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The Fox from Bajiazui (Qingyang, Central China) and an Update on Early Pleistocene Foxes from China

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Abstract: (1) Background: despite the fact that nowadays the genus *Vulpes* Frisch, 1775, is the most diverse among extant Canidae, its fossil record is utterly scarce, especially in the Asian Pliocene. The sparse nature of this record further complicates the reconstruction of the evolutionary scenario to fit these taxa with extant species. The situation seems to change slightly in the Early Pleistocene when two species are recorded: *Vulpes alopecoides* (Del Campana, 1913) in Europe and *Vulpes chikushanensis*, Young, 1930, in Asian localities. Unlike the former, which has an extensive record, the remains of the Chinese *V. chikushanensis* are sporadic and the validity of the taxon has also been questioned. (2) Methods: the study of the specimens from the Early Pleistocene site of Bajiazui (1.8–1.2 Ma, Qingyang, Gansu) in comparison to an extensive sample of *Vulpes* spp. The Pliocene–Early Pleistocene is relevant for the delimitation of fossil foxes variability; (3) Results: morphologically and morphometrically, the specimens of Bajiazui fit with the specimens of *V. chikushanensis* from other Chinese localities of the Early Pleistocene, e.g., Longdan (Gansu) and Huiyu (Fangshang), highlighting some difference with the latest Early Pleistocene forms of Jigushan fox; (4) Conclusions: the revision of the Asian fossil record of *Vulpes* is crucial in our attempt to understand and reconstruct the evolution of carnivoran guild during the late Early Pleistocene (1.8–0.8 Ma). The fox remains from Bajiazui, although fragmentary, add a valuable piece to our knowledge of *V. chikushanensis*, a species possibly strongly related to the extant *Vulpes corsac* (Linnaeus, 1768).

Keywords: *Vulpes*; carnivora; eastern Asia; Pleistocene



Citation: Bartolini-Lucenti, S.; Jiangzuo, Q.; Jiang, H.; Li, Z.; Xie, K.; Madurell-Malapeira, J. The Fox from Bajiazui (Qingyang, Central China) and an Update on Early Pleistocene Foxes from China. *Quaternary* **2023**, *6*, 57. <https://doi.org/10.3390/quat6040057>

Academic Editor: Juan Manuel López García

Received: 2 July 2023

Revised: 22 September 2023

Accepted: 7 November 2023

Published: 20 November 2023



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1. Introduction

Foxes of the genus *Vulpes* Frisch, 1775, are today the most diverse monophyletic group of extant Canidae [1,2], with twelve recognized species that inhabit almost the entire planet with the exception of Antarctica and South America [2,3]. Despite the present diversity, their fossil record is one of the most fragmentary within the subfamily Caninae.

The oldest documented fossil evidence of foxes dates back to the Late Miocene period of North America and the Old World. This coincided with the spread of dry and open environments, which followed the global cooling trend that began precisely in the latest Miocene [4]. However, fossil fox occurrences are sporadic and scattered across the North

American, Eurasian, and African continents [5,6]. The earliest species are the Late Miocene (~9 Ma) North American *Vulpes stenognathus* Savage, 1941, and *Vulpes kernensis* Tedford et al., 2009 [5]. *Vulpes* reached Eurasia and Africa pretty early in its record, as *Vulpes riffautae* de Bonis et al., 2007, was already present in Chad around 7 Ma [7]. The earliest Eurasian records of the genus are the Pliocene ones of *Vulpes qiuzhudingi* Want et al., 2014, from the Zanda basin [8], *Vulpes beihaiensis* Qiu and Tedford, 1990, from the Yushe Basin and Çalta-1 [9,10], *Vulpes rooki* Bartolini Lucenti, 2021, from the Yushe Basin [11], as well as *Vulpes 'praecorsac'* from Odessa Catacombs [12] and *Vulpes* sp. from Musselievo [13].

These early records are, despite apparent diversity, rather scattered and fragmentary. Indeed, of these taxa, only *V. beihaiensis*, *V. qiuzhudingi* and *V. rooki* are well characterized taxa, and there is general consensus on their taxonomy, ecology and, plausibly, systematics. The Tibetan *V. qiuzhudingi* and the Chinese *V. rooki* stand out as peculiar, with their hyper-carnivorous dentition and adaptations, especially in *V. qiuzhudingi* [8,11]. The small-sized *V. beihaiensis* is interesting for its plausible affinity with the extant *Vulpes corsac* (Linnaeus, 1768), as proposed by [9], but also with the Early Pleistocene *Vulpes chikushanensis*, Young, 1930 [14,15], and the contemporaneous *Vulpes alopecoides* (Del Campana, 1913) [10]. Indeed, *V. beihaiensis* might have originated *V. chikushanensis* in the Late Pliocene of eastern Asia and then, in turn, the extant *V. corsac*, while in western Asia, it gave origin to the lineage of *Vulpes vulpes* (Linnaeus, 1758) (through *V. alopecoides*) [10,16].

During the Late Pliocene and the Early Pleistocene, the situation changed. There was a reduction in diversity, probably prompted by an increase in carnivoran intraguild competition, as only the two distinct forms *V. alopecoides* and *V. chikushanensis* are recorded [6,15,17]. The first record of the former is in the Georgian site of Kvabebi, recently redated to 2.85 Ma [18], whereas the latter appeared in the Gansu site of Longdan (2.4–2.2 Ma) [15]. Both these taxa apparently remained confined to the two sides of Eurasia with numerous occurrences (see an in-depth discussion of [6]). By the beginning of the Middle Pleistocene, the extant *V. corsac*, *Vulpes lagopus* (Linnaeus, 1758), and *V. vulpes* appeared in the Asian fossil record: the corsac and the red fox are recorded in the earliest Middle Pleistocene layers of Zhoukoudian Loc. 1 [19,20], whereas the arctic fox is present in the deposits of the Middle Pleistocene of Oloyr fauna (Russian Federation) [21].

Here, we describe for the first time the remains of a fox from the Early Pleistocene site of Bajiazui (Qingyang, Gansu Province, China) (Figure 1).

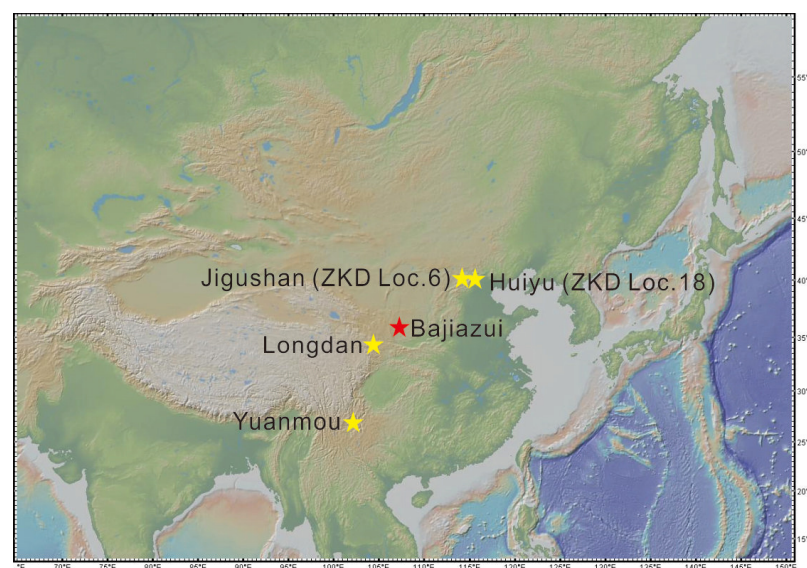


Figure 1. Localization of the late Early Pleistocene (1.8–1.2 Ma) site of Bajiazui (Qingyang, Gansu), red star, compared to other sites cited in the text, yellow stars. Abbreviations: ZKD, Zhoukoudian.

