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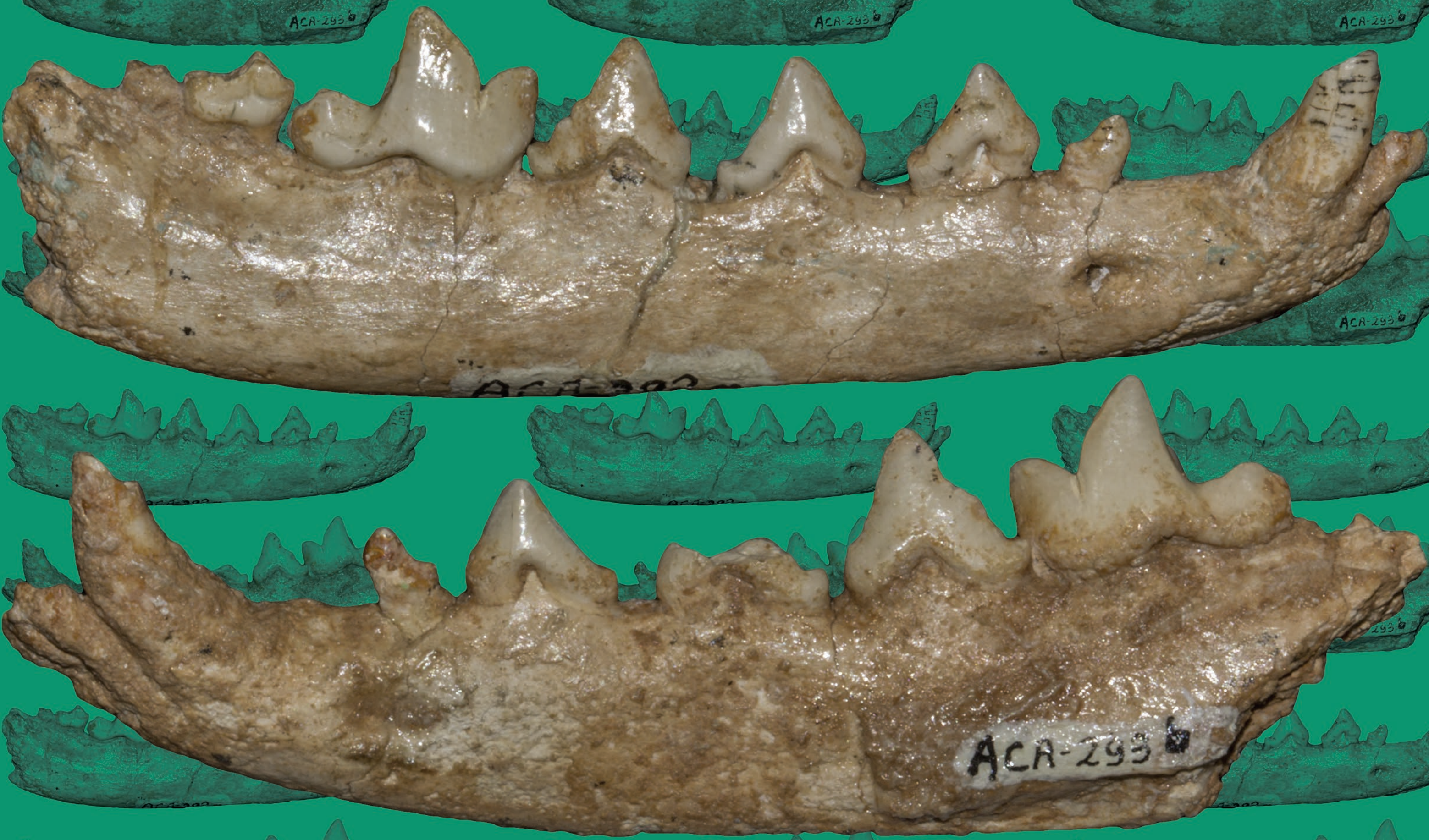
2021 • 20 • 29

Ancestral foxes at the gates of Europe: the Pliocene fox from Çalta-1 (Turkey) and their relationships with Asian and European Plio-Pleistocene foxes

Saverio BARTOLINI-LUCENTI & Joan MADURELL-MALAPEIRA



art. 20 (29) — Published on 13 July 2021
www.cr-palevol.fr

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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / *print*): 1631-0683/ ISSN (électronique / *electronic*): 1777-571X

Ancestral foxes at the gates of Europe: the Pliocene fox from Çalta-1 (Turkey) and their relationships with Asian and European Plio-Pleistocene foxes

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Submitted on 2 May 2020 | Accepted on 14 June 2020 | Published on 13 July 2021

urn:lsid:zoobank.org:pub:1ACE41D1-37C8-4110-ABDA-AD5F57DB74B8

Bartolini-Lucenti S. & Madurell-Malapeira J. 2021. — Ancestral foxes at the gates of Europe: the Pliocene fox from Çalta-1 (Turkey) and their relationships with Asian and European Plio-Pleistocene foxes. *Comptes Rendus Palevol* 20 (29): 619-626. https://doi.org/10.5852/cr-palevol2021v20a29

ABSTRACT
The Pliocene record of genus *Vulpes* Frisch, 1775 in Eurasia is scarce, coming from few sparse localities. The lack of a comprehensive and integrated revision led to the description of numerous different taxa, often only tentatively related to extant species but not with one another. Çalta-1 is an important Pliocene site located in the Anatolian region of Turkey, dated to 4.0 Ma. In the present review, we reappraise the interesting record of *Vulpes galatica* Ginsburg, 1998. Morphological and morphometric evidence suggests a strong similarity between this taxon and the early Late Pliocene *V. beihaiensis* Qiu & Tedford, 1990, recovered from the Chinese Yushe Basin. Such evidence favors the parsimonious interpretation of synonymy between the two species, under the name *V. beihaiensis*. This hypothesis opens a new interpretation on the biogeography of the Pliocene-Early Pleistocene foxes of Eurasia. *Vulpes beihaiensis* links the Asian and European records, with its affinity to *V. alopecoides* (Del Campana, 1913) and, eventually, to the extant red fox (*Vulpes vulpes* (Linnaeus, 1758)).

