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Latest Early Pleistocene wolf-like canids from the Iberian Peninsula

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ABSTRACT

Several species of the genus *Canis* (Carnivora: Canidae) have been recorded from the European Early Pleistocene, but the phylogenetic relationships among them and in relation to extant members of this genus are still unclear. This is particularly true for the medium-sized and wolf-like extinct species *Canis mosbachensis*. It has been considered by many researchers as a descendant of the larger *Canis etruscus* and as a likely putative ancestor of extant wolves (*Canis lupus*). Other scholars, in contrast, have advocated instead for a closer relationship between *C. mosbachensis* and the extinct *Canis arnensis*, and even a close relationship between *C. mosbachensis* and *C. lupus* has been questioned. Here we describe the previously unpublished medium-sized *Canis* remains from the late Early Pleistocene site of Vallparadís Estació, along with additional new *Canis* material from the roughly coeval site of Cueva Victoria (both in the Iberian Peninsula), and compare them qualitatively and morphometrically with both extant and extinct species of this genus. The described material most closely resembles in craniodental size and shape the remains from Central and Southern Europe that have been previously assigned to *C. mosbachensis*, to which they are hence formally attributed. The excellent preservation of the newly described specimens (which include the most complete skull of this taxon) enables the description of features previously unknown for this species, which further support a close phylogenetic link with living wolves. Based on the described material, we review the role played by *C. mosbachensis* in the evolutionary history of European fossil canids, and conclude that this extinct species is most closely related to *C. lupus* and other closely-allied species, such as *Canis anthus* and *Canis latrans*.

1. Introduction

The earliest fossil representatives of the genus *Canis* come from late Miocene deposits of the southern United States and Mexico (Miller and Carranza-Castañeda, 1998). Numerous Pliocene Asian sites have provided remains of canines spreading across Eurasia. For example, Flynn et al. (1991) reported a 3.4 million-years-old *Canis* sp. from Mazegou Formation in the Yushe Basin (Shanxi Province, China) that was later identified as *Canis* cf. *etruscus* (Qiu and Flynn, 2013; Qiu and Tedford 2013). Three species have been customarily distinguished from the Late Pliocene-Early Pleistocene of Asia: the large *Canis antonii* Zdansky, 1924, which is a likely junior synonym of the European *Lycaon falconeri* (see Rook, 1994); the large-sized *Canis chihliensis* Zdansky, 1924, similar to *L. falconeri* but more plesiomorphic; and the smaller *Canis palmidens* Teilhard de Chardin and Pivetau, 1930. An earlier, but highly disputed, evidence of the genus *Canis* in Europe comes from the Turolian (late Miocene; ca. 8–7 Ma) of the Teruel Basin (Spain). It consists of a partial mandible with p3–m2 from Concud that was used to erect "*Canis*" *cipio* Crusafont Pairó, 1950, as well as of an isolated m1 from Los Mansuetos that was later attributed to the same taxon (Pons-Moyà and Crusafont-Pairó, 1978). Rook (1992) questioned the inclusion of this species in the genus *Canis*, and subsequently it was considered "a form at *Eucyon* level of differentiation rather than a true *Canis*" (Wang and Tedford, 2007: 12). Rook (2009) agreed with this interpretation, and Tedford et al. (2009) deemed this species as a basal member of the subtribe Canini, or even more primitive.

Based on current evidence, the genus *Canis* is not recorded in

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Europe until the Early Villafranchian (Late Pliocene)—a summary of the chronological distribution of Late Pliocene and Pleistocene medium- and large-sized canids of Europe is provided in Fig. 1. Historically, from a biochronological viewpoint, the first appearance datum of *Canis* spp. in Western Europe marked the onset of the so-called "Wolf event", dated to ca. 2.0–1.8 Ma (Azzaroli, 1983; Azzaroli et al., 1988). However, subsequent discoveries have indicated an earlier dispersal of canids into Europe, based on scarce specimens attributed to *Canis* cf. *etruscus* from Coste S. Giacomo FU (late Middle Villafranchian, Italy; Rook and Martínez-Navarro, 2010) and specimens of *Canis* sp. from the Vialette (Early Villafranchian, ca. 3 Ma; Lacombat et al., 2008). These finds not only predate the Wolf event as classically defined, but show its diachronous nature (Sotnikova and Rook, 2010), thus questioning its significance as a biochronological event (Sardella and Palombo, 2007). Because of this fact, some authors (Martínez-Navarro, 2010; Rook and Martinez-Navarro, 2010) have suggested to redefine the faunal turnover that took place ca. 2 Ma as the "*Pachycrocuta brevirostris* event", based on the dispersal of this large superscavenger hyenid into Eurasia.