2. Geological and Geographical Background

Bajiazui fauna was found at the bottom of the Wucheng loess in Qingyang, Gansu province. The site has yielded a rich amount of fossils that belong to a diverse mammal community, including the *Talpinae* gen. et sp. indet., *Eospalax* sp., *Allosiphneus arvicolinus*, *Ochotona* sp.1, *Ochotona* sp.2, *Hystrix* sp., *Canis chihliensis*, *Vulpes chikushanensis* (here described), *Meles teilhardi*, *Pachycrocuta brevirostris*, *Megantereon inexpectatus*, *Homotherium* cf. *crenatidens*, *Coelodonta nihowanensis*, *Proboscideipparion sinensis*, *Equus qingyangensis*, *Equus wangi*, *Equus teilhardi*, *Sus lydekkeri*, *Eucladoceros* sp., *Gazella sinensis*, *Bison palaeosinensis*, and *Leptobos* cf. *amplifrontalis* [22,23]. The age of the fauna is still not fully resolved. Wang [23] believed that the age of the fauna is similar to that of Xiashagou of Nihewan, as the ratio of the extinct species is similar, while Xue et al. [24] believed that the age of the fauna could be younger, ranging from 1.8–1.2 Ma, therefore being slightly younger than Classic Nihewan fauna. We follow Xue et al. [24] that Bajiazui fauna is somewhat between 1.8–1.2 Ma based on the evolutionary level of Carnivora, including hypercarnivorous dentition of *Canis chihliensis*, reduced P4 protocone of *Megantereon* and *Homotherium*, and reduced m1 talonid cusp of *Pachycrocuta*, all derived within their lineages (Jiangzuo in prep.).

3. Material and Methods

This study is based on comparative morphological and morphometric analyses of *Vulpes* from Bajiazui compared to other Pliocene to Early Pleistocene *Vulpes* species of Eurasia. The fossils studied come from the collections of the Department of Geology, Institute of Cenozoic Geology and Environment, Northwest University. As comparative fossil material, we studied the collections of several European and Chinese localities (AMNH, AUTH, DST-UNIFI, HVM, HNHM, ICP, IGF, IVPP, MAFI, MdC, MG-GNM, MHNL, MNHN, UCBL-1; see abbreviations below) and inspected all the relevant literature on Eurasian fossil *Vulpes* [8–10,12,15,18,25–28].

Fossil species considered for comparison include *V. alopecoides* (sensu [6]) from numerous sites throughout Europe (see the sample [6]); *V. beihaiensis* from Baihaicun, Zhaozhuang, Zhangwagou (Yushe Basin, China) [9], and Alta-1 [10]; *V. chikushanensis* from Huiyu–Zhoukoudian Loc. 18 [13] and Longdan [15]; *V. qiuzhudingi* from the Himalayan–Tibetan Plateau (Zanda and Kunlun Pass Basins, China) [8]; *V. ‘praecorsac’* from the Odessa Catacombs (Ukraine) [12]; and *Vulpes* sp. from Musselievo (Bulgaria) [13].

Extant samples of *V. corsac*, *V. lagopus*, and *V. vulpes* from AMNH, HNHM, IVPP, IOZ, and MZUF were used for morphological and morphometric comparisons.

3.1. Abbreviations

3.1.1. Site and Institutional Abbreviations

AMNH, the American Museum of Natural History, New York (USA); AUTH, Aristotle University Thessaloniki (Greece); DST-UNIFI, Earth Science Department of the University of Florence (Italy); HVM, Hezheng Palaeozoological Museum, Linxia, Gansu (China); HNHM, Hungarian Natural History Museum, Budapest (Hungary); ICP, Institut Català de Paleontologia Miquel Crusafont, Barcelona (Spain); IGF, Geological and Paleontological Section of the Natural History Museum of the University of Florence (Italy); IOZ, Institute of Zoology, Chinese Academy of Sciences, Beijing (China); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (China); LGPUT, reference for the specimens in the Museum of Geology-Palaeontology-Palaeoanthropology of Aristotle University Thessaloniki (Greece); MAFI, Hungarian Institute of Geology and Geophysics, Budapest (Hungary); MdC, Musée des Confluences, Lyon (France); MG-GNM, S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi, Georgia); MGPT-PU, Geology and Paleontology Museum of the University of Turin (Italy); MZUF, La Specola, Zoological Section of the Natural History Museum of the University of Florence (Italy); NWU, Northwest University, Xi’an, China, UCBL-1, Université Claude-Bernard Lyon-1, Lyon (France).

3.1.2. Measurement Abbreviations

Dentition: C–M2 L, mesiodistal length from the mesial side of the canine to the distal side of the M2; ECW, external canine width of the muzzle measured at the level of the canines; GPW, greatest palatal width; L, mesiodistal length; LMR, upper molars row length; P4–M2 L, mesiodistal length from the mesial side of the P4 to the distal side of the M2; td, talonid; trd, trigonid; W, buccolingual width.

Teeth nomenclature follows Bartolini-Lucenti and Spassov [29].

4. Systematic Paleontology

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Canidae Fischer, 1817

Subfamily Caninae Fisher, 1817

Tribe Vulpini Hemprich and Ehrenberg, 1832

Genus *Vulpes* Frisch, 1775

Vulpes chikushanensis, Young, 1930

(Figure 2 and Table 1)

