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Jaramillo-aged carnivorans from Collecurti (Colfiorito Basin, Italy)

Joan Madurell-Malapeira^{1,2,3,*}, Saverio Bartolini-Lucenti^{4,5}, Maria Prat-Vericat¹, Leonardo Sorbelli¹, Alessandro Blasetti⁶, Marco P. Ferretti⁷, Alessandro Goro⁷, Marco Cherin³

¹ Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain. joan.madurell@icp.cat

² Department of Geology, Universitat Autònoma de Barcelona, Facultat de Ciències, Edifici C, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

³ Department of Physics and Geology, University of Perugia, Via A. Pascoli, 06123 Perugia, Italy

⁴ Earth Science Department, Paleo[Fab]Lab, University of Florence, Via La Pira 4, 50121 Firenze, Italy.

⁵ Natural History Museum, Geology and Paleontology Section, University of Florence, Via La Pira 4, 50121 Firenze, Italy.

⁶ Museo delle Scienze, Università degli Studi di Camerino, Via Gioco del Pallone 5, 62032 Camerino, Italy

⁷ Scuola di Scienze e Tecnologie, Sezione di Geologia, Università degli Studi di Camerino, Via Gentile III da Varano, 62032 Camerino, Italy

Abstract

Late Early Pleistocene vertebrate assemblages in the Mediterranean area have sparked the interest of the scientific community in the last two decades mainly thanks to the discovery of fossils and/or stone tools testifying to the presence of early *Homo*. However, our knowledge of most of these assemblages is biased by the lack of well-constrained chronological data, especially for those close to or related to the Jaramillo magnetostratigraphic subchron (ca. 1.0 Ma). As a matter of fact, the available European paleontological assemblages chronologically close to the Jaramillo interval are overall scarce, especially for the period prior to the so-called “0.9 Ma event”. This long and cold glacial period was characterized by profound changes in ecosystems and important faunal turnover in Europe, including the replacement of most Villafranchian species by typical Galerian ones. Here, we report on the carnivoran remains from Collecurti (central Italy), that is, one of the few available Jaramillo-dated assemblages in Europe. The Collecurti

sample includes the species *Canis (Xenocyon) lycaonoides*, *Canis mosbachensis*, and *Ursus deningeri* and is here described in detail for the first time and compared with those from similar-aged European sites.

Keywords Carnivora, Early Pleistocene, Early-Middle Pleistocene Transition, Epivillafranchian, Italy.

*Corresponding author

1. Introduction

The late Early Pleistocene (Calabrian Age; ca. 1.8–0.78 Ma) in Mediterranean Europe has been one of the most deeply investigated geological periods since the 1990s, thanks to mostly unexpected finds of hominin direct and indirect remains (e.g., fossils and stone tools) in several Iberian, French, and Italian sites (Moullé et al. 2006; Arzarello et al. 2007; Carbonell et al. 2008; Toro et al. 2013; Vallverdú et al. 2014; Despriée et al. 2017, 2018 and references therein). In this scenario, the Italian paleontological record has provided plenty of valuable information in order to add new pieces of evidence to the knowledge of the Mediterranean late Early Pleistocene, thanks to the recent reappraisal of classical sites and the discovery and/or description of new ones (Rook et al. 2013 and references therein). In fact, if we look at the whole interval from ca. 2 Ma to the Early-Middle Pleistocene boundary, the available information on the composition of faunal assemblages and, consequently, on the structure of ecosystems is biased by the number and richness of paleontological sites. In particular, the European record is quite continuous and the data are quite abundant for two intervals, i.e., that between ca. 2.0–1.2 Ma corresponding to the Late Villafranchian Land Mammal Age (LMA) in the European large mammal-based biochronological scheme (Gliozzi et al. 1997; Rook and Martínez-Navarro 2010), and that between ca. 0.9–0.78 Ma corresponding to the end of the Epivillafranchian stage (Kahlke et al. 2011; Madurell-Malapeira et al. 2014, 2017). The first interval, in which Villafranchian large mammal taxa are still dominant components of the assemblages, is well represented in all Mediterranean Europe including Italy (e.g., Olivola, several localities in the Upper Valdarno, Tiber and Valdichiana Basins, Pietrafitta, Monte Argentario, Pirro Nord; Azzaroli

1983; De Giuli 1987; Pavia et al. 2012; Petrucci et al. 2013; Rook et al. 2013; Cherin and Rook 2014; Iurino and Sardella 2014; Martinetto et al. 2014; Bartolini-Lucenti and Rook 2016; Cherin et al. 2018a, 2018b, 2019; Sardella et al. 2018; Sorbelli et al. 2021a), Iberia (e.g., several sites in the Guadix-Baza Basin; Madurell-Malapeira et al. 2014 and references therein), southern France (e.g., Creux de Peyrolles; Valli et al. 2006), and Greece (e.g., several sites in the Mygdonia Basin, Libbakos; Koufos 2001; Konidaris et al. 2021). The second interval is similarly well known especially thanks to the outstanding record from Iberia (e.g., sites of the Atapuerca Complex and Vallparadís Section Middle Unit; Madurell-Malapeira et al. 2010, 2014 and references therein) and secondarily thanks to some sites from Italy (e.g., Slivia; Ambrosetti et al. 1979; Cherin et al. 2020) and France (e.g., Durfort; Palombo and Valli 2004). On the other hand, the intermediate interval (ca. 1.2–0.9 Ma), corresponding to the beginning of the Epivillafranchian and including the Jaramillo magnetostratigraphic subchron (1.07–0.99 Ma; MIS 31) is still poorly known. Two remarkable exceptions in this timespan are layers EVT10–12 of the Vallparadís Section (Madurell-Malapeira et al. 2010, 2014, 2017, 2019a) and Untermassfeld (Kahlke 2006), both documenting the Jaramillo subchron. The latter site, although located in Germany, yielded a vertebrate fauna which is clearly indicative of warm climatic conditions (Kahlke et al. 2011) in fact, showing several taxonomic affinities with roughly coeval sites of the Mediterranean area. Few other fossiliferous sites spanning the 1.2–0.9 Ma interval are available in Mediterranean Europe, among which Cueva Victoria in Iberia (Madurell-Malapeira et al. 2014; Bartolini-Lucenti et al. 2017); Le Vallonnet and Bois-de-Riquet in

France (Moullé et al. 2006; Bourguignon et al. 2016), Arda River and Monte Peglia in Italy (Sardella and Iurino 2012; Bona and Sala 2016; Petronio et al. 2020).

In this context, one of the most interesting but least investigated sites is undoubtedly that of Collecorti (Italy; Fig. 1). Discovered in the late 1980s (Borselli et al. 1988), this Jaramillo-aged site has been the subject of in-depth geological, taphonomic, and paleoenvironmental studies (Torre et al. 1996; Coltorti et al. 1998; Bertini 2000; Mazza and Ventra 2011). Conversely, with the exception of some works on the arvicolid remains from the site (Ficcarelli et al. 1990; Masini and Santini 1991; Abbazzi et al. 1998), the large mammal fauna, represented by fossils in exceptional state of preservation, has been described only briefly (Ficcarelli and Mazza 1990; Ficcarelli and Silvestrini 1991). Despite this, the importance of Collecorti as a crucial site to investigate the end-Villafranchian faunal turnover, already recognized by Ficcarelli and Silvestrini (1991) and Masini et al. (1994), was confirmed by the formal choice of this local faunal assemblage as representative of the homonymous Collecorti Faunal Unit (misspelled as “Colle Curti”) in the Italian biochronological scheme based on large mammals (Gliozzi et al. 1997; Masini and Sala 2007; Palombo and Sardella 2007; Palombo et al., 2008, 2009; Rook and Martínez-Navarro 2010).

This article represents the first contribution of our review project on the large mammals from Collecorti. In particular, we present here the first detailed description of the remains of Carnivora from the site and their comparison with the available samples from other European sites of comparable age.

1.1 Biochronological background

The European carnivoran guild remains more or less stable throughout the Late Villafranchian (Madurell-Malapeira et al. 2010; 2014, 2019a; Kahlke et al. 2011; Cherin et al. 2013) despite the continuously changing paleoenvironmental conditions from more open (grasslands and forested steppes) to forested landscapes following the obliquity-forced glacial-interglacial periodicity of ca. 41 ka (Leroy et al. 2011; Magri et al. 2017). Not considering the small carnivorans (i.e., foxes and mustelids), the Late Villafranchian guild includes the two saber-toothed cats *Homotherium* and *Megantereon*; the giant cheetah-like felid *Acinonyx pardinensis*; the puma-like felid *Puma pardoides*; the Eurasian jaguar *Panthera gombaszoegensis*; the lynx *Lynx issiodorensis*, replaced by *Lynx pardinus* in the latest Villafranchian; two species of mesocarnivorous canids, *Canis etruscus* and *Canis arnensis*, both replaced by *Canis mosbachensis* in the latest Villafranchian; the hypercarnivorous wild dog-like canid *Canis (Xenocyon) falconeri*, replaced by *Canis (Xenocyon) lycaonoides* during the second half of the late Villafranchian; the bear *Ursus etruscus*; and the giant hyena *Pachycrocuta brevirostris* (Rook and Martínez-Navarro 2010; Madurell-Malapeira et al. 2014, 2019a). In fact, the competition between carnivorans in the Late Villafranchian must have been very high (Rodríguez et al. 2012) and finds in some way an “ecological equivalent” in the present-day carnivoran guild of East Africa (Cherin et al. 2013). In addition, noteworthy is the ecological influence of the arrival of early *Homo* in Europe in the same period, which as a hunter certainly interacted with carnivorans –in still debated ways– to the exploitation of prey (e.g., Hemmer et al. 2011; Espigares et al. 2013).

