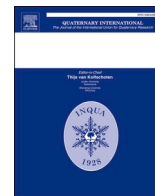




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Hominin paleoenvironment in East Asia: The Middle Paleolithic Xuchang-Lingjing (China) mammalian evidence

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ABSTRACT

The Chinese open-air site Xuchang-Lingjing (Henan) is located near the border between the Palearctic and the Oriental biozone in a lowland depression at the southern edge of the North China Plain. The site yielded a Middle Palaeolithic assemblage that includes the two fragmented, incomplete human (possibly Denisovan) skulls (Xuchang 1 and Xuchang 2), more than 15,000 artefacts and more than 40,000 mammalian remains representing at least 20 taxa. The composition of the faunal assemblage is biased by hominin hunting activities; it is, however, diverse and “natural” enough to be used as a proxy to reconstruct the paleoenvironmental condition during the human occupation of the site. The Palearctic faunal assemblage indicates a grassland-dominated palaeoecological environment, with a mosaic of scattered forest and mixed forest vegetation as well as along rivers and/or lakes the occurrence of swampy areas and with bushes. The OSL-dates and the assumed correlation with the last interglacial (MIS 5) palaeosol strongly suggest that we are dealing with an interglacial fauna. However, the fact that the Lingjing assemblage represents the southernmost Palearctic fauna questions the assumption that the Lingjing Middle Palaeolithic finds date from an interglacial period. A late Middle Pleistocene (MIS 6) or Late Pleistocene glacial or stadial phase (MIS 4) seems more likely.

1. Introduction

The discovery of hominin remains generally triggers questions about the age of the finds as well as about the environmental conditions in which the discovered hominin operated. The question about the palaeoenvironmental circumstances is in particular relevant for hominins that lived in the northern hemisphere where Quaternary climatic fluctuations resulted in major environmental changes (Roebroeks et al., 1992; Dennell et al., 2020). The contrast between the climatic conditions during the interglacial and the glacial phases can be big, in particular in Western and Central Europe where phases with a dominance of densely vegetated deciduous forest alternated with the open non-analogue Mammoth Steppe biome. In order to know how hominins/humans coped with these fluctuations it is important to have insight in the palaeoenvironmental conditions in a specific region during

hominin/human occupation. Different proxies (e.g., botanical, zoological as well as stable isotope data) can be used to reconstruct the palaeoenvironment, depending on the available fossil record.

The Chinese open-air site Xuchang-Lingjing (Henan) yielded a Middle Palaeolithic assemblage with two eastern Eurasian late archaic hominin (incomplete) skulls (Li et al., 2017a; Trinkaus and Wu 2017), >15,400 artefacts and a large number of vertebrate remains representing >20 taxa. Molluscs, insects as well palaeobotanical remains are missing. Hence, the vertebrate record is so far the only proxy that has been used to reconstruct the palaeoenvironment. The faunal analyses of the finds excavated in 2005 and 2006 resulted in an extensive list of large mammal taxa published in a number of papers (the majority in Chinese language with an English summary) (Li and Dong 2007; Dong and Li, 2008, 2009; Zhang 2009). The succeeding excavations (2007–2017) resulted in an increased number of fossil remains and in

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the discovery of “new” taxa as well as in the revision of previous identified species. An update of the mammalian information is presented in this paper. The data form the base of an updated palaeoenvironmental reconstruction of the region during human occupation and the deposition of the find horizon.

The Xuchang-Lingjing (Henan Province; 34°04'N, 113°41'E) site is located in a lowland depression at the southern edge of the North China Plain, between the eastern foot of the Songshan Mountains and the Huang-Huai Plain, about 120 km south of the Yellow River (Figs. 1 and 2) (Li et al., 2017a). The open-air site was discovered in 1965 by Zhou Guoxing (Zhou, 1974) and in 2005, researchers from the Henan Provincial Institute of Cultural Relics and Archaeology started to excavate the site. In the years 2005–2017, more than 550 m² were excavated, most of the area to a depth of ca. 9 m. Eleven geological layers were identified (Fig. 2) (Li et al., 2017a) and three archaeological horizons were discovered. Layers 1–4 yielded archaeological remains ranging in age from the Neolithic to the Shang-Zhou Bronze Age. Layer 5, dated to ca. 13,500 ± 406 yrs BP, contains microblade technology, microcores, bone artefacts, perforated ostrich eggshells, ochre, faunal remains, and the first regional evidence of pottery (Li and Ma, 2016; Li et al., 2017b). Layer 5 yielded, in addition, an exceptionally well-preserved, Palaeolithic miniature carved bird figurine (Li et al., 2020). Layer 6–9 are sterile; they did not yield any stone artefacts or bone material. Rich in Middle Palaeolithic lithic artefacts and fossil human and animal remains are the base of Layer 10 and the upper part of Layer 11. Layer 10 with a thickness of ≈1.6 m consists, just as Layer 9, of brownish ferruginous silt with vertical root hole-like structures and Layer 11, the lowest level, consists of sage-green silt. Only the upper ca. 1.3 m of Layer 11 has been excavated; the total thickness of Layer 11 is unknown (Li et al., 2017a).

Two OSL samples collected from layer 10 were dated to ~96 ± 6 kyr and ~102 ± 2 kyr (Nian et al., 2009). OSL samples from Layer 11 are dated to ≈105 ka - ≈125 ka, corresponding to the early Marine Isotope Stage 5 (MIS 5; MIS 5e to 5d) and to the last interglacial palaeosol S1 in the Loess Plateau of China (Nian et al., 2009; Li et al., 2017a).

The faunal remains from the base of Layer 10 and the upper part of

Layer 11 are regarded and treated as a single faunal assemblage because of the uninterrupted rather uniform distribution of the finds as well as the species they represent. Human remains were only found in Layer 11.

Li et al. (2018) concluded that the integrity of the Lingjing Layer 10 and 11 assemblage is high and that human behavioural information is well preserved. A variety of sedimentary and archaeological indicators show that the disturbance is limited. They also concluded that the uninterrupted vertical distribution (up to >1 m) of the Middle Palaeolithic finds throughout the Layers 10 and 11 sequence along with the large number of faunal remains representing different taxa, demonstrates that the site was occupied by humans repeatedly over a relatively long period (Li et al., 2018).

2. Material and methods

2.1. Materials

2.1.1. Middle Palaeolithic finds

A relatively small number of lithic artefacts, animal bones and small pebbles was recovered from the base of Layer 10. The largest archaeological assemblage with more than 50,000 finds (including lithic artefacts, animal bones) was collected in Layer 11. The material is stored in Henan Provincial Institute of Cultural Relics and Archaeology, Zhengzhou, China.

The lithic assemblage is, with >15,400 artefacts rather rich. It includes cores, flakes, and tools (i.e., scrapers, notches, denticulates, borers and points (Li et al., 2019a; Zhao et al., 2020)). The lithic assemblages show characteristics (e.g., the discoidal core preparation) that allows the attribution to Chinese Middle Palaeolithic (Doyon et al., 2018, 2019; Li et al., 2019a). The abundance of debitage flakes and evidence for use wear on lithic artefacts suggests that the manufacture, use, re-sharpening and discard of lithic tools occurred at the site (Doyon et al., 2019; Li 2007; Li et al., 2019a).

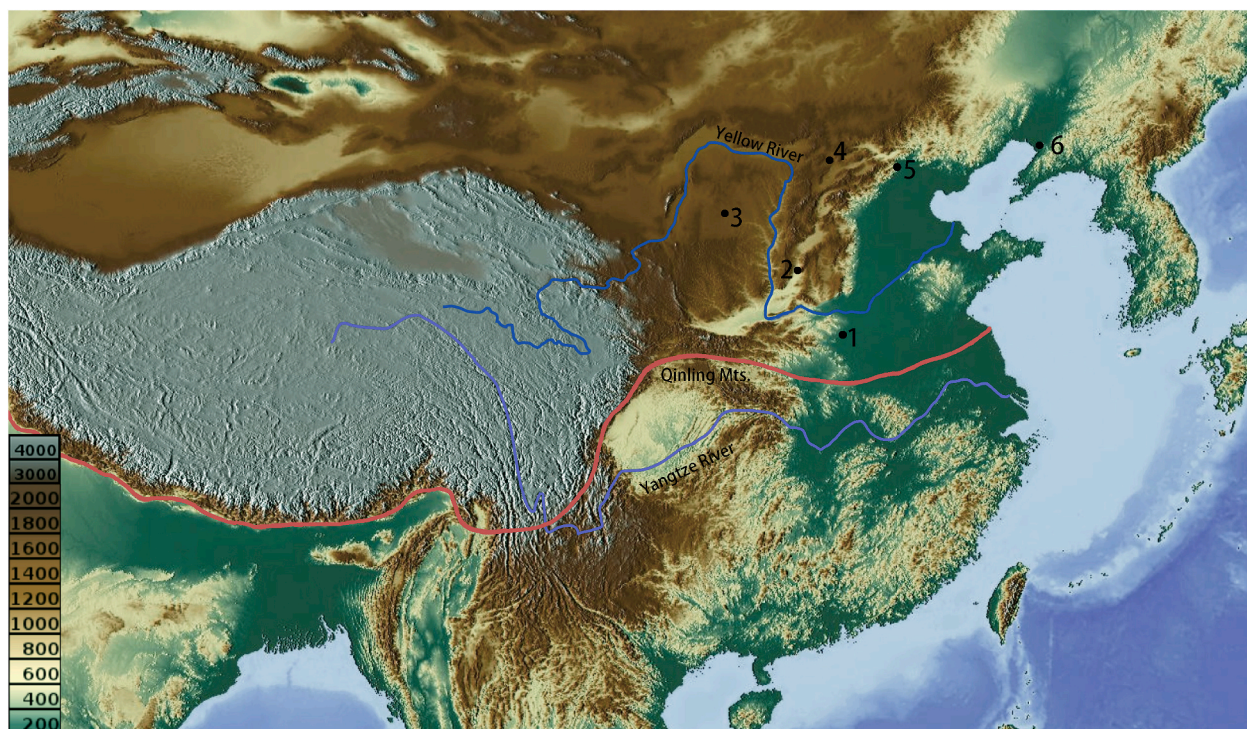


Fig. 1. Geographical position of the boundary (red line) between the northern Palearctic and the southern Oriental biogeographic zones and the location of Lingjing (Henan) (1) and other sites mentioned in the paper: 2. Dingcun (Shanxi); 3. Salawusu (Inner Mongolia); 4. Xujiayao (Shanxi); 5. Zhoukoudian; 6. Xiaogushan (Liaoning). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

