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Teeth of *Canis orcensis* n. sp. from Venta Micena, *Canis arnesis* Del Campana, 1913 from the Upper Valdarno, and *Canis mosbachensis* Soergel, 1925 from Piro Nord. Author of photos: Saverio Bartolini Lucenti.

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ABSTRACT

The site of Venta Micena (Orce, Spain), c. 1.6 Ma, preserves one the best paleontological records of the early Pleistocene large mammals fauna in Europe. Here we describe the specimens of the genus *Canis* Linnaeus, 1758 in the context of the late Villafranchian and Epivillafranchian fossil dogs from Eurasia. Anatomical and metric data suggest that the Venta Micena *Canis* form differs from the classical

KEY WORDS

Canis orcensis n. sp.,
carnivora,
Canidae,
late Villafranchian,
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new species.

MOTS CLÉS

Canis orcensis n. sp.,
Carnivora,
Canidae,
Villafranchien supérieur,
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espèce nouvelle.

records of *Canis etruscus* Forsyth Major, 1877 and *Canis arnensis* Del Campana, 1913, and that it forms part of the younger *Canis mosbachensis* Soergel (1925) lineage, also recorded in two slightly younger sites of the Orce site complex, Barranco León and Fuente Nueva-3, dated to *c.* 1.4 Ma. The anatomy of the Venta Micena fossil material shows features that resemble the *Canis* forms from the Caucasian site of Dmanisi, dated to 1.8 Ma, and *Canis ex gr. C. mosbachensis*. Nevertheless, dental peculiarities support the creation of a new chrono-species, *Canis orcensis* n. sp., from the town of Orce. Morphological and paleoecological data suggest that this species probably consumed more vertebrate flesh than other similar sized early Pleistocene canids (i.e., a trend to hypercarnivory), which had more omnivorous dietary habits.

RÉSUMÉ

Une nouvelle espèce de chien du site du Pléistocène inférieur de Venta Micena (Orce, bassin de Baza, Espagne). Le gisement de Venta Micena (Orce, Espagne), 1.6 Ma environ, possède un des plus importants registres paléontologiques de faune de grands mammifères du Pléistocène inférieur d'Europe. Dans ce travail, nous décrivons des spécimens attribués au genre *Canis* Linnaeus, 1758 dans le contexte des chiens fossiles du Villafranchien supérieur et de l'Epivillafranchien d'Eurasie. Les données anatomiques et métriques suggèrent que le *Canis* de Venta Micena diffère des espèces courantes à ces époques, *Canis etruscus* Forsyth Major, 1877 et *Canis arnensis* Del Campana, 1913. Il se place à la base de la lignée plus récente appelée *Canis mosbachensis* Soergel (1925), déjà mentionnée dans deux gisements du complexe d'Orce légèrement plus récents, Barranco León et Fuente Nueva-3, datés d'1,4 Ma environ. L'anatomie primitive du fossile de Venta Micena, avec des caractères semblables à ceux du *Canis* caucasien de Dmanisi, daté de 1,8 Ma, conforte la création d'une nouvelle chrono-espèce de canidé, *Canis orcensis* n. sp., qui prend son nom de la ville d'Orce. Les données paléoécologiques suggèrent que cette espèce consommait plus de viande (i.e., une tendance à la hypercarnivorie) que d'autres canidés de taille semblable du Pléistocène inférieur qui avaient des régimes alimentaires plus omnivores.

INTRODUCTION

The town of Orce (Granada, Baza Basin, SE Spain) is reknown in the paleontological literature since 1981, when the site of Venta Micena was first published (Moyà-Solà *et al.* 1981). Since then, the region of Orce became one of the most important Quaternary paleontological and prehistoric sites of all Europe. In fact, in the site of Barranco León, dated to 1.4 Ma, a deciduous tooth was unearthed, which is at the moment the earliest fossil hominin of the European continent (Toro-Moyano *et al.* 2013). Moreover, this site and Fuente Nueva-3, which is close in age to BL (see review in Palmqvist *et al.* 2016), preserve huge assemblages of Oldowan tools and evidence of anthropic action on large mammal bones, including megafauna (Espigares *et al.* 2013, 2019).

In this context, the site of Venta Micena, found in 1976 by a team directed by J. Gibert, is the best-known paleontological locality of Orce. Dated to *c.* 1.6 Ma, it is an 80-120 cm thick horizontal stratum with *c.* 1 km² of areal extent that encloses a dense accumulation of fossil remains of vertebrates beautifully preserved in micritic limestone (e.g. in the 360 m² surface excavated up to date, >24.000 fossils of large mammals have been unearthed). For this reason, it probably represents the best early Pleistocene paleontological record of all the European continent (Moyà-Solà *et al.* 1987; Martínez-Navarro 1991; Martínez-Navarro & Palmqvist 1995; Palmqvist *et al.* 1996, 1999, 2003, 2008, 2011; Arribas & Palmqvist 1998; Espigares 2010; Martínez-Navarro *et al.* 2011, 2014; Ros-Montoya *et al.* 2012).

THE GENUS *CANIS* IN THE EARLY PLEISTOCENE OF WESTERN EUROPE: A BRIEF INTRODUCTION

Although in eastern Asia the earliest record of *Canis* Linnaeus, 1758 dates to 3.4 Ma (Qiu & Flynn 2013; Qiu & Tedford 2013), the first undisputed record of this genus in Europe is found in the Middle Villafranchian (Early Pleistocene) Italian site of Coste S. Giacomo, tentatively dated to 2.2-2.3 Ma (Rook & Martínez-Navarro 2010; see also fig. 1 in Bartolini Lucenti *et al.* 2017). Historically, the arrival of *Canis* was regarded as a biochronological marker, the "Wolf-event" (Azzaroli 1977, 1983; Azzaroli *et al.* 1988), dated to *c.* 2.0 Ma. However, canids are not the only relevant carnivores that colonized Europe at this time, and the arrival of the giant, short-faced hyena coming from Africa, *Pachycrocuta brevirostris* Gervais, 1850, is especially important. This supercarnivore-eater is known from the Iberian Peninsula to China and Indonesia, being the most important generator of large mammals taphocoenoses during the rest of the Early Pleistocene throughout the Eurasian continent (Palmqvist *et al.* 2011). For this reason, Martínez-Navarro (2010) renamed this faunal event as "the *P. brevirostris* event".

The European record of *Canis* is characterized at the base of the Late Villafranchian by the occurrence of two medium-sized species, *Canis etruscus* Forsyth Major, 1877 and *Canis arnensis* Del Campana, 1913. Both species were first described in the Italian deposits of the Upper Valdarno (*c.* 1.8 Ma) and later found in other Italian localities of similar chronology (Torre 1967; Cherin *et al.* 2014; Bartolini Lucenti & Rook 2016). Outside Italy, they are recorded in France (Martin 1973), Greece (Koufos 1987, 2014) and Spain (Garrido & Arribas 2008).

The Spanish site of Fonelas P-1 (1.9–1.8 Ma) preserves a small crashed cranium, which was ascribed to a new species, *Canis accitanus* Garrido & Arribas, 2008. However, other scholars have suggested a different interpretation: e.g. focusing on size, Brugal & Boudadi-Maligne (2011) ascribed this specimen to *C. arnensis*. Nevertheless, its dental features do not differ markedly from those specimens of *C. etruscus* described from the same site, which suggests that it probably represents a small-sized individual of the latter species. After 1.8 Ma, an important faunal turnover led to a change in the composition of the canid guild of western Europe (Palombo *et al.* 2008). The medium-sized forms *C. etruscus* and *C. arnensis* were replaced by a primitive form of the *Canis mosbachensis* Soergel, 1925 lineage, a wolf-like canid somewhat intermediate in size between the two earlier species. It should be noted that this turnover affected also the large-sized wild dog-like species *Lycaon falconeri* (Forsyth Major, 1877), which was ecologically substituted by the more advanced hypercarnivorous *Lycaon lycaonoides* (Kretzoi, 1938), according to Martínez-Navarro & Rook (2003).

From this moment onwards, the *C. mosbachensis* lineage became a common element of the late early and middle Pleistocene faunas of Europe (see e.g. Sotnikova 2001; Martínez-Navarro *et al.* 2009; Petrucci *et al.* 2013). Some authors (e.g. Tedford *et al.* 2009) put forward the idea that the Asian *Canis variabilis* Pei, 1934 might be related to *C. mosbachensis*, which would imply a wide Palearctic geographic range for this *C. mosbachensis*-*C. variabilis* group. This hypothesis was recently supported by Jiangzuo *et al.* (2018), who suggested the attribution of *C. variabilis* to the subspecies *C. mosbachensis variabilis*. Both the wide geographical distribution of *C. mosbachensis*-like taxa and their time-extended record support the hypothesis of a close relationship with the *C. lupus*-lineage (Bartolini Lucenti *et al.* 2017). Indeed, several scholars consider *C. mosbachensis* as the ancestor of *Canis lupus* Linnaeus, 1758 (among others, Torre 1967; Sotnikova 2001; Sotnikova & Rook 2010; Flower & Schreve 2014), although the phylogenetic position of the various members of the tribe Canini is still subject to debate (i.e., Gopalakrishnan *et al.* 2018; Stoyanov 2020; Machado & Teta 2020).

Here we re-describe the fossil material ascribed to the genus *Canis* from the site of Venta Micena. The taxonomic attribution of this sample has been a matter of debate in the literature. The first reviews of fossil material from this canid by Pons-Moyà (1987) described the medium-sized specimens as *C. etruscus mosbachensis* and *Cuon priscus* Thenius, 1954 according to their size, morphology and, in case of the latter attribution, to a badly restored lower carnassial, which resembled those of extant dholes. Later, after a new restoration, this specimen and the other ascribed to *C. etruscus mosbachensis* were attributed to *C. etruscus* by Martínez-Navarro (1991, 1992). Rook (1993) and Rook & Torre (1996) pointed out the resemblance of this Venta Micena canid to *C. aff. arnensis*, which is comparable in size to the canid from the Italian site of Pirro Nord. Finally, Martínez-Navarro (2002) ascribed this material to *C. mosbachensis*, which would represent the earliest occurrence of this species in Europe (Bartolini Lucenti *et al.* 2017).

