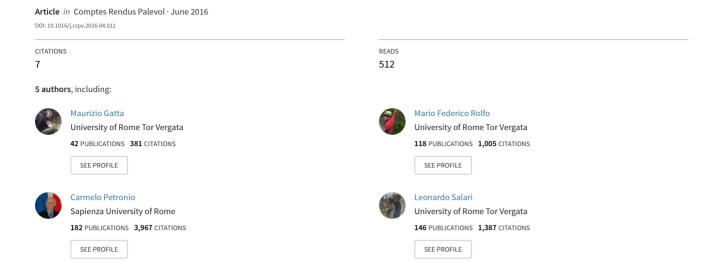
Late Pleistocene skeleton of Canis lupus L., 1758 from Grotta Mora Cavorso (Jenne, Latium, central Italy)



ELSEVIER

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Late Pleistocene skeleton of *Canis lupus* I., 1758 from Grotta Mora Cavorso (Jenne, Latium, central Italy)



Squelette de Canis lupus retrouvé dans le Niveau 7 de la Grotta Mora Cavorso (Latium, Italie centrale) datant du Pléistocène supérieur

Maurizio Gatta ^{a,*}, Mario F. Rolfo ^b, Carmelo Petronio ^c, Leonardo Salari ^c, Letizia Silvestri ^d

- ^a Department of Archaeology, BioArch Environment, Wentworth Way, York YO10 5NG, United Kingdom
- ^b Dipartimento di Storia, Patrimonio culturale, Formazione e Società, Università di Roma "Tor Vergata", Via Columbia 1, 00163 Roma, Italy
- ^c Dipartimento di Scienze della Terra, "Sapienza" Università di Roma, Piazzale Aldo Moro 5, 00185 Roma, Italy
- ^d Department of Archaeology, Durham University, South Road, DH1 3LE Durham, United Kingdom

ARTICLE INFO

Article history: Received 20 December 2015 Accepted after revision 24 April 2016 Available online 24 June 2016

Handled by Lars van den Hoek Ostence

Keywords: Wolf MIS 3 Morphometric variability Taphonomy Palaeontology

ABSTRACT

This paper describes the skeleton of *Canis lupus* found in Layer 7 of Grotta Mora Cavorso (Latium, central Italy), correlated with the MIS 3. Research on the deposition dynamics of this find is still in progress, but the action of human or other predators can be excluded. This specimen consists of a near complete articulated skeleton, lacking only the calvarium. The age at death was estimated at around six years old. Preliminary morphometric analyses and comparisons with samples of Italian Late Pleistocene wolf and extant Apennine wolf (*C. lupus italicus*) remains, show that the dimensions of the teeth and long bones are among the biggest known from the Italian Late Pleistocene and larger than the extant Apennine wolf

© 2016 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

RÉSUMÉ

Cette étude porte sur un squelette de *Canis lupus* retrouvé dans le Niveau 7 de la Grotta Mora Cavorso (Latium, Italie centrale), corrélé avec le MIS 3. Les dynamiques de dépôt sont actuellement en cours d'étude, bien qu'on puisse exclure l'action de l'homme ou d'autres prédateurs. Ce spécimen, auquel il manque la calotte crânienne, était en connexion anatomique. L'âge au décès est de six ans environ. Des analyses morphométriques préliminaires et des comparaisons effectuées avec d'autres loups du Pléistocène supérieur italien, ainsi que sur un échantillon de loup actuel des Apennins (*C. lupus italicus*), ont montré que les dimensions des dents et des os longs sont parmi les plus grandes dans le Pléistocène supérieur italien et plus grandes que chez le loup actuel des Apennins.

© 2016 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

Mots clés :

Taphonomy
Paléontologie

* Corresponding author.

E-mail address: maurizio.gatta@york.ac.uk (M. Gatta).

Loup MIS 3 Variabilité morphométrique

1. Introduction

This paper describes the Late Pleistocene skeleton of a wolf from Grotta Mora Cavorso (Jenne, Simbruini Mountains, central Italy), anatomically articulated but lacking its calvarium.

Grotta Mora Cavorso (Fig. 1A) is located in the territory of Jenne (Latium, central Italy), at 715 m a.s.l., along the upper Aniene River Valley. This site is mostly known for

holding the largest human burial deposit of Early Neolithic central Italy (Rolfo et al., 2012 with references).

Extant wolf, *Canis lupus*, probably originates in the early Middle Pleistocene of Beringia (Tedford et al., 2009) and it reaches western Europe during the second half of middle Pleistocene (Boudadi-Maligne, 2012; Bertè and Pandolfi, 2014). *C. lupus* first occurs in Italy in the late Middle Pleistocene of Polledrara di Cecanibbio (Rome), correlated with the Marine Isotope Stage 9 (MIS 9) (Palombo et al., 2003).

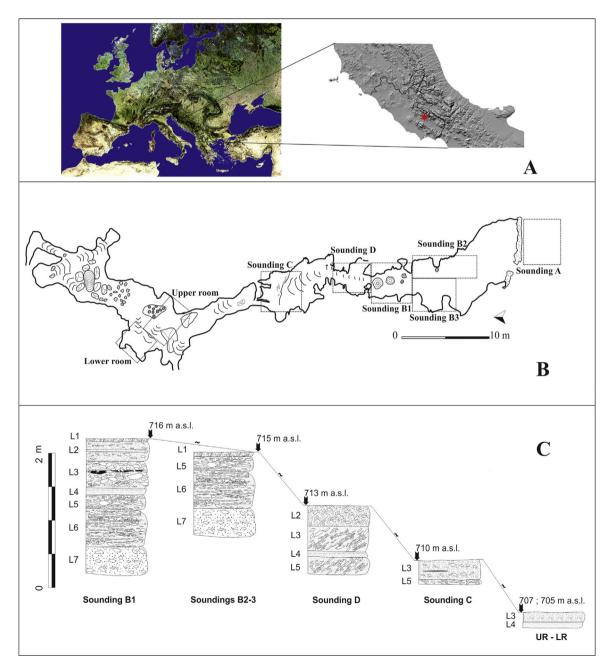


Fig. 1. Grotta Mora Cavorso: A) location of the site; B) plan of the cave with location of the soundings; C) stratigraphic sequences of archaeological soundings and their height above sea level.

