MIDDLE PLEISTOCENE FOX FROM THE VALLPARADÍS SECTION (VALLÈS-PENEDÈS BASIN, NE IBERIAN PENINSULA) AND THE EARLIEST RECORDS OF THE EXTANT RED FOX

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Abstract. Dentognathic remains of European Middle Pleistocene Vulpini are scarce and fragmentary. They have classically been attributed to several species, but many taxonomic and phylogenetic uncertainties remain. Here we describe a fox well-preserved maxilla with associated mandible from the Middle Pleistocene layers of the Vallparadís Section (EVT3; ca. 0.6 Ma; Vallès-Penedès Basin, NE Iberian Peninsula) and compare them with the known fossil record of *Vulpes* from roughly contemporary European localities. The studied *Vulpes* remains described here differ from Early Pleistocene *Vulpes alopecoides* (including its junior synonyms *V. praeglacialis* and *V. praecorsac*) in several dentognathic features (less individualized P4 protocone; M2 paracone larger than the metacone; more robust mandibular corpus, and stouter m1 with reduced metaconid) and most closely resemble extant *Vulpes vulpes*. The large size of the described remains also contrasts with the small dimensions of *V. alopecoides* and fits better within the variability of the extant red fox. We conclude that the studied specimens, like other available Middle Pleistocene fox remains from Europe, are attributable to the extant species *V. vulpes*. Therefore, the EVT3 remains represent the first well-dated appearance datum of the species in Europe.

INTRODUCTION

The European Plio-Pleistocene fossil record of the genus *Vulpes* is fragmentary and patchy, and available remains mostly come from old collections and are poorly dated. This hinders the reconstruction of their taxonomic affinities and has led to the proliferation of a large number of species names of doubtful taxonomic validity. The following three species were traditionally recognized from Pliocene to Middle Pleistocene sites of Europe (Bartolini Lu-

centi & Madurell-Malapeira 2020): *Vulpes alopecoides* (Del Campana, 1913), *Vulpes praeglacialis* (Kormos, 1932), and *Vulpes praecorsac* Kormos, 1932.

The absence of clear diagnostic features to differentiate these three similar-sized species has led to a confusing taxonomic allocation of several samples from Western Europe. Late Pliocene and earliest Pleistocene remains have often been ascribed to *V. alopecoides*, whereas late Early to Middle Pleistocene fossils have been assigned to either *V. praeglacialis* or *V. praecorsac* on the basis of size (large vs. small, respectively). Bartolini Lucenti & Madurell-Malapeira (2020) recently allocated all Early Pleisto-

cene samples to *V. alopecoides*—thereby synonymizing with the latter multiple species distinguished by previously authors (Bonifay 1971; García et al. 1997; Moigne et al. 2006)—based on their overall similarities compared to the high intraspecific variation typical of extant foxes (Daitch & Guralnick 2007; Szuma 2008a, 2008b, 2008c; Gimranov et al. 2015; Gimranov 2017)

Despite the taxonomic confusion, *V. alopecoides* was generally regarded as the ancestor of the extant red fox, *Vulpes vulpes* (e.g., Rabeder 1976; Bartolini Lucenti & Madurell-Malapeira 2020). The European Middle Pleistocene record of *V. vulpes* is utterly scarce. It is first recorded in the French localities of l'Escale (ca. 0.6 Ma; Bonifay 1971) and Caune de l'Arago (ca. 0.6-0.45 Ma; Moigne et al. 2006). In the Iberian Peninsula, red foxes have been identified from Sima los Huesos (MIS12, ca. 0.45 Ma; García et al. 1997) and Galería (ca. 0.3 Ma; García & Arsuaga 1998) in Atapuerca. In Italy, it appears probably slightly later, at the MIS 12-11 transition (ca. 0.43 Ma; Petronio et al. 2019), in sites such as Malagrotta (Capasso Barbato & Minieri 1987) and Torre in Pietra (Caloi & Palombo 1978). However, the precise chronology of the appearance of *V. vulpes* and its phylogenetic affinities with previous late Early Pleistocene *V. alopecoides* has never been subject to in-depth scrutiny. Here we describe the unpublished fox remains from the early Middle Pleistocene (ca. 0.6 Ma) Vallparadís Section and compare them with roughly coeval *Vulpes* remains from other European sites.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

