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Canis mosbachensis (Canidae, Mammalia) from the Middle Pleistocene of Contrada Monticelli (Putignano, Apulia, southern Italy)

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KEY WORDS - Carnivorans, Taxonomy, Biochronology, Paleobiogeography.

ABSTRACT - Herein we describe for the first time a canid partial cranium from the Contrada Monticelli site. Morphological and biometrical studies allow the fossil remains to be referred to the Middle Pleistocene wolf Canis mosbachensis*. Associated taxa include* Paleoloxodon antiquus*,* Stephanorhinus hundsheimensis*, cervids, equids and bovids, whose biochronological occurrence allows the site to be referred to the Galerian Mammal Age. Diagnostic characters normally used to distinguish* Canis mosbachensis *from* Canis lupus *are herein discussed. These carnivorans show a wide range in body-size and morphological variability, related to an extensive geographical distribution. The analyzed fossil can be considered as the smallest European specimen referable to the Mosbach wolf and represents the southernmost occurrence of this taxon in Italy.*

RIASSUNTO - [*Canis mosbachensis* (Canidae, Mammalia) dal Pleistocene Medio di Contrada Monticelli (Putignano, Puglia, Italia meridionale] *- In questo lavoro descriviamo per la prima volta un cranio parziale di canide dal sito di Contrada Monticelli. Lo studio morfologico e biometrico ha permesso di attribuire il reperto al lupo del Pleistocene Medio* Canis mosbachensis*. L'esemplare studiato è stato trovato in associazione con* Palaeoloxodon antiquus*,* Stephanorhinus hundsheimensis*, cervidi, equidi e bovidi, la cui distribuzione biocronologica permette di attribuire il deposito al Galeriano. Vengono qui discussi i caratteri diagnostici che permettono di distinguere* Canis mosbachensis *da* Canis lupus*. Questi carnivori presentano un'ampia variabilità dimensionale e morfologica, legata alla loro ampia distribuzione geografica. Il fossile in esame può essere considerato il più piccolo esemplare europeo riferibile al lupo di Mosbach e rappresenta la testimonianza più meridionale di questa specie in Italia.*

INTRODUCTION

The site of Contrada Monticelli is located about 5 km south-east of Putignano (Bari) (Fig. 1), near the crossroad between the Strada Statale 172 Putignano-Alberobello and the Strada Comunale Monticelli. In the late 1970s, the excavation for building a house exposed a deposit bearing abundant fossil vertebrate bones. The works were followed by E. Luperto Sinni, who guided the rescue of the materials. The fossiliferous deposit consisted by the filling of a karst cavity (locally known as "grave") formed into a Cretaceous calcarenite (Altamura limestones Formation).

The deposit was about 11 m thick, consisting of reddish sands and some interbedded cinerite levels (Luperto Sinni & Colucci, 1985). Unluckily, the fossil remains were in a poor state of preservation. Luperto Sinni & Colucci (1985) suggested that such a condition could have been related to a prolonged transport of bones prior to final deposition. The faunal assemblage includes *Palaeoloxodon antiquus* (Falconer, 1857), *Stephanorhinus hundsheimensis* Tuola, 1902, bovids, equids, cervids and the canid cranium described herein (Mazza & Varola, 1999). *Palaeoloxodon antiquus* is represented by a long tusk, the other ungulates are poorly preserved and no clearly diagnostic elements have been found. Rhinoceros is the best represented taxon (a cranium, a mandible, and some limb bones) and the only one that up to now has been studied in detail (Mazza & Varola, 1999). The co-occurrence of the straight tusked elephant and the Hundsheim rhinoceros suggests that this assemblage can be referred to the Galerian Mammal Age (Middle Pleistocene).

The faunal assemblage includes a partial skull of the middle-sized wolf *Canis mosbachensis* Soergel, 1925. Despite only the palatal portion has been preserved, a biometrical comparison of the dental remains is possible. Since at present this fossil represents the southernmost evidence of this canid in Italy, description of the fossil and its comparison with other Early and Middle Pleistocene fossils from Italy and Europe are worthy of note. This study aims to represent a starting point for further analyses on wolf evolution; we will be focusing in particular in this article on the relationships between *Canis mosbachensis* and *Canis lupus* Linnaeus, 1758.