KEY WORDS
Carnivora,
Vulpes,
Pliocene,
Eurasia,
biogeography.

RÉSUMÉ
Anciens renards aux portes de l'Europe : le renard pliocène de Calta-1 (Turquie) et ses relations avec les renards européens et asiatiques du Plio-Pléistocène.
Le signalement pliocène du genre *Vulpes* Frisch, 1775 en Eurasie est peu abondant, du fait de quelques localités éparses. L'absence d'une révision intégrée et exhaustive a conduit à la description de nombre de taxons souvent reliés, à titre d'essai, à des espèces actuelles, mais non l'un à l'autre. Calta-1 est un important site pliocène localisé dans la région anatolienne de Turquie, daté de 4 Ma. Dans cet article, nous réexaminons l'intéressant signalement de *Vulpes galatica* Ginsburg, 1998. Des preuves morphologiques et morphométriques suggèrent une importante similitude entre ce taxon et *V. beihaiensis* Qiu & Tedford, 1990 du début du Pliocène supérieur, récolté dans le bassin d'Yushe, en Chine. De telles preuves plaident en faveur de l'interprétation parcimonieuse d'une synonymie entre les deux espèces, sous le nom de *V. beihaiensis*. Cette hypothèse permet une nouvelle interprétation des renards d'Eurasie au Plio-Pléistocène-Pléistocène inférieur. *Vulpes beihaiensis* relie les registres européens et asiatiques, avec son affinité à *V. alopecoides* (Del Campana, 1913) et, éventuellement, au renard rouge actuel (*Vulpes vulpes* (Linnaeus, 1758)).

MOTS CLÉS
Carnivora,
Vulpes,
Pliocène,
Eurasie,
biogéographie.

INTRODUCTION

Fossil record of the genus *Vulpes* Frisch, 1775 is often fragmentary and scattered, making it difficult to reconstruct phylogenetic affinities among them, which often leads to the proliferation of numerous specific names with problematic taxonomy. The European Plio-Pleistocene record was historically characterized by the existence of three taxa: *Vulpes alopecoides* (Del Campana, 1913), *Vulpes praeglacialis* (Kormos, 1932) and *V. praecorsac* Kormos, 1932. Additionally, Spassov (2000) ascribed to *Vulpes* sp. a single right P4 from the Pliocene site of Musselievo (Bulgaria, MN15; Fig. 1). The first is a typical form of the Late Pliocene-Early Pleistocene, whereas the latter two species are described from the Early Pleistocene, although the sample from Odessa Catacombs (Ukraine, MN15, Early Pliocene; Fig. 1) was referred to *V. praecorsac* (Odintzov 1965). The virtual absence of clear diagnostic features between these three similar-sized species has led to confused taxonomy of samples from Western European localities. Generally, older samples were ascribed to *V. alopecoides,* whereas younger large-sized remains were attributed to *V. praeglacialis* and small-sized ones to *V. praecorsac*. Recently, Bartolini-Lucenti & Madurell-Malapeira (2020) proposed to synonymize the Early Pleistocene samples under the specific name of *V. alopecoides*, based on the low interspecific variance of the fossil compared to the elevated degree of intraspecific variability typical of extant foxes [*Vulpes corsac* (Linnaeus, 1768), Gimranov *et al.* 2015; Gimranov 2017; *Vulpes lagopus* (Linnaeus, 1758), Daitch & Guralnick 2007; Szuma 2008a; *Vulpes vulpes* (Linnaeus, 1758), Szuma 2008b, 2008c]. This with the notable exception of *V.* "*praecorsac*" from Odessa, whose features contrast significantly with the morphologies of *V. alopecoides*, therefore the former taxon could not be included in alopecoid fox (Bartolini-Lucenti & Madurell-Malapeira 2020).

The Plio-Pleistocene Asian record includes four species: the small-sized Early Pliocene *Vulpes beihaiensis* Qiu & Tedford, 1990 from Yushe Basin sites (*c.* 3.3-3.0 Ma; Fig. 1); *Vulpes chikushanensis* Young, 1930 from several Early-Middle Pleistocene Asian localities, e.g. Longdan (Qiu *et al.* 2004); *Vulpes galatica* Ginsburg, 1998 from the Early Pliocene site of Çalta-1 (*c.* 4.0 Ma; Turkey; Fig. 1); and the hypercarnivorous and large-sized *Vulpes qiuzhudingi* Wang, Tseng, Li, Takeuchi & Xie, 2014 from the Himalayan-Tibetan Plateau (China, *c.* 5.1-3.6 Ma, Wang *et al.* 2014; Fig. 1). The relationships between these extinct species are currently unclear, although some hypotheses have been made. Qiu *et al.* (2004) suggested a link between the Odessa sample and *V. chikushanensis*. The Chinese *V. beihaiensis* is considered the closest relative of *V. corsac* (Qiu & Tedford 1990), whereas *V. qiuzhudingi* might be the ancestor of *V. lagopus* (Wang *et al.* 2014). Ginsburg (1998) described *V. galatica* (note that "galaticus" violates the International Code on Zoological Nomenclature, 1999, as reported in Bartolini-Lucenti & Madurell-Malapeira 2020) as a highly carnivorous species, the earliest member of the genus *Vulpes* and the ancestor of modern *V. vulpes* and *V. lagopus*. According to this view, *V. alopecoides* would represent the intermediate, both ecologically and phylogenetically, between *V. galatica* and *V. vulpes* (Ginsburg 1998). In the Ginsburg original publication (Ginsburg 1998), *V. alopecoides* was the only fossil species considered as a comparison.