The described remains were collected from layer EVT3 of the Vallparadís Estació (EVT) site, which is part of the well-dated Vallparadís Composite Section (VCS; Vallès-Penedès Basin, northeastern Iberian Peninsula) together with the fossil site of Cal Guardiola (CGR; Madurell-Malapeira et al. 2010; 2017). The section has a total thickness of 20 m and multiple stratigraphic horizons. Specifically, the EVT site is a 14 m-thick succession composed by alternations of conglomerates and mudstones, divided into two units separated by an erosive angular unconformity (Madurell-Malapeira et al. 2010). All these sediments can be interpreted as the result of an alluvial fan system paired by the influence of close colluvial processes (Madurell-Malapeira et al. 2010; 2017). Magnetostratigraphic and biostratigraphic correlations indicate that the VCS spans from before the Jaramillo paleomagnetic subchron (ca. 1.2-1.1 Ma) to the early Middle Pleistocene (layer EVT3, ca. 0.6 Ma; Madurell-Malapeira et al. 2010, 2014, 2017; Minwer-Barakat et al. 2011).

During the excavations carried out between 1997 and 2008 from CGR and EVT, more than 30,000 vertebrate fossil remains were recovered. Mesowear and microwear analyses performed on a large sample of ungulate dental remains indicate that around 0.9 Ma the environment of VCS shifted from an open dry grassland with clear seasonality (layer EVT12; ca. 1.0 Ma; MIS 31) to more humid and probably even more seasonal woodlands (layer EVT7; ca 0.86 Ma; MIS 21), in agreement with data from other Southern European roughly coeval sites (Strani et al. 2019). Specifically, the analysis of the EVT3 (ca. 0.6 Ma) remains suggests paleoenvironmental conditions characterized by heterogeneous landscapes, possibly including the predominance of open habitats, as further indicated by the relatively high abundance of horse remains. This spread of open grasslands around 0.6 Ma is also attested at Isernia la Pineta (Italy), where herbaceous plants are the most abundant in the pollen record (Strani et al. 2019).

MATERIALS AND METHODS

The described specimen from EVT3 (IPS120168) is housed in the Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain. It is compared on qualitative morphological as well as morphometric grounds with other Early to Middle Pleistocene foxes belonging to the extinct species *V. alopecoides* (sensu Bartolini Lucenti & Madurell-Malapeira 2020; see therein for the morphological and biometrical criteria used in this article) and fossil *V. vulpes* from selected European sites. In particular, the inspected comparative fossil material is housed in the following institutions (see abbreviations below): DST-UNIFI, HNHM, and IGF. We also inspected all the relevant literature on Eurasian fossil *Vulpes* (Odintzov 1965; Rabeder 1976; Qiu & Tedford 1990; Ginsburg 1998; Qiu et al. 2004; Koufos 2014; 2018; Wang et al. 2014). In turn, the extant comparative material includes specimens of *Vulpes corsac*, *Vulpes lagopus*, and *V. vulpes* from the AMNH, HNHM, and MZUF.

Institutional abbreviations: ICP, Institut Català de Paleontologia Miquel Crusafont; DST-UNIFI, Earth Science Department of the University of Florence (Italy); IGF, Geological and Paleontological Section of the Natural History Museum of the University of Florence (Italy); MZUF, La Specola, Zoological Section of the Natural History Museum of the University of Florence (Italy); PP, site abbreviation of the Pirro Nord material housed in the collection of Geological and Paleontological Section of the Natural History Museum of the University of Florence (Italy).

Systematic Paleontology

Order **Carnivora** Bowdich, 1821
Family Canidae Fisher, 1817
Subfamily Caninae Fisher, 1817
Tribe Vulpini Hemprich & Ehrenberg, 1832
Genus *Vulpes* Frisch, 1775

Vulpes vulpes (Linnaeus, 1758)
Figs. 1-3

Referred specimens: IPS120168a: left maxillary fragments with P2, P4-M2; IPS120168b: right M2; IPS120168c: partial left hemimandible with c1, p2, p4-m1; IPS120168d: right c1 and right m1. All these specimens display the same degree of dental wear and comparable biometric dimensions, probably corresponding to the same individual.
Measurements: See Table 1.