Fig. 1. Grotta Mora Cavorso: A) localisation du site; B) planimétrie de la grotte avec la localisation des fouilles; C) séquences stratigraphiques des fouilles archéologiques et de leur altitude au-dessus du niveau de la mer.

Records of *C. lupus* are relatively abundant in the Italian Late Pleistocene, under both temperate-warm and cold climate conditions, and the species persists into the Holocene (Petronio et al., 2011; Sansalone et al., 2015).

C. lupus is currently distributed throughout Eurasia and North America. Its presence in Italy is ascertained in the Apennines and part of the western Alps, and probably in north-eastern Italy (Ciucci and Boitani, 2003; Lapini et al., 2010; Mech and Boitani, 2010). It is also found in the Simbruini Mountains, mainly in wooded areas with access to pastures and valleys between 800 and 1600 m. a.s.l. (Bernardini et al., 2005).

2. The Grotta Mora Cavorso

Grotta Mora Cavorso is a karst cavity, inside the Simbruini Mountains Regional Natural Park, which holds a succession of rooms and ducts. Following the fortuitous discovery of human bones inside the cave, archaeological investigations started by Tor Vergata University of Rome.

Excavations of the entrance room (Fig. 1B) started in 2007 and provided interesting information suggesting a longer sequence of human frequentation of the site (Fig. 1C), including a Late-Pleistocene sequence (Salari et al., 2011, 2014). In particular, soundings B1, B2, C and D held, with some discontinuities, archaeological and palaeontological finds ranging from the Late Pleistocene to historical times (Rolfo et al., 2013, 2016, and references therein).

Sounding B2 in Room 1 yielded Holocene levels (Layers 1–4), which were archaeologically associated with the Neolithic, the Bronze Age and the historic period. In these layers, bones of domestic and wild species were found, including a few wolf remains from the Bronze Age (3762 \pm 340 BP, CNR Montelibretti – 849 C) and from the 5–6th centuries AD (Rolfo et al., 2013, 2016, and references therein). Layer 5 is the most recent Pleistocene layer, radiometrically dated to 13,460 \pm 50 BP (CNRS Lyon–4568). Within this layer, an Epigravettian flint industry and abundant Lateglacial mammal remains were found. Layer 6 is about 60-cm thick and has been associated with the Last Glacial Maximum, according to its stratigraphic position and faunal assemblage (Rolfo et al., 2016; Salari et al., 2011, 2014).

Below this, Layer 7 showed a significant chronological hiatus and different climate conditions. The semi-complete skeletons of a chamois, studied using the same biochronological approach as this work (Salari et al., 2014), and a marmot were found. The faunal assemblage of this layer also includes *Lepus* sp., *Capra ibex*, *Cervus elaphus elaphus*, *Sus scrofa*, *Arvicola amphibius*, *Glis glis*, *Microtus arvalis* and other micromammal remains. Several finds of *C. lupus*, including a fragmented calvarium, were also discovered therein and radiometric dating performed on a fragment of this skull proved it older than 43,500 years BP (Beta Analytic Inc., Miami – 365375).

The lower portion of Layer 7 held the skeleton of *C. lupus* described in this work. The associated fauna and the abovementioned radiometric dating suggested correlation of this layer with a temperate oscillation of MIS 3 (Salari et al., 2014; Rolfo et al., 2016). So far, human artefacts or activities

have not been detected in this layer, although archaeological investigations are still ongoing.

A few wolf remains have also been retrieved in other sectors of the cave (Sounding B1 and D) and have been stratigraphically attributed to the Lateglacial and the Early Holocene (Rolfo et al., 2016; Salari et al., 2011).

3. Materials and methods

The excavation of the specimen was carried out during the 2014 campaign in Sounding B2, bottom of Layer 7, at an average depth of $-191\,\mathrm{cm}$. Each bone was assigned a find number and recorded with its grid coordinates and depth within a $1\times 1\,\mathrm{m}$ excavation grid system. Finds were mostly concentrated in grid square b2. The soil was fully sieved with a 2 mm mesh in the field.

All the bones of *C. lupus* from Grotta Mora Cavorso have been examined at the Laboratory of Prehistory of the University of Rome Tor Vergata. The comparative samples of extant Apennine wolf, *C. lupus italicus*, were sourced from the Scientific Services' Office of the "Ente Autonomo Parco Nazionale d'Abruzzo, Lazio e Molise" (=PNALM) of Pescasseroli. Late Pleistocene wolf remains from Ingarano and Avetrana were sourced from the Department of Earth Science of Sapienza University of Rome (Appendix 1).

Measurements of wolves from Late Pleistocene and Holocene of Grotta Mora Cavorso, Ingarano and Avetrana and of extant Apennine wolves from PNALM were taken by the authors with a vernier digital calliper, according to the methodology of von den Driesch (1976). Other measurements of *C. lupus* from several Late Pleistocene sites of Italy and from the Holocene site of Grotta delle Ossa (Trieste Karst, in Škocjan, Slovenia) were taken from the literature (Table 1).

