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CANIS LUPUS (MAMMALIA, CANIDAE) FROM THE LATE PLEISTOCENE DEPOSIT OF AVETRANA (TARANTO, SOUTHERN ITALY)

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Abstract. Here we described the remains of *Canis lupus* from the bed 8 of Avetrana karst filling (Late Pleistocene; Taranto, Southern Italy). The studied specimens are larger than those collected from the early Late Pleistocene Apulian localities and those referred to the recent Italian wolf. Moreover, the remains from Avetrana are morphometrically close to *Canis lupus maximus* from France and to *C. lupus* collected from Central and Northern Italian localities, chronologically related to MIS 2 and MIS 3. Morphologically, the studied specimens slightly differ from both *C. l. maximus* and other Pleistocene Apulian wolves. The dimensional differences between the Avetrana wolves and those collected from the other early Late Pleistocene Apulian localities could be explained through a spread of a large-sized morphotype from the Northern Italy.

Introduction

The hypothesis of a strict phylogenetic relationship between the modern wolf (*Canis lupus*) and the small Middle Pleistocene *Canis mosbachensis* is widely accepted in literature (Torre 1967, 1974, 1979; Kurtén 1968; Martin 1973; Sotnikova 1989, 2001; Rook 1993; Brugal & Boudadi-Maligne 2011; Ghezzo et al. 2014; Cherin et al. 2014; Sardella et al. 2014). The earliest record of the modern wolf is reported at Olyor (Siberia) and Cripple Creek Sump (Alaska), Middle Pleistocene in age, suggesting an origin of *C. lupus* in Beringia (Sher 1986; Tedford et al. 2009). The first occurrence of the modern wolf in Europe is at Lunel-Viel (France) with the subspecies *Canis lupus lunellensis* (Bonifay 1971). The site of Lunel-Viel is chronologically related to the Middle Pleistocene, MIS 11-10 (Argant & Mallye 2005; Mallye 2007; Croitor et al. 2008; Boudadi-Maligne 2010; Kahlke et al. 2011). The subspecies *C. lupus santenaiensis* (Santenay site, MIS 6-5), *C. lupus mediterraneus* and *C. lupus maximus* (Jaurens Cave, MIS 3) are also reported (Bonifay 1971; Argant 1991; Brugal & Boudadi-Maligne 2011; Boudadi-Maligne 2012) in the Pleistocene deposits of France. Moreover, according to Brugal and Boudadi-Maligne (2011), a dimensional trend characterizes the Pleistocene wolves.

In Italy, the wolf appears during the late Middle Pleistocene at La Polledrara di Cecanibbio, chronologically related to MIS 9 (Gliozzi et al. 1997; Anzidei et al. 2012; Sardella et al. 2014). The remains of wolf from La Polledrara di Cecanibbio are morphologically similar to the modern wolves collected from the Apennine area.

The modern Italian wolves collected from the Apennine area are referred to the subspecies *C. lupus italicus* (Altobello 1921; Randi et al. 2000; Nowak & Federoff 2002; Nowak 2003; Fabbri et al. 2007; Pilot et al. 2010), however in Italy no subspecies of wolf has been recognized during the Pleistocene and the several Italian remains have not been considered in recent contributions on the morphometric variations of *Canis lupus* during the Pleistocene (cfr. Brugal & Boudadi-Maligne 2011; Boudadi-Maligne 2012; van der Made et al. 2013).

The goal of this paper is to describe the new material of *Canis lupus* from Avetrana (Fig. 1) and to compare it with other Apulian and Southern European

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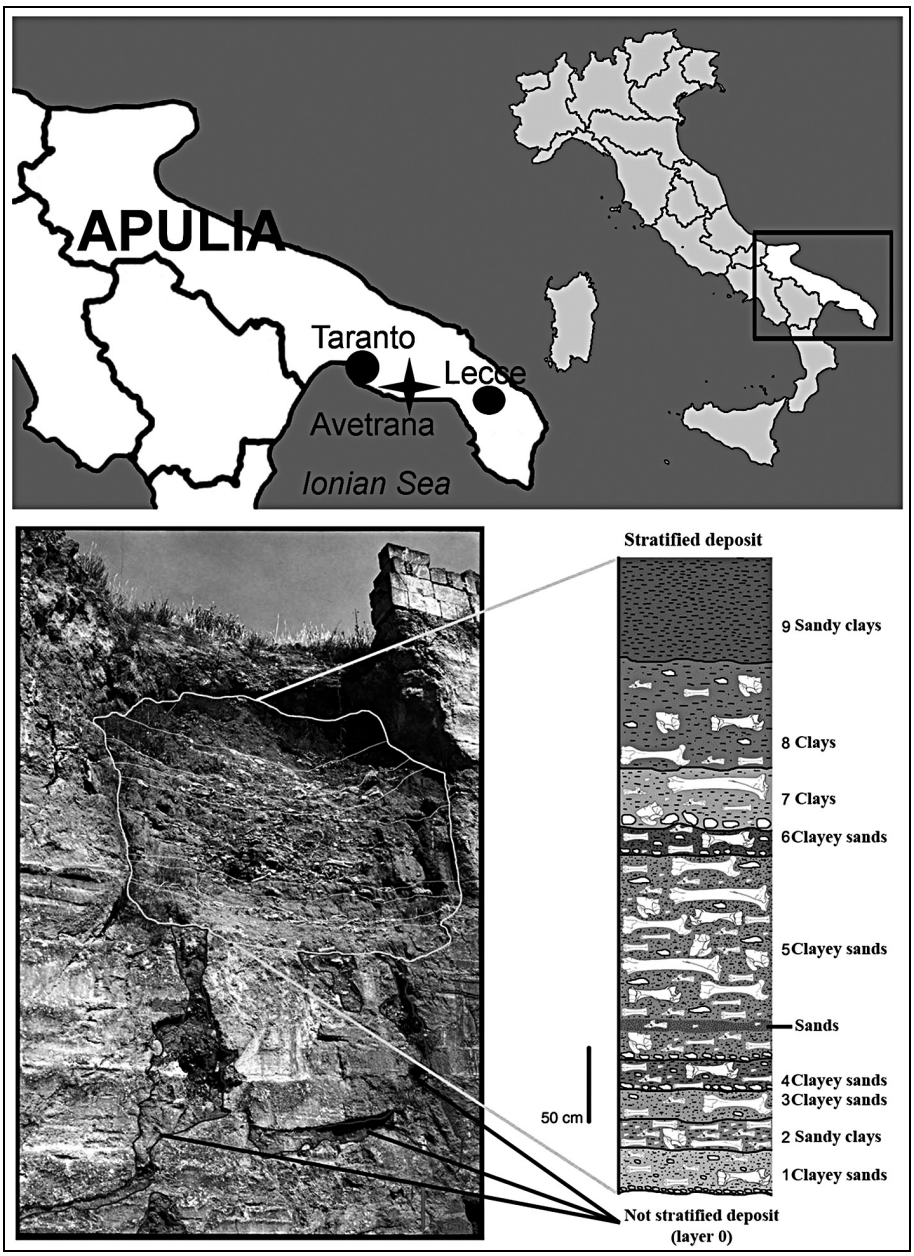

