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A NEW LARGE-SIZED PLIOCENE FOX (CARNIVORA, CANIDAE) FROM YUSHE BASIN (SHANXI, CHINA)

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*Abstract***.** The Yushe Basin (Shanxi, China) represent one of the most renowned location of China for its Upper Miocene-Lower Pleistocene fossiliferous beds, with an outstanding record of vertebrates, often reference to other Asian localities. Fossils from the town of Xiakou are considered among the oldest records (late Gaozhuang-earliest Mazegouan) of *Eucyon davisi* in the Basin. Nevertheless, the study of some Early Pliocene specimens of this sample attributed to *E. davisi* possess several features typical of *Vulpes*. The revision of this material in comparison with that of other fossil fox species from Asia revealed the peculiarity of the *Vulpes* from Xiakou, both metrically and morphologically, leading to the description of a new species, *Vulpes rooki* sp. nov. Dental features and proportions suggest that this large-sized fox had probably a hypercarnivorous diet, unlike the similar-sized *E. davisi.* Following other results in literature, the considerably diverse fossil record of canids in the Yushe Basin supports the interpretation of niche partitioning among these species during the Early Pliocene.

INTRODUCTION

Extant diversity of the species of *Vulpes* in Asia is higher compared to that of the other continents. Of the twelve living species, seven of these dwells and thrive in Asian rich and diverse environments (Nowak 2005, Castelló 2018). Nowadays, three different species of foxes live in China: *Vulpes ferrilata* Hodgson, 1842, *Vulpes corsac* (Linnaeus, 1768) and *Vulpes vulpes* (Linnaeus, 1758). The extant red fox is one of the most widespread carnivorans, being present in five continents, and particularly in Eurasia and North America (Larivière & Pasitschniak-Arts 1996). It appeared in the early Middle Pleistocene in Eurasia (Kurtén 1968), and the oldest Asian record is that of the Chinese Locality 1 of Zhoukoudian, as reported by Pei (1934) (ca. 0.8-0.7 Ma; see also Li et al. 2014; Bartolini Lucenti & Madurell-Malapeira 2020). The corsac fox is a small-sized fox that inhabits arid steppes and desertic areas of central and southern Asia (Clark et al. 2009). The earliest record of this species also comes from Zhoukoudian Loc. 1 (Pei 1934), and it is dated to the earliest Middle Pleistocene (Li et al. 2014). Fossil evidence suggests that during the Middle-Late Pleistocene, its range was wider than the extant one, probably reaching eastern Europe (Kurtén 1968). The Tibetan sand fox is a short-legged and thickly-furred canid, well-adapted to steppe and arid environments of Tibet and central-southwestern China (Clark et al. 2009). At present, no fossil record

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of this species is known. Despite previous interpretations, molecular analyses revealed that *V. ferrilata* is closely related to *V. corsac* (Bininda-Emonds et al. 1999; Zhao et al. 2016).

The Asian fossil record of the genus *Vulpes* starts in the Early Pliocene. Wang et al. (2014) described the large-sized and hypercarnivorous *Vulpes qiuzhudingi* Wang, Tseng, Li, Takeuchi, Xie, 2014 from the Zanda Basin (correlated to a large timespan between 5.0 and 3.6 Ma). From the 4.0 Myr-old site of Çalta (Turkey) comes the small-sized *Vulpes galatica* Ginsburg, 1998. This species is only known for two hemimandibles, probably of the same individual and three isolated teeth, and has never been studied in detail since its description. Another Asian record of *Vulpes* is that of *Vulpes beihaiensis* Qiu and Tedford, 1990, dated around 3.3-3.2 Ma (Mazegouan; see Qiu et al. 2013) from the localities of Zhangwagou and Zhaozhuang of the Yushe Basin (Qiu & Tedford 1990). As opposed to the record of *V. qiuzhudingi*, *V. beihaiensis* was a small and corsac-like species known from fairly well-preserved cranial and mandibular specimens. After the early Mazegouan *V. beihaiensis*, no other fossil record of *Vulpes* is reported from China and more widely from Asia, at least until the beginning of the Nihewanian (Gelasian, Early Pleistocene; see Bartolini Lucenti & Madurell-Malapeira 2020), when arose *Vulpes chikushanensis* Young, 1930. This taxon is known from a number of fossil sites such as, from the earliest to the most recent: Longdan (ca. 2.4-2.2 Ma; see Qiu et al. 2004), Classic Nihewan fauna (ca. 2 Ma; see Teilhard de Chardin & Piveteau 1930) and Yuanmou (Wang et al. 2013) and the Jigushan/Zhoukoudian Loc. 6 (ca. 0.7 Ma; the type locality of Young 1930).

Here, two crania from the Yushe Basin locality of Xiakou (Nihe Subbasin), F:AM 97027 and F:AM 97058, previously attributed to *Eucyon davisi* (Merriam, 1911) (in Tedford & Qiu 1996), are restudied and ascribed to a new species of *Vulpes*. The exact locality from where the fossils come is not precisely located being reported as from "close to the town of Xiakou" (according to Tedford & Qiu 1996). These authors mentioned that the fauna associated with *E. davisi* and the new taxon include two hipparionines taxa: *Cremohipparion licenti* Qiu, Huang, Guo, 1987 and *Proboscidipparion pater* Matsumuto, 1927. *C. licenti* appears to be present in the Yushe basin until the late Gaozhuang age (ca 4.2-4.0 Ma, Qiu et al. 1987; 2013; Bernor et al. 2018). Similarly, the earliest appearance of the *P. pater* is in the Early Pliocene (5.0 Ma; Qiu et al. 2013; Bernor & Bo-Yang 2015; Bernor et al. 2018). Therefore, a late Gaozhuang age for the record of Xiakou locality appears to be supported. Nevertheless, some authors expressed doubts regarding the exact origin of some of the fossil specimens acquired in Xiakou village (Xiakoucun) (e.g., Li 2014), taking into consideration the different color of the fossils and the enclosing sediment. Such caution should be extended to "*Eucyon*" specimens, thus considering them slightly younger in age (ca. 4.0-3.0 Ma, late Gaozhuang-early Mazegouan, L. Flynn, Z. Qiu, and X. Wang personal communication).

MATERIALS AND METHODS

This study is based on comparative morphological analyses of the *Vulpes* species of the Pliocene to Early-Middle Pleistocene Eurasia. The examined fossil material derives from the Chinese locality of Xiakou (Yushe Basin, Shanxi). The described fossils are housed at the AMNH (see abbreviations below). As comparative fossil material, we studied the collections of several European institutions (ICP, IGF, HNHM, MHNL, MNHN, UCBL) and inspected all the relevant literature on Asian fossil *Vulpes* (Qiu & Tedford 1990; Qiu et al 2004; Wang et al. 2014). Furthermore *E. davisi* material from North America (Clay Bank Quarry, Redington Quarry, e.g., F:AM 63009, F:AM 63010; F:AM 63183) and Asia (Yushe basin localities like Zhaozhuang, Xiakou; e.g., F:AM 97056, F:AM 97057) from AMNH collections and casts of the type and paratype materials (UCMP 545; UO 26742; UOMNH F-3241) of IGF were studied in detail. Fossil species considered as comparison include *V. alopecoides* from Europe (sensu Bartolini Lucenti & Madurell-Malapeira 2020); *V. beihaiensis* from Zhaozhuang and Zhangwagou (Yushe Basin, China; Qiu & Tedford 1990); *V. chikushanensis* from Jigushan (Young 1930) and Longdan (Gansu, China; Qiu et al. 2004); *V. galatica* from Çalta (Turkey, Ginsburg 1998); and *V. qiuzhudingi* from the Zanda Basin (China, Wang et al. 2014). 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* sp. from Xiakou and other fossil and extant species. Molar ratio method (Asahara & Takai 2016; Bartolini Lucenti 2019) to estimate diet preferences of the considered taxa of *Vulpes*. Calculating the ratio between the areas of lower molars, this method has proved to be effective discriminator of the subtle intraspecific differences in diet of other canids (namely *Nyctereutes* Temminck, 1838).

Measurements were taken with a digital caliper to the nearest 0.1 mm following Driesch (1976) and Tedford et al. (2009).

Institutional abbreviations

AMNH, American Museum of Natural History, New York (United States of America); **HMHN**, Hungarian Museum of Natural History, Budapest (Hungary); **IGF**, Museum of Natural History, Geological and Paleontological section, University of Florence (Italy); **MNHN**, Musée National d'Histoire Naturelle, Paris (France); **MHNL**, Musée des Confluences, Lyon (France); **MZUF**, Museum of Natural History, "La Specola" Zoology section, University of Florence (Italy); **UCBL**, Université Claude Bernard Lyon-1, Lyon (France).

