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Chronological and palaeoecological insights into the Dayakou fauna in Yanjinggou, Chongqing, China: Responses of large mammals to the Early-Middle Pleistocene Climate Transition

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ABSTRACT

The Yanjinggou fauna has long been recognized as the quintessential Middle Pleistocene fauna in South China. However, the recent discovery of the Dayakou fauna in the same region has unveiled a fossil assemblage indicative of the Early Pleistocene. Our new excavations at the Dayakou pit have yielded a substantial increase in fossil materials, which not only enriched the composition of the local fauna but also play a pivotal role in reconsidering the geochronology of the faunal complex in Yanjinggou area. The newly recovered fossil remains from the Dayakou pit comprise at least ten mammal taxa, including carnivorans (*Homotherium* sp., *Neofelis nebulosa*, *Panthera tigris* and *Ailuropoda melanoleuca wulingshanensis*), proboscidean (*Stegodon huananensis*), perissodactyls (*Hesperotherium sinense*, *Tapirus sinensis* and *Rhinoceros* cf. *sinensis*), and artiodactyls (Cervini gen. et sp. indet. and *Leptobos* sp.). thereinto, *A. m. wulingshanensis*, *T. sinensis* and *Leptobos* sp. represent the first discoveries of their kinds in the Yanjinggou area. The faunal combination, along with the combined ESR and U-series dating of the *Stegodon* tooth, resulting in an age estimate of 1010 ± 115 ka, suggests that the geologic age of the mammalian assemblage of the Dayakou pit corresponds to transition phase from the middle to late Early Pleistocene. Our study challenges preconceived notions and provides a more sophisticated understanding of the temporal framework for the Yanjinggou faunal complex, offering new insights into the Pleistocene mammalian faunas of South China. Furthermore, the Dayakou fauna is proposed to mark the onset of Early-Middle Pleistocene Transition mammalian faunas in South China, reflecting an ecosystem of mountainous subtropical forest mixed with arbor and shrub vegetation. The Dayakou locality witnesses the first appearances of modern clouded leopards and tigers in Asia, prompting the origin and early dispersal considerations of these two species.

1. Introduction

The Yanjinggou area, located in Wanzhou District of Chongqing municipality, is renowned as one of the most diverse and fossil-rich regions in South China for mammalian fossils (Matthew and Granger, 1923; Hooijer, 1947; Colbert and Hooijer, 1953). The faunal assemblage is identified as a typical representative of the *Ailuropoda* - *Stegodon* fauna during the Quaternary Period, with the majority of the species originating from the Indian subcontinent, including *Hystrix subcristata*, *Ailuropoda melanoleuca baconi*, *Ursus thibetanus*, *Stegodon orientalis*,

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Megatapirus augustus, *Dicerorhinus sumatrensis*, (*Bos*) *Bibos gaurus granger* (Matthew and Granger, 1923; Colbert and Hooijer, 1953; Zheng, 1993; Chen et al., 2013). However, the caves and pits where the Central Asiatic Expeditions of AMNH collected mammal fossils during the winters of 1921–1921, 1922–1923 and 1925–1926 cannot be matched with the fossils described by researchers of AMNH (Matthew and Granger, 1923; Colbert and Hooijer, 1953). This is due to the lack of detailed field records and the subsequent disturbance of fossil sites by agricultural and mining activities spanning over a century, so do the fossiliferous sites studied by Young C. C (Young, 1935, 1939). Currently, four pit locations have been confirmed in the Yanjinggou area, comprising the Upper Cave of Pingba (Zheng, 1993; Hu et al., 2023a), the Lower Cave of Pingba (Zheng, 1993), the Dayakou pit (Chen et al., 2013) and the Sifangdi cave (Hu et al., 2023b), along with one cave site, the Meiren cave (Chen et al., 2013).

Controversies concerning the geochronology of the Yanjinggou fauna have been ongoing for over a century in light of the scarcity of detailed locality descriptions and stratigraphic records in historical excavations (Matthew and Granger, 1923; Granger, 1932; Colbert and Hooijer, 1953). In essence, the age of the Yanjinggou fauna has predominantly been inferred through the examination of mammalian assemblages rather than through absolute geochronological experiments, with only two recent localities undergoing such studies (Hu et al., 2023a, 2023b). Initially assigned to Late Pliocene (Matthew and Granger, 1923), the geological age of the Yanjinggou fauna was later revised to Early Pleistocene (Teilhard de Chardin et al., 1935; Young, 1939). Subsequently, it was reassessed as Middle Pleistocene (Colbert, 1940), a designation that has been widely accepted by later studies (Colbert and Hooijer, 1953; Kahlke, 1961; Ji, 1980; Li, 1981; Zheng, 1993; Jin et al., 2008). Furthermore, recent biochronological studies of the Dayakou fauna, as well as the Upper and Lower Caves and the Meiren cave faunas, suggest a revised geochronology for the Yanjinggou faunal complex, placing it between the middle Early Pleistocene and the late Pleistocene (Chen et al., 2013, 2017, 2021). The assertion that the geological age of the Yanjinggou fauna ranges from Middle Pleistocene to Late Pleistocene was partly supported by numerical dating of the Upper Cave of Pingba (ca. 0.35–0.26 Ma, based on Hu et al., 2023a) and the Sifangdi cave (ca. 134 ± 22–133 ± 30 ka, based on Hu et al., 2023b). However, the chronological conclusion of Early Pleistocene (Chen et al., 2013) remains somewhat unconvincing due to the absence of typical species of the middle Early Pleistocene and a lack of numerical age references.

Here we present further findings of the Dayakou fauna in Chongqing, China, offering additional biochronological evidence and an absolute age, illuminating the Early Pleistocene components of the Yanjinggou fauna complex and discussing the significance of implications in the Eurasian context.

2. Materials and methods

2.1. Materials

The materials studied in this paper were recovered from the 3rd layer of the Dayakou pit and are currently housed in CYPL, comprising isolated teeth, incomplete skulls and postcranial bones of large mammals (Table 1).

Institute Abbreviations: AMNH, American Museum of Natural History; CTGIM, Chongqing Three Gorges Immigration Memorial; CTGIP, Chongqing Three Gorges Institute of Paleoanthropology, China Three Gorges Museum of Chongqing; CYPL, Chongqing Key Laboratory of Paleontology and Paleoenvironment Co-evolution (Sichuan-Chongqing Joint Construction), No. 208 Hydrogeological and Engineering Geological Team, Chongqing Bureau of Geological and Mineral Resource Exploration and Development, Chongqing, China.

2.2. Methods

The osteological and osteometrical terminologies in this papaer are after von de Driesch (1976), Evans and de Lahunta (2012) and Zheng (2004). The dental nomenclatures of *S. huananensis*, *A. m. wulingshanensis*, *Hesperotherium sinense*, *T. sinensis* and *Rhinoceros* cf. *R. sinensis* follow those of Maglio (1973), Jiangzuo et al. (2018, 2023), Qiu (2002), Hulbert Jr. (2010) and Tong (2004a,b), respectively. The methodology for measuring limbs of ruminants is accordance with Duvernois and Guérin (1989), Duvernois (1990) and Mead et al. (2014). All measurements were taken using a vernier caliper with an accuracy of 0.1 mm.

Osteological and Measurement abbreviations of Teeth: Uppercase letters are applied to designate upper teeth while lowercase letters are used for lower teeth. D/d prefix indicates deciduous teeth. H, height of the crown; L, mesiodistal length; W, buccolingual width; Wa, greatest width of anterior lobe (measured across paracone or trigonid for *Ailuropoda*, measured across the protoloph or protolophid near the base of the crown for tapirs and rhinoceros as well as *Hesperotherium*); Wp, greatest width of posterior lobe (measured across metacone or talonid for giant pandas, measured across the metaloph or hypolophid for tapir and rhinoceros as well as *Hesperotherium*); MAW, maximal buccolingual width; MIW, minimal buccolingual width; LLD, labial-lingual diameter.

Osteological and Measurement abbreviations of long bones: DAPdist, distal antero-posterior diameter (¼distal depth); DAPprox, proximal antero-posterior diameter (¼proximal depth); DTdiaph, least

Table 1
List of large mammal assemblages from the 3rd layer of Dayakou pit.

Materials			Field No.	Catalog No.	Horizon	Repository
Number	Species	Skeletal elements				
1	*Stegodon huananensis*	left M3	DYK1-1	CYM0006	3rd layer	CYPL
2	*Panthera pardus*	right P4	DYK55	CYM0007		
3	*P. tigris*	right m1	DYK67	CYM0008		
4	*Homotherium* sp.	left I2	DYK60-1	CYM0009		
5		left m1	DYK60-2	CYM0010		
6	*A. m. wulingshanensis*	fragmentary mandible	DYK103 (1)	CYM0011		
7	*Hesperotherium sinense*	left M2	DYK86	CYM0012		
8		left M3	DYK35	CYM0013		
9		right m2	DYK2-3 (2)	CYM0014		
10	*Rhinoceros* cf. *sinensis*	left dp2-dp3	DYK32	CYM0015		
11	*T. sinensis*	almost complete skull	DYK110	CYM0016		
12	Cervini gen. et sp. indet.	left humerus	DYK98	CYM0017		
13		left tibia	DYK xin18	CYM0018		
14	*Leptobos* sp.	right humerus	DYK82 (1)	CYM0019		
15		partial left humerus	DYK91(1)	CYM0020		
16		left tibia	DYK92(2)	CYM0021		
17		right metatarsal	DYK85	CYM0022		

transverse diameter of diaphysis (¼least width of diaphysis); DTdis, distal transverse diameter (distal width); DTprox, proximal transverse diameter (¼proximal medial-lateral width); GL, greatest length.