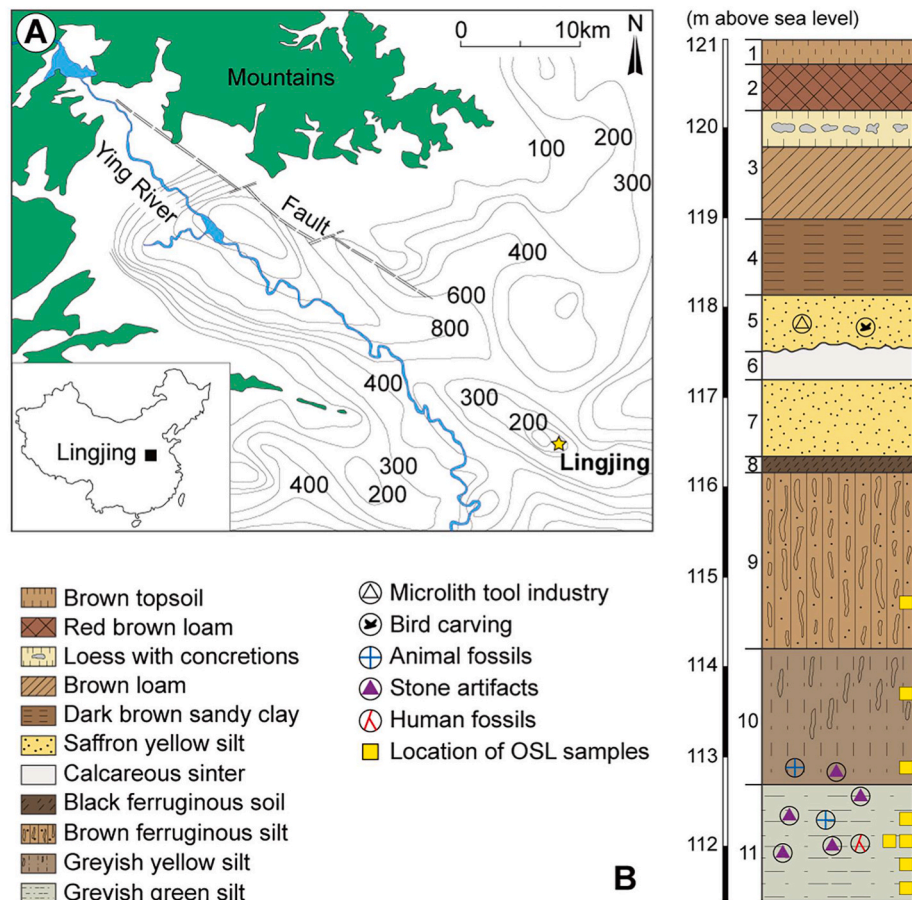


Fig. 2. a) Location of Lingjing (Henan, China); b) stratigraphy indicating the geological and cultural layers (after Doyon et al., 2018).

2.1.2. Human remains

Among the most spectacular finds from Lingjing Layer 11 are the two fragmented, incomplete human skulls (Xuchang 1 and Xuchang 2) excavated in situ in 2007 and 2014. The Xuchang Man skulls derive from young adults. Xuchang 1 (26 pieces) is the most complete skull; it retains most of the neurocranial vault and portions of the cranial base, as well as part of the left frontal bone. Xuchang 2 (16 pieces) is less complete with a large part of the occipital bone and the temporal bones (see Li et al., 2017a). Both skulls exhibit external auditory exostoses, most pronounced in Xuchang 2, implying conductive hearing loss (Trinkaus and Wu 2017). The skulls exhibit a mosaic of morphological features with differences from and similarities with their western contemporaries. Given their low and broad neurocrania with the maximum breadth inferiorly, they are considered as eastern Eurasian late archaic hominins (Li et al., 2017a; Trinkaus and Wu 2017). Taken into account the stratigraphical age of the skulls as well as the geographical position of the site, we might deal with Denisovan skulls as suggested by Martínón-Torres et al. (2017) and Dennell et al. (2020). This proposition needs to be confirmed by the results of further studies.

2.1.3. Faunal remains

The Middle Palaeolithic find horizon yielded a large number of vertebrate fossils; molluscs, insects as well palaeobotanical remains are, unfortunately, missing. The vertebrate record from the lower part of Level 10 and from Level 11, with more than 40,000 specimens, shows a high diversity in terms of the number of taxa. Mammalian remains dominate the Middle Palaeolithic fossil record. Reptilia (Order Testudines) are represented by ca. 10 carapace and plastron fragments of a turtle. The fossil bird (Aves) assemblage includes a small collection of ca. 10 bones/bone fragments; the bird collection represents different

species. Both categories have not been studied in detail so far.

The mammalian record is dominated by rather well preserved, although highly fragmented remains of large mammals. The smaller mammals are limited to bones and bone fragments of, so far unidentifiable, rodent species (Rodentia fam. gen. et sp. indet. 1; Rodentia fam. gen. et sp. indet. 2) and a representative of the Order Lagomorpha (Lagomorpha fam. gen. et sp. indet.) (Li and Dong, 2007).

The faunal analyses of the finds excavated in 2005 and 2006 resulted in an extensive list of large mammal taxa (Li and Dong 2007; Dong and Li, 2008, 2009; Zhang 2009). The succeeding excavations (2007–2017) resulted in an increased number of fossil remains and in the discovery of “new” taxa as well as in the revision of previous misidentified species. The revised list of large mammalian species is presented in Table 1. This paper presents a systematic summarizing overview of the fossil materials as well as the most significant diagnostic features of the large mammal species encountered in the Middle Palaeolithic horizon of Lingjing Layer 10 and 11.

2.2. Methods

Measurements, presented in the text, were taken following the standard guide published by von den Driesch (1976). Capital letters refer to upper cheek teeth, lower case letters refer to lower cheek teeth. Abbreviations used in the description of the material are: I/i = incisor; C/c = canine; DP/dp = deciduous molars; P/p = premolars; M/m = molars; dext. = dextral/right; sin. = sinistral/left; fam. = family; gen. = genus; sp. = species; indet. = indeterminate; fam. gen. et sp. indet. = family, genus and species indeterminate; cf. = confer/compare; MNI = the minimum number of individuals.

Table 1

Larger mammal taxa represented in the Lingjing Layer 10 and 11 faunal assemblage. N. spec. - the number of specimens assigned so far; MNI - the minimum number of individuals.

	N. spec.	MNI
Carnivora		
<i>Panthera tigris</i>	19	2
<i>Crocuta crocuta</i>	10 (+copr.) ^a	2
<i>Canis cf. lupus</i>	5	1
<i>Nyctereutes cf. procyonoides</i>	2	1
<i>Vulpes cf. vulpes</i>	17	3
<i>Ursus sp.</i>	5	2
<i>Meles cf. meles</i>	7	2
Proboscidea		
<i>Palaeoloxodon sp.</i>	2	1
Perissodactyla		
<i>Equus cf. przewalskii</i>	378 ^b	18
<i>Equus hemionus</i>		
<i>Stephanorhinus kirchbergensis</i>	3 ^c	1
<i>Coelodonta antiquitatis</i>	101 ^c	9
Artiodactyla		
<i>Sus lydekkeri</i>	29	2
<i>Hydropotes pleistocenicus</i>	3	1
<i>Cervus (E.) elaphus</i>	89	7
<i>Cervus nippon</i>	4	1
<i>Elaphurus davidianus</i>	1	1
<i>Sinomegaceros ordosianus</i>	6	2
<i>Bos primigenius</i>	432 ^d	38
<i>Procapra przewalskii</i>	45	20

^a copr. = coprolites.

^b Total nr. of dental elements and metapodial bones (the remaining equid remains have not been recorded so far and the record of both species has only partly been assigned to one of the two equid species).

^c Number of dental elements; postcranial elements have not been recorded so far.

^d The sum of the number of horn-cores, dental elements and metapodial bones (the remaining large bovid remains have not been recorded so far).

3. Systematic description of the large mammals

3.1. Order Carnivora

Family Felidae Gray, 1821

Genus *Panthera* Oken, 1816

Panthera tigris (Linnaeus, 1758) - tiger.

Materials: skull fragment dext. with P4, skull fragment sin. with P3 and P4, skull fragment dext. with P4, mandible sin. with p4 and m1, mandible dext. with canine and p4, lower canine, p3 dext., humerus sin., ulna dext., radius dext., femur dext., astragalus dext., astragalus sin., cuboid dext., 3rd cuneiform dext., 2 metatarsals II dext., metatarsals III dext., metatarsals V dext.

Fig. 3a–d; Table 2.

In total, 19 specimens, representing at least 2 individuals, were assigned to *Panthera tigris* based on their characteristic morphological features and dimensions. The cranial bones are incomplete. Two maxilla fragments, one from the right side (with a P4) (Fig. 3a) and one from the left side (with a P3 and P4) (Fig. 3b) are partly covered by sediment concretions. The premolars show major traces of damage: the antero-lateral side of the P3 is missing and both P4s show clear traces of heavy wear. The similarity in wear suggests that both fragments are most probably from the same adult individual. The third skull fragment is from a young individual. The erupting P4 is only slightly worn; the P3 has not been erupted.

The two mandibles are both incomplete: a fragment from the left side (Fig. 3d) includes a p4 and a heavily damaged m1. The p4 shows minor traces of wear. The second mandible is from the right side; only heavily damaged remnants of the canine and the p4 are present. The faunal assemblage contains, in addition, a lower canine and an isolated p3 dext. of a large felid.