Here, we restudy the material of *V. galatica* from Çalta-1 in the light of the diversity of Plio-Pleistocene *Vulpes*. The position of this site, both in time and space (see the following section), and the systematic position of this taxon might offer crucial insights on the evolution of *Vulpes* species in the Pliocene and Early Pleistocene times, as the first well-chronologically constrained record of *Vulpes* in Eurasia.

GEOLOGICAL AND PALEONTOLOGICAL SETTINGS

Çalta-1 is an important Early Pliocene site located in Central Anatolia, northwest of Ankara (Turkey; Fig. 1), in the Kazan Basin (Lunkka *et al.* 1998). The rich record of verte-

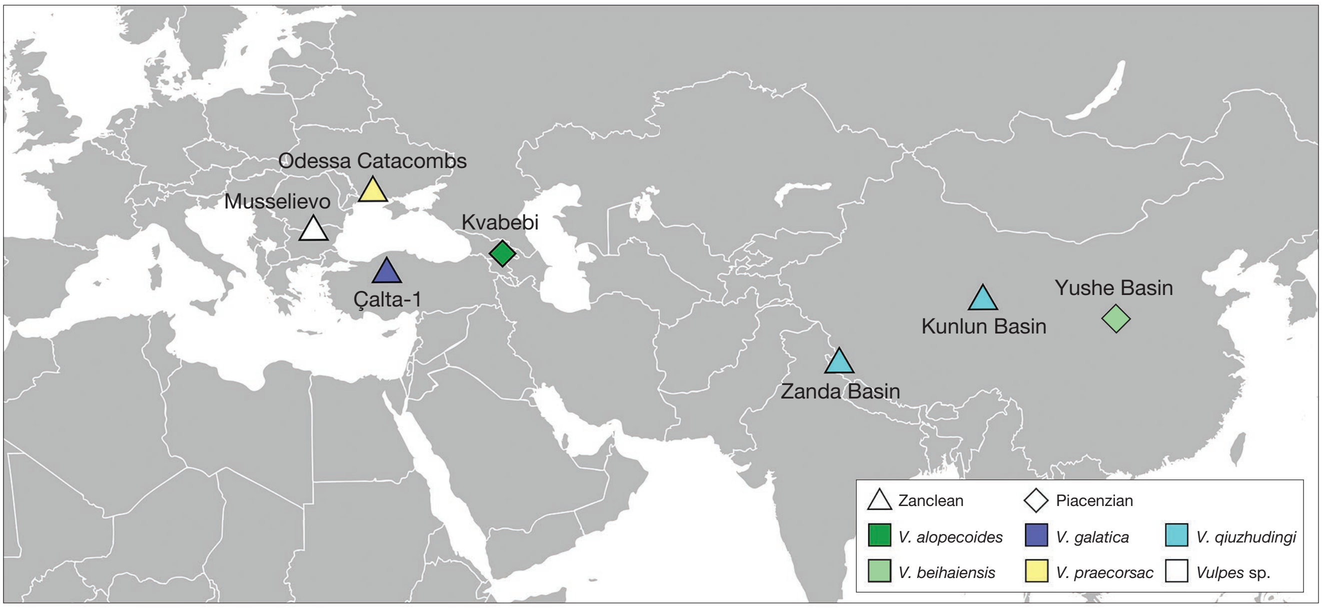

FIG. 1. — Geographic localization of the Pliocene localities with *Vulpes* Frisch, 1775 record.

brates recovered from this site was described in an extensive monography published in *Geodiversitas* (Sen 1998). The fossil-bearing succession of Çalta-1 is located in the Çalta member, the youngest of the Sinap Formation (Lunkka *et al.* 1998, 2003). A second site, named Çalta-2, is related to the upper part of the Kavakdere member (underlying Çalta member in the scheme of Lunkka *et al.* 1998; Sen & Saraç 2018). The Sinap Formation is characterized by fluviolacustrine deposits mainly characterized by the alternance of conglomerates, sandstone and mudstone of alluvial system. The Çalta member, at the top of the succession, is composed of floodplain deposits, represented by massive mudstones, channeled by thin conglomerates and sandstones. Upper portion of these massive mudstones contained the fossil specimens (Lunkka *et al.* 1998). Along with a rich associated fauna (Sen 1998), five carnivoran taxa were reported by Ginsburg (1998) from this site: the hyenid *Chasmaporthetes kani anatolicus* Ginsburg, 1998; the felids *Machairodus giganteus* (Wagner, 1848) (synonym of *Amphimachairodus giganteus* following Beaumont, 1978) and *Lynx issiodorensis* (Croitzer & Jobert, 1828); and the canids *Nyctereutes donnezani* (Depéret, 1890) and *V. galatica*. Chronologically the site is related to the late Ruscinian (MN15), *c.* 4 Ma (Sen 1998; Bernor & Sen 2017).

MATERIAL AND METHODS

This study is based on the comparative morphological and morphometric analyses of *Vulpes galatica* from Çalta-1 (Turkey) in comparison to other Pliocene to Early Pleistocene species of Eurasia. The studied fossils come from the collections of the MNHN (see abbreviations below). As comparative fossil material, we studied the collections of several European and Chinese localities (AMNH, DST-UNIFI, HNHM, IGF, MG-GNM, MHNL, MNHN, UCBL) and inspected all the relevant literature on Eurasian fossil *Vulpes* (Odintzov 1965; Qiu & Tedford 1990; Qiu *et al.* 2004; Wang *et al.* 2014; Bartolini-Lucenti 2021). Fossil species considered as comparison include *V. alopecoides* (*sensu* Bartolini-Lucenti & Madurell-Malapeira 2020) from selected site of Europe (i.e., the Pliocene record of Kvabebi, Georgia; and the Early Pleistocene one of Pirro Nord, Italy); *V. beihaiensis* from Zhaozhuang and Zhangwagou (Yushe Basin, China; Qiu & Tedford 1990); *V. qiuzhudingi* from the Himalayan-Tibetan Plateau (Zanda and Kunlun Pass Basins, China, Wang *et al.* 2014); *V.* "*praecorsac*" from Odessa Catacombs (Ukraine; Odintzov 1965); *Vulpes* sp. from Musselievo (Bulgaria; Spassov 2000). Extant specimens of *V. corsac*, *V. lagopus* and *V. vulpes* from the AMNH, HNHM, and MZUF were used for morphological and morphometrical comparisons. Log ratio diagrams (Simpson 1941; Simpson *et al.* 1960) on selected cranial and dental variables were used to assess the degree of similarity or difference between *Vulpes* from Çalta-1 other fossil and extant species.