Fig. 1 - Location map of the fossiliferous locality of Avetrana (Taranto, Southern Italy) and stratigraphy of the Avetrana karst filling (from Petronio et al. 2008; Pandolfi et al. 2011, 2013a).

wolves of Late Pleistocene. The results of the morphological and morphometric studies have enabled us to define a new biochronological and palaeobiogeographical framework of the Italian and Southern European wolves.

Geological and palaeontological framework of Avetrana karst filling

The faunal assemblage of Avetrana, chronologically related with the early Late Pleistocene, includes birds such as *Perdix perdix*, *Otis tarda*, *Columba livia*, *Athene noctua*, *Pyrrhocorax graculus* and *P. pyrrhocorax*, and mammals such as *Erinaceus europaeus*, *Terricola savi*, *Hystrix vinogradovi*, *Lepus* cf. *europaeus*, *Oryctolagus cuniculus*, *Canis lupus*, *Vulpes vulpes*, *Meles meles*, *Crocuta crocuta*, *Lynx lynx*, *Felis silvestris*, *Panthera leo*, *Stephanorhinus hemitoechus*, *Hippopotamus amphibius*, *Sus scrofa*, *Dama dama dama*, *Cervus elaphus elaphus* and *Bos primigenius* (Petronio et al. 2008; Pandolfi & Petronio 2011; Pandolfi et al. 2011, 2013a). Petronio et al. (2008) and Pandolfi et al. (2013a) have recognized several layers in the depositional sequence of Avetrana karst filling (Fig. 1). Based on the stratigraphical observations, the deposit of Avetrana can be divided into nine beds and two discrete infillings or pockets (Petronio et al. 2008, Fig. 1). The beds were probably deposited rapidly during a short time span by exceptional events, producing the rapid accumulation of carcasses in the karst cavity (Petronio et al. 2008; Pandolfi et al. 2011, 2013a). The abundance of the remains, many of them still articulated, their state of preservation, the absence of skulls strongly suggest that the remains were accu-

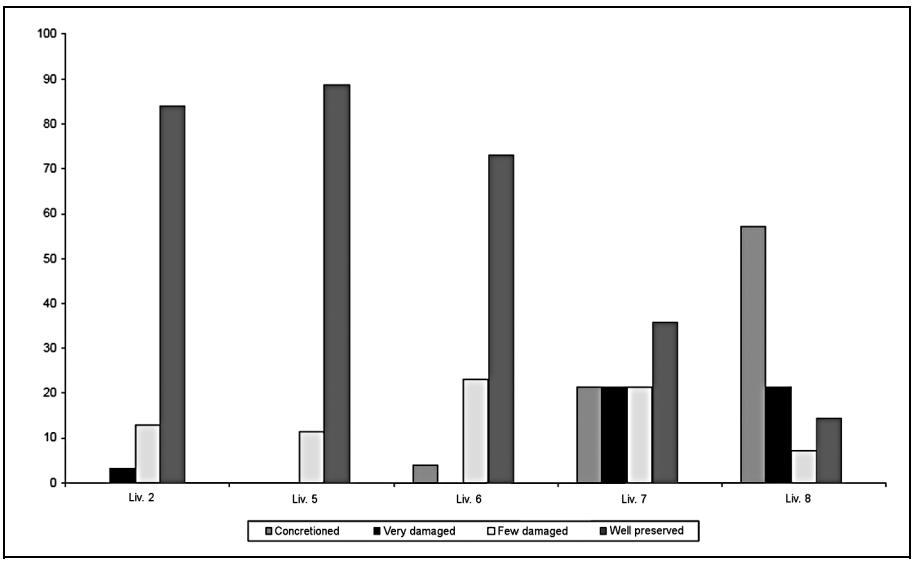

Fig. 2 - Percentages of preservation of the bones and teeth recovered in the different levels of Avetrana (from Pandolfi et al. 2013a).

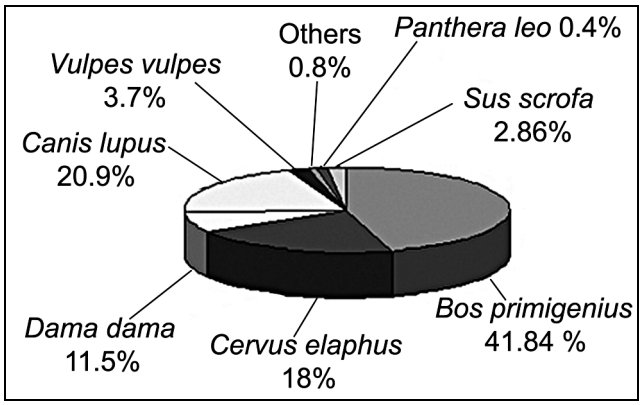

Fig. 3 - Graphic of taxa percentage for level 8 (modified from Petronio et al. 2008).

mulated by water during several catastrophic events in the area (Pandolfi et al. 2013a). In particular, layers 2, 5 and 7 were deposited over a short time and probably each one represents a single depositional event. By contrast, beds 3, 4, 6 and 8, which are characterized by scarce fossil remains and abundant clay-sandy matrix, are interpreted as layers deposited over a longer time span. At last, the bed 8 is characterized by a high percentage of concreted bones and relatively high and a very high percentage of carnivore remains, the wolf in particular (Fig. 2, Fig. 3). The sedimentological characteristics of bed 8, at the top of the stratigraphical sequence, suggest the presence of abundant water (also suggested by the presence of calcareous concretions and the occurrences of two species of Anura and *Arvicola amphibius*: Kotsakis, pers. comm; Kotsakis et al., in prep.). Due to the occurrence of the genus *Microtus* (which occurs in Italy during MIS 4-2: unpublished material, Kotsakis pers. comm.) and of the rhinoceros *Stephanorhinus hemitoechus* (which occurs in Italy until MIS 3: Pandolfi & Petronio 2011; Pandolfi et al. 2013b), the level 8 of the Avetrana karst filling can be interpreted younger in age than the beds 2-7, and referred to a time span between MIS 4 and MIS 3. According to Pandolfi et al. (2013a), the high percentage of wolf in the bed 8 may be due to a common presence in the area of this canid. However, the role of a natural trap of the cavity, where the carnivores could be attracted by the presence of carcasses, has not been deeply ruled out (Pandolfi et al. 2013a).

