

Early dispersal and niche partitioning in Canidae from an Early Pleistocene site of Spain (Fonelas P-1, Guadix-Baza basin, Granada)

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ABSTRACT - The Fonelas P-1 site in southern Spain (~2.0 Ma) offers an exceptional window into the Early Pleistocene canid diversity and ecology in Europe. This study identifies two medium-sized canid morphotypes from the site, corresponding to the species *Canis arnensis* Del Campana, 1913 and *Canis etruscus* Forsyth Major, 1877. Morphological and ecomorphological analyses, integrating cranial, dental, and mandibular features, confirm their taxonomic identities and ecological differentiation. *Canis arnensis* at Fonelas P-1 expands the geographic and temporal range of this species, providing robust evidence of its presence in southern Europe before 2 Ma. The co-occurrence of *C. arnensis* and *C. etruscus* at this well-dated site underscores their ecological divergence, with *C. arnensis* exhibiting a mesocarnivorous dietary niche and *C. etruscus* showing adaptations closer to hypercarnivory. These findings illuminate the complexity of Early Pleistocene canid guilds, offering critical insights into their dispersal patterns, adaptive strategies, and interactions within taphocenoses.

INTRODUCTION

Western European Early Pleistocene Canis: biochronology, diversity and the role of Fonelas P-1

The dispersals of Caninae (Canidae Fischer, 1817) across Eurasia and Africa represented major biochronological events of the mammal assemblages of these areas. Starting from the Miocene (Wang et al., 2008), Vulpini and Canini arrived in eastern Eurasia and then radiated into different forms all across the Old World (Sotnikova & Rook, 2010; Geraads, 2011; Marciszak et al., 2023b; Rook et al., 2024). Especially in Western Europe, their record has been used historically to mark changes of faunal compositions across the continent and in a determinate region (e.g., Gliozzi et al., 1997). The importance was underlined by the pivotal work by Augusto Azzaroli (1983) in which he proposed for the first time the concept of “Wolf event”: a gradual turnover of land mammals marked by the arrival of *Canis etruscus* Forsyth Major, 1877 (the eponymous “wolf”-like canid following to Azzaroli, 1983) in the Olivola Faunal Unit, and of *Canis arnensis* Del Campana, 1913 and of *Xenocyon falconeri* (Forsyth Major, 1877) in Tasso Faunal Unit (Azzaroli, 1983; Azzaroli et al., 1988). The intuition of Azzaroli was to link the evolution of previous mammalian faunas with global climatic changes and the progressive cooling and aridity trend recorded in Western Europe (Gibbard & Head, 2020). This opened environments, which became characterised by “warm” steppes, during glacials, and temperate deciduous forests, during interglacials (Bertini,

2010, 2013; Bertini et al., 2010; Martinetto et al., 2020). This was interpreted as the reason for the spreading of canids as well as new taxa, e.g., *Hippopotamus antiquus* Desmarest, 1822, *Pachycrocuta brevirostris* (Gervais, 1850) or *Panthera toscana* (Schaub, 1949) (among others Azzaroli, 1983; Sardella & Palombo, 2007; Palombo et al., 2008; Iannucci et al., 2023).

In the last twenty years, numerous and compelling evidence suggested that the biochronological picture is rather more complex, especially for canids. Several discoveries have anticipated substantially the dispersal of hypercarnivorous canids of grade *Xenocyon*, up to 2.6 Ma (Roca-Neyra, 2.6 Ma in Nomade et al., 2014 and Bartolini-Lucenti & Spassov, 2022; Rębielice Królewskie 1A and Zamkowa Dolna Cave A, both 2.4-2.2 Ma, Marciszak et al., 2023b), and of *Canis* cf. *etruscus* to 2.4-2.2 Ma (Rębielice Królewskie 1A and Zamkowa Dolna Cave A, both 2.4-2.2 Ma, Marciszak et al., 2023b; Coste San Giacomo, ca 2.1 Ma, Rook & Torre, 1996; Bellucci et al., 2012). *Canis arnensis*, typical of 1.9-1.8 Ma Southern European localities (Il Tasso, Poggio Rosso, Upper Valdarno, Frattaguida, Libakos; Del Campana, 1913; Bartolini-Lucenti & Rook, 2016; Petronio & Salari, 2021; Koufos & Tamvakis, 2022), might actually derive from the earlier forms of *Liventsovka* (~2.4 Ma; Sotnikova et al., 2002) and of *Senèze* (2.1 Ma, Paquette et al., 2021; Martin, 1973) referred to *Canis senezensis* Martin, 1973. Regarding this latter taxon there is a generalised consensus in regarding it as a probable synonym of *C. arnensis* (Schaub, 1943; Rook & Torre, 1996; Brugal &

Boudadi-Maligne, 2011; Bartolini-Lucenti & Rook, 2016; Argant, 2025). Furthermore, along with these clear and solid records, other fragmented, uncertain or undescribed ones are known in literature (Reumer & Piskoulis, 2017; Marciszak et al., 2023b; Spassov, 2024), the earliest of which is ?*Canis* sp. from Viallette (~3 Ma, Lacombat et al., 2008) (Fig. 1). Thus, the validity of a Wolf “event” as a single, synchronous and biochronologically significant marker, coincident with climatic changes and opening of environments, has been questioned by several authors (Martínez-Navarro, 2010; Sotnikova & Rook, 2010). Nowadays, it is not recognised as a valid one (Rook & Martínez-Navarro, 2010), despite some reinterpretations proposed (e.g., Iannucci et al., 2023; Spassov, 2024). Their discussion is out of the scope of the present manuscript. What is clear, as many have noticed (recently Spassov, 2024), after 2.2 Ma and before the Epivillafranchian, the canid diversity in Europe increased greatly: at least five but up to nine species of medium- to large-sized canids (depending on the authors) can be traced in Europe (Bartolini-Lucenti et al., 2017, 2020; Koufos, 2022) (Fig. 1). Apart from the aforementioned species, three other medium-sized species were described: *Canis accitanus* Garrido & Arribas, 2008 from the Spanish 2-My-old Fonelas P-1, a *C. arnensis*-like form (Garrido & Arribas, 2008; see further on). The renown and well-characterised *Canis mosbachensis* Soergel, 1925 appeared in Europe in the mid Calabrian (Martínez-Navarro et al., 2021) and remained present until the half of the Middle Pleistocene (Ghezzo et al., 2014; Mecozzi et al., 2017). Many authors support a close relationship with the extant gray wolf, *Canis lupus* Linnaeus, 1758 (Brugal & Boudadi-Maligne, 2011). Koufos & Kostopoulos (1997) described *Canis apolloniensis* Koufos & Kostopoulos, 1997 from the Greek site of Apollonia-1. This locality has always been referred to the Epivillafranchian with an age of ~1.2 Ma, according to biochronological inferences of the taxa (Spassov, 2003; Koufos & Kostopoulos, 2016; Koufos, 2018) but more recently Konidaris & Kostopoulos (2024) proposed a wider time range for the faunal unit of this locality (i.e., 1.5-0.9 Ma). The extension back in time fits with analyses by other authors (Bartolini-Lucenti et al., 2022a, b). The identity of this canid has been questioned (Garrido & Arribas, 2008; Sotnikova & Rook, 2010; Brugal & Boudadi-Maligne, 2011) and, despite new descriptions (Koufos, 2018), its true taxonomic status is still uncertain. The site of Apollonia-1 is also the last

occurrence of *C. etruscus* (Koufos, 2018). Last but not least, the outstanding record of the earliest Calabrian of Dmanisi (Georgia) includes a peculiar species, *Canis borjgali* Bartolini-Lucenti et al., 2020. The morphology of this species is more derived compared to *C. etruscus* and *C. arnensis*, more reminiscent of that of *C. mosbachensis* or more derived species of *Canis* (e.g., *C. lupus* Linnaeus, 1758), as discussed by Bartolini-Lucenti et al. (2020), among others.

In this context, the record of Fonelas P-1 Trench B (what is commonly known as simply Fonelas P-1) is considerably relevant for the faunal evolution in the mid-Early Pleistocene of Europe (Viseras et al., 2006; Arribas et al., 2009). The palaeontological record is remarkable (see following sections) and so is the record of Canidae. From the site, four taxa were reported in literature (Garrido, 2008; Garrido & Arribas, 2008): *Canis etruscus*, *C. accitanus*, *X. falconeri* (scarce and fragmentary material) and *Vulpes alopecoides* (Del Campana, 1913). The present manuscript aims to revise the taxonomy of the medium-sized forms and investigate the ecological implications of the coexistence of related taxa in the same palaeoenvironment.

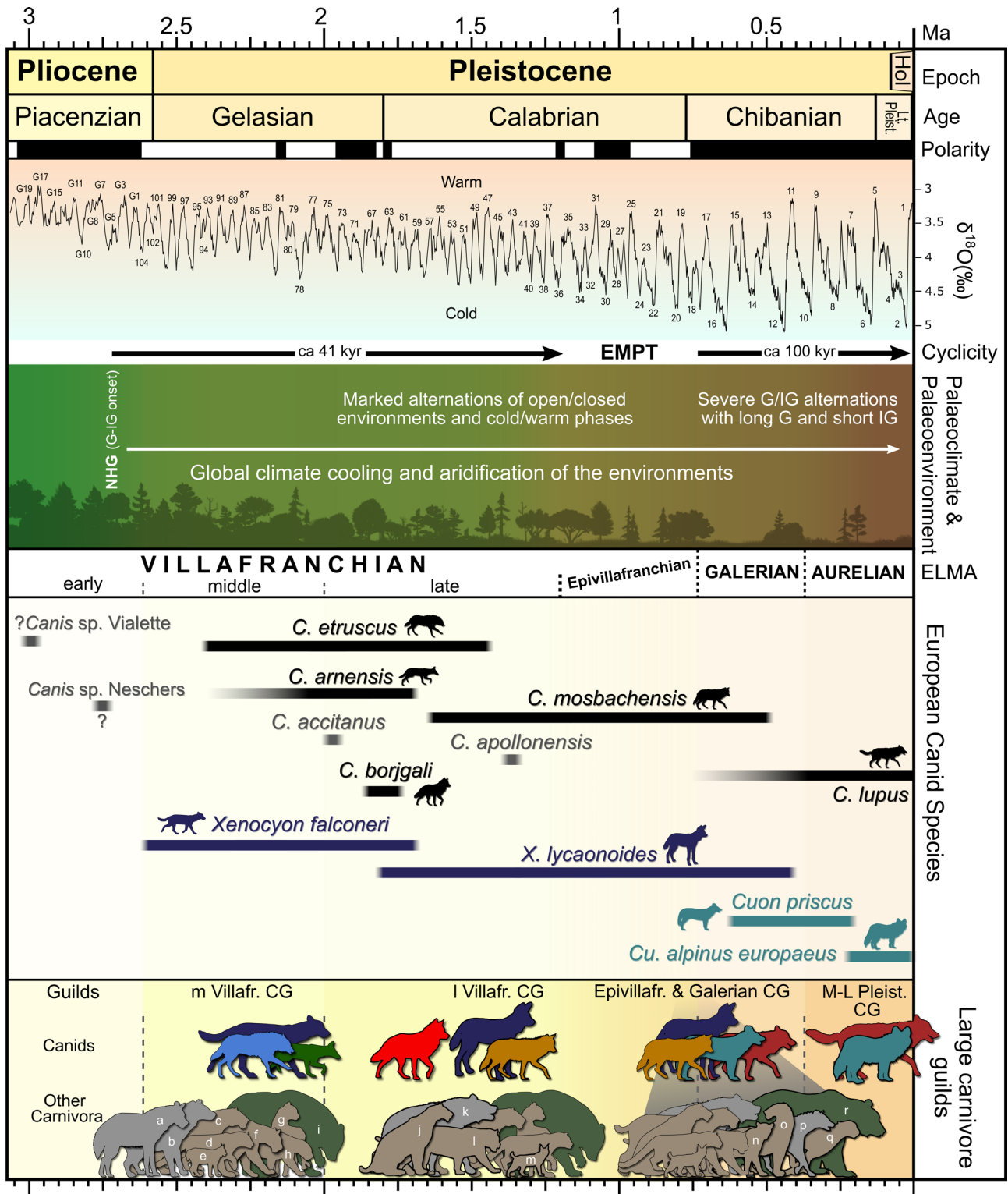
Canids ecological variability and coexistence in the same palaeoenvironment