2.3. *Geographic and geologic setting*

The Dayakou pit (coordinates: 30° 37′ 37.1″ N, 108° 26′ 56.9″ E, elevation 910 m), a natural karst shaft of 5 m long and wide and 9.5 m deep, lies on a SE-NW hillside near the Dayakou village of Xintian town, Wanzhou District, Chongqing, China (Fig. 1a–c), surrounded by the limestone from the Jialingjiang Formation of the Lower Triassic. The upper deposits (1st and 2nd layers, as well as the top part of 3rd layer) were excavated by a united team from both CTGIP and CTGIM between 2010 and 2011 (Chen et al., 2013), while the remaining part of the 3rd layer was excavated by CYPL between 2015 and 2016 (Fig. 1 d). Based on lithology and taphonomy, three layers can be recognized from top to bottom:

1st layer (<1.5 m). Brownish-red clay. *Rhinoceros* cf. *sinensis* and *Bos* (*Bibos*) sp. were uncovered in the bottom. The layer's thickness varies due to partial disturbance by agricultural activities (Chen et al., 2013).

2nd layer (2.5 m). Brownish-yellow sandy clay with grey breccia. This layer contains multiple stalactite fragments and calcareous concretions. A significant number of mammal fossils were unearthed, including *Rhizomys troglodytes*, Muridae gen. et sp. indet., *Homotherium* sp., *Panthera palaeosinensis* (previously identified as *P. pardus*), Felidae gen. et sp. indet., *Stegodon huananensis* (previously identified as *S. orientalis*), *Dicerorhinus sumatrensis*, *Hesperotherium sinense, Sus* sp., *Cervavitus fenqii*, *Cervus* sp. *and Muntiacus* sp. (Chen et al., 2013).

3rd layer (5.5 m). Brownish-yellow clay with greyish-black huge breccia. The clay is dense and intermixed, containing numerous limestone breccias. Abundant large mammal dental and cranial and postcranial fragments were found, including *Homotherium* sp., *Neofelis nebulosa*, *P. tigris*, *Ailuropoda melanoleuca wulingshanensis*, *S. huananensis*, *H. sinense*, *Rhinoceros* cf. *R. sinensis*, *Tapirus sinensis*, Cervini gen. et sp. indet. and *Leptobos* sp.

2.4. *Geological dating*

We carried out radiometric dating analysis at the Yunnan Key Laboratory of Earth System Science, Yunnan University, China. Owing to

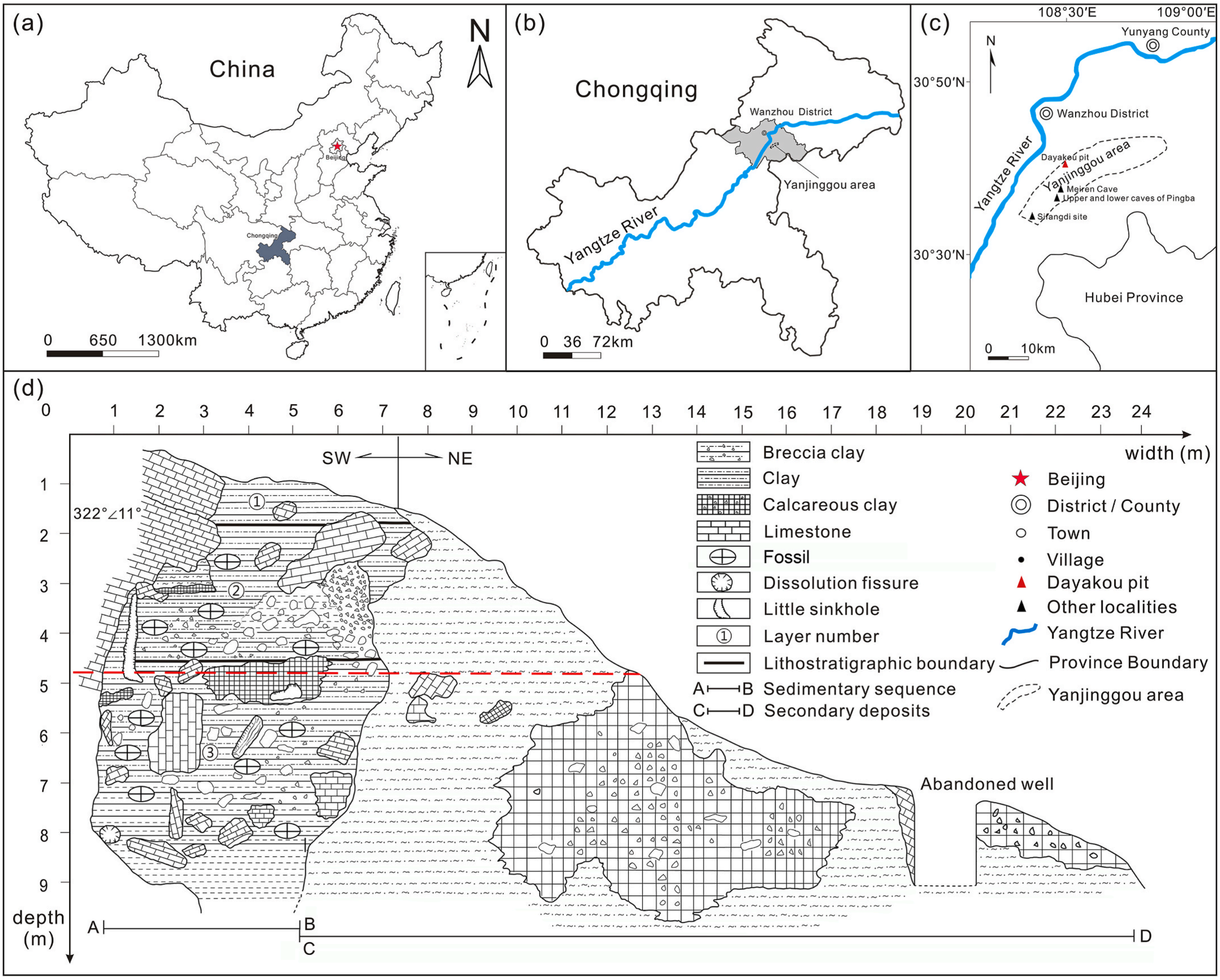

Fig. 1. The geographic map and sedimentary sequence of the Dayakou pit. (a–c), sketch map of China indicating the location of the Dayakou pit in Yanjinggou area of Wanzhou District of Chongqing Municipality, China. (d), the sedimentary sequence of the Dayakou pit, the section above the red dashed line was excavated by a united team from CTGIP and CTGIM in 2010 and 2011, while that below was recently excavated by CYPL in 2015 and 2016. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the unavailability of the materials yielded from the 1st and 2nd layers, a molar fragment of *S. huananensis* (DYKWZ1-6) collected from the 3rd layer was prepared for the combined electron spin resonance (ESR) and uranium series (U-series) dating. The dental tissues (enamel and dentine) were separated mechanically by the dental tools in the first place. The enamel was then grounded and crushed into powder, the 100–200 μm component was sieved and divided into aliquots for irradiation. The samples were irradiated at CENIEH with dose steps of 50, 100, 200, 400, 800, 1200, 1800, 2500, 3500, 5000, 8000, 12500, 20000, 32000 and 50000 Gy. The irradiated aliquots were left for a month before the ESR measurement. The ESR dating process was carried out under room temperature on a Bruker 5000 ESR X-band spectrometer at Yunnan Key Laboratory of Earth System Science in Yunnan University (Han et al., 2022), with the following measurement parameters: modulation frequency 100 kHz, modulation amplitude 0.1 mT, microwave power 2 mW, and 10 times scans. The dose points were fitted by a double saturation exponential (DSE) function to determine the equivalent dose (De). The uranium content and radioisotopic ratios of the dental tissues were measured by MC-ICPMS using the protocol of Shao et al. (2016). The external gamma dose rate of the fossil samples was reconstructed based on the U, Th and K content of the sediments surrounding the sample measured by the HpGe laboratory gamma spectrometer. The ESR/U-series age of the sample was calculated by the DATA program with the parameters listed in Table 2. The ESR/U-series dating of the fossil teeth from the Dayakou site yielded an Early Pleistocene age of 1010 ± 115 ka, with a total dose rate of 2987 ± 228 mGy/ka (a detailed account of the ESR/U-series dating analysis, see in Supplymentary Data 1).

3. Results

3.1. *Systematic paleontology*

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Felidae Batsch, 1788

Genus *Neofelis* Gray, 1867

Neofelis nebulosa Griffiths, 1821

Referred specimen: right P4 (Fig. 2c, CYM0007).
Measurements: H = 11.2 mm, L = 20.6 mm, W = 10.3 mm.

Description and comparisons: The right P4 is well-preserved. Given its small size and distinctive morphological characteristics, such as the underdeveloped ectoparastyle, the slightly undulating buccal border and notably advanced protocone compared to those of *Panthera pardus* and *P. tigris* (Christiansen and Kitchener, 2011; Jiangzuo and Liu, 2020; Jiangzuo et al., 2022a), it can be confidently assigned to *N. nebulosa*.

Genus *Panthera* Oken, 1816

Panthera tigris Linnaeus, 1758

Referred specimen: right m1 (Fig. 2d, CYM0008).
Measurements: H = 17.8 mm, L = 24.2 mm, W = 12.9 mm.

Description and comparisons: Despite the presence of several fissures on the protoconid, the right m1 exhibits a clear talonid and larger in size relative to those of *P. pardus* and *P. palaeosinensis* (Jiangzuo and Liu, 2020; Jiangzuo et al., 2022a). Consequently, it can be attributed to *P. tigris*.

Family Felidae Batsch, 1788

Subfamily Machairodontinae Gill, 1872

Genus *Homotherium* Fabrini, 1890

Homotherium sp.

Table 2
The ESR and U-series data of the dated fossil sample and its age result.