MATERIAL AND METHODS

The specimen QF28, here described for the first time, is stored at the Dipartimento di Scienze della Terra e Geoambientali, Università di Bari (Italy). Craniodental measurements of the studied specimen were taken to the nearest 0.01 mm with a digital calliper. Due to the bad state of preservation and the incompleteness of QF28, only few measures were collected following Driesch (1976): two for the cranium and seven for the teeth (Tab. 1). The biometric data of wolf from Contrada Monticelli were

Fig. 1 - Location of Contrada Monticelli (Apulia, southern Italy).

compared with various specimens of *C. mosbachensis* from the Early-Middle Pleistocene of Italy (Pirro Nord, Cerè, Soave, Loreto) (Caloi & Palombo, 1979; Capasso Barbato et al., 1998; Petrucci et al., 2013; Bertè, 2014; Ghezzo et al., 2014), Europe (Apollonia, Cueva Victoria, Gombaszöeg, Huescar, Hundsheim, L'Escale, Punta Lucero, Petralona, Stranskà Skàla, Untermassfeld, Vallparadìs, Venta Micena, Vertesszöllös, Westbury sub-Mendip, Wurzburg) (Kretzoi, 1938; Kurtén & Poulianos, 1977; Alcalá & Morales, 1989; Janossy, 1990; Koufos & Kostopoulos, 1997; Sotnikova, 2001; Boudadi-Maligne, 2010; Baryshnikov, 2012; Gomèz-Olivencia et al., 2015; Bartolini Lucenti et al., 2017), Levant ('Ubediya) (Martínez-Navarro et al., 2009) and Caucasus (Kudaro) (Boudadi-Maligne, 2010). The statistical analysis was performed with the Sofware R (R Core Team, 2000).

SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowditch, 1821
Family Canidae Fischer von Waldheim, 1817
Subfamily Caninae Fischer von Waldheim, 1817
Tribe Canini Fischer von Waldheim, 1817

Genus *Canis* Linnaeus, 1758
Type species *Canis mosbachensis* Soergel, 1925

Canis mosbachensis Soergel, 1925
(Fig. 2)

Referred specimen - Incomplete cranium QF28 from Contrada Monticelli, including the palatal area with left M^1-M^2 and right P^4-M^2 (Fig. 2).

Description - The state of preservation is poor. Only the palate and the basicranium are preserved, while the whole dorsal portion as well as the zygomatic arches are missing. The bones of the ventral part are strongly fragmented and partially embedded in a brown-reddish limestone (Fig. 2). The caudoventral portion is strongly damaged. Despite both the tympanic bullae are broken, in section they appear to be rounded and expanded.

The palate is narrow and elongated, the upper teeth are missing except for the left M^1-M^2 and right P^4-M^2. The upper toothrow is long, with the alveoli of the canine, the P^1 and the P^2 that lie on the same axis. The latter is less curved in correspondence of the P^3-P^4 junction and shows a more abrupt angle between P^2-P^3. All the alveoli are filled by the sediment with the exception of the left P^4 whose broken roots are still in situ (Fig. 2). The anterior palatine foramina are elongated and their caudal border extends to the caudal edge of the canine alveolus.

In occlusal view, P^4 has a well-developed protocone, the paracone is high and stout with slightly worn apex, while in lateral view the paracone is mesially inclined. M^1 has a well-defined labial cingulum, the paracone is larger than the metacone, the protocone, the metaconule and the hypocone are well evident and the basin of the tooth is deep. M^2 is relatively large, in occlusal view it is sub-rectangular shaped with four evident cusps (paracone, metacone, protocone and metaconule). In all the teeth the enamel is crossed by several narrow fracture lines and some small fragments are missing.