The family Canidae is among the most diversified of extant Carnivora (Nowak, 2005; Wilson & Mittermeier, 2009). Ecologically, most of canids are considered mesocarnivores (i.e., carnivores whose diet is composed for the 50-70% of vertebrate meat; Crusafont-Pairó & Truyols-Santonja, 1956; Van Valkenburgh, 1989; Biknevicius & Van Valkenburgh, 1996) compared to other carnivorans. Although within the family there is a certain dietary variability (Van Valkenburgh & Koepfli, 1993; Van Valkenburgh & Wayne, 1994; Slater et al., 2009), from hypocarnivorous small- to medium-sized forms to hypercarnivorous large-sized species. In many extant environments, more or less phylogenetically related canids live in the same environments only partially with overlapping ecologies and preferred diet. For instance, in the Balkan area coexist the gray wolf (*Canis lupus*), the golden jackal (*Canis aureus* Linnaeus, 1758), the red fox (*Vulpes vulpes* Linnaeus, 1758) and recently the raccoon-dog (*Nyctereutes procyonoides* [Gray, 1834]) is steadily spreading across Central and Southeastern Europe (Castelló, 2018; IUCN, 2024). Similarly, in central South

Fig. 1 - (color online) Time, climatic and environmental calibration of the stratigraphic distribution of medium-large-sized canids in Western Eurasia from the Late Pliocene to present from literature (Sotnikova et al., 2002; Lacombat et al., 2008; Tedford et al., 2009; Berté, 2013; Madurell-Malapeira et al., 2013; Ghezzo et al., 2014; Bartolini-Lucenti et al., 2017, 2021; Koufos, 2018; Marciszak et al., 2021, 2023a, b; Martínez-Navarro et al., 2021; Bartolini-Lucenti & Spassov, 2022; Spassov, 2024). Color code: black, widely accepted *Canis* species; blue, Eurasian *Xenocyon* species; gray, uncertain species (in terms of taxonomy and time correlation); ming light blue, fossil *Cuon* taxa. $\delta^{18}\text{O}$ and palaeoenvironmental reconstructions follow Fidalgo et al. (2023). List of the silhouettes of the large carnivore guild: a, *Chasmaporthetes lunensis* (Del Campana, 1914); b, *Pliocrocuta perrieri* (Croizet & Jobert, 1828); c, *Homotherium crenatidens* (Fabrini, 1890); d, *Viretailurus pardoides* (Owen, 1846); e, *Lynx issiodorensis* (Croizet & Jobert, 1828); f, *Megantereon cultridens* (Cuvier, 1823); g, *Acinonyx pardinensis* (Croizet & Jobert, 1828); h, *Panthera toscana*; i, *Ursus etruscus* Cuvier, 1823; j, *Megantereon whitei* (Broom, 1937); k, *Pachycrocuta brevirostris*; l, *Panthera gombaszoegensis* (Kretzoi, 1938); m, *Lynx pardinus* (Temminck, 1827); n, *Panthera pardus* Linnaeus, 1758; o, *Panthera fossilis* (von Reichenau, 1906); p, *Crocuta spelaea* Goldfuss, 1823; q, *Acinonyx pleistocaenicus* (Zdansky, 1925); r, *Ursus deningeri* von Reichenau, 1906. Color and style code of the large carnivore guild: brown, Felidae; gray, Hyaenidae; green, Ursidae; stronger borders indicate new elements in the guilds. Early Villafranchian guilds were not included because of the lack of medium- to large sized canids of the grade-*Canis*, and for Middle-Late Pleistocene guilds we only reported canids as they are the subject of the present work. The silhouettes of the taxa were scaled according to their reconstructed proportions, following Madurell-Malapeira et al. (2021). Particularly those of the canids following the estimation from literature (e.g., Palmqvist et al., 2002; Marciszak et al., 2021; Bartolini-Lucenti & Spassov, 2022).

America the bushdog (*Speothos venaticus* Lund, 1842), the maned wolf (*Chrysocyon brachyurus* [Illiger, 1815]) and the crab-eating fox (*Cerdocyon thous* Linnaeus, 1766) live in the same forested and wooded-plain ecosystems (Castelló, 2018; IUCN, 2024). Focusing on Canini, nowadays there are several taxa of the subtribe Canina (all the forms more related to the wolf than to *Cerdocyon*, sensu Tedford et al., 2009) share habitats and survive in ecologically distinct niches, e.g., *C. lupus*, *Canis rufus*

Audubon & Bachman, 1851 and *C. latrans* Say, 1823 in North America (Bekoff & Gese, 2003); *Speothos venaticus*, *Cerdocyon thous*, *Chrysocyon brachyurus* and *Lycalopex vetulus* (Lund, 1842) in South America (Castelló, 2018; IUCN, 2024); *Cuon alpinus* Pallas, 1811 and *C. aureus* in Asia south of Himalaya (Castelló, 2018; IUCN, 2024); *Canis lupaster* Hemprich & Ehrenberg, 1833, *Lupulella adusta* (Sundevall, 1847), *L. mesomelas* (Schreber, 1775) and *Lycaon pictus* Temminck, 1820 in



East Africa (Van Valkenburgh & Wayne, 1994; Johnson et al., 1996).

In the fossil record, many scholars reported the coexistence between different taxa of canids in the same palaeoenvironment, e.g., *Canis teilhardi* Qiu et al., 2004, *Canis longdanensis* Qiu et al., 2004, *Xenocyon brevcephalus* (Qiu et al., 2004) and *Sinicuon cf. dubius* (Teilhard de Chardin, 1940) in the Early Pleistocene (Gelasian) site of Longdan (Gansu, China; Qiu et al., 2004). Nevertheless, the problem of taxonomic misidentification, of time averaging and of taphonomic biases in some of these reported occurrences must not be disregarded. Among them, there is the classical Upper Valdarno faunal complex with the presence of three species of medium- to large-sized canids, i.e., *Canis arnensis*, *Canis etruscus* and *Xenocyon falconeri* (Torre, 1967, 1979; Rook et al., 2013) all historically cited as members of the “Tasso Faunal Unit” of the Italian biochronological scheme (Gliozzi et al., 1997, ~1.8 Ma). Unfortunately, the majority of the occurrences of the Upper Valdarno Basin are not well time-constrained or stratigraphically characterised. This casts some doubts on the chronological interpretation on these records (Rook et al., 2013). Other disputed records of coexistence of *Canis* are those of Gerakarou (early Calabrian, Greece; Koufos, 2014) or Libakos (where the specimens of *C. etruscus* have to be reascribed to *C. arnensis*; cf. Koufos & Tamvakis, 2022) and of Ceyssaguet (late Calabrian, France; Tsoukala & Bonifay, 2004). These records need to be revised because the taxonomic attributions reported in literature might be updated in the light of more recent discoveries. The record from Fonelas P-1 represents a valid and potentially unique occasion to study ecological distinction between two long-renowned species like *C. arnensis* and *C. etruscus* here recorded from the same layers, within the same environment and same timeframe.

GEOLOGICAL SETTINGS

The canid remains analysed in the present manuscript were found at the Fonelas P-1 palaeontological site, located within the Guadix-Baza Basin (Granada, Betic Ranges, southeastern Spain) (Arribas et al., 2001). This locality is understood to have been a hyaenid den situated on a dry floodplain associated with a fluvial system (Viseras et al., 2006). The palaeontological assemblage at Fonelas P-1 was discovered in situ, with the fossils representing an accumulated association (Viseras et al., 2006; Garrido et al., 2010). These remains exhibit distinct evidence of activity by the hyaenid *Pachycrocuta brevirostris*. Thousands of fossils have been unearthed at this site, representing a significant part of the terrestrial mammal ecosystem from the basal Early Pleistocene of Western Europe. These remains include 24 identified species of large mammals and various other vertebrate taxa, such as the giant tortoise *Titanochelon* (Garrido, 2006; Arribas, 2008; Arribas et al., 2009; Pérez-García et al., 2017).

Fonelas P-1 has been dated using biostratigraphic and magnetostratigraphic methods. The faunal assemblage corresponds to the late Villafranchian (Early Pleistocene), specifically to the MNQ18 zone (~2 Ma), with slightly more advanced members than those from the French site of Senèze (Guérin, 1989; Mein, 1989; Arribas et al., 2009; Pla-Pueyo et al., 2011; Nomade et al., 2014). Magnetostratigraphic studies in the Guadix Basin, focusing on this site, have determined that Fonelas P-1 lies within a reversed polarity layer (subchronozone C2r.1r), positioned between the Reunion and Olduvai normal subchrons (ca. 2.128–1.945 Ma; Fig. 3) and 5 meters below the base of the latter. Based on these findings, the site's age has been estimated at 2.0 Ma (Arribas et al., 2009; Pla-Pueyo et al., 2011).

Fonelas P-1 is located in a predominantly fluvial section of the Guadix-Baza Basin infill (Fig. 2). The palaeontological site spans a minimum surface area of 1,000 m². Its systematic excavation, carried out in 2001, 2002, 2004, and 2007, focused on two trenches: trench B (the main focus of research until 2009) and trench A, which fossils unpublished until now (Fig. 3).

The vertebrate palaeontological record is primarily associated with a set of facies (facies association E, known as “Unidad de Limos con Intraclastos Arcillosos” or with the acronym ULIA) linked to subaerial exposure and bioturbation caused by hyaenid activity in a fluvial context with an estimated chronology of 2 Ma (Arribas et al., 2009; Pla-Pueyo et al., 2011). This process resulted in a dry plain occupied by these carnivores, characterised by intense evidence of trampling and shallow excavations on the substrate (Trenches A and B; see, for instance, Garrido et al., 2010, fig. 5).

Within the site's context, another unit (the one called “Arenas Negras Fossilíferas”, acronym ANF, part of the facies association A) has also been identified with an estimated chronology between 2.128 and 2.0 Ma (Figs 2–3). This unit, yielded in Trench A various fossil remains, including an exceptionally well-preserved *Canis* partial skeleton, described here for the first time.

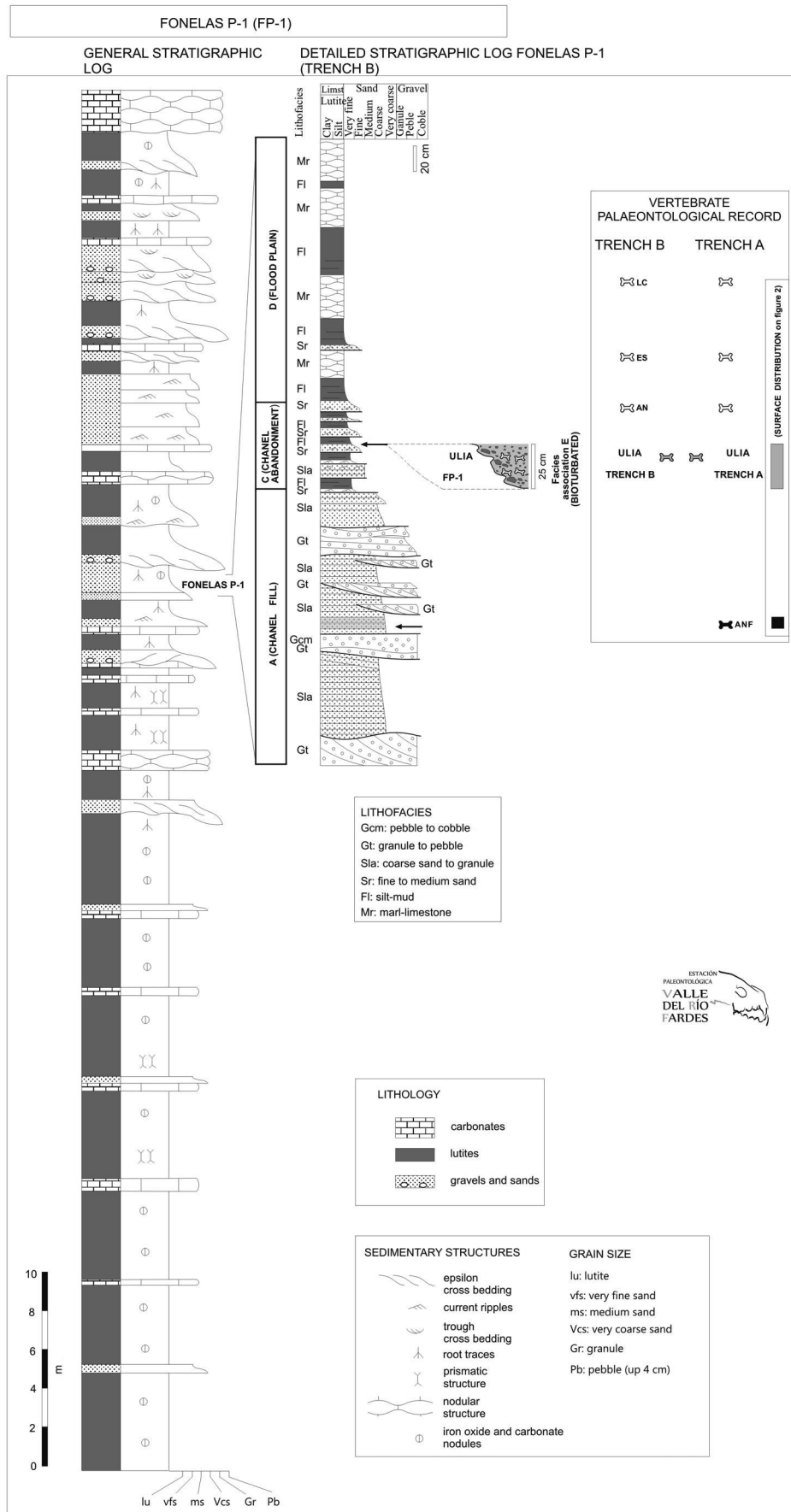
From a detailed chronological perspective, and considering that the entire fossil assemblage of Fonelas P-1 belongs to subchronozone C2r.1r (Arribas et al., 2009), the stratigraphic column and spatial arrangement of the trenches (Figs 2–3) indicate that unit ANF (part of facies association A) in Trench A is slightly older than unit ULIA (facies association E) found in both Trench A and Trench B.