Catalog No.	P2		P4		M1		M2	
	L	W	L	W	L	W	L	W
IPS120168a	10.2	3.5	15.9	6.7	10	12.9	6.1	9.4
IPS120168b							6.0	9.2

Catalog No.	c1		p2		p4		m1		Hp3	Hm1
	L	W	L	W	L	W	L	W		
IPS120168c	7.0	4.8	8.6	3.1	10.6	4.2	17.2	6.8	13.0	15.3
IPS120168d	7.2	4.9					17.3	6.6		

Tab.1 - Dentognathic measurements of the *Vulpes vulpes* specimen from Vallparadís Section layer EVT3. L, mesiodistal length; W, buccolingual width; Hp3, corpus height at the p3 level in buccal view; Hm1, corpus height at the m1 level in buccal view.

Description of Vallparadís material

Upper teeth. The P2 is narrow, with a moderately high protocone and a distal portion wider than the mesial. On the distal side of the protocone, a small accessory cusp is visible. The P4 is rather buccolingually wide relative to length, with a moderately developed protocone, a high and pointed paracone, and a moderately mesiodistally elongated metastyle. The protocone is more mesially located than the mesial crown margin. There is no mesiobuccal cingulum but a parastyle is present. The distolingual cingulum is prominent, especially distally. The M1 buccal portion is mesiodistally larger than the lingual one. There is a prominent shelf-like buccal cingulum that extends from the mesial wall of the paracone to the distal wall of the metacone. The two buccal cusps are similar in size, with the paracone only slightly higher than the metacone. On the mesiobuccal corner of the M1, there is a marked parastyle. The protocone is well developed and high, the protoconule is faint, and the metaconule is prominent but lower than the protocone. The hypocone is separated from the lingual cingulum by a marked furrow. The trigon basin is round and wide, and as deep as the talon basin, which is undulated but not compressed. The M2 has a buccolingually elongated occlusal contour. The paracone is larger than the metacone. The protocone is well developed and distally the metaconule is evident (Fig. 1A-H).

Mandible. The corpus is deep and stout, becoming mediolaterally thicker ventrally. There are two mental foramina: a larger one below the p2, and a smaller below the p3 that emerges more dorsally than the former (Fig. 1I, J, K). There is no m3 alveolus.

Lower teeth. The p2 is buccolingually compressed, with a distal portion more inflated than the mesial one. It lacks distal accessory cuspulids and distal cingulid. The p4 has a high, sharp and pointed protoconid; distal to the protoconid there is a prominent and large cuspulid, as well as a marked distal cingulid. The m1 is buccolingually stout and high, especially at level of the trigonid. The paraconid is short whereas the protoconid is stout and large. The metaconid is large and distinct from the protoconid but quite short. The hypoconid is large and high, smaller than the entoconid. The talonid basin is round and wide, partially closed lingually by an accessory cuspulid –the entoconulid– which is located distal to the metaconid rather than closer to the entoconid. Distally, there is a prominent cingulid (Fig. 1I-P).