The postcranial part of the skeleton is represented by (in)complete front and hind leg elements from both sides of the body. The distal end of

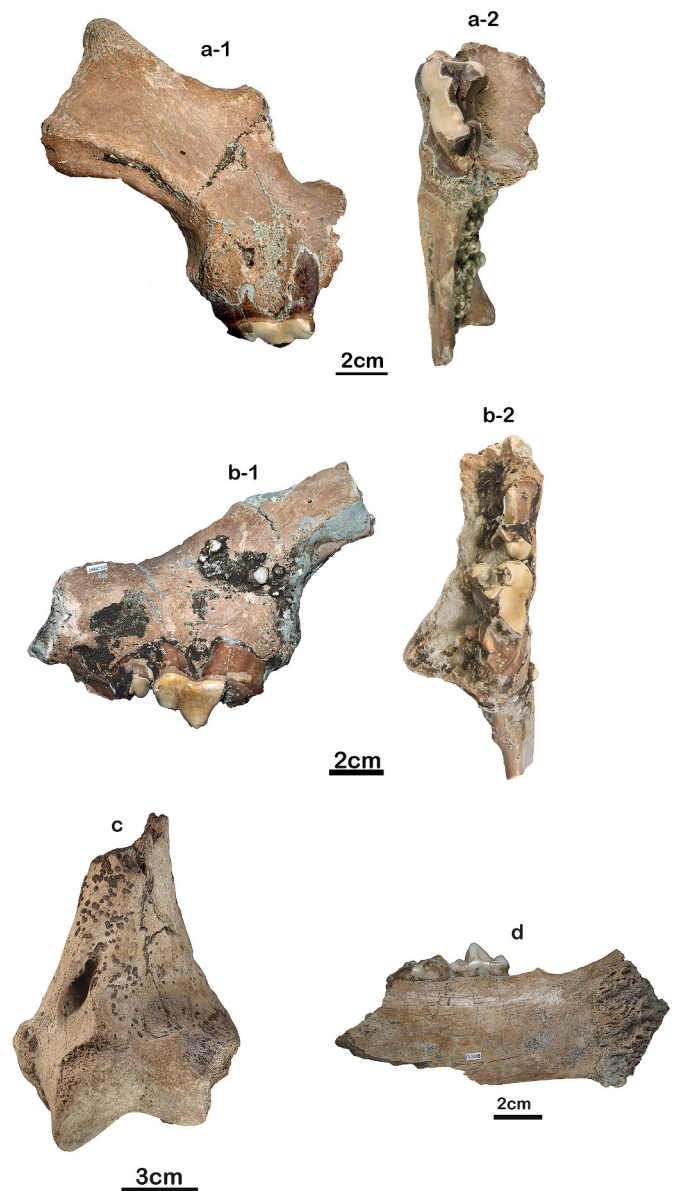


Fig. 3. Lingjing - *Panthera tigris*. 3a: maxilla fragment dext. with P4 (16L3098): a-1: labial view; a-2: occlusal view; 3b: maxilla fragment sin. with P3 and P4 (16L3097): b-1: labial view; b-2: occlusal view; 3c: distal part of humerus sin. (14L853); 3d: mandibula sin. with p4 and m1 (07L3465).

the humerus (Fig. 3c) shows the presence of a supracondyloid foramen, a diagnostic feature that is mainly characteristic for members of the Felidae family.

The dimensions of the Lingjing dental elements assigned to *Panthera tigris* (Table 2) show that the size of the Lingjing tiger is comparable to that of fossil tigers from the Chinese localities Yanjinggou of Wanxian (Wanhsien) (Sichuan) and Zhoukoudian (Choukoutien) (Beijing) locality 1 and to the living *Panthera tigris amoyensis* from Southern China. Recent tigers living on Java (*P. tigris sondaica*) and Sumatra (*P. tigris sumatrae*) are a little smaller in size (Table 2; Hooijer 1947). The greatest width of the distal epiphyse of the Lingjing humerus (78.78 mm) is smaller than that of a fossil humerus from Yanjinggou (82 mm) and just outside of the range of the greatest distal width of humeri of the living *P. tigris sondaica* from Java (68–75 mm; N = 2) (Hooijer, 1947). The astragali from Lingjing (greatest length: 58.35–58.40 mm) are also smaller than those from Yanjinggou (greatest length: 61–64 mm) (Hooijer, 1947).

Table 2

Dimensions of upper and lower premolars of *Panthera tigris* from Lingjing compared to those of the fossil tiger remains from the Chinese localities Wanxian (Wanhshien) (Sichuan) and Zhoukoudian (Choukoutien) (Beijing) locality 1 and the living tigers from Java (*P. tigris sondaica*) (N = 4) and from Southern China (*P. tigris amoyensis*) (N = 5). Data from Hooijer (1947).

<i>Panthera tigris</i>	Lingjing	Wanxian	Zhoukoudian – Loc. 1	Java - Recent	Southern China - Recent
P3 - length	27.32	19.3–24.5	22.3–24.0	18.8–22.5	20–23.8
P4 - length	35.72–36.12	33.3–38.1	33.0–35.0	30.0–33.7	31–36
p3 - length	17.55	14.9–18.0	15.5–20.3	13.5–16.8	15–17.3
p4 - length	25.82	22.8–25.7	22.2–25.5	19.7–22.9	21–24.3

Family Hyaenidae Gray, 1869

Genus *Crocota* Kaup, 1828.

Crocota crocuta (Erxleben, 1777) – spotted hyena.

Materials: posterior part of a skull, upper incisor, upper P4, mandible sin. with p2 and p3, mandible dext. with p3 and p4, 2 lower p2 dext., lower p3 dext., ulna sin., tibia sin., more than 30 coprolites.

Fig. 4a and b; Table 3.

Li and Dong (2007) presented 3 hyena specimens discovered in the Lingjing Layer 10 and 11 faunal assemblage excavated in 2005 and 2006. More recent excavations yielded additional remains that are, based on their characteristic morphological features and dimensions, assigned to *Crocota crocuta*. The material is fragmented; the posterior skull fragment (Fig. 4a) is characterised by the presence of large occipital condyles and a well-developed sagittal crest. The lower premolars (Fig. 4b1–3) are large and massive triangular cusps and a well-developed cingulum. The amount of wear is in most elements large; the crown of the upper P4 is almost entirely worn.

The dimensions of the Lingjing dental elements assigned to *Crocota crocuta* (Table 3) show that the size of the Lingjing hyena is comparable to the fossil hyena from the locality Penghu Trench described by Tseng and Chang (2007).

Apart from the fossil remains listed above, there are dozens of coprolites from a medium-sized carnivore, most likely a hyena (Wang et al., 2015). The assignment is based on their characteristic shape and size. Wang et al. (2015) described an assemblage of microbiological remains such as parasites, fungi and hairs, encountered in some of the coprolites. The data provides information about the diet and health condition of ancient hyaena species. Detailed analyses of the animal hairs indicated the consumption of a feline by hyenas (Wang et al., 2015).

Li and Dong (2007) assigned the Lingjing 2005, 2006 hyena finds to *Pachycrocota cf. sinensis*. However, during the end of the Early Pleistocene/first half of the Middle Pleistocene, the genus *Pachycrocota* was replaced by the *Crocota crocuta* (Tseng and Chang, 2007; Marciszak et al., 2021). Baryshnikov (1999) refers all Pleistocene discoveries of the genus *Crocota* to *Crocota spelaea* because of their more carnivorous specialisation. The Lingjing hyena record is, however, too fragmentary

Table 3

Dimensions of the lower premolars of *Crocota* from Lingjing compared to those of the fossil hyena remains from Penghu Trench (N = 2). Data from Tseng and Chang (2007).

<i>Crocota crocuta</i>	Lingjing	Penghu Trench
p2		
length	16.46	16.50–16.81
width	12.18	10.51–13.24
p3		
length	20.90–25.16	22.58–22.91
width	15.84–18.61	16.48–17.22

and too limited to draw conclusions about the level of carnivorous specialisation. Werdelin and Solounias (1991) suggested to include all fossil taxa of the genus *Crocota* in one species, the extant spotted hyena *C. crocuta*. Sheng et al. (2014) confirmed their suggestion after analysing morphological and ancient DNA data.

Family Canidae Fischer de Waldheim, 1817.

Genus *Canis* Linnaeus, 1758

Canis cf. lupus Linnaeus, 1758 - wolf.

Materials: a fragment of a lower m1 dext., an incomplete metacarpal (Mc III), a caput of a femur, the shaft and the distal end of a tibia, calcaneum.

Fig. 5a.

A limited number of finds are similar in morphology and size to skeletal elements of the modern wolf *Canis lupus*. The lower m1 (Fig. 5a) shows a well-developed metaconid which excludes assignment of the molar to a Dhole, the genus *Cuon* (Dhole) (Ripoll et al., 2010).

Genus *Nyctereutes*, Temminck, 1838

Nyctereutes cf. procyonoides (Gray, 1834) – raccoon dog.

Materials: humerus sin., radius dext.

Fig. 5e and f; Table 4.

Two finds, a humerus and a radius (Fig. 5e and f), are assigned to *Nyctereutes cf. procyonoides* because of the similarities in morphology and dimensions (Table 4) with skeletal elements of the raccoon dog

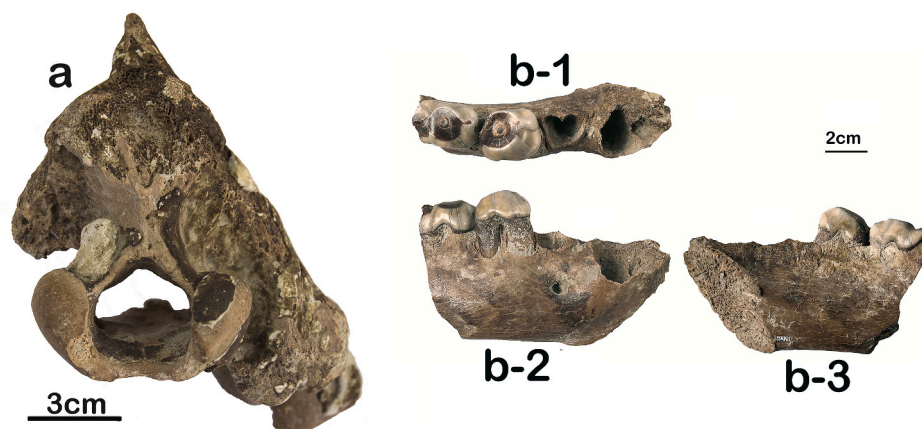


Fig. 4. Lingjing - *Crocota crocuta*. 4a: posterior part of a skull (10L3146); 4b: mandible dext. with p3 and p4 (6L179); 4b1: occlusal view; 4b2: lateral view; 4b3: lingual view.



Fig. 5. Lingjing – 5a: *Canis cf. lupus* - fragment of a lower m1 dext. (9L0087); 5b–d: *Vulpes cf. vulpes*: 5b: mandible dext. with p3 and p4 (14L313); 5c: mandible dext. with p2, p3 and p4 (9L0078); 5d: mandible sin. with p3, p4 and m1 (14L62); 5e–f: *Nyctereutes cf. procyonoides*: 5e: humerus sin. (6L2556); 5f: radius dext. (5L245).