MATERIALS AND METHODS

Considered specimens and comparative sample

This study is based on comparative morphological and ecological analyses of the cranial and dentognathic material of the medium-sized canids from Early Pleistocene of Fonelas P-1 (Trenches A and B) in comparison to selected extant and fossil taxa. The examined fossils are housed at the Centro Nacional Instituto Geológico y Minero de

Fig. 2 - General stratigraphic log of Unit VI near the Fonelas P-1 site and detailed stratigraphic log of trench B showing the facies associations (updated and modified after Viseras et al., 2006). The positions of the different fossiliferous units in relation to trenches B and A are indicated, highlighting the “Unidad de Limos con Intraclastos Arcillosos” (ULIA) and “Arenas Negras Fossilíferas” (ANF) units.



España (IGME)-CSIC (see abbreviations below). As comparative fossil material, we used data acquired by some of us (S.B.L.) studying the collections of MGPUF, DSTUF, GNM, ICP, AUT and inspected all the relevant literature on Early Pleistocene medium-sized canids from Eurasia. Comparative fossil species include *Canis arnensis* from Poggio Rosso, Upper Valdarno localities (e.g., Il Tasso, or unspecified ones held in the collection of MGPUF) (Torre, 1967, 1979; Bartolini-Lucenti & Rook, 2016); *Canis etruscus* from Olivola, Pantalla, and Upper Valdarno (Torre, 1967, 1979; Cherin et al., 2014); *Canis mosbachensis* from Pirro Nord, Cueva Victoria, Vallparadis Section (Rook & Torre, 1996; Petrucci et al., 2013; Bartolini-Lucenti et al., 2017); and *Canis borjgali* from Dmanisi (Bartolini-Lucenti et al., 2020). The extant comparative sample includes specimens of thirty-two species of nine genera: *Atelocynus microtis* (Sclater, 1883); *Canis*, with *C. aureus*, *C. latrans*, *C. lupus*, *Canis simensis* Rüppel, 1835; *Cerdocyon thous*; *Chrysocyon brachyurus*; *Cuon alpinus*; *Lupulella*, with *L. adusta* and *L. mesomelas*; *Lycalopex* including *Lc. culpaeus* Molina, 1782, *Lc. griseus* Gray, 1821, *Lc. gymnocercus* Fischer, 1814, *Lc. sechurae* Thomas, 1900, *Lc. vetulus* (Lund, 1842); *Lycaon pictus*; *Nyctereutes procyonoides*; *Otocyon megalotis* Desmarest, 1822; *Speothos venaticus*; *Urocyon* including *U. cinereoargenteus* Schreber, 1775 and *U.*

littoralis (Baird, 1858); *Vulpes* including *V. bengalensis* Shaw, 1800, *V. cana* Blanford, 1877, *V. chama* Smith, 1833, *V. corsac* Linnaeus, 1768, *V. ferrilata* Hodgson, 1842, *V. lagopus* Linnaeus, 1758, *V. macrotis* Merriam, 1888, *V. pallida* Cretzschmar, 1827, *V. rueppelli* (Schinz, 1825), *V. vulpes*, *V. zerda* Zimmermann, 1780.

Ecological methodology

Selected morphometric ratios (as described by Van Valkenburgh, 1989; Van Valkenburgh & Koepfli, 1993; Friscia et al., 2007; Bartolini-Lucenti & Rook, 2021) were used to investigate the dietary habits of Fonelas P-1 canids in comparison to related fossil taxa and extant species. The ratios used here, and their descriptions, are reported in the abbreviations list below. The selected indices are a subset of those reported by Van Valkenburgh & Koepfli (1993) and Martínez-Navarro et al. (2021), centred on mandibular ratios because the majority of the cranial specimens from Fonelas P-1 are crushed and deformed.

The four of the dietary groups defined by Van Valkenburgh & Koepfli (1993) i.e., Group 1 (G1): hypercarnivorous group-hunter canids, Group 2 (G2): hypercarnivorous canids hunting small prey, Group 3 (G3): mesocarnivorous canids, and Group 4 (G4): hypocarnivorous canids, were used in the ecological investigation of fossil taxa from Fonelas P-1 and in the comparative sample.

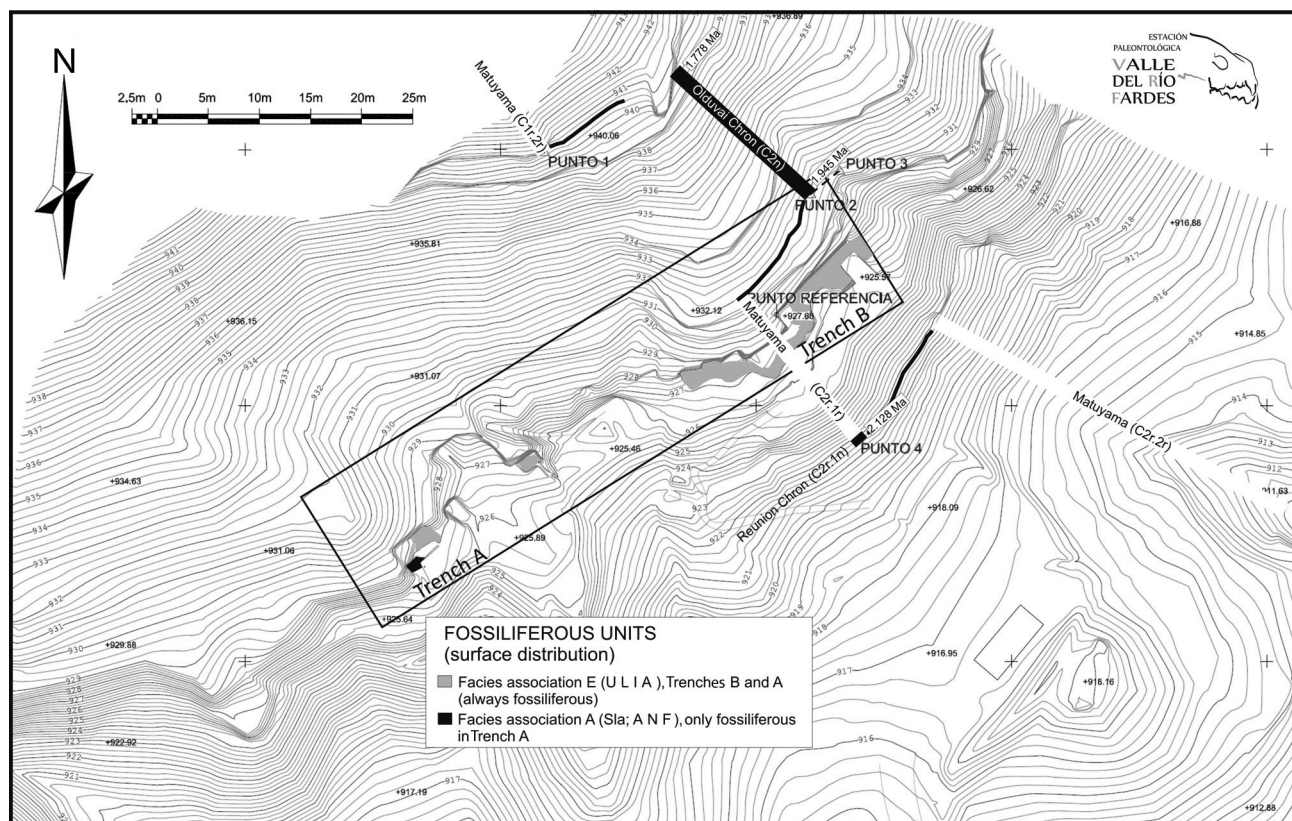


Fig. 3 - Topographic map (plan view) of the Fonelas P-1 site area (coordinate system: ETRS89, projection: UTM-30N; orthometric heights referenced to the EGM08 REDNAP geoid model; contour interval: 0.25 m. Scale 1:250). The map shows: the distribution of magnetostratigraphy in the field, with the chronozones and subchronozone identified in the site area (data from Arribas et al., 2009), including the topographic points (points 1 to 4) of polarity change; the location of the trenches; and the surface distribution of the fossiliferous units, specifically the ULIA unit in both Trench A and Trench B, and the ANF unit, which is fossiliferous only in Trench A. The rectangle indicates the area currently occupied by the Fonelas P-1 Palaeontological Center, part of the Fardes River Valley Palaeontological Station of IGME-CSIC in Fonelas (Granada; see <https://www.igme.es/servicios-e-infraestructuras/estacion-paleontologica-valle-del-rio-fardes/>).

Analyses were performed in the software RStudio (v. RStudio 2024.04.0+735 “Chocolate Cosmos” Release (a00d0e775dbc93e0d79a1bf474e3e8e8de677383, 2024-04-24; RStudio Team, 2024) in R environment (v. 4.3.2, R Core Team, 2024). A biplot of two dietary ratios (RJD and RtrigL, see abbreviation below) based on a complete dataset of extant canids and the fossil canids from Fonelas P-1, together with *Canis arnensis* from Upper Valdarno and Poggio Rosso and *Canis etruscus* from Olivola and Upper Valdarno as comparative fossil material, was obtained with *ggplot()* (*‘ggplot2’* package v.3.4.0; Wickham et al., 2016). A log-transformed dataset of nine indices (i.e., RBL, RLGA, m1BS, m2S, Ixp4, Ixm2, RAMP3, RAMP4, MAM, see abbreviation below) of selected canids of the four dietary groups of Van Valkenburgh & Koepfli (1993; i.e., *C. aureus*, *C. latrans*, *C. lupus*, *C. simensis*, *Cu. alpinus*, *L. adusta*, *L. mesomelas*, *Ly. pictus*, *V. corsac*, *V. lagopus*, *V. vulpes*), of the canids from Fonelas P-1, of *Canis arnensis* from Upper Valdarno and Poggio Rosso, and *Canis etruscus* from Olivola and Upper Valdarno were used to perform a between-group principal component analysis (bgPCA). The dataset of ratios used is reported as Supplementary Online Material (SOM) 1. The bgPCA was performed using *groupPCA()* (*‘Morpho’* package v. 2.12; Schlager, 2017) on the comparative extant and fossil sample; the specimens from Fonelas P-1 were plotted a posteriori to check their affinity to any of the a priori groups (i.e., ecological groups for extant or specific for the fossil *Canis arnensis* and *Canis etruscus*). We did this by centring the observations on the preliminary dataset and then the centred new observations were projected into the bgPCA space by calculating the dot product of each centred observation with the bgPCA loadings. This was done row-by-row using the *apply()* function (*‘base’* v. 4.3.2, R Core Team, 2024) to ensure compatibility with the matrix format of the loadings. The plots were obtained with *ggplot()* and *pch3D()* (*‘rgl’* v. 1.2.1; Adler et al., 2003).