Comparisons were made based either on single skeletal elements, mean values or, where the samples were relatively numerous and/or with wide variability, with the minimum, maximum and mean values. The age of death was estimated according to Gipson et al. (2000); the body mass and the body length was calculated according to Boudadi-Maligne (2010, tables 20 and 21):

- log body mass = log (length \times breadth of lower carnassial) \times 1.0701 1.1596;
- log body mass=log maximum length of mandible × 2.8816 – 4.9853;
- log body mass=log greatest length of radius × 2.9445 – 5.2903;
- log body mass = log greatest length of tibia × 2.6615 – 4.7585;
- log body length = log (length × breadth of lower carnassial) × 0.32852 0.6343;
- log body length = log maximum length of mandible × 0.7629 – 1.5357;
- log body length=log greatest length of radius × 0.8666 – 1.8166;
- log body length = log greatest length of tibia × 0.7054x - 1.4768.

Table 1
List of comparative sites, their age and geographic area.
Tableau 1
Liste des sites comparés, leur datation et zone géographique.

Site	Age	Geographic area	References		
Melpignano - Maglie	Late Pleistocene, MIS 5	Apulia	Sardella et al., 2014; Bertè and Pandolfi, 2014		
San Sidero 3	Late Pleistocene, MIS 5	Apulia	De Giuli, 1983		
Avetrana (layers 5-6)	Late Pleistocene, MIS 5	Apulia	Pandolfi et al., 2013; this work		
Valle Radice	Late Pleistocene, MIS 4	Latium	Biddittu et al., 1967		
Grotta Sant'Agostino	Late Pleistocene, MIS 4-3	Latium	Tozzi, 1970		
Grotta Tina	Late Pleistocene, MIS 4-3	Campania	Martini et al., 1974		
Ingarano	Late Pleistocene, MIS 4-3	Apulia	Bertè and Pandolfi, 2014; this work		
Sternatia	Late Pleistocene, MIS 4-3	Apulia	Rustioni et al., 1994		
Grotta Romanelli	Late Pleistocene, MIS 4-3	Apulia	Sardella et al., 2014; Bertè and Pandolfi, 2014		
Grotta Veja A	Late Pleistocene, MIS 3	Veneto	Bertè and Pandolfi, 2014		
Caverna Pocala	Late Pleistocene, MIS 3	Friuli Venezia Giulia	Bertè and Pandolfi, 2014		
Buco del Frate	Late Pleistocene, MIS 3	Lombardy	Bertè and Pandolfi, 2014		
Avetrana (layer 8)	Late Pleistocene, MIS 3	Apulia	Bertè and Pandolfi, 2014; this work		
Riparo di Fumane	Late Pleistocene, MIS 3-2	Veneto	Cassoli and Tagliacozzo, 1991		
Caverna Arene Candide	Late Pleistocene, MIS 2	Liguria	Cassoli and Tagliacozzo, 1994		
Grotta Paglicci	Late Pleistocene, MIS 2	Apulia	Boscato, 1994; Bertè and Pandolfi, 2014		
Škocjan	Holocene, Iron age	Slovenia	Riedel, 1977		

Finally, the withers height was calculated following the methodology proposed by Harcourt (1974) for prehistoric domestic dogs.

4. Taphonomic observations

The dimensions of specimen 2823 match those of a wolf or a large domestic dog. It is evident that this is not a deposition of an archaic domestic dog for both the archaeological and chronological context and the morphological characters. The sub-rectilinear profile of the lower mandibular edge, the alignment of the premolars, as well as a hypoconid of the lower carnassial much greater than the entoconid indeed, exclude archaic domestic dog (Bonifay, 1971: Ciucci and Boitani, 2003; Germonpré et al., 2015).

The skeleton was well preserved in a reddish clay layer, not very compact and with small rock inclusions, about 50 cm thick and rich in vertebrate remains. The specimen occupied about 1 m² and was lying below a large natural chimney. The bones showed an advanced state of fossilisation, with a yellow patina and overall good robustness, except for the most fragile bones such as ribs and the right scapula. The specimen was lying on its left side and showed almost full anatomical articulation (Fig. 2); teeth are all permanent and the long bone epiphyses are all fused to their diaphysis. The skull, of which only the lower mandible and some upper teeth were preserved, was aligned but not connected to the spine, due to the dislocation of the two cervical vertebrae posterior to the axis. However, the matching position between the mandible and the body indicates a minimal impact of post-depositional movements. The absence of the calvarium remains unexplained. The presence of the upper canine, correctly seated in the mandibular diastema between the lower canine and the p1 (Fig. 3A), suggests that the removal of the calvarium followed the dismembering of the carcass and preceded its full burial. The central axis of the torso was in a good state of preservation, with a fragmentary sternum and most of the ribs still present. Atlas and axis were leaning against the mandible, with the first being overturned and having the

facette that articulates with the cranium facing upwards, and the second still in its correct anatomical position. The remaining part of the spine was in full anatomical articulation between the second thoracic and the first four lumbar vertebrae. All the other cervical vertebrae were shifted but present, whereas the last four lumbar and most of the caudal ones were missing.

The right scapula, the only one recovered, was smashed next to the first thoracic vertebrae and lacked the shoulder joint. The poor preservation caused fragmentation at the time of the retrieval.

The collarbones, which were not in connection, were lying at the sides of the spine. The pelvis was almost completely missing and only a few left coxal fragments were found next to the proximal epiphysis of the femur. The fore-limbs, located alongside the body, had lost their connection with the thorax. The right limb, lacking the ulna and the humeroradial joint, was slightly overlapping the left one. The latter preserved all the long bones connections and partial carpal connections. The right foot was close to the right radius. The metacarpal and carpal bones were found grouped together, whilst some phalanges were missing.



Fig. 2. Grotta Mora Cavorso, Sounding B2: the skeleton of wolf. **Fig. 2.** Grotta Mora Cavorso, Fouille B2: le squelette du loup.