Table 4

Dimensions of the humerus and radius from Lingjing assigned to *Nyctereutes cf. procyonoides* compared to those of the modern raccoon dog *Nyctereutes procyonoides* in the zoological comparative collection of the Institute of Cultural Heritage, Shandong University.

<i>Nyctereutes cf. procyonoides</i>	Lingjing	modern
humerus (6L2556)		
proximal width	20.25	20.61
radius (5L245)		
distal width	10.80	10.20

Nyctereutes procyonoides. Both specimens indicated the presence of a raccoon dog in the Lingjing Layer 10 and 11 faunal assemblage.

Genus *Vulpes* Frisch, 1775

Vulpes cf. vulpes (Linnaeus, 1758) – red fox.

Materials: mandible dext. with p2, p3 and p4, mandible sin. with p3, p4 and m1, mandible dext. with p3 and p4, mandible dext., ulna dext., metacarpal IV dext., metacarpal V dext., 3 tibia sin., metatarsal II dext., metatarsal III dext., metatarsal IV dext., 3 metapodial fragments, phalange 1.

Fig. 5b–d; Table 5.

The Lingjing Layer 10 and 11 faunal assemblage includes 17 specimens of a small canid. The remains have the size and the morphology of those of a red fox *Vulpes vulpes*. The minimum number of individuals is 3 based on the presence of 3 distal ends of tibia sinistral. The dimensions of the Lingjing dental elements are within the range of those of the modern red fox from Poland (Table 5). Assignment to the Corsac or Steppe fox (*Vulpes corsac*) has been rejected because of the latter's smaller size.

Family Ursidae Gray, 1825

Genus *Ursus* Linnaeus, 1758

Ursus sp.

Materials: upper canine dext., upper canine sin., mandible sin. with p4 and m2, 2 m³ dext.

Table 5

Dimensions (range, mean, number of specimens (N)) of the lower premolars of *Vulpes* sp. from Lingjing compared to those of the modern red fox (*Vulpes vulpes*) from Poland (Szuma, 2000).

	Lingjing	Poland - modern males	Poland - modern females
p3			
length	8.57–9.64	7.67 to –10.77 (9.24; N = 587)	7.33–10.19 (8.91; N = 495)
width	2.90–3.27	2.78–4.20 (3.37; N = 603)	2.55–4.37 (3.23; N = 500)
p4			
length	9.21–10.05	8.40–11.06 (9.73; N = 602)	7.94–10.62 (9.39; N = 498)
width	3.03–4.04	3.33–5.03 (4.13; N = 611)	3.01–4.78 (3.96; N = 510)
m1			
length	14.91	13.69–18.03 (15.67; N = 574)	12.87–17.94 (15.15; N = 483)
width	5.43	5.12–7.51 (6.08; N = 573)	4.87–6.84 (5.88; N = 488)

Fig. 6a and c; Table 6.

Li and Dong (2007) presented a lower m3, assigned to *Ursus* sp., discovered in the Lingjing Layer 10 and 11 faunal assemblage excavated in 2005 and 2006. More recent excavation yielded additional remains that are, based on their characteristic morphological features and dimensions, assigned to a bear of the genus *Ursus*. The canines are robust and the lower m2 and m3 are characterised by the presence of a large number of small cusps. The dimensions of the Lingjing *Ursus* molars (Table 6), in particular the dimensions of the m3, are outside of the range of the molars of the extant *Ursus arctos*; they correspond well with the dimensions of the molars that have been assigned to the large speleoid cave bears *Ursus deningeri* and *U. spelaeus*. The lower m2 shows, in addition, a clear central constriction, a feature that is more strongly developed in the lower m2 of the larger cave bears (Wagner and Cermák, 2012). *U. deningeri* is known from Zhoukoudian Loc. 1 and Zhoukoudian Upper Cave (Jiangzuo et al., 2018); the occurrence of *U. spelaeus* is listed by Li and Dong (2007) in the fauna from Zhoukoudian - Upper Cave. The number of remains in the Lingjing faunal assemblage is too limited to assign the remains to one of the large speleoid cave bears and is therefore listed as *Ursus* sp.

Family Mustelidae Fischer 1817

Genus *Meles* Brisson, 1762

Meles cf. meles (Linnaeus, 1758) - badger.

Materials: mandible sin. with p2 and p3, mandible dext. with m1, 2 radius dext., 1 radius sin., pelvis dext., tibia sin.

Fig. 6b; Table 7.

The remains listed above show morphological features that are more or less identical with those of skeletal remains of a modern badger *M. meles* (Henan coll.216–002) in the zoological comparative collection of Henan Provincial Institute of Cultural Relics and Archaeology, Zhengzhou, China. The mandibles are short, the m1 is relatively large but almost completely worn. The Lingjing mandibles differ from the modern *Meles meles* mandibles by a less anteriorly extended masseteric fossa. The right mandible with the m1 has been published by Li and Dong (2007). The authors assigned the specimen to *Viverra cf. zhibetha*. Because of the close resemblance with the *Meles meles* mandibles, we prefer to assign the mandible to *Meles cf. meles*.

3.2. Order Proboscidea

Family Elephantidae Gray, 1821

Genus *Palaeoloxodon* Matsumoto, 1924

***Palaeoloxodon* sp.** - elephant.

Materials: 2 fragments of distal part of a tusk.

Fig. 7a and b.

Two fragments of a distal part of a tusk (Fig. 7a) indicate the occurrence of an elephant at the site Lingjing Layer 10 and 11. The total length is ca. 36 cm and the max. diameter at the proximal end is ca. 10.5 cm. A second specimen assigned to *Palaeoloxodon* sp. has been described

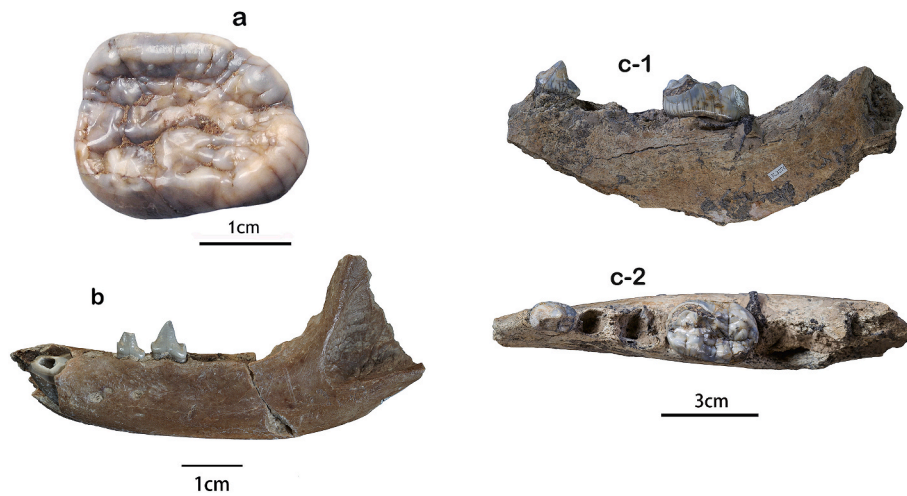


Fig. 6. Lingjing – 6a and 6c: *Ursus* sp.: 6a: m3 dext. (6L1517) (occlusal view); 6c: mandible sin. with p4 and m2 (17L3270); 6c1: lateral view; 6c2: occlusal view; 6b: *Meles* cf. *meles* - mandible sin. with p2 and p3 (9L0079).

Table 6

Dimensions (range, mean, number of specimens (N)) of the upper canines and the lower (pre)molars from Lingjing compared to the dimensions of *Ursus deningeri* from Zhoukoudian (Jiangzuo et al., 2018), those of *Ursus deningeri* from sites located in the Czech Republic and Poland (Wagner and Čermák, 2012), *Ursus spelaeus* from Zoolithen Cave (Germany) (Baryshnikov, 2006) and of the extant *Ursus arctos* with different geographical origin (Balkan, Siberia, Tibet, Kamchka) (Wagner and Čermák, 2012).

	<i>Ursus</i> sp. - Lingjing	<i>Ursus deningeri</i> - Zhoukoudian	<i>Ursus deningeri</i>	<i>Ursus spelaeus</i>	<i>Ursus arctos</i>
upper canine					
length	35.22				
width	24.30–25.97				
lower p3					
length	14.94				
width	8.90				
lower m2					
length	27.43	26.22–29.60 (27.4; N = 3)	24.9–32.8 (28.97; N = 39)	25.7–36.3 (29.70; N = 57)	20.5–27.4 (23.91; N = 108)
width	18.11	12.72–16.38 (14.2; N = 4)	14.8–19.2 (17.18; N = 39)	15.6–21.9 (18.44; N = 57)	12.4–17.2 (14.76; N = 107)
lower m3					
length	26.13–26.29		20.0–28.0 (24.62; N = 41)	21.4–31.1 (25.87; N = 55)	16.2–23.3 (19.79; N = 76)
width	18.15–21.19		15.9–21.4 (17.82; N = 42)	16.9–22.4 (18.92; N = 55)	12.3–17.5 (14.52; N = 79)

Table 7

Dimensions of the dental elements of from Lingjing assigned to *Meles* cf. *meles* compared to those of the modern badger *Meles meles* in the zoological comparative collection of the Institute of Cultural Heritage, Shandong University.

	Lingjing - <i>Meles</i> cf. <i>meles</i>	<i>Meles meles</i> - extant
p3		
length	5.06	4.74
width	2.80	3.12
p4		
length	5.79	5.72
width	3.41	3.76
m1		
length	16.34	16.92
width	6.75	7.42

by Li and Dong (2007).

The transversal cross-section of the tusk (Fig. 7b) clearly shows the presence of so-called “Schreder lines” as well as the “Schreder pattern” i. e., the angle between the Schreder lines. The Schreder pattern can be used to discriminate the Elephantinae taxa (Palombo and Villa, 2001). The angle between the Schreder lines is, at the Lingjing specimen, very wide (ca. 140°); the value falls outside of the range of the angles observed in *Mammuthus primigenius* (65°–90°). Tusks of the straight-tusked elephant *Palaeoloxodon antiquus* show an angle that is

much wider (between 90° and 132°) (Palombo and Villa, 2001). Ábelová (2008) showed that the angle between the Schreder lines increases towards the tusk surface. This might explain the high value observed at the Lingjing *Palaeoloxodon* specimen. The available data do not allow assignment to *Palaeoloxodon namadicus* or to *Palaeoloxodon naumanni*, the two common species of the genus *Palaeoloxodon* in China.