GEOLOGICAL AND PALEONTOLOGICAL BACKGROUND

GEOLOGICAL SETTING

The paleontological site of Venta Micena is located in the Baza and Guadix Depression (Fig. 1), a NE-SW elongated sedimentary basin (c.110 km long) that covers a surface of c. 4000 km² and is situated in the contact between the external and internal zones of the Betic Cordillera (Oms *et al.* 2011; García-Aguilar *et al.* 2013, 2014, 2015). After its uplift around 8 Ma (Hüsing *et al.* 2010, and references therein) the depression was characterized by an old set of sediments (Late Miocene marine deposits), overlapped by a modern set of sediments with an angular unconformity (latest Miocene to middle Pleistocene continental deposits) (Vera 1970; García-Aguilar & Martín 2000; Viseras *et al.* 2005; García-Aguilar & Palmqvist 2011; García-Aguilar *et al.* 2014). The Baza and Guadix Depression includes two different depocenters: the Guadix Basin, in the southwestern sector, and the Baza Basin, in the northeastern one (García-Aguilar *et al.* 2013, 2014, 2015). The Plio-Pleistocene continental infilling was deposited under an endorheic regime and consists of a c. 600 m-thick continuous succession and has been historically divided into three formations (with different facies that change laterally): 1) the Guadix Formation, which includes alluvial-fluvial sediments (Guadix Basin); 2) the Gorafe-Huélago Formation, formed by carbonate lacustrine sediments (Guadix Basin); and 3) the Baza Formation, consisting of lacustrine limestones, marls and gypsum (Baza Basin) (Vera 1970).

The badlands landscape visible nowadays in the sedimentary depression is the result of an intense erosion that took place after the capture of its hydrographic network by a tributary of the Guadalquivir River (the Gadiana Menor River) during latest middle Pleistocene times (García-Tortosa *et al.* 2008), which led to an exorheic regime.

All the formations of the Baza and Guadix Depression preserve abundant Plio-Pleistocene paleontological assemblages (Martínez-Navarro 1992; Martínez-Navarro *et al.* 1997, 2010, 2014; Arribas & Palmqvist 1998; Oms *et al.* 2000, 2011; Palmqvist *et al.* 2005, 2011; Espigares 2010; Espigares *et al.* 2013, 2019; Ros-Montoya 2010). Vera *et al.* (1985) recognized three members within the Baza Formation, composed of (from bottom to top): 1) limestones with lignite clay intercalations; 2) a “red detrital member”, with fluvio-alluvial plain mudstones; and 3) limestones and carbonate silts precipitated in a shallow lacustrine context with local fluvial contributions (Oms *et al.* 2000). The Early Pleistocene site of Venta Micena is located at the bottom of the uppermost member. Its local stratigraphy (Fig. 1) consists of six units in a 20-m-thick section of calcareous sediments (for further details of these units, see Anadón *et al.* 1987; Turq *et al.* 1996).

THE PALEONTOLOGICAL RECORD OF VENTA MICENA

The vertebrate assemblage unearthed from the site is composed of 35 taxa, including *Homotherium latidens*, *Megantereon whitei*, *Panthera* cf. *gombaszoegensis*, *Lynx* sp., *Pachycrocuta brevirostris*, *Lycaon lycaonoides*, *Canis orcanis* n. sp., *Vulpes alopecoides*, *Ursus*

etruscus, *Meles* sp., *Mammuthus meridionalis*, *Stephanorhinus* aff. *hundsheimensis*, *Equus altidens*, *Hippopotamus antiquus*, *Bison* sp., *Hemibos* aff. *gracilis*, *Hemitragus albus*, *Praeovibos* sp., *Soergelia minor*, *Praemegaceros* cf. *verticornis*, *Metacervoceros rhenanus*, *Prolagus calpensis*, *Oryctolagus* cf. *lacosti*, *Hystrix major*, *Allophaiomys ruffoi*, *Apodemus mystacinus*, *Castillomys rivas*, *Eliomys intermedius*, *Galemys pyrenaicus*, *Asoriculus gibberodon*, *Testudo* sp., *Lacerta* sp., *Ophidea* indet., *Rana* sp., and Charadriiformes indet. aff. Laridae (Martínez-Navarro 1991, 1992; Martínez-Navarro & Palmqvist 1995; Palmqvist & Arribas 2001; Palmqvist *et al.* 1996, 2003, 2005, 2011; Martínez-Navarro *et al.* 2003, 2010; Abbazzi 2010; Agusti *et al.* 2010; Ros-Montoya 2010; Ros-Montoya *et al.* 2012; Duval *et al.* 2011; Madurell-Malapeira *et al.* 2014; Medin *et al.* 2017; Bartolini Lucenti & Madurell-Malapeira 2020). In addition, some avian specimens currently in study point to the presence of a crow (*Corvus* sp.), a common shell-duck (*Tadorna tadorna* Linnaeus, 1758) and a large Ciconiiformes. This faunal assemblage is typical of the *Allophaiomys plioceanicus* Kormos, 1933 (synonym of *A. ruffoi*) zone (MmQ2 biozone: Agustí *et al.* 1986), although new studies suggest that *A. plioceanicus* Kormos, 1933 is the ancestor of *A. ruffoi* (see López-García *et al.* 2015). In any case, Venta Micena is biochronologically placed in between the older Georgian site of Dmanisi and the younger Italian site of Pirro Nord.

MATERIAL AND METHODS

The studied material was formerly stored at the Institut de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain) until 1998, later at the Museo Municipal de Prehistoria y Paleontología (Orce, Granada, Spain) until 2016 and, since then, at the Museo Arqueológico de Granada (Spain). As comparative fossil material, we studied: *Canis apolloniensis* Koufos & Kostopoulos, 1997 from Apollonia 1 (housed at AUT) *Canis arnensis* from Upper Valdarno and Poggio Rosso (housed at IGF); *Canis chihliensis* Zdansky, 1924 from Yushe Basin (housed at AMNH); *Canis etruscus* from Olivola and Upper Valdarno (housed at IGF and MPM); *Canis borjgali* Bartolini Lucenti *et al.*, 2020 from Dmanisi (housed at MG-GNM); *Canis mosbachensis* from Cueva Victoria, Pirro Nord, Vallparadís Estació, and Vértesszölös II (housed at ICP, DST-UniFI, HNHN); *Canis palmidens* Teilhard de Chardin & Piveteau, 1930 from Yushe Basin (housed at AMNH) and Nihewan Basin (housed at MNHN; for institution abbreviations, see below). Additional comparative material of extant and late Villafranchian canids was taken from the literature (Del Campana 1913; Crusafont 1950; Thenius 1954; Torre 1967, 1974; Kurtén 1974; Pons-Moyà & Crusafont 1978; Pons-Moyà 1981; Rook 1993; Koufos & Kostopoulos 1997a, b; Sotnikova 2001; Garrido & Arribas 2008; Lacombat *et al.* 2008; Martínez-Navarro *et al.* 2009; Tedford *et al.* 2009; Tong *et al.* 2012; Petrucci *et al.* 2013; Koufos 2014; Cherin *et al.* 2014; Bartolini Lucenti & Rook 2016; Bartolini Lucenti *et al.* 2017, 2020). Extant specimens used for morphological and statistical comparisons were taken from the collection of the “La Specola” Zoological Section of the Museum

of Natural History of the University of Florence. This sample includes specimens of the following species: *C. lupus*, *Canis latrans* Say, 1823, *Canis lupaster* Hemprich & Ehrenberg, 1832, *Canis aureus* Linnaeus, 1758, *Lupulella mesomelas* (Schreber, 1775), *Lupulella adusta* (Sundevall, 1847) and *Lycaon pictus* (Temminck, 1820). Craniodental measurements of the studied specimens were taken with digital calipers to the nearest 0.1 mm, following Von Den Driesch (1976), with few modifications. Metric data from modern canid species were kindly provided by Blaire Van Valkenburgh and additional measurements were taken from Torregrosa (2008).

To depict the difference in proportions among several fossil Eurasian species (i.e., *C. etruscus* from Olivola, Upper Valdarno and Pantalla; *C. arnensis* from Upper Valdarno; *C. mosbachensis* from Cueva Victoria, Vallparadís Section and Pirro Nord; *C. accitanus* from Fonelas P1; *C. apolloniensis* from Apollonia 1) and extant ones (i.e., *Lupulella mesomelas*, *L. adusta*, *C. aureus*, *C. lupaster* and *C. lupus*) of Canini, log-ratio diagrams were used (Simpson 1941; Simpson *et al.* 1960). Log-transformed dental measurements of the considered taxa were plotted. They have the double advantage of showing the absolute differences in the same dimension for different specimens of the same taxon (i.e., the vertical difference of the same feature) and the relative size differences among all taxa (i.e., distance between the reference taxon/specimen and other taxa/specimens). This second advantage is the most important as, in a very simple way, the log-ratio diagrams provide information on the shape differences between the various taxa/specimens considered in the analysis. We also used the ratio between the length of the P4 and the length of M1-M2 (index A of Bonifay 1971; here CI) to consider differences in the relative proportions of carnassials and molars. Moreover, paleoecological inferences were also derived from carbon- and nitrogen-isotope ratios measured in the members of the carnivoran guild of Venta Micena (data from Palmqvist *et al.* 2008) and also from craniodental ratios that allow differentiating among modern species of canids according to their dietary habits; the metric variables used in the latter ratios were selected from discriminant analyses performed to differentiate among hypercarnivorous, mesocarnivorous and hypocarnivorous extant canids.

ABBREVIATIONS

Site and institutional

AMNH	American Museum of Natural History, New York;
AUT	Aristotle University of Thessaloniki, Thessaloniki;
DST-UniFI	Earth Sciences Department, University of Florence, Florence;
HNHN	Hungarian Natural History Museum, Budapest;
ICP	Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Bellaterra, Barcelona;
IGF	Geology and Paleontology section of the Natural History Museum, University of Florence, Florence;
MG-GNM	Georgian National Museum, Tbilisi;
MNHN	Museum national d'Histoire naturelle, Paris;
MPM	Museo Paleontologico di Montevarchi, Arezzo;
MZUF	“La Specola” Zoology section of the Natural History Museum, University of Florence, Florence;
VM	Site abbreviation for Venta Micena, Orce.