The sexual dimorphism in the genus *Canis* is often quite modest, but males generally have larger body size, a more pronounced sagittal crest, longer muzzle and wider frontal bones than females (Boitani et al., 2003). Due to the bad state of preservation and the lack of the whole dorsal portion of the cranium, these characters are not observable, therefore it was not possible to define the sex of the specimen from Contrada Monticelli. Despite the small size, the teeth are permanent and show a slight wear of the cusps, indicating an adult but not an old individual. Unfortunately, other diagnostic features (such as cranial suture closures) are unavailable.

Measurements - See Tab. 1.

Morphometric comparison - The size and proportions of the teeth in the described specimen are compared to those of *C. mosbachensis* reported in scientific literature (Kretzoi, 1938; Kurtén & Poulianos, 1977; Caloi & Palombo, 1979; Alcalá & Morales, 1989; Janossy, 1990; Koufos & Kostopoulos, 1997; Sotnikova, 2001; Martínez-Navarro et al., 2009; Boudadi-Maligne, 2010;

Cranium		Teeth		
Total basal length	154.9	P^4	length	19.3
Greatest width of the occipital condyles	31.2		width	6.4
			greatest width	8.2
		M^1	length	11.0
			width	14.6
		M^2	length	6.2
			width	10.4

Tab. 1 - Craniodental measurements (mm) of *Canis mosbachensis* Soergel, 1925 from Contrada Monticelli (Apulia, southern Italy).

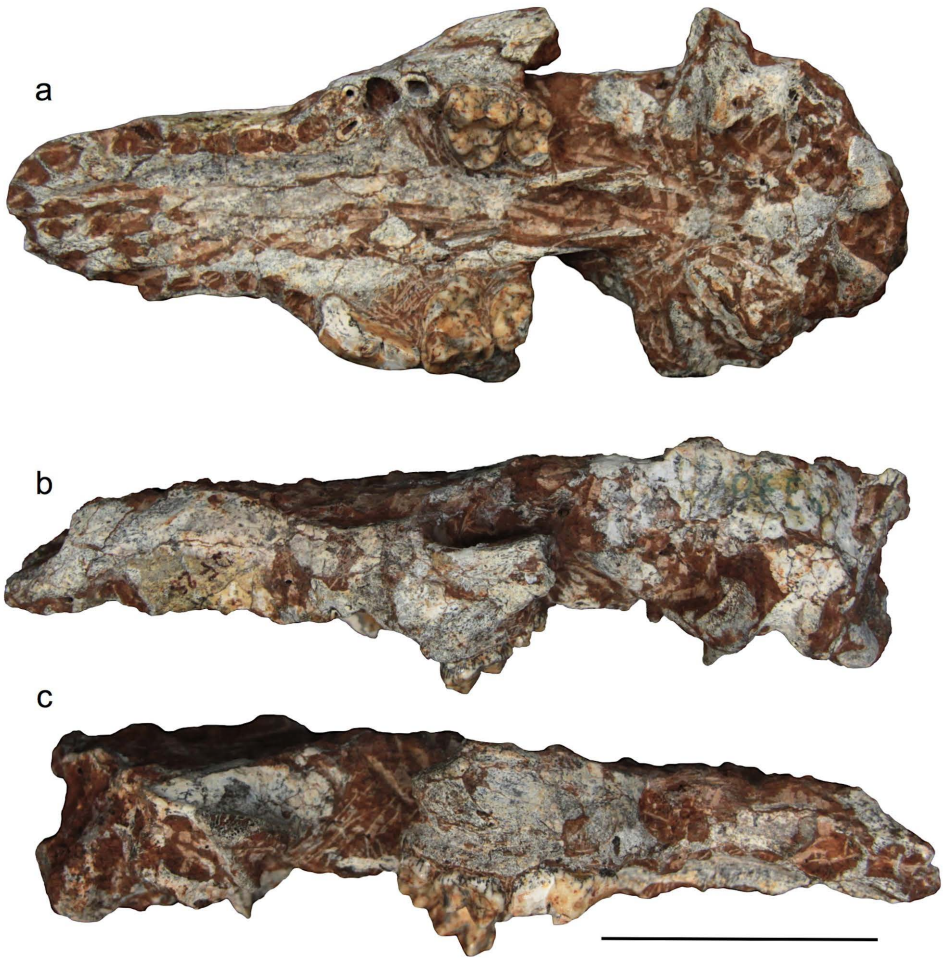

Fig. 2 - (Color online) *Canis mosbachensis* Soergel, 1925 (QF28) from Contrada Monticelli (Apulia, southern Italy) in: a) occlusal, b) left lateral and c) right lateral views. Scale bar corresponds to 50 mm.