Materials and methods

Despite the high number of specimens, the remains of *Canis lupus* from Avetrana (Fig. 4) are fragmented and the morphology of the whole skull cannot be observed, therefore our work has been focused on the teeth. The studied material from Avetrana is temporarily stored at Sapienza, Università di Roma and it will be transferred to the Soprintendenza of Taranto (Southern Italy) where the most part of Avetrana findings are currently housed. The specimens included in this study have been collected in the beds 8 of the Avetrana karst filling, during a fieldwork in the winter 2013, and include several fragmented maxillae and hemimandibles, isolated teeth and few fragmented postcranial remains (Tabs 1, 2).

Morphometric data were taken with standard calliper. The measures taken are length and breadth for each tooth, the greatest breadth of P^4 and the talonid length of M_1, as reported by von den Driesch (1976). The Avetrana measurements were compared with fossil wolves from other Late Pleistocene sites of Italy (e.g., Grotta Romanelli, Melpignano and San Sidero, Ingarano, Grotta Paglicci, Buco del Frate) (Tab. 3). A morphometric comparison with the Late Pleistocene wolves from France, reported by Boudadi-Maligne (2010) and Brugal and Boudadi-Maligne (2011), was also carry out (Tab. 3). Data on recent *C. lupus* from the Apennine area were taken from Bertè (2013) and include 115 individuals (52 males and 63 females) belonging to the Italian medium-size subspecies *C. lupus italicus* (Nowak & Federoff 2002; Boitani et al. 2003). All the specimens considered for morphological comparison are reported in Appendix.

All the statistical analysis are performed with the software PAST version 2.08 (Hammer et al. 2001). A Principal Component Analysis (PCA) was performed to visualise variance in teeth measurements across samples using Principal Component vectors. The analyses were run separately for upper and lower teeth. A Multivariate Analysis of Variance (MANOVA) was also performed; it is the multivariate

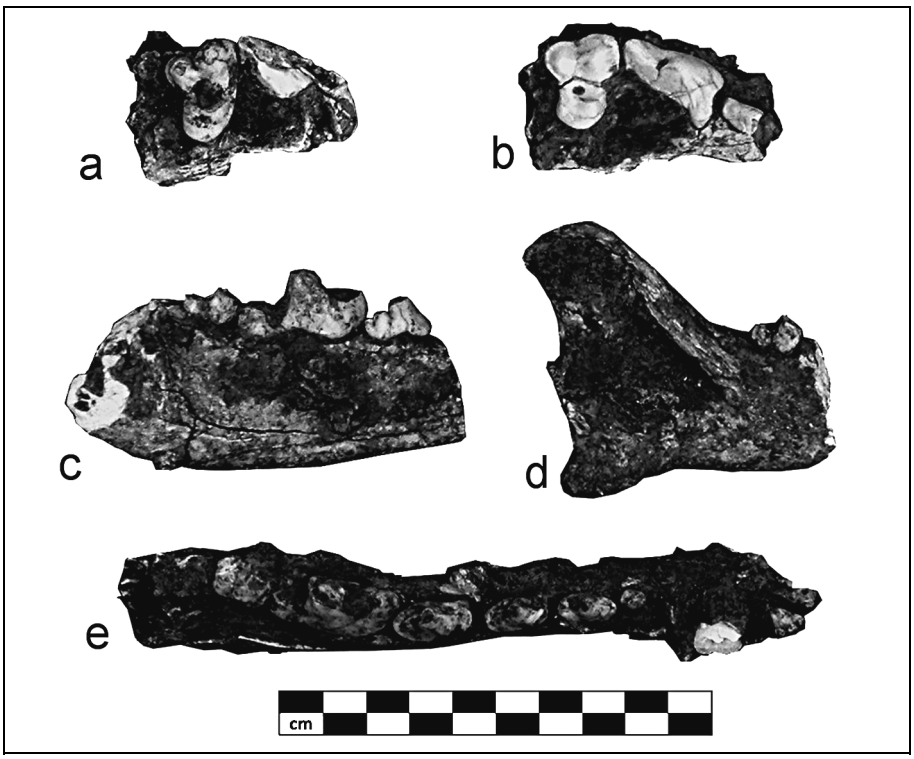

Fig. 4 - *Canis lupus* remains of Avetrana bed 8. A) P4-M1 (A8C9); B) P4-M1 (A8-32); C) P4-M2 (A8C1); D) fragmentary mandible with vertical ramus and M2 (Ave8-10); E) horizontal ramus of mandible with P1-M2 (Ave8-1).

version of the univariate ANOVA, testing whether several samples have the same mean. Wilk's lambda value is reported. If the MANOVA shows significant overall difference between groups, the analysis can proceed by pairwise comparisons. The Bonferroni correction for multiple test is applied and *p* values (multiplied by the number of pairwise comparisons) is reported.

A ANOVA is performed only on PC1. If the ANOVA shows significant inequality of the means (small *p*), is used the "post-hoc" pairwise comparisons, based on Tukey's HSD (Honestly Significant Difference) test. Sample sizes do not have to be equal for the version of Tukey's test used. Sample smaller than five specimens are removed from the analysis.

A discriminant analysis was also performed on the data for confirming or rejecting the hypothesis that two species are morphologically distinct.

Description and morphological comparison

Upper teeth

P^4 of the Avetrana specimens has a round-shaped protocone that is well delineated and isolated from the edge of the tooth. The protocone is anterior-lingually

Tab. 1 - List and measurements (mm) of the upper teeth of *Canis lupus* collected at Avetrana and included in this study. L = length; W = width; W max = maximal width.