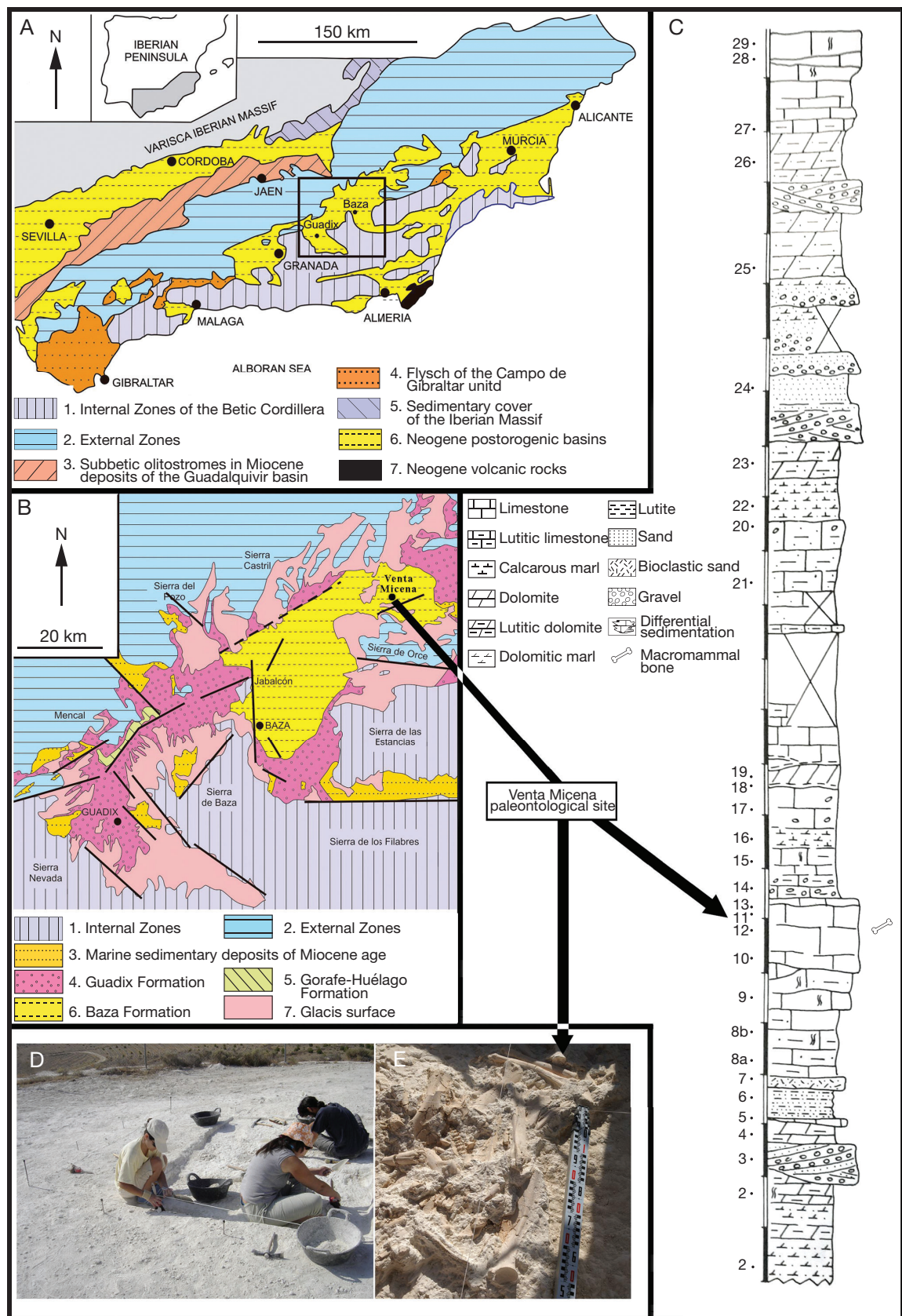


FIG. 1. — **A**, Geographic and geologic map of the Betic Chain (from García-Aguilar *et al.* 2014); **B**, geologic map of the Baza and Guadix Basin (from García-Aguilar *et al.* 2014); **C**, stratigraphic series of Venta Micena (from Anadón *et al.* 1987); **D**, excavation at Venta Micena during the 2005 season; **E**, detail of the excavation during the 2005 season.

Cranial and Dentognathic abbreviations

Upper dentition

LRCR	mesiodistal length of the upper cheek toothrow (P1-M2 L);
LMR	mesiodistal length of the upper molar row (M1-M2 L);
LPR	mesiodistal length of the upper premolar row (P1-P4 L).

Mandible and lower dentition

HR	height of the mandible ramus;
LLMR	mesiodistal length of lower molar row;
LLPR	mesiodistal length of lower premolar row;
M m1 H	mandibular corpus height distal to m1 alveolus;
M p2 H	mandibular corpus height distal to p2 alveolus;
M p4 H	mandibular corpus height distal to p4 alveolus;
tdm1	talonid of m1;
trm1	trigonid of m1.

Other abbreviations

CI	P4 L/M1-M2 L (Bonifay (1971));
L	mesiodistal length;
W	buccolingual width.

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
 Family CANIDAE Fischer, 1817
 Subfamily CANINAE Fischer, 1817
 Tribe CANINI Fischer, 1817
 Genus *Canis* Linnaeus, 1758

Canis orcensis n. sp.
 (Figs 2; 3)

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Canis etruscus mosbachensis – Agustí *et al.* (1986) — Pons-Moyà (1987): 110-112, figs 3, 4.

Cuon priscus – Agustí *et al.* (1986) — Pons-Moyà (1987): 113-114, fig. 7.

Canis etruscus – Martínez-Navarro 1992: 28-30, pls. 5, 8, 9.

Canis aff. *arnensis* – Rook (1993): 72-80, pls. 20-21.

Canis mosbachensis – Martínez-Navarro (2002) — Boudadi-Maligne (2010) — Brugal & Boudadi-Maligne (2011) — Ros-Montoya *et al.* (2012) — Madurell-Malapeira *et al.* (2014).

SYNTYPES. — VM-2253, right hemimandible with p4-m2; VM-2258, maxillary fragment with P4-M2; and VM-4109, right M1 and M2.

DIAGNOSIS. — Medium-sized canid; M1 paracone higher and enlarged compared to the metacone; strong and lobed buccal cingulum; large M1 protocone and crest-like metaconule; M2 hypocone reduced; p3 alveolus lower than those of p2 and p4 on the alveolar plane of the mandible; short-crowned lower premolars; buccolingually compressed m1; m1 metaconid reduced; sinuous crista transversa connecting m1 hypoconid and entoconid; m1 entoconid reduced; m2 metaconid reduced compared to the development of the protoconid and hypoconid.

DERIVATIO NOMINIS. — From the town of Orce, in the vicinity of which the site of Venta Micena is located.

HYPODIGM. — **Cranial fragments.** VM-2258, maxillary fragment with P4-M2; VM-2260, maxillary fragment with P4-M2; VM-2262, maxillary fragment with M1-M2; VM-10308, maxillary fragment with M1-M2.

Upper teeth. VM-10375, right I2; VM-10405, left I2; VM-10378, right I3; VM-10479, left I3; VM-10376, left P2; VM-10498, right P2; VM-10488, right P3; VM-10379, right P4; VM-10467, left P4; VM-10480, left P4; VM-10494, left P4; VM-10495, left P4; VM-4109_1, right M1; VM-10408c, left M1; VM-10466, left M1; VM-10470, left M1; VM-4109_2, right M2; VM-4585, left M2; VM-10382, left M2; VM-10497, left M2.

Mandible. VM-2253, right hemimandible with p4-m2; VM-2254, right hemimandible with m2; VM-10408a, hemimandible with m2; VM-13295_4, right hemimandible.

Lower dentition. VM-10390, right i1; VM-10391, left i1; VM-10361, left i2; VM-10388, left i2; VM-10483, right p1; VM-10484, left p1; VM-10360, left p2; VM-10485, right p2; VM-10468, left p4; VM-13295_1, right p4; VM-9322, right m1; VM-10403, left m1; VM-10404, left m1; VM-13295_2, left m1; VM-13306, right m1; VM-4440_1, right m2; VM-4440_2, right m2; VM-10406, left m2; VM-10408d, right m2; VM-13295_3, right m2 (Table 1).

DESCRIPTION

Upper dentition

The I1 and I2 have two small basal cusps, one on each side of the main cusp. The I3 is caniniform, with no accessory cusplids, and shows a well-developed distobuccal cingulum. The upper canine is flattened buccolingually, with an oval outline in occlusal view. The P1 is single-rooted, with a conical crown. The P2 has no accessory cusps. The P3 is similar in morphology to the P2 but shows a single accessory cusp. The P4 has a reduced protocone, poorly expanded lingually and rather close to the paracone. The latter is well-developed and stout. The cingulum extends on the distolingual part of the tooth. Of the buccal cusps of M1, the paracone is larger and higher than the metacone. The protocone is well-developed, prominent and individualized. No protoconule is present. The postprotocrista is shallow and connects the protocone directly to the distal cingulum, as the metaconule is reduced to a shallow crista. The hypocone is prominent and rather individualized from the lingual cingulum. The trigon basin is wider and deeper than the talon basin. The latter is shallow and well-developed. The M2 is smaller than the M1, but similar in occlusal morphology. It is buccolingually elongated. The M2 paracone is larger than the metacone, the protocone is well-developed and the hypocone is cingular. The cingulum is well-developed (Fig. 2).

Mandible

The corpus is low and slender, with a curved ventral border and a slightly arched toothrow with labial convexity, in dorsal view. When observed in lateral view, the ramus is high and forms a right angle with the corpus. On the buccal side of the mandible, the masseteric fossa is deep and broad. VM-2253 is the best-preserved hemimandible and may belong to an adult individual not displaying the p1 and m3 alveoli (though the former seems to have been reabsorbed after the tooth was lost during life). The condyloid process is developed and medially inclined (Fig. 3).

TABLE 1 — Dental measurements of *Canis orcensis* n. sp. from Venta Micena (in mm).