Anatomical abbreviations

Cranium: **AB**, height of the cranium without the sagittal crest (akrokranion-basion); **BL**, basal length of the cranium**; CBL**, condylobasal length of the cranium; **ECW**, external C1 alveoli width; **Eu**, greatest breadth of the braincase; **FL**, facial length; **GNL**, greatest length of the nasals; **GWOC**, greatest width of occipital condyles; **M2B,** ventral length of the neurocranium between the distal side of the M2 to the rostral side of the bulla tympanica; **MOH**, height of the maxilla-orbit area, from M1 to the infraorbital margin; **NCL**, neurocranium length; **PL**, palatal length; **PoCW**, least width of the postorbital constriction; **SH**, skull height (with sagittal crest); **TL**, total length of the cranium.

Dentition: **AC-M2 L**, alveolar length of the upper toothrow, from the distal side of the C to the distal side of the M2; **c-m2 L**, length of the lower toothrow between c-m2, from the mesial side of the canine to the distal margin of the m2; **c-m3 L**, length of the lower toothrow between c-m3, from the mesial side of the canine to the distal margin of the m3; **L**, mesiodistal length; **LLMR**, length of the lower molar row; **LLPR**, lower premolar row length; **LMR**, upper molar row length (M1-M2); **LPR**, upper premolar row length (P1-P4); **trm1**, trigonid of m1; **tdm1**, talonid of m1; **W**, buccolingual width.

Mandible: **Mm1B**: breadth of the mandibular corpus below the m1; **Mm1H**: mandibular corpus height distal to m1 alveolus; **Mp4H**: mandibular corpus height distal to p4 alveolus.

SYSTEMATIC PALEONTOLOGY

Order **Carnivora** Bowdich, 1821
Suborder **Caniformia** Kretzoi, 1943
Family Canidae Fischer, 1817
Subfamily Caninae Fischer, 1817
Tribe Vulpini Hemprich & Ehrenberg, 1832
Genus *Vulpes* Frisch, 1775

Vulpes rooki sp. nov.

Fig. 1; Table 1

1996 *Eucyon davisi* Tedford & Qiu

Holotype: F:AM 97027, cranium with left I3, P2, P4-M2 and right P3-M2.

Locality & Age: Xiakou (Nihe Subbasin, Yushe Basin, Shanxi, China), late Gaozhuang-early Mazegouan age, between 4.0-3.0 Ma (L. Flynn, Z. Qiu, and X. Wang personal communication).

Referred material: F:AM 97058, skull with left P2-M2 and right C-P2, P4-M2, and mandible with left i2-m3 and right i1-m3.

Diagnosis: medium-sized canid, larger than most, known fossil *Vulpes* species and similar to *Eucyon* taxa, in size; rostrocaudally elongated cranium; robust muzzle; laterally everted zygomatic bone; presence of the vulpine crease on the dorsal surface of zygomatic process of the frontal; marked postorbital constriction; parasagittal crests fuse slightly after the frontoparietal suture into a high sagittal crest, as visible in lateral view; nuchal crest enlarged dorsally but reduced lateral constriction, resulting in a modest bell-like caudal shape of the occipital; caudorostrally convergent medial side of the tympanic bullae; palate ends at level the mesial side of M2; I3 reduced and incisor-like; mesiodistally short C alveolus; stout P4; reduced P4 protocone; elongated P4 metastylar blade; enlarged M1 paracone, much higher than metacone; prominent protocone and hypocone compared to the reduced metaconule; M2 paracone considerably larger than metacone; M2 protocone large and metaconule nearly absent. Shallow mandible corpus. Lower protoconids of premolars are distally arched, in lateral view; m1 metaconid and entoconid are reduced; wide talonid basin; elongated m2, with developed buccal cuspids; reduced m2 entoconid, barely visible.

Derivatio nominis: The species is named after Prof. Lorenzo Rook, for his contributions to international Vertebrate Paleontology, from Mio-Pleistocene carnivorans, particularly Canidae, to Primate evolution and ecology.

Description

Cranium - Rostrocaudally elongated cranium with a rather robust muzzle, especially at level of the canines, and an inflated and pear-shaped braincase. Although broken in the type specimen F:AM 97027, the zygomatic bone of F:AM 97058 shows a laterally eversion of its dorsal margin. The frontal sinus is absent, as revealed from the broken portion of the frontal in F:AM 97027. Moreover, the dorsal surface of the zygomatic process of the frontal possesses a marked depression, as visible in dorsal and lateral views. In dorsal view, these processes are developed and sharply pointed. The postorbital constriction is rather marked. The parasagittal crests are prominent bone structures. They fuse just caudally to the frontoparietal suture into a high sagittal crest, especially caudally, in lateral view. Although the right bulla is missing and the ventral surface of the left one is broken, the tympanic bullae appear inflated and large, in lateral view. The acoustic meatus is oval in shape and large, nearly half the height of the bulla. In caudal view, the occipital region shows a modest bell-like shape. The nuchal crest is enlarged on its dorsal portion but does not possess almost no lateral constriction. In ventral view, the medial walls of the tympanic bullae markedly appear to be caudorostrally convergent. No paraoccipital process has preserved. Part of the palate is broken along all its length, but the right palatine bone is fairly complete. Both the greater and the lesser foramina palatina are visible. The caudal margin of the palate ends at level of the mesial side of M2. Short diastemata are present between C-P1 and P1-P2.

Upper teeth - The I3 appear to be reduced, with its alveolus closely attached to that of I2. The basal cingulum is visible but not so enlarge or marked,