Comparisons

IPS120168 possesses several features that differ from *V. alopecoides* (sensu Bartolini Lucenti & Madurell-Malapeira 2020; see Figs 2-3). For instance, in the upper teeth, the P4 protocone of *V. alopecoides* is more individualized from the paracone compared to that of IPS120168. The M1 of *V. alopecoides* has a proportionally smaller protocone and a generally larger metaconule, compared to that of IPS120168. The M2 of *V. alopecoides* is shorter mesiodistally, whereas it is longer in IPS120168 and *V. vulpes*. In the latter, the M2 paracone is conspicuously larger than the metacone and the protocone is broader compared to that of *V. alopecoides*. The mandibular corpus of *V. alopecoides* is slender and thin compared to that of IPS120168 and *V. vulpes*, particularly in its ventral part. On the buccal side of
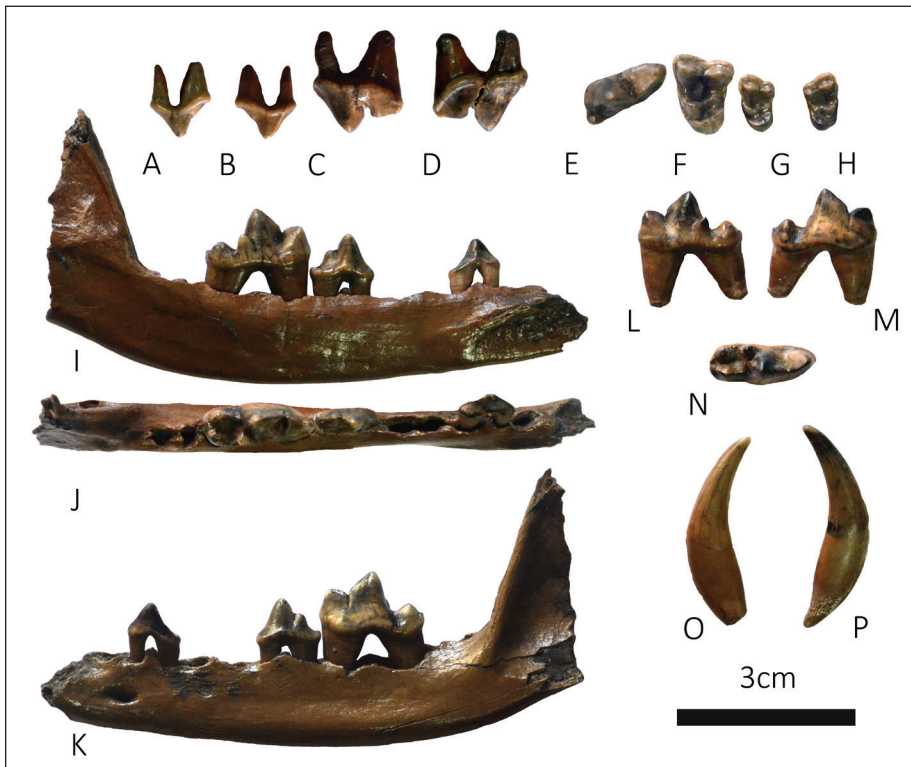
Fig. 1 - Dentognathic remains of *Vulpes vulpes* from Vallparadís Estació layer EVT3 – IPS120168a, left P2 and P4-M2: P2 in buccal (A) and lingual (B) views; P4 in buccal (C), lingual (D), and occlusal (E) views; M1 (F) and M2 (G) in occlusal views. IPS120168b, right M2 in occlusal view (H). IPS120168c, left hemimandible with c1, p2, and p4-m1 in lingual (I), occlusal (J), and buccal (K) views. IPS120168d, right c1 and m1: m1 in lingual (L), buccal (M), and occlusal (N) views; c1 in lingual (O) and buccal (P) views.

the mandible, the mental foramina emerge on the same line in *V. alopecoides* whereas in IPS120168, like in *V. vulpes*, the posterior mental foramen is not aligned with the anterior one. The m1 is buccolingually stouter (i.e., wider relative to length) in IPS120168, like in *V. vulpes*, and possesses a small metaconid, as opposed to *V. alopecoides*.

Biometrical comparisons. Despite the restricted sample available from EVT3, some relevant comparisons are feasible relative to both extant *V. vulpes* and extinct *V. alopecoides* from Europe (Fig. 4). For all dental measurements analyzed, *Vulpes* from EVT3 falls outside the variation of both species by being larger, particularly for m1 length and specially as compared with *V. alopecoides* (Fig. 4B, C). Nevertheless, this larger overall size do no contradict with the morphological similarities found above, and support the attribution of the EVT sample to *V. vulpes*.

Discussion

The earliest record of *V. vulpes* is from the French site of L'Escale, dated to ca. 0.6 Ma (Palombo & Valli 2003). Bonifay (1971) first described the fox from L'Escale and assigned the material to three different taxa *V. praeglacialis*, *V. vulpes jansoni*, and *V. vulpes*. The author described at least 12 individuals from the 'couche H' and two hemimandibles from the 'niveau B' including both layers in the Late Mindel (Bonifay 1971). Brugal et al. (2020) placed l'Escale in the interval MIS 19-16 (ca. 790-676 ka).

According to Bonifay's (1971) descriptions, specimens of *V. v. jansoni* would be characterized by a P4 protoconid more individualized than in the extant red fox; M1 with sharp paracone and metacone, strong lingual cingulum, and distinct metaconule and hypocone; and M2 with a larger hypocone than in *V. vulpes*. Nevertheless, Bonifay (1971) concluded that the main difference between *V. v. jansoni* from l'Escale and the extant red fox is the development of the P4 protocone. Nevertheless, the position, inclination, and size of the P4 protocone is variable in extant populations of *V. vulpes* (Bartolini Lucenti & Madurell-Malapeira 2020). Bonifay (1971) further described the mandible and lower premolars of *V. v. jansoni* as similar to those of the extant red fox and the m1 with an individualized metaconid and a bicuspid talonid. To sum up, based on Bonifay's (1971) descriptions, we do not find any taxonomically relevant difference between the L'Escale specimens, the red fox, and the studied specimens from EVT3, in agreement with García (2003).