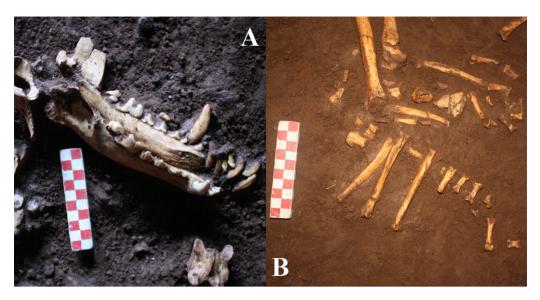


Fig. 3. Grotta Mora Cavorso, Sounding B2: the skeleton of wolf; A) detail of the mandibles; B) detail of the hind foot. **Fig. 3.** Grotta Mora Cavorso, Fouille B2: le squelette du loup; A) détail des mandibules; B) détail de la patte arrière.

Except for the left radius, all the long bones of the forelimbs are fractured along the diaphysis. Hindlimbs, found in crouch position, are more incomplete and disturbed. Both limbs miss a large part of tarsal and metatarsal bones and phalanges, with those identified being quite widespread in the area (Fig. 3B). Their position appears to indicate a shift of these remains along the south-north axis, possibly caused by water flow or small mammal disturbance. Overall, the left portion of the skeleton was better preserved, i.e. the side on which the body was lying and that was probably first buried in the sediments.

The degree of skeletal articulation, including that of several small bones, suggests a rather fast burying of the carcass, most likely caused by the sediments falling from the overlying chimney. The missing elements must have been lost before the burial completed.

At present, the arrangement dynamics of the wolf cannot be fully explained, although some hypotheses can be drawn. Human or predator action is not visible, therefore a fall through the chimney of the carcass or of the live animal could be considered. This hypothesis is corroborated by the presence of other semi-complete skeletons, of a chamois and a marmot, in the same area (Salari et al., 2014). However, the absence of compound fractures, expected in this type of fall, might instead suggest a natural death of the carnivore, after sheltering in the cave. In this case, the fractures of almost every long bone diaphysis might be explained by the pressure exerted by the sediments, and the shift of the cervical joint and of some phalanges by the aforementioned post-depositional disturbance. Future investigations at the site might provide new information about the taphonomic dynamics of the context and shed light on this question.

The calvarium of *C. lupus* found prior to the skeleton examined in this work and identified at the same depth yet two metres northward, is not referable to the same individual, based on different tooth wear and the presence of the two first upper premolars.

5. Descriptions and comparisons

Upper incisors of this wolf (Specimen 2823) are small and their dimension increases outwards. The front (labial) surface is smooth and rounded, the back (lingual) one is concave; first and second incisors are trilobate, the third has one long and sharp lobe. The upper canine is relatively robust, slightly curved. The mesio-distal section is elliptical and its diameter (13.8 mm) is consistent to those of females of PNALM, while males have a mesio-distal diameter comprised between 14.3 and 15.0 mm. These values are larger than those of Grotta S. Agostino (12–13.5 mm; mean 12.7 mm) although there is not any information about the sex of the latter specimens. The P1 is small, with a simple and ogival crown.

The mandible is robust, with a high coronoid process. The condyle process is slightly oblique to the mandibular axis. The angular process is short and almost horizontal, the lower edge of the horizontal ramus is sub-rectilinear, with a slight convexity towards the molars. Maximum length (angular process-infradentale: ~184 mm) is longer than the extant wolves of the PNALM (162-175 mm, mean 167.5 mm) and comparable with the mean value of the Iron Age C. lupus from Škocjan (186.2 mm). Basing on this measurement, using Brinkman and Dahar's indexes (von den Driesch, 1976), the basal length of the skull (basion - prosthion) was estimated between 218.4 and 232.7 mm. Experimental confirmation of the estimates was provided by the skulls of the extant wolves of the PNALM, especially with regard to the mean value of the Brinkman indexes, whereas the Dahar index tends to overestimate the calculated basal length of the skull compared to the measured one (Table 2).

The lower incisors are bilobate and increase in dimension outwards. The lower canine is similar to the upper one, except for the slightly rounder mesio-distal section and the cusp facing outwards. The lower jugal teeth have

Table 2Basal length (basion - prosthion) of skull, measured and calculated according the Brinkman and Dahar indices (von den Driesch, 1976). **Tableau 2**

Longueur basale (basion - prosthion) du crâne, mesurée et calculée selon les indices de Brinkman et Dahar (von den Driesch, 1976).

Dahar
232.7
197.3
218.2
203.1
200.8
204.8
201.9

usually greater mesio-lingual diameter (length) than the vestibular-lingual diameter (breadth). Premolars increase in dimension backwards, with the first having a simple crown, the others having two secondary mesial cusps. The first one leans on the second, the third on the fourth, which is slightly imbricate with the first molar. The latter, i.e. the carnassial, is big, has a high crown and is divided in two parts: a cutting front (trigonid) and a grinding back (talonid). The m2 is slightly smaller and has three main cusps. The m3 is rounded and similar in size to the first premolar.

The length of the m1 (28.9 mm) is longer than in the extant wolves of the PNALM (26.3–27.8 mm, means 27.2 mm) and is among the longest of the comparative ones, whereas the width (11.0 mm) is relatively small (Fig. 4). This tooth was probably not very robust, yet very sharp. The trigonid length/total tooth length ratio shows a possible strong carnivore tendency (Boudadi-Maligne, 2010; Petronio et al., 2006). The value obtained (71.3%) falls in the range of the extant wolves of the PNALM (69.2–72.6%; mean 71.8%). It is on average longer than the Pleistocene wolves of Grotta Romanelli (68.7–70.9%, mean 70.3%) and Ingarano (67.5–73.8, mean 70.0%), smaller than the other Pleistocene wolves of Grotta Mora Cavorso (72.2–77.3%, mean 74.5%), but comparable with that of the historical age of this cave (71.9%).

Overall, the tooth wear shows that the wolf died at about six years. The wear stage of canines, lower carnassials and first and second incisors match this estimate. The left i3 is less worn (4–6 years), whereas the wear of the right one is so strong that reaches the external lobe (\sim 8 years), indicating that the animal had anomalous chewing behaviour, for instance gnawing bones mostly on one side.