N specimen	P4 L	P4 W	P4 W max	M1 L	M1 W	M2 L	M2 W
A8-12				14.5	18.4		
A8-15				15.5	18.8		
A8-16	22.5	9.4	12.5				
A8-65				16.3	18.9		
A8C9	25.5			17.2	21.6		
Ave8-32	24.7	10.6	12.2	16.4	19.6		
Ave8-33	22.6	11.3	12.9	15.3	19.8	8.9	11.9
Ave8-34	22.0	10.8	12.1	16.2	18.0		
Ave8-35	24.5	11.3	13.2				
Ave8-36				18.1	20.6	9.6	12.6
Ave8-37	25.5	10.4	14.2	17.1	19.3		
Ave8-38				14.8	19.1		
Ave8-39				16.8	18.7		
Ave8-40				16.1	19.0		
Ave8-41	25.8	10.4	13.2		21.2	8.8	12.2
Ave8-42	21.7	9.1	12.0				
Ave8-43	22.8	10.0					
Ave8-44	22.3	9.7	13.3				
Ave8-45	25.0		13.5	14.3	19.3	9.2	11.9

N specimen	Lt	Lp	Lm	p1 L	p1 W	p2 L	p2 W	p3 L	p3 W	p4 L	p4 W	m1 L	m1 W	Ltal	m2 L	m2 W	m3 L	m3 W
Ave8-1	98.3	53.0	47.0	5.5	4.9	12.8	6.2	13.9	7.3	17.0	8.7	27.5	11.7	8.9	13.3	9.4		
Ave8-3												27.3	11.2	8.4				
Ave8-4															12.6	9.3	6.0	5.1
Ave8-5			45.3									26.4	11.0	7.6	12.6	9.1		
Ave8-6												30.0	12.0	9.0				
Ave8-7		46.0										28.7						
Ave8-8															11.4	8.2		
Ave8-9												28.0	11.4	8.0				
Ave8-10															12.2	9.3		
Ave8-11								15.0	7.0									
Ave8-12										14.5		27.0	11.9					
Ave8-13												28.1	11.2	9.0				
A8C6										12.5	8.1	31.4	13.0	9.5				
Ave8-14	95.7	50.0	48.4			13.9	6.5	15.0	7.2	17.0	8.4	31.0	12.4	7.8	13.1	9.0		
Ave8-15		49.7										28.8						
A8C1			47.8							15.6	7.7	29.5	11.6	9.7	11.8	8.6		
A8C2			49.0									29.2	12.2	10.0				
A8C3										14.7	7.2	26.0	10.1	9.3				
A8C5										16.5	8.3	29.3	12.1	9.0				
A8-2(16)			45.0									28.2	12.0	8.5	12.5	8.6		
A8C4										15.5	7.7	29.7	11.6	9.0				
Ave8-16										15.8	7.3	27.8						
Ave8-17															11.5	8.1		
Ave8-18						12.6	5.4	14.0										
A8-11						11.5	6.1											
Ave8-19													11.6					
Ave8-20										15.8								
Ave8-21						13.0	6.0	15.2	6.6									
Ave8-22						13.6	6.0											
Ave8-23														8.1				
Ave8-24															11.1	8.2		
Ave8-25						11.0	5.7											
Ave8-26						12.6	6.1	13.8	6.8									
Ave8-27			45.0												12.6	9.2		
Ave8-28			47.5							16.0	8.3	28.5	12.0	8.5				
Ave8-29						11.1	6.0	13.4	6.8									
Ave8-30						11.6	6.3	13.2	6.4									
Ave8-31						13.7	6.1											
A876						13.0	5.5											
A84								14.2	5.7									

Tab. 2 - List and measurements (mm) of the lower teeth of *Canis lupus* collected at Avetrana and included in this study. Lt = length of the tooth row; Lp = length of the premolars; Lm = length of the molars; L = length; W = width; Ltal = length of the talonid.

oriented and makes an obtuse angle with the anterior rim of the paracone. Moreover, P^4 displays a little concavity in the labial side between the paracone and the metastyle; the ridge of the paracone, in anterior direction, is well delineated and marked.

The protocone of the P^4 is rounded as in modern wolves and in the Late Pleistocene Apulian specimens, whereas the specimens from Jaurens have a tight protocone, pointed and more lingually oriented on the palate.

In M^1 the paracone is clearly larger than the metacone; the protocone is well developed, whereas the metaconule is little developed, the basin is not much deep, the hypocone is well developed but lesser high than the protocone. The hypocone is broad around the talon and joined with the dental cingulum; the metaconule is evident.

In the sample here considered, M^2 is well separated from M^1 and the only contact point is at the level of the metacone of M^1. M^2 is separated from the M^1 as in the all specimens of Grotta Romanelli. In the modern wolf, the contact point between M^1 and M^2 is along their whole lateral side. In the occlusal view, the M^2 is sub-rectangular, the paracone is more developed than the metacone, the protocone and the metacone are not much tall and the basin does not appear deep.

Area	Site	Age	MIS	References
Italy	Melpignano and San Sidero	Late Pleistocene	5a–5b	Bertè 2013; Sardella et al. 2014; this work
Italy	Grotta Romanelli	Late Pleistocene	4–3	Cassoli et al. 1994; Sardella et al. 2014; this work
Italy	Avetrana	Late Pleistocene	4–3	Petronio et al. 2008; Pandolfi et al. 2013a; this work
Italy	Veja grotta A	Late Pleistocene	3	this work
Italy	Pocala	Late Pleistocene	3	this work
Italy	Buco del Frate	Late Pleistocene	3	Bona pers. com.; this work
Italy	Ingarano	Late Pleistocene	3	Bertè 2013; Sardella et al. 2014; this work
Italy	Grotta Sant'Agostino	Late Pleistocene	3	Tozzi 1970; this work
Italy	Grotta di Ladrenizza	Late Pleistocene	3	this work
Italy	Grotta Mora Cavorso	Late Pleistocene	2	Salari et al. 2011; this work
Italy	Covoli di Velo	Late Pleistocene	2	this work
Italy	Grotta Paglicci	Late Pleistocene	2	Bartolomei 1975; this work
Italy	Grotta Bella	Holocene, ancient	1	Guerreschi et al. 1992; this work
Italy	Colle Cappuccini	Holocene, ancient	1	Wilkens 1990; this work
Italy	Central Italy, Apennine area	Holocene, recent	1	Bertè 2013, this work
France	Aven de l'Arquet	Late Pleistocene	3	Boudadi-Maligne 2010, 2012; Brugal & Boudadi-Maligne 2011
France	Jaurens	Late Pleistocene	3	Boudadi-Maligne 2010, 2012; Brugal & Boudadi-Maligne 2011
France	Maldidier	Late Pleistocene	3	Boudadi-Maligne 2010, 2012; Brugal & Boudadi-Maligne 2011
France	Igue du Gral	Late Pleistocene	2	Boudadi-Maligne 2010, 2012; Brugal & Boudadi-Maligne 2011

Tab. 3 - List of the fossiliferous localities yielded remains of *Canis lupus* included in this study.

Lower teeth

P_2 possesses just only the principal cusp and does not have any secondary cusps or cingulum; the principal cusp is vertically oriented and located in the anterior half of the teeth.