Sample No.	Tissue	U (ppm)	±	$^{234}U/^{238}U$	±	$^{230}Th/^{234}U$	±	Equivalent dose (D_E) (Gy)	±	Total dose rate (μGy/a)	±	US-ESR age (ka)	±	n-enamel	±	p-dentine	±
DYKWZ1-6	Enamel	4.017	0.001	1.1264	0.0007	1.0229	0.0017	3005.3	272.1	2987	228	1010	115	−0.0011	0.0001		
	Dentine	67.694	0.010	1.3217	0.0006	0.5440	0.0008									6.35	0.89

Note:
1. Alpha efficiency of tooth enamel kα = 0.13 ± 0.02 (Grün and Katzenberger-Apel, 1994).
2. The water content in enamel and dentine tissues were assumed as 0 and 7 ± 3% respectively.
3. The total thickness of enamel layer is 788 ± 79 μm, and the removed thickness on the sediment side (S1) and dentine side (S2) were 62 ± 6 μm and 38 ± 4 μm respectively.
4. No Rn loss was assumed in the dental tissues.
5. The radioelements U, Th and K in the sediments were measured by HpGe gamma spectrometer.
6. Cosmic dose rate were estimated based on the burial depth of 7 m.

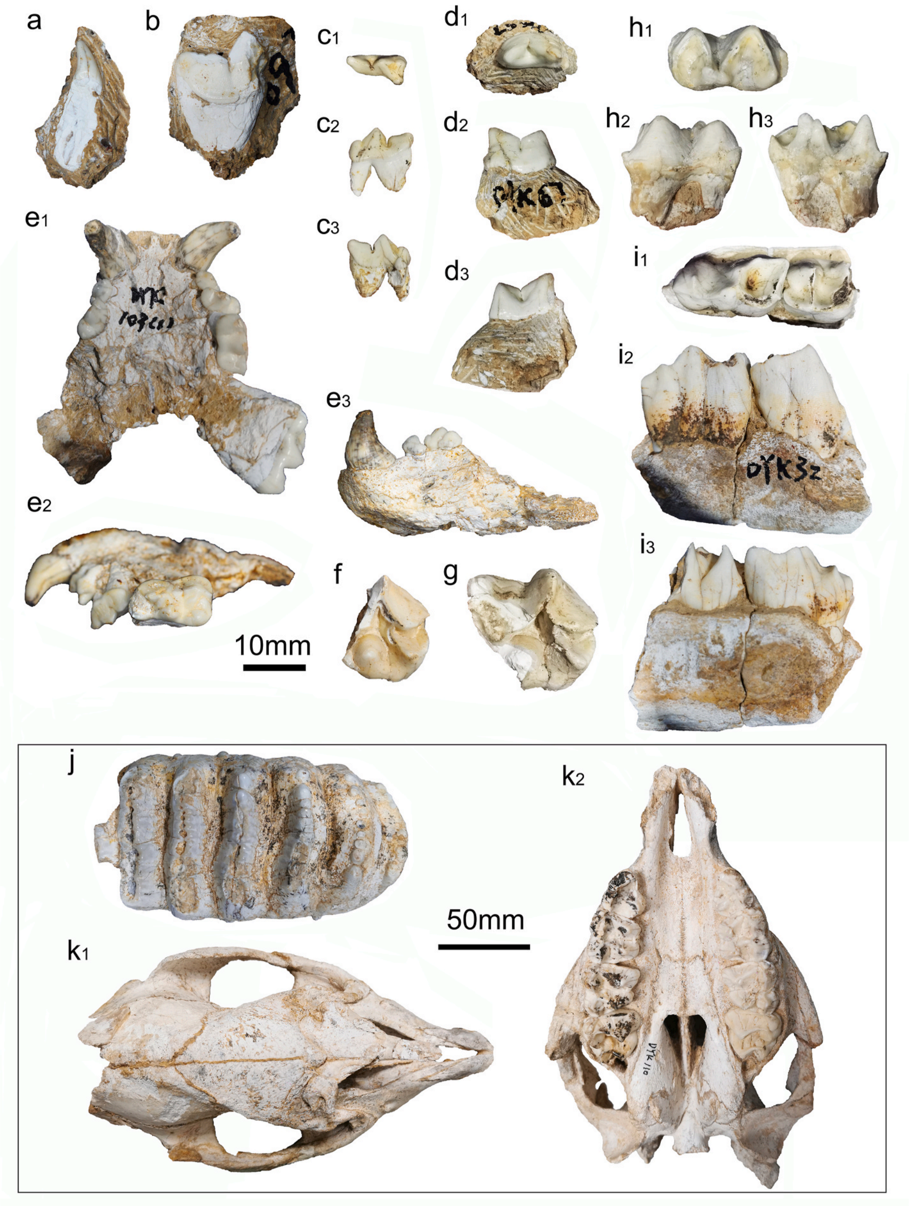

Fig. 2. Teeth of proboscideans, carnivorans and perissodactyls from the faunal association in the third layer in the Dayakou pit. a-b. *Homotherium* sp., a. left I2, CYM0009, b. left m1, CYM0010; c. *Neofelis nebulosa*, right P4, CYM0007; d. *P. tigris*, right m1, CYM0008; e. *A. m. wulingshanensis*, partial mandible with lower canines, lower premolars and right m1, CYM0011; f-h. *H. sinense*, f. left M2, CYM0012, g. left M3, CYM0013, h. right m2, CYM0014; i. *Rhinoceros* cf. *R. sinensis*, left dp2-dp3, CYM0015; Scale bar (a–i) equals 10 mm. j. *S. huananensis*, left M3, CYM0006; k. *T. sinensis*, an almost complete skull with complete deciduous cheek teeth, CYM0016. k1, dorsal view; k2, ventral view; c1, d1, e1, e2, f1, g, h1, i1, j, occlusal views; a, b, c2, d2, e3, h2, i2, buccal views; c3, d3, h3, i3, lingual views. Scale bar (j–k) equals 50 mm.

Referred specimen: left I2 (Fig. 2a, CYM0009), left m1 (Fig. 2b, CYM0010).

Measurements: I2, H = 15.9 mm, LLD = 9.5 mm, H = 23.9 mm; m1, L > 30.0 mm, H = 11.0 mm.

Description and comparisons: The left I2 and the left m1 preserve most of their crowns, but the latter shows heavily worn on the paraconid and protoconid. Notwithstanding these two isolated teeth do not provide conclusive evidence for species identification, they can be tentatively allocated to *Homotherium* due to the rostrally arched upper incisor and the sharp paraconid and protoconid of the m1, similar to those found in the Renzi Cave in Fanchang, Anhui Province (Liu and Qiu, 2009).

Family Ursidae Batsch, 1788

Tribe Ailuropodini Grevé, 1892

Genus *Ailuropoda* Milne-Edwards, 1870

Ailuropoda melanoleuca wulingshanensis Wang et al. (1982)

Referred specimen: mandible (Fig. 2e, CYM0011).

Measurements: see Table 3.

Description and comparisons: The heavily deformed mandible only preserved the symphysis and most of the left and right bodies, lacking the lower incisors, the left p4 and m1, as well as the m2 and the m3. Although slightly larger than *A. microta* but smaller than *A. m. baconi* and modern giant pandas, and sharing the same dental morphology with giant pandas from other localities (Han et al., 1975; Wang et al., 1982; Zhang and Feng, 2004; Échassoux et al., 2008; Wu, 2010), specimen CYM0009 can be classified as *A. m. wulingshanensis*. Based on the minimal dental wear, this specimen is recognized as a young adult. The

Table 3
Measurements and comparisons of the lower teeth of Quaternary giant pandas from different localities in southern China (mm).

Species or Subspecies		*Ailuropoda microta*	*A. m. wulingshanensis*							*A.m.baconi*	Modern *A. melanoleuca*
Locality		*Gigantopithecus* cave, Guangxi (Pei, 1987)	Dayakou pit, Chongqing		Longgudong, Hubei (Zhang and Feng, 2004)	Dongpaoshan site, Hunan (Wang et al., 1982)	Bijiashan site, Guangxi (Han et al., 1975)	Yunxian Man site, Quyuanhekou, Hubei (Échassoux et al., 2008)		UPC, Chongqing (Hu et al., 2023a,b)	Unknown localities (Jiangzuo et al., 2018) and IVPP (Hu et al., 2023a,b)
Teeth		–	left	right	–	–	–	left	right	–	–
c	L (anterior-posterior diameter)	–	16.5	16.8	–	–	–	–	–	19.4–21.5	14.8–19.9
	W (bucco-lingual diameter)	–	13.6[a]	11.9	–	–	–	–	–	14.2–16.5	11.3–14.1
	H	–	19.5	19.8	–	–	–	–	–	21.6[a]-27.5	21.6–24.9
p2	L	–	9	9.1	10.1–13.4	–	12.6	8.2	8.6	11.8–13.0	10.4–12.3
	W	–	5.7	5.6	6.1–7.8	–	6.3	5.6	5.2	6.9–7.4	6.0–7.3
p3	L	11.8–12.0	12.6	13.0	12.3–15.4	–	15.5–15.8	–	13.7	18.1–18.4	15.4–18.7
	W	7.4–7.8	7.7	7.7	7.4–9.4	–	8.4–9.5	–	7.9	9.9–10.7	7.8–10.5
p4	L	16.2–19.1	–	19.4	16.3–23.4	–	–	20.0	20.1	25.8–26.4	21.5–25.0
	W	9.5–11.0	–	11.5	9.0–13.2	–	–	11.8	11.5	13.8–15.0	11.5–14.0
m1	L	23.0–26.0	–	27.6[a]	26.0–33.0	28.1	32.9	30.8	29.3	34.9–35.7	30.0–35.8
	W	14.0–17.2	–	17.1	15.4–20.2	17.4	21.1	17.6	19.5	21.6–22.8	18.7–22.5