Limb bones are robust, slender and with prominent muscle attachments. The distal scapula shows a net coracoid apophysis and relatively deep glenoid cavity. The humerus is sub-rectilinear, with the diaphysis slightly expanding towards the extremities; in the proximal portion, which is more developed anteroposteriorly, the deltoid mark is oblique; in the distal epiphysis, the supratrochlear foramen is located just above the condyle, in a median position. The radius is rectilinear, with the diaphysis flattening anteroposteriorly and elliptical epiphyses; the proximal one shows a central depression, the distal one is slightly rounder and ends in a lateral extension (styloid apophysis). The right radius has a slightly smaller proximal epiphysis and is ~3 mm longer than the

Table 3

Measurements (mm) of post-cranial remains of the specimen 2823 from Grotta Mora Cavorso and of some Late Pleistocene, Holocene and living wolves. Measurement abbreviations: GL: greatest length; GLC: greatest length from caput (femur); Bp: breadth of proximal end; Dp: depth of the proximal end (humerus); SD: smallest breadth of the diaphysis; Bd: breadth of distal end.

Tableau 3

Mesures (mm) de restes postcrâniens de l'Échantillon 2823 de Grotta Mora Cavorso et de certains loups du Pléistocène supérieur, de l'Holocène et vivants. Abréviations des mesures : GL : longueur maximale ; GLC : longueur à partir du caput (fémur) ; Bp : largeur de l'extrémité proximale ; Dp : épaisseur de l'extrémité proximale (humérus) ; SD : largeur minimale de la diaphyse ; Bd : largeur de l'extrémité distale.

Humerus	GL	Dp	SD	Bd		
Mora Cavorso 28223 dx	207.0	52.2	14.8	40.9		
Mora Cavorso 28223 sn			15.0	40.9		
PNALM min	177.0	49.2	14.8	40.4		
PNALM max	203.0	53.2	16.8	44.4		
PNALM med	193.5	51.6	15.6	42.8		
Škocjan med	221.6	56.0	17.6	44.9		
Grotta Tina	199.0	51.8	14.5	39.5		
Radius	GL	Вр	SD	Bd		
Mora Cavorso 28223 dx	201.0	23.8	17.5	31.1		
Mora Cavorso 28223 sn	198.0	24.4	17.5	30.3		
Mora Cavorso Bb3	216.0	24.7	17.8	33.0		
PNALM min	176.0	21.2	15.2	29.4		
PNALM max	200.5	23.8	16.1	31.7		
PNALM med	187.6	22.5	15.6	30.4		
Škocjan med	217.1	24.8	17.1	33.5		
Valle Radice	183.5	20.1	14.5	28.4		
Grotta Sant'Agostino	196.0	23.0		31.0		
Femur	GLC	Вр	SD	Bd		
Mora Cavorso 28223 sn	223.0	50.8	16.0	39.1		
PNALM min	198.0	45.1	14.8	37.5		
PNALM max	216.0	51.2	17.5	41.1		
PNALM med	208.5	48.5	15.9	39.2		
Škocjan med	233.8	52.0	17.8	44.1		
Avetrana 8	208.0	42.2	15.0	35.8		
Tibia	GL	Вр	SD	Bd		
Mora Cavorso 28223 dx	226.0	41.6	16.5	28.7		
Mora Cavorso 28223 sn	225.0	41.1	16.4	28.7		
Mora Cavorso Bb3	240.0	49.2	18.5	30.6		
PNALM min	196.0	40.2	15.0	24.0		
PNALM max	227.0	45.4	16.8	29.3		
PNALM med	211.0	42.2	15.9	27.8		
Škocjan med	239.0	45.9	16.5	29.8		
Melpignano	206.0		15.0	25.6		
Grotta Paglicci	232.0			27.9		
Caverna Arene Candide	213.0		14.7	28.6		

left one (Table 3), whereas the other measurements of the left and right bones are almost identical. No bone malformations or neo-formations are present. The ulna is curved towards the extremities, with a distally narrowing diaphysis; the proximal extremity is wide and robust, with the top of the olecranon showing a groove and with a rather prominent beak. The femur is rectilinear; in the proximal area, the caput is detached from the bone body and the third trochanter is laterally dislocated. The tibia is elongated, with a tibial ridge reaching the proximal fourth of the bone, which gives it a slender aspect. The diaphysis is almost rectilinear and ends with a slightly widening distal epiphysis.

Lengths of the limb bones are generally longer than extant wolves of the PNALM and of the other Pleistocene Italian wolves, but shorter than Škocjan and of the other wolves from Layer 7 of Grotta Mora Cavorso (Table 3). The

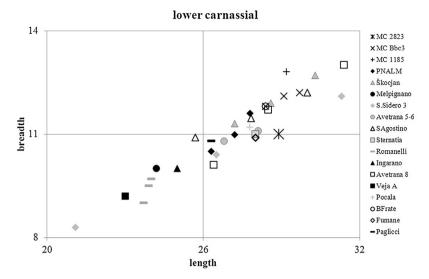


Fig. 4. Scatter diagram of breadth versus maximum length of lower carnassial (mm) of the Specimen 2823 from Grotta Mora Cavorso (=MC) compared with some Late Pleistocene, Holocene and living wolves.

Fig. 4. Diagramme de dispersion de la largeur et de la longueur maximale de la carnassière inférieure (mm) de l'échantillon 2823 de Grotta Mora Cavorso (=MC), par rapport à celles des loups du Pléistocène supérieur, de l'Holocène et de loups vivants.