Around 1.2 Ma, the beginning of the Epivillafranchian biochron roughly coincides with a major climatic event in the Earth history, the so-called *Early-Middle Pleistocene Transition*

(EMPT; ca. 1.2-0.4 Ma in its wider sense; Head and Gibbard 2015). During this period, several geological proxies record a progressive increase of amplitude of the climate oscillations driven by the shift from obliquity-dominated 41-ka cycles to eccentricity-dominated 100-ka cycles. This shift caused the increase of average global ice volume, the intensification of seasonality, and the establishment of strong asymmetry in global ice volume cycles (Head and Gibbard 2005; Maslin and Ridgwell 2005). Furthermore, a long-term (ca. 80 ka) and extreme glaciation, known as the “0.9 Ma event”, occurred in correspondence to MIS 24 and MIS 22. During this period, surface sea temperatures reached the lowest values of the EMPT in the North Atlantic (Clark et al. 2006; Head and Gibbard 2015; Maslin and Brierley 2015). All these climatic shifts had important repercussions on the ecosystems and the vertebrate faunal composition in Europe, particularly at high latitudes but also in the Mediterranean area (Kahlke et al. 2011; Head and Gibbard 2015; Magri and Palombo 2013). As a matter of fact, these deep ecological changes are the main reason why many researchers proposed the validity of the Epivillafranchian itself as a formal biochron (Kahlke 2006; Kahlke et al. 2011; Madurell-Malapeira et al., 2010, 2017). From about 1.0 Ma, most of members of the Villafranchian carnivoran guild started vanishing from European ecosystems. Indeed, most of the aforementioned taxa of medium- to large-sized carnivorans were last recorded at MIS 21 (ca. 0.86 Ma; Madurell-Malapeira et al. 2010) and were replaced by species of African origin such as *Panthera fossilis*, *Panthera pardus*, and *Crocuta crocuta* (Madurell-Malapeira et al. 2014, 2019a), which dominated Europe in the Middle Pleistocene.

In this context, any novel information on the composition of the Epivillafranchian carnivoran guild is able to add pieces of information crucial to understanding the EMPT.

1.2. Geological, magnetostratigraphic and paleoenvironmental background

Systematic field surveys were carried out in the Colfiorito area –in the Collecurti-San Martino basin and in the neighboring one of Cesi, dated to the early Middle Pleistocene (Ficcarelli et al. 1997)– by researchers of the Universities of Camerino and Firenze between 1987 and 2012.

The majority of the Collecurti vertebrate fauna occurs in a 10–15 cm bed of gravels (U3 in Fig. 1B), within the middle part of the Pleistocene fluvio-lacustrine deposits of the Collecurti basin. This is a small intermountain basin of tectonic-karstic origin, located in the Umbria-Marchean Apennines at about 850 m above sea-level (Coltorti et al. 1998). The Jurassic to Oligocene carbonate bedrock was affected by extensional tectonics in the Early to Middle Pleistocene causing the formation of various tectonic depressions in the area (Fig. 1A). The Collecurti basin is filled by approximately 100 m of clastic sediments, consisting of coarse gravels at the bottom and at the top of the sequence, and an interposed 40 m-thick clay deposit. These represent the gradual development of a shallow lake environment from an initial braidplain, in the lower to middle part of the succession and a final re-establishment of a fluvial plain. At the main excavation site, the upper gravely portion of the Collecurti succession is not present, due to erosion, so that the intermediate lacustrine clayey unit is directly exposed on the surface. The main bonebed is located here about 1 m below the surface (Fig. 1B) and is contained within a medium gravel layer interbedded in clays representing the lower part of the lacustrine episode, stratigraphically at about 45 m from

the base of the complete Collecureti succession. Two paleomagnetic reversals were recorded along the Collecureti lacustrine sequence, one just below the main fossiliferous layer, whose sediments show a normal polarity (Coltorti et al. 1988). The short normal episode is identified as the Jaramillo subchron (C1r.1n), a conclusion supported by the systematic composition of the vertebrate fauna and a Ar/Ar dating of 424 ka obtained on sanidine crystals from pyroclastic sediments occurring at the top of the Collecureti succession (Coltorti et al. 1988). Based on these results, the Collecureti fauna can be confidently correlated with the beginning of the Jaramillo subchron, at about 990 ka.

Taphonomic studies explained the origin of the Collecureti mammal assemblage as the result of debris-flow events triggered in the upland areas of the basin margin, where they swept away sparse bones from disarticulated skeletons. Later, the same flows reached a lacustrine environment covering several hippopotamus carcasses that were lying in advanced degree of decomposition (Mazza and Ventra 2011).

General tectonic and geomorphological evidence for this area of the Apennine chain, suggests that the Collecureti basin was set at an elevation not exceeding 400 m a.s.l. during the Middle Pleistocene (Coltorti et al. 1991). The paleoenvironment was likely characterized by a montane coniferous forest dominated by *Tsuga* and *Cedrus*, based on palynological analyses of the Collecureti deposits (Bertini 2000). It is worth noting that *Tsuga* disappeared from Europe during the early part of the Brunhes Chron (ca. 700 ka.), with the onset of more arid conditions. Integrated faunal and floral proxies suggest that during the formation of the Collecureti vertebrate deposit the climate was humid, with mild winter temperature. Available data seems thus to support the hypothesis that the Collecureti fossil horizon represents an

interglacial phase, tentatively correlated with MIS31 (Bertini 2000). As for the remained of the fluviolacustrine sequence, bracketed between the Collecorti fossil layer and that at the nearby Cesi site, spanning ca. 400 ka, palynological studies indicated an alternation between intervals of prevalent montane coniferous forest and intervals of prevalent open vegetation, as well as changes between more humid and colder, drier phases.

2. Materials and methods

The specimens described in this paper are housed in the collections of the Science Museum of the University of Camerino (SMUC; Italy). They were compared on qualitative morphological as well as biometric grounds with several samples of Early to Middle Pleistocene carnivorans from Europe, housed in the following institutions: Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain), Museu Arqueològic Comarcal de Banyoles (Banyoles, Spain), Museo Arqueológico de Granada (Granada, Spain), Centre Européen de Recherches Préhistoriques (Tautavel, France), Musée de Préhistoire Régionale (Menton, France), Earth Science Department of the University of Florence (Italy), Geological and Paleontological Section of the Natural History Museum of the University of Florence (Italy), Department of Earth Sciences, Sapienza University of Rome (Italy), Department of Physics and Geology, University of Perugia (Italy). In addition, we included in the comparative analysis morphological and biometric data on the following extant species: *Lycaon pictus*, *Canis lupus*, *Cuon alpinus*, *Vulpes vulpes*, *Vulpes lagopus*, *Ursus arctos*, *Ursus americanus*, and *Ursus maritimus*, taken from skeletons stored at the Royal Museum for Central Africa (Tervuren, Belgium), Natural History Museum of Barcelona (Spain), and La Specola,

Zoological Section of the Natural History Museum, University of Florence (Italy).

Morphological nomenclature used in the descriptions and comparisons is taken from Barone (1999) and Tedford et al. (2009).

3. Results

Order Carnivora Bowdich, 1821

Family Canidae Fischer, 1817

Subfamily Caninae Fischer, 1817

Tribe Canini Fischer, 1817

Genus *Canis* Linnaeus, 1758

Subgenus *Xenocyon* Kretzoi, 1938

Canis (Xenocyon) lycaonoides (Kretzoi, 1938)

Fig. 2

Referred specimens—SMUC 52457, right corpus with p3, m2, and alveoli of p1-p2, p4-m1, and m3.

Measurements—Table 1

Description—The studied specimen preserves most of the corpus, which is high and stoutly built. The masseteric fossa is deep, reaching anteriorly the level of the m3 alveolus. The p3 shows in labial view a high and asymmetric protoconid, an individualized distal accessory cuspid, and a strong distal cingulid (Fig. 2B). The m2 displays an oval occlusal outline, with two trigonid cusps, i.e., a large and sharp protoconid, and a strongly reduced and lingually-situated metaconid. The m2 talonid only shows a reduced and labially-

situated hypoconid. A well-developed cristid develops along the lingual side of the talonid (Fig. 2C).

Discussion—Attribution of SMUC 52457.