3.3. Order Perissodactyla

Family Equidae Gray, 1821

Genus *Equus* Linnaeus, 1758

Equus cf. *przewalskii* Poliakov, 1881 - Przewalski’s horse and.

Equus hemionus Pallas 1775 - Onager.

Materials (recorded so far): 168 isolated upper premolars and molars, mandible sin. with p2 and p3, mandible sin. with p4 and m1, mandible sin. with p4-m2, mandible dext. with p2-p4, mandible dext. with p3-m1, mandible dext. with m2 and m3, 153 isolated lower premolars and molars, 10 metacarpals sin., 3 metacarpals dext., 9 metatarsals sin., 5 metatarsals dext., 23 distal metapodia fragments.

Figs. 8 and 9; Table 8.

So far only part of the equid remains has been recorded. Dental elements have been listed and measured and the equid metapodials have been studied in more detail in the frame of the study of metapodial bone hammers in the Lingjing assemblage. Dental as well as postcranial remains of *Equus* cf. *przewalskii* and *Equus hemionus* are abundant. The

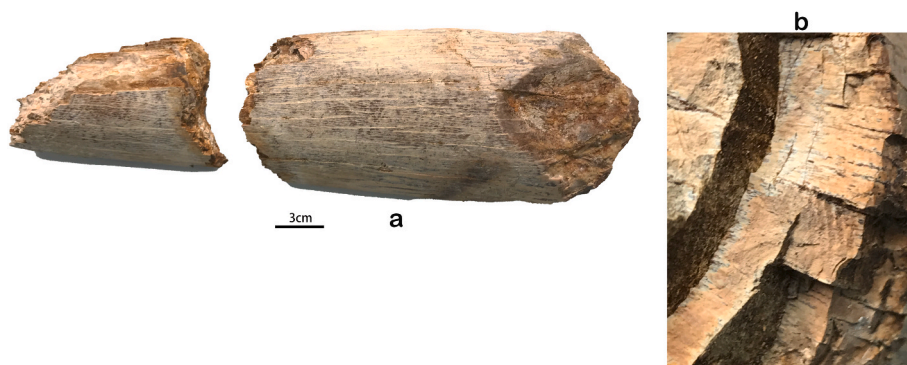


Fig. 7. Lingjing – *Palaeoloxodon* sp.; 7a: fragments of a distal part of a tusk; 7b: transversal cross-section of the tusk.

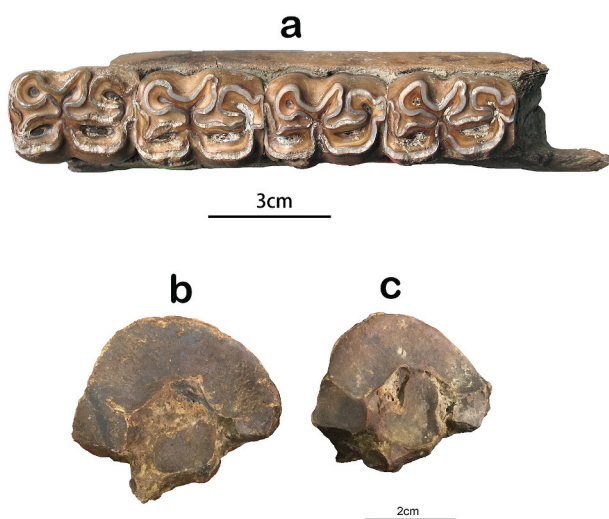


Fig. 8. Lingjing – *Equus* cf. *przewalskii* and *Equus hemionus*. 8a: *Equus* cf. *przewalskii*: mandible sin. with p3 – m2 (6L1516) (occlusal view); 8b: *Equus* cf. *przewalskii*: metatarsal sin. (10L3171) (proximal view); 8c: *Equus hemionus*: metatarsal sin. (6L1400) (proximal view).

fossil equid assemblage includes at least 18 lower m3s from the left side of the skull, indicating a minimum number of equid individuals of 18. Many of the metapodial remains have been assigned to either *Equus* cf. *przewalskii* or *Equus hemionus* based on the dimensions. The metapodials of *Equus* cf. *przewalskii* are more robust; the *Equus hemionus* ones are more slender (Fig. 8b and c; Fig. 9). Based on the dimensions of the equid remains it is apparent that the majority of the equid remains should be assigned to the more slender Onager or Asiatic wild ass *Equus hemionus*.

There are only two complete metapodial bones in the Lingjing assemblage; two metatarsals sin. The dimensions of the Lingjing Onager bones (Table 8) indicate that they are, compared with the modern *E. hemionus hemionus* from the Gobi of Mongolia, rather large and robust.

Table 8

Dimensions (range, mean, number of specimens (N)) of the *Equus hemionus* metatarsus from Lingjing Layer 10 and 11 compared to the dimensions of the metatarsi of the extant *E. hemionus hemionus* from the Gobi of Mongolia (Schöpke et al., 2012).

<i>E. hemionus</i>	Lingjing	<i>E. hemionus hemionus</i> Gobi, Mongolia
metatarsal		
greatest length	262–283	222 - 280 (267.11; N = 18)
greatest distal width	39.28–46.60 (41.73; N = 18)	35.9–39.8 (38.34; N = 18)

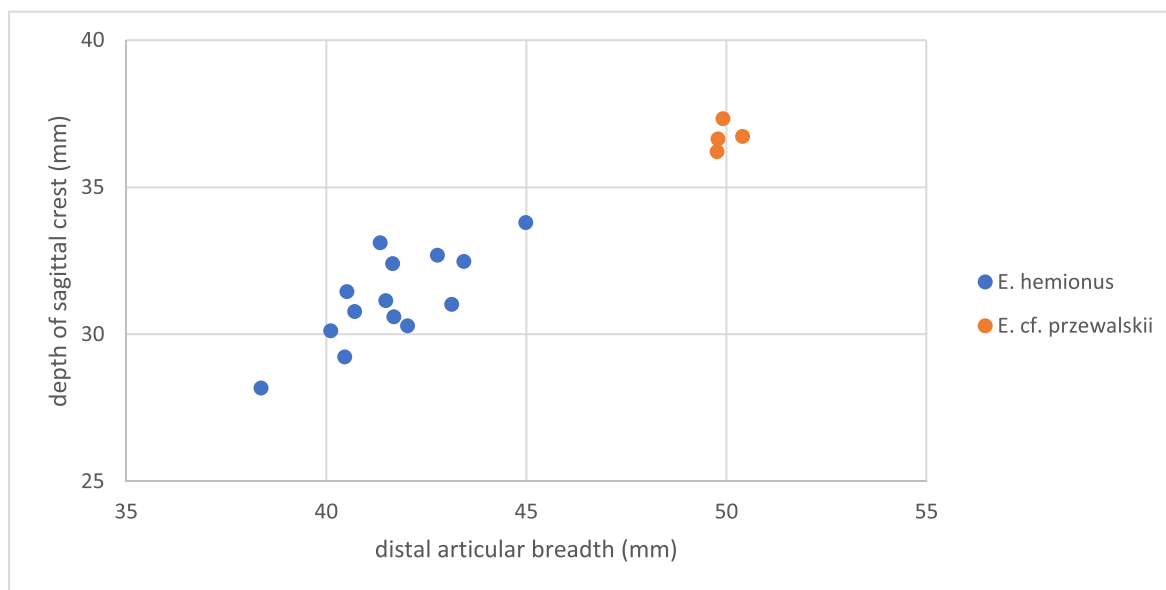


Fig. 9. Scatter diagram showing the distal articular breadth/depth of sagittal crest ratio of the metapodials of the equids *Equus* cf. *przewalskii* and *Equus hemionus* in the Lingjing Layer 10 and 11 faunal assemblage.

Deciduous molars are missing in the collection of more than 320 dental elements and the vast majority of the premolars and molars are still rather high crowned. This indicates that we are dealing with a population of subadult equids and that juvenile as well as old individuals are missing.

Li and Dong, 2007 gave an extensive description of the morphological features of the Equid dental material and assigned the premolars and molars to *Equus caballus* and *Equus hemionus*. In more recent publications (e.g., Dong et al., 2010) the species name of the more robust late Middle Pleistocene/Late Pleistocene equid has been replaced by *Equus przewalskii*. However, molecular research has indicated that the modern *Equus przewalskii* shows signs of domestication (although in a minor degree) (Orlando, 2019). The Lingjing robust horse lived long before the domestication process started; therefore, we prefer to assign the more robust equid, which shows many similarities with the modern Przewalski's horse, to *Equus cf. przewalskii*.

Family Rhinocerotidae Owen, 1845

The family of the Rhinocerotidae is represented in the Lingjing faunal assemblage by two species; a conclusion that is based on the morphological characters of the dental remains. The faunal assemblage includes dental as well as postcranial material. In this paper we only present the dental data; the postcranial elements have not been recorded systematically so far. Li and Dong (2007) presented data of a limited number of rhinoceros remains collected during the 2005 and 2006 excavations. More recent excavations yielded additional material.

Genus *Stephanorhinus* Kretzoi, 1942.

Stephanorhinus kirchbergensis (Jäger, 1839) – extinct rhinoceros.

Materials: upper P3 dext., upper P4 dext., lower p3? sin.

Fig. 10a–c; Table 9.

The dental elements listed above (Fig. 10a–c) are characterised by a smooth enamel surface. The upper premolars listed above are assigned to *Stephanorhinus kirchbergensis* because of the absence of a closed medifossette, a feature that is characteristic for the upper molars of the woolly rhinoceros *Coelodonta antiquitatis*. In addition, the premolars are also large. The ectoloph of the upper premolars is rather flat and slightly

Table 9

Dimensions (range, mean, number of specimens (N)) of the upper premolars, P3 and P4, and the lower p3 of *Stephanorhinus kirchbergensis* from Lingjing Layer 10 and 11 compared to the dimensions of the premolars from Rhino Cave (Shennongjia, Hubei) assigned to *Stephanorhinus kirchbergensis* (Tong and Wu, 2010) and to the dimensions of dental elements from various European locations presented by Guérin (1980) originally assigned to *Stephanorhinus mercki* (a synonym of *Stephanorhinus kirchbergensis*).