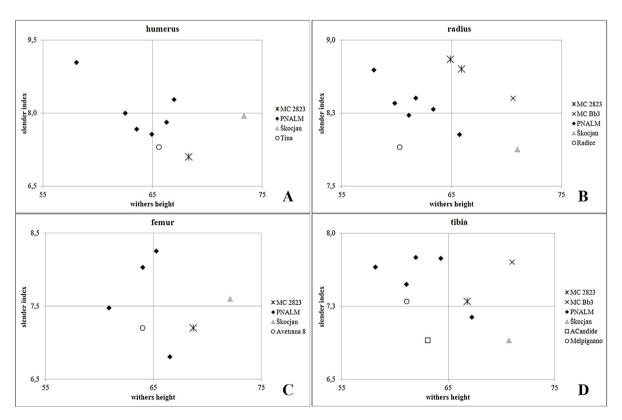


Fig. 5. Scatter diagram of slenderness index (smallest breadth of the diaphysis \times 100/maximum length) versus withers height (cm) according to Harcourt (1974) of the specimen 2823 from Grotta Mora Cavorso compared with some Late Pleistocene, Holocene and living wolves; A) humerus [withers height=(maximum length \times 3.43 – 26.54)/10]; B) radius [withers height=(maximum length \times 3,18 + 19,51)/10]; C) femur [withers height=(maximum length \times 3,14 – 12,96)/10]; D) tibia [withers height=(maximum length \times 2,92 + 9,41)/10].

Fig. 5. Diagramme de dispersion de l'indice d'élancement (la plus petite largeur de la diaphyse \times 100/longueur maximale) par rapport à la hauteur au garrot (cm) selon Harcourt (1974) de l'échantillon 2823 de Grotta Mora Cavorso par rapport à des loups du Pléistocène supérieur, de l'Holocène et de loups vivants ; A) humérus [hauteur au garrot = (longueur maximale \times 3,43 - 26,54)/10] ; B) radius [hauteur au garrot = (longueur maximale \times 3,14 - 12,96)/10] ; D) tibia [hauteur au garrot = (longueur maximale \times 2,92 +9,41)/10].

maximum diameters of the epiphyses and minimum one of the diaphysis (i.e. the transverse diameters, except for the anteroposterior one of the humerus proximal epiphysis) fall instead in the variability pattern of the extant wolves of the PNALM, more often close to their maximum values, but they are always smaller than Škocjan's Holocene wolves (Table 3). These measurements are comparable with the other Pleistocene wolves, except for the radius from Valle Radice, whose values for the transverse diameters are also smaller, and for the more robust radius and tibia of the other wolves from Layer 7 of Grotta Mora Cavorso (Table 3).

In order to draw a picture of the specimen's original aspect, withers height (ranging between 65.4 and 68.7 cm, with a mean of 67.3 cm), estimated from various bones, and the slenderness index of each item were considered (Fig. 5). As can be noted, the specimen analysed in this work falls almost always to the right side of the graphs, because of the medium-high lengths, and in the middle-bottom region. except for the radius, due to the long and slender limbs. Extant wolves of the PNALM, with a withers height ranging between 57.9 and 67.2 cm and a mean of 62.9 cm, fall instead mainly to the left side and in the middle-top part of the graphs, due to shorter and relatively more robust limbs. The other Pleistocene wolves from Grotta Mora Cavorso were likely to be taller and more robust than Specimen 2823, that from Grotta Tina would be of average height with slender limbs, those from Valle Radice and Melpignano of modest height with relatively robust limbs, whereas the Holocene wolves from Škocjan would be the biggest and most slender.

Maximum limb and mandible lengths, along with the lower carnassial surface, were also used to estimate the body mass (ranging between 30.3–34.8 kg, with a mean of 32.6 kg) and length (ranging between 150 and 156 cm, with a mean of 153.3 cm) of Specimen 2823. The same methodology showed that the extant wolves of the PNALM's body mass would likely range between 21.0 and 33.5 kg, and the body length between 135 and 155 cm, with a mean of 146 cm.

According to Toschi (1965) the weight of the extant European wolves ranges between 25 and 50 kg, with a mean of 31.9 kg, whereas Boudadi-Maligne (2010) reported that for the Portuguese extant wolves it probably ranges between 27.5 and 39.0 kg, with a mean of 31.9 kg. Based on a sample of Apennine wolves that died between 1974 and 1990, the body length on average ranged between 109 and 148 cm and the withers height between 49 and 73 cm (Ciucci and Boitani, 2003).

Values of body mass and withers height of Specimen 2823 thus fall in the variability pattern of the extant wolves, whereas the body length is significantly longer.

6. Conclusive considerations

The specimen that lived during the MIS 3 was probably a 6-year-old female. Its withers height probably ranged between 65 and 69 cm, body length between 150 and 156 cm and body mass between 30 and 35 kg. It showed robust mandible and hindlimbs, longer and more slender forelimbs, and a similar height/mass ratio to the modern Apennine wolves, but a more slender body overall.

Morphometric data show that it is not the biggest Pleistocene individual from Grotta Mora Cavorso, although it is better preserved and suitable to an extensive study, and it still falls among the biggest Italian wolves published in literature.

The remains, concentrated in a limited area and mostly in anatomical articulation, were well preserved and in an advanced state of fossilisation, bearing no traces of human or animal action. However, the orientation of the specimen and the absence of some bones indicate slight post-depositional disturbance prior to the burial of the carcass. The dynamics of deposition of the specimen are not clear and future investigations are necessary to shed light on this query. Currently a natural death of the wolf, voluntarily sheltered in the entrance of the cave, seems the most likely hypothesis and the fracture of most of the long bone's diaphyses may be explained by the soil pressure. However, the fall of the animal, dead or alive, from the overlying natural chimney cannot be firmly excluded. This hypothesis could be supported by the discovery of a chamois and marmot skeletons in the upper zones of the same layer 7 (Salari et al., 2014).