Baryshnikov, 2012; Petrucci et al., 2013; Bertè, 2014; Ghezzo et al., 2014; Gomèz-Olivencia et al., 2015; Bartolini Lucenti et al., 2017). Standard bivariate plots of width vs. length of the P^4-M^2 show a distinctly small size for the QF28 specimen, as evidenced by the proportions of each tooth (Fig. 3).

All the measurements fall within the lowest values recorded for this taxon, with a difference of about 5 mm with respect to the larger specimens of the available sample (Cerè Cave) and about 4 mm from the sample from L'Escale (Fig. 3). Only the upper carnassial is comparable in size with the smaller specimens from the Early Pleistocene site of Pirro Nord, while M^1 and M^2 are dimensionally smaller (Fig. 3a). The upper molars are very small and resemble in size and shape those of *Canis* sp. reported from the Middle Pleistocene site of Loreto (South Italy) (Caloi & Palombo, 1979) (Fig. 3b-c).

THE MOSBACH WOLF

The original description of *C. mosbachensis* Soergel, 1925 is based on a mandible fragment with a complete P_4. The incomplete status of the type specimen generated confusion in scholars to identify diagnostic characters for this taxon (Musil, 1972) which triggered a long and complex debate about the taxonomical status of this canid. Several authors (Soergel, 1925; Musil, 1972; Sotnikova, 2001; Tedford et al., 2009; Baryshinokov, 2012; Ghezzo et al., 2014) regarded *C. mosbachensis* as a distinct species, while others (Bonifay, 1971; Pons-Moyà, 1981; Argant, 1991; Brugal & Boudadi-Maligne, 2011) suggested it is an advanced form of *Canis etruscus* Forsyth Major, 1877 (Bonifay, 1971; Agustí et al., 1986) or an ancestral form of *Canis lupus* (Thenius, 1954; Adam, 1959; Schutt, 1974; Kurtén & Poulianos, 1977; Pons-Moyà, 1987; Alcalà & Morales, 1989). Moreover, some authors suggested that the Mosbach wolves can be considered instead as a distinct form linked to modern jackals (Rook & Torre, 1996; Garrido & Arribas, 2008). Despite this long debate, there is a general consensus in considering *C. mosbachensis* as the ancestor of *C. lupus* (Torre, 1967; Sotnikova, 2001; Sotnikova & Rook, 2010; Sardella et al., 2014 among others). *Canis mosbachensis* became a common element of the carnivoran guild during the late Early Pleistocene and the Middle Pleistocene (e.g., Sotnikova, 2001; Martínez-Navarro et al., 2009; Petrucci et al., 2013; Bartolini Lucenti et al., 2017). Its first occurrence in the Italian fossil record is reported from the Early Pleistocene site