The secondary cusp on P_2 is present in some specimens from Melpignano (e.g. in the specimens MPE2 and MPD4. See Appendix for more details), but it is absent in the specimens from Grotta Romanelli. The secondary cups occurs in several specimens of modern wolf but it is not always evident.

P_3 has a principal cusp, a secondary cusp, and a little mesial accessory cusp developed from the cingulum.

The principal cusp on P_4 is high as the paraconid of M_1. Two secondary cusps are present in mesial position. The small cusp is developed from the rising of the dental cingulum. It can also be observed on P_4 in some specimens from Romanelli and Melpignano (e.g. in the specimens R3592 and MPE2. See Appendix for more details). In occlusal view, the tooth is massive and wide and lingually extends, near second cusp, is present.

In the modern wolf, as it occurs in the specimens of Avetrana, this cusp is usually absent. The talonid on M_1 is short respect to the length of the trigonide, the metaconid is poorly developed, small, low, and not well-isolated from the protoconid. The hypoconid and the entoconid are well-delineated, whereas the entoculid is not well evident or absent. The metaconid of M_1 is always well-marked and isolated from the protoconid as occurs in the modern wolf.

In occlusal view, M_2 is sub-squared, the protoconid and the metaconid are well-marked and similar in size, the hypoconid is slightly taller than the protoconid and the entoconid is not well clear. The entoconid of M_2 is well evident in the specimens of Avetrana, whereas it is absent or poorly developed in some specimens from Melpignano (e.g. in the specimen MPE2. See Appendix for more details) or in the modern wolves.

Mandible

The mandibles are generally fragmented and none is completely preserved. The mandibular ramus is high and the masseteric fossa is much deep. In occlusal view, the tooth row is S-shaped as appears in the modern wolves.

Morphometric comparisons

Comparison with fossil specimens

For the upper teeth, the analysis was limited to the jugal teeth. The MANOVA analysis show that the differences between mean are significant (Wilk's lambda: 0.1277; p: 1.397E-09). MANOVA revealed that the Avetrana wolves differ from those of Grotta Romanelli (p-value= 0.0018) and Melpignano (p-value = 0.0007) but not from those of Ingarano (p-value = 0.0688) and San Sidero (p-value = 0.9064) (Tab. 4). A discriminant analysis, performed to test the differences between the Avetrana specimens and the other fossil wolves, is significant (p= 0.00268) and the specimens correctly classified are 80,6%. The PCA performed on the upper teeth shows similar differences (Fig. 5; Tab. 6). The first component PC1 (on the horizontal axis) accounts for the 68,43% of the total variance, and has is loadings for the length of P^4. The second component (vertical axis) explain 16,57% of the variance and is mainly influenced

Tab. 4 - Comparative dimensions (mm) of the upper teeth of *Canis lupus* of Avetrana and those of several Southern Italian localities and Apennine area.

Site		P4 L	P4 B	GB P4	M1 L	M1 B	M2 L	M2 B
Melpignano/San Sidero	Mean	21.9	8.7	11.1	13.1	16.7	8.3	12.1
	N	9	9	8	5	5	3	3
Grotta Romanelli	Mean	22.1	8.9	10.8	13.9	17.0	8.3	12.0
	N	5	5	3	6	6	6	6
Veja Grotta A	Mean	27.0	10.7	13.0	16.4	19.0	10.0	13.6
	N	1	1	1	1	1	1	1
Buco del Frate	Mean	26.0	10.6	13.9	16.0	19.3	8.9	13.1
	N	13	13	13	11	11	6	6
Ingarano	Mean	23.5	9.0	12.2	14.7	18.1	8.7	12.0
	N	5	5	5	7	7	4	4
Grotta Sant'Agostino	Mean	24.9		13.2	17.3	22.0		
	N	3		2	3	3		
Grotta Ladrenizza	Mean	23.9	9.5	14.4	15.2	18.2	8.8	12.1
	N	2	2	2	2	2	2	2
Avetrana	Mean	23.7	10.3	12.9	16.0	19.5	9.2	12.2
	N	12	10	10	13	14	3	3
Grotta Mora Cavorso	Mean	24.87		15.1	17.5	23.4		
	N	2		2	2	2		
Covoli di Velo	Mean	25.4	10.2	15.0	17.0	19.5	9.3	13.4
	N	2	2	2	1	1	2	2
Grotta Paglicci	Mean	22.7	8.9	11.9				
	N	1	1	1				
Appennine area	Mean	24.2	9.7	12.8	15.3	18.4	8.3	12.8
	N	250	250	250	252	253	253	252
Aven de l'Arquet	Mean	25.7	10.3	13.6	16.3	21.5	9.0	13.5
	N	27	26	27	16	16	15	15
Jaurens	Mean	26.6	10.7	14.5	16.6	20.0	8.8	14.0
	N	8	8	7	5	5	5	5
Maldidier	Mean	27	11.07	14.8	16.2	21.95	9.2	14.5
	N	3	3	3	2	2	4	4
Igue du Gral	Mean	25.47	10.36	13.9				
	N	10	10	10				

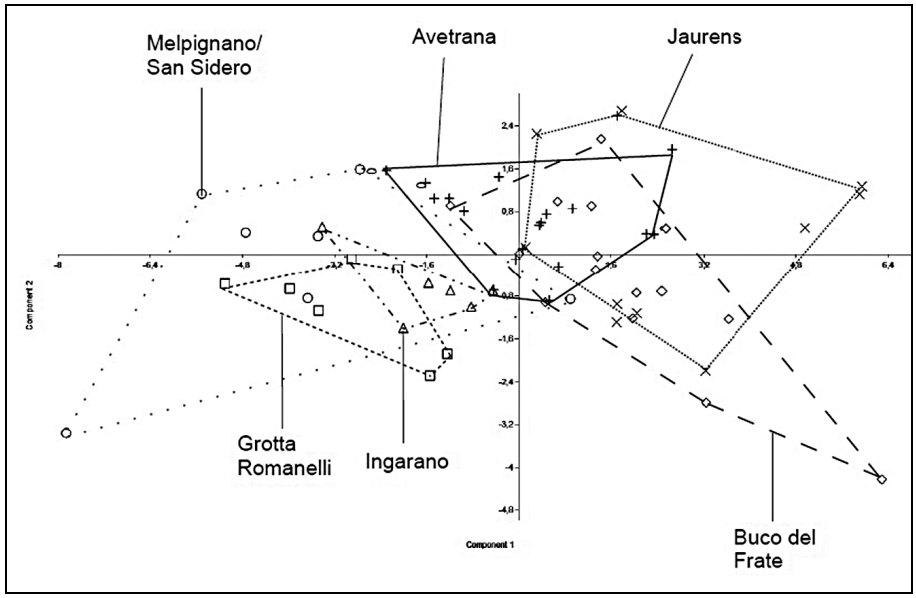

Fig. 5 - Principal Component Analysis performed on the upper teeth. Cross, full line: Avetrana; circle, big pointed line: Melpignano/San Sidero; triangle, point and line: Ingarano; asterisk, no line: Grotta Paglicci; square, small dashed line: Grotta Romanelli; diamond, big dashed line: Buco del Frate; X, small pointed line: Jaurens.