[a] Means reference measurements of fragmentary or transformed teeth.

symphysis terminates at least at the level of the m1s, and the left mental foramen lies below the boundary of the parastylid and paraconid of the p4, albeit vertically flattened. Moreover, the dimensions of the lower premolars of specimen CYM0009 are closer to those from the Yunxian Man site at Quyuanhekou in Hubei (Échassoux et al., 2008) and smaller than those from other localities (Han et al., 1975; Wang et al., 1982; Zhang and Feng, 2004), suggesting potential sexual dimorphism differences. Additionally, several intrasubspecific variations can be observed in *A. m. wulingshanensis*. The mandibular diastema of specimen CYM0009 is mesiodistally shorter than that of *A. m. wulingshanensis* from the Yunxian man site (Échassoux et al., 2008). The longitudinal orientations of both the p2 and the p3 of specimen CYM0009 are further from the cheek teeth line compared to those of *A. m. wulingshanensis* from the Longgudong and Yunxian Man sites (Zhang and Feng, 2004; Échassoux et al., 2008). What's more is that the absence of the p1s on specimen CYM0009 is similar to *A. m. wulingshanensis* found in the Yunxian Man site (Wu, 2010), corroborating the variations in the presence or absence of the first lower premolars not only in *A. m. baconi* (Hu et al., 2023a) and extant pandas (Peng et al., 2001) but also in *A. m. wulingshanensis*.

Order Proboscidea Illiger, 1811

Family Stegodontidae Osborn, 1918

Genus *Stegodon* Falconer and Cautley, 1857

Stegodon huananensis, Chen (2011).

Referred specimen: left M3 (Fig. 2j, CYM0006).

Measurements: L > 180.0 mm, MAW = 94.0 mm, MIW = 67.6 mm.

Description and comparisons: The left M3 suffered moderate wear on the anterior plates, with the anterior two or three plates being damaged. Despite the absence of the anterior portion, seven plates are preserved, and each plate has eight to eleven mammillae that can be easily recognized (nine plates shown for the well-preserved M3, based on Chen et al., 2013). Previous research erroneously allocated specimens of *Stegodon* in the 2nd layer to *S. orientalis* (L: 235 mm, MAW: 95 mm, based on Chen et al., 2013) due to slightly more plates and larger mammillae with respect to *S. huananensis* (Chen, 2011). However, a reassessment reveals a markedly lower number of plates and larger mammillae, as well as smaller tooth measurements compared to *S. orientalis* (L: 286 mm, MAW: 105–109 mm, based on Colbert and Hooijer, 1953; Tong et al., 2018). Consequently, all *Stegodon* specimens from the Dayakou pit are more appropriately assigned to *S. huananensis*, which show a slightly more advanced state than those from other localities, such as the Longgupo site in Wushan, Chongqing (Huang and Fang, 1991) and the Longgudong in Jianshi, Hubei (Chen, 2004b).

Order Perissodactyla Owen, 1848

Family Chalicotheriidae Gill, 1872

Genus *Hesperotherium* Qiu, 2002

Hesperotherium sinense Owen, 1870

Referred specimen: left M2 (Fig. 2f, CYM0012), left M3 (Fig. 2g, CYM0013), right m2 (Fig. 2h, CYM0014).

Measurements: See Table 4.

Description and comparisons: The left M2 suffered moderately worn, with the paracone and parastyle and most of the anterior cingulum broken off. The left M3 shows slight wear and lacks most of parastyle, paracone, protocone and the entire anterior cingulum. Despite being poorly preserved, the left M2 can be easily recognized by its relatively flat outer wall of the ectoloph, moderately developed hypocone, and narrow and shallow postfossette. The left M3 is characterised by a concave outer ectoloph, a well-developed hypocone and a wide and deep postfossette. The right m2 is well preserved and slightly worn, featured by a wider talonid than the trigonid, a deep external syncline, a smaller anterior valley than the posterior, and an extremely developed posterior cingulum. The morphological features of these specimens are consistent with those of *H. sinense* described at the Longgudong in Jianshi, Hubei (Tong, 2004a,b), supporting to the assignment to *H. sinense*. Considering the limited availability of reported teeth materials and measurement differences across various localities, it is likely that there is a broader range of dental variation within this species.

Family Rhinocerotidae Owen, 1845

Genus *Rhinoceros* Linnaeus, 1758

Rhinoceros cf. *sinensis* Owen, 1870

Referred specimen: left dp2-dp3 (Fig. 2i, CYM0015).

Measurement: See Table 5.

Description and comparisons: The well-preserved left dp2 is slightly

Table 4
Measurements and comparsion of teeth of *Hesperotherium* from Early Pleistonece localities in China (mm).

Species		*Hesperotherium sinense*	*H. sinense*	*H. sinense*	*H. sinense*	*Hesperotherium* sp.	*H. sinense*
Localities		Dayakou pit (3rd layer)	Longgupo site, Chongqing (Huang et al., 1991)	*Gigantopithecus* cave, Guangxi (Tong, 2006)	Tianzhen site, Shanxi (Qiu, 2002)	Longgudong, Hubei (Tong, 2004a)	Dayakou pit (2nd layer: (Chen et al., 2013; Chen et al., 2017)
M2	L	>28.3	40.0	36.1–40.0	–	–	–
	W	35.2	43.2	36.8–42.6	–	38.0	–
M3	L	>45.4	48.0	36.7–43.5	–	–	–
	W	41.1	44.2	38–47.5	–	–	–
m2	L	40.3	40.5	34.5	42.4	–	40.1
	W	22.8	20.5	19.5	26.3	–	21.5

Table 5
Measurements and comparison of teeth of Pleistonece rhinos in South China (mm).

Species		*Rhinoceros sondaicus*	*R. unicornis*	*Rhinoceros* cf. *R. sinensis*	*R. sinensis*	*S. kirchbergensis*	*D. sumatrensis*	
Localities		Baxian cave, Chongzuo, Guangxi (Yan et al., 2023)	South Asia (Colbert and Hooijer, 1953)	Dayakou pit (3rd layer)	Longgudong, Jianshi, Hubei (Zheng and Yang, 2004)	Yangtze valley (Chen et al., 2021; Tong and Wu, 2010)	Dayakou pit (2nd layer: (Chen et al., 2013; Chen et al., 2017; Chen et al., 2021)	Yanjinggou area (Chen et al., 2021)
dp2	L	27.3–33.1	31–33	35.7	28.0–31.0	27.5–38.8	20.1	23.1–23.7
	W	10.5–15.5	18–19	19.6	15.0–15.6	15.8–20.0	12.2–12.9	13.2–13.9
dp3	L	37.5–43.9	42–46	>30.9	37.3–40.0	41.1–50.8	35.6–36.9	35.0–35.4
	W	18.1–20.4	23–24	21.6	17.4–21.5	20.4–25.5	20.3	19.0–20.2

worn and characterized by its low crown and thin enamel. The protoconid, metaconid, hypoconid and entoconid are all of equal height. The talonid basin is deep and enclosed, surrounded by a short protolophid and well-developed metaconid, hypolophid and entolophid, resulting in a notably extended posterolingual corner. The paraconid and parastylid are moderately developed and smaller than the metaconid. The paralophid is almost equal in length to the protolophid but positioned lower. The anterior valley is wide and irregular, bordered by the paraconid and paralophid anteriorly, the protolophid buccally, and the metaconid and protolophid posteriorly. The anterior cingulum is less developed, while the posterior cingulum is slightly developed. The left dp3 shows moderate wear, with damage to the posterior part. Identified features include a weak anterior cingulum, a well-developed parastylid, a deep anterior valley, an acute protoconid, and a blunt metaconid. It is easy to distinguish *R. sinensis* from *D. sumatrensis* and *R. sondaicus* in South China based on larger measurements (Table 5). Compared to *R. unicornis*, the specimen CYM0013, with a slightly larger dp2 and a smaller dp3, exhibits a markedly extended posterolingual corner and a wide anterior valley for the dp2, along with a much more elongated paralophid for the dp3. Although similar to *S. kirchbergensis* on measurements, the dp2 of specimen CYM0013 has a smaller talonid and a markedly extended posterolingual corner than the materials from Rhino Cave in Shennongjia, Hubei (Tong and Wu, 2010). The dp3 features an extremely developed parastylid as *R. sinensis* from the Longgudong in Jianshi, Hubei (Zheng and Yang, 2004). The talonid basin of the dp2, which is completely closed in specimen CYM0013 but lingually open in those from the Longgudong in Jianshi, Hubei (Zheng and Yang, 2004), appears to be variable. Therefore, we prefer to regard this specimen as *Rhinoceros* cf. *sinensis*.

Family Tapiridae Burrett, 1830

Genus *Tapirus* Brisson, 1762

Tapirus sinensis Owen, 1870

Referred specimen: an almost complete juvenile skull (Fig. 2k, CYM0016).

Table 6
Measurements and comparsion of the deciduous upper premolars *Tapirus sanyuanensis*, *T. sinensis*, *T. augustus* and *T. indicus* (mm).