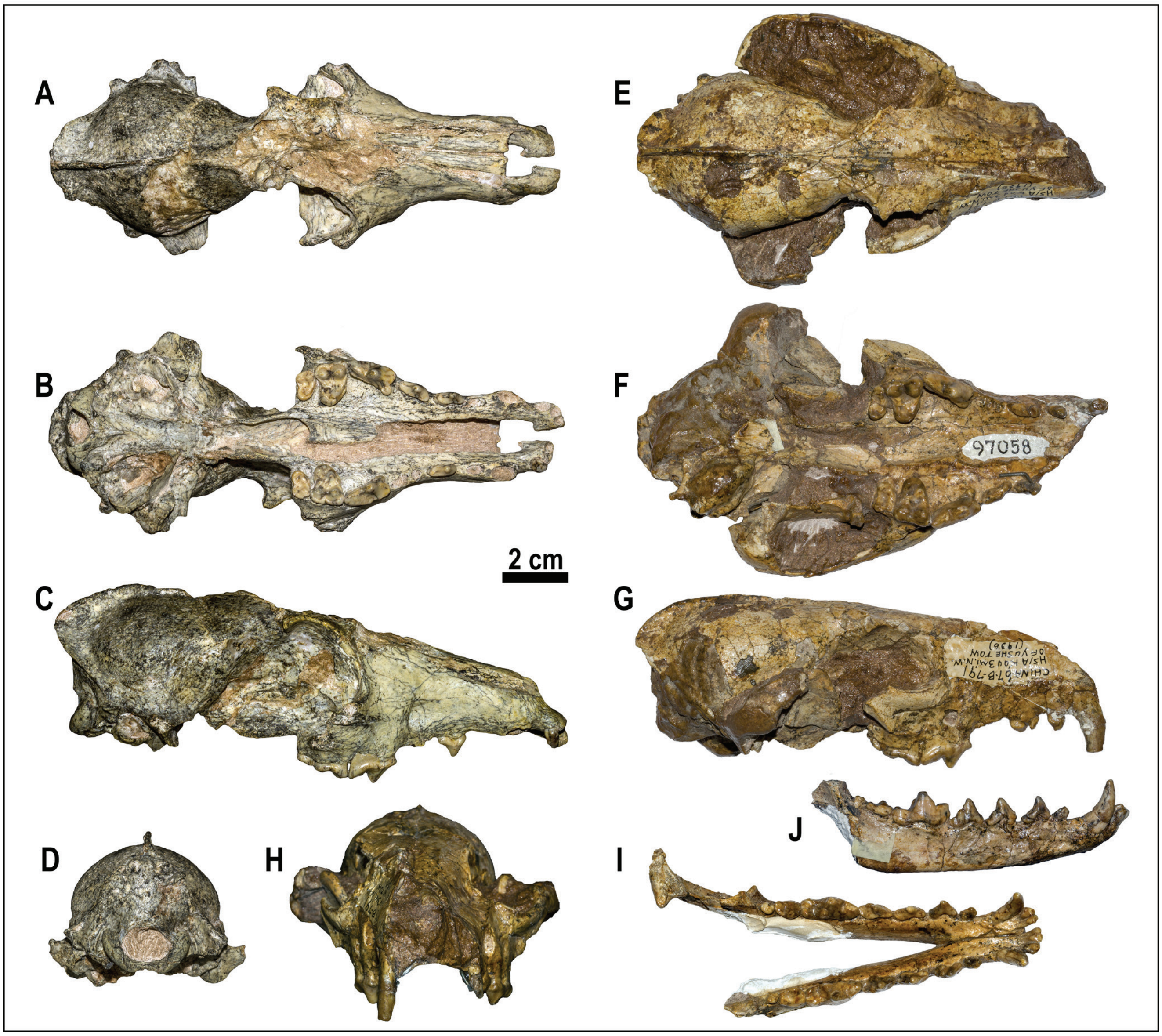

Fig. 1 - *Vulpes rooki* sp. nov. from Xiakou. A-D - F:AM 97027, cranium. A) Dorsal view. B) Ventral view. C) Right lateral view. D) Occipital view. E-J - F:AM 97058, skull. E) Dorsal view. F) Ventral view. G) Right lateral view. H) Frontal view. I) Mandible in occlusal view. J) Right hemimandible in buccal view.

but it possesses a swelling of the enamel in shape of a small cuspule, on its lingual side. The canine alveolus of F:AM 97027 is reduced in mesiodistal length compared to the alveolus of the I3 or of the premolars. The slenderness of the canine is confirmed by that of F:AM 97058, although broken. The upper premolars show a distal curvature of the protocone. The P1 is single-cusped, enlarged in the mesial portion and an elongated distally portion. The P2 is buccolingually compressed and elongated in mesiodistal sense. The P3 is larger than the P2, with larger mesial portion compared to the distal one, in F:AM 97027. The P4 is stout and well developed. It possesses an evident cingulum on its mesiobuccal side. The P4 protocone is reduced compared to the size of the P4, and only slightly advanced compared to the mesial margin of the paracone. The metastyle is sharp and long, similar in mesiodistal length to the paracone. On the distolingual side, there is a rather prominent cingulum, almost connected to the one on the mesiolingual part of the tooth. The M1 paracone is larger and much higher than metacone. The M1 is modestly arched distally, as the distal molar notch is wide and not marked, in occlusal view. A parastyle is present on the mesiobuccal corner of the paracone but it is not so prominent. Lingually, the protocone and the hypocone are considerably enlarged, especially in comparison to the reduced

	F:AM 97027	F:AM 97058		F:AM 97058
TL	153.0	–	**c L**	8.9
NCL	66.9	–	**c W**	5.1
FL	94.7	–	**p1 L**	5.1
Eu	46.8	47.6	**p1 W**	3,0
PoCW	22.1	23.75	**p2 L**	8.8
SH	39.7	42.0	**p2 W**	3.7
AB	34,0	31.8	**p3 L**	9.8
GWOC	25.3	–	**p3 W**	3.9
BL	138.4	–	**p4 L**	10.6
PL	75.4	–	**p4 W**	4.9
CBL	144.8	–	**m1 L**	18.3
ECW	25.7	–	**m1 W**	6.8
MOH	23.8	19.7	**trm1 L**	11.8
M2B	35,0	36.2	**tdm1 W**	6.4
AC-M2L	59.4	–	**m2 L**	7.9
P1-P4L	–	45.5	**m2 W**	5.6
M1-M2L	15.7	17.6	**m3 L**	4.4
C L	–	7.9	**m3 W**	3.6
C W	–	5,0	**Mm1H**	16.4
P1 L	–	5.6	**Mm1B**	8.4
P1 W	–	3.4	**Lc1m2L**	74.4
P2 L	8.2	–	**Lc1m3L**	78.3
P2 W	3.4	–	**LLPR**	36,0
P3 L	9.3	10.2	**LLMR**	29.7
P3 W	4.2	3.8		
P4 L	15.8	16.5		
P4 W	7.7	7.9		
M1 L	10.1	11.5		
M1 W	12.4	13.6		
M2 L	5.3	6.2		
M2 W	7.9	8.8		

Tab. 1 - Measurements of the *Vulpes rooki* sp. nov. from Xiakou.

metaconule. This cuspule is reduced and separated from the protocone, close to the distal margin of the M1. A small protoconule arises on the mesiobuccal side of the protocone. The buccal, mesial and even distal cingula are well developed, more markedly in F:AM 97027 compared to F:AM 97058. Distally, the lingual cingulum ends on the lingual side of the reduced metaconule. The trigon basin in wide and deep, compared to the reduced and S-shaped talon one. The M2 paracone is considerably larger than the metacone. No buccal notch is evident between these cusps, whereas the distal one is marked. The latter feature gives to the lingual portion of the M2 a distinct distally-curved occlusal morphology. The M2 protocone is large and conspicuous, whereas the metaconule nearly absent. The two cusps are connected by an evident postprotocrista. The M2 hypocone is cingular.

Mandible - The corpus of F:AM 97058 is rather thin and shallow. Its ventral margin is gently arched. No ramus is preserved as the with corpus is broken at the level of the m3 and the left one is broken dorsally and ventrally to the condyloid process.

Lower teeth - The canine is high in lateral view and buccolingually compressed in occlusal view. There are no diastemata between premolars. The protoconids of the lower premolars are arched distally. The p1 is well-developed, slightly elongated distally in an oval occlusal shape. The p2 shows an enlarged distal half and has no distal accessory cuspulid. The p3 is similar to the p2, but possesses a small accessory cuspulid emerging from the distal side of the protoconid. Distally, a shallow but evident cingulid bounds the distal portion of p1, p2 and p3. The p4 possesses a large distal accessory cuspulid; the right p4 of F:AM 97058 shows an incipient second, accessory cuspulid. The m1 is stout and moderately elongated. The metaconid is relatively reduced and fairly individualized from the protoconid. The entoconid is considerably smaller than the hypoconid and tend to be displaced distolingually on the talonid. The talonid basin is wide with no accessory cuspulids on the lingual side. The m2 is elongated mesiodistally and rather compressed buccolingually. The tooth in occlusal view has an ovoidal-shape with a larger mesial portion compared to the distal one. This results from the reduced size of the m2 entoconid, barely visible on the lingual margin. The m2 protoconid and hypoconid are enlarged. The m3 has two cuspulids, the buccal appears to be larger compared to the lingual one.

Comparisons

Comparison to *Eucyon davisi* from Yushe Basin and North America

Several cranial features differ between the specimens of *Vulpes* from Xiakou and *E. davisi* from Yushe Basin localities (see Tedford & Qiu 1996) and North America (Tedford et al. 2009). F:AM 97027 and F:AM 97058 possess an elongate neurocranium (Fig. 2A1) compared to the that of *E. davisi* specimens (e.g., F:AM 97056 or F:AM 97057) (Fig. 2A2). As evident from Fig. 2A1-A2, the postorbital constriction of *E. davisi* is poorly marked whereas in F:AM 97027 and F:AM 97058 it is narrow and pronounced. On the dorsal side of the zygomatic processes the presence of the vulpine crease on the of the frontals on F:AM 97027 and F:AM 97058 (Fig. 2B1, B3) differs from the inflated condition of *E. davisi* (Fig. 2B2). Another difference on the