Site		p1 L	p1 W	p2 L	p2 W	p3 L	p3 W	p4 L	p4 W	m1 L	m1 W	Ltal	m2 L	m2 W	m3 L	m3 W
Melpignano/San Sidero	Mean	5.3	4.2	11.7	5.4	13.0	6.1	14.8	7.0	24.2	10.0	7.4	11.1	7.8	5.5	4.8
	N	4	4	8	8	10	10	10	10	7	7	7	6	6	3	3
Grotta Romanelli	Mean	5.4	4.0	10.5	5.0	12.0	5.1	13.7	6.2	23.9	9.5	7.1	10.8	7.5	4.3	4.0
	N	2	2	3	3	2	2	5	5	4	4	4	4	4	2	2
Veja Grotta A	Mean									23.0	9.2	6.8	10.2	7.2		
	N									1	1	1	1	1		
Pocala	Mean	5.7	4.4	13.2	6.2	13.0	6.3	15.6	7.8	27.8	11.2	8.5	11.7	8.4		
	N	1	1	1	1	2	2	3	3	7	7	7	3	3		
Buco del Frate	Mean	5.9	5.0	12.3	7.7	14.1	7.5	16.2	8.2	28.4	11.8	7.7	11.8	8.7		
	N	1	1	11	11	10	10	17	17	27	27	27	14	14		
Ingarano	Mean			10.9	5.3	12.7	6.0	14.0	6.6	25.0	10.0	7.0	11.6	7.9		
	N			3	3	2	2	2	2	5	5	5	3	3		
Grotta Sant'Agostino	Mean									28.2	11.3					
	N									5	5					
Avetrana	Mean	5.5	4.9	12.5	6.0	14.2	6.7	15.5	8.0	28.5	11.7	8.8	12.2	8.8	6.0	5.1
	N	1	1	12	12	9	8	11	9	19	17	16	11	11	1	1
Grotta Mora Cavorso	Mean									29.1	12.1					
	N									3	3					
Grotta Paglicci	Mean			11.9	5.3	12.7	5.8	14.6	6.8	26.3	10.8	6.3				
	N			1	1	1	1	3	3	1	1	1				
Grotta Bella	Mean									28.3						
	N									4						
Grotta Cappuccini	Mean									28.6						
	N									1						
Appennine area	Mean	5.7	4.3	11.6	5.7	13.1	6.2	14.9	7.1	27.2	10.8	7.6	10.9	8.0	5.2	4.8
	N	167	167	248	248	247	247	254	254	251	251	249	247	247	198	198
Aven de l'Arquet	Mean	6.2	4.9	12.6	6.1	13.2	6.8	16.1	8.0	28.2	11.4	10.2	11.8	8.8	5.9	6.0
	N	7	7	17	17	15	14	18	18	28	28	28	21	21	1	1
Jaurens	Mean	6.6	5.0	12.7	6.2	14.6	7.2	16.5	8.5	29.5	12.0	10.2	12.0	8.9		
	N	4	4	10	10	13	13	15	15	19	19	19	9	9		
Maldidier	Mean	6.2	5.0	13.0	6.7	15.0	7.7	17.2	8.9	30.3	12.4	10.6	10.6	8.5	5.5	5.3
	N	4	4	4	4	4	4	5	5	3	3	3	2	2	3	3
Igue du Gral	Mean	6.1	5.0	12.7	6.4	14.5	7.3	16.7	8.5	29.3	11.9	11.0	12.0	9.2	6.0	5.5
	N	6	6	10	10	10	10	12	12	10	10	10	7	7	7	7

Tab. 5 - Comparative dimensions (mm) of the lower teeth of *Canis lupus* of Avetrana and those of several Southern Italian localities and Apennine area.

by the breadth of M^1. ANOVA analysis on PC1 and PC2 have significant result (Tukey pairways test p= 0.0001095).

In the analysis on the lower teeth the specimens from Melpignano and San Sidero are considered as the same population and the sample from Grotta Paglicci was removed because is too small. A MANOVA performed on the lower teeth reveals that some means are significantly different (Wilks lambda: 0.145; p: 2.752E-23). After the Bonferroni correction the Avetrana wolves differ from those of Grotta Romanelli (*p*-value = 0.033158), Buco del Frate (*p*-value= 0.008824) and Jaurens (*p*-value= 4.15949E-06) but not from those of Ingarano (*p*-value= 0.144342), Melpignano (*p*-value = 0.0738477) (Tab. 5). The PCA performed on the lower teeth shows similar differences (Fig. 6; Tab. 6). The first component PC1 (on the horizontal axis) accounts for the 55,5% of the total variance, and has is loadings for the length of M_1. The second component (vertical axis) explain 16,0% of the variance and is mainly influenced by the breadth of P_2. ANOVA analysis was performed on PC1 and PC2 (Tukey pairways test p= 8,761E-06). The dimensional range of the length of M_1 is similar to that of the French localities of Jaurens and Aven de l'Arquet, in addition it is similar to that of Buco del Frate, Pocala and other Northern and Central Italian localities, chronologically related to MIS 3 and MIS 2 (Fig. 7). The mean value of the ratio between the total length and the talonid length of M_1 shows similar values to the samples under investigation (Tabs 4, 5).

The specimens of Avetrana are not significantly different, both for upper and lower teeth, from the populations of Buco del Frate, and Jaurens.