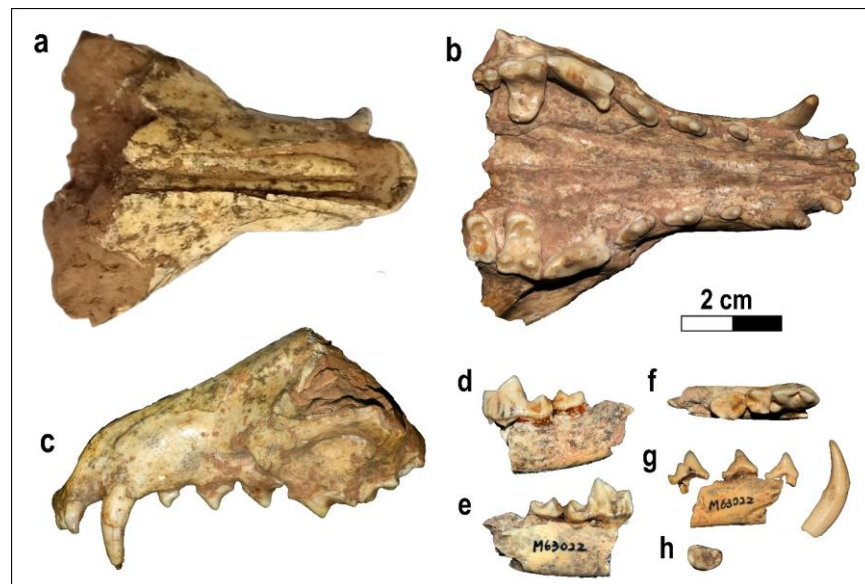


Figure 2. Early Pleistocene fossil fox remains from Bajiazui (Qingyang, Gansu), China. (a–c) MLS028, cranial fragment in dorsal (a), ventral (b), and left lateral (c) views. (d–h) M63022, left and right mandibular fragments with teeth; left hemimandible fragment with m1–m2 in buccal (d), lingual (e), and occlusal (f) views; right hemimandible fragment with p3 and isolated c, p2, and p4 (g) in buccal view; right m2 (h) in occlusal view.

Table 1. Measurement table for upper and lower teeth expressed in millimeters. Abbreviations: C–M2 L, mesiodistal length from the mesial side of the canine to the distal side of the M2; ECW, external canine width of the muzzle measured at the level of the canines; GPW, greatest palatal width; L, mesiodistal length; LMR, upper molars row length; P4–M2 L, mesiodistal length from the mesial side of the P4 to the distal side of the M2; td, talonid; trd, trigonid; W, buccolingual width.

	C L	C W	P1 L	P1 W	P2 L	P2 W	P3 L	P3 W	P4 L	P4 W	M1 L	M1 W	M2 L	M2 W	LMR	C–M2 L	P4–M2 L	GPW	ECW
MLS028	5.10	3.40	3.80	2.30	6.80	2.60	7.7	3.2	12.2	6.3	8.2	10.9	5.7	8.5	13.65	55.90	23.40	37.70	19.00
	c L	c W	p2 L	p2 W	p3 L	p3 W	p4 L	p4 W	m1 L	m1 W	m1td L	m1td W	m1trd L	m2 L	m2 W				
M63022	5.6	3.4	6.8	2.6	7.3	2.8	8.2	3.4	14	5.2	4.2	5	9.8	6.5	5.3				

4.1. Referred Specimens

Cranial fragment—MLS028, rostral portion of the cranium with complete dentition (I1–M2 from both sides).

Mandible—M63022, fragments of left and right hemimandibles with left m1–m2 and right c, p2–p4, and m2.

4.2. Description

Cranial specimen—The specimen MLS028 (Figure 2a–c) consists of part of the cranium, particularly the muzzle, with complete dentition. The specimen is partially deformed, with right to left compression. As a result, the nasals sank into the nasal cavity. Despite the plastic deformation, some features can still be identified. The muzzle is not particularly elongated rostrocaudally. In lateral view, the caudal margin of the infraorbital foramen is located at the level of the distal margin of the P3. In ventral view, the palate is not enlarged neither rostrally, at the level of the canines, nor caudally at the level of the molars. The palatine foramina are well developed, and two marked furrows extend rostrally from them. The incisors are very similar to each other, as the I3 is not particularly enlarged, showing only a low cingulum on its lingual side. There is no space between I2 and I3. The canines have a high and mesiodistally thin crown. There are diastemata between C1–P1 and P1–P2, and a small one between P2 and P3. The premolars are compressed buccolingually and fairly elongated distally, marked by a fairly low crown. The single-rooted P1 has a single, rather low, cusp. The P2 and the P3 do not show differentiation among each other, apart from the larger size and a mesiolingual enlargement visible in the occlusal view of the P3. In occlusal view, the P4 have a mesially projected protocone, markedly placed forward compared to the mesial margin of the paracone, and rather individualized. In the same view, the paracone and the metastylar blade have comparable length. No prominent cingula or accessory crests are visible. The molars have a rectangular and elongated buccolingual occlusal shape, marked by the lingually projecting talons and hypocones. The M1 paracone is only slightly enlarged compared to the metacone. The lingual cusps are fairly worn down, but the presence of protocone and developed metaconule seem plausible. Lingually, there is a cingular hypocone. The buccal cingulum is prominent. Even in the M2, the paracone is slightly larger than the metacone. The protocone appears to have developed but is not connected to the distal side, as there is a furrow extending buccally from the talon.

Mandibular specimens—The mandibular remains of Bajiazui are rare and fairly poorly preserved (Figure 2d–h). The lower canine is high-crowned and slender, characterized by a crescent-like lateral shape. The premolars are compressed buccolingually and have a moderately high crown. Only the p4 is slightly rounded, in the occlusal view. The p2 and p3 have very similar morphologies, despite the larger size of the latter. In addition, the p3 displays a shallow distal accessory cuspid, distally to the protoconid, and a shallow but pointy distal cingulid. The p4 is larger compared to the other premolars and has a prominent distal accessory cuspid and a high, pointy distal cingulid. The m1 of M63022 has a developed trigonid compared to the talonid, as evident in the buccal and occlusal views (Figure 2d,f). In the occlusal view, it is slender and compressed buccolingually. The paraconid is mesiodistally short compared to the prominent protoconid. The metaconid is enlarged in the occlusal view, projected lingually and distally (it is even visible in the buccal view). On the talonid, the principal cuspid is the hypocone, which is enlarged, and placed buccally. The entoconid is reduced in height and width and is placed at the distolingual corner of the talonid. There is no transverse cristid between the entoconid and hypoconid. From the mesial to the entoconid, there is a shallow cuspid, which does not close the talon lingually. A hypoconulid shelf bounds the distal margin of the tooth with a central hypoconulid. The m2 has three principal cuspid: protoconid, metaconid, and hypoconid. Mesially, a cristid departs from the protoconid and reaches the mesial margin of the m2, but no paraconid seems to be present. The protoconid and the metaconid are of similar size. On the distolingual side of the tooth, a shallow entoconid is evident. The cingulid is prominent mesiobuccally.

4.3. Morphological Comparisons

The fox from Bajiazui is a medium-sized fox, comparable in size to the extant *V. corsac*, *V. lagopus*, and close to the extinct *V. chikushanensis* and *V. alopecoides* of the Early Pleistocene of China and Europe, respectively [6,15]. MLS028, due to its fragmentary nature, has few cranial characteristics valuable for comparison with other taxa. Possibly, only the slenderness of the muzzle can be used as a comparative feature. In this sense, the specimen from Bajiazui differs from *V. alopecoides* from Europe (e.g., Kastritsi, and Villány 3) [5,28] and the existing *V. vulpes* or *V. lagopus*, in which the muzzle is generally wider rostrally (cf. to the cranium of Bajiazui, Figure 2).

The slenderness is more consistent with the shape of *V. chikushanensis* (e.g., from Longdan or Huiyu) and the extant *V. corsac*.