The teeth number and morphology are suggestive of an attribution of the specimen SMUC 52457 to a large-sized canid. The stoutness of corpus and the development of the buccal cuspulids of the lower second molar support the attribution to the group of hypercarnivorous *Canis* (*Xenocyon*). The mandible from Collecurti shares several characters with other Late Villafranchian and Epivillafranchian European samples referred to *C. (Xenocyon) lycaonoides* (Rook 1994; Palmqvist et al. 1999; Sotnikova 2001; Martínez-Navarro and Rook 2003; Moullé et al. 2006; Madurell-Malapeira et al. 2013; Petrucci et al. 2013; Vislobokova and Agadjanian 2015; Bartolini-Lucenti et al. 2021 and references therein), namely the high and stout mandibular corpus; relatively low premolars with strong distal accessory cuspid; sharp and well-developed m2 labial cuspids (protoconid and hypoconid) compared to the lingual ones (metaconid and entoconid, which is absent in SMUC 52457) (Fig. 3). The premolar morphology of SMUC 52457 is noteworthy. While in the majority of the samples of *Canis* (*Xenocyon*) the premolars are relatively short, in some specimens such as those from Venta Micena and Vallparadís Estació, the premolars are significantly longer and higher (Madurell-Malapeira et al. 2013), as observed in the specimen from Collecurti. Furthermore, the presence of distal accessory cuspids on the p2 and p3 is a common feature in late Early Pleistocene *C. (Xenocyon) falconeri* and *C. (Xenocyon) lycaonoides* and also in *L. pictus* (Fig. 3; Madurell-Malapeira et al. 2013).

Regarding the m2, the morphology of the Collecorti specimen (especially the protruding and sharp protoconid and the relatively reduced metaconid) fits that of Epivillafranchian samples of *C. (Xenocyon) lycaonoides* from Vallparadís Estació, Untermassfeld, Cueva Victoria, and Le Vallonnet (Pons-Moyà and Moyà-Solà 1978; Sotnikova 2001; Moullé et al. 2006; Madurell-Malapeira et al. 2013). The reduction in size of the metaconid as compared to the protoconid observed in all Epivillafranchian wild dogs is different from the typical morphology of *L. pictus*, in which the metaconid is absent, but also from that observed in the m2 of earlier (i.e., Late Villafranchian) *Canis (Xenocyon)* (e.g., Upper Valdarno, Pirro Nord, Venta Micena, among others), in which the metaconid is only slightly smaller than the protoconid (Madurell-Malapeira et al. 2013; Fig. 3).

Overview of large-sized hypercarnivorous canids of the Early Pleistocene.

Canis (Xenocyon) lycaonoides was a large-sized hypercarnivorous species that arose during the in the Early Pleistocene in Asia and then dispersed across the Old World (Martínez-Navarro and Rook 2003; Bartolini-Lucenti et al., 2021). This canid was a particularly successful carnivorans that became a common element of Eurasian and African faunas. It persisted in Europe until the latest Early Pleistocene (Madurell-Malapeira et al. 2013; Bartolini-Lucenti et al., 2021). It reached north-eastern of portion of Russia (Sher 1986), managing even to reach North America (Tedford et al. 2009). The origin of this species has always been related to the earlier and more primitive (in terms of dental adaptations to hypercarnivory) *C. (Xenocyon) falconeri* (Rook 1994), probably arising from some Asian form. There is general consensus in regarding *Canis (Xenocyon) lycaonoides* as the possible ancestor of the extant African wild dog *L. pictus* (Stiner et al. 2001; Martínez-

Navarro and Rook 2003; Tedford et al. 2009; Madurell-Malapeira et al. 2013; Petrucci et al. 2013; Koufos 2018; Bartolini Lucenti et al., 2021), also fitting some genetic evidence (Chavez et al. 2019). Hence the choice of some authors to refer the species of *Canis* (*Xenocyon*) to the genus *Lycaon* (e.g., Madurell-Malapeira et al. 2013). However, some researchers expressed doubts on this systematic interpretation (e.g., Geraads 2011). Recently, Hartstone-Rose et al. (2010) proposed a new species as the ancestor of the African wild dog lineage, *Lycaon sekowei* from two South African sites (Cooper's Cave and Gladysvale, 1.9 Ma and 1.0-0.7 Ma respectively; Pickering et al. 2007). Yet the morphology of the premolars, that is, one of the distinctive features of *L. sekowei*, is considerably variable in *L. pictus* as well as in *Canis* (*Xenocyon*) (Sotnikova 2001; Madurell-Malapeira et al. 2013). Considering therefore that an African origin of wild dogs is debated and currently based on scanty fossils, we favour the more widely accepted hypothesis of a Eurasian origin of this group, which subsequently dispersed into Africa around 1.8 Ma (Rook and Martínez-Navarro 2010; Madurell-Malapeira et al. 2013; Bartolini-Lucenti et al., 2021). To complete the picture, it is worth mentioning that results coming from recent phylogenetic analyses is conflicting. According to molecular data, *Lycaon* and *Cuon* are generally accepted as basal to *Canis* (Gopalakrishnan et al. 2018), although studies based on mitochondrial and nuclear DNA may produce slightly different results (Koepfli et al. 2015). In the phylogenetic tree by Zrzavý et al. (2018), in which morphological, developmental, ecological, behavioural, and molecular data are combined, *Lycaon* is basal to a wide clade including extant *Canis*, *Lupulella*, and *Cuon*, as well as several extinct species (unusual pattern that contrasts both morphological and molecular analyses; see respectively Tedford et al. 2009 and Perri et al.

2021). Among these, *C. (Xenocyon) lycaonoides* (= *Xenocyon lycaonoides*) results as the sister group of *Cuon*, and their common ancestor is part of a polytomy which also includes *C. (Xenocyon) falconeri* (= *Canis falconeri*). Based on these conflicting interpretations, we prefer to keep the wild dog-like Villafranchian-Epivillafranchian species into the subgenus *Canis (Xenocyon)* pending resolute phylogenetic studies.

Genus *Canis* Linnaeus, 1758.

Canis mosbachensis Soergel, 1925

Figure 4

Referred specimens—SMUC 52459, left tibia lacking proximal epiphysis.

Measurements—Table 1.

Description—Approximately the proximal third of the tibia is not preserved. The preserved part of the diaphysis is crossed by several fractures. It appears lightly-built and almost rectilinear. The distal epiphysis displays an evident rounded pit in its posterior part, almost certainly interpretable as a bite mark (Fig. 4B). The malleolus is prominent medially, and distally projected in both anterior and posterior views (Fig. 4A-B). On its lateral side, the distal tibial notch is relatively shallow and wide. The distal articular surface is well preserved (Fig. 4C). The lateral and medial articular grooves are similar in size and depth and separated by a low and wide transverse crest.

Discussion—*Attribution of SMUC 52459.*

The tibia SMUC 52459 has typical morphologies (e.g., the trapezoidal outline of the distal epiphysis in distal view) and size of medium-sized canid, suggesting a plausible attribution to *Canis*. Although the morphology of the postcranial skeleton is rather conservative in members of the genus *Canis*, some features might be pointed out. In comparison to *C. etruscus* from Olivola and Upper Valdarno, the specimen SMUC 52459 is rather slender and laterally compressed especially at level of the distal epiphysis. In contrast, *C. etruscus* has a stouter diaphysis. Moreover, *C. etruscus* has a broader and more medially expanded malleolus. Similar is the development of the lateral part of the epiphysis, that is much more reduced in the Collecorti specimen SMUC 52459, compared to the morphology of the sample of *C. etruscus* from, e.g., Olivola (Torre 1967). Lastly, the distal notch on the cranial surface of the tibia is wider compared to that of the Collecorti specimen. Compared to *C. arnensis* from Upper Valdarno, there are also some features that worth to be pointed out. Firstly, the diaphysis of *C. arnensis* appears narrower compared to that of the Collecorti specimen SMUC 52459. Moreover, the outline of the cranial notch of the distal epiphysis of the tibia is narrower in *C. arnensis* compared to that of SMUC 52459, although its proximal development is comparable to that of both *C. etruscus* and SMUC 52459. In contrast to the latter, *C. arnensis* and *C. etruscus* show similar morphologies in the cranial and plantar outlines of the distal articular surface. In the two Early Pleistocene species, the cranial outline of the surface shows an evident and sharp-pointed process, lying just laterally to the notch. This process is blunt and much lower in the specimen SMUC 52459. On the plantar surface, the outline of the articular surface in *C. arnensis* is characterized by a developed distally concavity, more arched than in specimen SMUC

52459. Furthermore, in the same view, the distal epiphysis of *C. arnensis* shows a slender, shelflike morphology on the lateral side, unlike the rounded morphology of SMUC 52459. Lastly the groove on the plantar side of the malleolus is deeper and more marked in *C. arnensis* than in SMUC 52459. In contrast with these primitive western Eurasian canids, the specimen from Collecureti shows some characters recognized in the tibiae of *C. mosbachensis* from several sites, including L'Escaze (Bonifay 1971; Boudadi-Maligne 2010), Stránská-Skála (Musil 1972), Trinchera Dolina 6 (García and Arsuaga 1999), Untermassfeld (Sotnikova 2001), and Ceysaguet (Tsoukala and Bonifay 2004). In particular, the straight morphology of the distal part of the diaphysis and the shape of the distal notch resembles the specimens from Stránská-Skála, Trinchera Dolina 6, and L'Escaze. The similarity above all with the rich sample from L'Escaze is confirmed by the biometric comparisons on the distal epiphysis (Fig. 5). The specimen from Collecureti falls in the middle of the L'Escaze range (with the exception of three very large individuals from this site) and is relatively smaller than the tibiae of *C. mosbachensis* from the other considered localities. However, the position in the graph of the few available tibiae of the Villafranchian *C. etruscus* and *C. arnensis* (Fig. 5) evidence that a size-only approach is not sufficient to distinguish *C. mosbachensis* from the other species.

The wolf-like Canis mosbachensis in Early Pleistocene times.