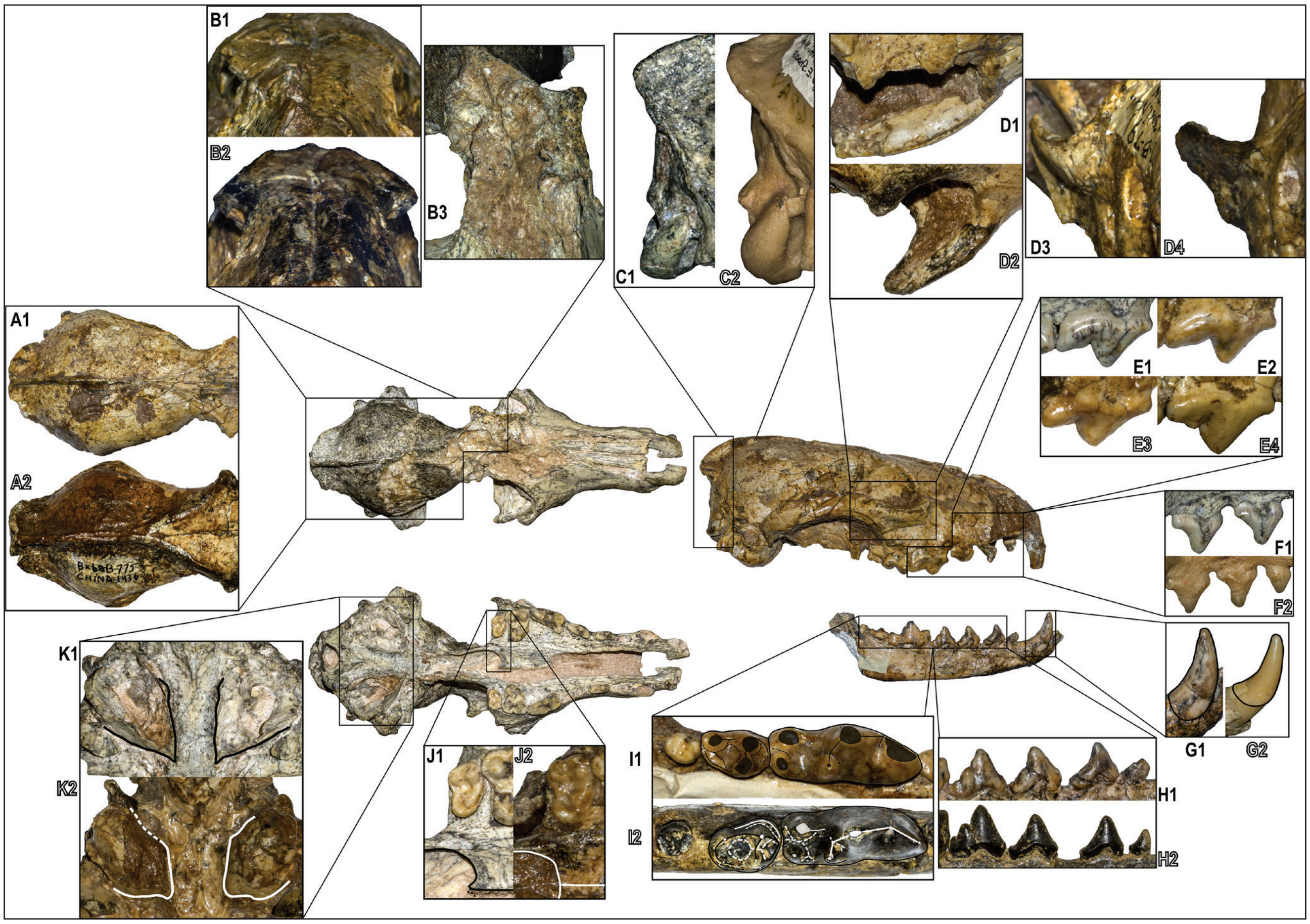

Fig. 2 - Comparison between the cranial and dentognathic features of *Vulpes rooki* sp. nov. (solid letters) and *Eucyon davisi* (outlined text).

neurocranium can be seen in lateral and caudal views: the nuchal processes of *E. davisi* are prominent and jutting processes (Fig. 2C2) as opposed to the reduced ones of *Vulpes* sp. (Fig. 2C1). The rostrolateral portion of the zygomatic bone of F:AM 97027 and F:AM 97058 is everted (Fig. 2D1) and, in rostral view, appears thick and flattened (Fig. 2D3). The dorsal margin of the zygomatic bone in *E. davisi* does not everts laterally (Fig. 2D2) and is thinner and sharper in rostral view (Fig. 2D4). In ventral view, the tympanic bullae of F:AM 97027 and F:AM 97058 possess a convex rostromedial portion (Fig. 2K1). On the contrary this area in *E. davisi* is concave (Fig. 2K2). Moreover, the bulla of *E. davisi* is larger in ventral view, but less inflated when observed in lateral view. In F:AM 97027 and F:AM 97058 bullae are markedly inflated in lateral view but rather narrower if observed ventrally. In the *Vulpes* sample from Xiakou the palate ends at the level of the medial side of the M2 (Fig. 2J1), whereas in *E. davisi* the caudal margin of the palatines extends till the distal margin of the M2 or beyond it (Fig. 2J2). This caudal margin differs in the two taxa: in *E. davisi* show a single concavity with poorly evident nasal processes; in *Vulpes* from Xiakou the palate is evidently biconcave (each palatine bone has a concave margin) (Fig. 2I1). Upper and lower premolars of *Vulpes* sp. show a distal curvature of the principal cusps/cuspids (Fig. 2F1, H1) in contrast to the upright morphology of those of *E. davisi* (Fig. 2F2, H2). The P4 of *Vulpes* sp. from Xiakou is stouter, buccolingually, compared to that of *E. davisi*. Moreover, in F:AM 97027 and F:AM 97058, it shows a longer and buccolingually slender metastylar blade compared to that of *E. davisi* (Fig. 2E1-E2), which in turn possesses a longer and stouter paracone (Fig. 2E3-E4). The features of the M1 of *Vulpes* from Xiakou as opposed to *E. davisi* are the larger and higher paracone, the enlarged and lingually displaced protocone and the wide trigon basin. The M2 of *E. davisi* has a generally lobed buccal outline of the buccal cingulum, unlike in *Vulpes* from Xiakou. Furthermore, it is mesiodistally enlarged in the specimens of the *E. davisi*, unlike the more slender morphology of latter, in occlusal view (Fig. 2J1-J2). The canines, especially the lower ones, of *Vulpes* from Xiakou have a higher crown compared to those of *E. davisi* (Fig. 2G1-G2). The larger M2 paracone characterizes *Vulpes* from Xiakou as opposed to the equal-sized buccal cuspulids of *E. davisi*. The height of the p4 protoconid, conspicuously higher compared to the m1 paraconid, characterizes F:AM 97058 as opposed to *E. davisi* specimens. The m1 entoconid in *E. davisi* is smaller than the hypoconid but still a developed cuspulid (Fig. 2I2), whereas in F:AM 97058 is displaced distolingually on the talonid (Fig. 2I1) and more reduced. The talonid basin of F:AM 97058 is wider than in *E. davisi* (e.g., F:AM 97031). The m2 of F:AM 97058 is elongated, with enlarged protoconid and hypoconid (Fig. 2I1). In *E. davisi*, the m2 possesses an enlarged buccal cingulid, extending distally till the hypoconid (Fig. 2I2), unlike F:AM 97058. The m2 entoconid of *E. davisi* is more developed compared to that of F:AM 97058 (Fig. 2I2), in which it is greatly reduced, barely evident on the lingual side of the tooth(Fig. 2I1). The m3 is bicuspid in both *E. davisi* and *Vulpes* sp. from Xiakou but in the former, protoconid and metaconid are equal in size whereas in *Vulpes* sp. the buccal protoconid is considerably enlarged compared to the lingual cuspulid (Fig. 2I). The peculiarity of *Vulpes* sp. from Xiakou as opposed to *E. davisi* is also testified to by cranial ratios showed in Fig. 3. Particularly, in the relative width the occipital condyles, the relative proportion of the muzzle and the neurocranium and the breadth of the palate at level of the canines show marked difference between the large-sized fox and *E. davisi*.

Comparison to other Asian fossil *Vulpes* spp.