Species		*T. sanyuanensis*	*T. sinensis*					*T. augustus*	Modern *T. indicus*		
Localities		Renzi Cave, Anhui (Tong and Qiu, 2009)	Unknown localities from *Sichuan* (Koken, 1885)	Longgudong, Hubei (Tong, 2004b)	Yunxian Man site, Quyuanhekou, Hubei (Échassoux et al., 2008)	Dayakou pit		Yanjinggou area (Hooijer, 1947)	Unknown localities (collected by AMNH)	Unknown localities (collected by IVPP) OV 535	
		–	–	–	–	left	right	–	–		
DP1	L	20.0–21.5	19	21–24	22.4	20.5	20.7	26–27	19–21	17.8	18.6
	W	18.5	17.5	18–21	–	18.8	19.2	22–24	15–18	14.9	15.7
DP2	L	–	–	25	21.8	24.8	25.1	30–32	23–25	22.8	23.0
	Wa	–	–	25	–	22.8	22.6	27–28	19–22	19.4	19.6
	Wp	–	–	–	–	23.9	23.3	30–31	22–25	20.7	20.9
DP3	L	23.5	–	28	24.2	27	26.3	31–33	24–25	22.5	22.8
	Wa	27.0	–	16	–	26.4	26.0	31–32	23–26	22.2	22.4
	Wp	24.5	–	20	–	23.1	22.6	30	21–24	20.4	20.5
DP4	L	26.0	–	–	26.6	26.8	26.1	33–35	23–26	23.9	24.2
	Wa	28.0	–	–	28.6	27.6	27.7	36–37	25–27	24.5	24.8
	Wp	24.5	–	–	–	22.4	22.2	32–33	22–24	21.6	22.0
DP1-DP4 L		–	–	–	–	94.1	93.9	–	–	84.2	84.8

Measurement: Tooth measurement sees Table 6.

Description and comparisons: The cranium is nearly complete, lacking only the left rostrolateral part of nasal, the interparietal, the occipital bones, and all incisors and canines. It belongs to a young juvenile with fully erupted DP1-DP4 and erupting M1s (Hulbert, 2010). The tooth measurements of specimen CYM0014 are within the range of *T. sinensis*, being slightly larger than those of *T. sanyuanensis* and extant *T. indicus*, but significantly smaller than those of *T. augustus* (Table 6). As this is the most complete skull of young juvenile *T. sinensis* ever reported, a detail description and discussion of its phylogenetic significance will be provided in a forthcoming paper. Here, only the taxonomic rank and tooth measurements are presented.

Order Artiodactyla Owen, 1848

Family Cervidae Gray, 1821

Tribe Cervini Weber, 1928

Cervini gen. et sp. indet.

Referred specimen: left humerus (Fig. 3e, CYM0017); left tibia (Fig. 3f, CYM0018).

Measurement: Humerus: GL = 264.2 mm, DTdiaph = 24.9 mm, DTprox = 52.9 mm, DTdist = 55.4 mm, DAPdist = 56.1 mm; Tibia: GL = 212.8 mm, DTdiaph = 18.3 mm, DTprox = 46.7 mm, DTdist = 33.9 mm.

Description and comparisons: The left humerus lacks the greater tubercle and most of the medial and lateral supracondylar crests, showing multiple fissures on the shaft and distal portion. The left tibia, from another individual, has damage to the tibial tuberosity, the crest of tibia, the medial condyle and the medial malleolus. It is challenging to establish the generic and specific ranks based solely on a humerus and a tibia, given the presence of multiple genera and species of Cervini from Early Pleistocene localities. Owing to their small sizes and slender bodies, the two specimens have been tentatively assigned to Cervini gen. et sp. indet.

Family Bovidae Gray, 1821

Subfamily Bovinae Gill, 1872

Genus *Leptobos* Rütimeyer, 1877–1878

Leptobos sp.

Referred specimen: a left humerus (Fig. 3a, CYM0019), a partial right humerus (Fig. 3b, CYM0020), a left tibia (Fig. 3c, CYM0021), a right metatarsal (Fig. 3d, CYM0022).

Measurement: See Table 7.

Description and comparisons: Despite the absence of tooth materials, the identification of *Leptobos* is still feasible based on the morphology and measurements of the appendicular skeletal elements. In other words, when compared with *Bibos gaurus granger* and *Bubalus bubalis* (Colbert and Hooijer, 1953), the trochlea of the humerus (specimen CYM0019 and CYM0020) is relatively slenderer, and the shaft is more rotated. Furthermore, the shaft of the tibia (specimen CYM0021) is straighter, and the proximal and distal ends of the metatarsal (specimen CYM0021) are slightly broader than the shaft. Even so, it remains challenging to differentiate *L. crassus* from *L. brevicornis* without comparing related cranial and dental morphologies. Therefore, the three samples can be classified as *Leptobos* sp.

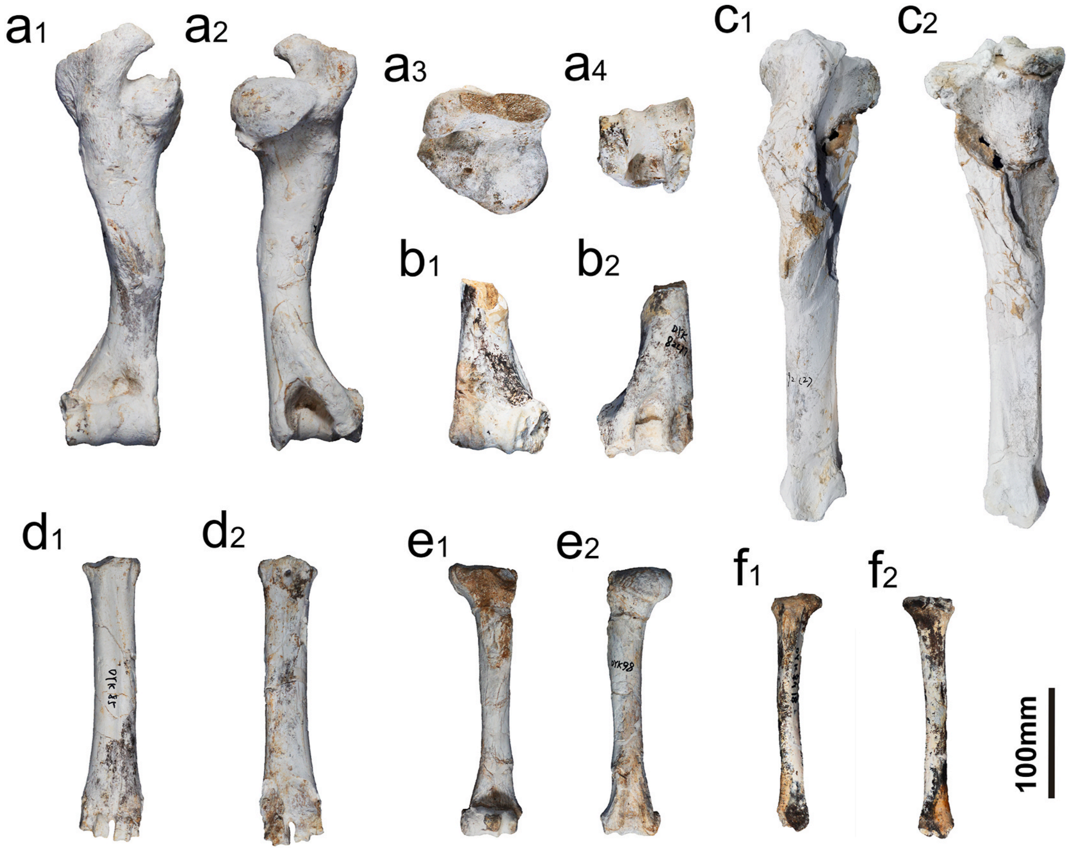

Fig. 3. Postcranial bones of artiodactyls from the faunal association in the third layer in the Dayakou pit. a-d. *Leptobos* sp., a. right humerus, CYM0019; b. partial left humerus, CYM0020; c. left tibia, CYM0021; d. right metatarsal III + IV, CYM0022; e-f. Cervini gen. et sp. indet., e. left humerus, CYM0017; f. left tibia, CYM0018; a1, b1, c1, d1, e1, f1, anterior views; a2, b2, d2, e2, f2, posterior views; a3, proximal view; a4, distal view. Scale bar equals 100 mm.

Table 7
Measurements and comparsion of skeletal elements of *Leptobos* from localities of southern China (mm).

Species		*Leptobos* sp.	*Leptobos crassus*	*Leptobos brevicornis*	*B. bubalis*	*B. g. grangeri*
Localities		Dayakou pit	Renzidong, Anhui (Mead et al., 2014)	Yunxian Man site, Quyuanhekou, Hubei (Échassoux et al., 2008)	Yanjinggou area (Colbert and Hooijer, 1953)	Yanjinggou area (Colbert and Hooijer, 1953)
humerus	GL	376.2	375.0	\	\	471
	DTprox	125.7	118.0–125.0	\	\	\
	DAPprox	123.6	153.0	\	\	\
	DTdist	83.8	90.0–92.1	96.0	\	\
	DAPdist	78.7–87.1	94.3	90.0	\	\
	DTdiaph	42.1–44.4	44.1–45.6	56.0–59.3	\	\
tibia	GL	444.8	452.0	\	\	536
	DTprox	118.2	128.7–129.2	126.0	\	\
	DAPprox	114.9	129.7	\	\	\
	DTdist	64.9	76.3–76.4	\	\	\
	DAPdist	50.4	56.0–56.4	\	\	\
	DTdiaph	46.9	40.8–43.6	\	\	\
metatarsal	GL	262.6	286.0	254.0–281.0	213–226	301–312
	DTprox	53.8	60.8	53.3–78.0	64–72	59–72
	DAPprox	49.6	59.3	57.0	\	\
	DTdist	>55.0	61.4–63.5	51.1–77.0	81–87	63–77
	DAPdist	>31.6	37.5–38.9	34.0–47.5	\	\
	DTdiaph	37.4	40.3–41.7	32.6–41.0	46–50	38–47