Canis mosbachensis is a late Early-Middle Pleistocene medium-sized species that was widely spread in Eurasia (Rook and Torre 1996; Sotnikova 2001; Martínez-Navarro et al. 2009; Sotnikova and Rook 2010; Petrucci et al. 2013; Bartolini-Lucenti et al. 2017; 2020; Jiangzuo et al. 2018; Mecozzi et al. 2020; Martínez-Navarro et al. 2021). Its taxonomical

status is debated, being considered as a separate species (e.g., Sotnikova 2001; Jiangzuo et al. 2018) or a subspecies of *C. lupus* (e.g., Thenius 1954; Kurtén 1968), or even a subspecies of *C. etruscus* (e.g., Bonifay 1971; Agustí et al. 1987). Today, the first interpretation is rather consolidated, as is the phylogenetic reconstruction according to which *C. mosbachensis* is an intermediate species between *C. etruscus* and *C. lupus* along the same lineage (Torre 1967; Kurtén 1968; Musil 1972; Sotnikova 2001; Brugal and Boudadi-Maligne 2010). However, a recent revision of the canid material from the early Late Villafranchian site of Dmanisi (Georgia; ca. 1.8 Ma), previously attributed to *C. etruscus* (Vekua 1995), has recognized several derived features in this sample as compared with *C. etruscus*, hence the referral to the new species *Canis borjgali* (Bartolini-Lucenti et al. 2020). The morphological affinity between *C. borjgali* and *C. mosbachensis* led to the reconsideration of the putative lineage *C. etruscus*-*C. mosbachensis*-*C. lupus* supporting the stronger affinity between the Georgian form and *C. mosbachensis* and, in turns with *C. lupus* (Bartolini-Lucenti et al. 2020).

The earliest reported occurrence of *C. mosbachensis* in Europe is from the Orce site complex (Venta Micena, Barranco León, Fuente Nueva 3; ca. 1.5-1.2 Ma; Duval et al. 2011, 2012; Madurell-Malapeira et al. 2014; Martínez-Navarro et al. 2021), that is, the arrival of this species is almost contemporaneous with the spread of *C. (Xenocyon) lycaonoides* in Europe (Sotnikova and Rook 2010; Bartolini-Lucenti et al. 2017). These events are part of the turnover that involved the European carnivoran guild during the latest Villafranchian (see Palombo et al. 2008). Some canid samples of latest Villafranchian and Epivillafranchian age are regarded by some authors as different species, such as *Canis apolloniensis* from

Greece (Koufos 2018) *Canis orcensis* from Venta Micena (Martinez-Navarro et al. 2021) and *Canis tamanensis* from the Azov Sea area (Sotnikova and Titov 2009). However, it is very likely that these samples could indeed be included into *C. mosbachensis*, also considering the presence of this species in China at least since the mid-late Early Pleistocene (see Jiangzuo et al. 2018 for *C. mosbachensis* occurrences in eastern Asia). After the westward dispersal in Europe, *C. mosbachensis* became a common element of the continental carnivoran guild at least until the mid-Middle Pleistocene, when it was replaced by the modern wolf (Sardella et al. 2014).

Family Ursidae Bowdich, 1821

Genus *Ursus* Linnaeus, 1758

Ursus deningeri Von Reichenau, 1904

Figure 6

Referred specimens— SMUC 52458, right maxillary fragment with P4 and mesial fragment of M1.

Measurements—Table 1.

Description— The studied maxillary fragment preserves a complete P4 with a sharp and narrow paracone without parastyle, low metacone without visible metastyle, and narrow protocone attached to the metacone without accessory cuspids. The P4 general occlusal outline is narrow, with the mesial and distal parts of similar width (Fig. 6C). Only the mesial part of the M1 is preserved. The massive paracone is connected mesially with a small and vertical parastyle.

Discussion— Attribution of SMUC 52458

The available fragmented specimen from Collecurti (SMUC 52458), although fragmented clearly shows dental features of members of the genus *Ursus*. It displays some plesiomorphic characters shared by other latest Early Pleistocene *Ursus* specimens (i.e., Vallparadís Estació, Le Vallonnet, Trinchera Dolina, and Untermassfeld) namely: (1) labiolingually compressed P4 without accessory cusps (Fig. 7); (2) sharp P4 paracone with mesial margin inclined distally with an angle of ca. 45°; (3) labiolingually compressed and unicuspid P4 deutocone attached to the metacone, and (4) M1 with well-developed and vertically implanted parastyle. It is worth noting that these dental characters, as well as other, can be subject of a certain intra-sample variation in ursids. For instance, the only P4 recorded at Untermassfeld (IQW 1983/1955) or some P4 from Le Vallonnet (e.g., Vall. A6C 6902) show a less sharp paracone and a labiolingually inflated protocone, respectively (J.M.-M. pers. observ.; Moullé 1992; Musil 2001). A similar morphology (i.e., relatively wide P4, with blunter mesial profile of the paracone) is also observed in the nearly coeval Frantoio locality (Bona and Sala 2016). On the contrary, differently from the Collecurti specimen, most of the later (i.e., Middle Pleistocene) samples of *U. deningeri* and especially *U. spelaeus* s.l. display (1) a vertical and blunt P4 paracone, (2) P4 main cusps (paracone, metacone, protocone) with accessory cusps, (3) relatively wide P4 (especially the protocone), and (4) M1 with mesially directed parastyle (J.M.-M. pers. observ.).

Taking into consideration the above comparisons, we conclude that the most parsimonious option is to include the Collecurti specimen SMUC 52458 into the *U. deningeri* hypodigm.

The Ursus lineages of the late Early Pleistocene-Late Pleistocene

Since the pioneering works of Björn Kurtén (see a synthesis in Kurtén 1976), the cave bear history has been traditionally seen by most palaeontologists as an example of gradual evolution, beginning in the late Early Pleistocene with *Ursus etruscus*, through the Middle Pleistocene with *U. deningeri*, and ending in the Late Pleistocene with *Ursus spelaeus* s.l. This vision is followed by one of us in recent publications (Madurell-Malapeira et al. 2009, 2010, 2014; Medin et al. 2017, 2019). Nevertheless, in the last two decades, the taxonomy of European Epivillafranchian ursids has been subject to an intense debate. In fact, two new species, putatively displaying several plesiomorphic characters, were described: *Ursus dolinensis* from Trinchera Dolina in Atapuerca (Spain; ca. 1.0–0.8 Ma; García and Arsuaga 2001) and *Ursus rodei* from Untermassfeld (Germany; ca. 1.0 Ma; Musil 2001). The former was diagnosed on the basis of a mixture of primitive “arctoid” and derived “speleoid” characters, which supposedly distinguish it from all other European Pleistocene bears. Furthermore, García and Arsuaga (2001) considered this species very close to the ancestor of *Ursus arctos*. On the other hand, *U. rodei* would be characterized by a typically arctoid cranial morphology. Musil (2001) argued that the presence of anterior premolars and the planar morphology of the glabella point to a close relationship with *U. etruscus*, although this last species shows overall a more primitive morphology. Subsequently, García (2004) attributed the Untermassfeld material to *Ursus* cf. *dolinensis*, emphasizing the sharing of primitive characters with *U. etruscus* and further highlighting strong resemblance between the Untermassfeld sample and those from other late Early Pleistocene sites, including the type locality of Trinchera Dolina (TDW4) and Le Vallonnet (France; ca. 1.2–1.1 Ma)—see

Moullé's (1992) original description for more discussion. According to García (2004), *U. dolinensis* belongs to the *U. spelaeus* lineage. This phylogenetic interpretation contrasts with that of Argant (2006), who considered *U. dolinensis* from Spain as a primitive form belonging to the brown bear lineage. Conversely, the fossils from Untermassfeld and Le Vallonnet would represent an intermediate form between *U. etruscus* and the *U. spelaeus* lineage (Argant 2006). Adding more complexity to this tangle, Rabeder et al. (2010) analyzed in detail the ursid collection from the Austrian site of Deutsch-Altenburg 2 (ca. 1.3–1.0 Ma), concluding that all the previously-described latest Early Pleistocene European ursids should be accommodated in the subspecies *U. arctos suessenbornensis*. The taxonomy of Epivillafranchian ursids remains confused even in the more recent literature. In the monography on Cueva Victoria (Spain, ca. 0.9 Ma), we referred the very scanty ursid remains from the site to *U. deningeri* based on detailed comparisons with the nearly coeval Vallparadís Estació sample (Madurell-Malapeira et al. 2015). On the contrary, Bona and Sala (2016) ascribed to *U. dolinensis* some remains, including a partial cranium and a mandible, from the Frantoio site, Arda River (Northern Italy; ca. 1.1–0.99 Ma). In the first description of the large mammal assemblage from Barranc de La Boella (Spain; ca. 1.0–0.9 Ma), we attributed the scanty ursid material to *U. deningeri* (Madurell-Malapeira et al. 2019b). Finally, in a recent review of the assemblage from Monte Peglia (Italy; ca. 1.0 Ma) – which is normally correlated with Collecorti (Gliozzi et al. 1997) – the few recorded bear remains were referred to *Ursus* cf. *etruscus* (Petronio et al. 2020).

