., Götherström A., Hiller J., Collins M.J., Wes T. & Alt K.W. (2004) Molecular phylogeny of the extinct lion-like cat *Panthera leo spelaea. Mol. Phyl. Evol.*, 30: 841-849, Amsterdam.
- Fabiani R. (1919) I mammiferi quaternari della regione Veneta - *Mem. Ist. geol. Univ.*, 5: 1-174, Padova.
- Groiss J. Th. (1996) Der Höhlentiger *Panthera tigris spelaea* (Goldfuss) *N. Jb. Geol. Paläont. Mh.*, H. 7: 399-414, Stuttgart.
- Gužvica G. (1988) Panthera spelaea (Goldfuss, 1810) from North-Western Croatia - Geol. Croat., 51/1: 7-14, Zagreb.
- Koby F.E. (1946) A propos des grands chats des caverns. *Ecl. Geol. Helv.*, 39: 367-371, Basel.
- Kurtén, B. (1985) The Pleistocene lion of Beringia. *Ann. Zool. Fennici*, 22: 117-121, Helsinki.
- Leonardi P. (1935) Nuovi resti di mammiferi pleistocenici della caverna Pocala (carso triestino). *Atti Mus. Civ. Storia Nat. Trieste*, 13: 1-26, Trieste.

- Maviglia C. (1954) Resti di fauna Pleistocenica rinvenuti a Zandobbio (Bergamo). *Natura*, 46 (3): 120-157. Milano.
- Paganoni A. & Zambelli R. (1981) Catalogo delle grotte settore bergamasco *Riv. Mus. Sc. Nat. Bg.*, III: 1-159, Bergamo.
- Piccoli G., Franco F., Mior S., Bacchin M.L., Maretto P. & Taruna M.F. (1979) Grandi carnivori fossili quaternari conservati nel museo universitario padovano di geologia e paleontologia (macherodonti, leoni, iene, orsi cavernicoli). *Mem. Sc. Geol. Univ. Padova*, 32: 4-21, Padova.
- Riedel A. (1982) Il grande felino della Grotta Tilde (The lion of the Tilde Cave). Atti Mus. Civ. Stor. Nat. Trieste, 34 (1): 9-47, Trieste.
- Sala B. (1990) Panthera leo fossilis (V. Reich, 1906) (Felidae) de Isernia La Pineta (Pléistocène Moyen Inférieur d'Italie). Geobios, 23 (2): 189-194, Lyon.
- Schütt G. (1969) Untersuchungen am Gebiß von *Panthera leo fossilis* (V. Reichenau 1906) und *Panthera leo spelaea* (Goldfuss, 1810). *N. Jb. Geol. Paläont. Abh.*, 134 (2): 192-220, Stuttgart.
- Schütt G. & Hemmer H. (1978) Zur evolution des löwen (*Panthera leo* L.) im europäischen Pleistozän. *N. Jb. Geol. Paläont. Abh.*, 4: 228-255, Stuttgart.
- Smuts G. L.; Anderson J. L. & Austin J. C. (1978) Age determination of the African lion (*Panthera leo*). *J. Zool.*, 185: 115-146, Cambridge.
- Sotnikova M. & Nikolskiy P. (2003) Systematic position of lion-like cat (*Panthera spelaea*)(L) abstract of 3rd International Mammoth conference, Yukon.
- Torre D. (1967) Analisi di alcune differenze nell'apparato masticatorio dei leoni e delle pantere. *Atti Soc. Tosc. Sc. Nat. Mem.*, B, 74: 59-70, Pisa.
- Turner A. (1984) Dental sex dimorphism in European lions (*Panthera leo* L.) of the Upper Pleistocene: palaeoecological and palaeoethological implications. *Ann. Zool. Fennici*, 21: 1-8, Helsinki.
- Turner A. & Anton M. (1997) The Big Cats and their Fossil Relatives. Columbia University Press, 234 pp., New York.
- Vialli V. (1957) I vertebrati della breccia ossifera dell'interglaciale Riss-Würm di Zandobbio (Bergamo). *Atti Soc. It. Sc. Nat.*, 96: 51-75, Milano.