Dental morphologies allow more considerations (Figures 3 and 4). The P4 of MLS028 is fairly slender, especially for the reduction in a distolingual cingulum, similar to the morphologies of *V. chikushanensis* from Jigushan [21] and the existing *V. corsac*. In fact, it contrasts with the morphology of *Vulpes* sp. from Odessa [12] as P4 is enlarged and stout, with a poorly individualized protocone. Likewise, the morphologies of *V. rooki*, as well as its size, do not fit the morphology of *Vulpes* from Bajiazui. Apparently, the specimens from Bajiazui has a more slender P4 compared to the published specimens of *V. chikushanensis* from Longdan [15], although some specimens, for example, X1805 and X1806, are definitely similar to MLS028 (Figure 3). In fact, the slenderness of P4 appears to be a variable feature in *V. alopecoides* and *V. vulpes* [6]. However, the development of the P4 protocone is comparable to that of *V. chikushanensis* from Longdan [15], Huiyu (Zhoukoudian Loc. 18) [13], Jigushan [25], and the existing *V. corsac*, unlike the generally large and individualized one of *V. alopecoides* from Europe and the existing *V. vulpes* (Figure 3). On the contrary, the Pliocene *V. beihaiensis* from the Yushe Basin has a smaller protoconid [8]. The arctic fox, *V. lagopus*, generally possesses a larger P4 compared to the specimen of Bajiazui. In the upper molars, the European *V. alopecoides* and Holarctic *V. vulpes* tend to display a moderately mesiodistally enlarged M1 compared to that of Bajiazui *Vulpes*, while M2 shares the slender, buccolingually elongated morphology (Figure 3 and [6]). However, the buccal M2 cusps of *V. alopecoides* generally differ in size, with the paracone being slightly larger compared to the metacone (Figure 3) [6]. The upper molar morphology of the specimen from Odessa [12] and of *V. rooki* differ greatly from the *Vulpes* from Bajiazui. In the Odessa specimens, there is a notable enlargement of the paracone relative to the metacone in the M1–M2, along with an enlargement of the M1 hypocone, as observed through parameters such as the mesiodistal width of the M1. In *V. rooki*, the enlargement of the cingula and that of the buccal cusps as well as of the protocone mark the distinction with the fox from Bajiazui. The *Vulpes beihaiensis* type AMNH F:AM 97062 has a larger M1 compared to MLS028 and is less lingually elongated (Figure 3). The buccal side of the M2 of *V. beihaiensis* is enlarged compared to the shortened shape of *Vulpes* from Bajiazui (Figure 3). Moreover, *V. beihaiensis* shows an evident metaconule, possibly linked to the protocone by postprotocrista. This contrasts with the morphology of *Vulpes* of Bajiazui and *V. chikushanensis* of Longdan, in which the metaconule is reduced or absent and there is no postprotocrista connecting the protocone to the distal side (Figure 3). The similarity between M2 paracone and metacone resembles that of *V. chikushanensis* from Longdan. In this regard, *Vulpes* from Bajiazui differs from *V. corsac*. The mesiodistal slenderness of the molars suggests a close similarity with *V. chikushanensis* from Chinese localities such as Longdan or Huiyu (Zhoukoudian Loc. 18) [14,15].

Regarding the lower dentition (Figure 4), the premolars are higher crowned compared to those of *V. alopecoides* from Eurasia and *V. vulpes* (despite the low degree of variability). Their morphology is consistent with that of *V. chikushanensis* from Longdan [15] and Jigushan [21] or extant *V. corsac*. The morphology of *V. qiuzhudingi*'s lower carnassial and m2, with strongly derived hypercarnivorous features (Figure 4), allow immediate distinction between this Pliocene taxon and the fox from Bajiazui. Similarly, *V. rooki* cannot be regarded as comparable to *Vulpes* from Bajiazui given the enlargement of buccal cuspids and the

parallel reduction in lingual ones. The m1 in buccal view, differs from *V. alopecoides* from Eurasia (e.g., Dafnero 1; La Puebla de Valverde; Apollonia-1) due to the more mesiodistally reduced paraconid and the stouter protoconid compared to other Eurasian species (Figure 4). Furthermore, m1 of *V. alopecoides* tends to possess buccolingually wider talonids compared to Asian forms, such as *V. beihaiensis*, *V. chikushanensis*, *V. corsac*, and M63022 (Figure 4). Compared to *V. beihaiensis*, the fox from Bajiazui possesses a proportionally larger hypoconid and a more reduced entoconid. These cusps are more similar in *V. beihaiensis*, where the entoconid is enlarged in the talonid. The morphologies of *Vulpes* from Bajiazui are close to those of *V. chikushanensis* from Longdan and Jigushan and to those of extant *V. corsac*, although they are stouter, especially mesially on the trigonid compared to the latter two. The m2 of *V. beihaiensis* is more squared, unlike the oval morphology of M63022, which has a more oval, occlusal shape (Figure 4). This morphology resembles that of *V. chikushanensis* from Longdan, although the latter have a more developed entoconid. On the contrary, this cuspid is very reduced. The morphology also bears some similarity to that of *V. corsac*, although the corsac fox generally possesses a definitely prominent mesial cingulid. In comparison, *V. alopecoides* has a wider talonid and a generally more prominent buccal cingulid (Figure 4).