As mentioned above, our opinion on the evolutionary history of European Pleistocene bears is close to Kurtén's early hypothesis, according to which the last representatives of *U.*

etruscus are probably recorded in the Late Villafranchian Orce site complex in a context of climatic stability (ca. 1.6–1.3 Ma; Medin et al. 2017). After that phase and probably relating to the climatic shifts associated to the EMPT, cave bears begin to depend on cave/karstic environments, their average body mass grows significantly, and an ever-increasing trend towards hyperherbivorism is observed (Prat-Vericat et al. 2020). In the light of the relatively scarce available data, we strongly support the most parsimonious scenario, that is, including all the Epivillafranchian European ursids into the hypodigm of *U. deningeri* (Madurell-Malapeira et al. 2009, 2010, 2013, 2014; Medin et al. 2017, 2019; Prat-Vericat et al. 2020).

4. Conclusions

The carnivorans identified at Collecurti are here reattributed to *C. (Xenocyon) lycanoides*, *C. mosbachensis*, and *U. deningeri*, while the presence of a hyaenid in the assemblage, reported in the first papers describing the site (Borselli 1988; Coltorti et al. 1998) is not confirmed. These species are typically recorded in other latest Early Pleistocene European sites such as Untermassfeld, Le Vallonnet, Vallparadís Estació (Lower and Middle Unit), and Cueva Victoria, in a chronological time span from 1.2 to 0.8 Ma (Madurell-Malapeira et al. 2019a; Fig. 8). This fits well with the chronology of the Collecurti assemblage within the Jaramillo subchron, MIS 31 (Coltorti et al. 1998; Mazza and Ventura 2011).

Our comparative analysis highlights that *C. (Xenocyon) lycaonoides* and *U. deningeri* from Colleculti exhibit clear morphological adaptations toward hypercarnivory and hyperherbivory, respectively, which are comparable with what is observed in specimens from Untermassfeld, Vallparadís Estació layers EVT12 and EVT7, and Le Vallonnet (Moullé 1992; Musil 2001; Sotnikova 2001; Madurell-Malapeira et al. 2010, 2013). Moreover, the postcranial element previously referred to *C. arnensis* is here reattributed to the *C. mosbachensis* thanks to its morphological and biometrical features.

The systematic study of the whole Colleculti fauna is still in progress. At the state of the art, we can point out that the persistence of taxa with Villafranchian affinity at Colleculti – including *C. (Xenocyon) lycaonoides*, but also *Mammuthus meridionalis* and *Hippopotamus antiquus* (Mazza and Ventura 2011)– reinforces the significance of the Epivillafranchian as a transitional biochron in Europe (Kahlke et al. 2011; Madurell-Malapeira et al. 2014). Moreover, it confirms that several Villafranchian large mammals did not become extinct before the Early-Middle Pleistocene boundary or at least before the “0.9 Ma event”, as evidenced both in the Iberian and Italian Peninsulas (Madurell-Malapeira et al. 2010, 2014, 2015, 2017, 2019a, 2019b; Strani et al. 2019; Fig. 8).

Similar transitional features are suggested also by the paleoenvironmental evolution of the area reconstructed from the pollen record. The lower part of the Colleculti stratigraphic succession yielded pollen of mesophilous tree taxa such as *Tsuga* and *Cedrus*, associated to and progressively replaced by *Picea* and *Abies* in the upper part (Coltorti et al. 1998; Bertini 2000). Thermophilous arboreal taxa with Villafranchian or even Ruscinian affinity (e.g., Taxodiaceae) are almost absent (Bertini 2000). The paleoenvironment

reconstructed for the earlier phase (i.e., Jaramillo) at Collecorti is that of a small lake basin at medium altitude (ca. 400 m a.s.l.) surrounded by coniferous forests and scattered open areas, in a relatively mild and humid climatic context (Coltorti et al. 1998; Bertini 2000; Mazza and Ventra 2011). This reconstruction is well compatible with the taxonomic composition of the Collecorti fauna, whose remains were concentrated in a bonebed enclosed in a gravel layer, stratigraphically located just below the lowermost *Tsuga* and *Cedrus*-rich pollen assemblage (Bertini 2000; Mazza and Ventra 2011). The large mammal assemblage is largely dominated by *H. antiquus* (402 identifiable specimens over a total of 443 from the bonebed; Mazza and Ventra 2011), which probably found in the Collecorti lake a habitat suitable for its ecological requirements (Martínez-Navarro et al. 2015). The co-occurrence of *M. meridionalis*, *Stephanorhinus* cf. *hundsheimensis*, *Dama vallonnetensis* and *Praemegaceros verticornis* (Coltorti et al. 1998; Mazza and Ventra 2011), as well as *C. (Xenocyon) lycaonoides*, *C. mosbachensis*, and *U. deningeri* described herein, confirms the presence of a mosaic of habitats with coniferous forests and open areas.

The cool and humid phases marked by the aforementioned abundance of conifers are alternated with significantly drier phases, with much more open environments dominated by herbaceous plants (Coltorti et al. 1998; Bertini 2000). In a broader view, when the composite section of Collecorti and Cesi (i.e., about 1.0–0.6 Ma) is considered, a trend of increasing aridity and decreasing temperature can be recognized (Ficcarelli et al. 1997; Bertini, 2000). Such an interpretation perfectly fits the general paleoenvironmental transitions characterizing the EMPT (Magri and Palombo 2013). Despite the relatively poor diversity of the Collecorti and Cesi mammal assemblages, similar conclusions are suggested

by the taxa recognized so far. As a matter of fact, while the Collecrti fauna still shows a certain Villafranchian appearance, the Cesi one (dated at ca. 0.7 Ma) is more typically Galerian (Ficcarelli et al. 1997; Coltorti et al. 1998), as demonstrated by the presence of a caballine horse, the deer *Megacerooides solilhacus* and *Cervus elaphus*, and an advanced form of *Bison schoetensacki* (Ficcarelli et al. 1997; Sorbelli et al. 2021b). The occurrence of *Dama clactoniana* and *S. hundsheimensis* at Cesi (Ficcarelli et al. 1997) needs to be verified.

Pending a detailed reappraisal of the whole assemblages from these Italian localities and their comparison with putatively coeval unpublished ones (e.g., Ellera di Corciano; Cherin et al. 2012), this first contribution on the carnivorans from Collecrti reinforces the key importance of this site –and of the homonymous Faunal Unit– for the European biochronology and, in general, for an ever better understanding of the paleoenvironmental changes during the EMPT.

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Figure Captions

Figure 1. A, Schematic geological section of the Collecureti basin. 1: Recent talus (Holocene), 2: Fluvio-lacustrine deposits of the Collecureti basin (Middle Pleistocene), 3 Mesozoic-Paleogene carbonate bedrock (redrawn from Serva et al., 2002). B, Stratigraphic units of the lacustrine sequence exposed at the Collecureti excavation site. Unit 3 (U3) represents the fossiliferous layer and is composed by a clast-supported gravel, with a sandy to silty clay matrix. Units 1 and 5 are made up by massive silty clay (from Mazza and Ventra, 2011).

Figure 2. *Canis (Xenocyon) lycaonoides* from the Epivillafranchian of Collecureti. SMUC 52457, partial right hemimandible with p3 and m2 in labial (A), lingual (B), and occlusal (C) views. Abbreviations: cgd, cingulid; dacd, distal accessory cuspid; Hd, hypoconid; MasFos, masseteric fossa; Med, metaconid; Prd, protoconid.

Figure 3. Comparative pictures of different specimens of Early Pleistocene *Canis (Xenocyon)* from Mediterranean Europe. A-B, IGF 865, right hemimandible of *Canis (Xenocyon) falconeri* from Il Tasso (Upper Valdarno) in A, labial view; B, detail of m2 in occlusal view. C-D, VM2255, left hemimandible of *Canis (Xenocyon) lycaonoides* from Venta Micena in C, labial view (reversed); D, detail of m2 in occlusal view (reversed). E-F, SMUC 52457, right hemimandible of *Canis (Xenocyon) lycaonoides* from Collecureti in E, labial view; F, detail of m2 in occlusal view. G-H, EVT22434, right hemimandible of *Canis (Xenocyon) lycaonoides* from Vallparadís Estació layer EVT7 in G, lingual view; H, detail of m2 in occlusal view.

Figure 4. *Canis mosbachensis* from the Epivillafranchian of Collecort. SMUC 52459, left tibia in anterior (A), posterior (B), and distal (C) views. Abbreviations: dep, distal epiphysis; diaph, diaphysis; gro, groove; mall, malleolus; not, notch.

Figure 5. Plot of the anteroposterior diameter of the distal epiphysis of the tibia (DAPD) versus its transversal diameter (DTD). The specimen from Collecort (red diamond) is compared with several European samples of *Canis etruscus*, *Canis arnensis*, and *Canis mosbachensis*.