Anatomical and metric abbreviations

Abbreviations and explanation of morphometric ratios (in alphabetical order): Ixm2, relative resistance of the dentary to bending in the parasagittal plane as estimated by the second moment of area at the interdental gap between m1 and m2 relative to the dentary length (rostrocaudal length between the mesiobasal side of the lower canine and the caudal margin of the mandibular condyle); Ixp4, relative resistance of the dentary to bending in the parasagittal plane as estimated by the second moment of area at the interdental gap between the third and fourth lower premolars relative to the dentary length (measured as in as in Ixm2); m1BS, length of the m1 trigonid relative to the dentary length, estimated as the ratio between the mesiodistal length of the trigonid and the dentary length (rostrocaudal length between the mesiobasal side of the lower canine and the caudal margin of the mandibular condyle); m2S, relative size of the m2 estimated as the area of the lower m2 and the dentary length (Area is measured as in RLGA and dentary length as in Ixm2); MAM, mechanical advantage of the masseter muscle, measured as the distance from the mandibular condyle to the ventral border of the mandibular angle divided by dentary length (measured as in Ixm2); RAMP3, relative

section area of the mandible behind the p3, calculated as the square root of the area of the mandible idealised as an ellipse divided by the dentary length (measured as in as in Ixm2); RAMP4, relative section area of the mandible behind the p4, calculated as the square root of the area of the mandible idealised as an ellipse divided by the dentary length (measured as in as in Ixm2); RBL, relative blade length of the lower carnassial, obtained dividing the length of the trigonid part of the lower carnassial by the maximum length of the m1; RJD, the relative depth of the mandible measured at the interalveolar spaces between m1 and m2, calculated dividing the height of the mandible distally to the m1 by the dentary length (measured as in Ixm2); RLGA, the relative lower grinding area measured as the square root of the summed areas of the m1 talonid and m2, divided by the length of the m1 trigonid. Area was estimated as the product of the width and length of the talonid of m1 and of the m2; RtrigL, relative length of the trigonid, obtained dividing the mesiodistal length of the m1 trigonid by the sum of the length of the m1 talonid and the greatest mesiodistal length of the m2.

Systematic abbreviations

C., *Canis*; *Ch.*, *Chrysocyon*; *Cu.*, *Cuon*; *L.*, *Lupulella*; *Lc.*, *Lycalopex*; *Ly.*, *Lycaon*.

Institutional abbreviations

DGAUT, Department of Geology, Aristotle University of Thessaloniki (Thessaloniki, Greece); DSTUF, Dipartimento di Scienze della Terra, Università di Firenze (Florence, Italy); GNM, Georgian National Museum (Tbilisi, Georgia); ICP, Institut Català de Paleontologia Miquel Crusafont (Cerdanyola del Valles, Barcelona, Spain); IGME-CSIS, Centro Nacional Instituto Geológico y Minero de España (IGME)-CSIC; MGPUF, Museo di Geologia e Paleontologia dell’Università di Firenze (Florence, Italy); MPM, Museo Paleontologico di Montevarchi (Montevarchi, Arezzo, Italy).

RESULTS

In the deposits of Fonelas P-1, despite a generalised deformation of the specimens, which are affected especially by laterolateral compressions and dorsoventral flattenings, the morphologies of the specimens can be ascribed to two morphotypes. A slenderer form and a generally larger and stouter taxon can be identified. In previous papers these differences were referred to, respectively, *Canis accitanus* and *Canis etruscus*. We here compare them with other Gelasian and early Calabrian record of medium-sized canid. For this purpose, we initially refer them to as a morphotype 1 (the slender one) and morphotype 2 (the stouter one). The morphotypes are present both in Trench A and Trench B with a subtle but relevant distinction. Morphotype 1 was recovered in all fossiliferous facies of the association of the site, i.e., in unit ANF, part of facies A, from Trench A, in unit ULIA, facies E, from Trenches A and B. Morphotype 2 was recovered only from unit ULIA in both Trench A and Trench B. See Figs 2-3 for stratigraphic interpretations and Appendix for list of specimens of the two morphotypes and chronological references.

Morphological comparisons of morphotypes 1 and 2 (Trenches A and B)

The canid with morphotype 1 is characterised by slender muzzle with a globose neurocranium (as in FP1-2007 3148, Figs 4-5) like in *C. arnensis* from Upper Valdarno localities (Del Campana, 1913; Bartolini-Lucenti & Rook, 2016). On the contrary, in dorsal view, the morphotype 2 (see Appendix for list of specimens) is characterised by stout muzzle and neurocranium (as in FP1-2007 3064, Fig. 6), despite the deformation affecting the specimens. The nasals of morphotype 1 do not extend beyond the maxillofrontal suture in FP1-2001 434, FP1-2004 2709 and FP1-2007 3148, unlike those of morphotype 2 (Figs 4-6). The condition of morphotype 1 is reminiscent of *C. arnensis* from Il Tasso (Torre, 1967) or Poggio Rosso (Bartolini-Lucenti & Rook, 2016), whereas that of morphotype 2 of *C. etruscus* from Upper Valdarno or Olivola, in *C. mosbachensis* from Cueva Victoria (Bartolini-Lucenti et al., 2017) or Untermassfeld (Sotnikova, 2001) or *C. borjgali* from Dmanisi (Bartolini-Lucenti et al., 2020). The cranial specimens of morphotype 1 resemble *C. arnensis* in the morphology of the zygomatic process of the frontals, which are lobed and rounded in dorsal view (Torre, 1967; Bartolini-Lucenti & Rook, 2016) (Figs 4-5). Opposed to this shape, morphotype 2 shows pointy and sharper frontal processes when observed in dorsal view (as FP1-2001 849, Fig. 6) like *C. borjgali*, *C. etruscus* and *C. mosbachensis* (cf. Torre, 1967; Sotnikova, 2001; Bartolini-Lucenti et al., 2017, 2020). The medial walls of the tympanic bulla in both morphotypes (Figs 4-6) are parallel to the parasagittal axis of the cranium, resembling the morphology of *C. etruscus* and *C. arnensis*, in sharp contrast with *C. borjgali* and *C. mosbachensis*

(Bartolini-Lucenti et al., 2017, 2020). Other features of the cranium of both the morphotypes are masked by the deformation of the specimens (Figs 4-6).

Dentally, the upper incisor and canines bear very little diagnostic significance at a specific level and are coherent with the morphologies of Early Pleistocene *Canis* species. The P3 in FP1-2004 2709 and FP1-2007 3148 (Figs 4-5) show a relatively low major cusp, with a distally curved distal margin. This morphology of the P3 contrasts with the proportionally higher-crowned one of morphotype 2 (e.g., FP1-2002 1100, Fig. 6). In comparison to fossil canids of Western Eurasia, morphotype 1 is similar to *C. arnensis*, whereas morphotype 2 recalls the premolar morphology of *C. etruscus* from Olivola, Upper Valdarno or Pantalla (Torre, 1967; Cherin et al., 2014). Both morphotypes possess small distal accessory cusps on the P3 (Figs 4-6). This additional cusplule is possessed by all the comparative species considered here: *C. arnensis* from Poggio Rosso and Upper Valdarno (Torre, 1967; Bartolini-Lucenti & Rook, 2016), *C. borjgali* (Bartolini-Lucenti et al., 2020), *C. etruscus* from Upper Valdarno and Pantalla (Torre, 1967; Cherin et al., 2014), and *C. mosbachensis* from Cueva Victoria, Pirro Nord, Vallparadis Section, Untermassfeld (Sotnikova, 2001; Petrucci et al., 2013; Bartolini-Lucenti et al., 2017). Nevertheless, in *C. borjgali* and *C. mosbachensis* the distal accessory cusplule (dac) of the P3 is more basal in the crown, whereas in morphotype 1 (FP1-2004 2709 and FP1-2007 3148, Figs 4-5), in morphotype 2 (FP1-2001 434 and FP1-2002 1100, Fig. 6), in *C. arnensis* and in *C. etruscus*, the dac is attached to the principal cusp of the P3 (Torre, 1967; Cherin et al., 2014; Bartolini-Lucenti & Rook, 2016). The P4 of morphotype 1 is slender and not enlarged buccolingually,

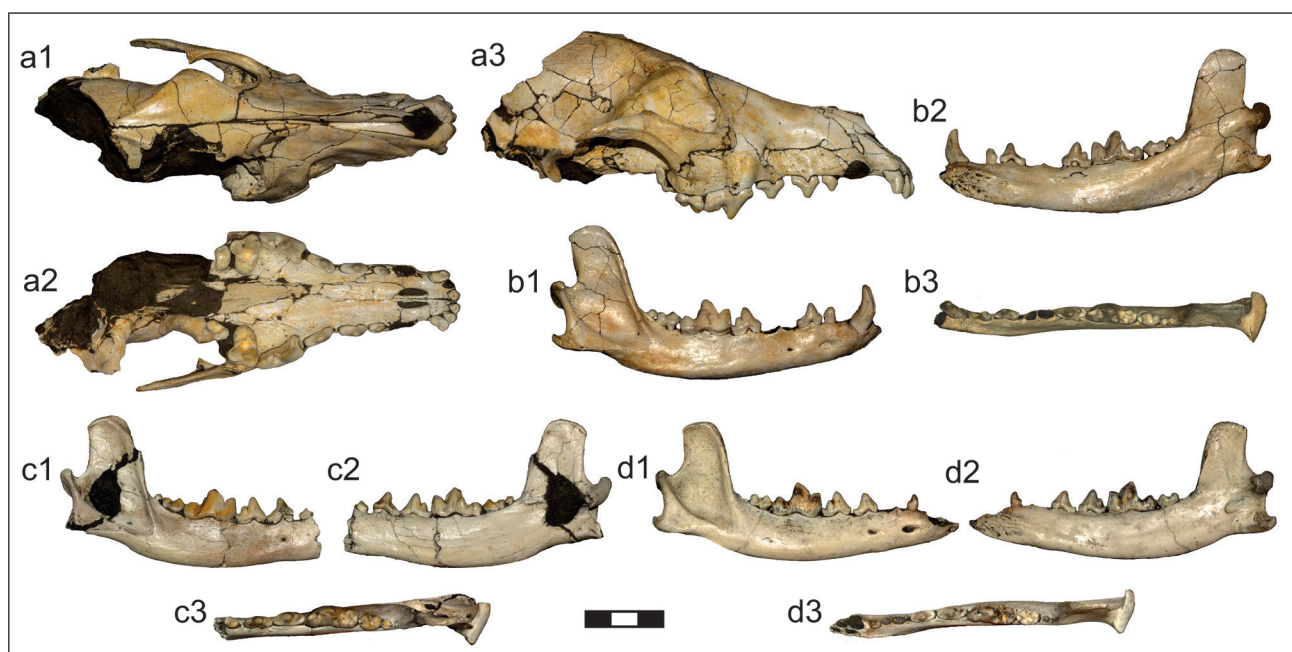


Fig. 4 - (color online) Morphotype 1 from Fonelas P-1 Trench A, *Canis arnensis* Del Campana, 1913. a1-a3) FP1-2004 2709, cranium recovered from unit ANF of facies association A, in dorsal (a1), ventral (a2) and reflected left lateral (a3) views. b1-b3) FP1-2004 2708, right hemimandible associated to the cranium FP1-2004 2709, probably belonging to the same individual (recovered from unit ANF part of facies association A) in buccal (b1), lingual (b2) and occlusal (b3) views. c1-c3) FP1-2007 3669, right hemimandible recovered from unit ULIA, facies association E, in buccal (c1), lingual (c2) and occlusal (c3) views. d1-d3) FP1-2007 3604, right hemimandible recovered from unit ULIA, facies association E, in buccal (d1), lingual (d2) and occlusal (d3) views. Scale bar equals 3 cm.