ABBREVIATIONS

Institutions

AMNH	American Museum of Natural History, New York;
DST-UNIFI	Earth Science Department of the University of Florence, Florence;
HNHM	Hungarian Natural History Museum, Budapest;
IGF	Geological and Paleontological Section of the Natural History Museum of the University of Florence, Florence;
MG-GNM	S. Janashia Museum of Georgia, Georgian National Museum, Tbilisi;
MGPT-PU	Geology and Paleontology Museum of the University of Turin, Turin;
MZUF	La Specola, Zoological Section of the Natural History Museum of the University of Florence, Florence;
UCBL	Université Claude-Bernard Lyon-1, Lyon.

Table 1. — Measurements of the *Vulpes beihaiensis* Qiu & Tedford, 1990 from Çalta (Turkey). Abbreviations: **H**, height; **L**, greatest mesiodistal length in case of teeth and rostrocaudal one in case of the astragalus; **Mm1H**, mandibular height distal to the m1; **Mm1W**, mandibular width at level of the m1; **Mp4H**, mandibular height distal to the p4; **W**, buccolingual width.

Specimens		**L**	**W**	**H**
MNHN.F.ACA-293	c	5.2	3.7	–
	p1	3.2	1.9	–
	p2	6.5	2.4	–
	p3	7.5	2.7	–
	p4	8.3	3.3	–
	m1	11.9	4.8	–
	trm1	7.9	–	–
	tdm1	–	4.5	–
	m2	5.5	4.3	–
	m3	3.1	2.7	–
	Mp4H	–	–	11.0
	Mm1H	–	–	11.6
	Mm1W	–	5.6	–
MNHN.F.ACA-357	P4	14.3	6.0	–
MNHN.F.ACA-302	astragalus	22.9	–	–

Anatomy

c	lower canine;
M	upper molar;
m	lower molar;
P	upper molar;
p	lower molar.

Measurements

L	length;
H	height;
W	width.

SYSTEMATIC PALAEONTOLOGY

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

Vulpes beihaiensis Qiu & Tedford, 1990
(Fig. 2)

Vulpes beihaiensis Qiu & Tedford, 1990: 28.

Vulpes galaticus Ginsburg, 1998: 380-382, figs 1-2. — Sen & Saraç 2018: 536.

Vulpes galatica – Bartolini-Lucenti & Madurell-Malapeira 2020: 2.

Holotype. — AMNH F:AM 97062, cranium laterally compressed in Qiu & Tedford (1990).

Type locality. — Zhanwagou (Yushe Basin, Shanxi, China).

Chronostratigraphic distribution. — Early Pliocene (*c.* 4.0-3.0 Ma)

Geographic distribution. — Asian continent, from Central China to Turkey.

Referred material. — MNHN.F.ACA-357, left P4 (L: 14.3 mm; W: 6.0 mm); MNHN.F.ACA-293, mandibular corpora with left i1-m1 (MNHN.F.ACA-293b) and right i3-m3 (MNHN.F.ACA-293a); MNHN.F.ACA-302, right astragalus.

Measurements. — See Table 1.

Description

Upper teeth

The P4 is rather stout, with a large protocone a high paracone and modestly elongated metastyle, slightly shorter mesiodistally compared to the paracone. The protocone is advanced compared to the mesial margin of the P4. A cingulum bounds the lingual side of the tooth and another one is evident on the mesially, reaching the buccal margin of the paracone, at level of the feeble parastyle. The cingulum is prominent around the protocone.

Mandible

The mandible corpus is shallow with a scaphoid ventral margin. The mesial mental foramen is located under the p1 and a smaller one under p3 in MNHN.F.ACA-293a whereas MNHN.F.ACA-293b apparently has only the mesial one. The right mandible is broken distal to the m3 whereas the left one at level of the distal root of m1.

Lower teeth

Incisors are reduced, flattened teeth. The canine is buccolingually compressed but rather stout. The diastema between c1 and p1 is considerably wide. Premolars have upright protoconids and enlarged distal portions compared to the mesial ones, in lateral and occlusal views. The p1 is monocuspid with a distal cingulid. The p2 does not have distal accessory cuspulids. The p3 and p4 display high, sharp and pointed protoconids. On the distal side of the p3 protoconid, a feeble accessory cuspulid is visible. Distally, a cingulid arises from the margin of the tooth. The p4 possesses a mesial shelf-like morphology with an accessory cuspulid. Distal to the protocone MNHN.F.ACA-293a has two cuspulids, whereas in MNHN.F.ACA-293b there is a single larger one. The distal cingulid is fairly marked. The m1 paraconid is considerably lower than the p4 protoconid. The m1 protoconid is high, sharp and stout, in buccal view. The metaconid is relatively reduced and attached to the protoconid. Although smaller than the hypoconid, the entoconid is not so reduced. Talonid basin is round and rather wide, partially closed lingually by an accessory cuspulid, mesial to the entoconid, and distally by a prominent cingulid. The later continues on the buccal side, reaching the level of the hypoflexid. The m2 is rectangular in occlusal view. The protoconid and the metaconid are similar in size. On the talonid the hypoconid is large but the entoconid is not reduced. The buccal cingulid is prominently and enlarged till the distal side of the tooth. The m3 is oval-shaped, with two equal-sized cuspulids and a cingulid bounding the distal margin.