Concerning the *V. praeglacialis* specimens from the couche H of L'Escale, Bonifay (1971) described them as possessing an individualized and high P4 protocone; a reduced M1 metaconule (similar to

Fig. 2 - Upper fourth premolar and molars of fossil *Vulpes* from selected European localities and extant *Vulpes vulpes* in occlusal view (original photos made by the authors). A-C) Upper teeth of *Vulpes alopecoides*: A - IGF12110 (holotype), right M1-M2 from the Early Pleistocene of Il Tasso (Italy); B - IPS36793, left (reversed) P4-M2 from the Early Pleistocene of Villarroya (Spain); C - PP789, left (reversed) P4-M2 from the Early Pleistocene of Pirro Nord (Italy). D-F) Upper teeth of *V. vulpes*: D - IPS120168a, left (reversed) P4-M2 from the Middle Pleistocene of Vallparadís Estació layer EVT3 (Spain); E - MZUF-12426, right P4-M2 (extant); F - MZUF-3632, right P4-M2 (extant).
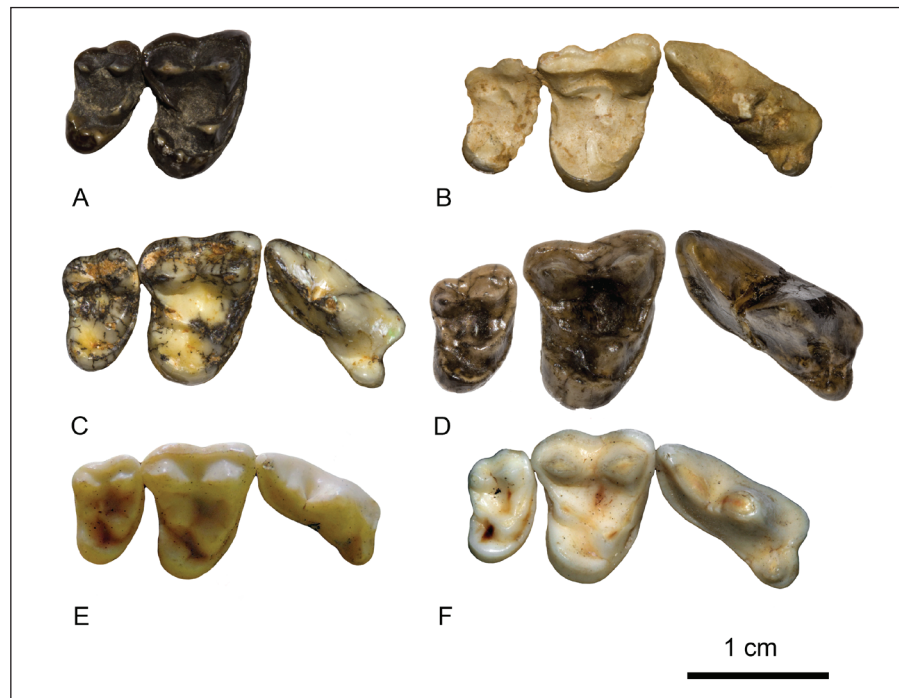