ID	Element		P4 L	P4 W	M1 L	M1 W	M2 L	M2 W
VM-2258	maxillary fr.	R	21.0	10.7	15.4	17.1	9.1	11.8
VM-2260	maxillary fr.	R	19.1	9.5	14.4	15.6	7.7	9.8
VM-2262	maxillary fr.	R	—	—	14.5	16.8	9.0	10.8
VM-10308	maxillary fr.	L	—	—	15.4	16.4	8.7	9.6
VM-10308	maxillary fr.	R	—	—	15.2	16.4	8.4	9.8

ID	Element		p4 L	p4 W	m1 L	m1 W	trm1 L	tdm1 W	m2 L	m2 W	Mp4H	Mm1H	m1-m2 L
VM-2253	hemimandible	R	13.0	6.0	21.6	8.7	14.0	7.6	8.7	6.3	20.4	22.7	30.9
VM-2254	hemimandible	R	—	—	—	—	—	—	10.1	—	—	24.4	—
VM-10408a	hemimandible	R	—	—	—	—	—	—	10.1	7.4	—	—	—

ID	Element		L	W	trm1 L	tdm1 W
VM-10390	i1	L	2.8	4.1	—	—
VM-10391	i1	R	2.7	4.0	—	—
VM-10361	i2	L	4.4	4.6	—	—
VM-10388	i2	L	4.27	3.5	—	—
VM-10485	p2	R	11.6	4.8	—	—
VM-10468	p4	L	14.0	5.5	—	—
VM-13295_1	p4	R	14.2	6.5	—	—
VM-9322	m1	L	—	8.8	—	—
VM-13295_2	m1	R	6.8	7.9	—	—
VM-10403	m1	L	21.9	8.9	14.8	8.1
VM-10404	m1	R	24.4	9.0	16.3	8.3
VM-4440_1	m2	R	10.0	6.7	—	—
VM-4440_2	m2	R	10.6	7.0	—	—
VM-10406	m2	L	9.6	7.0	—	—
VM-10408d	m2	R	9.3	7.3	—	—
VM-13295_3	m2	R	11.0	8.0	—	—
VM-10375	l2	R	3.5	5.4	—	—
VM-10405	l2	L	5.38	5.35	—	—
VM-10378	l3	R	5.4	8.2	—	—
VM-10479	l3	L	4.7	6.9	—	—
VM-10498	P2	L	9.7	4.5	—	—
VM-10488	P3	L	13.4	5.5	—	—
VM-10379	P4	L	20.9	—	—	—
VM-4109_1	M1	L	13.6	15.8	—	—
VM-10408c	M1	L	14.4	15.7	—	—
VM-10466	M1	L	14.2	17.0	—	—
VM-10470	M1	R	14.0	—	—	—
VM-4109_2	M2	L	7.3	9.7	—	—
VM-4585	M2	L	8.9	10.9	—	—
VM-10382	M2	L	6.6	8.5	—	—

Lower dentition

The incisors are flattened buccolingually, with a single distal accessory cuspid. The p1 is single-rooted and single-cusped. The p2 is elongated mesiodistally, with a slightly enlarged distolingual portion and a small distal accessory cuspid on the distal cingulid. The p3 is similar to the p2 but mesiodistally larger. It has a high protoconid and a small cuspid on the distal cingulid. The p4 is mesiodistally larger than the p3, being elongated mesiodistally with the distolingual portion slightly inflated. It has two well-developed accessory cuspids, individualized from the distal cingulid. A small cuspid is evident on the mesiolingual cingulid. The m1 paraconid is well-developed and higher compared to the p4 protoconid, if observed in buccal view. The mesial margin of the paraconid is inclined distally. The m1 has a high and distally inclined protoconid as well as a smaller mesial paraconid. The metaconid is reduced but rather individualized from the protoconid. Its tip is pointed distally, especially in VM-10403. Regarding the talonid cuspids, the hypoconid is larger than the entoconid. There is a prominent

transverse cristid between both cuspids, with a prominent sinuous outline in occlusal view. The talonid basin is deep, although it is small and closed lingually by a cristid-like entoconulid. Mesially to this cuspid, there is a shallow cristid that develops to the distal side of the metaconid. The mesial margin of the hypoconid shows a crest. A small accessory tubercle is present on the distobuccal wall of the protoconid. The distal portion of the lower carnassial generally shows a variably developed cristid-like cingulid, which separates a shallow space between the hypoconid and the entoconid. A distobuccal cingulid is present. VM-10403 also possesses a mesiolingual cingulid. The m2 has an almost oval shape, in occlusal view. The mesiobuccal cingulid is markedly enlarged, especially compared to the distal portion of the tooth. The m2 possesses two mesial cuspids, a large and stout protoconid and a smaller metaconid. Distally, the well-developed hypoconid is the only cuspid of the talonid. The protoconid is generally higher than the other two cuspids. A high cristid bounds the distolingual margin of the tooth, enclosing the well-developed talonid basin (Fig. 3).

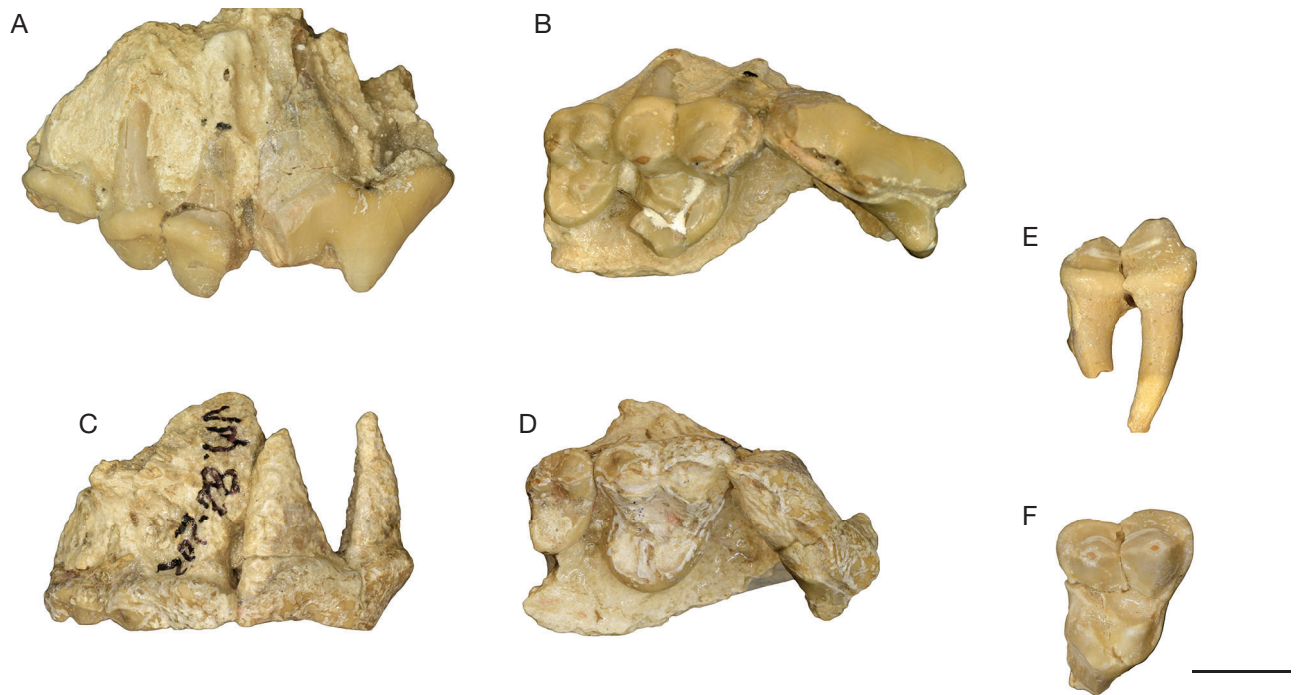


FIG. 2. — *Canis orcanis* n. sp. from Venta Micena: **A, B**, VM-2258, right maxillary fragment with P4-M2, in buccal (**A**) and occlusal (**B**) views; **C, D**, VM-2260, right maxillary fragment with P4-M2, in buccal (**C**) and occlusal (**D**) views; **E, F**, VM-4109, left M1, in buccal (**E**) and occlusal (**F**) views. Scale bar: 1 cm.

MORPHOLOGICAL AND MORPHOMETRIC COMPARISONS

Comparisons with C. arnensis and C. etruscus from Italy

The general size and tooth morphology are close to *C. arnensis* (and *C. mosbachensis*) but smaller than *C. etruscus* (see Figs 4; 5). In upper teeth morphology, *C. orcanis* n. sp. differs from the type sample of *C. arnensis* from Il Tasso and that of Poggio Rosso (Bartolini Lucenti & Rook 2016) as well as from that of *C. etruscus* from Olivola, Upper Valdarno and Pantalla (Cherin *et al.* 2014) in several features, including a P4 protocone that is reduced in lingual development and does not possess a sharp-pointed cusp, unlike *C. arnensis* and *C. etruscus*. In *C. orcanis* n. sp., the M1 paracone is considerably larger than the metacone, which differs from *C. arnensis*, where the cusps are of similar size, but also from *C. etruscus*, in which the difference is less marked and the metacone is generally girdled by a prominent cingulum. In the latter, the molars are elongated buccolingually in occlusal view, whereas in *C. orcanis* n. sp. they do not, and show a marked distolingual curvature. The trigon basin in the M1 of *C. orcanis* n. sp. is deeper than the talon one, whereas these basins have equal depth in both *C. etruscus* and *C. arnensis* (Fig. 5), and the talon basin does not tend to reduction as in *C. orcanis* n. sp. Moreover, the M2 of *C. etruscus* is mesiobuccally enlarged compared to the more-slender morphology of *C. orcanis* n. sp. in occlusal view. Additionally, *C. orcanis* n. sp. lacks other peculiar features of *C. arnensis* from Il Tasso and Poggio Rosso, and of *C. etruscus* from Olivola, Upper Valdarno and Pantalla, like e.g., the well-developed metaconid of m1, generally lingually displaced; the strongly developed P4 protocone and the absence of cusplids on the lingual margin of m1

of *C. etruscus*; as well as the reduced difference between the hypoconid and entoconid of m1; and the presence of accessory cusplids on the lingual side of m2 of *C. arnensis*.