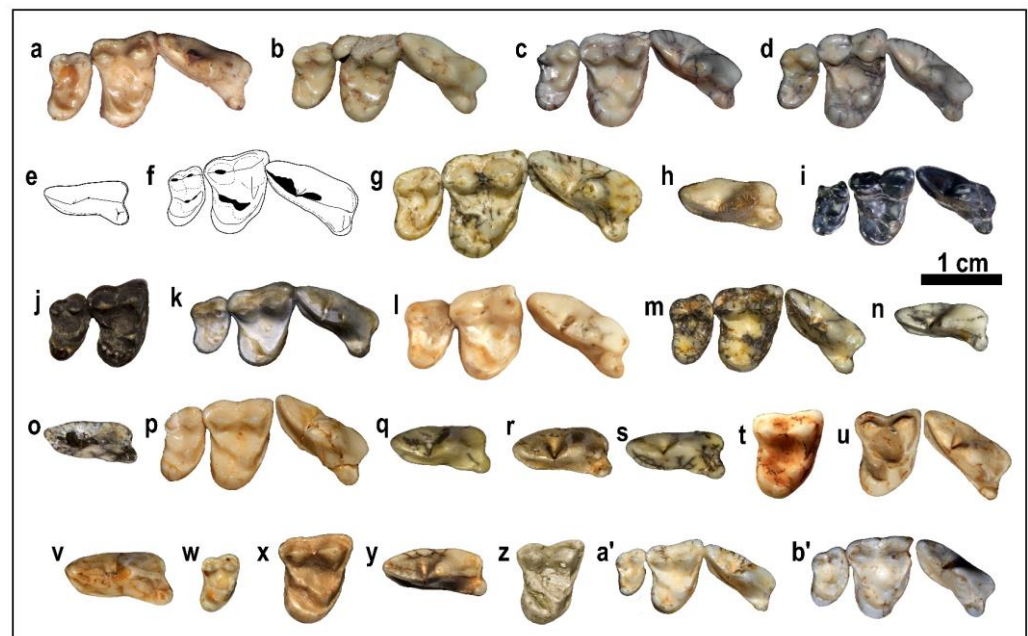


Figure 3. Comparison of upper teeth morphologies (occlusal view of P4–M2) of various *Vulpes* spp. from Eurasia. (a) *Vulpes* from Bajiazui (China), MLS028, left P4–M2 (mirrored). (b–d) *Vulpes chikushanensis* from Longdan (Gansu, China): (b) X1805, left P4–M2 (mirrored); (c,d) V.13533, right (c) and left mirrored (d) P4–M2. (e) *Vulpes* sp. from Musselievo (Bulgaria) [13], right P4 with catalogue number. (f) *Vulpes* sp. from Odessa Catacombs (Ukraine) [12], O-7764, right P4–M2. (g) *Vulpes rooki* from Xiakou (Yushe basin, China), AMNH F:AM 97027, right P4–M2. (h,i) *Vulpes beihaiensis* from Asia (Turkey and China): (h) MNHN.F.ACA-357, left P4 (mirrored) from Çalta-1 (Turkey); (i) AMNH F:AM 97062, right P4–M2 right from Baihai, Yushe Basin (China). (j–b′) *Vulpes alopecoides* from European localities: (j) IGF 12110, right M1–M2 (type specimen of the species) from Il Tasso (Il Tasso); (k) MHNL 20.161684, right P4–M2 from St. Vallier (France); (l) PP 789, left P4–M2 (mirrored) from Pirro Nord (Italy); (m) MGPT-PU104618, right P4 from Pirro Nord (Italy); (n) MGPT-PU104805, left P4 (mirrored) from Pirro Nord (Italy); (o) KSR-PO221, P4–M2 (mirrored) from Kastritsi (Greece); (p) V.61.1401, left P4–M2 (reversed) from Villany 3 (Hungary); (q) APL-20, right P4 from Apollonia-1 (Greece); (r) V.13.04696.3, left P4 (mirrored) from Nagyarsanyhegy 4 (Hungary); (s) VER.2018.2676, left P4 (mirrored) from Somssich Hill 2 (Hungary); (t) VER.2018.2682, right M1 from Somssich Hill 2 4 (Hungary); (u) V.61.2164_1, left P4–M1 (mirrored) from Villany 8 (Hungary); (v) V.61.2164_2,

right P4 from Villany 8 (Hungary); (w) unnumbered specimen, left M2 (mirrored) from Villany 3 (Hungary); (x) unnumbered specimen, right M1 from Villany 3 (Hungary); (y) unnumbered specimen, left P4 from Villany 3 (Hungary); (z) IPS 45634 (cast), right M1 from Venta Micena (Spain); (a') UWPI 2275/13/10, left P4-M2 (mirrored) from Deutsch Altenburg 2C (Austria); (b') UWPI 2275/13/11, right P4-M2 from Deutsch Altenburg 2C (Austria).