particularly at the level of the paracone (Figs 4-5). The occlusal morphology is close to that of *C. arnensis* from Poggio Rosso and Upper Valdarno (Torre, 1967; Bartolini-Lucenti & Rook, 2016). On the contrary, the one of morphotype 2 resembles that of *C. etruscus*, *C. borjgali* and *C. mosbachensis* for its stoutness, especially FP1-2002 1100 (Fig. 6). Particularly, the specimens of morphotype 2 share with *C. etruscus*, *C. borjgali* and *C. mosbachensis* the enlargement of the paracone and of the protocone (Cherin et al., 2014; Bartolini-Lucenti et al., 2020; Martínez-Navarro et al., 2021). The M1 is developed in both morphotypes, characterised by a buccal cingulum with a marked ectoflexus between paracone and metacone (Figs 4-6). The M1 of morphotype 1 is characterised by similarly developed M1 paracone and metacone, evident metaconule and protoconule (especially in FP1-2001 434 and FP1-2007 3148, Figs 4-5), and a lingually enlarged hypocone. The similar size of the buccal cusps contrasts sharply with *C. borjgali*, *C. etruscus* and *C. mosbachensis* (Cherin et al., 2014; Bartolini-Lucenti

et al., 2020). On the contrary, the M1 of morphotype 2 is marked by an enlarged M1 paracone in comparison with the metacone, a pointy parastyle, absence of protoconule, a reduced metaconule and enlarged protocone and hypocone (Fig. 6). The morphology is close to *C. etruscus* from Pantalla and Upper Valdarno (Torre, 1967; Cherin et al., 2014) as *C. borjgali* and *C. mosbachensis* generally have a prominent protocone and a lower hypocone (cf. Petrucci et al., 2013; Bartolini-Lucenti et al., 2017; Martínez-Navarro et al., 2021). The trigon and talon basins of the two morphotypes are of similar depth, like in *C. arnensis* and *C. etruscus* (Torre, 1967; Cherin et al., 2014; Bartolini-Lucenti & Rook, 2016). The M2 of morphotype 1 shows a mesiodistally slender occlusal shape. It possesses an enlarged paracone, a smaller metacone and lingually a protocone, protoconule and a metaconule (connected to the protocone), as visible in FP1-2001 434, FP1-2004 2709 and FP1-2007 3148 (Figs 4-5). The occlusal morphology recalls that of *C. arnensis* (Torre, 1967; Bartolini-Lucenti & Rook, 2016) and some

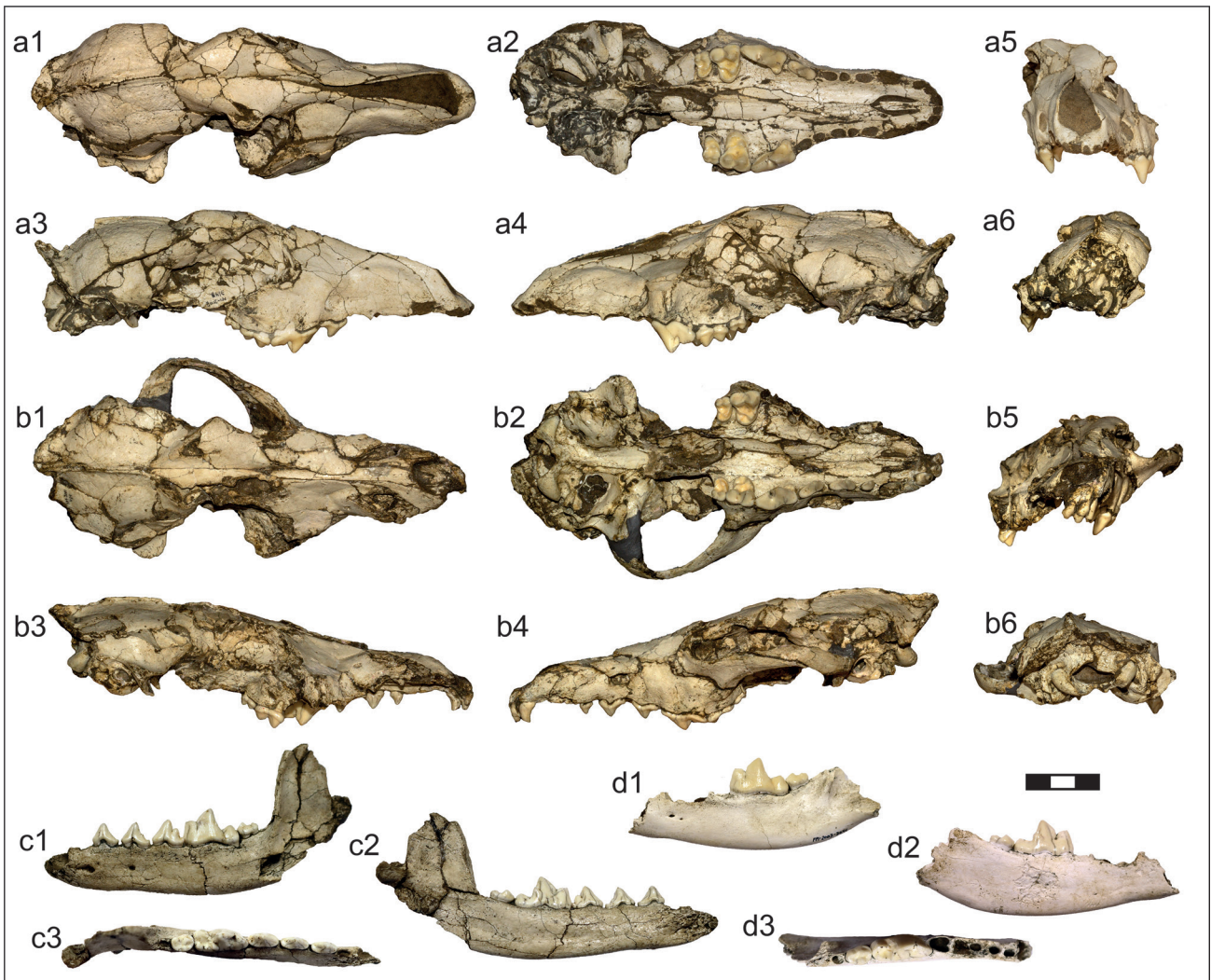


Fig. 5 - (color online) Morphotype 1 from Fonelas P-1 Trench B (all recovered from unit ULIA, facies association E), *Canis arnensis* Del Campana, 1913. a1-a6) FP1-2007 3148, cranium in dorsal (a1), ventral (a2) right lateral (a3), left lateral (a4), rostral (a5) and occipital (a6) views. b1-b6) FP1-2001 434, cranium (type of *Canis accitanus*) in dorsal (b1), ventral (b2) right lateral (b3), left lateral (b4), rostral (b5) and occipital (b6) views. c1-c3) FP1-2007 3001, left hemimandible in buccal (c1), lingual (c2) and occlusal (c3) views. d1-d3) FP1-2007 3044, left hemimandible in buccal (d1), lingual (d2) and occlusal (d3) views. Scale bar equals 3 cm.

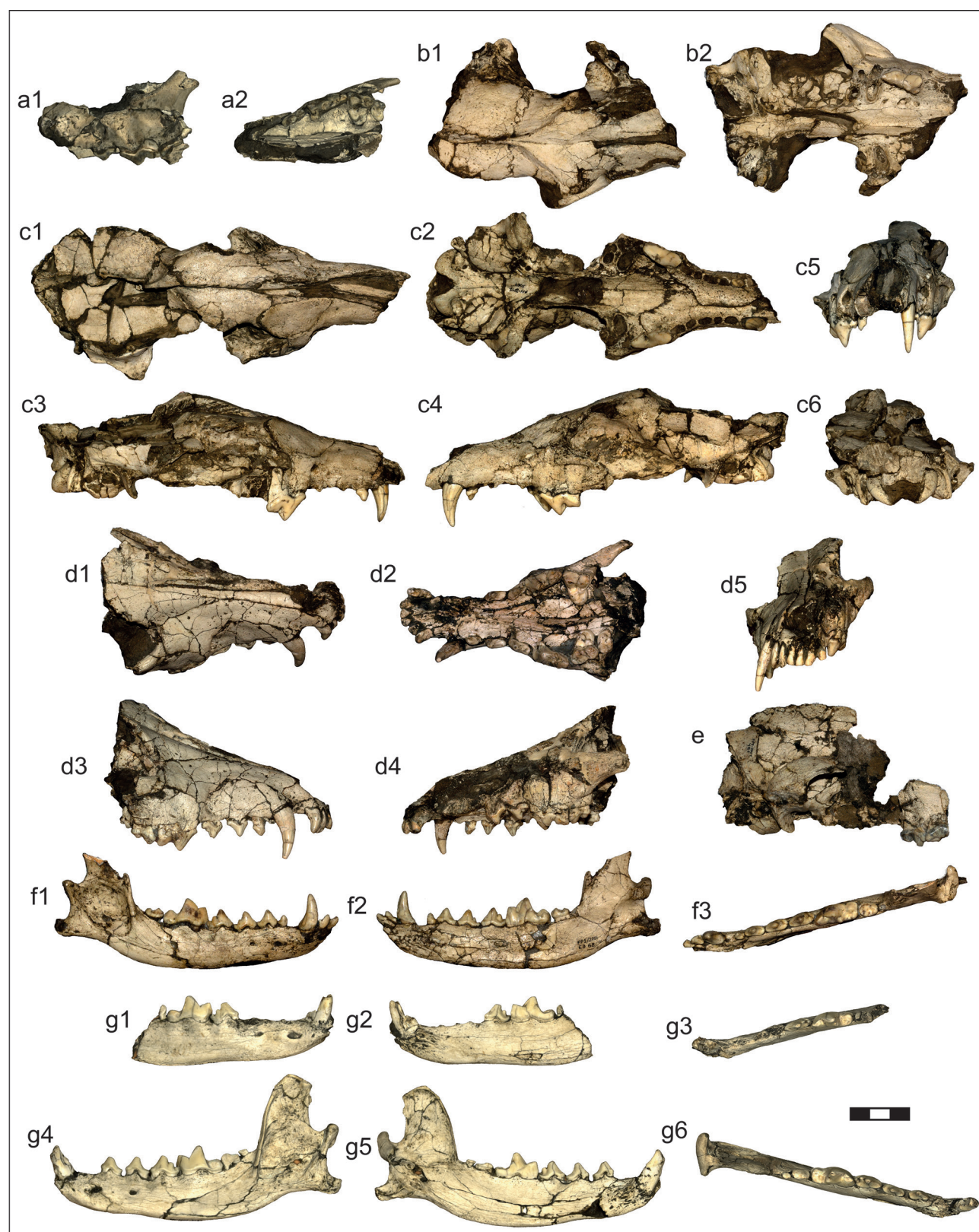


Fig. 6 - (color online) Morphotype 2 from Fonelas P-1 Trenches A and B (all from unit ULIA, facies association E), *Canis etruscus* Forsyth Major, 1877. a1-a2) FP1-2004 2766, left cranial fragment with P3-M2 recovered from Trench A shown in lateral (a1) and occlusal (a2) views. b1-b2) FP1-2001 849, fragment of cranium with right P4 from Trench B in dorsal (b1) and ventral (b2) views. c1-c6) FP1-2007 3064, cranium with left canine and P4 and right P4 from Trench B in dorsal (c1), ventral (c2), right lateral (c3), left lateral (c4), rostral (c5) and occipital (c6) views. d1-d5) FP1-2002 1100, cranium fragment with left I1-M1 and right I1-M2 from Trench B in dorsal (d1), ventral (d2), right lateral (d3), left lateral (d4) and rostral (d5) views. e) FP1-2001 481, cranial fragment with right P4 from Trench B in right lateral view. f1-f3) FP1-2001 E3 68, right hemimandible with i2-m2 in buccal (f1), lingual (f2) and occlusal (f3) views. g1-g6) FP1-2007 3252, left and right mandibular fragments from Trench B; the left one has a broken canine, p4-m1 and a broken m2, in buccal (g1), lingual (g2) and occlusal (g3) views; the right one possesses c-m3 and is shown in buccal (g4), lingual (g5) and occlusal (g6) views. Scale bar equals 3 cm.

C. mosbachensis, e.g., from Untermassfeld (Sotnikova, 2001). Morphotype 2 shows mesiodistally larger M2 in comparison to that of morphotype 1, and possesses an enlarged protocone, as evident in FP1-2002 1100 (Fig. 6). Lingually there is no metaconule, if not a distal cingulum, despite a postprotocrista departing from the prominent protocone. The features just mentioned are comparable to those of *C. etruscus* from Olivola, Pantalla and Upper Valdarno (Torre, 1967; Cherin et al., 2014).