Compared to other Late Pliocene and Early Pleistocene Asian species, *Vulpes* sp. from Xiakou is larger and the cranium is, in general, more robust. For instance, *V. beihaiensis* is considerably more slender and smaller. The muzzle of *Vulpes* from Xiakou is enlarged and stouter. In comparison, both in *V. beihaiensis* and *V. chikushanensis* from Longdan possess slender and elongated muzzle. In lateral view, the orbit of the latter two species is proportionally larger than in *Vulpes* from Xiakou. The braincase of *Vulpes* from Xiakou is longer rostrocaudally compared to both *V. beihaiensis* and *V. chikushanensis* from Longdan and Jigushan. Other prominent differences with *V. beihaiensis* are the high parasagittal and sagittal crests, in lateral view, and the laterally expanded nuchal crests in dorsal view, whereas *V. beihaiensis* have reduced and lyre-shaped sagittal crest and, in dorsal view, the nuchal crest is prominent only in the area of the external occipital protuberance. Similarly, *V. chikushanensis* from Longdan resembles *V. beihaiensis* in the dorsal morphology of the parasagittal crests. In lateral view, the meatus acusticus of *Vulpes* from Xiakou is oval and large although proportionally smaller compared to that of *V. beihaiensis*, in which it is greatly inflated and bulging. The distal margin of the palate in *V. chikushanensis* from Longdan reaches the distal margin of the M2, unlike *Vulpes* from Xiakou, in which the palatine bone extends only to the mesial half of the M2. The P4 of *V. beihaiensis*, *V. chikushanensis* and *V. galatica* is considerably more slender and thinner compared to that of *Vulpes* from Xiakou, especially on the paracone and distally on the metastyle. The P4 protocone is proportionally reduced in *Vulpes* from Xiakou compared to *V. beihaiensis*, *V. chikushanensis* and *V. galatica*, in which it is developed. The cingula of the M1 in *Vulpes* from Xiakou are greatly marked compared to those of *V. beihaiensis*. In occlusal view, the M1 of *Vulpes* from Xiakou is distally arched, whereas in *V. beihaiensis* is elongated in buccolingual sense. In the latter taxon, the M1 paracone is similar or slightly larger compared to the metacone, but in F:AM 97027 and F:AM 97058 the M1 paracone is considerably larger compared to the other buccal cusp. The development of the trigon basin is similar in the two taxa but the talon one is wider in *V. beihaiensis* compared to *Vulpes* from Xiakou, in which is reduced by the expansion of the hypocone. The M1 metaconule is proportionally larger and higher in *V. beihaiensis* and *V. chikushanensis*, whereas *Vulpes* from Xiakou possesses a very shallow one. The mesiodistally enlarged M2 of *Vulpes* from Xiakou contrasts with the slender occlusal morphology of *V. beihaiensis* and *V. chikushanensis*. The M2 of *V. galatica* is more elongated mesiodistally compared to that of the latter two species. *V. chikushanensis* shares with *Vulpes* from Xiakou the enlarged M2 paracone compared to the metacone, whereas both *V. beihaiensis* and *V. galatica* has equal-sized M2 buccal cusps. No metaconule appears on the distal side of the M2 of *V. chikushanensis* and *V. galatica*, whereas the latter possess a reduced but evident metaconule. The mandible corpus is deeper compared to that

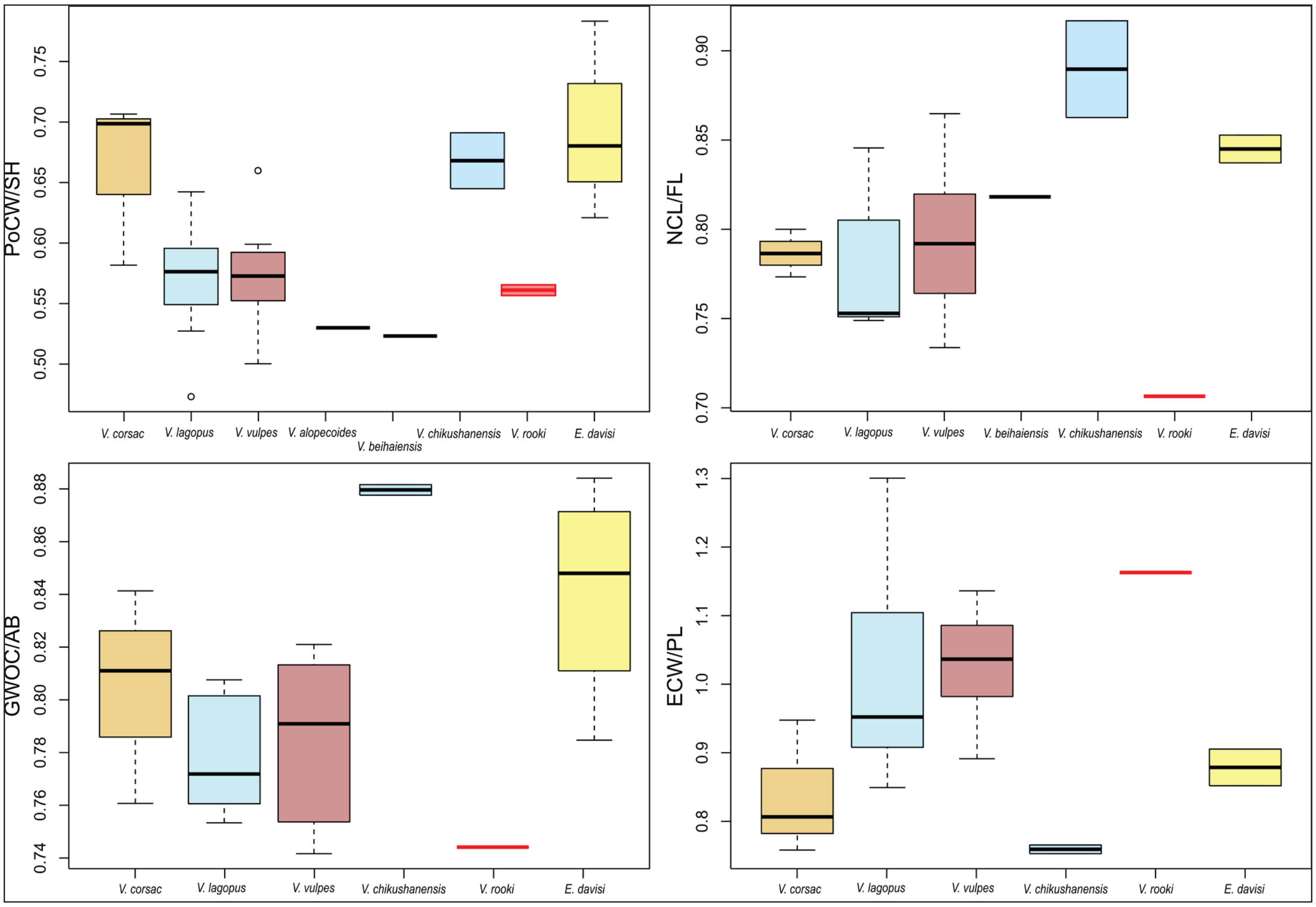

Fig. 3 - Boxplot of selected cranial ratios in fossil and extant species of *Vulpes* and in *E. davisi* (from North America and China). Abbreviations (see also Materials and Methods): AB, height of the cranium without the sagittal crest (akrokranion-basion); ECW, width of the muzzle across the canines; FL, facial length; GWOC, greatest width of the occipital condyles; NCL, neurocranial length; PL, palate length; PoCW, width of the postorbital constriction; SH, skull height, comprising the sagittal crest.

of *V. beihaiensis* and *V. galatica*. It proportionally resembles that of *V. chikushanensis* and *V. qiuzhudingi* from the Zanda Basin (Wang et al. 2014), although larger than these species. The arched ventral margin of the mandible corpus is similar to the other *Vulpes* species. The lower premolars distal curvature contrasts with the morphology of *V. beihaiensis* from Yushe Basin and *V. galatica*, in which their protoconids are fairly high and upright, and of *V. qiuzhudingi* from the Zanda Basin (Wang et al. 2014). *Vulpes chikushanensis* from Longdan shares with *Vulpes* from Xiakou the distally curved morphology of the lower premolars. This curvature is not so evident in *V. chikushanensis* from Jigushan. Unlike *Vulpes* from Xiakou and *V. qiuzhudingi*, *V. beihaiensis*, *V. galatica* and *V. chikushanensis* possess evident distal cingulid on the lower premolars. In *V. chikushanensis* the p1 is reduced, unlike in *Vulpes* from Xiakou. The distal portion of the p2 in *Vulpes* from Xiakou, and even more in *V. qiuzhudingi* from the Zanda Basin, is enlarged compared to the mesial one. On the contrary, *V. beihaiensis*, *V. galatica* and *V. chikushanensis* show similar-sized mesial and distal portions. The p4 of *V. beihaiensis*, *V. galatica* and *V. chikushanensis* from Longdan possess a feeble mesial accessory cuspulid not present in *Vulpes* sp. from Xiakou. *V. galatica* from Çalta shows an incipient second distal accessory cuspulid on a p4 as in *Vulpes* sp. from Xiakou. which is present. The lower carnassial of *V. beihaiensis* and *V. galatica* is shorter mesiodistally compared to that of *Vulpes* from Xiakou. *Vulpes qiuzhudingi* from the Zanda Basin show a stout m1 trigonid (robust paraconid and protoconid) with a considerably reduced metaconid, individualized from the protoconid but not jutting lingually. The m1 metaconid of *V. chikushanensis* from Longdan is developed unlike that of *Vulpes* from Xiakou. On the talonid, the m1 entoconid of *V. beihaiensis*, *V. galatica* and *V. chikushanensis* from Longdan is prominent and not reduced, yet being smaller that the hypoconid. Thus, differing from *Vulpes* from Xiakou. The m1 talonid of *V. qiuzhudingi* is greatly reduced in mesiodistal