<i>Stephanorhinus kirchbergensis</i>	Lingjing	<i>St. kirchbergensis</i> Rhino Cave - Shennongjia, Hubei	<i>St. mercki</i> (Guérin, 1980)
P3			
length	41.07		43 - 51 (46.63; N = 8)
width	52.76		50 - 62 (57.23; N = 13)
P4			
length	56.96		43.5–58 (51.06; N = 26)
width	74.86		54–69.5 (62.71; N = 29)
p3			
length	45.11	34.5–36.8 (35.6; N = 4)	35 - 46 (40.0; N = 13)
width	32.21	25.9–28.6 (27.2; N = 4)	27–35.5 (30.19; N = 13)

convex. A cingulum is only weakly developed. The trigonid of the lower p3 has a round shape; the talonid is crescent-shaped. The lower premolars and molars of *Coelodonta antiquitatis* have, in contrast, a more rectangular shaped trigonid. The lower p3 is clearly larger than those from the Rhino Cave in Shennongjia, Hubei, described by Tong and Wu (2010) which have been assigned to *Stephanorhinus kirchbergensis*. The dimensions of the Lingjing materials (Table 9) fall, with exception of the width of the P4, within the range of the dimensions of dental elements from various European locations presented by Guérin (1980).

Genus *Coelodonta* Bronn, 1831

Coelodonta antiquitatis (Bumenbach, 1799) – woolly rhinoceros.

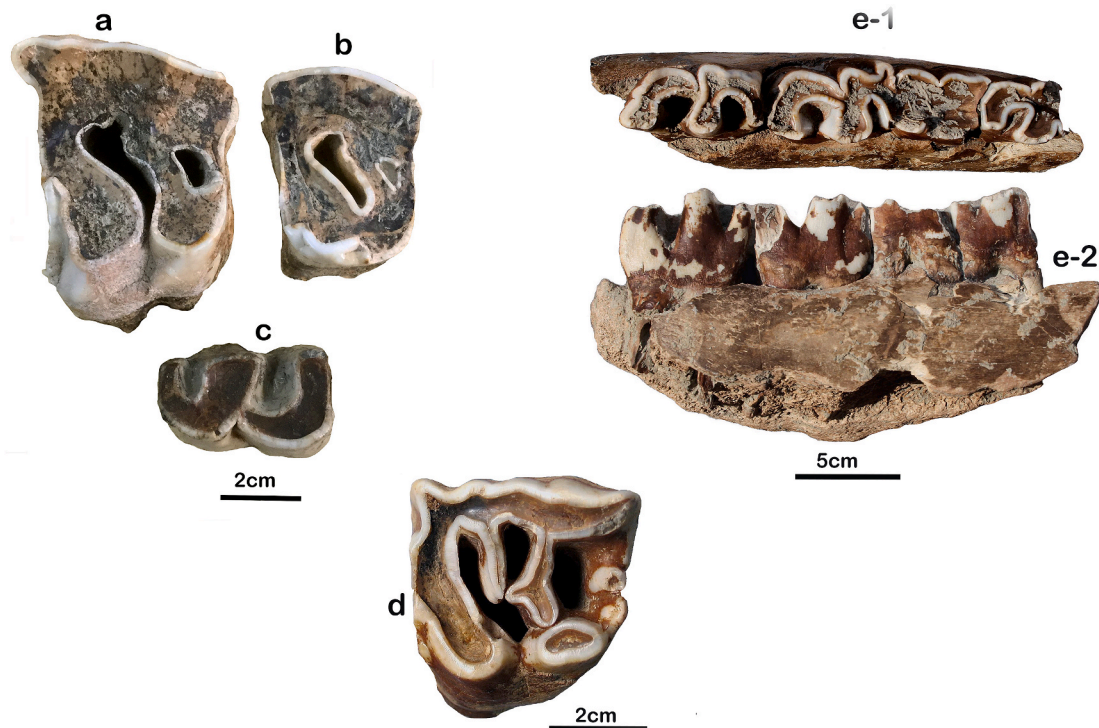


Fig. 10. Lingjing – *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis*. 10a–c: *Stephanorhinus kirchbergensis*. 10a: Upper P4 sin. (13L4174); 10b: Upper P3 sin. (17L2180); 10c: lower p3? sin. (5L167); 10d–e: *Coelodonta antiquitatis*. 10d: P3 sin. (6L778); 10e: mandible sin. with p4-m3 (14L258).

Materials: DP2 dext., 2 DP4s dext., P2 dext., 3 P3s sin., 2 P3s dext., 3 P4 sin., 5 P4s dext., M1 sin., M1 dext., M2 sin., 2 M2s dext., 4 M3s sin., 4 M3s dext., 31 upper molar fragments, mandible dext., with p4-m3, mandible dext. with p4-m2, mandible fragment, 3 dp2s sin., 2 dp2s dext., dp3/dp4 dext., p2 sin., p2 dext., p3 dext., m1 sin., m1/m2 dext., 2 m2s dext., 5 m3s sin., 3 m3s dext., 10 lower molar fragments, 5 M fragments.

Fig. 10d and e; Tables 10 and 11.

The enamel of the dental elements assigned to the woolly rhinoceros (Fig. 10d and e), is often covered with crown cement and is not as smooth as the enamel of the premolars of *Stephanorhinus kirchbergensis*, described above. The upper molars show the presences of a medifossette, a woolly rhinoceros feature. The trigonid of the lower premolars and molars is rectangular with clear angles; the talonid is crescent-shaped. The dimensions (Table 10) of the Lingjing Materials fall within the range of the dimensions of the *Coelodonta antiquitatis* dental elements from various European locations presented by Guérin (1980).

The woolly rhinoceros *Coelodonta antiquitatis* remains include at least 9 different individuals (the majority is juvenile (Table 11)). Remarkable is the large number of milk molars whereas very old individuals are missing in the assemblage. This conclusion is based on the wear stages of different elements.

3.4. Order Artiodactyla

Family Suidae Gray, 1821

Genus *Sus* Linnaeus, 1758

Sus lydekkeri Zdansky, 1928 – wild boar.

Materials: mandible anterior part with i1 sin., i2 sin., i1 dext., i2 dext., mandible anterior part with alveoli for incisors and canines, mandible fragment dext. with alveoli for p2, p3 and p4, mandible dext. with m1, m2 and m3, mandible sin. with m2 and m3, mandible fragment with m3 dext., upper canine, upper canine fragment, 3 fragments of an

Table 10

Dimensions (range, mean, number of specimens (N)) of upper (DP4, P3, P4, M3) and lower (dp2, m3) dental elements of *Coelodonta antiquitatis* from Lingjing Layer 10 and 11 compared to the dimensions of dental elements from various European locations presented by Guérin (1980).

<i>Coelodonta antiquitatis</i>	Lingjing	<i>C. antiquitatis</i> - Guérin (1980)
DP4		
length	48.75	44 - 57 (48.60; N = 20)
width	41.69–44.03 (42.86; N = 2)	39 - 55 (43.35; N = 23)
P3		
length	34.18–38.48 (36.34; N = 4)	33 - 43 (38.28; N = 56)
width	39.29–51.26 (44.52; N = 5)	35–47.5 (42.06; N = 57)
P4		
length	38.77–44.71 (42.09; N = 6)	37–51.5 (43.17; N = 47)
width	47.66–59.64 (52.57; N = 7)	44–55.5 (48.53; N = 52)
M3		
length	55.75–64.44 (61.64; N = 4)	44 - 70 (58.0; N = 69)
width	50.98–56.98 (54.04; N = 5)	37.5–55 (49.88; N = 42)
dp2		
length	27.84–29.86 (28.85; N = 2)	26–29.5 (27.23; N = 11)
width	14.40–15.59 (15.09; N = 3)	15–18.5 (16.33; N = 12)
m3		
length	51.71–58.02 (54.56; N = 6)	47 - 62 (53.50; N = 49)
width	28.10–37.71 (33.10; N = 5)	28 - 37 (31.36; N = 351)

Table 11

Age categories and minimum number of individuals of the woolly rhinoceros (*Coelodonta antiquitatis*) remains from Lingjing Layer 10 and 11 based of the wear stages of the different elements.

<i>Coelodonta antiquitatis</i> - individual age	MNI
Age 0, not/just born (based on dp2 unworn)	2
very young (based on slightly worn dp2)	1
young (based on very worn dp2)	1
semi adult (based on p2 slightly worn); upper P2 hardly worn	1
adult but not very old (based on the wear and the number of lower m1 dext)	3
old individual (based on advanced wear stage of a number of molar fragments)	1
Total MNI	9

upper canine, upper DP4, upper M1 or M2, lower incisor i1, lower m1, 2 lower m3, 7 M fragments, incomplete scapula, caput of a femur.

Fig. 11a and b.

The chisel-like incisors (Fig. 11b), the characteristic upper canines and the bunodont premolars and molars (Fig. 11a) indicate the occurrence of a wild boar of the genus *Sus*. The upper canines are robust and based on their large dimensions assigned to a male. The Lingjing wild boar is larger than the modern wild boar *Sus scrofa* in dental elements. The dimensions of the Lingjing finds are about similar to those of fossils from Zhoukoudian, Locality 1 attributed to *Sus lydekkeri* (Dong and Li, 2008).

Family Cervidae Goldfuss, 1820

The Lingjing Layer 10 and 11 faunal assemblage includes ca. 50 antler fragments. Many fragments show morphological features that enables the assignment to a specific species. In addition, there are ca. 80 dental elements and postcranial materials. Detailed investigation of the Cervidae remains is in progress; only a restricted number of diagnostic elements are presented in this paper.

Genus *Hydropotes* Swinhoe, 1870

Hydropotes pleistocenica (Teilhard de Chardin & Pei, 1941) – extinct water deer.

Materials: a left upper canine, an upper M3, a mandible fragment with p2, p3 and p4.

Fig. 12a–c.

The characteristic upper canine (Fig. 12a and b) is long and slender, with enamel layers on both, lingual and labial, sides. The latter character excludes, according to Dong and Li (2008) the assignment to the genus *Moschus*. The upper molar (Fig. 12c) and the lower premolars are small in size. The dimensions are similar to those of comparable elements found in Zhoukoudian, Locality 13, attributed to *Hydropotes pleistocenica* (Dong and Li, 2008).

Genus *Cervus* Linnaeus, 1758

Cervus elaphus Linnaeus, 1758 – red deer.