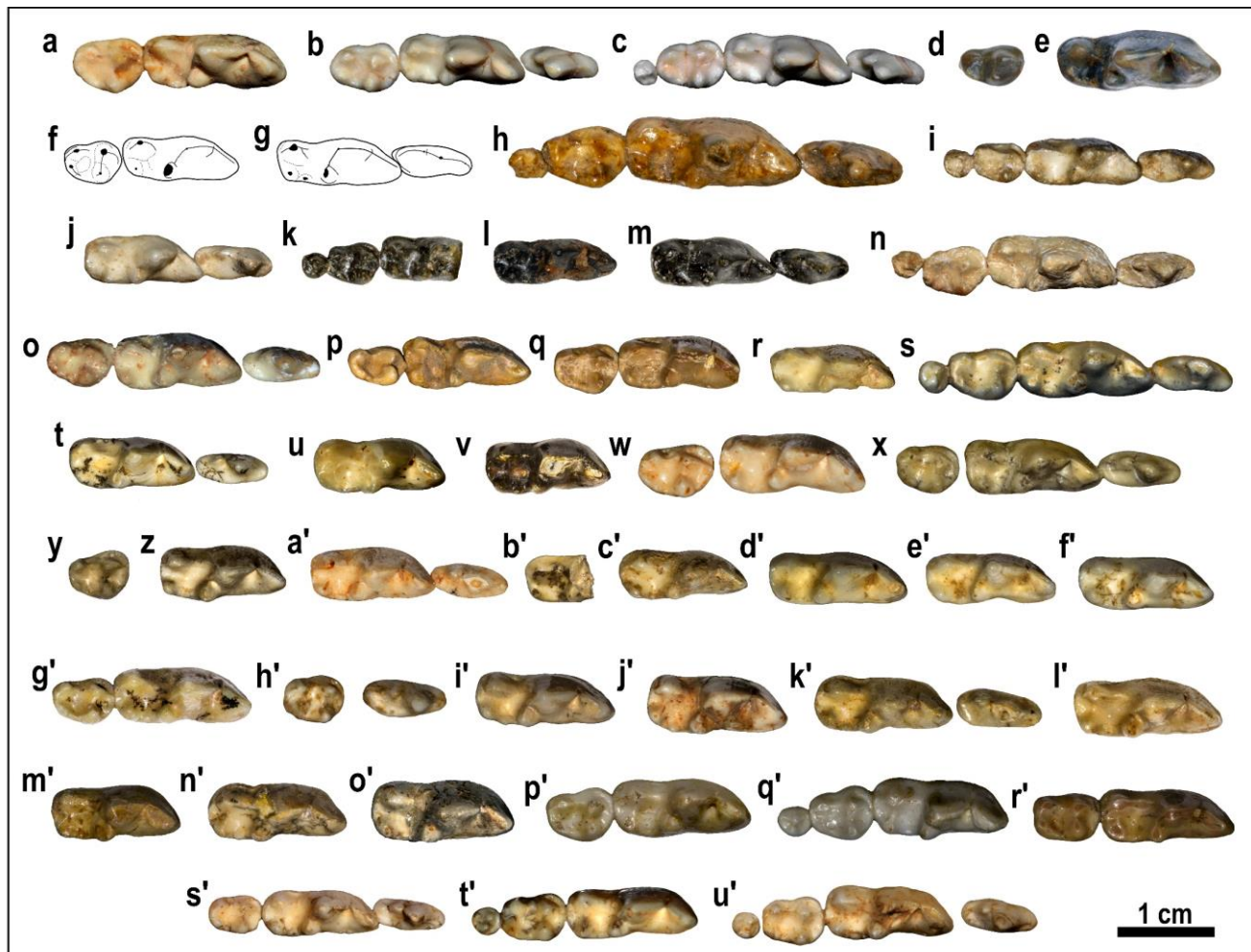


Figure 4. Comparison of lower teeth morphologies (occlusal view of p4–m3) of various *Vulpes* spp. from Eurasia. (a) *Vulpes* from Bajiazui (China), M63022, left m1–m2. (b,c) *Vulpes chikushanensis* from Longdan (Gansu, China): (b,c) V.13533, left p4–m2 (b) and right mirrored p4–m3 (c). (d,e) *Vulpes qiuzhudingi* from Himalayan–Tibetan Plateau (China): (d) IVPP V19060, left m2 from IVPP locality KL0605, Kunlun Pass Basin (China); (e) IVPP V18923, left m1 from Zanda Basin (China). (f,g) *Vulpes* sp. from Odessa Catacombs (Ukraine) [12]: (f) O-1519, left m1–m2; (g) O-1520, right p4–m1 (mirrored). (h) *Vulpes rooki* from Xiakou (Yushe basin, China), AMNH F:AM 97058, right p4–m3 (mirrored). (i–m) *Vulpes beihaiensis* from Asia (Turkey and China): (i) MNHN.F.ACA-293b, left m1–m2 from Çalta-1 (Turkey); (j) MNHN.F.ACA-293a, right p4–m3 (mirrored) from Çalta-1 (Turkey); (k) AMNH F:AM 97068, right m1–m3 (mirrored) from Zhuangwagou, Yushe Basin (China); (l) AMNH F:AM 97071, left m1 from Zhaozhuang, Yushe Basin (China); (m) AMNH F:AM 97070, left p4–m1 from Zhaozhuang, Yushe Basin (China). (n–u') *Vulpes alopecoides* from European localities: (n) LGPUT DFN-22, left p4–m3 from Dafnero-1 (Greece); (o) LGPUT DFN-172, right p4–m2 (mirrored) from Dafnero-1 (Greece); (p) MG-29-2013/461, right m1–m2 (mirrored) from Kvabebi (Georgia); (q) IPS 27246, left m1–m2 from La Puebla de Valverde (Spain); (r) IPS 27248, right m1 (mirrored) from La Puebla de Valverde (Spain); (s) IPS 27259, right p4–m3 from La Puebla de Valverde (Spain); (t) PN 28, left p4–m1 from Pirro Nord (Italy); (u) MGPT-PU104721, right m1 (reversed) from Pirro Nord (Italy);

(v) MGPT-PU106227, right m1 (reversed) from Pirro Nord (Italy); (w) V.61.1401, right m1–m2 (mirrored) from Villany 3 (Hungary); (x) LGPUT APL-11, right p4–m2 (mirrored) from Apollonia-1 (Greece); (y,z) V.13.04696.0, right m2 (mirrored) and left m1 from Nagyarsanyhegy 4 (Hungary); (a') V.61.1372, left p4–m1 from Villany 8 (Hungary); (b') V.13.04785.0, right m1 talonid (mirrored) from Püspökfurdö/Betfia 2 (Romania); (c') VER.2018.2630, left m1 from Somssich Hill 2 (Hungary); (d') VER.2018.2638, right m1 (mirrored) from Somssich Hill 2 (Hungary); (e') VER.2018.2641, left m1 from Somssich Hill 2 (Hungary); (f') VER.2018.2676, left m1 from Somssich Hill 2; (g') V.2014.2.5.1, right m1–m2 (mirrored) from Villany 3 (Hungary); (h') VER.2018.2678, left p4 and m2 from Somssich Hill 2 (Hungary); (i') V.2014.5.1.2, right m1 (mirrored) from Villany 3 (Hungary); (j') unnumbered specimen, right m1–m2 (mirrored) from Villany 3 (Hungary); (k') V.2014.2.5.2, left p4–m1 from Villany 3 (Hungary); (l') V. 2014.2.5.4, right m1 (mirrored) from Villany 3 (Hungary); (m') V.13.3632_c, right m1 (mirrored) from Villany 3 (Hungary); (n') V.13.3632_d, left m1 from Villany 3 (Hungary); (o') V.13.10754.1, right m1 (mirrored) from Püspökfurdö/Betfia 2 (Romania); (p') LGPUT PET-1600, left m1–m2 from Petralona (Greece); (q') LGPUT PET-1602, right m1–m3 (mirrored) from Petralona (Greece); (r') IPS 14748, right m1–m2 (mirrored) from Cal Guardiola (Spain); (s') UWPI 2275/13/17, left p4–m2 from Deutsch Altenburg 2C (Austria); (t') UPWI 2275/13/1, right p4–m3 (mirrored) from Deutsch Altenburg 2C (Austria); (u') UPWI 2275/13/26, right m1–m3 (mirrored) from Deutsch Altenburg 2C (Austria).

4.4. Morphometric Comparisons

Comparisons of the upper and lower teeth measurements of *Vulpes* of Bajiazui with the Plio–Pleistocene and extant species of Eurasia are visible in Figures 5 and 6 (and 3D plots in the Supplementary Material). Figure 5 reports the principal component analysis on the upper teeth (length and width P3–M2).

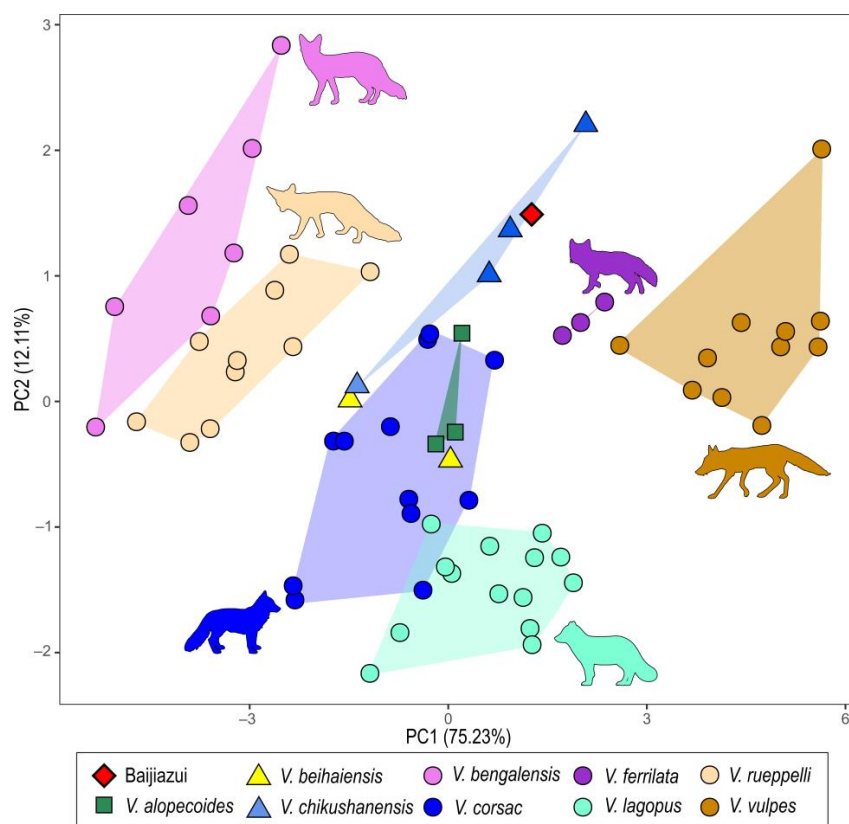


Figure 5. Principal component analysis on upper teeth variables (P3–M2 length and width) on extant and fossil *Vulpes* species. Symbols are explained in the legend. The red diamond is MLS028. *Vulpes chikushanensis* specimens from Jigushan (China) [25] are reported in light cerulean whereas that of Longdan (China) [15] in dark cerulean.