DISCUSSION

In the original description by Ginsburg (1998), a P3 and M2 were included in the sample. Nevertheless, their morphology

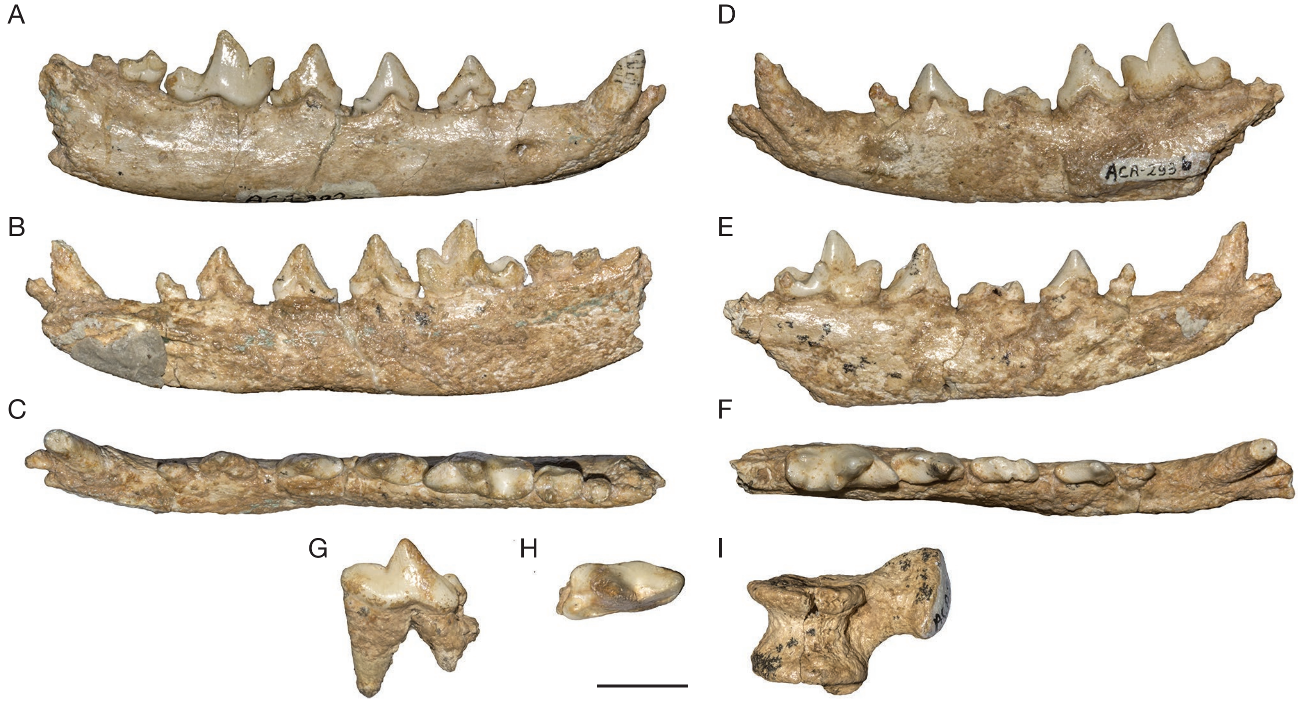

FIG. 2. — *Vulpes beihaiensis* Qiu & Tedford, 1990 from Çalta-1. **A**-**F**, MNHN.F.ACA-293, mandibles: **A**-**C**, right hemimandible in buccal (**A**), lingual (**B**) and occlusal (**C**) views; **D**-**F**, left hemimandible in buccal (**D**), lingual (**E**) and occlusal (**F**) views. **G**-**H**, MNHN.F.ACA-357, left P4 in buccal (**G**) and occlusal (**H**) views. **I**, MNHN.F.ACA-302, right astragalus in proximal view. Scale bar: 1 cm.

(e.g. lobed buccal cingulum on M2) does not fit with general one of *Vulpes*, probably belonging to a different canid (*Nyctereutes* Temminck, 1838 or other). We therefore excluded them from the sample here described.

COMPARISON WITH ASIAN PLIO-PLEISTOCENE *VULPES*

In dental morphology, the specimens from Çalta-1 do not differ greatly from Yushe Basin, as visible Fig. 3. There are only slight differences, among which: 1) *V. beihaiensis* from Yushe Basin has a more compressed buccolingually P4 at the level of the metastyle (Fig. 3A-C); 2) a cingulum does not girdle the P4 protocone; 3) more evident P4 parastyle; 4) more evident distal cingulid on the lower premolars (Fig. 3I-M); and 5) generally lower m1 protoconid (although F:AM 97071 has the same morphology of Çalta-1 specimens). In size and dental proportions, the two taxa differ only slightly (Fig. 4). On the contrary, the hypercarnivorous *V. qiuzhudingi* greatly differs from Çalta-1 *Vulpes* in many respects, morphological and metrical ones (Figs 3; 4) such as: 1) the corpus of *V. qiuzhudingi* is considerably deeper and stouter compared to *Vulpes* from Çalta-1; 2) the p2 protoconid of *V. qiuzhudingi* is lowered compared to the upright one of *Vulpes* from Çalta-1; 3) *V. qiuzhudingi* does not show the high m1 protoconid (Fig. 3I, J, T, U); 4) the hypercarnivorous characteristics of *V. qiuzhudingi* (e.g. enlarged buccal cuspulid on m1-m2; reduced metaconid; cristid-like entoconid) cannot be found in the specimens of Çalta-1 (Fig. 3I, J, T, U); and 5) the biometrical dimensions of *V. qiuzhudingi* are considerably larger as compared to the taxon from Çalta-1 and its saw-toothed pattern contrast with the latter (Fig. 4).