Materials: 1 unshed antler fragments sin., 9 shed antler fragments sin., 5 shed antler fragments dext.; 34 upper premolars and molars (fragments), 10 mandible fragments, 30 lower premolars and molars (fragments).

Fig. 13a and b.

Most of the antlers are shed. The antlers that are assigned to *Cervus (E.) elaphus* show the presence of a burr with a brow tine at their base and a bez tine at a short distance above the burr (Fig. 13a and b). This antler shape is characteristic for semi-adult and adult males of the red deer *Cervus (E.) elaphus*. The angle between the brow tine and the beam is large in the specimens assigned to *Cervus elaphus*; the angle is smaller in the antlers identified as *Cervus (Sika) nippon*. The fossil assemblage also includes a distal fragment of a right antler with three tines that form a 3-dimensional terminal “crown” (Dong and Li, 2008).

The mandible fragments and isolated premolars and molars are from a large deer and are assigned to *Cervus elaphus* based on their dimensions. The lengths of the third lower molars (31.54–36.51 mm, x = 33.76, N = 7) overlap with the length range of *C. elaphus* molars from a number of British fossil assemblages (Lister et al., 2010). Most of the

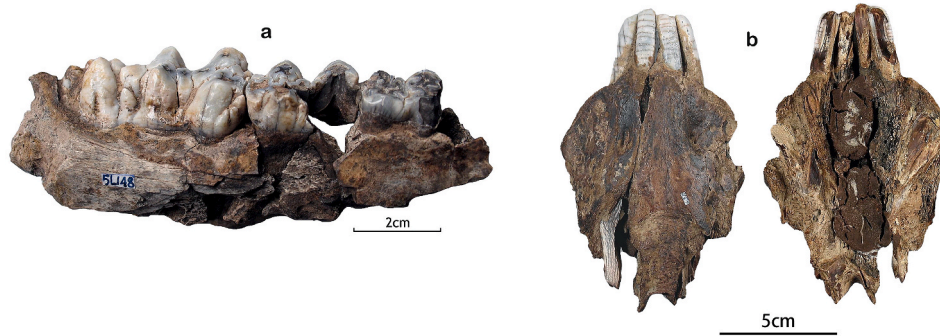


Fig. 11. Lingjing – *Sus lydekkeri*. 11a: mandible dext. with m1, m2 and m3 (5L148); 11b: mandible anterior part with i1 sin., i2 sin., i1 dext., i2 dext (6L876); left: outer/ventral view; right: inner/dorsal view.

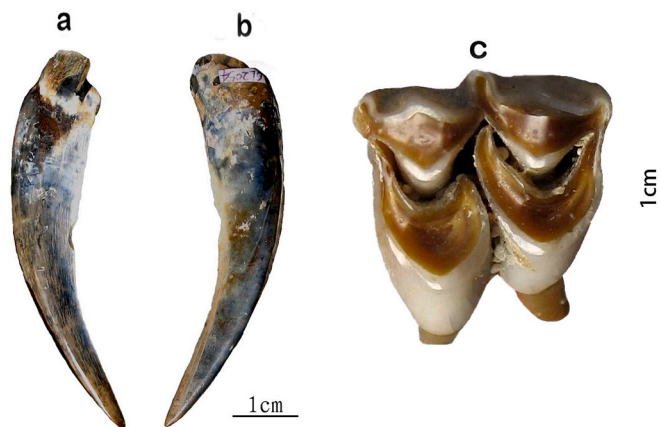


Fig. 12. Lingjing – *Hydropotes pleistocenica*. 12a–b: upper canine sin. (6L2054); 12a: labial view; 12b: lingual view; 12c: upper M3 sin. (6L828) – occlusal view.

molars are only slightly worn. This indicates that we are dealing with a prime-adult dominated populations. Deciduous molars are absent. The MNI in the assemblage is 7; a number that is based on the total number of lower p4 dext.

Cervus nippon Temminck, 1838 - Sika deer.

Materials: 2 shed antler fragments sin., 2 shed antler fragments dext. Fig. 13d and e.

Four basal antler fragments in the Lingjing fossils assemblage are from antlers with about the same size as those assigned to *Cervus elaphus*. However, their shape is different. The antlers (Fig. 13d and e) have close to the burr a so-called brow tine but a bez tine, characteristic for *Cervus elaphus*, is missing. The angle between the brow tine and the beam is smaller than in *Cervus elaphus* antlers.

Dong and Li (2009) assigned the antlers to a new cervid subspecies, *Axis shansius lingjingensis*. However, we do not agree with this identification. The morphology of the four antler basal parts is similar to the shape of antlers of the East Asian medium-sized sika deer (*Cervus nippon*).

Genus *Elaphurus* H. Milne-Edwards, 1872

Elaphurus davidianus A. Milne-Edwards, 1866 - Père David's deer.
Material: antler fragment.

Fig. 13c.

The antler fragment (Fig. 13c) is characterised by the relatively high number of (tiny) bifurcations within a short distance, a feature that does not occur in *Cervus elaphus* and *Cervus nippon* antlers. Size and morphology correspond with antlers of the Père David's deer.

Genus *Sinomegaceros* Dietrich, 1933

Sinomegaceros ordosianus Young, 1932 – extinct giant deer.

Materials: proximal part of a left antler with a pedicle, M1 sin., p3 sin., mandible sin. with m1-m3, mandible dext. with m2 and m3, m3 sin.

Fig. 13f.

Dimensions: burr: maximum diameter 103.3 mm, minimum diameter 98; pedicle is thick and short - the distance from the frontal bone to the horn ring on its medial edge is 25 mm.

Dong and Li (2008) described the giant deer remains encountered in the Lingjing Layer 10 and 11 fossil assemblage. The antler (Fig. 13f) is unshed; it is the basic part (proximal part) of the beam of a left antler; remnants of a brow tine are visible at the very base of the antler just above the burr, the brow tine is very broad, a feature that is characteristic for East Asian giant deer. The dental remains that are listed, are (slightly) larger than the comparable elements assigned to *Cervus elaphus*.

Dong and Li (2008) assigned the larger cervid remains to *Megaloceros ordosianus*. van der Made and Tong (2008), however, prefer the assignment to the genus *Sinomegaceros*, an extinct genus of deer known from the Early to Late Pleistocene of East Asia. It is considered to be part of the group of "giant deer" taxa (often referred to collectively as members of the tribe Megacerini), with a probable close relationship to *Megaloceros*.

Family Bovidae Gray, 1821

Genus *Bos* Linnaeus, 1758

Bos primigenius Bojanus, 1827 - Aurochs.

Materials (recorded so far): 2 horn-cores, maxilla dext. with P3 – M1; 85 isolated upper premolars and molars, 5 upper molar fragments, mandible dext. with m2 and m3, 113 isolated lower premolars and molars, 33 lower molar fragments, 38 metacarpals sin., 38 metacarpals dext., 25 metatarsals sin., 22 metatarsals dext., 69 distal metapodial fragments (mainly isolated distal epicondyles).

Fig. 14a–c.

So far only part of the large bovid remains has been recorded. Dental elements have been listed and measured and the metapodials have been studied in more detail in the frame of the study of metapodial bone hammers in the Lingjing assemblage.

The long, curved and twisted horn-cores show features (such as a circular cross section and a diameter that slowly decreases towards the terminal end) (Fig. 14a) that support the identification as Aurochs *Bos primigenius* (Dong and Li, 2008) and excludes the assignment to species of the genera *Bubalus* and *Bison*.

Isolated dental elements form a large part of the large bovid remains of the Lingjing Layer 10 and 11 faunal assemblage. The collection of dental elements with ca. 200 specimens includes only 2 deciduous molars, an upper DP2 and a lower dp4. Young individuals are apparently missing. This assumption is supported by the fact that the proximal and/or distal epiphyses of all the metapodials are completely fused. The upper and lower premolars and molars are relatively high-crowned; heavily worn elements are missing. Based on these data it can be concluded that the majority of the individuals are (sub)adult in age.

Distal parts of metacarpal as well as metatarsal bones are well represented in the large bovid fossil assemblage. Based on the large