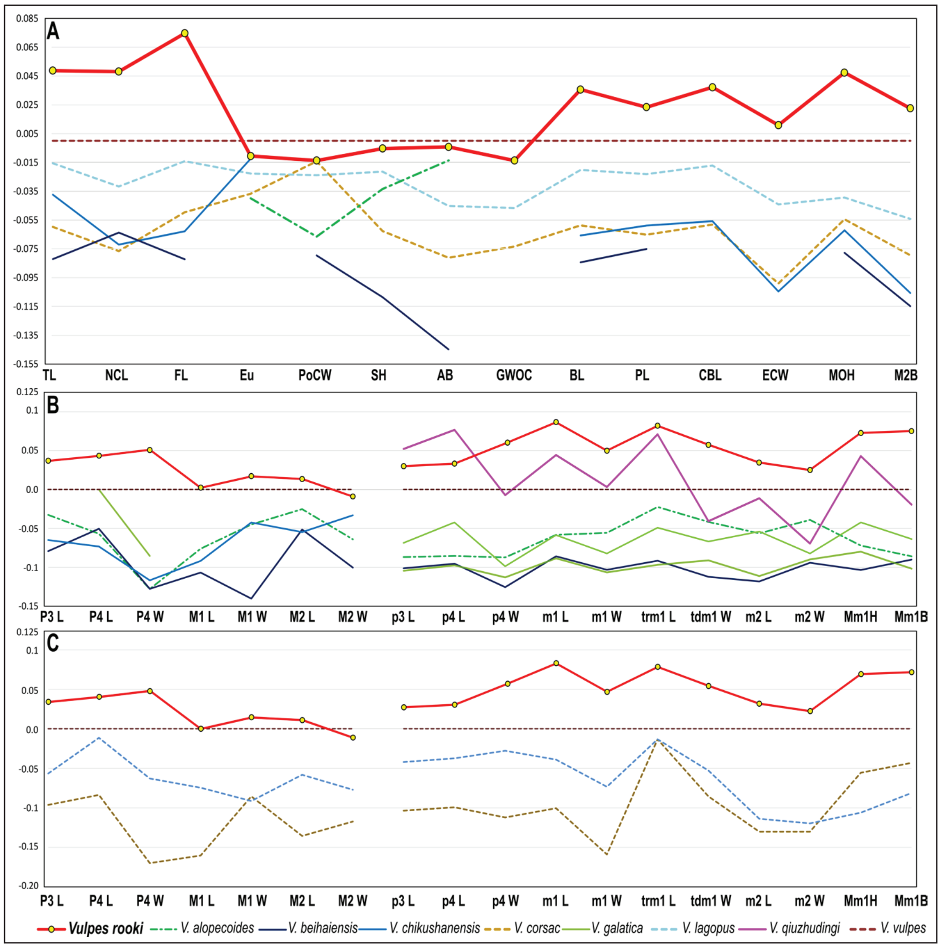

Fig. 4 - Log-ratio diagram based on selected cranial (A) and dentognathic variables (B-C) in the described as well as in other Plio-Pleistocene species of *Vulpes* (*V. alopecoides* from Europe; *V. beihaiensis* from the Yushe Basin, *V. chikushanensis* from Longdan, *V. galatica* from Çalta, *V. qiuzhudingi* from the Zanda Basin data taken from the literature: Qiu et al. 2004; Wang et al. 2014) as compared to extant *V. corsac*, *V. lagopus* and *V. vulpes* (the latter used as the reference baseline).

length, unlike that of *Vulpes* from Xiakou. The m1 hypoconid occupies the majority of the talonid in the species from the Zanda Basin, as the entoconid is considerably reduced, more compared to *Vulpes* from Xiakou. In *V. qiuzhudingi*, the talonid basin is a small, round basin, closed lingually by a cristid arising from the mesial side of the entoconid, as opposed to the wider and lingually-open talonid basin of *Vulpes* sp. from Xiakou. In contrast to this condition and to *Vulpes* from Xiakou, *V. beihaiensis*, *V. galatica* and *V. chikushanensis* from Longdan possess an m1 entoconulid, particularly developed in the latter. A distal cingulid bounds the distal side of the m1 in *V. beihaiensis* and in *V. chikushanensis* from Longdan, and in the latter it extends on the buccal side of the tooth. Several features of the m2 of *V. beihaiensis* and of *V. galatica* contrast with that of *Vulpes* from Xiakou: the rectangular-like shape, the expanded buccal cingulid bounding the buccal margin reaching the hypoconid; the similarity in size between protoconid and metaconid; and the presence of a developed entoconid and, in *V. beihaiensis*, of an entoconulid. *V. chikushanensis* from Longdan and *V. qiuzhudingi* share with *Vulpes* from Xiakou the reduction of the buccal cingulid on the m2, not extended distally until the hypoconid. The m2 talonid of *V. chikushanensis* from Longdan is not reduced lingually as in *Vulpes* from Xiakou. The entoconid is not large but evident in *V. chikushanensis* from Longdan and on its mesial side there is an accessory cuspulid. Moreover, the m2 hypoconid of *V. chikushanensis* from Longdan is proportionally reduced as opposed to that of *Vulpes* from Xiakou. The occlusal morphology of the m2 of *V. qiuzhudingi* is ovoidal, with a greatly enlarged mesial portion and a narrow and short talonid one. Mesially, *V. qiuzhudingi* shows a conspicuously enlarged protoconid compared to the metaconid, unlike *Vulpes* from Xiakou. Moreover, these two cuspulids tend to coalesce together, whereas in *Vulpes* from Xiakou are separated. Distally, the hypoconid of *V. qiuzhudingi* is considerably enlarged and centralized. Lingually, there is not sign of cristid or cuspulids. In contrast to *Vulpes* from Xiakou and *V. beihaiensis*, *V. qiuzhudingi* and some specimens of *V. chikushanensis* from Longdan, do not possess the m3. The m3 of *V. beihaiensis* and *V. galatica* is large round with similar-sized cuspulids, whereas in *Vulpes* from Xiakou the m3 is oval with buccal cuspulid larger than the lingual one.

The peculiarities of *Vulpes* sp. from Xiakou are visible in its cranial and dental proportions (Figs. 3-4). Indeed, the pattern displayed by this taxon is unique among the known species of the fossil record. As for the case of *E. davisi*, the relative size of *Vulpes* sp. from Xiakou differ greatly from the other fossil *Vulpes* species (Fig. 3). The values of its ratios fall in the range of the extant *V. lagopus* and *V. vulpes*, although out of their typical variance. With the exception of the relative length of the neurocranium, in comparison to the length of the muzzle.

In general proportions, *Vulpes* from Xiakou is larger compared to the average *V. vulpes*, and considerably larger compared to *V. lagopus, V. corsac* and the considered fossil species. The only exceptions are the width of the braincase, the marked postorbital constriction, the skull height, the width across the occipital condyles, and the buccolingual width of the M2, all traits in which *V. vulpes* is larger.

Besides the larger size, cranial values testify to the peculiarity of *Vulpes* sp. from Xiakou. The longer muzzle (FL) and the proportionally narrow and short cranium (as visible from the pattern of e.g., Eu, PoCW, SH, Fig. 4A), are distinctive features that distinguish the new species from Xiakou from the other considered taxa. In some proportions, *Vulpes* sp. from Xiakou resembles *V. lagopus* and *V. corsac*, despite its size. Apart from the reduced difference between skull height considering the sagittal crest and cranial height without the crest (SH-AB), *V. lagopus*' pattern follows that of *Vulpes* sp., although smaller. *V. corsac* resembles the proportions of *Vulpes* sp. especially in ventral lengths (BL-CBL), the width of the muzzle at canines the height of the maxilla (MOH) and the ventral length of the neurocranium (M2B). Similarly, can be said for the pattern *V. chikushanensis*, for the values CBL-M2B. Dentally (Fig. 4B-C), the pattern of the upper teeth of *Vulpes* sp. from Xiakou does not deviate considerably from that of *V. vulpes*, a part from the longer P4 and the buccolingually shorter M2 as in *V. lagopus* (Fig. 4C). Even in lower teeth the arctic fox does not differ considerably from *Vulpes* sp., despite the proportionally smaller m2 and the thicker mandible in the former (Fig. 4C). *Vulpes* sp. from Xiakou differs markedly from the other fossil Asian species and also from *V. alopecoides* from Europe (Fig. 4B). It shares with *V. beihaiensis*, *V. chikushanensis* and *V. qiuzhudingi* the longer and narrower m1 compared to those of *V. vulpes* (Fig. 4B). In contrast to *Vulpes* sp. from Xiakou, *V. qiuzhudingi* has a considerably reduced width of the m1 talonid and of the m2, whereas *V. beihaiensis* shows a buccolingually enlarged m2.

