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The wolf from Grotta Mora Cavorso (Simbruini mountains, Latium) within the evolution of *Canis lupus* L., 1758 in the Quaternary of Italy

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ABSTRACT

This paper describes the Late Pleistocene and Holocene remains of *Canis lupus* from Grotta Mora Cavorso (Latium, Italy), with a particular focus on the anatomically connected skeleton found in Layer 7, radiometrically dated to over 43,500 years BP and correlated with Marine Isotopic Stage 3. The studied specimens were compared with wolf remains collected from numerous Middle and Late Pleistocene and Holocene sites in Italy, France, Austria and Slovenia. Additional comparisons were made with a sample of the extant Apennine wolf, *Canis lupus italicus*. The Late Pleistocene and Holocene wolves from Grotta Mora Cavorso range between 6 and 10 years of age at death, 64–75 cm in height at the withers, 150–162 cm in body length, and 30–39 kg in body mass. They are morphometrically close to *Canis lupus maximus*, a Late Pleistocene chrono-subspecies of France. The late Middle and Late Pleistocene wolves of Italy show a great variability in body size. This prevents the recognition of a progressive increase of size in Italian wolves with any resulting biochronological implications. The Holocene reduction in body size of the extant Apennine wolf was more recent than previously thought, probably because of genetic isolation, and the rarefaction and subsequent local extinction of large-sized prey, such as red deer. In addition, the 6 year old anatomically connected specimen discovered at Grotta Mora Cavorso, probably a female, allows some considerations on the functional morphology of Pleistocene wolves.

1. Introduction

According to Brugal and Boudadi-Maligne (2011) a dimensional trend characterizes the Pleistocene genus *Canis*, from *Canis etruscus* Forsyth Major, 1877 to *Canis mosbachensis* Soergel, 1925 and then *Canis lupus* Linnaeus, 1758 (see also Torre, 1979; Rook and Torre, 1996; Sotnikova, 2001; Cherin et al., 2013; Flower and Schreve, 2014). A similar trend would have involved the evolution of *C. lupus* in Western Europe, with a steady increase in body size from their first appearance to the so-called "Würm maximum" *Auctorum* (see Boudadi-Maligne, 2010; Boudadi-Maligne, 2012).

The earliest occurrences of *Canis lupus* are during the Middle Pleistocene at Olyor (Eastern Siberia, Russia), Cripple Creek Sump (Alaska, U.S.A.) and Old Crow (Yukon, Canada), indicating the probable origin of the modern wolf in the early Middle Pleistocene of Beringia (Sher, 1986; Tedford et al., 2009). In Western Europe this species first occurs in the second half of Middle Pleistocene, at Lunel-Viel (Hérault, France), correlated to the Marine Isotope Stage (= MIS) 11-10 (Brugal and Boudadi-Maligne, 2011; Bertè and Pandolfi, 2014). Based on the earliest remains from Lunel-Viel, the chrono-subspecies *Canis lupus lunellensis* Bonifay, 1971 was described as very similar to (but smaller than) extant wolves (Bonifay, 1971; Boudadi-Maligne, 2012); afterwards, based on the remains from Santenay (Côte d'Or, France; MIS 6/5), the chrono-subspecies *Canis lupus santenaisiensis* Argant, 1991 was described as of intermediate size (Argant, 2009), while the chrono-subspecies *Canis lupus maximus* Boudadi-Maligne, 2012 from Jaurens (Corrèze, France; MIS 3), was of very great size (Boudadi-Maligne, 2012).

In Italy, *C. lupus* occurs for the first time in the late Middle Pleistocene at Polledrara di Cecanibbio (Rome), correlated with MIS 10/9 (Gliozzi et al., 1997; Anzidei et al., 2012; Marra et al., 2014). Records of *C. lupus* are relatively abundant in the Late Pleistocene of Italy, under both temperate-warm and cold climate conditions, and the wolf

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persists into the Holocene (Petronio et al., 2007, 2011; Bertè and Pandolfi, 2014; Sansalone et al., 2015).