Some fox remains were also unearthed from the western Asian site of Kuruksay (Tajikistan; MN17; Sharapov 1986). These former dentognathic remains, ascribed to *Vulpes* aff. *corsac*, differs from the Çalta-1 record for several features: the proportionally longer lower premolars, with more prominent distal cingulid. Çalta-1 specimen possesses a reduced mesial portion of the p4, whereas in Kuruksay ones such portion is evident. Some other differences worth to be mentioned between the Kuruksay taxon and Çalta-1 specimens are: the larger m1 protoconid and a stouter hypoconid, in buccal view, in the former compared to the latter and the metaconid is more developed in Kuruksay taxon compared to Çalta-1.

COMPARISON WITH EUROPEAN PLIOCENE AND EARLY PLEISTOCENE *VULPES*

The P4 from the Pliocene Bulgarian site of Musselievo differs considerably from that of Çalta-1. For instance, the P4 of the former is buccolingually compressed, with a longer paracone compared to metastyle; the P4 protocone lies at the level of the mesial margin of the tooth; and a prominent buccal cingulid is visible (Fig. 3A and D). In size, it is considerably smaller and its proportions resemble those of *V.* "*praecorsac*" from Odessa (Fig. 4).

Vulpes "*praecorsac*" in the sample from Odessa display evident differences as compared with Çalta-1 specimens, namely: 1) the P4 of the former is stouter compared to Çalta-1, with a longer paracone compared to the metastyle and more prominent buccal cingulum (Fig. 3E); 2) the P4 protocone in *V.* "*praecorsac*" from Odessa is reduced in height