DISCUSSIONS

Taxonomic interpretation of *Vulpes* material from Xiakou

Although ascribed to *E. davisi* by Tedford & Qiu (1996), the specimens F:AM 97027 and F:AM 97058 from Xiakou (Yushe Basin, China) possess several morphological features unfitting with the typical and diagnostic morphologies of *E. davisi* from the same and other localities of the Yushe Basin (Tedford & Qiu 1996) and also from North America (Tedford et al. 2009) (Figs. 1-2). Some of them suggest the plausible reascription of the specimens to the genus *Vulpes*, like: the marked eversion of the zygomatic bone, the presence of the vulpine crease, the reduction of the frontal sinuses (not inflated towards the tip of the zygomatic process of the frontals), or the marked postorbital constriction, high-crowned canine (see Fig. 2). This is also confirmed by cranial ratios (Fig. 3). The relevance of the cranial ratios as discriminating elements between canid taxa was pointed out by several authors (e.g., Cherin et al. 2014).

Considering the mensural variability of the fossil foxes, *Vulpes* from Xiakou is larger compared to all other species, as visible in Fig. 4, being close only to *V. qiuzhudingi*. Moreover, its morphometric pattern does not resemble that of any other fossil species. Some proportions are similar to those of other species e.g., reduced width of the M2 of *V. alopecoides*, *V. beihaiensis* and *V. galatica*, or the longer and narrower m1 and longer trigonid like *V. beihaiensis*, *V. galatica* and *V. qiuzhudingi*.

Although some cranial ratios of *Vulpes* from Xiakou are close to *V. lagopus* and *V. vulpes* (Fig. 3), its cranial proportions (Fig. 4A) are different from those of the other fossil and extant species, . For instance, despite its large size, the slender dorsal outline of the neurocranium, the marked postorbital constriction the comparatively short cranium in height, when observed in lateral view, are close to

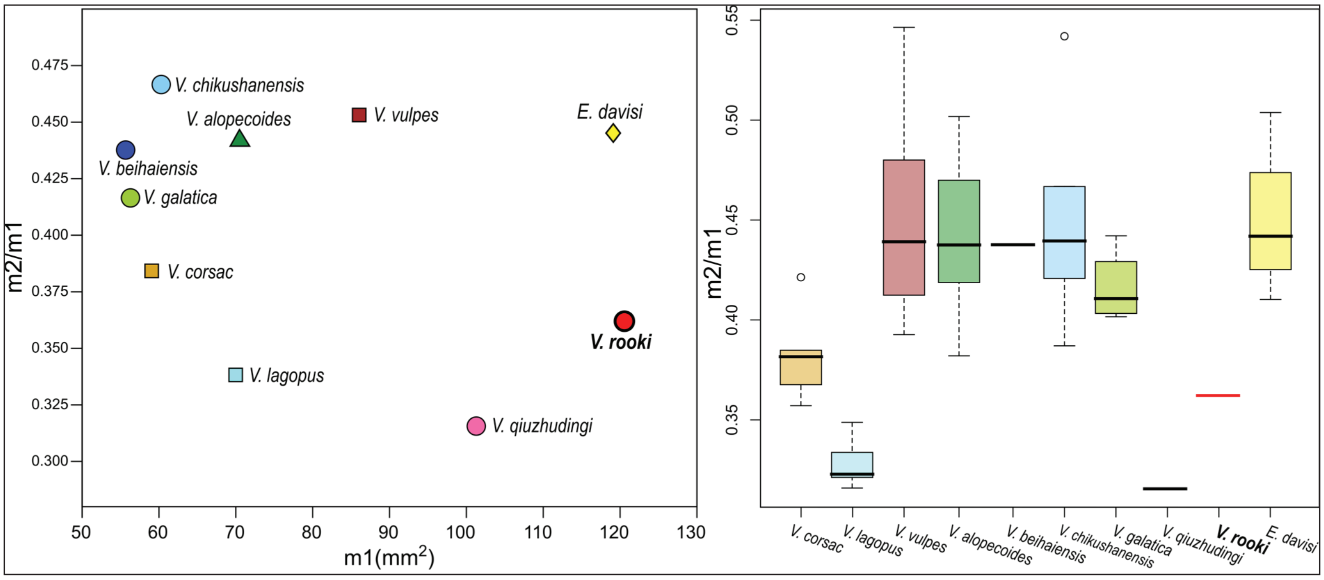

Fig. 5 - Left, biplot of the m2/m1 scores against the m1 occlusal surface (following Asahara & Takai 2016) in various fossil and extant species of *Vulpes* and in *E. davisi*. Squares are extant species; circles are extinct Asian taxa; triangle is the European *V. alopecoides* (sensu Bartolini Lucenti & Madurell-Malapeira 2020); diamond is *E. davisi* from Yushe Basin. Right, boxplots showing the range of variance of the molar ratios in fossil and extant species of *Vulpes* and *E. davisi*.

those of extant *V. vulpes*. This ends in the narrow and rostrocaudally elongate appearance of the cranium (Fig 1). *Vulpes lagopus* and *V. corsac* shares similar proportions with the taxon from Xiakou, especially the former. Unlike them, *Vulpes* from Xiakou possesses a long neurocranium (NCL) and a proportionally higher occipital triangle (AB). Whereas, *V. lagopus* shares the comparable basal proportions, *V. corsac* has proportionally high maxilla and ventral side of the neurocranium. Despite its size, *Vulpes* from Xiakou is somewhat intermediate between the morphometric patterns of *V. lagopus* and *V. corsac*. Besides the fragmentary status of the fossil record of Asian foxes, none of the fossil species resemble the pattern of *Vulpes* sp. from Xiakou. For instance, *V. chikushanensis* from Longdan and Jigushan show a more marked reduction of the cranium at the level of canine (ECW) and ventral length of the neurocranium (M2B) compared to the condylobasal length as opposed to *Vulpes* from Xiakou. Indeed, the morphological features of this taxon differ with those of *V. beihaiensis* from Yushe Basin and also of *V. chikushanensis* from Longdan and Jigushan. For instance, *Vulpes* from Xiakou shows a high sagittal crest, marked straight parasagittal ridges and a high occipital triangle, whereas the two smaller species possess lyre-shapes or caudally curved parasagittal ridges and a short occipital triangle (with an arched caudal morphology of the braincase, in lateral view). At present, no cranial specimen of *V. galatica* nor of *V. qiuzhudingi* is known.

Dentally, *Vulpes* from Xiakou contrast with the marked sawtooth-like pattern of proportions showed by other fossil species (i.e., *V. beihaiensis*, *V. chikushanensis*, *V. galatica* and *V. qiuzhudingi*) (Fig. 4A). *V. alopecoides* does not resemble the proportions of *Vulpes* from Xiakou, both in upper and lower teeth (Fig. 4A). The morphological features of *V. alopecoides* from Europe (Bartolini Lucenti & Madurell-Malapeira, 2020), *V. beihaiensis* from Yushe Basin, *V. chikushanensis* from Longdan and Jigushan, and *V. galatica* differ markedly from those of *Vulpes* from Xiakou, confirming the morphometric evidence. Compared to *V. vulpes* the latter taxon has longer P4, buccolingually shorter M2 and a considerably longer m1 trigonid.