Fig. 3 - Lower fourth premolar and first molar of fossil *Vulpes* from selected European localities and extant *Vulpes vulpes* in occlusal view. A-D) Lower teeth of *V. alopecoides*: A - IPS27259, right (reversed) p4-m1 from the Early Pleistocene of La Puebla de Valverde (Spain); B - PN28, left p4-m1 from the Early Pleistocene of Pirro Nord (Italy); C - APL-11, right (reversed) p4-m1 from the Early Pleistocene of Apollonia-1 (Greece); D - IPS14748, right (reversed) m1 from the Early Pleistocene of Cal Guardiola (Spain). E-H) Lower teeth of *V. vulpes*: E - IPS120168d, right (reversed) m1 from the Middle Pleistocene of Vallparadís Estació layer EVT3; F - IPS120168c, left p4-m1 from the Middle Pleistocene of Vallparadís Estació layer EVT3; G - MZUF-4363, right (reversed) p4-m1 (extant); H - MZUF-6445, left p4-m1 (extant).
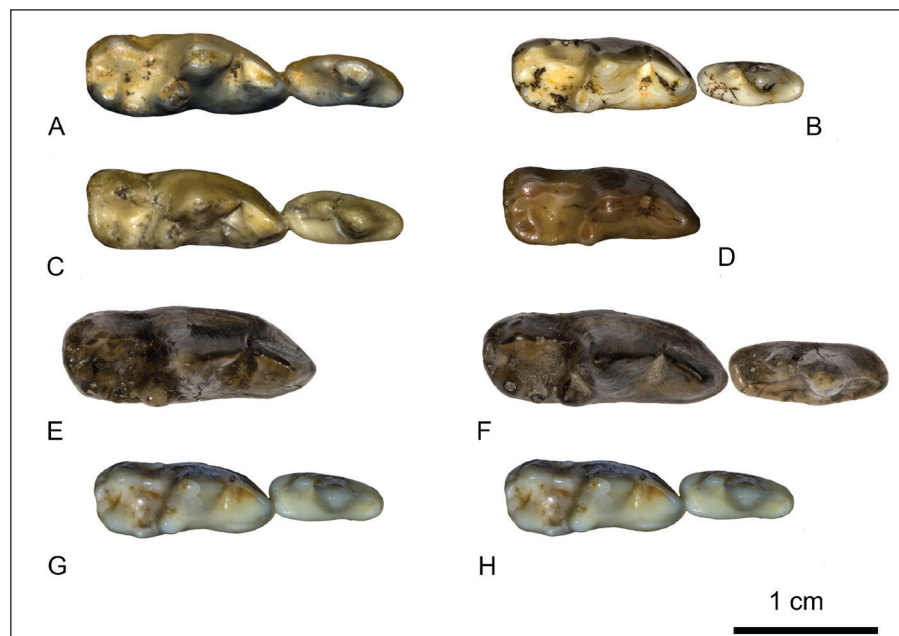
that of *Vulpes lagopus*); an M2 buccolingually wide; sharp lower premolars; and m1 with protoconid and paraconid forming a sharp angle (as in *V. lagopus*), a bicuspid talonid with a hypoconid clearly larger than the entoconid, and a visible metastylid. Bonifay (1971) did not figure the upper dentition, but in her drawings of the lower dentition (Bonifay 1971: fig. 23) the position of the cuspids of the trigonid and talonid as well as the development of the transverse cristid are similar to the morphology observed in the EVT3 specimen and in the extant red fox. Therefore, the material attributed to *V. praeglacialis* by Bonifay (1971) seems indistinguishable from extant *V. vulpes* and also similar the EVT3 remains—although more detailed comparisons of the upper teeth would be required to confirm this statement.
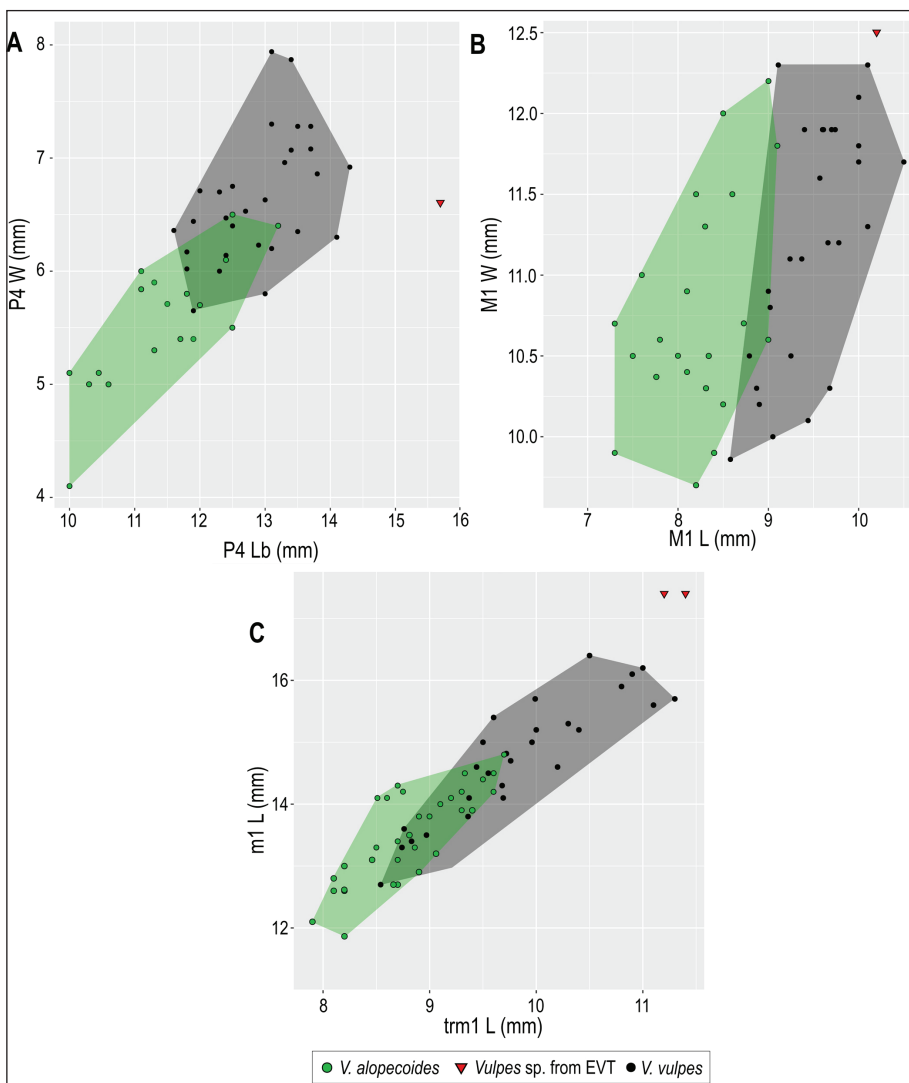
Fig. 4 - Bivariate scatterplots showing the dental variation of *Vulpes* remains from EVT3 compared with extinct *Vulpes alopecoides* (sensu Bartolini Lucenti & Madurell-Malapeira, 2020) and both extant and fossil *Vulpes vulpes*: A) P4 width (P4 W) vs. buccal length (P4 Lb); B) M1 width (M1 W) vs. length (M1 L); C) m1 length (m1 L) vs. m1 trigonid length (m1 trL).