The mandible of morphotype 1 has a fairly slender corpus with a curved ventral margin especially below the m1, in contrast with morphotype 2 mandible that is stouter, with a higher corpus (e.g., FP1-2001 E3 68, FP1-2007 3252, Figs 4-6) and characterised by the markedly deep masseteric fossa. The masseteric fossa on the mandible of morphotype 1 is developed but shallower compared to that of morphotype 2, when observed in lateral view (Figs 4-5). The lower canine in morphotype 2 seems higher-crowned compared to that of morphotype 1 (Fig. 6). In both morphotypes 1 and 2, the p3 tip is lower compared to that of p4 in some specimens (e.g., FP1-2007 3604 in Trench A or FP1-2001 E3 68, Figs 4-6) whereas the majority are of the same height. The position of the p3 alveolus in the mandible is an important feature for *C. mosbachensis* and *C. borjgali*, in which it sets at a lower level compared to p2 and p4 in the majority of the specimens (Sotnikova, 2001; Petrucci et al., 2013; Bartolini-Lucenti et al., 2017, 2020) resulting in a shorter p3. On the contrary, in *C. etruscus* and *C. arnensis* the alveoli are at the same level between one another. Yet few specimens of *C. etruscus* and *C. arnensis* from Poggio Rosso and Upper Valdarno have p3 tips slightly lower than of the p4 (see Torre, 1967; Tedford et al., 2009; Bartolini-Lucenti & Rook, 2016), similar to the condition seen in morphotypes 1 and 2 of FoneLas P1. The premolars in both the morphotypes (Figs 4-6) have high crowns like *C. etruscus* and *C. arnensis* (Torre, 1967; Bartolini-Lucenti & Rook, 2016), with p4 protoconid higher than the m1 paraconid. These two features sharply contrast with *C. borjgali* (Bartolini-Lucenti et al., 2020) or *C. mosbachensis* (e.g., from Cueva Victoria or Vallparadis Section, Bartolini-Lucenti et al., 2017; or Untermassfeld, Sotnikova, 2001). The p3 possesses a reduced distal accessory cuspid, comparable to that of *C. arnensis*, *C. borjgali* and *C. mosbachensis* (Torre, 1967; Sotnikova, 2001; Bartolini-Lucenti et al., 2020). The p4 of morphotype 1 shows a large distal accessory cuspid and basal cingulid (Figs 4-5), unlike that of morphotype 2 (e.g., FP1-2001 E3 68 and the left hemimandible FP1-2007 3252, Fig. 6) and of *C. etruscus* from Olivola and Upper Valdarno (Torre, 1967; Cherin et al., 2014) that generally possesses an additional secondary cuspid and a cuspid-like cingulum. In both morphotypes, the p4 protoconid is slender and as high as the m1 paraconid, in buccal view like in *C. arnensis* and *C. etruscus* (Torre, 1967; Bartolini-Lucenti & Rook, 2016) (Figs 4-6). The m1 of morphotype 1 is buccolingually slender and it is characterised by a developed metaconid, projected on the lingual side (e.g., FP1-2004 2708 and FP1-2007 3044, Figs 4-5). On the contrast the morphotype 2 has a proportionally stouter carnassial, with a reduced metaconid (e.g., FP1-2001 E3 68 and FP1-2007 3252, Fig. 6). On the talonid of morphotype 1, the hypoconid is larger than the entoconid, but the latter is not considerably

reduced like in morphotype 2 (cf. FP1-2004 2708 to FP1-2001 E3 68 or FP1-2007 3252, Figs 4-6). The morphology of morphotype 2 recalls that of *C. etruscus* from Olivola and Upper Valdarno (Torre, 1967), whereas the one of morphotype 1 that of *C. arnensis* from Upper Valdarno (Bartolini-Lucenti & Rook, 2016). Moreover, on the lingual side of the talonid of morphotype 1 there is an evident entoconulid, comparable to *C. arnensis* from Valdarno (Bartolini-Lucenti & Rook, 2016) or some *C. mosbachensis* specimens (Sotnikova, 2001; Petrucci et al., 2013; Ghezzi et al., 2014; Bartolini-Lucenti et al., 2017; Martínez-Navarro et al., 2021). Only one specimen of morphotype 2 (i.e., FP1-2001 E3 68, Fig. 6) possesses the entoconid, a feature seldomly present in *C. etruscus* from Olivola and Upper Valdarno (Torre, 1967; Bartolini-Lucenti et al., 2017). The m2 of morphotype 1 is elongated distally and shows three major cuspulids and a reduced, but evident entoconid (Figs 4-5). *Canis arnensis* from Poggio Rosso and Valdarno has a comparable morphology, characterised by an elongated m2 talonid and entoconid. Furthermore, the m2 in morphotype 1 has protoconid and metaconid of comparable size, unlike *C. borjgali*, *C. etruscus* and *C. mosbachensis* (see Torre, 1967; Bartolini-Lucenti et al., 2017, 2020). Moreover, *Canis etruscus* normally does not have the m2 entoconid or at maximum a cuspid-like lingual cingulum (Torre, 1967), and similarly does *C. borjgali* (Bartolini-Lucenti et al., 2020). The m2 of *C. mosbachensis* normally does not show an entoconid, with few exceptions (see Bartolini-Lucenti et al., 2017). On the contrary, the m2 of morphotype 2 are similar to those of *C. etruscus* for the mesiodistally reduction of the tooth, especially of the talonid, the relative size of the protoconid (almost twice the time of the metaconid in occlusal view, e.g., in FP1-2001 E3 68, Fig. 6) and the expansion of the buccal cingulid. In all, morphotype 1 evidently recalls *C. arnensis* whereas morphotype 2 is consistent with *C. etruscus*.

Ecological analyses of FoneLas P-1 canids

The use of mandibular ratios as the relative length of the m1 trigonid (RtrigL) and the relative depth of the mandible corpus (RJD) allow to easily separate extant canid ecological groups. In Fig. 7 the extant canids separate in two clusters and some isolated observations: the group-hunter hypercarnivores (G1 from hereafter) on the top right, a large cluster of the left side of the variability mainly composed by hypocarnivores (G4 from now on) but with mesocarnivores (of group 3, G3 onward), and some small-prey hypercarnivores (i.e., *C. simensis*, *V. lagopus*, and *V. macrotis*; group 2, G2 from now on). Far from these clusters, *Otocyon* occupies the lowest position in the variability, especially as far as RtrigL values are concerned. The fossil species considered here occupy an intermediate position between G1 and G3-G4 clusters, particularly the averaged *C. arnensis* from Upper Valdarno and *C. etruscus* from Olivola and Upper Valdarno. The variability of the comparative sample of *Canis etruscus* is large and placed towards the cluster of G1, whereas that of *C. arnensis* is much smaller and partially overlapping with the lower range of RJD of the Etruscan wolf. The two taxa from FoneLas P-1 are well separated from one another. The morphotype 1 lies within the variability of *C. arnensis* from Poggio Rosso and other Upper Valdarno

localities (confirming the morphological similarity to *C. arnensis*). Similarly, specimens of morphotype 2 are placed within the variance of *C. etruscus* from Olivola and Upper Valdarno (confirming the morphologically similarity described above), and close to G1 species e.g., the averaged values of *C. lupus* and *Ly. pictus*. Considering additional dentognathic ratios, we performed a between-group PCA (bgPCA), whose results are reported in Fig. 8. The first axis (bgPC1) accounts for 79.47% of the variance with positive and similar loadings for almost all analysed variables (see SOM2). It is positively influenced by the relative area of the mandible at p3 (RAMp3), resistance to bending in the parasagittal plane between m1-m2 (Ixm2) and mechanical advantage of the masseter muscle (MAM) and negatively by relative lower grinding area (RLGA) and relative area of the m2 (M2S). Along this axis, we can identify two distinct clusters: one consists of the species of G2, G3, G4 and *C. arnensis* (with the specimens of Fonelas P-1) which all share negative or low positive values of bgPC1. The second cluster includes the species of G1 and *C. etruscus* (with also the specimens from Fonelas P-1). The bgPC2, which accounts for 15.63% of the variability, is positively affected only by the RAMp3 and the relative length of the carnassial blade (RBL). Negative loadings include the M2S, RLGA and the relative length of the trigonid (M1BS). Along axis 2, the groups are much less differentiated from one another, especially the G1 that occupies positive and negative values along bgPC2 (particularly *Cu. alpinus* on the positive end and most of the *C. lupus* and *Ly. pictus* on the negative one). On the contrary G2 is limited to the positive portion of axis. G3 shows a rather dispersed pattern in the morphospace. On this axis, *C. arnensis*, *C. etruscus*, the specimens from Fonelas P-1 share similar negative values. Overall, observing the distribution of the taxa in the morphospace of Fig. 8a, we see that three of the extant groups (i.e., G1-G3) are well separated from one another. Regarding the fossils, there is a clear

separation between *C. arnensis* and *C. etruscus*, with the former more closely attached to the variability of G3 canids. On the contrary, *C. etruscus* variability lies close and partially overlapping that of extant *C. lupus*. A permutation MANOVA performed on bgPC1-bgPC2 values of a priori ecological groups and fossil taxa show statistically significant distinction between all the groups but also between the comparative sample of *C. arnensis* and *C. etruscus* from Upper Valdarno (Tab. 1). The canids from Fonelas P-1, plotted a posteriori on the bgPCA variability, fall in the convex hulls of two other fossil species. Particularly morphotype 1 is enclosed within the variability of *C. arnensis*, whereas morphotype 2 is in the variability of *Canis etruscus*. Thus, confirming the morphological results in both instances. Moreover, the two canids from Fonelas P-1 are clearly distinct from an ecological point of view, considering the distant position they both occupy in the bgPC1-bgPC2 plot. The 3D plot of the bgPCA here performed (Fig. 8b-c) confirms the same pattern just described. Although, accounting for a limited portion of variability (i.e., 3.97%), the bgPC3 further shows the distance between morphotype 1 and morphotype 2, placing them respectively in the variability of *C. arnensis* and *C. etruscus*. The bgPC3 is positively influenced by RLGA, RAMp3 and the relative area of the mandible at p4 (RAMp4), whereas it is negatively influenced by M1BS and RBL (in decreasing order of magnitude).

DISCUSSION

The variability of Fonelas P-1 medium-sized canids and their implications

The analysis of the material coming from Fonelas P-1 has revealed the presence of two morphotypes of medium-sized canids as previously reported in literature (Garrido, 2008; Garrido & Arribas, 2008). The first

	Df	SumsOfSqs	F.Model	R2	p-value	p-adjusted
<i>Canis etruscus</i> vs <i>Canis arnensis</i>	1	0.01410	12.85085	0.68171	0.01798	0.02075
<i>Canis etruscus</i> vs G4	1	0.21569	36.12914	0.73539	0.00200	0.00272
<i>Canis etruscus</i> vs G1	1	0.03387	9.01523	0.23107	0.00200	0.00272
<i>Canis etruscus</i> vs G3	1	0.06291	27.40884	0.46136	0.00100	0.00167
<i>Canis etruscus</i> vs G2	1	0.17743	22.08401	0.51258	0.00100	0.00167
<i>Canis arnensis</i> vs G4	1	0.06839	10.03180	0.47698	0.01299	0.01623
<i>Canis arnensis</i> vs G1	1	0.06268	15.94340	0.36282	0.00100	0.00167
<i>Canis arnensis</i> vs G3	1	0.00511	2.16628	0.06735	0.13187	0.13187
<i>Canis arnensis</i> vs G2	1	0.04627	5.29327	0.21789	0.01998	0.02141
G4 vs G1	1	0.76460	147.76638	0.80850	0.00100	0.00167
G4 vs G3	1	0.13139	34.27198	0.48086	0.00100	0.00167
G4 vs G2	1	0.13241	14.51876	0.35832	0.00100	0.00167
G1 vs G3	1	0.53029	161.83289	0.74981	0.00100	0.00167
G1 vs G2	1	0.65029	102.72326	0.70492	0.00100	0.00167
G3 vs G2	1	0.18989	36.67933	0.44906	0.00100	0.00167

Tab. 1 - Results of the MANOVA on the first two bgPCs obtained from the between-group principal component analysis on *Canis arnensis* and *Canis etruscus* and the ecological groups.