4. Discussion

4.1. Taphonomic and palaeoecological significance of the Dayakou fauna

The Dayakou pit is a relatively rare vertical fissure, especially considering the diverse middle and late Early Pleistocene mammalian localities discovered in South China over the last decades (Zheng, 2004; Échassoux et al., 2008; Jin et al., 2009, 2014; Wang et al., 2014, 2017). This suggests a unique taphonomic condition and corresponding palaeoecological significance. The excellent preservation of three skeleton of *S. huananensis* (once identified as *S. orientalis* in previous research), skulls of juvenile *T. sinensis* and *D. sumatrensis*, including fragile nasal and zygomatic arch bones, along with isolated or associated teeth and postcranial bone fragments of other mammals (Chen et al., 2013, 2017, 2021), characterizes the fossil accumulation as a blend of autochthonomous and heterochthonous burial. The accumulation of the perfectly preserved cranial or postcranial bones mirrored the deposition pattern of giant panda bones deposited in the Jiangdong Mountain, Yunnan Province (Jablonski et al., 2012). Undoubtedly, the Dayakou pit, a vertical fissure approximately 5 m in diameter and 9.5 m in depth, cannot be a predator's nest or a shelter for large animals owing to the unsuitability for habitation and the inevitable rainwater accumulation through the open entrance, as well as the absence of marks of animal or human activities, such as gnaw marks on bones or ichnofossils like coprolites and stone tools. In other words, it appears that the Dayakou pit served as a deathtrap for unsuspecting animals, its entrance possibly concealed by the surrounding lush vegetation. Large animals such as *S. huananensis*, *D. sumatrensis* and *T. sinensis*, wandering near, might have stumbled into the pit and perished immediately upon burial by mud or soil carried by rainwaters or torrential floods. Additional events resulting in the deposits of isolated or associated teeth and fragmentary postcranial bones could be explained by naturally scattered and damaged teeth or bones being flushed into the pit by fluids and eventually deposited with sediments. The presence of mandibles of *R. troglodytes* (Chen et al., 2013) is likely due to live rodents reaching the bottom of pit during periods of sedimentary events. They could have inhabited and multiplied in the pit until the arrival of the next sedimentary events, contributing to the abundance of remains in the deposits.

Statistics on the elements of the Dayakou fauna reveal that 94.7% of the total elements belong to the Indian subcontinent, with the Palaearctic genus of *Leptobos* being the only exception. Within the Dayakou fauna, tropical to subtropical forest mammals predominate, indicative of a warm and humid climate. Species like *A. m. wulingshanensis* and *R. troglodytes* were dwellers of bamboo forests (Wang et al., 1982; Zhang and Feng, 2004; Échassoux et al., 2008), while *T. sinensis* thrived in forests near water sources at various altitudes (Tong, 2004b, 2007; Jin et al., 2009; Wang et al., 2017). *Stegodon* and *Hesperotherium* were associated with arboreal forests rich in tender leaves (Tong, 2007; Tong et al., 2018). *Neofelis* are highly adapted to an arboreal lifestyle (Yuan et al., 2023). *Sus*, *Cervus*, *Muntiacus* and *Leptobos* suggest environmental conditions of shrub forests and mountainous regions (Chen, 2004a; Yang, 2006; Wilting et al., 2007; Smith and Yan, 2009; Dong and Bai, 2021). Moreover, the absence of primates in the Dayakou fauna appears to be due to non-preservation of fossils rather than the actual absence of these taxa, seeing that abundant primate fossils (*Rhinopithecus*, *Hylobates*, *Gigantopithecus*, *Procynocephalus* and *Macaca*) were discovered in neighbouring localities such as the Longgupo site in Wushan (Huang and Fang, 1991) and the Longgudong in Jianshi, Hubei (Zheng, 2004). Considering previous studies that *Rhinopithecus, Hylobates, Gigantopithecus, Procynocephalus and Macaca* are more or less referred to habitats of subtropical dense forest and hills (Smith and Yan, 2009; Zhang et al., 2010; Zhao et al., 2011; Zhao and Zhang, 2013), the possible explanation for the absence of primate fossils is that the bodies of apes and monkeys are too flexible to be confined in such a fissure, or their intelligence helped them avoid falling into the deathtrap themselves. Consequently, the palaeoecological system around the Dayakou pit suggests a mountainous subtropical forest, characterized by a mixture of arbor and shrub vegetation near rivers (Fig. 4).

4.2. Faunal remains and biochronological implications of the Dayakou fauna

With reference to previous researches (Chen et al., 2013, 2017, 2021), the mammalian fauna in the 2nd layer of the Dayakou pit encompasses five orders, eight families, twelve genus and species, composed of *R. troglodytes*, Muridae gen. et sp. indet., *Homotherium* sp., *P. palaeosinensis*, Felidae gen. et sp. indet., *S. huananensis*, *D. sumatrensis*, *H. sinense*, *Sus* sp., *C. fenqii*, *Cervus* sp. and *Muntiacus* sp. What's more, in terms of morphology and taxonomy, the mammalian assemblage in the 3rd layer can be unequivocally assigned to four orders, eight families, ten genera, and ten species, including *P. tigris*, *N. nebulosa*, *Homotherium* sp., *A. m. wulingshanensis*, *S. huananensis, H. sinense, Rhinoceros* cf. *R. sinensis*, *T. sinensis*, Cervini gen. et sp. indet. and *Leptobos* sp. Givening the co-occurrence of *Homotherium* sp., *S. huananensis*, and *H. sinense*, and the absence of primitive species or subspecies, as well as the sedimentary

Fig. 4. Palaeoecological reconstruction and faunal affinity of the Dayakou during the mid-late Early Pleistocene.

succession, it is suggested that faunal associations in the 2nd and 3rd layers belong to the same faunal unit. Totally, the Dayakou fauna comprises nineteen species, including *R. troglodytes*, Muridae gen. et sp. indet., *Homotherium* sp., *P. palaeosinensis*, *P. tigris*, *N. nebulosa*, Felidae gen. et sp. indet., *A. m. wulingshanensis*, *S. huananensis*, *H. sinense*, *T. sinensis*, *D. sumatrensis*, *Rhinoceros* cf. *R. sinensis*, *Sus* sp., Cervini gen. et sp. indet., *C. fenqii*, *Cervus* sp., *Muntiacus* sp. and *Leptobos* sp.

A significant number of Early Pleistocene mammalian localities have been discovered in southern China over the past few decades, suggesting the identification of three biostratigraphic stages due to succession and geochronological analysis (Han, 1987; Pei, 1987; Huang and Fang, 1991; Zheng, 2004; Échassoux et al., 2008; Jin et al., 2008, 2009, 2014; Jin and Liu, 2009; Wang et al., 2014, 2017). Specifically, the early stage (in the early Pleistocene: approximately 2.58–1.95 Ma) is characterized by small-sized *Gigantopithecus blacki*, *A. microta*, *Megantereon microta*, *S. huananensis*, *T. sanyuanensis*, and large-sized jackal (*Sinicuon dubius*), and Neogene relict species such as *Sinomastodon*, *Hesperotherium*, *Dicoryphochoerus*. Representative localities include the Longgupo site in Wushan, Chongqing (Huang and Fang, 1991), the *Gigantopithecus* cave in Liucheng (Pei, 1962), the Baikong cave in Chongzuo, Guangxi (Jin et al., 2014), and the Mohui cave in Bubing Basin, Guangxi (Wang et al., 2005, Wang, 2013). The middle stage (in the middle Early Pleistocene: approximately 1.95–1.24 Ma) is marked by small-sized *G. blacki*, *A. m. wulingshanensis*, *Cuon antiquus* and *T. sinensis*, with representative sites such as the Longgudong in Jianshi, Hubei (Zheng, 2004), the Sanhe cave in Chongzuo (Jin et al., 2009), the Juyuan Cave in Boyue Mountain (Wang et al., 2017), the Bijiashan site in Liuzhou, Guangxi (Han et al., 1975) and the Yuanmou homonid site in Yunnan (Ji and Li, 1979). The late stage (in the late Early Pleistocene: approximately 1.24–0.78 Ma) is featured by mammals of large size, including moderate-sized *G. blacki*, *A. m. baconi* and *T. augustus*, with notable faunal remains from the Yunxian Man site in Quyuanhekou, Hubei (Li et al., 1999; Échassoux et al., 2008), the Gongwangling site in Lantian, Shaanxi (Hu and Qi, 1978) and the Queque cave in Wuming, Guangxi (Wang et al., 2007; Jin et al., 2008, 2014) and the Black cave in Daxin, Guangxi (Han, 1982).

Within the Dayakou fauna, *Homotherium*, *Hesperotherium* and *Cervavitus* are elements of the Neogene relict genera. *Homotherium* seems to have become extinct in southern China in the Middle Pleistocene but survived until the late Pleistocene in Europe (Tong et al., 2019). *Hesperotherium* remains from Gongwangling in Shaanxi Province represent the latest records in China, suggesting a chronological implication of late Early Pleistocene (Hu and Qi, 1978). *C. fenqii* once existed in South China from the early to middle Early Pleistocene (Jin et al., 2009; Chen et al., 2013). The co-occurrences of *Homotherium* sp., *H. sinensis* and *C. fenqii* indicate that the age of the Dayakou fauna does not exceed the time span from the early to middle Early Pleistocene. Moreover, *A. m. wulingshanensis* and *T. sinensis* first appeared in the middle Early Pleistocene (Zhang and Feng, 2004; Wang et al., 2017). As a consequence, the biochronology of the Dayakou fauna is worth comparing with faunas in the middle Early Pleistocene.