Cregut (1979) first described the fox remains from the Middle Pleistocene French site of Caune de l'Arago (ca. 0.6-0.5 Ma) and assigned them to *Vulpes* cf. *praeglacialis* and *Vulpes* sp. However, a more recent work reassigned the material to *V. vulpes* and *V.* aff. *praeglacialis* (Moigne et al. 2006). The remains originally ascribed by Cregut (1979) to *V.* cf. *praeglacialis* basically consist of two m1, which according to the author are smaller than a single m2 assigned to *Vulpes* sp. (Cregut, 1979). Unfortunately, the later author did not provide detailed morphological comparisons or good pictures enabling the comparison of the studied material with the Arago collection.

In the Iberian Peninsula, the earliest records of *V. vulpes* are reported from the Middle Pleistocene sites of Trinchera Galería (ca. 0.3 Ma; García & Arsuaga 1998) and Sima de los Huesos (MIS 12; ca. 0.45 Ma; García et al. 1997), in the Atapuerca site complex. Although the Atapuerca fox remains have not been described in detail, those from Galería were metrically compared with living and fossil foxes by García (2003), who noted close similarities with the extant species. The only available figures (García 2003: figs. III.3.26-27) do show similarities with both the extant red fox and EVT3 specimens (e.g., robust mandibular corpus and individualized m1 metaconid, developed cristid between entoconid and hypoconid), although the absence of pictures in occlusal view prevents more detailed comparisons.

The Italian Middle Pleistocene record of foxes is utterly scarce and fragmentary, with *V. vulpes* being recorded in some localities (e.g., Malagrotta, Torre in Pietra) referred to the Fontana Ranuccio and Torre in Pietra Faunal Units (MIS 11-9; ca. 0.43-0.33 Ma; Caloi & Palombo 1978; Capasso Barbato & Minieri 1987; Petronio et al. 2019). However, these reports are based on isolated postcranial elements, precluding comparisons with the EVT3 sample.

A single dental specimen of *V. vulpes* was described from the Middle Pleistocene layers of Westbury-Sub-Mendip (England; Bishop 1982). It is a m1 (M.33658) from Bed 5 (Bishop 1982: fig. 29), which resembles the EVT3 remains and the extant red fox in the small and individualized metaconid, the developed entoconid, and a visible transverse cristid connecting the talonid cuspids.

A maxillary fragment (Schö 13 II-4, 721) of *V. vulpes* from the Spear Horizon of Schöningen (Germany) described by van Kolfschoten (2003: fig. 1) only preserves a damaged P4, in which only a well-developed and individualized protocone is visible, thereby precluding detailed comparisons with either the EVT3 specimens or extant red foxes.