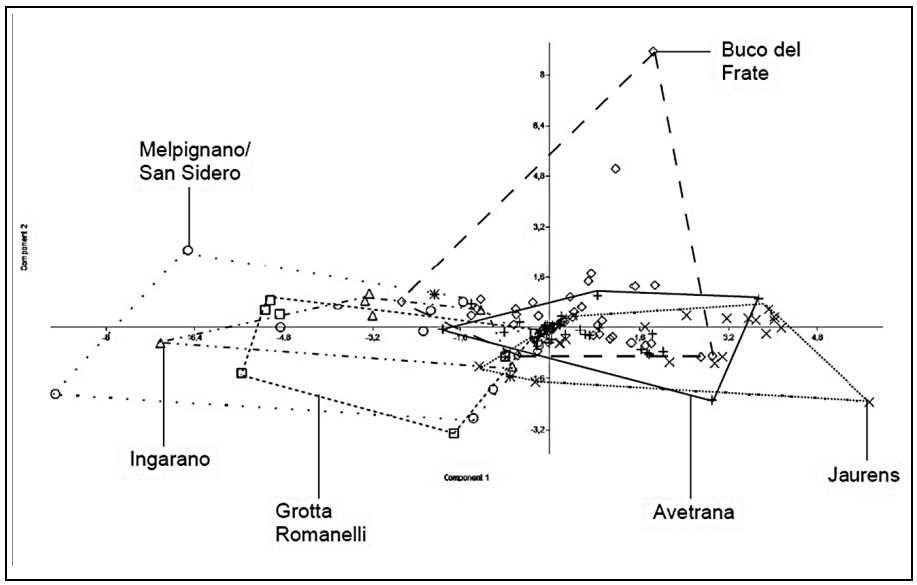

Fig. 6 - Principal Component Analysis performed on the lower teeth. Cross, full line: Avetrana; circle, big pointed line: Melpignano/San Sidero; triangle, point and line: Ingarano; asterisk, no line: Grotta Paglicci; square, small dashed line: Grotta Romanelli; diamond, big dashed line: Buco del Frate; X, small pointed line: Jaurens.

Comparison with extant wolves

The MANOVA analysis show that the differences between mean are significant (Wilks lambda: 0.0485; p= 2.24001E-06). The sample from Avetrana and the extant wolves are significant different (p-value: 2.24001E-06) and the p-value remains the same after the Bonferroni correction.

A discriminant analysis confirm that the two populations are different (p-value: 2.319E-06) and the percentage of corrected classified specimens is 77,59%.

A PCA analysis show that the first component PC1 (on the horizontal axis) accounts for the 48,25% of the total variance, and has is loadings for the length of P_4 and the breadth of M_1. The second component (vertical axis) explain 16,70% of the variance and is mainly influenced by M_2 breadth.

The values of the ratio between the talonid length and the total length in the lower carnassial are not significantly different within the considered sample. The widest populations of Italian fossil wolves, Avetrana and Buco del Frate, are dimensionally similar to the modern wolves and show the same variance (Tabs 4, 5). The subspecies *C. lupus maximus* is larger in the mean values than the Italian samples, but the maximal values fall into the variability of the modern wolf (Tabs 4, 5).

Eigenvalue	% variance
7.60821	68.43
1.84192	16.567

Eigenvalue	% variance
3.78962	55.502
1.82465	16.004

Tab. 6 - Variances of the major axes of the PCAs.

Discussion and conclusion

The population of *C. lupus* from the bed 8 of Avetrana represents the widest population of fossil wolves in Southern Italy. The studied specimens display important morphological and morphometric differences respect to those collected from the Apulian area. The dimensions of the early Late Pleistocene Apulian wolves are usually smaller than those of the modern wolf of the Apennine area. The teeth of *Canis lupus* collected from the bed 8 of Avetrana are larger and more robust than those of the early Late Pleistocene Apulian localities and in some cases are larger than those of the modern wolves of the Apennine area.

The large carnassial teeth and the deep jaw suggest a strong bite force and a high resistance to the stress due to the torsion movements of big preys as already highlighted in previous contributions (Ewer 1973; Leonard et al. 2007). The ratio between the talonid length and the total length of the M_1 shows similar values in the considered populations, suggesting a low intra-specific variability. This character can be associated to an ecomorph specialized for hunting large prey and/or habitual scavenging (Leonard et al. 2007; Flower & Schreve 2014). As well-known in literature, wolves hunted wild ungulate species accordingly to their relative abundance in the faunal community (Mech & Peterson 2003; Vucetich et al. 2010; Nowak et al. 2011). *Bos primigenius* and *Cervus elaphus* represent the most common taxa in the fossil record of Avetrana bed 8 (cfr. Petronio et al. 2008; Pandolfi et al. 2013a). These taxa were probably the most common preys hunted by wolves. On the opposite, the most abundant species in

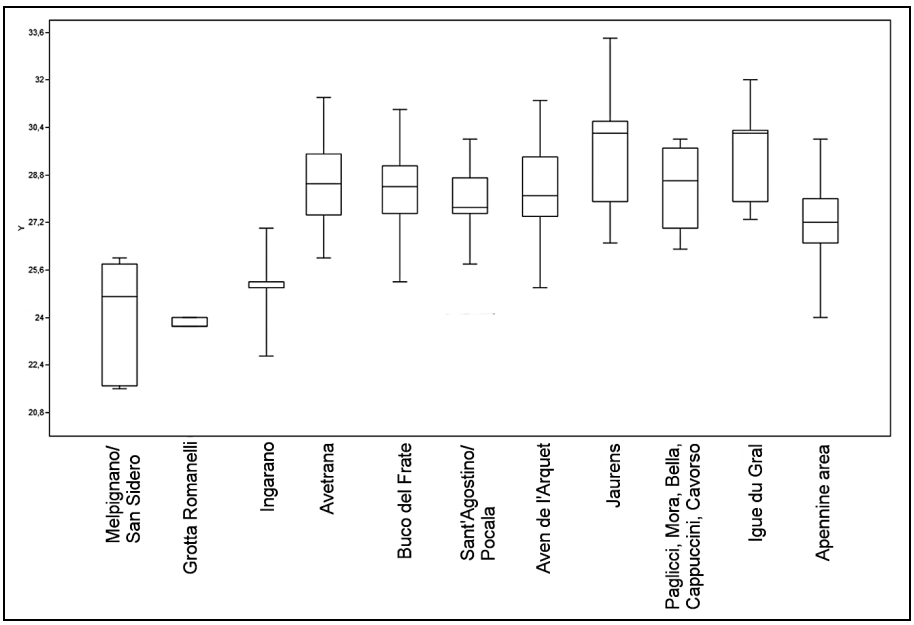

Fig. 7 - Box plot of variation in length of M_1 in *Canis lupus* of Melpignano-San Sidero (MIS5), Grotta Romanelli, Avetrana (MIS 4-3), Ingarano, Buco del Frate, Grotta Sant'Agostino, Pocala, Aven de l'Arquet, Jaurens (MIS 3), Paglicci, Mora Cavorso, Grotta Bella, Colle Cappuccini (MIS2-1), Igue du Gral (MIS 2-1), and Apennine area (recent).