In contrast to other mammal assemblages in the middle Early Pleistocene (see in Supplymentary data 2), the Dayakou mammalian fauna holds pronounced biochronological significance. When compared to the fossil assemblage from the Longgudong, Jianshi, Hubei (Zheng, 2004), seventeen species or subspecies (accounting for 89.4% of the total) of the Dayakou fauna were found to co-occur. The absence of *D. sumatraensis* in the Longgudong appears to be due to a lack of fossil records rather than true absence, considering its discovery at the early Pleistocene locality, such as the *Gigantopithecus* cave in Liucheng, Guangxi (Tong, 2006). With the absence of the primitive tapir (*T. sanyuanensis*) and the presence of the advanced *S. huananensis* in the Dayakou pit, the age of the Dayakou fauna is suggested to be later than that of the Longgudong fauna. Comparing it to the Sanhe faunal from Chongzuo, Guangxi (Jin et al., 2009), the Dayakou fauna shows similarities with twelve species or subspecies, accounting for a high percentage of 73.7%. The lack of *Homotherium*, *D. sumatraensis*, *H. sinense* and *Leptobos* in the Sanhe fauna is more likely to be non-preservation due to taphonomical bias rather than their actual absence, taking into consideration the existence of living *D. sumatraensis* in Southeast Asia (Radcliffe and Morkel, 2014) and the appearances of *Homotherium* and *Leptobos* at the Yunxian Man site in Hubei (late Early Pleistocene, based on Échassoux et al., 2008) and *Leptobos* at the Gongwangling site of Lantian in Shaanxi Province (late Early Pleistocene, based on Hu and Qi, 1978). The substantial overlap between the Dayakou and Sanhe faunas, together with the absence of both primitive and derived paleospecies or paleosubspecies, such as *A. microta* and *A. m. baconi*, *T. sanyuanensis* and *T. augustus*, contribute to similar biochronological results. Fossil similarities are also observed among the Dayakou cave and the Juyuan Cave in Boyue Mountain (Wang et al., 2017), the Bijiashan site in Liuzhou, Guangxi (Han et al., 1975) and the Yuanmou Hominoid site in Yunnan (You and Qi, 1973; Zhou and Zhang, 1984; Qian, 1985), although with fewer paleospecies or paleosubspecies co-occurred. However, *S. huananensis* from the Juyuan Cave and Bijiashan site are not as advanced as those found in the Dayakou and Yuanmou faunas. *R. fusuiensis* from the Juyuan Cave is more primitive than *R. sinensis* in other faunas (Yan et al., 2014, 2023). In light of this, the Dayakou fauna appears to be comparable to the Yuanmou fauna but more advanced than the Juyuan and Bijiashan faunas. Consequently, the Dayakou fauna is proposed to be approximately coincident with the Yuanmou fauna, following the Juyuan, Longgudong, Bijiashan and Sanhe faunas and preceding the Quyuanhekou and Gongwangling faunas.

4.3. The chronometric dating discussion of the Dayakou fauna

The ESR/U series dating of the Dayakou fauna, with an estimated age of 1.010 ± 0.115 Ma, aligns with its composition, indicating a transitional phase from the middle to late Early Pleistocene. The chronometric dating results can be examined notwithstanding differences in geochronological study levels and methods among the related Early Pleistocene localities (Table 8). In essence, the dating results of the Longgudong, the Sanhe Cave, the Dayakou pit and the Yunxian Man site are assessable using the ESR/U method. Concurrently, the dating results for the Longgudong, the Juyuan Cave, the Sanhe Cave, the Yunxian Man site and the Gongwangling can be examined using the paleomagnetic method. The age of the Dayakou fauna is comparable to that of Quyuanhekou fauna but younger than that of the Longgudong fauna and older than that of the Sanhe fauna based on the ESR/U datings (Shao et al., 2016; Han et al., 2022, 2024), which corresponds to their biochronological inference, except for the Sanhe and Quyuanhekou faunas. However, according to paleomagnetic datings, the age of the Sanhe fauna follows those of the Longgudong and Juyuan faunas but predates that of the Quyuanhekou fauna, which is consistent with their biochronological considerations in previous studies (Jin et al., 2008; Wang et al., 2017). The paleomagnetic dating result supports the biochronological inference for the Sanhe fauna rather than the ESR/U dating result, possibly due to a lack of horizon information of the herbivore tooth samples during the ESR/U dating experiment (Shao et al., 2015, 2016). Furthermore, despite dating tests relying on multiply methods (Aigner and Laughlin, 1973; Ma et al., 1978; Cheng et al., 1978; An and Ho, 1989; Heslop et al., 2000; Ding et al., 2002; Zhu et al., 2015; Tu et al., 2017; Pan et al., 2022), the paleomagnetic results for the Quyuanhekou (800–750 ka, based on Ma et al., 1978) and Gongwangling (936 ka, based on de Lumley and Li, 2008) faunas, and the ESR dating result for the Yuanmou fauna (1.6–1.1 Ma, based on Huang and Grün, 1998) appear to be more consistent with their biochronological inferences, considering the attributes of their fossil assemblages (You and Qi, 1973; Zhou and Zhang, 1984; Li et al., 1999; Jin et al., 2008). The possible reason why the age of the Yuanmou fauna appears older than that of the Dayakou fauna is the choice of different dating methods. Given the higher accuracy of the ESR/U results with respect to the regular ESR results (Shao et al., 2016), we propose that the numerical age of 1.0 Ma should be used to evaluate the chronology of the Yuanmou fauna in future research. Besides, the Queque fauna merit additional dating studies, as the paleomagnetic result (~1.0 Ma: Sun et al., 2014) does not agree with its biochronological inference, which suggests an age of a transitional time between the late Early Pleistocene and Middle Pleistocene close to those of Quyuanhekou and Gongwangling faunas (Jin et al., 2014).

4.4. The geochronological considerations of the Yanjinggou fauna complex

The classic Yanjinggou fauna has served as a crucial source for diagnosing and biochronologically comparing Quaternary mammalians in South China for decades, contributing to the identification of at least 38 large mammal species and 21 small mammalian species (Matthew and Granger, 1923; Colbert and Hooijer, 1953; Zheng, 1993; Chen et al., 2013; Hu et al., 2023a, 2023b). Although faunal associations from five well-documented localities, including the Dayakou pit, the Upper and Lower Caves of Pingba, the Sifangdi cave and the Meiren cave, suggest the geological age range of the Yanjinggou faunal complex spans from the Early to Late Pleistocene (Chen et al., 2013; Hu et al., 2023a, 2023b), the classic fauna, established based on mammalian fossils excavated by AMNH in 1921–1926 (Matthew and Granger, 1923; Colbert and Hooijer, 1953), faces age-related disputes due to the absence of detailed excavation records. Given the presence of numerous typical species and subspecies, including advanced *S. huananensis*, giant pandas, black bears, tapirs, and pigs, alongside the relicts of Neogene genus *Homotherium*, *Hesperotherium*, *Cervavitus* and *Leptobos*, the Yanjinggou fauna complex was previously interpreted as a Mid-Late Pleistocene fauna with a few middle Early Pleistocene elements (Chen et al., 2013). Considering the absence of typical paleospecies or paleosubspecies in the early Pleistocene, such as *Sinomastodon jiangnanensis, A. microta*, *T. sanyuanensis* and *R. fusuiensis* (Wang et al., 2017; Yan et al., 2023), the oldest age of Yanjinggou faunal complex is thought not to predate the middle Early Pleistocene. Furthermore, we have refined the division

Table 8

Comparisons of dating results of mammalian faunas in middle-late Early Pleistocene from southern China.

Catalgo No.	Faunal localities	Age estimate	Dating method	Dating material	Reference
1	Longgudong, Jianshi, Hubei	>2.14 Ma (below layer 6)	Paleomag	Sediment	Zheng (2004)
		1.512 ± 0.094 Ma (layer 8); 1.044 ± 0.053 Ma (layer 4)	ESR/U	Tooth remains	Han et al. (2024)
2	Juyuan Cave, Boyue Mountain, Guangxi	1.8 Ma	Paleomag	Sediment	Sun et al. (2014)
3	Sanhe Cave, Chongzuo, Guangxi	Sun et al. (2014)	Paleomag	Sediment	Sun et al. (2014)
		0.91–0.60 Ma	ESR/U	Tooth remains	Shao et al. (2015); Shao et al. (2016)
4	Bijiashan, Liuzhou, Guangxi	0.502 ± 0.06 Ma	Amino-acid	Tooth remains	Jin et al. (2008)
5	Yuanmou homonid site, Yunnan	1.54 ± 0.06 (0.11) Ma	^{26}Al/^{10}Be	Quartz sand	Luo et al. (2020)
		~1.7 Ma	Paleomag	Sediment	Zhu et al. (2008)
		1.6–1.1 Ma	ESR	Tooth remains	Huang and Grün (1998)
6	Queque Cave, Chongzuo, Guangxi	~1.0 Ma	Paleomag	Sediment	Sun et al. (2014)
7	Dayakou pit, Wanzhou, Chongqing	1.010 ± 0.115 Ma	ESR/U	Tooth remains	\
8	Yunxian Man site, Quyuanhekou, Hubei	1.10 ± 0.16 Ma	ESR/U & ESR	Tooth remains	Han et al. (2022)
		936 ka	Paleomag	Sediment	de Lumley and Li (2008)
9	Gongwangling, Lantian, Shaanxi	1.82 ± 0.12 Ma	^{26}Al/^{10}Be	Tooth remains & quartz sand	Tu et al. (2017)
		800-750 ka;	Paleomag	Sediment	Ma et al. (1978)
		1.0 Ma;			Cheng et al. (1978)
		1.15 Ma;			An and Ho (1989)
		1.63 Ma			Zhu et al. (2015)
		~1.15 Ma	Loess-palaeosol	Sediment	Heslop et al., 2000; Ding et al. (2002)
		700 ka	palynology	Spore and pollen	Aigner and Laughlin (1973)

proposed by Chen et al. (2013). The Yanjinggou faunal complex encompasses three temporal stages: the early stage (the transition fauna from the middle to late Early Pleistocene: the Dayakou fauna), the middle stage (the Middle Pleistocene fauna: such as the Upper and Lower Caves of Pingba faunas) and the late stage (the Late Pleistocene fauna: such as the Sifangdi and Meiren faunas).