morphotype is of a slender in generally smaller canid, comparable in all its features to the Italian and French *Canis arnensis*. In previous reports from site, a new species (i.e., *Canis accitanus*, Garrido & Arribas, 2008) was described and was interpreted as strictly related to *C. arnensis*. In the present paper we confirm the similarity between morphotype 1 canid from Fonelas P-1 (to which *C. accitanus* belongs to) and *C. arnensis* expanding and deepening the morphological and morphometric analyses, following the more recent revisions of the latter species (Bartolini-Lucenti & Rook, 2016; Bartolini-Lucenti et al., 2024). These reviews of the diagnostic features of *C. arnensis* have revealed that some of these characteristics were biased by taphonomic deformation obscuring real morphologies, thus hindering correct interpretations. As correctly identified by Garrido & Arribas (2008), *C. accitanus* only slightly differs from *C. arnensis* and the revision here provided confirms that the variability of *C. arnensis* from Poggio Rosso and other Upper Valdarno localities, can accommodate the specimens from Fonelas P-1 Trench B. Moreover, here we describe for the first time the remains from Trench A (slightly older than Trench B, see Geological Setting section) belonging at least to three individuals, one of which with a partial skeleton associated (i.e., cranium FP1-2004 2709 and correspondent mandible FP1-2004 2708). As far as the morphotype 2 is concerned, the size and morphology of the cranial and dentognathic specimens is consistent with an attribution to *C. etruscus*, confirming the interpretation reported in literature for some of the described fossils from Trench B (Garrido, 2008; Garrido & Arribas, 2008). What is relevant here is that *C. etruscus* is not only limited to the upper levels of the section (i.e., Trench B) but it is also present, though less abundant, also in the lower layers of Trench A. In this sense the record of Fonelas P-1 is interesting, far above the local or regional level. First of all, fossils from Fonelas P-1 attributable to *C. arnensis* (as shown in Figs 4-5) greatly expands the distribution area of this canid into southernmost Europe, adding to its punctiform record from Italy (where majority of its records are reported), France (Bartolini-Lucenti & Rook, 2016) and possibly Eastern Europe (Sotnikova et al., 2002). The pattern expressed by the records from Eastern and Western Europe fits with our understanding of westward expansion of canids from Asia into Europe (Sotnikova & Rook, 2010; Bartolini-Lucenti et al., 2020). Nevertheless, these occurrences were disputed for their isolated and scanty record. Unlike *C. etruscus*, which was already considered a member of the middle Villafranchian fauna of western Europe (Bellucci et al., 2012; Marciszak et al., 2023b), the presence of *C. arnensis* was confidently related only to Olduvai subchron (roughly 1.9-1.8 Ma), despite isolated reports of previous occurrences around 2 Ma. Any possible doubts on the scarce material of Senèze, assigned to this species by several scholars, are here resolved with specimens with clear morphological features and comparable characteristics since the record of *C. arnensis* in Fonelas P-1 is composed of abundant and undisputable cranial material. The occurrences in units ANF and ULIA (Figs 2-3) reinforces the idea of a biochronological arrival in Europe before 2 Ma, corroborating the occurrence in Senèze and the persistence of this taxon for the first part of the Calabrian. Moreover,

thanks to the expanded hypodigm, the record of Fonelas P-1 grants the possibility to observe the variability of the species with more precision, to test the soundness of previously suggested diagnostic features in the hope that it will enable future research to expand even more the biogeography of this species.

Ecomorphological considerations on European Gelasian medium-sized canids

The records of Fonelas P-1 are relevant also in terms of palaeoecology of these canids. Normally, the co-occurrence of taxa in the fossil record is difficult to ascertain properly considering time averaging, taphonomic biases and stratigraphic resolution. Speaking of European canids, the most exemplificative record is that of *C. etruscus*, *C. arnensis* and *X. falconeri* from Upper Valdarno, the first place where all of these species were described and are known since the end of the 19th and the beginning of the 20th Century (Forsyth Major, 1877; Del Campana, 1913). In their descriptions and subsequent work, scholars have tried to understand how it was possible to encounter three taxa in the same basin: the most parsimonious answer was to advocate ecological/trophic distinction. *Xenocyon* was, obviously, regarded as a hypercarnivore (Rook, 1994; Martínez-Navarro & Rook, 2003); *Canis etruscus* was always referred to as a wolf-like canid (Torre, 1967, 1979); whereas *C. arnensis* as a mesocarnivore (a side from the phylogenetic dilemma of its affinities; Torre, 1967, 1979; Kurtén, 1974; Bartolini-Lucenti & Rook, 2016). The few ecological analyses performed on some of these taxa substantially confirmed these interpretations (Flower & Schreve, 2014; Bartolini-Lucenti & Spassov, 2022) although, no stable isotope analyses nor microwear ones have yet been performed on these taxa. Despite these ecological interpretations, the historical fossil-bearing localities from which these species come from, if still preserved, are not easily identifiable nor stratigraphically constrained or described, with very few exceptions in terms of sites (Napoleone et al., 2003; Ghinassi et al., 2004; Mazza et al., 2004; Rook et al., 2013). Thus, although indeed they were recorded in Upper Valdarno sites generally accepted as coeval, there is no certainty of coexistence *C. etruscus* and *C. arnensis* in the same environment. Presently, there is no other site in Europe that reports the sure occurrence of *C. arnensis* and *C. etruscus* in the deposits and in the same geological layer. In this sense it is easy to understand the relevance of Fonelas P-1. It represents the only stratigraphically well-constrained record in Europe with the proved coexistence of these two taxa, recorded more than one layer and in both Trenches A and B. For this reason, Fonelas P-1 represents the perfect site in which to test the hypothesis of ecological distinction between *C. arnensis* and *C. etruscus* as well as other biological phenomena, rarely discernible in the fossil record, e.g., character displacement, niche partitioning, various degree of competitions (interspecific, intraspecific, intraguild). Character displacement – the reduction in phenotypic overlap between two or more closely related species compete over the same resources, to reduce the intensity of competition (e.g., Brown & Wilson, 1956; Slatkin, 1980; Meiri et al., 2011) – has been studied in extant canids by different authors (Dayan et al., 1992; Van Valkenburgh & Wayne, 1994; Davies et al., 2007;

Bubadué et al., 2016) but rarely investigated in fossils (see García & Virgós, 2007). Although out the scope of this manuscript, an interesting question to be answered might be: is there character displacement between *C. arnensis* and *C. etruscus* in the sites they co-occurred? Van Valkenburgh & Wayne (1994) identified four different possible manifestations of character displacement: divergence in size; divergence in shape; reduced morphological variability; reduced sexual dimorphism. Indeed, all the evidence known from literature and the one here reported point out to ecological character

displacement favouring reduced competition between *C. arnensis* and *C. etruscus*. First of all, the two species are different in size, with *C. etruscus* roughly one third larger than *C. arnensis* (Del Campana, 1913; Torre, 1967; Brugal & Boudadi-Maligne, 2011; Cherin et al., 2014; Bartolini Lucenti & Rook, 2016). Secondly, morphologically the two taxa can be easily distinguished based on cranial and dentognathic features (see Cherin et al., 2014; Bartolini-Lucenti & Rook, 2016; Bartolini-Lucenti et al., 2020) and their morphological variability indeed appears reduced (Cherin et al., 2014; Bartolini-Lucenti & Rook,

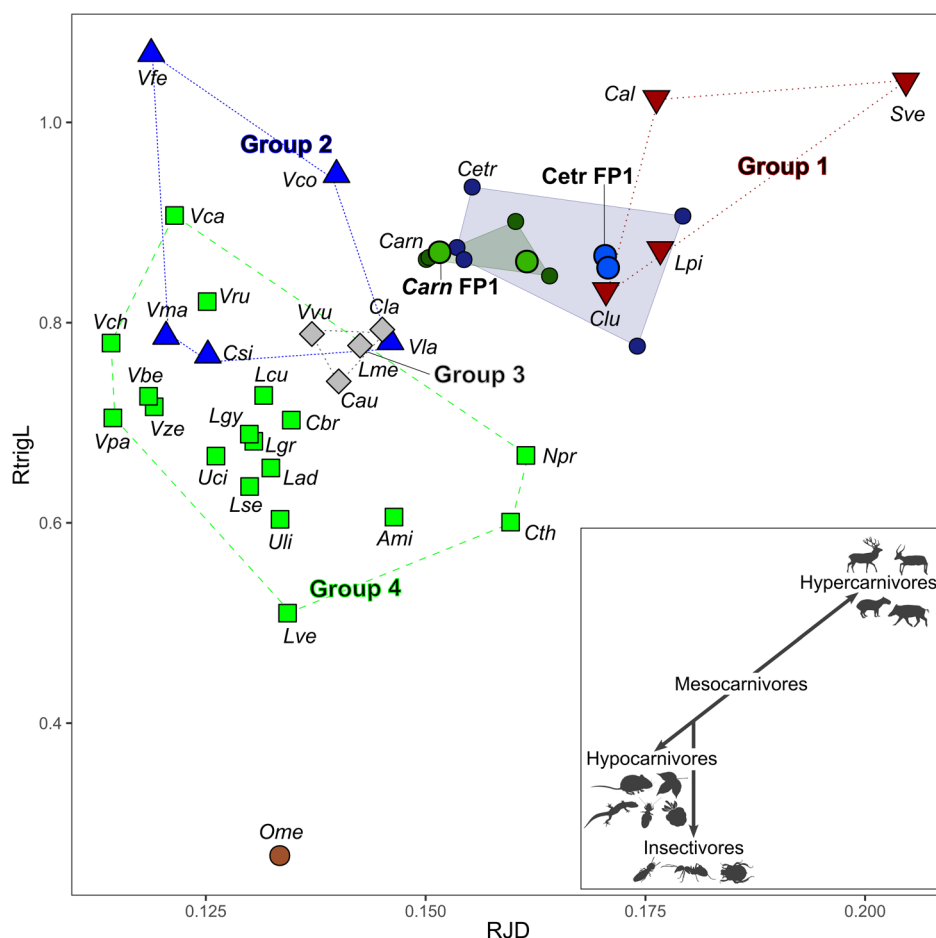


Fig. 7 - (color online) Biplot of the relative depth of the mandible (RJD), measured as the height of the corpus distal to the m1 and divided by the dentary length (see abbreviations in the Materials and Methods section), and of the relative length of the trigonid (RtrigL), measured as the mesiodistal length of the m1 trigonid divided by the sum of the lengths of the m1 talonid and of the m2 (following Martínez-Navarro et al., 2021). The distribution of the extant taxa reveals that the two variables allow to discriminate effectively dietary preferences. This is reported in the scheme in the bottom-right corner of the figure. Particularly it is evident that: large hypercarnivorous species (>70% meat in the diet, Crusafont-Pairó & Truyols-Santonja, 1956; Van Valkenburgh, 1989; corresponding to Group 1 canids of Van Valkenburgh & Koepfli, 1993) tend to place in the upper right corner. Opposite to this there are the hypocarnivores (< 50% of meat in the diet, Crusafont-Pairó & Truyols-Santonja, 1956; Van Valkenburgh, 1989; corresponding to Group 4 canids of Van Valkenburgh & Koepfli, 1993). In the middle morphospace between them lie the mesocarnivores (50-70% meat in the diet, Crusafont-Pairó & Truyols-Santonja, 1956; Van Valkenburgh, 1989; these percentage corresponds to those that define Group 3 canids of Van Valkenburgh & Koepfli, 1993). It should be noted that Group 2 canids of Van Valkenburgh & Koepfli (1993) (hypercarnivores feeding in only small vertebrate prey) are not greatly divided by these ratios. Lastly, insectivores (i.e., *Otocyon megalotis*) occupy the lowest position along the y-axis. Abbreviations: *Cal*, *Cu. alpinus*; *Carn*, *C. arnensis* from Upper Valdarno localities (Torre, 1967; Bartolini-Lucenti & Rook, 2016); *Carn FP1*, *C. arnensis* from Fonelas P-1; *Cau*, *C. aureus*; *Cbr*, *Ch. brachiurus*; *Cetr*, *C. etruscus* from Olivola and Upper Valdarno localities (Torre, 1967); *Cetr FP1*, *C. etruscus* from Fonelas P-1; *Clu*, *C. latrans*; *Chu*, *C. lupus*; *Csi*, *C. simensis*; *Cth*, *Ce. thous*; *Lad*, *L. adusta*; *Lcu*, *Lc. culpaus*; *Lgr*, *Lc. griseus*; *Lgy*, *Lc. gymnocercus*; *Lse*, *Lc. sechurae*; *Lve*, *Lc. vetulus*; *Lme*, *L. mesomelas*; *Lpi*, *Ly. pictus*; *Lse*, *Lc. sechurae*; *Npr*, *N. procyonoides*; *Ome*, *O. megalotis*; *Sve*, *S. venaticus*; *Uci*, *U. cinereoargenteus*; *Uli*, *U. littoralis*; *Vbe*, *V. bengalensis*; *Vca*, *V. cana*; *Vch*, *V. chama*; *Vco*, *V. corsac*; *Vfe*, *V. ferrilata*; *Vla*, *V. lagopus*; *Vma*, *V. macrotis*; *Vru*, *V. rueppellii*; *Vvu*, *V. vulpes*; *Vze*, *V. zerda*. Dietary silhouettes taken from Phylopic (www.phylopic.org) and used under public domain (CC0).