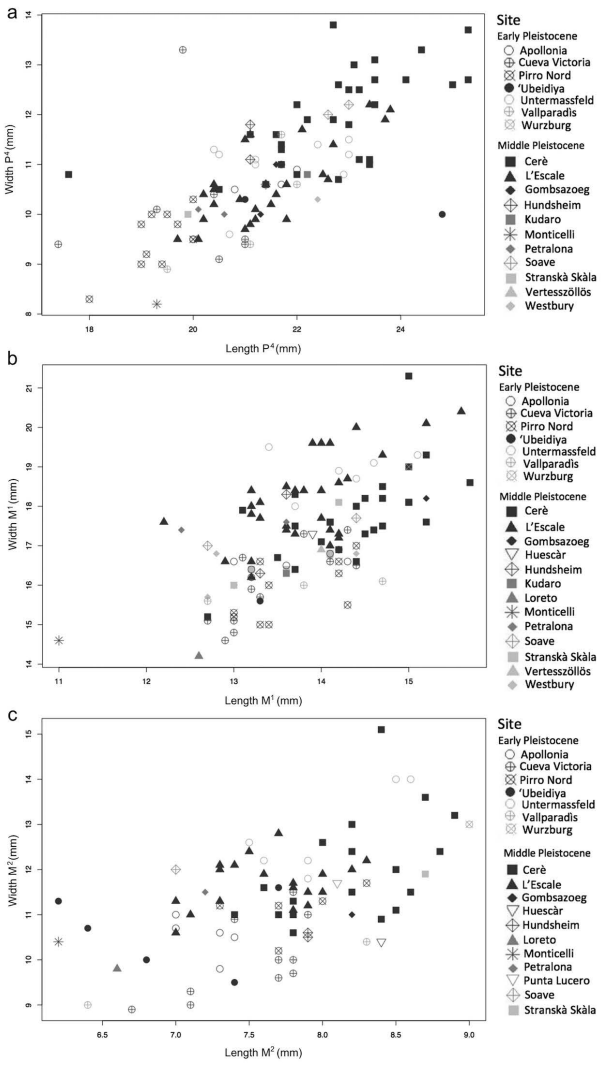

Fig. 3 - Standard bivariate plots of width vs. length of upper dentition of *Canis mosbachensis* Soergel, 1925 from various European localities: a) carnassial; b) first upper molar; c) second upper molar.

of Pirro Nord (Pavia et al., 2012; Petrucci et al., 2013). This canid occurs in several Early and Middle Pleistocene sites (Petrucci et al., 2013; Bertè, 2014; Ghezzo et al., 2014) until the first appearance of "true" *Canis lupus*, that is the bioevent selected to define the beginning of the Aurelian Mammal Age of the Italian large mammal biochronological scale (Gliozzi et al., 1997). The morphological study and statistical analysis of the sample from Cerè Cave, the largest fossil sample of this species, allowed to demonstrate that the intraspecific variability of this taxon is entirely comparable to that of modern *C. lupus* (Ghezzo et al., 2014). According to Bergmann's ecogeographical rule, the Mosbach wolf (as many terrestrial mammals with wide geographical distribution) shows a clinal gradient. In particular, the Early and Middle Pleistocene northern populations (e.g., Untermassfeld and Mosbach) are constituted by larger individuals than all the coeval southern populations (e.g., Venta Micena, L'Escale and Petralona) (Brugal & Boudadi-Maligne, 2011; Bertè, 2014). This clinal variation is similar to that observed both in modern and fossil populations of *C. lupus* (Macdonald & Sillero-Zubiri, 2004; Brugal & Boudadi-Maligne, 2011). In general, the Late Pleistocene "true wolves" are larger and stouter than the Middle Pleistocene ones (Flower & Schreve, 2014). Conversely, late Middle Pleistocene early *Canis lupus*, such as the relatively small and slender *C. lupus lunellensis* Bonifay, 1971 from Lunel Viel (France) (Brugal & Boudadi-Maligne, 2011; Sansalone et al., 2015), overlaps the size and morphology of the Mosbach wolf.

The main characters proposed in literature to distinguish *C. lupus* from *C. mosbachensis* are located in the cranium. These include the muzzle rostrocaudally longer and narrower at the level of the canine alveoli. The Mosbach wolf shows long nasals ending beyond maxillofrontal suture, straight in lateral view. It differs from modern wolves for its flattened frontals, less elevated over the rostrum. Furthermore, *C. lupus* can be distinguished from *C. mosbachensis* for the longer anterior palatine foramina, with the caudal border lying at the level of the distal part to canine alveoli. Regarding dental morphology, the Mosbach wolf shows a relatively longer tooth row, less curved at the P^3-P^4 junction, with mesiodistally more elongated and narrower premolars than in the grey wolf (Fig. 4, Tab. 2). The upper carnassial differs from those of *C. lupus* for a prominent protocone located slightly mesially and a strong lingual cingulum, while the upper first molar has a deeper and larger hypocone basin and a more developed and continuous labial cingulum. Finally, *C. mosbachensis* shows a larger upper second molar than *C. lupus*.