With regard to the methodologies used to calculate body mass, length and the withers height, it has to be noted that the values proposed in this work are estimates and that wolves' dimensions and body proportions are highly variable. For example, extant Portuguese wolves' condylobasal length of the skull and maximum mandible length are longer than the Italian wolves, whereas their upper canines and lower carnassials are smaller (Boudadi-Maligne, 2010, tabs 23 and 24); Bulgarian and Polish wolves, as well as those from the Russian district of Smolensk, are bigger than the Portuguese and Italian ones, although their proportions vary slightly (Boudadi-Maligne, 2010, tabs 23 and 24). The dimensions of the skeletal elements of the Specimen 2823 from Grotta Mora Cavorso are overall greater than the sample of extant wolves of the PNALM, therefore body mass and length values, as well as the withers height, were expected to be greater than (or, at least, close to the maximum values of) the extant Apennine wolves. This is only the case for the body length estimate. However, for the withers height an underestimated value was expected, as Harcourt's (1974) methodology had been elaborated for prehistoric domestic dogs rather than for the wolves. Discrepancies between the body mass and length of the other two estimates, elaborated by Boudadi-Maligne (2010) for Pleistocene wolves, might be explained with the relative exiguity of the Apennine wolves sample. Alternatively and more likely, the combined utilisation of actually measured values (Ciucci and Boitani, 2003) and estimates from the sample of extant wolves of the PNALM, might have caused a slight overestimation of the body length, as well as a slight underestimation of the body mass.

Acknowledgements

We wish to thank Paola Tollis of the Ente Autonomo Parco Nazionale d'Abruzzo, Lazio e Molise of Pescasseroli. We also wish to thank Charlotte Rowley for English corrections. Finally, we are grateful to the anonymous reviewers of this manuscript for their thoughtful and constructive comments that helped us enhance the quality of the paper.

Appendix A. Appendix A

List of the examined specimens:

- specimen 2823: 2 first and 2 second upper incisors, left third upper incisor, left upper canine, left first upper premolar, 2 mandibles with all teeth, atlas, axis, 5 cervical, 12 thoracic, 3 lumbar, 3 sacral and 3 caudal vertebrae, 4 sternal segments, 22 ribs, right scapula, 2 clavicles, 2 humeri, 2 radii, left ulna, carpal bones, 2 first, 1 right second, 1 left third, 1 right fourth and 2 fifth metacarpal bones, fragmented left coxal, left femur, 2 tibiae, left fibula, left calcaneus, left talus, tarsal bones, left second, 2 third, right fourth and 2 fifth metatarsal bones, 12 first, 10 second and 5 third phalanges (specimens from n. 2823/1 to 2823/124);
- other Grotta Mora Cavorso wolf remains (specimens n. Bb3, Bc3, 06est, 105B3, 1185, 1836, 1852, 2744, 2755, 2756, 2924, 2927 and some without number):
- ingarano (specimens n. 508, 509, 511, 634, 635,915 e 5095) and Avetrana (specimens n. A8C1, A8C4, 8-13, 8-17 and some without number) stored in the Department of Earth Science of "Sapienza" University of Rome;
- *C. lupus italicus* (specimens n. 112, 113, 122, 123, 125, 126, 128, 194, 197, 200, 207 and 221) stored at the Scientific Service Office of "Ente Autonomo Parco Nazionale d'Abruzzo, Lazio e Molise" of Pescasseroli.

References

- Bernardini, A., Guj, I., Lollobrigida, F., Sanfilippo, B., 2005. Guida ai servizi delle aree naturali protette del Lazio - Parco Regionale Monti Simbruini. Regione Lazio, 98 p.
- Bertè, D.F., Pandolfi, L., 2014. *Canis lupus* (Mammalia, Canidae) from the Late Pleistocene deposit of Avetrana (Taranto, southern Italy). Riv. Ital. Paleontol. S. 120, 367–379.
- Biddittu, I., Cassoli, P., Malpieri, L., 1967. Stazione musteriana in Valle Radice nel Comune di Sora (Frosinone). Quaternaria 9, 321–348.
- Bonifay, M.F., 1971. Carnivores quaternaires du Sud-Est de la France. Muséum National d'Histoire Naturelle 2, Paris, 377 p.
- Boscato, P., 1994. Grotta Paglicci: la fauna a grandi mammiferi degli strati 22-24 (Gravettiano antico Aurignaziano). Riv. Sc. Preist 46, 145–176.
- Boudadi-Maligne, M., 2010. Les Canis pléistocènes du Sud de la France: approche biosystématique, évolutive et biochronologique. Thèse, Univ. Bordeaux 1, 451 p.
- Boudadi-Maligne, M., 2012. Une nouvelle sous-espèce de loup (*Canis lupus maximus* nov. subsp.) dans le Pléistocène supérieur d'Europe occidentale. A new subspecies of wolf (*Canis lupus maximus* nov. subsp.) from the Upper Pleistocene of western Europe. C. R. Palevol 11, 475–484.
- Cassoli, P.F., Tagliacozzo, A., 1991. Considerazioni paleontologiche, paleoecologiche e archeozoologiche sui macromammiferi e gli uccelli dei livelli del Pleistocene superiore del Riparo di Fumane (VR). Scavi 1988/91. Boll. Mus. Civico Storia Nat. Verona 18, 349–445.
- Cassoli, P.F., Tagliacozzo, A., 1994. I macromammiferi dei livelli tardopleistocenici delle Arene Candide (Savona, Italia): considerazioni paleontologiche e archeozoologiche. Quaternaria Nova 4, 101–262
- Ciucci, P., Boitani, L., 2003. Canis lupus Linnaeus, 1758. In: Boitani, L., Lovari, S., Vigna Taglianti, A. (Eds.), Fauna d'Italia. Mammalia III. Carnivora-Artiodactyla. Calderini, Bologna, pp. 20–47.