2016). In addition to the morphological differences, the results of the ecomorphological analyses shown in Figs 7-8 suggest that indeed a distinction between the taxa exists and it is referable to a more mesocarnivorous diet in *C. arnensis* and more carnivorous diet in *C. etruscus*. Thus, corroborating the character displacement hypothesis. Figure 7 shows some overlapping in the selected dentognathic variables (relative jaw depth and the relative length of the trigonid) between *C. arnensis* and *C. etruscus* from Upper Valdarno, but the specimens from Fonelas P-1 are separated from one another. Considering more dentognathic indices in a bgPCA (Fig. 8) reveals even more interesting results. The distribution in Fig. 8 shows a nice separation of the extant ecological groups, all statistically significantly different (Tab. 1). The same can be said for the fossil species: indeed *C. arnensis* and *C. etruscus* from Upper Valdarno occupy distinct regions of the morphospace, with no overlapping and a statistically significant difference on the first two bgPCs (Tab. 1). Plotting a posteriori the specimens from Fonelas P-1 morphologically ascribe to *C. arnensis* (i.e., morphotype 1) and to *C. etruscus* (i.e., morphotype 2) produced two relevant results. A confirmation of the taxonomic attributions, but more importantly a clear ecological distinction between the Fonelas P-1 *C. arnensis* and *C. etruscus* following the pattern of the respective taxa from Upper Valdarno. Our results are the first of their kind since previous dietary inferences were principally made on only dental morphometrics (e.g., Flower & Schreve, 2014; Martínez-Navarro et al., 2021) and no analyses were performed on *C. arnensis*. Even in the case of *C.*

etruscus the dietary reconstructions were investigated in an evolutionary perspective, i.e., in comparison to taxa like *C. mosbachensis* and *C. lupus* (Flower & Schreve, 2014), and less in terms of intraguild distinction (Turner, 1995; Cherin et al., 2013). In these analyses, *C. etruscus* is less carnivorous than *C. mosbachensis* and *C. lupus* and our results are not in disagreement with them (considering the position of *C. etruscus* in Fig. 8 and the distinction from extant G1 canids; see also Tab. 1). Moreover, unpublished stable isotopes data for *C. mosbachensis* from the Calabrian of Piro Nord have comparable hypercarnivorous values to those of *Xenocyon*. What is more interesting is the comparison with intraguild competitors. Indeed, there are no certain records of co-occurrence between *C. etruscus* and *C. mosbachensis*, but it shared environment with *C. arnensis*. This canid lies close to the variability of mesocarnivorous canids (G3) and the MANOVA on bgPC1-bgPC2 fails to statistically discriminate between *C. arnensis* and G3 canids. Thus, the ecomorphometric results allow us to confirm previous assumptions of dietary preference of the mesocarnivorous *C. arnensis*, on the one side, and more carnivory *C. etruscus*, on the other. This reaffirms the ecological compatibility of these two forms in the same taphocoenoses as suggested from other fossil localities with less strict temporal constraints, possibly arose through character displacement. Moreover, such a coexistence in time and space is perfectly in line with some extant instances of co-existence between living canids in present ecosystems e.g., *C. lupus*, *C. rufus* and *C. latrans* in North America (Bekoff & Gese, 2003); or *C. lupaster*, *L. adusta*, *L. mesomelas* and *Ly. pictus* in East Africa

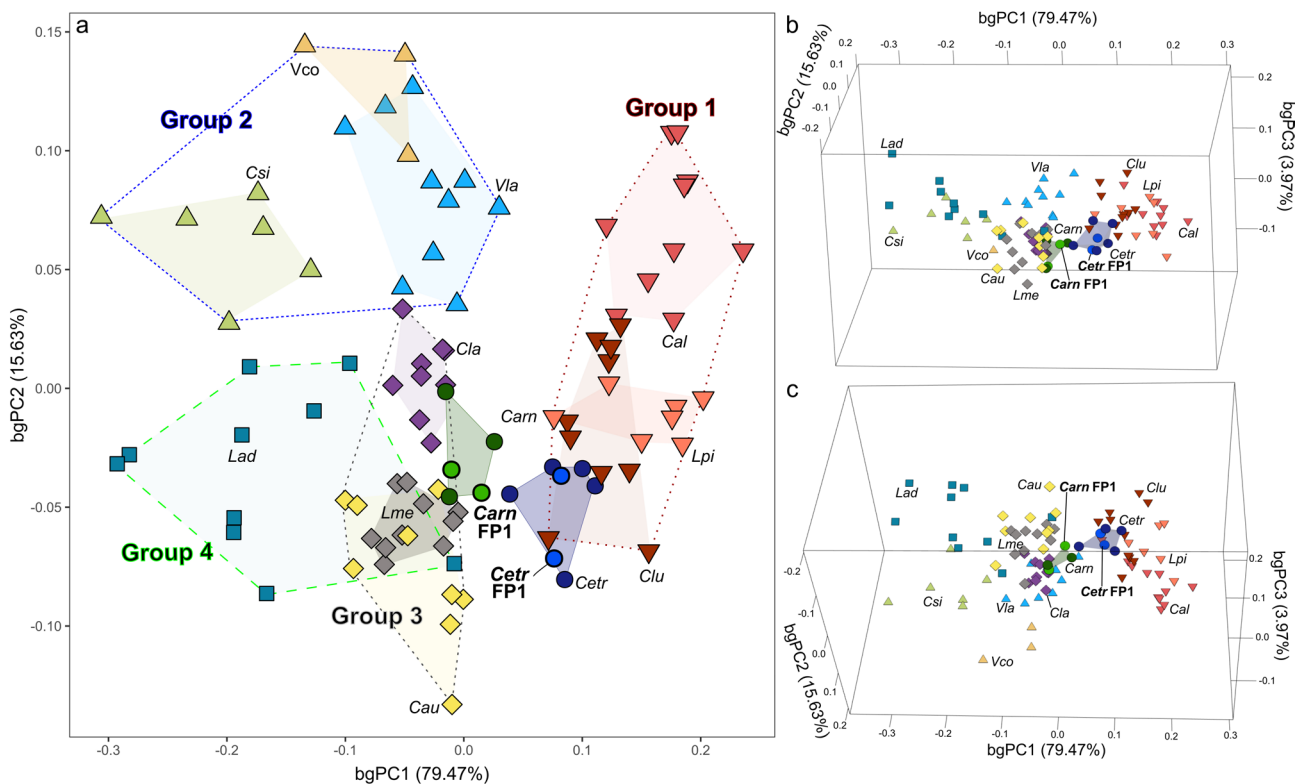


Fig. 8 - (color online) Between-group Principal Component Analysis (bgPCA) performed on a selection of log-transformed dentognathic ratios on select extant and fossil taxa. Panel (a) shows the biplot of the first two principal components (bgPCs) whereas panels (b-c) show the three-dimensional results of the same bgPCA, including the third bgPC. For abbreviation see the caption of Figure 7.

(Van Valkenburgh & Wayne, 1994; Johnson et al., 1996) (furthermore see Castelló, 2018; IUCN, 2024).

CONCLUDING REMARKS

The Fonelas P-1 site provides critical evidence for understanding the evolutionary dynamics of medium-sized canids during the Early Pleistocene in Europe. This study confirms the co-occurrence of two distinct canid species, *Canis arnensis* and *Canis etruscus*, within a well-constrained stratigraphic framework. The available data from the facies associations of Fonelas P-1 suggest that *C. arnensis* arrived slightly earlier to the Guadix-Baza basin than *C. etruscus* (as the former is recorded in the fossiliferous ANF unit, part of facies A, whereas the latter only in facies E, unit ULIA), and that they coexisted there (as both are recorded in facies E, unit ULIA). The comprehensive morphological and ecomorphological analyses conducted on the specimens highlight clear taxonomic and ecological distinctions between the two species, in line with ecological character displacement. *Canis arnensis* is characterised by features associated with a mesocarnivorous dietary strategy, while *C. etruscus* displays adaptations more aligned with a degree of hypercarnivory. These ecological differences likely facilitated their coexistence in the same palaeoenvironment without significant interspecific competition. The presence of *C. arnensis* at Fonelas P-1 extends its known biogeographic range to southern Europe and corroborates its earlier biochronological occurrence before 2 Ma (Sotnikova et al., 2002; Bartolini-Lucenti et al., 2016). This finding contributes to a more nuanced understanding of the dispersal and diversification patterns of canids during the Early Pleistocene, challenging previous assumptions of their geographic and ecological constraints. Moreover, the robust fossil evidence from Fonelas P-1 reinforces the validity of the palaeoecological interpretations for these taxa, providing an invaluable reference for future studies on carnivoran evolution and ecosystem dynamics in the Villafranchian of Europe. The record from Fonelas P-1 underscores the importance of integrating stratigraphically controlled fossil data with advanced ecomorphometric techniques to unravel the complex evolutionary histories of Pleistocene faunal communities. By demonstrating the ecological niche partitioning of *C. arnensis* and *C. etruscus*, this study highlights the adaptive versatility of Early Pleistocene canids and their critical role in shaping carnivore guilds in dynamic and changing environments.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data generated and analysed in this contribution are available on the BSPI website at: <https://www.paleoitalia.it/bollettino-spi/bspi-vol-641/>

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APPENDIX

Systematic Palaeontology of Fonelas P-1 canids

Morphotype 1

Order CARNIVORA Bowdich, 1821

Family CANIDAE Fischer, 1817

Tribe CANINI Fischer, 1817

Genus *Canis* Linnaeus, 1758*Canis arnensis* Del Campana, 1913

(Figs 4-5; SOM 3)

Occurrence - Fonelas P-1 Trench A, facies association A (ANF unit).*Chronology* - ca 2.05 Ma (range 2.128-1.945 Ma).*Cranial material* - FP1-2004 2708, right hemimandible with c-p2, p4-m3 (of the same individual of FP1-2004 2709); FP1-2004 2709, partial cranium with left I1-I3, P1-M2 and right I1, I3, P1-M2 (of the same individual of FP1-2004 2708).*Occurrence* - Fonelas P-1 Trench A, facies association E (ULIA unit).*Chronology* - ca 2.00 Ma (range 2.128-1.945 Ma).*Cranial material* - FP1-2007 3604, right hemimandible with p1, p3-m2; FP1-2007 3669, right hemimandible with fragmented p2, and p3-m3.*Occurrence* - Fonelas P-1 Trench B, facies association E (ULIA unit).*Chronology* - ca 2.00 Ma (range 2.128-1.945 Ma).*Cranial material* - FP1-2001 434, cranium with left I1-I3, P1-M2 and right P1, M1-M2 (type of *Canis**accitanus* in Garrido & Arribas, 2008); FP1-2007 3001, left hemimandible with p2-m2; FP1-2007 3044, left hemimandible with m1-m2; FP1-2007 3148, cranium with left P4-M2 and right P3-M2.

Morphotype 2

Canis etruscus Forsyth Major, 1877

(Fig. 6; SOM 3)

Occurrence - Trench A, facies association E (ULIA unit).*Chronology* - ca 2.00 Ma (range 2.128-1.945 Ma).*Cranial material* - FP1-2004 2766, left cranial fragment with P3-M2; FP1-2004 2757, left cranial fragment with M2; FP1-2004 2773, right p3; FP1-2004 2815, right C1; FP1-2004 2816, left i2; FP1-2004 2817, right i1; FP1-2004 2818, left i1; FP1-2004 2819, right I2; FP1-2004 2820, left m3; FP1-2004 2634, right C1; FP1-2004 2766, left cranial fragment with P3-M2; FP1-2007 3502, right hemimandible fragment p2, p3, m3; FP1-2007 3514, right cranial fragment.*Occurrence* - Fonelas P-1 Trench B, facies association E (ULIA unit).*Chronology* - ca 2.00 Ma (range 2.128-1.945 Ma).*Cranial material* - FP1-2001 481, cranial fragment with right P4; FP1-2001 849, fragment of cranium with right P4; FP1-2001 E3 68, right hemimandible with i2-m2; FP1-2002 1100, cranium fragment with left I1-M1 and right I1-M2; FP1-2004 2043, cranial fragment with left I3-M2 and right I2-P2; FP1-2007 3064, cranium with left canine and P4 and right P4; FP1-2007 3252, left mandibular fragment with a broken canine, p4-m1 and a broken m2 and right mandibular fragment, which possesses c1-m3.