Baryshnikov (2012) revised the diverse assemblages of two cave sites in the Caucasus, namely Kudaro 1 (360 ± 90 ka) and Kudaro 3 (less than 250± 50 ka), in which *V. vulpes* remains were reported. The material from Vallparadís does not differ significantly from those of *V. vulpes* from Kudaro caves. For instance, the P4 (IPS120168a) closely resembles ZIN 36492 from Kudaro Cave 3 (Baryshnikov 2012) in the development of the protocone, metastyle, and lingual cingulum (which also partially encircles the protocone), while the M1 (IPS120168c,d) resembles the morphology of ZIN 36488 and ZIN 36492 from Kudaro 1 and 3, respectively (Baryshnikov 2012). Similarly, no substantial differences can be found between the EVT3 m1 and those from Kudaro, either in the development of cuspids and cuspulids or in the distinct but small accessory cuspulid between the entoconid and metaconid (Baryshnikov 2012).

In contrast, it is difficult to compare the EVT3 material with the holotype of *Vulpes angustidens* from Hundsheim (Thenius 1954) because no m2 is available in our sample. Nevertheless, the m1 talonid from Hundsheim resembles those from EVT3 in the small size of the entoconid and the well-developed entoconulid. This species has also been reported from the Czech Epivillafranchian site of Stránská Skála I, alongside *V. "praeglacialis"* (= *V. alopecoides*)—the distinction between the two species being apparently based on the size of the teeth (Musil 1972). The specimens assigned to both species resemble those from EVT3 in the well-developed buccal cingulum of the M1, the sharp and high protoconid and distal accessory cuspulid of the p4, and the development of the m1 entoconid,

but differ in the presence of a more developed and mesiolingually projected P4 protocone and an enlarged m1 metaconid. The m1 entoconulid on the EVT3 specimens is also evident in some but not all of the specimens of *V. "praeglacialis"* and *V. angustidens* from Stránká Skála I (Musil 1972). The sample from the Czech site is more consistent with a single attribution to *V. alopecoides* (sensu Bartolini Lucenti & Madurell-Malapeira 2020).

Conclusions

Bartolini Lucenti & Madurell-Malapeira (2020) revised the European Early Pleistocene record of foxes and concluded that a single species, *V. alopecoides*, is recorded in Europe throughout this time span. They further argued that this species is the possible ancestor of extant *V. vulpes*. The scanty and fragmentary nature of the European Middle Pleistocene record of foxes, coupled with chronological uncertainties for fossils from several sites, seriously hinders testing further the aforementioned phylogenetic link between the two species, and even makes it difficult to determine the time and location of the earliest records of *V. vulpes* in Europe.

The *Vulpes* remains from EVT3 described herein (IPS120168) differ from the characteristic morphology of *V. alopecoides* (sensu Bartolini Lucenti & Madurell-Malapeira 2020) in the following dentognathic features: (i) P4 protocone less separated from the paracone; (ii) M1 with proportionally larger protocone and lingual cingulum bearing the hypocone; (iii) mesiodistally broader M2, compared to the slender morphology of *V. alopecoides*; (iv) M2 paracone conspicuously larger than the metacone; (v) robust mandibular corpus, particularly inferiorly; (vi) distal mental foramen not aligned with the mesial one; (vii) buccolingually stouter m1 with small metaconid (Figs 2-3). On the contrary, the described specimens from EVT3 only display slightly larger dental dimensions than extant *V. vulpes*, which they most closely resemble in the following features (Bartolini Lucenti & Madurell-Malapeira 2020): (i) marked and continuous P4 lingual cingulum; (ii) M1 buccolingually broader relative to mesiodistal length; (iii) M1 paracone and metacone of similar size and (iv) robust mandibular corpus. Additionally, the studied specimens display a stout m1 metaconid that is individualized from the protoconid, as

in *V. alopecoides* and extant *V. vulpes*, and larger than in *V. lagopus*; and a developed m1 entoconid transverse cristid connected with the talonid cuspids, as in *V. vulpes* and *V. alopecoides* (Bartolini Lucenti & Madurell-Malapeira 2020).

To sum up, the EVT3 remains described in this paper most closely resemble those of extant *V. vulpes*, merely being slightly larger, but can be distinguished from *V. alopecoides* on the basis of dental morphology. We therefore conclude that the EVT3 sample, dated to 0.6 Ma, represents one of the earliest records of *V. vulpes* in Western Europe, pending a more thorough revision of the roughly coeval sample from the French site of L'Escale.

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