DISCUSSION

The study of the partially preserved cranium from Contrada Monticelli and its comparison with other Early-Middle Pleistocene Mosbach wolves from Italy and Europe, support the attribution to *Canis mosbachensis* proposed by Mazza & Varola (1999).

The biometric comparison of QF28 with the European samples of Mosbach wolf shows very low values for the cranium length and especially for the teeth dimensions, so that the Contrada Monticelli specimen results as the smallest *C. mosbachensis* in the European fossil record. Standard bivariate plots of width vs. length of the M^1-M^2 (Fig. 3) show one additional specimen characterized by reduced molars: the maxillary fragment from the Middle Pleistocene site of Loreto (Apulia, South Italy), which was reported by Caloi & Palombo (1979) as *Canis* sp. In addition to the biometrical similarity, the morphological comparison of the molars also reveals a very strong resemblance of QF28 with the Loreto specimen. In fact, according to Sotnikova (2001), in *C. mosbachensis* M^1 has a well-defined labial cingulum, with a paracone larger than the metacone, the M^2 is relatively large compared to M^1 and, in occlusal view, it is sub-rectangular shaped with four evident cusps. These features are shared by both the specimens and lead us to refer also the Loreto canid to *C. mosbachensis*.

As claimed before, according to Brugal & Boudadi-Maligne (2011), the North European populations of *C. mosbachensis* from Unterssmasfeld and Mosbach, consist of individuals with body size larger than those reported

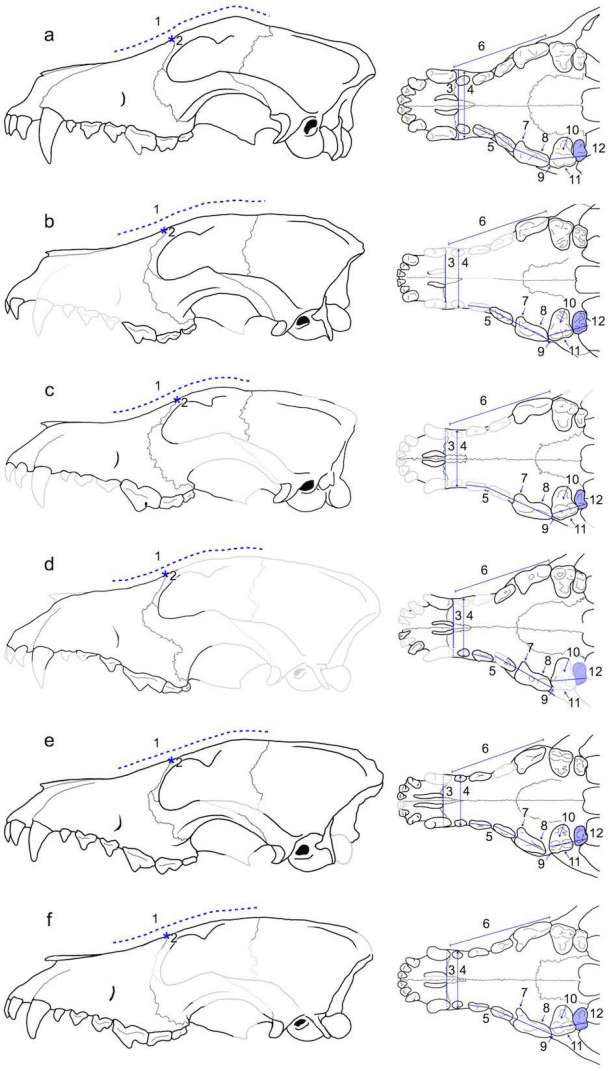

Fig. 4 - (Color online) Craniodental morphological features in normalized crania of: a) extant *Canis lupus* Linnaeus, 1758; b) *Canis lupus* Linnaeus, 1758 from Grotta Romanelli, Italy (Sardella et al., 2014); c) *Canis lupus lunellensis* Bonifay, 1971 from Lunel Viel, France (Bonifay, 1971); d) *Canis mosbachensis* Soergel, 1925 from Cerè Cave, Italy (Ghezzo et al., 2014); e) *Canis mosbachensis* Soergel, 1925 from Cueva Victoria, Spain (Bartolini Lucenti et al., 2017); f) *Canis mosbachensis* Soergel, 1925 from Untermassfeld, Germany (Sotnikova, 2001). Left column: left lateral view; right column: occlusal view. See Tab. 2 for the description of characters.