Today, the wolf is widely distributed across Eurasia and North America in a variety of habitats and with several subspecies. However, it shows notably restricted ranges in Europe, particularly in central-western regions, where the populations are extremely fragmented and their spread is strongly limited by human activities (Ciucci and Boitani, 2003; Mech et al., 2010), in contrast to their widespread Late Pleistocene distribution. In Italy, the wolf is considered an endangered species; after local extinctions of *C. lupus* in the Alps and in Sicily between 1920 and 1940, the Apennine wolf, *Canis lupus italicus* Altobello, 1921, reached a historic low in the 1970s (Zimen and Boitani, 1975; Nowak and Federoff, 2002; Mech et al., 2010). Today, it is vulnerable but present throughout the Apennines, part of the Western Alps and probably also in North-Eastern Italy (Ciucci and Boitani, 2003; Lapini et al., 2010; Marucco et al., 2010). It is also found in the Simbruini Mountains, mainly in wooded areas between 800 and 1600 m in altitude with access to pastures and valleys (Bernardini et al., 2005).

Recently, several studies have focused on the evolution and the palaeoecology of late Middle and Late Pleistocene *C. lupus* in Italy, based on the morphometry of the teeth and/or of the skull (e.g., Bertè and Pandolfi, 2014; Sardella et al., 2014; Sansalone et al., 2015), but none concerned the post-cranial bones.

The Late Pleistocene and Holocene wolf remains from Grotta Mora Cavorso (Jenne, Latium, Central Italy; hereafter GMC) are described in this paper. In particular, the finding of an anatomically connected skeleton (thereinafter GMC 2823) is an exceptional and interesting case study. Taphonomic observations and preliminary osteometric data of GMC 2823 are in Gatta et al. (2016). This find stimulated the analysis of all the wolf remains from GMC and the comparison with samples of Pleistocene, Holocene and extant wolves. The following data could provide new insights and considerations on the morphometric variability of the species through time.

2. Archaeological setting

GMC (Fig. 1) 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., 2009, 2012, 2016). Excavations of the entrance room started in 2007, providing interesting information on a long-established human frequentation of the site (Fig. 1B), including a Late Pleistocene sequence (Salari et al., 2011, 2014). In particular, soundings B1, B2, C and D (in Room 1, Room 2 and in the duct that connects them; Fig. 1C) held, with some discontinuities, archaeological and palaeontological finds ranging from the Late Pleistocene to historical times (Rolfo et al., 2013, 2016, and references therein).

Room 1 (sounding B2) revealed Holocene levels (Layers 1–4) archaeologically associated with late Antiquity (5-6th centuries AD), the Bronze Age (3762 ± 340 BP, CNR Montelibretti - 849C), the Neolithic (6505 ± 50 BP, CEDAD Lecce - LTL6124A) and the early Holocene (Preboreal or Boreal chronozone). In these layers, many artefacts and the bones of domestic and wild species were found, including wolf remains of both the Bronze Age and historical periods (Rolfo et al., 2013, 2016, and references therein).

Layer 5 is the most recent Pleistocene layer, radiometrically dated to 13,460 ± 50 BP (CNRS Lyon – 4568), and contained artefacts of the Epigravettian flint industry and abundant Lateglacial mammal remains, particularly *Marmota marmota*, as well as by *Cervus elaphus elaphus*, *Capra ibex*, *Rupicapra pyrenaica ornata*, *Lepus* sp., *Sus scrofa*, *Capreolus capreolus*, rare small carnivores, birds and microvertebrates. Layer 6 was about 60-cm thick and did not contain human artefacts. According to its stratigraphic position and to its faunal assemblage, characterized by the remarkable presence of *Microtus arvalis*, followed by *Arvicola amphibius* and rare remains of *Lepus* sp., *Martes martes*, *M. marmota*, *C. ibex*, *R. pyrenaica ornata*, *Bos primigenius*, *Mustela putorius*, various microvertebrates and birds, it can be referred to the Last Glacial Maximum (= LGM) (Salari et al., 2011, 2014; Rolfo et al., 2016).