the early Late Pleistocene localities of Apulia, such as in Romanelli and Melpignano, are *Dama dama*, *Equus hydruntinus* and other small and medium sized mammals, whereas large sized taxa, such as *Bos primigenius*, are scarcely represented (Blanc 1920; Cassoli et al. 1994; Bologna et al. 1996; Di Stefano 1994; Petronio et al. 2007). The Avetrana wolf resembles in dimension the populations of several Southern French localities of MIS 3 in which *C. lupus maximus* is recorded. Nevertheless, the population of Avetrana and the specimens referred to *C. lupus maximus* differ in the morphology of the upper carnassials (see the paragraph Description and comparisons). The morphometric similarities between the two samples could be related with evolutionary constraints (e.g. developmental constraints or allometric growth factors as discussed in Sardella et al. 2014) due to the same specialization and/or size increase. The latter could be influenced by local adaptation or climatic changes. However morphological and morphometric similarities between the Avetrana wolves and those collected from several Central and Northern Italian localities, chronologically related with MIS 3 and MIS 2 (e.g., Buco del Frate, Pocala), suggest a new dispersal event of the wolf in Italy rather than a local adaptation or a size increase due to climate changes. This dispersal event could be related with the expansion of the glacier during MIS 4 that forced the expansion of the areal distribution of the Central European wolves into Southern Europe with the replacement of native populations and/or the hybridisation between the different populations.

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Appendix 1

List of the Italian specimens considered for morphological comparison:

• *Canis lupus*

Museo Nazionale Preistorico-Etnografico "L. Pigorini", Roma - Grotta Romanelli: P3580; P3581.2; P3582; P3583; P3584; P35841; P3585.1; P3585.2; P3585.4; P3588; P3588.1; P3589; P3590; P3591; P3592; P3593; P3595.1; P3595.2.

Dipartimento di Geologia, Sapienza Università di Roma - Ingarano: IN110; IN505; IN507; IN509; IN511; IN517; IN604; IN634; IN635.

Dipartimento di Geologia, Sapienza Università di Roma - Melpignano: MPD4; MPD24; MPA3; MPC1; MPE2.

Dipartimento di Geologia, Università di Siena - Grotta Paglicci: USS 1034; USS 1035; USS 880; USS 879; USS 912; USS 278; USS 664; USS A; USS 1608; USS 1379; USS 1186; USS 1383; USS 833; USS 920; USS 1032; USS 877; USS 234; USS 748; USS 1346; V5767; V5770.

Museo Civico di Scienze Naturali di Brescia - Buco del Frate: Q1129; Q1130; Q1131; Q1133; Q1134; Q1135; Q1136; Q1137; Q1138; Q1139; Q1140; Q1141; Q1143; Q1144; Q1145; Q1146; Q1147; Q1148; Q1149; Q1150; Q1151; Q1152; Q1153;Q1154; Q1155; Q1156; Q1157; Q1158; Q1159; Q1160; Q1161; Q1162; Q1163; Q1164; Q1165; Q1166; Q1167; Q1168; Q1169; Q1170; Q1175; Q1176; Q1178; Q1182; Q1183; Q1184; Q1185; Q1186; Q1187; Q1188; Q1189; Q1190; Q1191; Q1192; Q1193; Q1194; Q1195; Q1196; Q1197; Q1198; Q1199; Q1200; Q1201; Q1202; Q1203; Q1204; Q1205; Q1206; Q1207; Q1208; Q1209; Q1210; Q1211; Q1212; Q1213; Q1214; Q1215; Q1218; Q1219; Q1220; Q1221; Q1222; Q1223; Q1224; Q1225; Q1226; Q1227; Q1231; Q1232; Q1233; Q1234.

Museo di Geologia di Padova - Grotta di Ladrenizza: MGP 26644.

Pocala: MGP 26626; MGP 26627; MGP 26628; MGP 26642; MGP 26643; MGP 26647.

Museo di Scienze Naturali di Verona - Grotta di Veja: V9996; V3078; V3079; V3080/1; V3080/2; V3081; V3082.

• *Modern wolves from Apennine area*

Istituto Superiore per la Protezione e la Ricerca Ambientale: ISPRA: 4399; ISPRA 6883; ISPRA 6885; ISPRA 7277; ISPRA 7284; ISPRA 7287; ISPRA 7770; ISPRA 7771; ISPRA 7775; ISPRA 7939; ISPRA 7945; ISPRA 7946; ISPRA; 9047; ISPRA 9048; ISPRA 9049; ISPRA 9052; ISPRA 9053; ISPRA 9054; ISPRA 9055; ISPRA 9056; ISPRA 9057; ISPRA 9058; ISPRA 9059; ISPRA 9060; ISPRA 9063; ISPRA 9064; ISPRA 9065; ISPRA 9068; ISPRA 9069; 9070; ISPRA 9076; ISPRA 9085; ISPRA 9087; ISPRA 9088; ISPRA 9100; ISPRA 9112; ISPRA 9182; ISPRA 9184; ISPRA 9185; ISPRA 9188; ISPRA 9189; ISPRA 9190; ISPRA 9605; ISPRA 9607; ISPRA 9608; ISPRA 9617; ISPRA 9618; ISPRA 9620; ISPRA 3899; ISPRA 3900; ISPRA 3901; ISPRA 3902; ISPRA 3903; ISPRA; 3904; ISPRA 45?; ISPRA 4847; ISPRA 5579; ISPRA 5897; ISPRA 5899; ISPRA 6735; ISPRA 6742; ISPRA 6743; ISPRA 6882; ISPRA 6884; ISPRA 6886; ISPRA 6896; ISPRA 6898; ISPRA 7031; ISPRA 7279; ISPRA 7291; ISPRA 7292; ISPRA 7772; ISPRA 7943; ISPRA 8508; ISPRA 9051; ISPRA 9094; ISPRA 9110; ISPRA 9111; ISPRA 9117; ISPRA 9119; ISPRA 9121; ISPRA 9132; ISPRA 9142; ISPRA 9191; ISPRA 9619.

Dipartimento di Zoologia di Roma: DZR (no num); DZR 0142CV; DZR 0143CV; DZR 1; DZR 2; DZR 3; DZR 5; DZR 6; DZR 7; DZR 8; DZR 9; DZR 10; DZR 13; DZR 14; DZR 16; DZR 18; DZR 19; DZR 20; DZR 21; DZR 22; DZR 23; DZR 24; DZR 25; DZR 27; DZR 28; DZR 29; DZR 30; DZR 32; DZR 33; DZR 34.