Subsequently from the oldest dispersal of true *Canis* into Europe, during the Pleistocene, several different species of canids are recorded in this continent. Ever since the pioneering study by Del Campana (1913), for many years the complex taxonomic status of extinct species of *Canis* in Europe has been investigated (summarized in Brugal and Boudadi-Maligne, 2011; Cherin et al., 2014; Bartolini Lucenti and Rook, 2016). At least three species are currently considered valid, being mostly distinguished on the basis of general size and proportions, as well as particular craniodental and/or postcranial features: *Canis etruscus* Major, 1877 (ca. 2.0 Ma, Olivola, Italy); *Canis arnensis* Del Campana, 1913 (ca 1.8 Ma, Upper Valdarno); and *Canis mosbachensis* Soergel, 1925 (ca 1.4 Ma, Southern and Central Europe). The taxonomic distinction of these species is relatively well founded based on the diagnostic features reviewed by several authors (respectively, Sotnikova, 2001; Cherin et al., 2014; Bartolini Lucenti and Rook, 2016), even if the taxonomic status of *C. mosbachensis* as a distinct species (instead of subspecies) from *C. lupus* is still debated (see Flower and Schreve, 2014). The phylogenetic relationships among these species and relative to extant species of the genus, in any case, are still highly debated (e.g., Kurtén, 1974; Tedford et al., 2009; Brugal and Boudadi-Maligne, 2011), and some additional species of more dubious taxonomic validity or generic ascription are distinguished by other authors (see below).

The earliest well-documented evidence of *Canis* from the Early Pleistocene of Europe comes from the Italian sites of Olivola (Val di

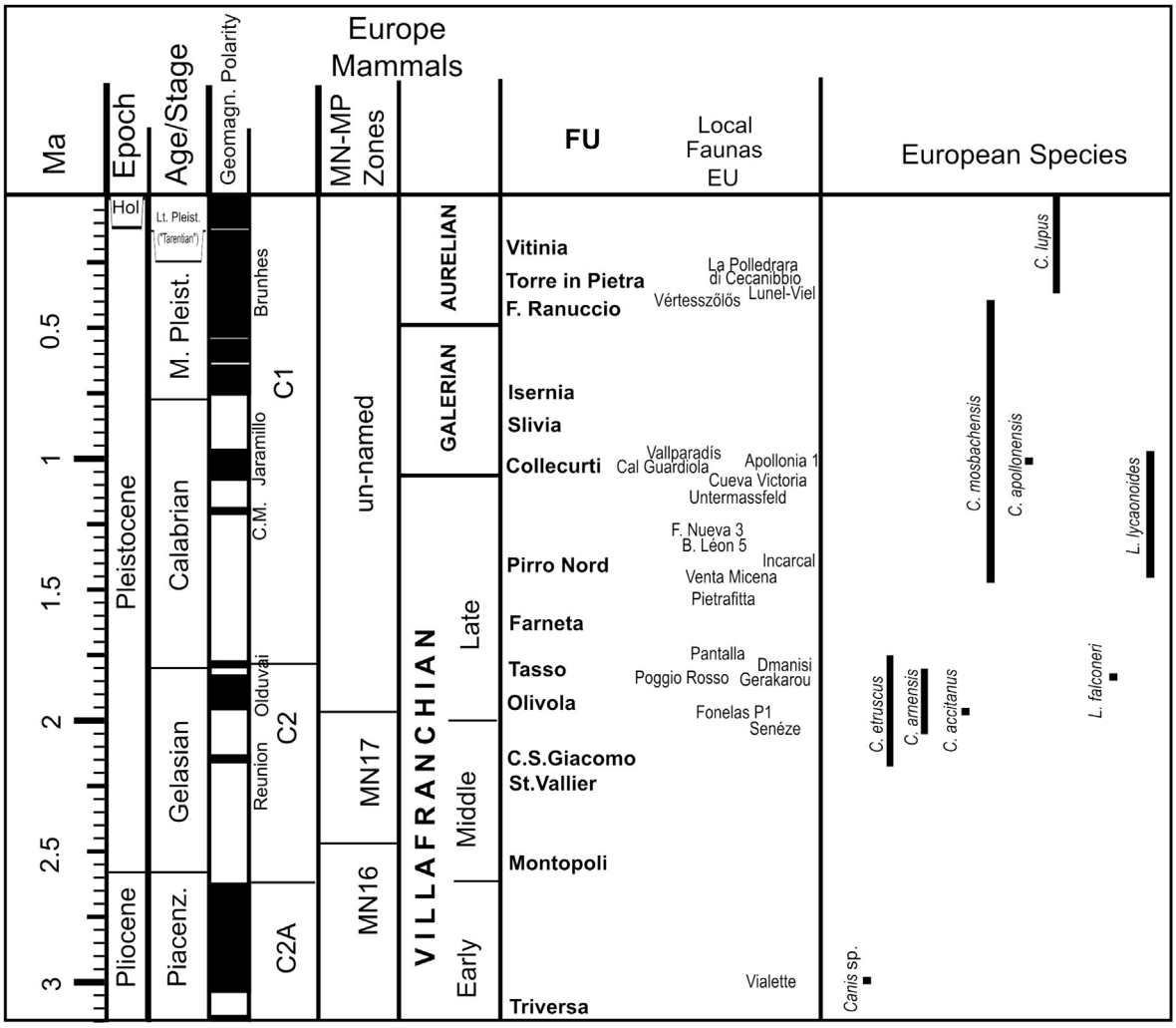

Fig. 1. Chronological distribution of medium- and large-sized canids during the late Pliocene and Pleistocene in Europe. Based on the following references: Koufos, 1987; Brugal and Boudadi-Maligne, 2011; Madurell-Malapeira et al., 2013; Petrucci et al., 2013; Cherin et al., 2014; Sardella et al., 2014; Bartolini Lucenti and Rook, 2016.