Comparisons with C. etruscus and C. accitanus from Fonelas P1 and C. borjgali from Dmanisi

As noted above, two small-to-medium-sized *Canis* species have been described in the Spanish site of Fonelas P1: *Canis etruscus*, and the species erected by Garrido & Arribas (2008), *C. accitanus*. In comparison to *C. etruscus* from this site, in addition to the above-mentioned differences, *C. orcanis* n. sp. shows a greater development of the M1 buccal cingulum as well as a M1 metacone (Fig. 5), a metaconule and a M2 protocone that are all proportionally reduced. In the type specimen of *C. accitanus*, the development of the P4 protocone does not resemble that of *C. orcanis* n. sp. In the former, it is large and expands lingually, whereas in the latter the protocone is less separated from the paracone, smaller and characterized by a blunt cusp. The cingula of the M1 (i.e., the buccal and the mesial ones) in *C. accitanus* are poorly developed compared to those of *C. orcanis* n. sp (Fig. 5). The former also shows an evident protoconule and a tubercular metaconule, in contrast to the features of the sample from Venta Micena. The M2 of *C. accitanus* possesses similarly sized buccal cusps, whereas *C. orcanis* n. sp. shows a markedly enlarged M2 paracone in comparison to the metacone. The buccal cingulum of *C. orcanis* n. sp. is continuous along the buccal side of the M2. In contrast, in *C. accitanus*, it girdles the buccal cusps and forms a feeble yet visible notch between them. Fonelas P1 is roughly coeval to the site of Dmanisi, which preserves one of the most remarkable records

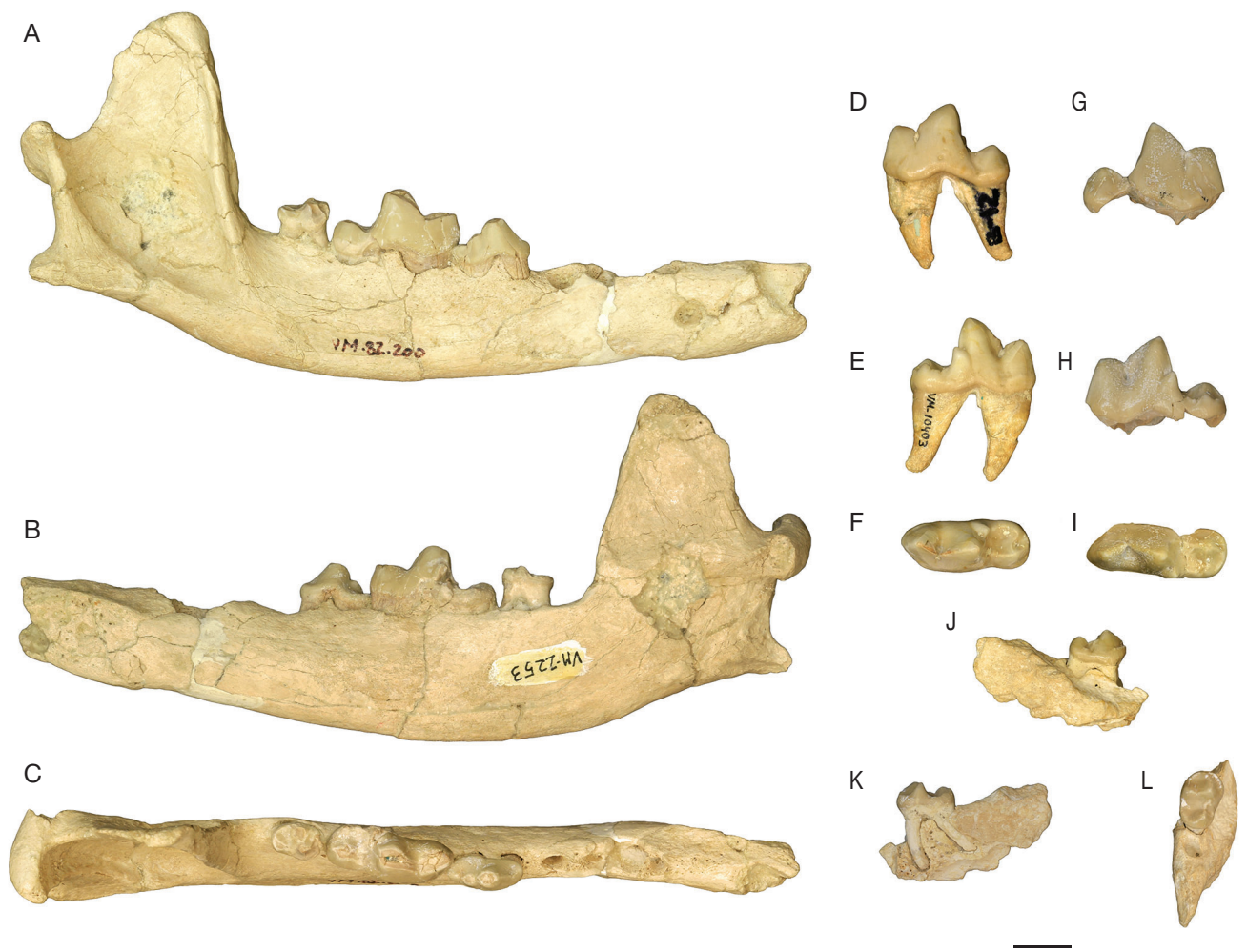


FIG. 3. — *Canis orcensis* n. sp. from Venta Micena: **A-C**, VM-2253, right hemimandible with p4-m2, in buccal (**A**), lingual (**B**) and occlusal (**C**) views; **D-F**, VM-10403, left m1, in buccal (**D**), lingual (**E**) and occlusal (**F**) views; **G-I**, VM-10404, left M1, in buccal (**G**), lingual (**H**) and occlusal (**I**) views; **J-L**, VM.10408, right hemimandible fragment, in buccal (**J**), lingual (**K**) and occlusal (**L**) views. Scale bar : 1 cm

of *Canis* historically attributed to *C. etruscus* (Vekua 1995). A recent revision questions this attribution due to the absence of several diagnostic features of *C. etruscus* (Bartolini Lucenti *et al.* 2020). Compared to *C. orcensis* n. sp., this sample shares also the differences above-mentioned, although it also shows some similarities. In the upper teeth, the P4 protocone is reduced, the M1 buccal cingulum is more developed compared to *C. etruscus* of Fonelas P1 and Italy, the M1 metaconule is reduced although still tubercular, rather than crest-like as in *C. orcensis* n. sp (Fig. 5). Of the features of the lower teeth that resemble *C. orcensis* n. sp., the most prominent are the short morphology of the lower premolars in buccal view, the reduction of the m1 metaconid compared to *C. arnensis* and *C. etruscus* from Fonelas P1 and the Italian sites, and the sinuous transverse cristid connecting the hypoconid and the entoconid.

Comparisons with latest Early

Pleistocene *C. mosbachensis* of Europe

Numerous features suggest a close affinity to *C. mosbachensis* from Pirro Nord, Untermassfeld (see Sotnikova 2001), Cueva

Victoria, and Vallparadís Section. For instance, the alveolus of the p3 sets lower level in the corpus of the mandible in comparison to those of p2 and p4. The morphology of the lower premolars resembles that of *C. mosbachensis*, with a mesiolingual stout expansion and a low inclined mesial border (state 3 of character 61 described by Prevosti 2010). *C. etruscus* from Olivola and Upper Valdarno and *C. arnensis* from Upper Valdarno differ to a large extent from these morphologies, e.g. in showing a higher angle of inclination of the premolar crown in lateral view (more similar to the condition of state 2 of character 61, Prevosti 2010). The lower carnassial testifies to this affinity to *C. mosbachensis*. For instance, the presence of a sinuous crest connecting the hypoconid and the entoconid of m1, or the metaconid separated from the protoconid but not projecting lingually. Other features are the depth of the M1 trigon basin, deeper than the talon basin or the M1 hypocone, and the protocone of similar height (see Fig. 5). These are all derived features commonly present in *C. mosbachensis*. Even the teeth proportions are suggestive of a close affinity to *C. mosbachensis* (see Fig. 4). In contrast to

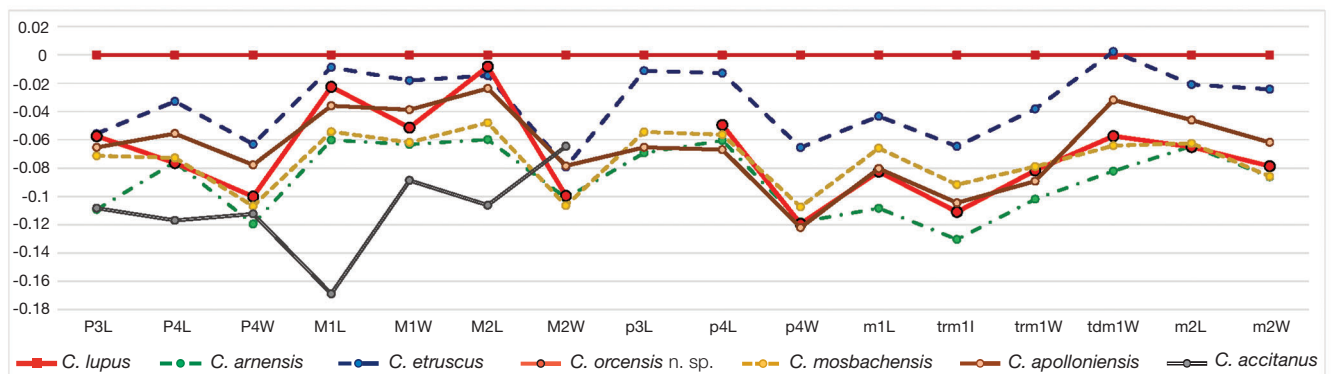


Fig. 4. — Log-ratio diagram based on selected dental variables in the described material as well as in other early Pleistocene species of *Canis* Linnaeus, 1758 (*C. etruscus* Forsyth Major, 1877, *C. arnensis* Del Campana, 1913, *C. mosbachensis* Soergel 1925, *C. apolloniensis* Koufos & Kostopoulos, 1997, and *C. accitanus* Garrido & Arribas 2008, data taken from the literature: Sotnikova 2001; Garrido & Arribas 2008; Martínez-Navarro *et al.* 2009; Petrucci *et al.* 2013) as compared to extant *C. lupus* Linnaeus, 1758 (used as the reference baseline).

the latter, *C. orcensis* n. sp. does not possess the protoconule of the M1 and the metaconule is strongly reduced, showing a crest-like shape in occlusal view. This morphology bears resemblance with the condition seen in the M1 of the type specimen of the primitive hypercarnivorous canid *Lycaon falconeri* Forsyth Major, 1877.