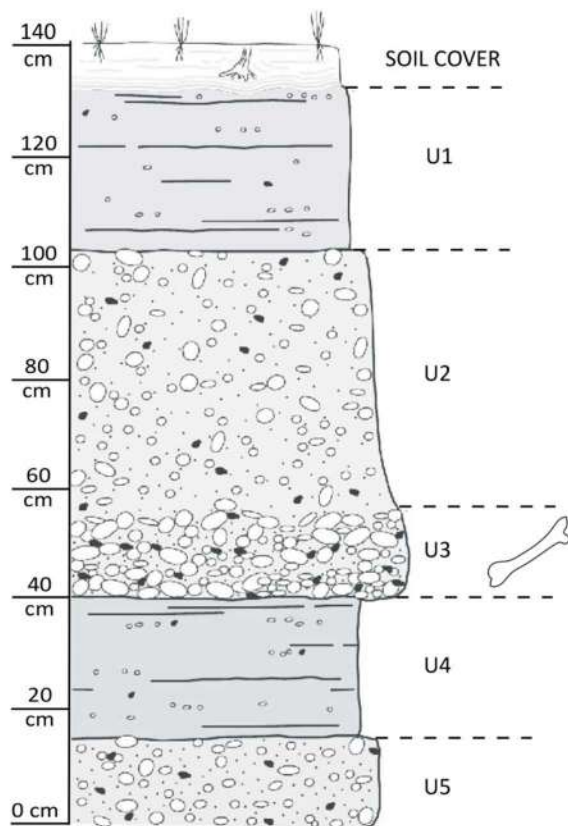
Figure 6. *Ursus deningeri* from the Epivillafranchian of Collecort. SMUC 52458, right maxillary fragment with P4 and mesial fragment of M1 in labial (A), lingual (B), and occlusal (C) views. Abbreviations: cg, cingulum; Hd, hypoconid; Me, metacone; Pa, paracone; Pr, protocone; Ps, parastyle.

Figure 7. Boxplot of P4 width (W) in different European Pleistocene *Ursus* species compared with the Collecort specimen. Biometric data are from Prat-Vericat et al. (2020).

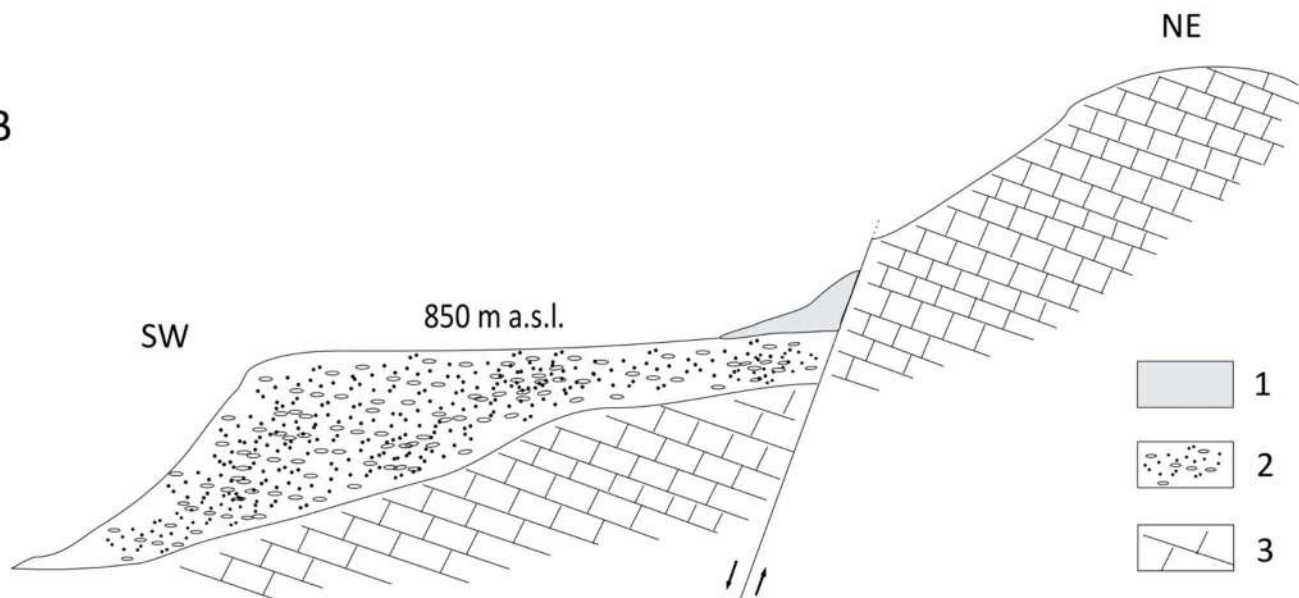
Figure 8. Chronological range of Late Villafranchian and Epivillafranchian carnivoran species recorded in European sites. a, *Homotherium latidens*; b, *Vulpes alopecoides*; c, *Canis* (*Xenocyon*) *lycaonoides*; d, *Meles meles*; e, *Megantereon whitei*; f, *Ursus etruscus*; g, *Panthera pardus*; h, *Panthera gombaszoegensis*; i, *Panthera* sp. (large size); j, *Canis*

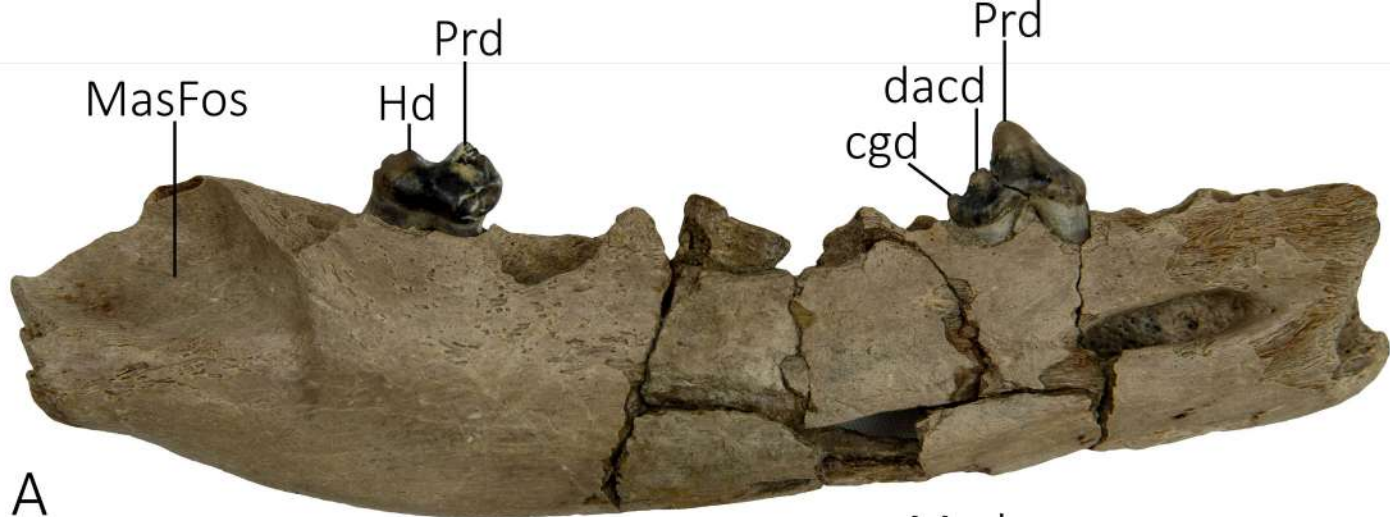
mosbachensis; k, *Pachycrocuta brevirostris*; l, *Crocuta crocuta*; m, *Ursus deningeri*; n, *Puma pardoides*; o, *Lynx pardinus*.