- De Giuli, C., 1983. Le faune pleistoceniche del Salento. 1. La fauna di San Sidero 3. Quaderni del Museo Comunale di Paleontologia di Maglie 1, 45–84
- Germonpré, M., Lázničková-Galetová, M., Losey, R.J., Räikkönen, J., Sablin, M.V., 2015. Large canids at the Gravettian Předmostí site, the Czech Republic: The mandible. Ouat. Internat. 359/360. 261–279.
- Gipson, P.S., Ballard, W.B., Nowak, R.M., Mech, L.D., 2000. Accuracy and Precision of Estimating Age of Grey Wolfes by tooth Wear. J. Wildl. Manag. 64, 752–758.
- Harcourt, R.A., 1974. The Dog in Prehistoric and Early Historic Britain. J. Archaeol. Sci. 1, 151–175.
- Lapini, L., Brugnoli, A., Krofel, M., Kranz, A., Molinari, P., 2010. A grey wolf (*Canis lupus* Linnaeus, 1758) from Fiemme Valley (Mammalia, Canidae; north-eastern Italy). Boll. Mus. St. Nat. Venezia 61, 117–129.
- Martini, F., Sala, B., Bartolomei, G., Tonon, M., Cattani, L., 1974. La grotta Tina a Marina di Camerota (Salerno), BPI 81, 27–79.
- Mech, L.D., Boitani, L., 2010. Canis lupus, The IUCN Red List of Threatened Species. Version 2015.2. (www.iucnredlist.org. Downloaded on 01 September 2015).
- Palombo, M.R., Anzidei, A.P., Arnoldus-Huyzendveld, A., 2003. La Polledrara di Cecanibbio: one of the richest *Elephas (Palaeoloxodon)* antiquus sites of the late Middle Pleistocene in Italy. Deinsea 9, 317–330
- Pandolfi, L., Petronio, C., Salari, L., 2013. Catastrophic death assemblages from the Late Pleistocene of Italy: the case of Avetrana karst filling (Taranto, southern Italy). Riv. Ital. Paleontol. S. 119, 109–124.
- Petronio, C., Bellucci, L., Martinetto, E., Pandolfi, L., Salari, L., 2011. Biochronology and palaeoenvironmental changes from the Middle Pliocene to the Late Pleistocene in central Italy. Geodiversitas 33, 485–517
- Petronio, C., Petrucci, M., Salari, L., 2006. La volpe nel Pleistocene superiore della Puglia: indicazioni paleoambientali. Boll. Mus. Civ. Stor. Nat. Verona, Geol.-Paleont,-Preist. 30, 59–78.
- Riedel, A., 1977. I resti animali della Grotta delle Ossa (Škocjan). Atti Mus. Civ. Stor. Nat. Trieste 30, 125–208.
- Rolfo, M.F., Lelli, R., Martinez Labarga, C., Passacantando, D., Scorrano, G., Salari, L., Rickards, O., 2012. La comunità neolitica di Grotta Mora Cavorso a Jenne (Roma): osservazioni deposizionali, paleobiologiche e faunistiche. Atti del 10° Incontro di Studi sulla Preistoria e Protostoria in Etruria "L'Etruria dal Paleolitico al Primo Ferro Lo stato delle ricerche", vol. I. Milano, pp. 131–143.
- Rolfo, M.F., Achino, K.F., Fusco, I., Salari, L., Silvestri, L., 2013. La grotta Mora Cavorso a Jenne (Roma). I livelli dell'antica-media età del Bronzo. Riv. Sci. Preist. 63, 95–123.
- Rolfo, M.F., Achino, K.F., Fusco, I., Salari, L., Silvestri, L., 2016. Reassessing human occupation patterns of the Inner Central Apennines in Prehistory: the case-study of Grotta Mora Cavorso. JAS Report 7, 358–367, http://dx.doi.org/10.1016/j.jasrep.2016.05.005.
- Rustioni, M., Mazza, P., Abbazzi, L., Delfino, M., Rook, L., Petrucci, S., Vianello, F., 1994. The Würmian fauna from Sternatia (Lecce, Apulia, Italy). B. Soc. Paleontol. Ital. 33 (2), 279–288.
- Salari, L., Passacantando, D., Rolfo, M.F., 2011. First data on the Latest Pleistocene Mammals from Mora Cavorso Cave (Jenne, Latium, central Italy). Il Quat. 24, 131–140.
- Salari, L., Rolfo, M.F., Petronio, C., 2014. The Late Pleistocene Apennine chamois from Grotta Mora Cavorso (Simbruini Mountains, central Italy). Riv. Ital. Paleontol. S. 120, 381–408.
- Sansalone, G., Bertè, D.F., Maiorino, L., Pandolfi, L., 2015. Evolutionary trends and stasis in carnassial teeth of European Pleistocene wolf Canis lupus (Mammalia, Canidae). Quat. Sci. Rev. 110, 36–48.
- Sardella, R., Bertè, D., Iurino, D.A., Cherin, M., Tagliacozzo, A., 2014. The wolf from Grotta Romanelli (Apulia, Italy) and its implications in the evolutionary history of *Canis lupus* in the Late Pleistocene of Southern Italy. Quat. Int. 328, 179–195.
- Tedford, R.H., Wang, X., Taylor, B.E., 2009. Phylogenetic systematics of the North American fossil Caninae (Carnivora: Canidae). Bull. Am. Mus. Nat. Hist. 325. 1–218.
- Toschi, A., 1965. Mammalia. Lagomorpha, Rodentia, Carnivora, Artiodactyla, Cetacea. Fauna d'Italia, Vol. VII. Calderini, Bologna, Italy, 647
- Tozzi, C., 1970. La Grotta di S. Agostino (Gaeta). Riv. Sci. Preist. 25, 3–87. von den Driesch, A., 1976. A guide to the measurement of animal bones from archaeological sites. Bull. Peabody Mus. Nat. Hist. 1, 1–137.