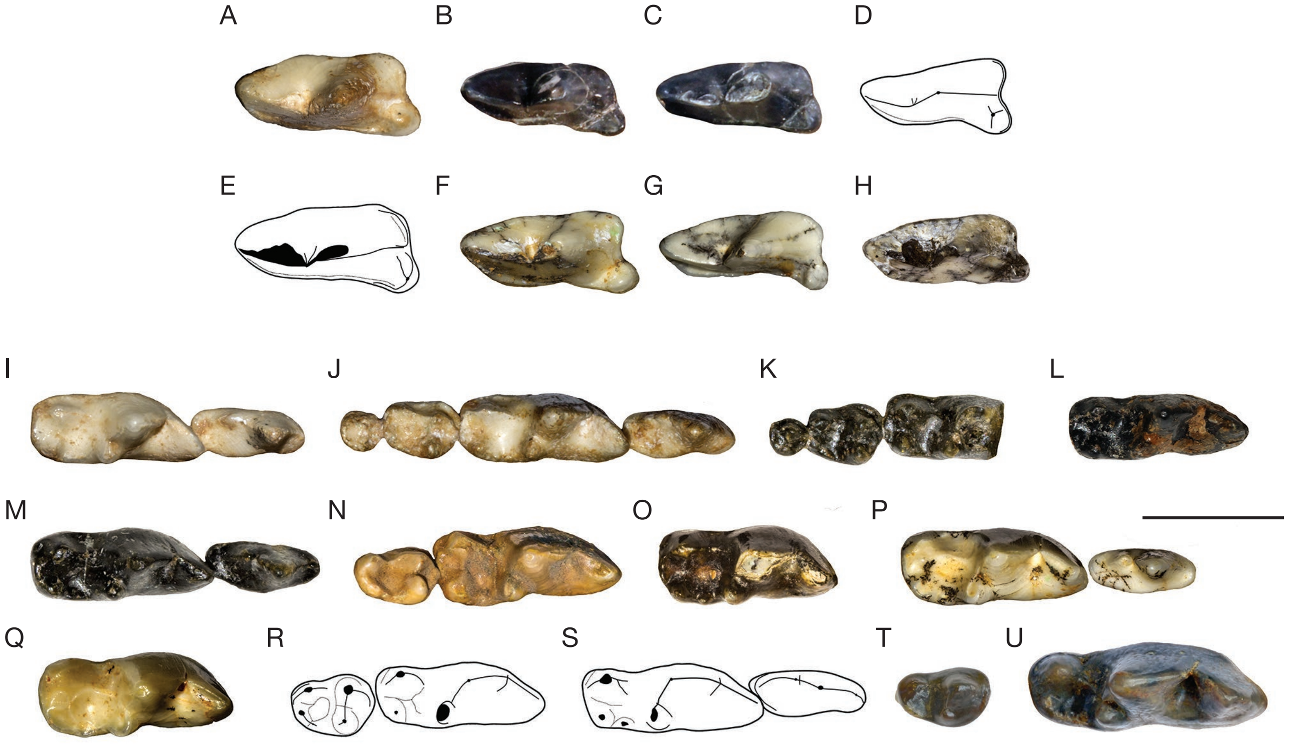

Fig. 3. — Comparison of dental morphologies (**A**-**H**, occlusal view of P4; **I**-**U**, occlusal morphology of lower teeth) of various *Vulpes* spp. from Eurasia: **A**, *Vulpes* Frisch, 1775 from Çalta-1 (Turkey), MNHN.F.ACA-357, left P4 (reversed); **B**, **C**, *V. beihaiensis* Qiu & Tedford, 1990 from Yushe Basin (China), AMNH F:AM 97062, right (**B**) and left reversed P4 (**C**); **D**, *Vulpes* sp. from Musselievo (Bulgaria; Spassov 2000), right P4; **E**, *V. "praecorsac"* Kormos, 1932 from Odessa Catacombs (Ukraine; Odintzov, 1965), O-7764, right P4; **F-H**, *V. alopecoides* (Del Campana, 1913) from Pirro Nord (Italy): **F**, PP789, left P4 (reversed); **G**, MGPT-PU104618, right P4; **H**, MGPT-PU104805, left P4 (reversed); **I**, **J**, *Vulpes* from Çalta-1: **I**, MNHN.F.ACA-293b, left m1-m2; **J**, MNHN.F.ACA-293a, right p4-m3 (reversed); **K**-**M**, *V. beihaiensis* from Yushe Basin (China): **K**, AMNH F:AM 97068, right m1-m3 (reversed); **L**, AMNH F:AM 97071, left m1 (reversed); **M**, AMNH F:AM 97070, left p4-m1; **N**-**Q**, *V. alopecoides* from Europe: **N**, MG-29-2013/461, right m1-m2 (reversed) from Kvabebi (Georgia); **O**, MGPT-PU106227, right m1 (reversed) from Pirro Nord (Italy); **P**, PN 28, left p4-m1 from Pirro Nord (Italy); **Q**, MGPT-PU104721, right m1 (reversed) from Pirro Nord (Italy); **R**, **S**, *V. "praecorsac"* from Odessa Catacombs (Ukraine, Odintzov 1965): **R**, O-1519, left m1-m2; **S**, O-1520, right p4-m1 (reversed); **T**, **U**, *V. qiuzhudingi* Wang, Tseng, Li, Takeuchi & Xie, 2014 from Himalayan-Tibetan Plateau (southwestern China): **T**, IVPP V19060, left m2 from IVPP locality KL0605, Kunlun Pass Basin (China); **U**, IVPP V18923, left m1 from Zanda Basin (China). Scale bar: 1 cm.

(Fig. 3A, E); 3) the mandible *V.* "*praecorsac*" is stouter compared to that of Çalta-1; 4) on the p4, *V.* "*praecorsac*" possess a developed shelf-like portion with an accessory cuspulid, which is reduced in MNHN.F.ACA-293 (Fig. 3I, J, R, S); 5) the m1 of *V.* "*praecorsac*" differs from MNHN.F.ACA-293 for its elongation and buccolingual compression; the rounded lingual margin of the talonid; the reduced entoconid compared to the hypoconid (Fig. 3I, J, R, S); and 6) the m2 of *V.* "*praecorsac*" differs from that of Çalta-1 for the peculiar straight morphology of the mesial-mesiolingual side; the mesially expanded buccal cingulid and for the narrower talonid. It is also proportionally longer compared to that of MNHN.F.ACA-293 (Fig. 4).

Few isolated remains of foxes were recently found in the Oldowan north-Caucasian site of Muhkai II (Amirkhanov *et al.* 2016). The former fragmentary remains were tentatively included in *Vulpes alopecoides* without describing it in detail. Only one partial mandibular corpus with p2-p4 were figured by Amorkhanov *et al.* (2016), which displays narrow premolars and a proportionally enlarged distal accessory cuspulids as compared with Çalta-1 specimens. Such features also contrast with the usual morphology of *V. alopecoides*, suggesting a possible different attribution of the specimens from Muhkai II.

In comparison with Early Pleistocene *V. alopecoides* from Europe (*sensu* Bartolini-Lucenti & Madurell-Malapeira 2020), the Çalta-1 specimens display many differences such as: 1) the studied material is stouter as compared to the average of *V. alopecoides* (Fig. 4); 2) in the European species the P4 lingual cingulum is less prominent whereas the P4 metastyle appear enlarged at its base compared to the latter; 3) the corpus of the mandible from Çalta-1 shares with some specimens of *V. alopecoides* the high position of the distal mental foramen (close to the alveolar plane); 4) the m1 trigonid of *Vulpes* from Çalta-1 resemble that of earlier forms of *V. alopecoides*, e.g. Kvabebi (Fig. 3I, N), in which it is slender compared the stouter morphology of Early Pleistocene forms, e.g. from Pirro Nord (Fig. 3P); 5) the m1 transverse cristid of Çalta-1 is incomplete like in *V. beihaiensis* (Fig. 3U), whereas in *V. alopecoides* it is generally complete (Fig. 3N-Q); 6) the m2 of *V. alopecoides* from Kvabebi (Fig. 3N) differs from that of Çalta-1 for its more mesiodistally elongated occlusal morphology, the larger trigonid cuspulids, the reduced lingual side, including the entoconid; and 7) with the exception