A

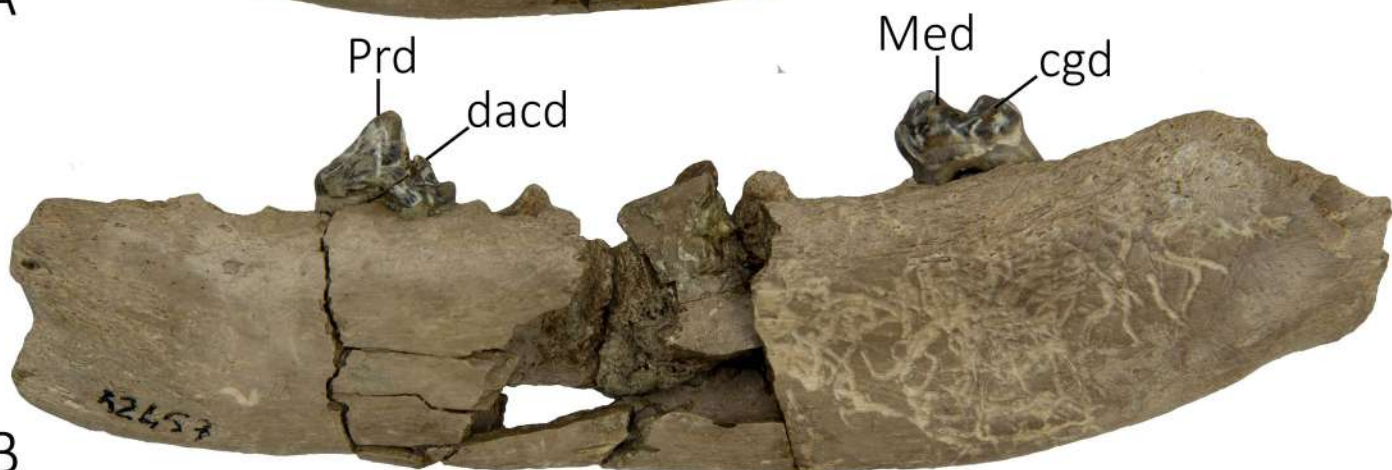


B





A



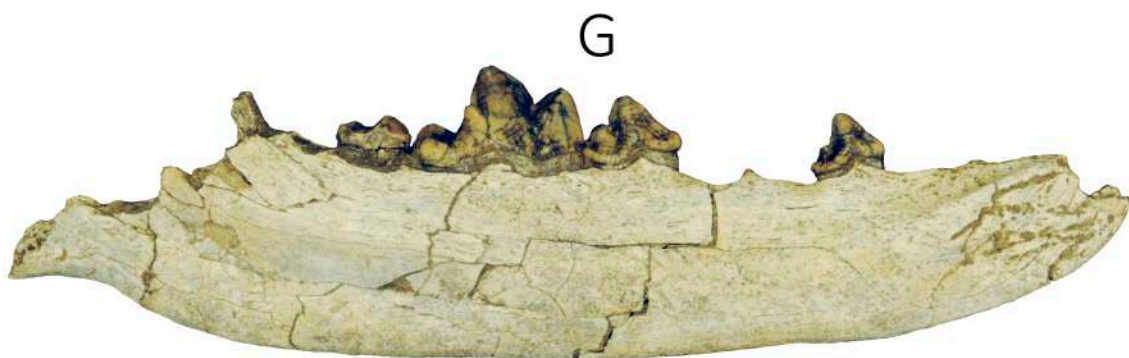
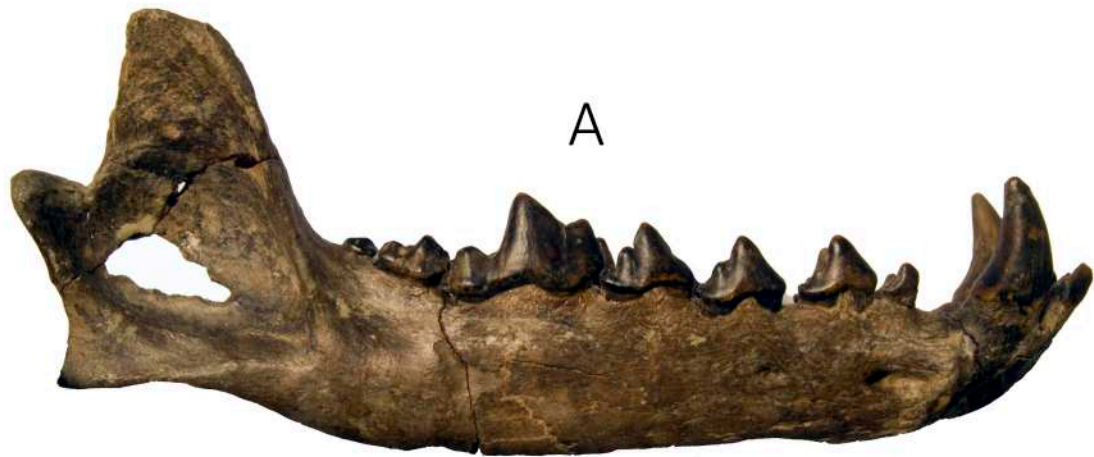
B