The subsequent Layer 7 did not hold human artefacts and showed a significant chronological hiatus as well as different climate conditions. Abundant *Lepus* sp. was found along with *C. ibex*, *C. elaphus elaphus*, *R. pyrenaica ornata*, *M. marmota*, *S. scrofa*, *A. amphibius*, *Glis glis*, *M. arvalis*, other microvertebrates, birds and several remains of *C. lupus*, including GMC 2823 (Fig. 2), found in the deepest portion of this layer. Radiometric dating performed on a fragment of wolf skull yielded an age older than 43,500 years BP (Beta Analytic Inc., Miami - 365375). The abovementioned radiometric dating and the mammal assemblage allowed this layer to be correlated with temperate oscillations of the MIS 3 (Salari et al., 2014, 2015; Rolfo et al., 2016). A few *C. lupus* remains have also been retrieved in other sectors of the cave (soundings B1 and D; Salari et al., 2011; Rolfo et al., 2016) and therefore support the view that the wolf occurs at GMC over 43,500 years BP and its occurrence is continuous across the MIS 3 (at least 5 individuals); it then disappears during the LGM to subsequently appear sporadically in the Lateglacial (2 individuals), early Holocene (1 individual), Bronze Age (1 individual) and finally in historical times (1 individual).

3. Materials and methods

3.1. Wolf remains from GMC

All the fossil remains of *C. lupus* from GMC are located in the Laboratory of Prehistory of the University of Rome "Tor Vergata". The bone remains of GMC 2823, i.e. 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, 10 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, 8 tarsal bones, left second, 2 third, right fourth and 2 fifth metatarsal bones, 12 first, 10 second and 5 third phalanges. These are numbered from 2823/1 to 2823/124; the other remains (skull, mandible and limb bones, sometimes fragmented) are the specimens n. 1852, 2744, 2755, 2756, 2928, 2929, 2930, 2931, 2932, 2933, 2936, 2937, 2938, 2939, 2940, 2941, 2942, 2943, 2944, 2945, 3051, 3052, 3053, 3054, 3055, 3056, US105, 105top, 06est, Bb3 and some without number from Layer 7 (MIS 3), the mandible fragments n. 2934 and 2935 and some isolated teeth without numbers from Layer 5 (Lateglacial), the maxillary fragment n. 1835 from Layer 4 (early Holocene) and the mandible n. 1185 from Layer 1 (Holocene, late Antiquity). Measurements of selected elements, expressed in mm, are reported in the Supplementary Material.

3.2. Comparative samples and methodology

Morphological and morphometric features of the *C. lupus* remains from GMC have been compared with late Middle and Late Pleistocene and Holocene wolf remains from several sites in Italy, Slovenia, Austria and France (Table S1), as well as with specimens belonging to the extant Apennine wolves, *C. lupus italicus* (specimens n. 112, 113, 122, 123, 125, 126, 128, 194, 197, 200, 207 and 221) housed at the Scientific Service Office of Ente Autonomo Parco Nazionale d'Abruzzo, Lazio e Molise (hereafter PNALM) in Pescasseroli (L'Aquila, Abruzzi).

Measurements of fossil remains from the sites reported in Table S1 are taken from the literature, in particular from Biddittu et al. (1967), Riedel (1968, 1974, 1977, 1985), Tozzi (1970), Martini et al. (1974), Cassoli (1977), Caloi and Palombo (1978), Sala (1979), De Giuli (1983), Vigne et al. (1986), Capasso Barbato and Minieri (1987), Wilkens (1988, 1990, 1997, 1999), Cassoli and Tagliacozzo (1991), Guerreschi et al. (1992), Bon and Boscato (1993), Boscato (1994), Cassoli and Tagliacozzo (1994a, 1994b), Rustioni et al. (1994), Barbera et al. (1995), Sala and Barbi (1996), Pacher and Döppes (1997),