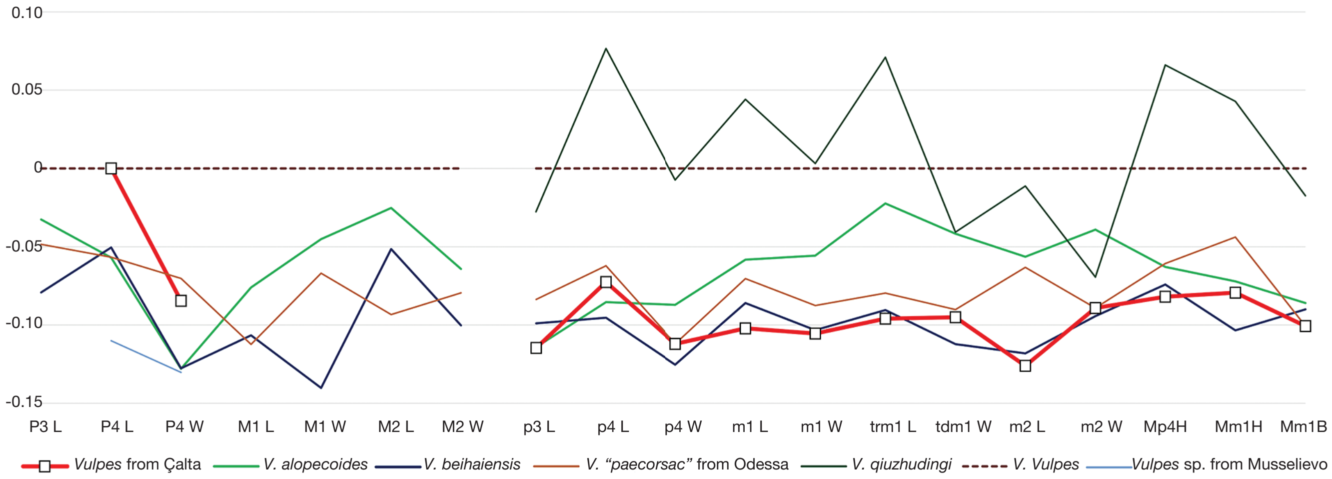

Fig. 4. — Log-ratio diagram based on selected dentognathic variables in *Vulpes* Frisch, 1775 from Çalta-1 and other Pliocene-Early Pleistocene species (*V. alopecoides* (Del Campana, 1913) from Europe *sensu* Bartolini-Lucenti & Madurell-Malapeira 2020; *V. "praecorsac"* Kormos, 1932 from Odessa; *V. beihaiensis* Qiu & Tedford, 1990 from Yushe Basin; *V. qiuzhudingi* Wang, Tseng, Li, Takeuchi & Xie, 2014 from Zanda Basin; and *Vulpes* sp. from Musselievo). The average values of *V. vulpes* (Linnaeus, 1758) are used as standard reference.

of the P4, *V. alopecoides* is generally larger than *Vulpes* from Çalta-1 (Fig. 4). Their pattern of proportions does not differ considerably one another.

CONCLUSIONS

In the framework of the Pliocene record of *Vulpes* across Eurasia, characterized by numerous taxa of uncertain affinities (Fig. 1), the record of Çalta-1 has a significant relevance. Firstly, for its geographical position, at the gates of Europe but close to the junction between three continents (Sen 1998). Secondly, for its chronology, representing one of the earliest well-calibrated occurrences of *Vulpes* in the Eurasian continent. As shown above, the similarity between the specimens from Çalta-1 and those of *V. beihaiensis* from Yushe Basin, both morphological and biometric, especially in comparison to that of other Pliocene localities, supports the parsimonious and plausible hypothesis of subjective synonymy between these taxa under the specific name of *V. beihaiensis* (following priority rule of the International Commission on Zoological Nomenclature 1999). Such a result contrasts with the interpretation by Ginsburg (1998). Nevertheless, this author did not compare the specimens from Çalta-1 to the Chinese material described by Qiu & Tedford (1990). Despite his specific attribution, we agree with Ginsburg (1998)'s interpretation of a plausible link between the *Vulpes* from Çalta-1 and the European Pleistocene *V. alopecoides*, yet considering them as distinct species.

Following the results described above, a new paleobiogeographic scenario for the Old-World foxes is here suggested. After their arise in the late Miocene of North America (*c.* 9.0-8.0 Ma), the center of origin and radiation of all Canidae (Wang & Tedford 2008; Tedford *et al.* 2009), members of the genus *Vulpes* reached the Old World rather early, as the oldest record is in Chad in the Tortonian (late Miocene, *c.* 6.8 Ma; de Bonis *et al.* 2007). Among the earliest occurrences of *Vulpes* in Eurasia, the first stratigraphically and chronologically well-constrained records of small- to medium-sized foxes is that of the described specimens of *V. beihaiensis* from Çalta-1 (*c.* 4.0 Ma). This species configures as one of the key species of the Pliocene of Eurasia, ranging across the Asian continent until the middle Late Pliocene, as testified to by the Mazegouan remains from Yushe Basin (Qiu & Tedford 1990). Subsequently, around 3.1 Ma, the first *V. alopecoides*-like fox – the species that characterized the Late Pliocene-Early Pleistocene record of Europe – appeared, in the eastern Georgian site of Kvabebi (Rook *et al.* 2017). Considering the morphological similarity between *V. beihaiensis* and *V. alopecoides*, like the Kvabebi *Vulpes*, it seems plausible that the latter species derives from a western population of *V. beihaiensis*, diverging from it between 4.0 and 3.1 Ma. In the Early Pleistocene *V. alopecoides* spread across Europe and became a common element of European Early Pleistocene faunas (Bartolini-Lucenti & Madurell-Malapeira 2020). Finally, during the Middle Pleistocene, as documented in western European site, the extant red fox (*Vulpes vulpes*) might have arisen from a yet unknown population of *V. alopecoides.*

Acknowledgements

The authors are thankful to the kindness and availability of following curators of universities and institutions: E. Cioppi and P. Agnelli, curators of the IGF and of the MZUF, respectively; M. Pavia of the Paleontology collection of the MGPT-PU; M. Bukhsianidze and D. Lordkipanidze of the MG-GNM; C. Argot, curator of the Paleovertebrate collection of the MNHN; J. Galkin and J. Men, curator of the fossil mammals collection of AMNH; M. Gasparik, curator of the Paleovertebrate collection of the HNHM. The MNHN gives access to the collections in the framework of the RECOLNAT national Research Infrastructure. We also thank S. Sen for the fruitful discussion on the site of Çalta-1 and its fauna and Dr X. Wang for kindly providing us the pictures of *V. qiuzhudingi.* The authors thank Prof. G. Koufos and an anonymous reviewer for their suggestions that improved the first version of the manuscript. This work has been funded by the Agencia Estatal de Investigación – European Regional Development Fund of the European Union (CGL2017-82654-P, AEI/FEDER-UE) and the Generalitat de Catalunya (CERCA Program). S.B.L. study visits of to AMNH and MG-GNM have been supported by the Earth Sciences Department, University of Florence (Ateneo funds, and International mobility funds) and by the Italian Ministry of Foreign Affairs (DGSP-VI funds). J.M.-M. is member of consolidated research group 2017 SGR 116 (AGAUR, Generalitat de Catalunya). This work is part of the "Augusto Azzaroli (1921-2015) centennial papers" by the Vertebrate Paleontology Group at the Earth Sciences Department, University of Florence.

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Submitted on 2 May 2020;
accepted on 14 June 2020;
published on 13 July 2021.