from South European sites (Venta Micena, Cueva Victoria, L'Escale, Petralona, Apollonia, Pirro Nord), suggesting for this taxon a latitudinal cline. Among the southern forms, the Mosbach wolves from Contrada Monticelli and Loreto are the smallest, and this condition may support the cline hypothesis, though in our opinion more data about the cranial and postcranial size variation would be required.

Both Mosbach and anatomically modern wolves were widespread in Europe during late Middle Pleistocene. A possible sympatry between the two species has been hypothesized by some authors (De Giuli, 1983; Mazza et al., 1992; Bologna et al., 1994; Capasso Barbato & Gliozzi, 1995; Boscato, 2001), although the overlap of many morphological features and biometric values among the last representatives of *C. mosbachensis* and early *C. lupus* makes the distinction very complex (Sardella et al., 2014).

In southern Italy, in particular, such a scenario was suggested mainly on the basis of the fossil record from the Late Pleistocene sites of Apulia. The small wolf found from the lower levels at Grotta Romanelli (Lecce) has been considered by some authors either a golden jackal (Blanc, 1920, 1928) or *Canis mosbachensis* (Sala et al., 1992; Masini & Sala, 2007). Recently, Sardella et al. (2014) considered the peculiar set of craniodental characters

	Characters	*Canis mosbachensis* Soergel, 1925	*Canis lupus* Linnaeus, 1758	Author
1	Frontals	Flat and less elevated above the rostrum	Rounded and elevated above the rostrum	Sotnikova, 2001
2	Nasals	End beyond the maxillofrontal sutura	End before the maxillofrontal suture	Tedford et al., 2009; Bartolini Lucenti et al., 2017
3	Anterior palatine foramina	Short, posterior border lies at or anterior to posterior end of canine alveolus	Long, posterior border lies posterior to canine alveolus	Tedford et al., 2009
4	Palate width at P^1	Narrow	Wide	Tedford et al., 2009
5	Toothrow	Long and less curved in junction of P^3 - P^1	Short and curved in junction of P^3 - P^4	Sotnikova, 2001
6	Premolars	Elongated anteroposteriorly and narrower	Wide	Sotnikova, 2001
7	P^4 protocone	Prominent and located slightly anteriorly	Less prominent	Sotnikova, 2001
8	P^4 lingual cingulum	Large	Small	Sotnikova, 2001
9	M^1 parastyle	Subdued but remains united with preparacrista	Preparacrista directed more anteriorly, lingual to parastyle	Tedford et al., 2009
10	M^1 hypocone basin	Deep and large	Small	Sotnikova, 2001
11	M^1 labial cingulum	Well developed and continuous	Subdued and often incomplete across paracone	Sotnikova, 2001; Tedford et al., 2009
12	M^2	Large	Small	Sotnikova, 2001

Tab. 2 - Diagnostic features of *Canis lupus* Soergel, 1925 and *Canis mosbachensis* Linnaeus, 1758 from the literature.

of this specimen suitable with the variability that can be observed in extant wolves, and noticed similarities with southern distributed forms or the Indian wolf *Canis lupus pallipes* Sykes, 1831.

In addition, also the earliest "true wolf" *Canis lupus lunellensis* is smaller and slender than Late Pleistocene and extant ones, showing a body size similar to Mosbach wolf.

However, the wide geographical distribution together with the uncertain age of some sites, do not allow defining a clear scenario for the evolution and dispersal of the "wolves" during the Middle-Late Pleistocene to the extant forms.

