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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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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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. alopexoides (Del Campana, 1913) and, eventually, to the extant red fox (Vulpes vulpes (Linnaeus, 1758)).

KEY WORDS
Carnivora, Vulpes, Pliocene, Eurasia, biogeography.
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 Plioceene site of Muscelievo (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), Gmrtanov et al. 2015; Gmrtanov 2017; *Vulpes lagopus* (Linnaeus, 1758), Daitch & Guralnič 2007; Suzma 2008a; *Vulpes vulpes* (Linnaeus, 1758), Suzma 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 alopecoïd 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 Calta-1 (c. 4.0 Ma; Turkey; Fig. 1); and the hypercarnivorous and large-sized *Vulpes ginzburgi* 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. ginzburgi* 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 reexamine the material of *V. galatica* from Calta-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-
brites 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 (Croizter & 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, MHN, 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. beihatenis from Zhaozhuang and Zhangwangou (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 Musselieve (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.
Bartolini-Lucenti S. & Madurell-Malapeira J.

**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.

*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 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 so reduced. The buccal cingulid is prominently and enlarged till the distal side of the tooth. The m3 is oval-shaped, with two equal-sized cuspsulids 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

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**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; Mm1W, mandibular width at level of the m1; Mp4H, mandibular height distal to the p4; W, buccolingual width.

| Specimens       | L (mm) | W (mm) | H (mm) |
|-----------------|--------|--------|--------|
| 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    |        |
| tdm1            | 7.9    | –      | –      |
| m2              | 5.5    | 4.3    |        |
| m3              | 3.1    | 2.7    |        |
| Mn1H            | –      | 11.0   |        |
| Mn1W            | –      | 11.6   |        |
| MNHN.F.ACA-293b | –      | 5.6    | –      |
| MNHN.F.ACA-357  | 14.3   | 6.0    | –      |
| MNHN.F.ACA-302  | 22.9   | –      | –      |

Anatomy

**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 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).

**Chronostatigraphic 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.

**Systematic Palaeontology**

**Order** CARNIVORA Bowdich, 1821

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**Genus** Vulpes Frisch, 1775

*Vulpes beihaiensis* Qiu & Tedford, 1990
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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 cuspid on m1-m2; reduced metaconid; cristid-like entoconid) cannot be found in the specimen from 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 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 cingulid (Fig. 3E); 2) the P4 protocone in *V. "praecorsac"* from Odessa is reduced in height.
Such features also contrast with the usual morphology of accessory cuspulids as compared with Çalta-1 specimens. Narrow premolars and a proportionally enlarged distal talonid. It is also proportionally longer compared to that of V. beihaiensis. The mesial-mesiolingual side; the reduced entoconid compared to the hypoconid (Fig. 3I, J, R, S); and 6) the m2 of 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 V18523, left m1 from Zanda Basin (China). Scale bar: 1 cm.

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 frischi, 1775 from Çalta-1 (Turkey), MNHN.F.ACA-357, left P4 (reversed); B, C, V. beihaiensis Gu & Tedford, 1990 from Yushe Basin (China), AMNH F:AM 97062, right (B) and left reversed P4 (C); D, Vulpes sp. from Musselevo (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 V18523, left m1 from Zanda Basin (China). Scale bar: 1 cm.

(Fig. 3A, E); 3) the mandible of 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 metaстыle 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
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). During 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 (*V. vulpes*) might have arisen from a yet unknown population of *V. alopecoides*.
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