C

5 cm

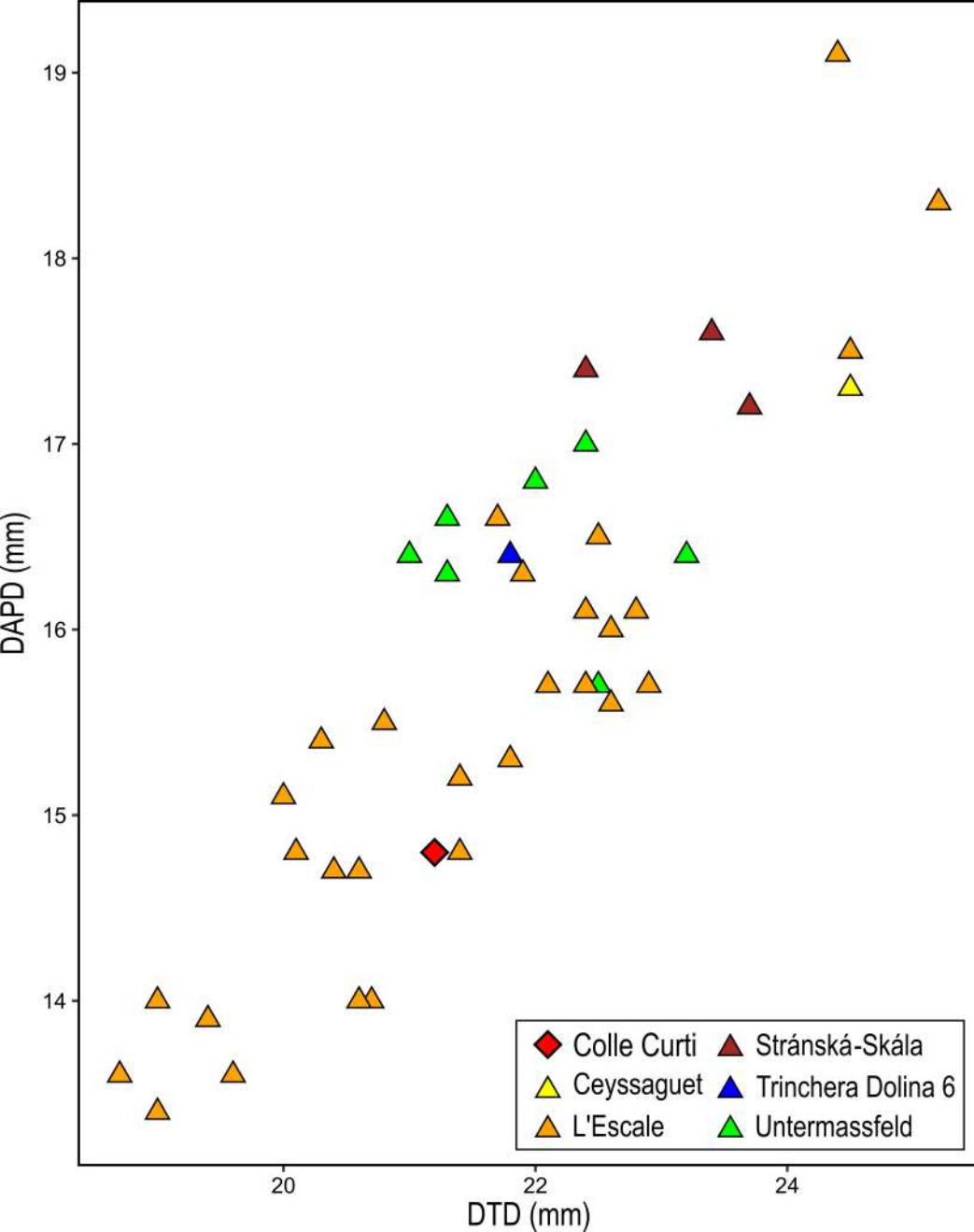


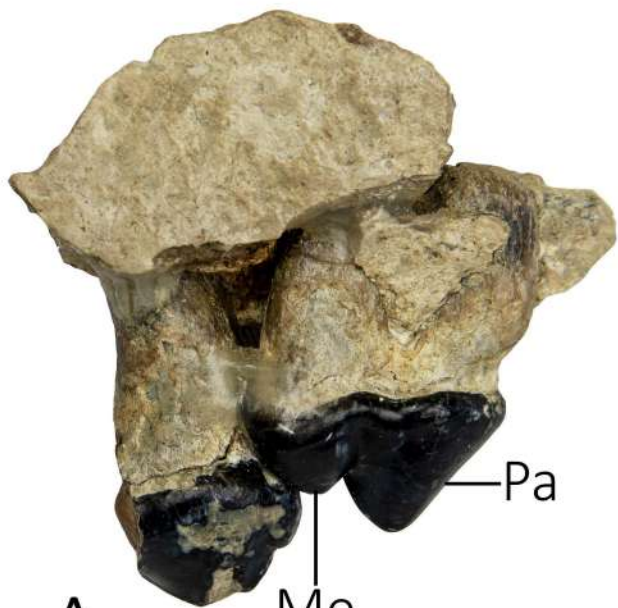


5 cm

2 cm



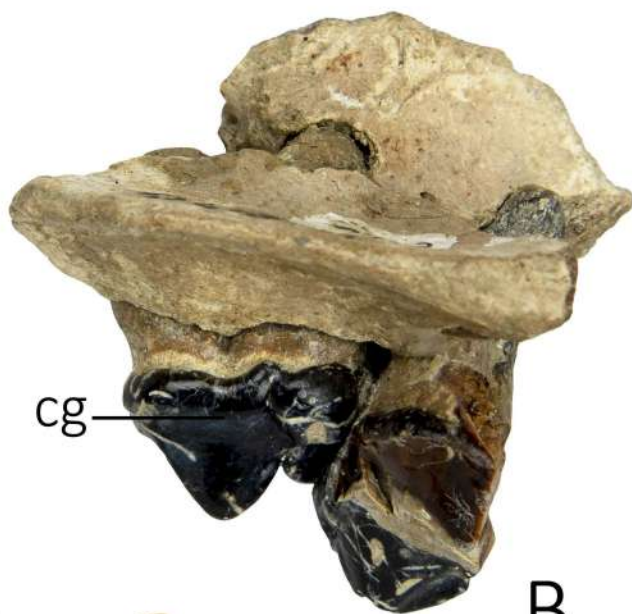




A

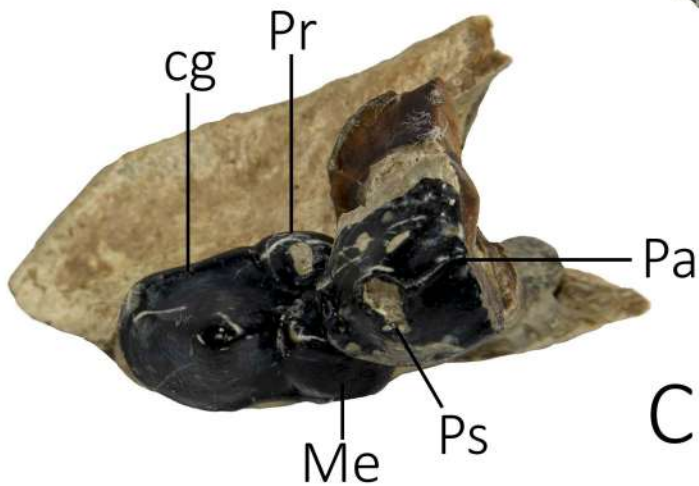
Me

Pa



B

cg



C

cg

Pr

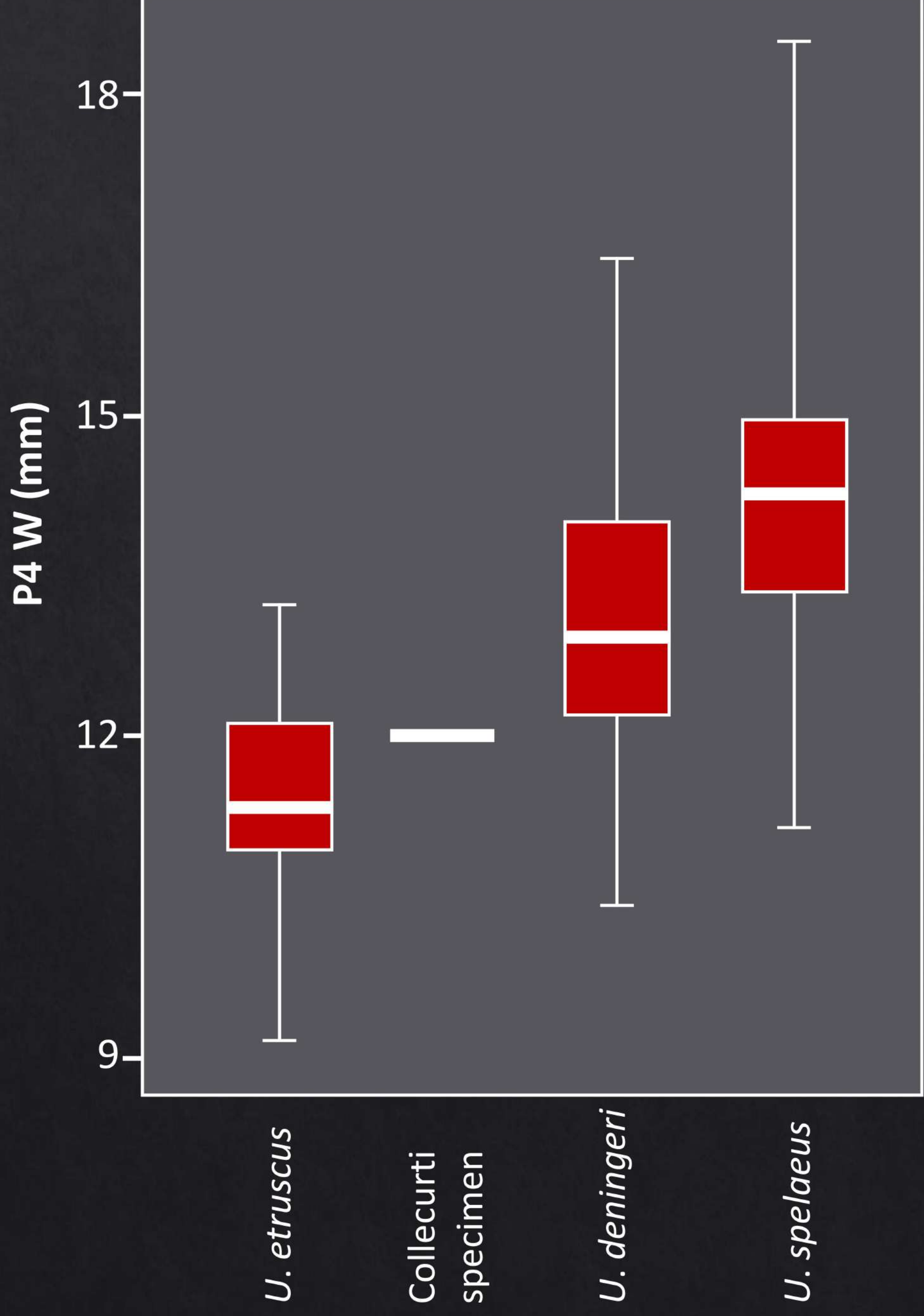
Pa

Me

Ps

5 cm





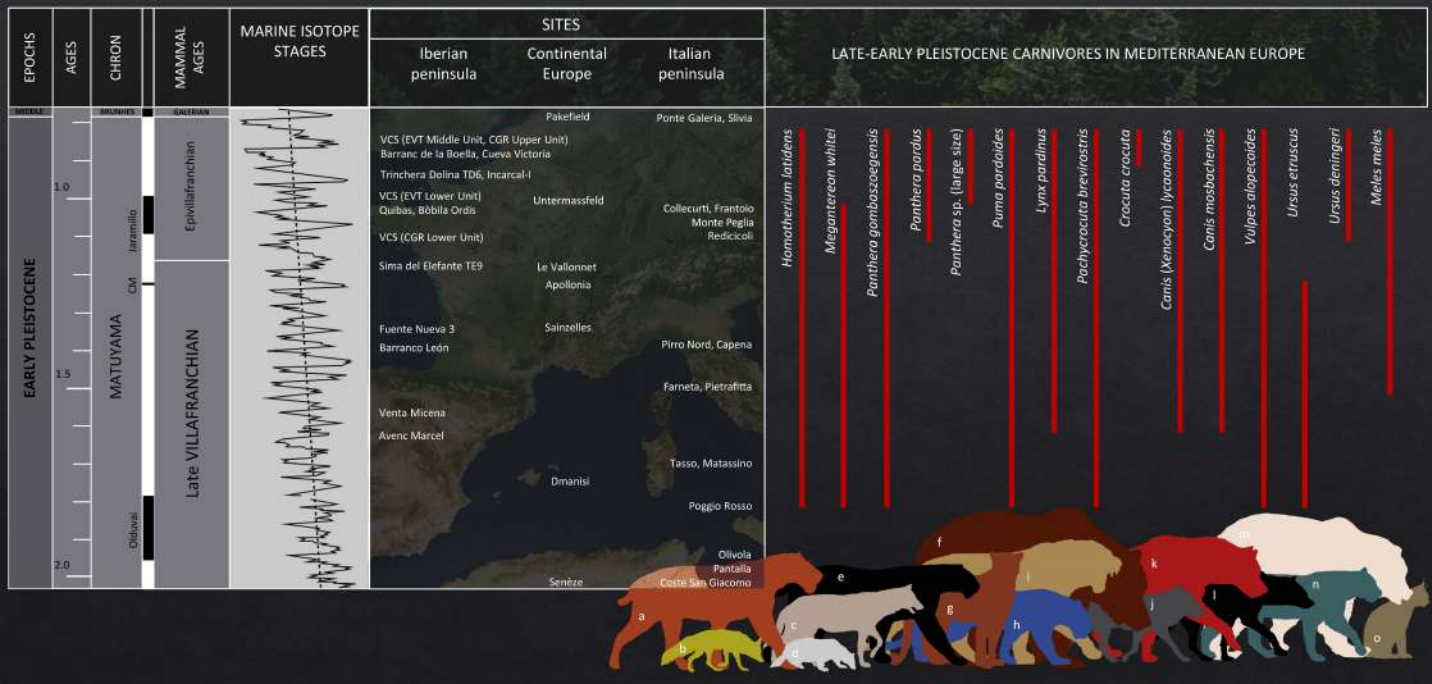


Table 1. Measurements (mm) of carnivoran specimens from Collocurti.

ID	Species	p3L	p3W	m2L	m2W	Hp3	Hm1
SMUC 52457	<i>Canis (Xenocyon) lycaonoides</i>	14.2	6.6	13	7.9	26.1	28.5
		DTM	DTD	DAPM	DAPD		
SMUC 52459	<i>Canis mosbachensis</i>	13.4	21.2	12	14.8		
		P4L	P4W	M1MW			
SMUC 52458	<i>Ursus deningeri</i>	19.5	12.1	18			

Abbreviations: **L**, length; **W**, width; **Hp3**, height of the mandibular corpus at the level of p3 measured on the labial side; **Hm1**, height of the mandibular corpus at the level of m1 measured on the labial side; **DTM**, mediolateral diameter of the tibia at midshaft; **DTD**, mediolateral diameter of the distal epiphysis of the tibia; **DAPM**, anteroposterior diameter of the tibia at midshaft; **DAPD**, anteroposterior diameter of the distal epiphysis of the tibia **MW**, mesial width.