4.5. The palaeoecological and palaeogeographic significances of the Dayakou fauna in Eurasia

The Early-Middle Pleistocene Transition (EMPT), a period spanning from the middle Early Pleistocene to the Middle Pleistocene (from 1.25 Ma to 0.41 Ma before present), is marked by significant climatic shifts and ecological changes (Lisiecki and Raymo, 2007; Head and Gibbard, 2015), which profoundly impacted hominins, vegetation, and large mammalian adaptations across Eurasia (Rook and Martínez-Navarro, 2010; Szymanek and Julien, 2018; Yang et al., 2021; Zhan et al., 2023). The effects of these climatic and ecological changes across the EMPT on the survival of large mammals in South China, at middle and low latitudes, have been somewhat underrated when compared to those at the same latitudes in Africa and high latitudes in Eurasia. Conversely, while large mammals in Africa appear to have remained stable throughout the EMPT (Head and Gibbard, 2015), those in South China reflected an extraordinary faunal turnover akin to those in high latitudes of Eurasia (Head and Gibbard, 2015; Zhou et al., 2018). The presence of advanced *S. huananensis* in the Dayakou and Yuanmou faunas (Zhou and Zhang, 1984) can be seen as the onset of large mammal evolutionary responses to the climatic and ecological changes during the EMPT in South China, implicating that giant herbivores may be more sensitive to climate fluctuations than other large mammals. Since then, large mammals underwent rapid evolution throughout the EMPT, with the majority being replaced by larger - bodied successor taxa such as *G. blacki*, giant pandas, black bears and tapirs (Pei, 1965; Zhang et al., 2015; Tong et al., 2019; Hu et al., 2023a, 2023b) while a minority (such as jackals and orangutans) were substituted by dwarf derived forms (Pei, 1965; Liao, 2024). At the same time, several genera became extinct, including *Sinomastodon*, *Homotherium*, *Hesperotherium*, *Cervavitus*, *Leptobos* (Dong, 2008; Wang et al., 2014; Chen et al., 2017; Tong et al., 2019).

Significantly, the extinction timelines of *Homotherium*, *Cervavitus*, *Leptobos* exhibit considerable diversity across Eurasia. *Homotherium* survived the entire EMPT, ultimately going extinct in the Late Pleistocene in Europe and Siberia (Antón et al., 2014; Jiangzuo et al., 2022b Lopatin et al., 2024), but disappeared regionally within China in the Middle Pleistocene (North China, late Middle Pleistocene; South China, middle Pleistocene, based on Tong et al., 2019). *Cervavitus,* a genus that became extinct in Europe at late Miocene and in the Central Asia and North China in Pliocene (Dong, 2011; Wang and Zhang, 2014), miraculously made its final appearance in South China during the early Middle Pleistocene (Tong et al., 2019; Zhang et al., 2022). *Leptobos* in China were shown to have been extirpated slightly later than those in Europe and the Eastern Mediterranean (China: around 0.8 Ma, Europe: around 1.0 Ma, based on Dong, 2008; Mead et al., 2014; Tong et al., 2017). *Homotherium* and *Leptobos* were dwellers in open environments (Antón et al., 2005; Mead et al., 2014), while *Cervavitus* preferred forests with irregular slopes (Dong, 2011). Four possible premises may explain the discrepancies of regional distinctions mentioned above: 1) Early Pleistocene is a period when the ecosystem of mountainous subtropical forests, mixed with arbor and shrub vegetation in South China, possessed a wide range and was relatively stable, providing a shelter for forest dwellers like *Cervavitus*. 2) The impact of climatic fluctuations and ecological changes across the EMPT on herbivorous inhabitants of open environments like *Leptobos* in Europe was slightly more severe than in China, leading to a comparatively earlier extinction; 3) Predators preferring open environment, like *Homotherium*, show greater potential for adaptation to environmental changes than herbivores and have a much longer survival protraction; 4) During the EMPT, more complex ecological systems in Europe than in China made it possible for predators like *Homotherium* to seek out more available habitats.

Equally noteworthy are the issues concerning the origins of modern clouded leopards and tigers. *N. nebulosa* has an exceedingly sparse fossil record (Werdelin et al., 2010), with documentation suggesting a Middle Pleistocene origin in mainland Southeast Asia (Olsen and Ciochon, 1990; Suraprasit et al., 2016). The earliest known remains of the clouded leopard in China were recovered from two Late Pleistocene localities: the Bailong cave in Yunxi, Hubei Province (Wu et al., 2007) and the Yanjiawan Cave 2 in Pingxiang, Jiangxi Province (Jiangzuo et al., 2018). As the oldest finding within China and Southeast Asia, *N. nebulosa* in the Dayakou fauna updates our understanding of modern clouded leopard and aligns its origin to the beginning of the EMPT.

In the case of *Panthera* fossils in China, there is an ongoing debate on taxonomy. Abundant teeth from localities in the early to middle Early Pleistocene have been identified as *P. pardus*, such as those from the Longgupo site in Wushan (ESR/U dating: 2.5–2.2 Ma, based on Huang and Zhong, 1991; Han et al., 2022), the *Gigantopithecus* Cave in Liucheng (ESR/U dating: 1.206–0.94 Ma; Pei, 1987; Deng et al., 2019), the Chuifeng Cave in Bubing Basin (ESR/U dating: 1.92 Ma, based on Shao et al., 2014; Liao et al., 2023), the Longgudong in Jianshi (ESR/U dating:1.5–1.0 Ma) (Han et al., 2024; Zhang and Feng, 2004), the Sanhe Cave in Chongzuo (Paleomagnetic dating: around 1.2 Ma, based on Jin et al., 2009; Sun et al., 2014) and the Yuanmou homonid site (ESR dating: 1.6–1.1 Ma, based on Zhou and Zhang, 1984; Huang and Grün, 1998). Isolated cheek teeth were sketchily described without measurements in the Longgupo site (Huang and Zhong, 1991), the Chuifeng and Sanhe Caves (Jin et al., 2009; Liao et al., 2023) as well as the Yuanmou homonid site (Zhou and Zhang, 1984), and the naming validity of *Panthera* cf. *P. pardus* or *P. pardus* still needs to be reexamined. Dental materials from *Gigantopithecus* Cave (Pei, 1987) and those previously described from the Dayakou pit appear larger than *P. pardus* and closer to *P. palaeosinensis* according to the measurement comparisons (Jiangzuo and Liu, 2020). *Panthera* fossil from Longgudong (Zhang and Feng, 2004) were assigned to *Panthera* sp. and need to be reevaluated with more complete materials, acting as a certain affinity to Asian pantherine cat (Jiangzuo et al., 2022a). It is generally agreed that living tigers are descended from *P. palaeosinensis*, with an oldest record from Pliocene sediments in North China (Qiu et al., 2003; Qiu, 2006). Either *P. tigris* or lager *P. pardus* from the localities in the early to middle Early Pleistocene could be assigned into *P. palaeosinensis* when it comes to dental measurements (Jiangzuo and Liu, 2020). Fossils of modern tiger were considered first appeared at Gongwangling site in Shaanxi, indicating an age reference of the late Early Pleistocene (Hu and Qi, 1978). Thus, the tiger remain studied in this paper reveals the oldest record of *P. tigris* in Asia, strengthening the assumption that modern tigers originated in Asia (Qiu, 2006). The coincidences of *P. palaeosinensis* and *P. tigris* can serve as an evolutionary index of large pantherine cats responding to climatic and ecological changes at the beginning of the EMPT.

5. Conclusion

This study reveals that the Dayakou fauna encompasses at least nineteen mammalian taxa, including *R. troglodytes*, Muridae gen. et sp. indet., *Homotherium* sp., *N. nebulosa*, *P. palaeosinensis*, *P. tigris*, Felidae gen. et sp. indet., *A. m. wulingshanensis*, *S. huananensis*, *H. sinense*, *T. sinensis*, *D. sumatrensis*, *Rhinoceros* cf. *R. sinensis*, *Sus* sp., Cervini gen. et sp. indet., *C. fenqii*, *Cervus* sp., *Muntiacus* sp. and *Leptobos* sp. The occurrence of *A. m. wulingshanensis*, *T. sinensis* and *Leptobos* sp. is recorded for the first time in the Yanjinggou of Chongqing. Based on ESR/U- series dating and faunal comparisons, it is proposed that the Dayakou fauna represents the earliest manifestation of the Yanjinggou fauna complex, potentially serving as a transition form from the middle to late Early Pleistocene (1010 ± 115 ka) mammalian fauna in South China. The Dayakou pit exhibits an accumulation of both well-preserved and fragmentary fossils, indicating a combination of autochthonomous and heterochthonous deposition. The palaeoecological reconstruction suggests a subtropical mountainous forest environment with arbor and shrub rivers nearby. It is particularly noteworthy that the Dayakou fauna is considered the onset of South China's mammalian faunas during the Early-Middle Pleistocene Transition, embracing the oldest records of modern clouded leopards and tigers in Asia, and reflecting the primary responses of large mammals to the climatic fluctuations and ecological changes in South China.

Data availability

Data will be made available on request.

Credit author statement

Haiqian Hu: Conceptualization, Methodology, Writing, Review & Editing; **Haowen Tong**: Conceptualization, Methodology, Review & Funding; **Fei Han**: Experimental design, Data analysis, Writing, Review, Editing & Funding; **Hui Dai, Wanbo Huang, Xunqian Wang and Yu Lin**: Field work, Fossil recognition & Supervising; **Qigao Jiangzuo**: Carnivore identification & Species origin discussion; **Paul Rummy**: Taphonomic and ecological discussions & English editing; **Guangbiao Wei**: Conceptualization, Methodology, Supervising, Review & Funding.

Declaration of competing interest

We declare that we have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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