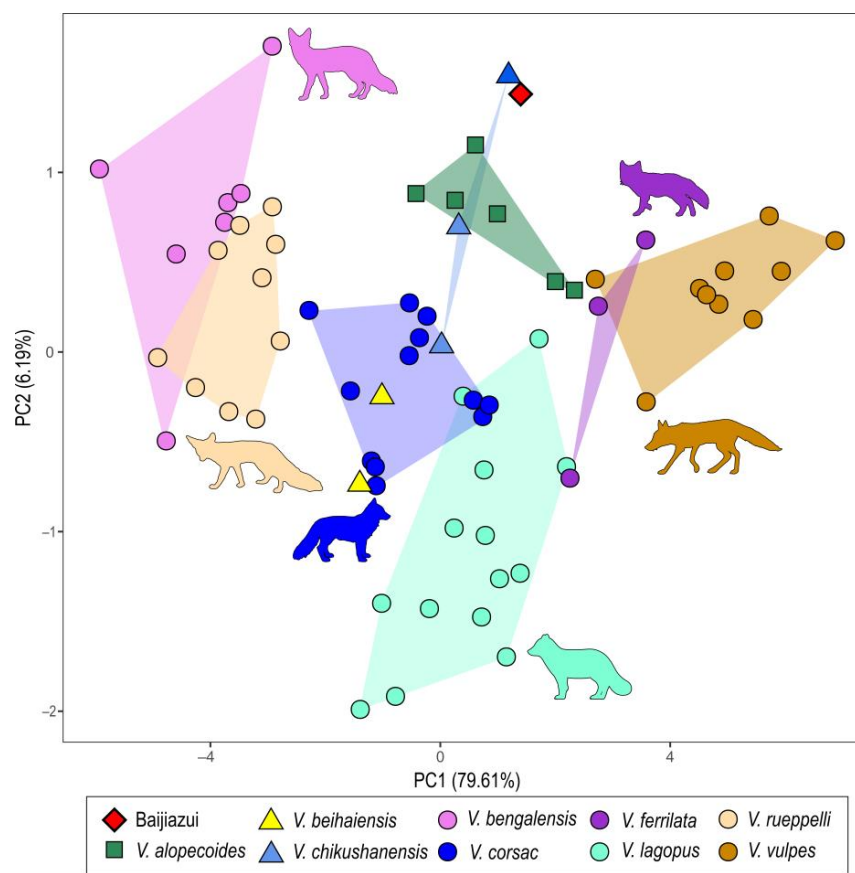


Figure 6. Principal component analysis on lower teeth variables (p3–m2 length and width) on extant and fossil *Vulpes* species. Symbols are explained in the legend. The red diamond is M63022. *Vulpes chikushanensis* specimens from Jigushan (China) [25] are reported in light cerulean whereas that of Longdan (China) [15] are in dark cerulean.

The PC1 represents 75.23% of the total variance and is positively influenced, in order, by the length of P4 and P3 and of the width of the P4 (see Table S1). Along this axis, the species are fairly well separated according to size, with *V. vulpes* occupying the positive end of the axis, whereas *V. bengalensis* and *V. rueppelli* have negative values. In between these extremes are medium-sized foxes, e.g., *V. corsac* and *V. lagopus*. The fossil species are in this latter group, with very low (positive and negative) values. The PC2 accounts for 12.11% of the variance and it is mainly influenced by the size of the upper molars, especially the width and length of the M2 and the width of the M1 (see Table S1). Along this axis, the extant species are clustered together: only *V. lagopus* is partially separated from the other species by its negative values. Fossil species range from very low negative values to positive values of *V. chikushanensis* and *Vulpes* from Bajiazui. In the analysis, *V. alopecoides*, *V. beihaiensis*, and *V. chikushanensis* from Jigushan are within the variability of the upper teeth of *V. corsac*. *Vulpes chikushanensis* has a wide variability, with the cranium from Jigushan having negative values of PC1 and low values of PC2, lying close to *V. beihaiensis* and *V. corsac*. In contrast, Longdan specimens have positive values for both PC1 and PC2. The fox of Bajiazui lies close to these specimens. Taking into account also PC3, which accounts for 4.12% of the variance and is positively influenced by the width of M2 and P3 (see Table S1), in a 3D plot (see Figure S1 and Supplementary Material), it is possible to confirm the pattern visible in Figure 5, with all taxa separated from one another and *Vulpes* from Bajiazui placed close to *V. chikushanensis* from Longdan.

Figure 6 shows the analysis of the principal components in the measures of the lower teeth (length and width p3–m2).

The PC1 here accounts for 79.61% of the variability and is mainly influenced by the length of m1, p4, and p3, respectively (see Table S2); the PC2 accounts for 6.19% of the total variance and is positively influenced by the length and width of m2 and by the width of the talonid m1 talonid (see Table S2). The distribution of the taxa is consistent with the PCA in the upper teeth (Figure 5) described above. Here, *V. alopecoides* is distinct from *V. corsac*. Again, *Vulpes* from Bajiazui lies close to the specimen from Longdan (V.13533). The 3D plot considering PC3 (accounting for 5.25% of the variability) confirms the distinction of the different species in the lower teeth (see Figure S1 and Supplementary Material).

5. Discussion

Taxonomical Attribution of the Bajiazui Specimens and the Status of V. chikushanensis

The fox specimens from the Early Pleistocene of Bajiazui described in this paper display several characteristics formerly attributed as characteristic of *Vulpes chikushanensis*, namely [9,15]: slender muzzle; slender P4 with reduced distolingual cingulum and reduced protocone; M1 not enlarged mesiodistally; M2 with reduced or absent metaconule; lower premolars with crowned lower premolars; m1 with larger hypoconid and reduced entoconid; and m2 with oval occlusal outline, narrow talonid and faintly buccal cingulid.

On the contrary, the studied specimens differ in some respects from other previously described species, specifically from the European *V. alopecoides*, which shows a larger muzzle; larger and individualized P4 protocone; mesiodistally enlarged M1; M2 slightly larger compared to the metacone; and m1 with a mesiodistally reduced paraconid and a stouter protoconid [6]. Finally, the Bajiazui specimens differ from *Vulpes corsac*, for example, in the deeper and wider outline of the zygomaticomaxillary suture, in lateral view; the stouter upper molars, especially in mesiodistal length at the mid level of the tooth; the similarity between M1 and M2 paracone and metacone; the m1 is more robust in occlusal view but with a proportionally shorter trigonid.