These features are shared with the hypercarnivorous *V. lagopus*, which shares a similar morphometric pattern compared to *Vulpes* from Xiakou (with the exception of a buccolingually reduced M1, smaller m2 and proportionally thicker mandible corpus in the arctic fox). Morphometric values consistent with hypercarnivorous diet are also evident in the pattern of *V. qiuzhudingi* from the Zanda Basin, e.g., the strongly elongate trigonid compared to the talonid or the reduced width of the m2. This taxon was described by Wang et al. (2014) as the possible ancestor of the modern *V. lagopus*. Surely, the features possessed by the type specimens clearly point out the hypercarnivorous diet of this Early Pliocene taxon, to some extent even more developed, both morphologically and morphometrically, than those of the extant *V. lagopus* (Wang et al. 2014). Certain morphologies of the *Vulpes* from Xiakou, e.g., the development of the buccal cuspids/cuspulids and the reduction of lingual ones such as the M1 metaconule, m1 and m2 entoconids, are suggestive of a possible adaptation to hypercarnivory, incipient compared to *V. lagopus* and surely less marked compared to that of *V. qiuzhudingi*. Nevertheless, the adaptation of *Vulpes* from Xiakou can neither be assimilated compared to those of the other fossil species from the Eurasia (i.e., *V. beihaiensis*, *V. chikushanensis*, *V. galatica*, *V. alopecoides*; see Qiu & Tedford 1990; Ginsburg 1998; Qiu et al. 2004; Bartolini Lucenti & Madurell-Malapeira 2020). Considering all the distinctive features possessed by the specimens of *Vulpes* sp. from Xiakou, the large-sized taxon cannot be ascribed to any known species and it is thus named as *Vulpes rooki* sp. nov.

Insights on the dietary preferences of fossil Eurasian foxes

Figure 5 shows the results of the analysis of molar ratios in the considered species of *Vulpes* and in *E. davisi*, and the variance of these ratios in the analyzed species. Higher values of m2/m1 index is the consequence of larger crushing surface of the lower molars (Asahara & Takai 2016; Bartolini Lucenti 2019). In turns this is connected to the tendency of the a more hypocarnivorous diet (i.e., less income of meat in the diet). The pattern of distribution of the extant species confirms this interpretation also in other Canidae (as shown by Asahara et al. 2016). *Vulpes vulpes*, a mesocarnivorous species (meat income in the diet around 50-70%, generally from small preys, Van Valkenburg & Koepfli 1993; Larivière and Pasitschniak-Arts 1996), has the highest scores of the extant species (m2/m1=0.453). *V. corsac* and *V. lagopus*, two hypercarnivorous species that prey on small-sized prey (Van Valkenburg & Koepfli 1993; Audet et al. 2002; Clark et al. 2009) have mean scores lower than 0.40, respectively m2/m1=0.384 and 0.338. The elongation of the trigonid portion of the lower carnassial and the reduction of the talonid, resulting in lower molar ratios, are common elements in hypercarnivorous species of Carnivora in general (Biknevicius & Van Valkenburgh 1996; Asahara et al. 2016) and in Canidae (Van Valkenburgh et al. 2003; Tedford et al. 2009; Bartolini Lucenti & Rook 2020). Fossil species are clearly divided in two groups: the first is made up by the small-sized species (lower values of m1 area). The molar ratios for these taxa point out a more hypocarnivorous diet, with values close to that of *V. vulpes*. *Vulpes beihaiensis* and *V. galatica* have indices close one another (m2/m1=0.438 and 0.422, respectively), and are also of similar size. The European *V. alopecoides* from Europe has the closest to the average score of *V. vulpes* (mean index= 0.442). *Vulpes chikushanensis* from Longdan have the largest molar index (m2/m1=0.468), suggesting that its diet was probably more hypocarnivorous compared to that of other fossil species and even to that of extant *V. vulpes*. The second group is composed of the large-sized species, *V. qiuzhudingi* and *V. rooki*. The molar ratio displayed by *V. qiuzhudingi* (m2/m1=0.316) confirms its interpretation of as hypercarnivorous species (Wang et al. 2014), even more specialized compared to extant *V. lagopus* (also evident from the morphology of the lower carnassial and the m2). The value of *V. rooki* (m2/m1=0.362), intermediate between *V. corsac* and *V. lagopus*, also support the morphological and morphometrical evidence presented here of a hypercarnivorous diet. Bartolini Lucenti and Rook (2020) showed that *E. davisi* probably had a mesocarnivorous diet and the morphological features and the high molar ratio value (m2/m1=0.444) fit in this interpretation. Therefore, Fig. 5 supports the distinction between the two taxa recorded in Xiakou, *E. davisi* and *V. rooki*, described above on morphological and morphometric ground. Despite the similar size, the two species had markedly different diet preferences probably facilitating the coexistence in the Chinese basin.

CONCLUSIVE REMARKS

Vulpes is a diverse genus that first occurred in the Late Miocene of North America and experienced taxonomic diversification and geographic range expansion into eastern Asia and into the rest of the Old World since the latest Miocene. In contrast to the attention that literature devoted to the evolutionary history of other members of the Caninae (*Nyctereutes*, *Eucyon, Canis*), studies on the genus *Vulpes* (despite its remarkable diversification with-in Eurasian and African canids, giving rise to the most diverse canine genus) are relatively rare and with generally less consideration in respect to other members of the subfamily.

The Mio-Pliocene transition is Eurasia is characterized by a marked turnover in the structure of the carnivore guild, especially characterized by the decrease (and disappearance) in canid-like morphotypes among hyaenids and the correspondent increase (either in number and ecological role) of representatives of the family Canidae (Werdelin & Turner 1996). The marked diversification recorded among the genus *Vulpes* (*V. beihaiensis*, *V. qiuzhudingi*, *V. rooki*) definitely contributes to the Early Pliocene maximum diversity that Caninae showed in Central Asia, while in western Eurasia, the peak of Early Pliocene canid diversification, in addition to the appearance of two species of the genus *Vulpes* (*V. alopecoides* in Kvabebi and *V. galatica* in Çalta) is more related to the taxonomic branching of the raccoon-dog *Nyctereutes* (Bartolini Lucenti 2018), the appearance of other Canini like the cryptic *"Canis" michauxi* Martin, 1971, together with the presence of advanced species of the genus *Eucyon* (Rook 2009). Nevertheless, *Vulpes* remains the one of the most elusive and most understudied genera of Eurasian canids. Recently, Wang et al. (2014) proposed the large-sized *V. qiuzhudingi* as a possible ancestor of the extant hypercarnivorous *V. lagopus*, whereas *V. corsac* might be related to *V. chikushanensis*, which is close is morphology (as suggested Qiu et al. 2004) but not in diet (Fig. 5). Of the Asian foxes, the Tibetan sand fox, *V. ferrilata*, does not have any known fossil record (Clark et al. 2008). The large size and hypercarnivory of *V. rooki* remind of this large-sized fox, which also has and a diet mainly composed of small mammals (Clark et al. 2008). Some features are also similar, e.g., the elongated cranium, diastemata between premolars, hinting a relationship between *V. rooki* and *V. ferrilata*.

The record of Yushe Basin is of outstanding relevance for our understanding of the Pliocene diversification of Canidae (Tedford et al. 1991; 2013; Wang et al. 2013). Fossil record of the Basin includes the typical genera of the Plio-Pleistocene canids of Eurasia (i.e., *Canis*, *Eucyon*, *Nyctereutes*, *Vulpes*), with the exception of large-sized hypercarnivorous taxa, although Tedford et al. (1991) reports a "*Cuon*" (Tedford et al. 1991: Table 1) from the younger beds of the basin (Haiyan Formation). Here, it is reported the description of a new species of fox from the locality of Xiakou (Nihe Subbasin) whose type material was previously included in *E. davisi*. Several features support the distinction between these two taxa, and the comparison with other Plio-Pleistocene species of *Vulpes* showed the peculiarity of this taxon favoring its description as *Vulpes rooki* sp. nov., probably with hypercarnivorous diet. The erection of a new species in the Yushe Basin with such ecological preferences, in addition to increasing the diversity of the Eurasian record, has important implications in the understanding of the co-occurrence fossil canid species. Rook et al. (2017) demonstrated the early occurrence of niche partitioning among three sympatric canids thanks to the contemporary occurrence of *Vulpes* with *Nyctereutes* and *Eucyon* in the Pliocene site of Kvabebi (Georgia, 3.09 Ma, Agustí et al. 2009). The highly diverse fossil record of the Yushe basin supports similar interpretations of niche partitioning among Caninae during the Early Pliocene, even for similar-sized species like *V. rooki* and *E. davisi*. The evidence presented here confirms the interpretation of Bartolini Lucenti and Rook (2020) on *E. davisi*'s mesocarnivorous diet in marked contrast to the tendency towards a hypercarnivorous diet of *Vulpes rooki* sp. nov. allowing the exploitation of different niches.

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