The ratio between P4 L/M1-M2 L (CI) for *C. orcensis* n. sp. has an average of 86.2. This value contrasts with the mean values of other Villafranchian canids of Western Europe, like *C. etruscus* (mean: 97.9), *C. arnensis* (mean: 99.1) and *C. mosbachensis* (mean: 97.1), as shown in Table 2

Comparisons with *C. apolloniensis*

Compared to late early Pleistocene species, *C. orcensis* n. sp. shows affinity to *C. apolloniensis* from Apollonia-1 (old and new material, see Koufos 2018). Indeed, the morphology of the upper and lower teeth, as well as the mandible are close to the Greek canid, although some slight but significant differences can be pointed out. For instance, *C. apolloniensis* shows upper molars that are more lingually elongated in occlusal view, and the M1 trigon basin is proportionally larger compared to that of *C. orcensis* n. sp. (Fig. 5). The metaconule is evidently cuspule-like in *C. apolloniensis*, as in *C. mosbachensis* from other European localities, whereas *C. orcensis* n. sp. has a crista-like M1 metaconule. The cingular hypocone of the M1 of *C. apolloniensis* is larger at its base and expands lingually, whereas in *C. orcensis* n. sp. it is stout and shorter, in buccolingual sense when observed in occlusal view (Fig. 5). The m1 of *C. apolloniensis* is more compressed buccolingually and the entoconid is less reduced compared to the new Spanish species (Fig. 3).

Comparisons with Early Pleistocene canids from eastern Asia

Compared to the medium-sized *C. palmidens* from the type locality of Nihewan Basin and from the Yushe Basin, or to the large-sized *C. chihliensis* from the Nihewan and Yushe Basin (Teilhard de Chardin & Piveteau 1930), there are several differences that can be noticed. The P4 paracone of *C. orcensis* n. sp. is slender in buccal view, and the metastyle

appears to be more elongated compared to the mesiodistally short one of *C. palmidens* and *C. chihliensis*. Particularly, the P4 of the latter species is considerably stouter and buccolingually large. Compared to *C. orcensis* n. sp. (and even more to *C. palmidens*), the P4 protocone of *C. chihliensis* is reduced and half fused to the paracone. The distolingual cingulum of the P4 is more prominent in *C. palmidens* from Nihewan and in *C. chihliensis* from Shanshenmiaozui and Yushe Basin in comparison to that of *C. orcensis* n. sp. The occlusal outline of the M1 of *C. orcensis* n. sp. differs from that of *C. palmidens* from Nihewan and Yushe Basins as well as from *C. chihliensis* from Yushe Basin. In the latter forms, it is buccolingually elongated, whereas in *C. orcensis* n. sp. this tooth is proportionally shortened and more distally arched. Unlike *C. orcensis* n. sp., the M1 metaconule of *C. palmidens* from Nihewan and Yushe Basins is a prominent cuspule, connected to the large protocone by a sharp postprotocrista. On the contrary, the morphology of the metaconule of *C. orcensis* n. sp. is similar to that of the specimen of *C. chihliensis* from Yushe Basin, where this cuspule is considerably reduced, close to the proportions depicted by fossil *Lycaon* spp. The hypocone is more prominent in *C. orcensis* n. sp. than in *C. palmidens* and the trigon basin is deeper than the talon in the Spanish taxon compared to the latter. In *C. chihliensis* the hypocone is greatly enlarged, compared to the two medium-sized taxa. The M2 is bean-shaped in *C. palmidens* from Nihewan and Yushe Basins, with a developed lingual lobe, whereas in *C. orcensis* n. sp. this portion is reduced in occlusal view. The notch on the distal side of the M2, visible in *C. palmidens*, is strongly reduced in *C. orcensis* n. sp. In *C. chihliensis* from Yushe Basin, the M2 is buccolingually reduced with no distal notch. The lower carnassial of *C. palmidens* shows a rather large metaconid and an entoconid slightly smaller compared to the hypoconid. *C. orcensis* n. sp. possesses a reduced metaconid, poorly individualized from the protoconid, although not as reduced as in *C. chihliensis* from Nihewan. The entoconid of *C. orcensis* n. sp. is proportionally smaller than those of *C. chihliensis* and *C. palmidens*, and it is connected to the hypoconid with a prominently sinuous transverse cristid. Although also

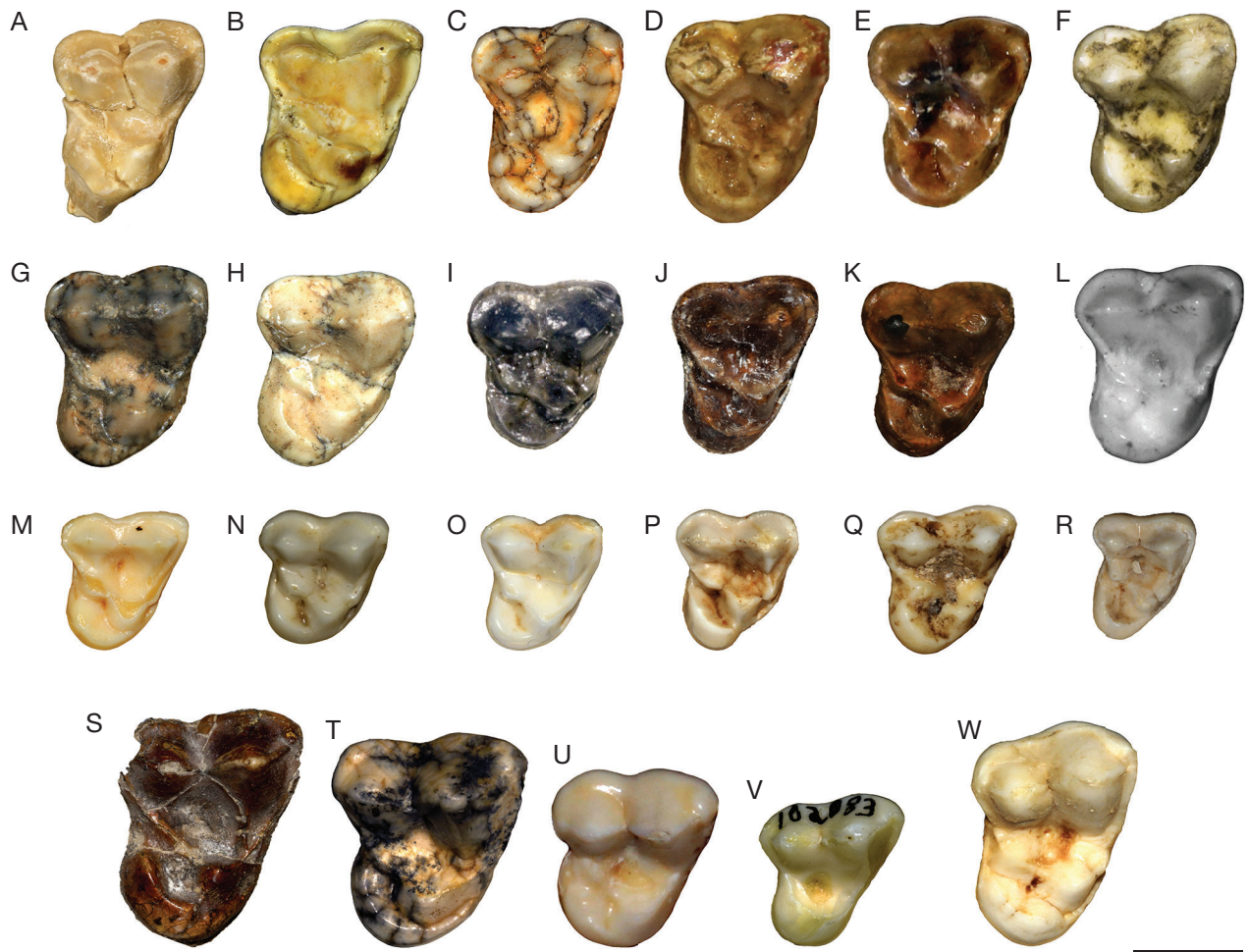


FIG. 5. — **A**, VM-2258, *Canis orcensis* n. sp. from Venta Micena; **B**, EVT-6530, *Canis mosbachensis* Soergel, 1925 from Vallparadís Section; **C**, DE2 ac, *Canis mosbachensis* Soergel, 1925 from Pirro Nord; **D**, IGF 4407, *Canis etruscus* Forsyth Major, 1877 from Olivola; **E**, IGF 12867, *Canis etruscus* Forsyth Major, 1877 from Matassino (Upper Valdarno); **F**, D2314, *Canis borjgali* Bartolini Lucenti *et al.*, 2020 from Dmanisi; **G**, APL-16, *Canis apolloniensis* Koufos & Kostopoulos, 1997 from Apollonia-1; **H**, APL-254, *Canis apolloniensis* Koufos & Kostopoulos, 1997 from Apollonia-1; **I**, IGF 7919V, *Canis arnesis* Del Campana, 1913 from Poggio Rosso; **J**, IGF 867, *Canis arnesis* Del Campana, 1913 from the Upper Valdarno; **K**, IGF 869, *Canis arnesis* Del Campana, 1913 from the Upper Valdarno; **L**, FP1-2001-0434, *Canis accitanus* Garrido & Arribas, 2008 from Fonelas P-1 (Garrido & Arribas 2008); **M**, AMNH-52049, *Lupulella adusta* (Sundevall, 1847) from Zaire; **N**, MZUF 1898, *Lupulella mesomelas* (Schreber, 1775) from Ethiopia; **O**, MZUF-1851, *Canis lupaster* Hemprich & Ehrenberg, 1832 from Somalia; **P**, MZUF-11879, *Canis aureus* Linnaeus, 1758 from Dalmatia; **Q**, CE-818, *Canis simensis* Rüppell, 1840 from Ethiopia; **R**, MZUF-418, *Canis latrans* Say, 1823 from Mexico; **S**, IGF 883, *Lycaon falconeri* (Forsyth Major, 1877) from the Upper Valdarno; **T**, PP 186, *Lycaon lycaonoides* (Kretzoi, 1938) from Pirro Nord; **U**, AMNH-82082, *Lycaon pictus* (Temminck, 1820) from Kenya; **V**, AMNH-102083, *Cuon alpinus* (Pallas, 1811) from Java; **W**, MZUF-11874, *Canis lupus* Linnaeus, 1758 from Italy. Scale bar: 1 cm.