In the past many authors considered the Middle Pleistocene small wolves as a chrono-subspecies of *Canis lupus* (Thenius, 1954; Adam, 1959; Schutt, 1974; Kurtén & Poulianos, 1977; Pons-Moyà, 1987; Alcalá & Morales, 1989), or a chrono-subspecies of the Early Pleistocene Etruscan wolf (Bonifay, 1971; Agustí et al., 1986). Recently many authors focused their studies on the description of new more complete fossil material and on the definition of the diagnostic characters (Boudadi-Maligne, 2010; Berté, 2014; Cherin et al., 2014; Ghezzo et al., 2014; Sardella et al., 2014; Bartolini Lucenti & Rook, 2016; Bartolini Lucenti et al., 2017).

In our opinion, most of these craniodental characters used to describe the "classic" *C. mosbachensis* (Tabs 2-3) could be less marked in some populations, due to geographical, chronological and intraspecific variability of *C. mosbachensis* as well as of the first "true wolves" (Tabs 2-3). As a matter of fact, the Mosbach wolf shares several morphological and biometrical features with the extant wolves, especially with the slender Indian *C. lupus pallipes*. This similarity, highlighted by several authors (Thenius, 1954; Sotnikova, 2001; Sardella et al., 2014), could be related to allometric development of the different craniodental portions as a result of ecological and environmental factors which have affected the body size (Milenković et al., 2010). In addition, the dental variation in these taxa is poorly known and it is not clear if a relationship between the dental size and the complexity of their structures exists, as demonstrated by Szuma (2002) in an extant population of red fox. Finally, it is worth nothing that all the considered diagnostic features are relative to craniodental and mandibular characters, and in general no postcranial elements have been considered for this purposes (see Brugal & Boudadi-Maligne [2011] for a discussion). Therefore, more efforts are required to recognize characters affected by morphological and morphometric variation due to body size, and to distinguish these characters from those of diagnostic value. At the same time, extending the analysis to limb bones and other postcranial element is needed.

CONCLUSIONS

Canids have a conservative body plan and relatively primitive craniodental features, therefore species recognition and classification is a complicated matter also for living species. The Middle Pleistocene wolf taxonomy is affected by these elements too, and the long chronological distribution gets the framework also more complex. Many scientists are putting their attention to the study of wolf evolution in Pleistocene times and any new single fossil can add elements for clarifying this issue. The diagnostic features are still matter of discussion and - up to now - focused on the craniodental characters. The analysis of the available data on the postcranial elements will provide a more detailed framework for improving the diagnosis of this taxon and to estimate the morphological variability within the Middle-Late Pleistocene wolf populations.

The specimen QF28 from the karst filling deposit at Contrada Monticelli, here described for the first time, represents the southernmost occurrence of *Canis mosbachensis* in Italy. This taxonomical determination is confirmed by morphological and morphometric data, and is compatible with the biochronological evidence.

The chronological attribution of the site as defined by the faunal assemblage is coherent with the occurrence of *C. mosbachensis*. The co-occurrence of the straigth-tusked elephant and of the Hundsheim rhinoceros is documented at Isernia La Pineta (Sala, 1996) and at Calorie (Mercure basin) (Cavinato et al., 2001; Petrosino et al., 2014) in a time span included between 0.6 and 0.5 my. Unfortunately, the deposit at Contrada Monticelli does not exist anymore, and a more accurate dating of the site is therefore impossible.

All the recognizable characters of QF28 fit those reported in the literature as diagnostic for *C. mosbachensis.* This set of characters, in our opinion, cannot be considered completely "reliable".

Previous studies highlighted that some characters supposed to be diagnostic for *C. mosbachensis* can be observed also in some *C. lupus* specimens. In particular, some "*mosbachensis* features" can be observed in early wolves (e.g., Lunel Viel, Grotta Romanelli) or modern wolves (e.g., slender Indian and African forms) (Bertè, 2017; Viranta et al., 2017). This overlapping of characters is probably due to the wide geographic distribution of *C. lupus*. The distribution in time and space of *C. mosbachensis* was at least as wide as that of *C. lupus*, and, in addition, the phyletic relationships between these two taxa are expressed by a mosaic of characters not yet firmly defined.

From a morphometric point of view, the specimen QF28 is the smallest *C. mosbachensis* of Europe, a feature that can be explained as a geographic cline according with the Bergmann's rule.

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