In summary, the reported evidence enables us to include the Bajiazui specimens in the Early Pleistocene Asian species, *Vulpes chikushanensis*, similar to that of Longdan (Gansu). The Jigushan fox was described by Young in 1930 in his revision of the mammalian fauna from a fossiliferous level near Zhoukoudian. This locality, known as Jigushan, 'Chicken Bones Hill' for its fossil accumulations, had already been investigated in the late 1910s by other paleontologists e.g., Zdansky, Andersson [30] and fossils unearthed. However, the study of the taxa recovered here was delayed by the discovery of the first tooth of the 'Pekin man' (*Homo erectus pekinensis*) by Zdansky [30]. Samples of *Vulpes* were fairly common in Jigushan [25] and were numerous. In his revision, Young [25] acknowledged the similarity envisioned by other scholars (e.g., Zdansky) of the fox from Jigushan to *V. corsac* reporting 'the clearest affinities of the *Vulpes* of Chi ku shan seem to be with the complex group of *V. corsac*' See Young [25] (p. 12). According to Young [25], the number of different forms of this 'group of *V. corsac*' justified the erection of a new species. After Young's description, all subsequent authors accepted this specific name and it was rooted in the literature as *V. chikushanensis* is reported from Huiyu (Zhoukoudian Loc. 18) [14], Longdan [15], Classic Nihewan fauna [31], Yuanmou [32,33]. Qiu and Tedford [9] pointed out the possibility that *V. chikushanensis* from the type locality might actually be conspecific of extant *V. corsac*, as at the time *corsac* fox was poorly known [9], or rather, it was its variability. The age of the site also might offer support to this interpretation, as Jigushan is early Middle Pleistocene. Nevertheless, subsequent authors have abandoned this hypothesis and put forward other ones, e.g., the possible conspecificity of *V. chikushanensis* and *Vulpes* sp. from Odessa Catacombs [15].

We agree that the specimens from Longdan, Huiyu (Zhoukoudian Loc. 18), and also Bajiazui show some differences from those described by Young [25], both morphologically and morphometrically (see Sections 4.3 and 4.4). Regarding the similarity between *V. chikushanensis* and *Vulpes* sp. of the Odessa Catacombs, the morphologies of the upper teeth of the cranium described by Odintzov [12] contrast strongly with those of Jigushan fox, but the lower teeth and the lateral shape of the mandible (see [12,15]) are indeed similar to

each other. Such a dichotomic condition and the revision needed for the taxon from Odessa Catacombs (currently undergoing, Ivanoff pers. comm.) favor caution in considering the two taxa as related or conspecific.

Taking into account the rarity of the Asian record and the current inaccessibility of the original specimens used by Young [25] in the collection from Zhoukoudian sites, it is difficult to adequately assess the degree of variability of *V. chikushanensis*. Modern species, for example *V. corsac*, *V. lagopus*, and *V. vulpes*, show high intraspecific variability [6,34,35], which could justify synonymizing historic taxa. However, discriminating between interspecific or intraspecific variability of Asian fossil foxes currently represents a challenge, unlike European ones [6]. Thus, we prefer to keep the specific name of *V. chikushanensis*, at least for the moment.

6. Concluding Remarks

We described for the first time the medium-sized fox remains coming from the Early Pleistocene of Bajiazui (Gansu, China). The dentognathic features of the studied material allowed us to include it in the species *V. chikushanensis*, a mesocarnivorous fox widely recorded in the earliest Pleistocene of China. Dental characteristics suggest a closer affinity of the latest from the Pliocene *V. beihaiensis* and possibly with the extant *V. corsac*. The available records of *V. chikushanensis* do not allow a precise comparison with the other widely recorded Eurasian form, e.g., *V. alopecoides*, either regarding dental variability or an eventual relationship between them. Despite these issues and the possible problematic status of the specific name, the discovery of a medium-sized fox-like *V. chikushanensis* in the late Early Pleistocene site of Bajiazui is relevant because it adds morphological and morphometric variance on this poorly known species.

The general cooling trend of the Northern Hemisphere started at the Latest Miocene intensified in the Latest Pliocene around 3 Ma. The former progressive aridification and the shift from subtropical environments to more open ones significantly affected the large mammal assemblages of Europe [36,37]. At the beginning of the Pleistocene the last tropical adapted species such as *Tapirus*, *Anancus*, or *Alephis* disappeared from Eurasian ecosystems being replaced by *Mammuthus*, *Leptobos*, or *Eucladoceros* [38]. Regarding carnivorans, at this time the first pursuit predators such as *Homotherium*, *Xenocyon*, or *Chasmaporthetes* were recorded in Eurasia [29,39,40]. More precisely, focusing on the small-to-medium-sized carnivores particularly influenced by climatic shifts, the initial appearances of the genera *Meles*, *Nyctereutes*, *Canis*, *Gulo*, and *Vulpes* were documented in Eurasia at the onset of the Early Pleistocene [38,39].

Certainly, the available records of Pliocene carnivorans are scanty, fragmented, and geographically distant and results easily compare the Late Pliocene to the Early Pleistocene ecosystems. Nevertheless, the loss of diversity of the fox group at the beginning of the Pleistocene seems significant, associated with the increase in diversity in the recorded small-to-medium-sized carnivorans and the change from hypercarnivorous forms such as *V. qiuzhudingi* and *V. rooki* to mesocarnivorous forms such as *V. alopecoides* and *V. chikushanensis*. In fact, the loss of diversity of the carnivoran guild in the latest Early Pleistocene [17] appears to be coeval with the second increase in diversity in the *Vulpes* group during the Early-Middle Pleistocene transition, when the first records of the arctic corsac and red foxes.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/quat6040057/s1>, Figure S1: 2D views of the 3D plot of PCA on upper teeth described in the main text; Figure S2: 2D views of the 3D plot of PCA on lower teeth described in the main text. Table S1: Loadings of the principal component analysis on upper teeth; Table S2: Loadings of the principal component analysis on lower teeth. Shtml file #1: PCA Upper teeth_3D PLOT; Shtml file #2: PCA Lower teeth_3D PLOT.

Author Contributions: Conceptualization, S.B.-L., J.M.-M. and Q.J.; writing—original draft preparation, S.B.-L.; writing—review and editing, S.B.-L., J.M.-M., Q.J., H.J., Z.L. and K.X.; photo making, Q.J.; analyses, figure preparation, S.B.-L. All authors have read and agreed to the published version of the manuscript.

Funding: S.B.-L. is supported by the Tuscany Region funds for young researchers “Giovani” (www.giovanisi.it (accessed on 1 May 2023)): ‘POR FSC 2014–2020’ funds for ‘Progetti di alta formazione attraverso l’attivazione di Assegni di Ricerca’.

Data Availability Statement: Data are available upon request to the corresponding author.

Acknowledgments: 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. Meng, curator of the fossil mammals collection of AMNH; M. Gasparik, curator of the Paleovertebrate collection of the HNHM. G. Koufos and D. Kostopoulos from the Earth Science Dept. of the AUTH; The MNHN gives access to the collections in the framework of the RECOLNAT national Research Infrastructure. We also thank X. Wang for kindly providing us the pictures of *V. qiuzhudingi*.

Conflicts of Interest: The authors declare no conflict of interest.

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