possessed by *C. chibliensis* from Nihewan and *C. palmidens* from Nihewan and Yushe Basins, in *C. orcensis* n. sp. this cristid is generally straight. On the m2 of *C. orcensis* n. sp., the entoconid is reduced, whereas it is more developed in *C. palmidens* from Nihewan and Yushe Basins. *Canis chibliensis* from Nihewan has conspicuously enlarged buccal cuspids on the m2, unlike the morphology possessed by *C. orcensis* n. sp. In comparison to the extensive record of the late early-middle Pleistocene *C. mosbachensis variabilis* from Zhoukoudian localities (Jiangzuo *et al.* 2018), some differences can be listed. Whereas the P4 paracone and metastyle are similar to those of *C. orcensis* n. sp., the P4 protocone is generally larger and tend to be well separated from the paracone. In occlusal morphology, the sample of *C. m. variabilis* from Zhoukoudian possess a rather elongated linguall M1 resembling the

condition of modern *C. lupus*, and unlike the specimens from Venta Micena. Other features of *C. m. variabilis* contrast with *C. orcensis* n. sp., e.g. the paracone circa two times the size of the metacone; the development of the metaconule; and the large hypocone lobe. For the same reasons, the sample of *C. aff. mosbachensis* from Ningyang differs from *C. orcensis* n. sp. Other Asian samples are more similar to *C. orcensis* n. sp., e.g. those of *C. mosbachensis* of Gongwangling (see Jiangzuo *et al.* 2018). Nevertheless, as for the European *C. mosbachensis*, the M1 hypocone of *C. orcensis* n. sp. is more developed and the metaconule is crest-like compared to the morphology of the sample from Gongwangling. Even in lower teeth morphology, the samples of *C. m. variabilis* from Zhoukoudian and *C. aff. mosbachensis* from Ningyang differ from *C. orcensis* n. sp. (see Jiangzuo *et al.* 2018). In the former Chinese taxon, the

TABLE 2. — Resuming table of the P4 L/M1-M2 L in various species of extant and fossil Canidae.

	<i>C. orcensis n. sp.</i>	<i>C. mosbachensis</i>	<i>C. etruscus</i>	<i>C. arnensis</i>	
min	85.9	94.7	94.8	93.4	
max	86.5	110.6	103.7	105.4	
mean	86.2	99.3	97.9	99.1	
st. dev.	0.4	5.2	2.7	3.8	
count	2	7	11	9	
	<i>C. lupus</i>	<i>C. aureus</i>	<i>C. lupaster</i>	<i>C. simensis</i>	<i>C. latrans</i>
min	91.3	81.6	76.8	77.2	91.8
max	119.0	92.5	97.2	84.7	111.6
mean	102.5	87.5	86.7	81.2	98.3
st. dev.	5.0	2.9	4.7	2.1	6.5
count	138	14	35	8	13
	<i>L. adusta</i>	<i>L. mesomelas</i>	<i>Ly. pictus</i>	<i>Cu. alpinus</i>	
min	67.8	72.5	85.2	104.4	
max	79.9	101.3	95.5	113.4	
mean	75.1	93.0	90.6	108.7	
st. dev.	2.9	5.8	3.0	4.5	
count	52	29	14	3	

hypocone is considerably enlarged and tends to be centralized compared to the position of the cuspids of *C. orcensis n. sp.* In the latter taxon, the entoconid is less reduced compared to *C. orcensis n. sp.*, and the crista transversa is straight instead of sinuous as in the Spanish form.

PALEOECOLOGY

Four out of 36 species of extant canids (the Eurasian and North American grey wolf, the African painted dog, the Indian dhole and the South American bush dog) are considered hypercarnivorous (i.e., vertebrate meat constitutes >90% of their diet). The other canid species are more omnivorous and can be further subdivided in three dietary groups, although their trophic characterization is not as accurate: mesocarnivores (>50% of meat in diet, mostly from small vertebrates), hypocarnivores (small vertebrates represent <50% of diet, with variable proportions of eggs, fruits, vegetal matter and insects making up the balance) and insectivores (>50% insects in diet).

According to Van Valkenburgh (1989, 1991) and Palmqvist *et al.* (1999, 2002), the trigonid blade of the lower carnassial (m1) is enlarged in the hypercarnivorous canids and three of them (the dhole, hunting dog, and bush dog) share a trenchant heeled shape in the talonid basin of this tooth, which bears a single, centrally positioned blade-like cusp, the hypoconid (the wolf shows a moderately trenchant talonid, asymmetrically bicuspid, with a large, buccally positioned hypoconid and a lingually reduced entoconid). The functional significance of this condition is a lengthening of the effective cutting blade of the carnassial. Other dental modifications associated with hypercarnivory include the reduction of the metaconid of m1 and the reduction (m2) or complete loss (m3) of the postcarnassial molars. In contrast, compared to the hypercarnivorous species, the more omnivorous canids show: 1) a similar size in the two cusps of the talonid basin; 2) a shorter trigonid (lower carnassial blade); and 3) a larger grinding area of the lower teeth (i.e., the talonid basin of m1 and the postcarnassial molars). For this reason, the length of the trigonid blade divided by the length of the talonid basin plus the second lower molar was used in

this study as a proxy for characterizing the dietary adaptations of the fossil populations analysed. Moreover, given that flesh-eating specialists use to have a deeper and shorter mandibular ramus compared to other carnivores (Figueirido *et al.* 2011), a second variable was estimated as the depth of the horizontal ramus, measured at the contact between m1 and m2, divided by the mandibular length between the distal (posterior) border of the lower canine and the tip of the jaw condyle. A number of canonical variates analyses performed among dietary groups in extant canids (i.e., insectivores, hypocarnivores, mesocarnivores, and hypercarnivores; Torregrosa 2008) helped to select the variables for both morphometric ratios.

The combination of these dentognathic indexes with functional significance (Fig. 6) allows to discriminate between the hypercarnivorous canids, which show a comparatively enlarged trigonid blade in the lower carnassial and a more stoutly built mandible, and those species not specialized in hunting prey of similar size or larger than themselves. Among the omnivores, although there is a substantial overlap between the mesocarnivores and hypocarnivores, the former take in most cases higher values in both morphometric indexes, and the two truly insectivorous species show a comparatively reduced trigonid in the lower carnassial. Concerning the fossil specimens, *C. orcensis n. sp.* from Venta Micena and the fossils of *C. mosbachensis* from Untermassfeld, which are very similar to those of Venta Micena (and probably belong to the new species), show values in both indexes closer to the hypercarnivores than those of other extinct forms like *C. mosbachensis* and *C. etruscus*. Moreover, *C. apolloniensis* from Apollonia and *C. borjgali* from Dmanisi show values that lie halfway between the mesocarnivores and the hypercarnivores, while *C. arnensis* from Upper Valdarno and *C. etruscus* from Olivola, Upper Valdarno and Pantalla take values close to the mesocarnivores. These results indicate that although there is substantial functional (and dietary) variability among the Early Pleistocene medium-sized canids, the dentition of the species from Venta Micena shows that it was adapted to consume a greater percentage of vertebrate meat than the other fossil forms.

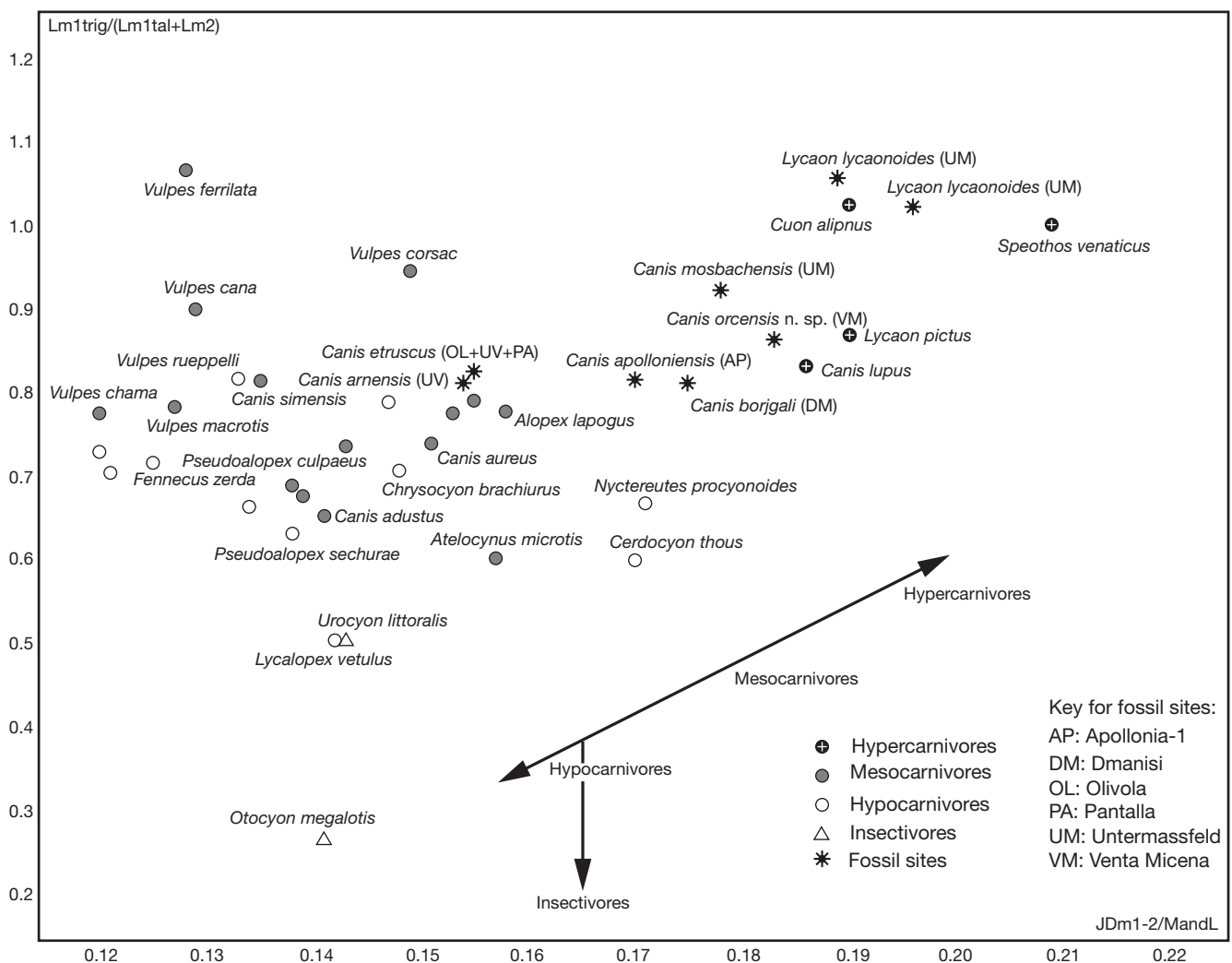


FIG. 6. — Scatterplot for the extant canid species and selected Early Pleistocene specimens of *Canis* Linnaeus, 1758 and *Lycaon* between the relative depth of the mandible (JDm1-2/MandL, X-axis), calculated as the depth of the horizontal ramus at the m1-m2 contact divided by mandibular length between the distal border of the lower canine and the tip of the jaw condyle, and the relative length of the carnassial blade (Lm1trig/(Lm1tal+Lm2), Y-axis), estimated as the ratio between the length of the m1 trigonid and the length of the m1 talonid plus the length of second lower molar. Mean values for modern species calculated from original data (measurements taken in 252 specimens) kindly provided by B. Van Valkenburgh and taken from Torregrosa (2008).

Moreover, isotopic data retrieved from bone collagen of the members of the carnivore guild from this site (Fig. 7) show that the $\delta^{15}\text{N}$ values of *C. orcensis* n. sp are lower than those of the hypercarnivore *L. lycaonoides*, which suggests a lower consumption of ungulate prey, but close to the values of the pantherine cat *P. gombaszoegensis* and, to a lesser extent, those of the sabre-tooth *M. whitei*, both hypercarnivores (Palmqvist *et al.* 2008). This confirms that the medium-sized canid from Venta Micena had more hypercarnivorous dietary habits than other early Pleistocene canids of similar size (except Untermassfeld) or the extant omnivorous species of this family.

DISCUSSION AND CONCLUSIONS

The taxonomy and systematics of the early Pleistocene canids of Europe and Asia is a much-debated topic. The middle/late Villafranchian faunal turnover, around 2.0 Ma, when the large

canids became common in western Asia and Europe, is well known in the Italian assemblages, especially in the Upper Valdarno, by the record of three species of large canids: *Lycaon falconeri*, *Canis etruscus* and *C. arnensis* (Forsyth-Major 1877; Del Campa 1913; Azzaroli 1977, 1983).

The large canids from Venta Micena, c. 1.6 Ma, have to be explained in this context. As it was interpreted by Martínez-Navarro & Rook (2003), the largest hypercarnivorous form is a more evolved chronospecies than *L. falconeri*, and it was ascribed to *L. lycaonoides*, together with the later forms of this lineage, found in late Villafranchian and Epivillafranchian assemblages (Rook & Martínez-Navarro 2010).

Similarly, the sample of *Canis* from Venta Micena possesses consistent differences with the first representatives of this genus in western Europe, i.e., the Italian populations of *C. etruscus* and *C. arnensis* from the Upper Valdarno at the sites of Tasso and Poggio Rosso. On the contrary, *C. orcensis* n. sp. shows a number of features (e.g. the mesiodistally

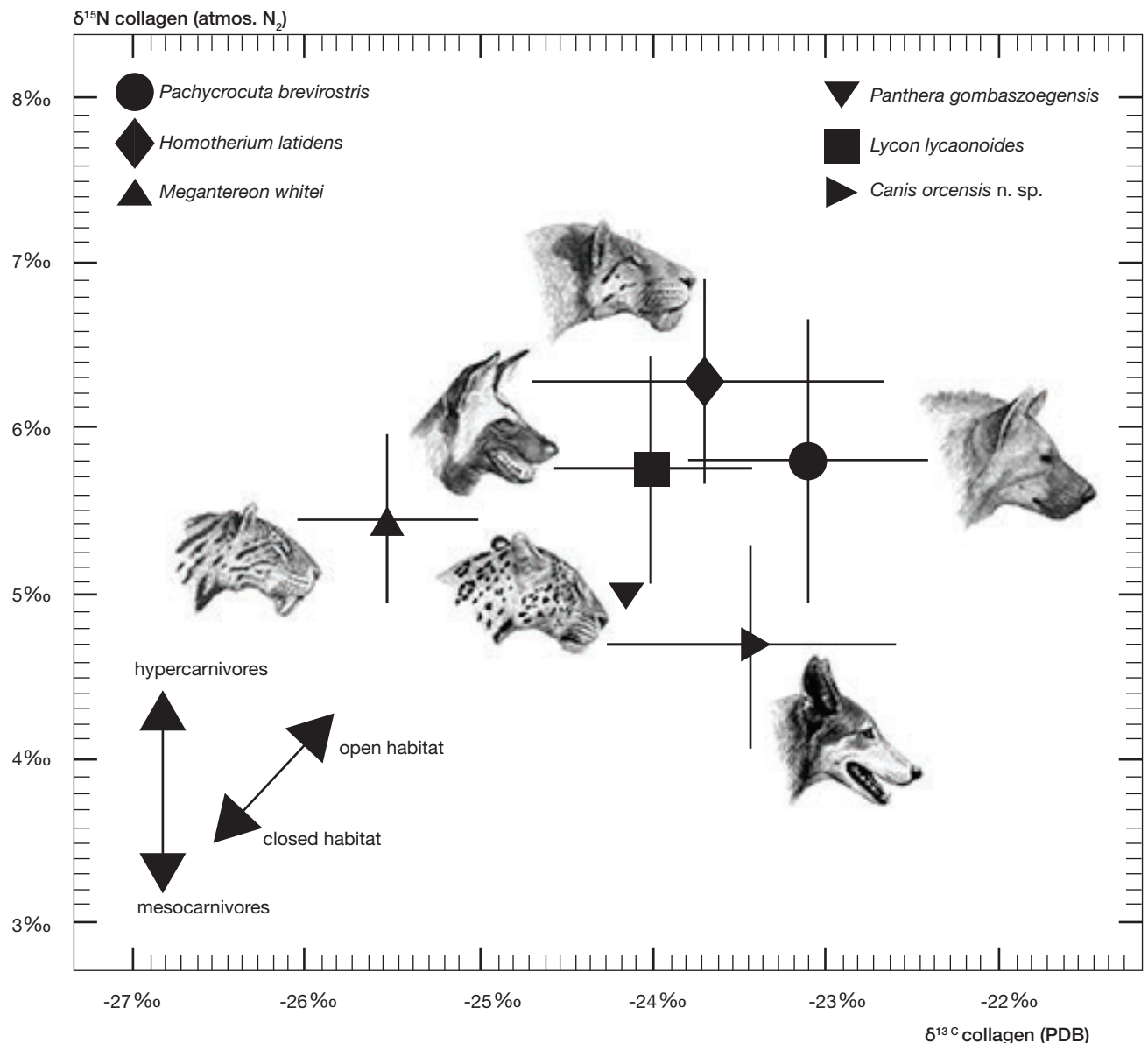


Fig. 7. — Isotopic data ($\delta^{13}\text{C}$ values, X-axis; $\delta^{15}\text{N}$ values, Y-axis) measured in samples of bone collagen from the carnivorous species identified in the early Pleistocene site of Venta Micena. The symbols indicate the species means and the lines represent one standard deviation below and above these means (data from Palmqvist *et al.* 2008). Specimens of *Canis orcensis* n. sp. analyzed (named as *Canis mosbachensis* in Palmqvist *et al.* 2008): VM-2254 (two samples from the same specimen, a left mandible from an adult individual with M2 and roots of P3-P4-M1) and VM-4440 (a right mandible of a subadult individual, in which the M1 shows non developed roots). Given the low abundance of carnivore remains at Venta Micena compared to those of ungulates, few specimens from each carnivore species could be sampled, although a minimum of three individual values were obtained from each species. Due to this limitation of sampling, this figure depicts the means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values plus one standard deviation, instead of plotting individual specimens.

elongated lower carnassials, with a rather reduced metaconid and a sinuous crista transversa connecting the hypoconid and entoconid) resembling *C. borjgali* from Dmanisi and also some late Early Pleistocene taxa ex gr. *C. mosbachensis* (e.g. *C. apolloniensis* from Apollonia-1, but particularly *C. mosbachensis* from Pirro Nord, Untermassfeld, Cueva Victoria and Vallparadís Section), as also noted by several authors in the literature (among others, Rook & Torre 1996). Nevertheless, *C. orcensis* n. sp. possesses peculiarities that contrast with the typical *C. mosbachensis*, such as the strong reduction of the

metaconule of M1 and the enlargement of the M1 paracone compared to the metacone. Most probably, *Canis orcensis* n. sp. is a chrono-species that connects the earlier forms of small-to-medium-sized canids from the middle-late Villafranchian transition located at the Faunal units of Olivola and Tasso, together with those from Dmanisi, to the posterior latest late Villafranchian and Epivillafranchian *Canis mosbachensis* in the European continent, and *Canis mosbachensis variabilis* from the late Early and Middle Pleistocene assemblages of eastern Asia (Jiangzuo *et al.* 2018). This species shows a number of

ecomorphological adaptations to an hypercarnivorous diet more developed than in other Late Villafranchian canids of similar size from Western Europe.

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