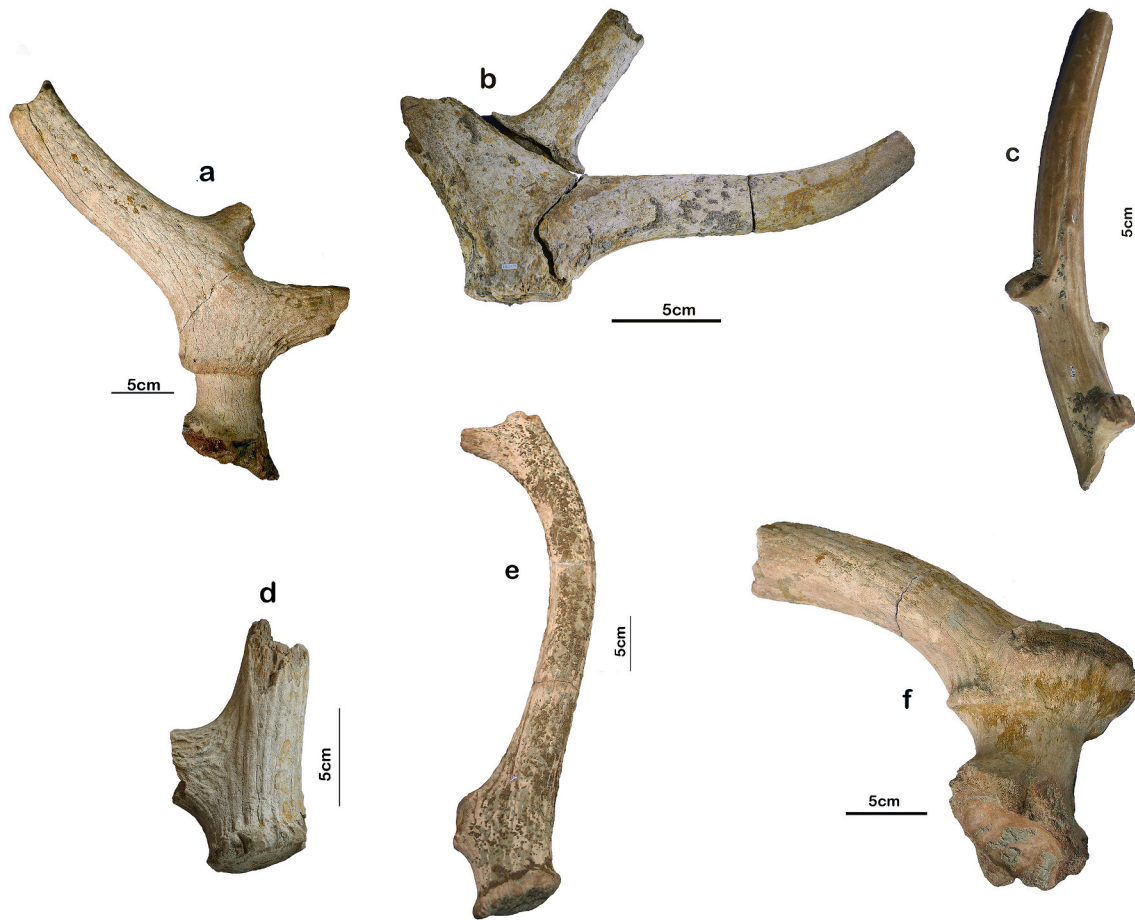


Fig. 13. Lingjing – *Cervus elaphus*, *Cervus nippon*, *Elaphurus davidianus* and *Sinomegaceros ordosianus*. 13a–b: *Cervus elaphus* – 13a: proximal part and pedicle of an antler sin. (6L732); 13b: antler base dext. (14L3439); 13c: *Elaphurus davidianus* – antler fragment (9L0151); 13d–e: *Cervus nippon* – 13d: antler sin. base (6L1209); 13e: antler sin. base (6L731); 13f: *Sinomegaceros ordosianus* – proximal part and pedicle of an antler sin. (6L1936).



Fig. 14. Lingjing – *Bos primigenius*. 14a: horn core sin./dext.; 14b–c: metatarsal – anterior view: 14b: metatarsal sin. (6L2424); 14c: metatarsal dext. (6L2457).

variation in size (Fig. 14b and c), it is concluded that both males and females are represented in the assemblage.

Genus *Procapra* Hodgson, 1846

Procapra przewalskii (Büchner, 1891) - Przewalski's gazelle.

Materials: 39 (almost) complete horn-cores and horn-core fragments, maxilla sin. with DP3-M1, upper M1 sin., 2 lower m1/m2 sin., 1 lower m1/m2 dext., m3 sin.

Fig. 15a–c.

Dimensions: the maximum diameter of the base varies between 29.03 and 39.6 mm (N = 18), the maximum length of the horn-cores is

up to 151 mm.

The Lingjing Layer 10 and 11 *Procapra* record includes a total of 39 (almost) complete horn-cores and horn-core fragments. The cores (Fig. 14a and b) show the occurrence of longitudinal, narrow grooves and ribs; the cross section is more or less oval in shape. The minimum number of individuals is based on the number of horn-cores at least 20. The dental elements (Fig. 15c; Table 12) are assigned to the species because of the hypsodont character and the dimensions of the molars.

Dong and Li (2008) assigned the small bovid remains to Przewalski's gazelle (*Procapra przewalskii*) and exclude the assignment to the

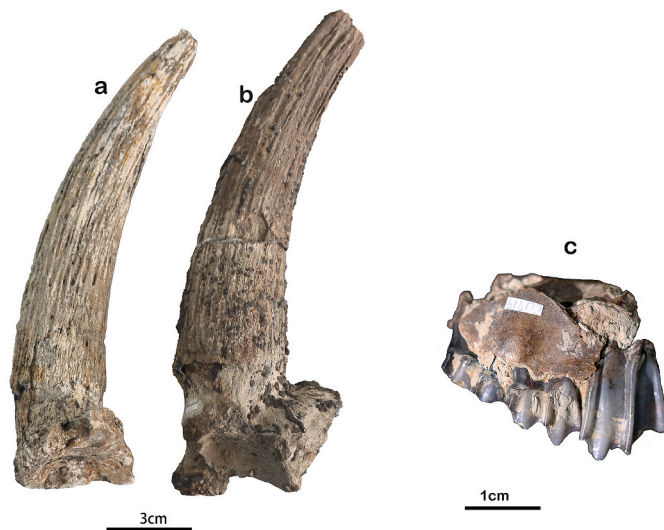


Fig. 15. Lingjing – *Procacpra przewalskii*. 15a–b: horn cores: 15a: horn core sin (5L078); 15b: horn core sin. (6L1908); 15c: maxilla sin. with DP3-M1 (6L1919) – lingual view.

Table 12

Dimensions (length and width) of the dental elements from Lingjing Layer 10 and 11 assigned to *Procacpra przewalskii*.

<i>Procacpra przewalskii</i>	length/width
DP3	9.70/8.90
DP4	12.00/10.50
M1	13.88/11.64–14.30/11.55
m1/m2	12.54/8.86–15.71/9.06–16.27/8.76
m3	20.71/9.18

Mongolian gazelle *P. gutturosa* (the horn-cores of the Mongolian gazelle are more curved) or to the Tibetan gazelle *Procacpra picticaudata*. Przewalski's gazelle is a species that was widespread during the Late Pleistocene while the present-day distribution of the small and endangered population is confined to an isolated, small area in the vicinity of Qinghai Lake in north-eastern Qinghai Province, China (Leslie et al., 2010).

4. Taphonomical aspects

A detailed study of the taphonomical aspects of the complete fossil assemblage excavated from the Layers 10 and 11, including the spatial distribution, is in progress. So far only preliminary data have been published (Zhang, 2009; Zhang et al., 2009, 2011a, 2011b, 2012; Doyon et al., 2019). Remarkable is the high degree of fragmentation. Doyon et al. (2019) investigated the bones excavated in 2017 and presented the following results: the Layers 10 and 11 yielded respectively 976 and 1260 finds: 85% of the finds from Layer 10 and 70% of the finds from Layer 11 are less than 5 cm long and many bone elements are heavily affected by weathering: Layer 10–58.6% of the finds, Layer 11–29.0% of the excavated elements. Concretion deposits are present on 51.2% of the finds from Layer 10 and on 67.9% of the finds from Layer 11; additional natural modifications include manganese staining and root-etching. Modifications by carnivores are, with <1%, very rare.

4.1. Hominin interference

The number of complete bones in the Lingjing assemblage is very low; almost all herbivore bones are fragmented and the breakage pattern

shows the occurrence of green-as well as dry-bone fractures, which suggests hominin exploitation of bone marrow. It is, however, well-known that hyenas, also represented in the associated fauna, have the capacity to break bones. Future analyses should clarify the role of the large carnivores in the fragmentation of the Lingjing bone assemblage.

Many bones, in particular the upper and lower limb bones, show the presence of cut marks. Zhang et al. (2011a) concluded that ca. 13% of the finds, excavated in 2005 and 2006, show cutmarks, predominantly (98.5%) on the midshafts of long bones (Zhang et al., 2011a, 2011b). The morphological characteristics of the marks as well as their location and orientation, indicate disarticulation and meat exploitation. Scraping marks are very rare which indicates, according to Zhang et al. (2011a) a non-intensive processing technique.

The Middle Palaeolithic bone assemblage yielded also a large number of bone tools: metapodial hammers (used to fracture the long bones) (Wang et al. in prep) and retouchers (Doyon et al., 2018, 2019) as well as deliberately knapped long bone fragments (Doyon et al., 2021). Lingjing, Layer 11 yielded, in addition, two bone fragments with ochred engravings (10 and 13 sub-parallel lines incised on weathered bone) (Li et al., 2019b).

Hominins played an important role in the accumulation of the Lingjing Middle Palaeolithic faunal assemblage. The mortality profiles of the two dominant prey species, i.e., the Onager *Equus hemionus* and the Aurochs *Bos primigenius*, are almost exclusively represented by prime-adult individuals (Zhang et al., 2009, 2011a, 2011b; van Kolfschoten et al., 2020), a feature that demonstrates the focussed hunting strategy of Xuchang Man. However, a natural component in the accumulation of the assemblage should not be excluded. The woolly rhinoceros assemblage is, for example, dominated by young individuals, a feature that suggests a natural accumulation. Although the composition of the faunal assemblage is biased by hominin hunting activities, we assume that the faunal assemblage is “natural” enough to be used as a proxy to reconstruct the paleoenvironmental condition during the human occupation of the site.

5. Paleoenvironmental conditions

The Lingjing Middle Palaeolithic faunal assemblage is with 20 identified taxa, rather diverse and it includes species that prefer to live in/adapted to different habitats. *Panthera tigris* occurs predominantly in forest but also inhabit grassland with sufficient vegetation cover. The hyena *Crocota crocota* is common in open, dry habitat. The grey wolf *Canis lupus* occupies a wide variety of habitats, from arctic tundra to forest, prairie, and arid landscapes. The raccoon dog *Nyctereutes procyonoides* prefers forest and forest borders and regions bordering water. The red fox *Vulpes vulpes* occurs, just as the grey wolf, in a wide range of habitats. It is generally assumed that cave bears, in Lingjing represented by *Ursus* sp., lived in a forested environment. The badger *Meles meles* are highly adaptable and live in a wide variety of habitats including forests adjacent to open fields. The straight-tusked elephant of the genus *Palaeoloxodon* is regarded as an open-forest dweller. Przewalski's wild horse *Equus przewalskii* and the onager *Equus hemionus* are adapted to live in areas with an open, steppe vegetation. The extinct, so-called woodland or forest rhinoceros *Stephanorhinus kirchbergensis* is supposed to live in close forests (Tong and Wu, 2010). The extinct woolly rhinoceros *Coelodonta antiquitatis* is a characteristic element of the Mammoth Steppe biome, an extensive non-analogue, highly productive ecosystem that was dominated by grasses, herbs and willow shrubs. However, the Woolly Rhinoceros in China had a wider ecological range expanding more to the south than the Woolly Mammoth *Mammuthus primigenius* (Xue et al., 2000; Li et al., 2012). The wild boar *Sus lydekkeri* inhabited areas with sufficient vegetation cover nearby a water source. We assume that the extinct Chinese water deer *Hydropotes pleistocenica* preferred the same habitat as the extant relative i.e., living among tall reeds and rushes along rivers, swampy regions and open grasslands. The red deer *Cervus (E.) elaphus* prefers open woodlands and avoid dense

unbroken forests. The Sika deer *Cervus nippon* is primarily a forest-dweller that particularly prefers forested areas with a dense understory (Nowak 1991). Père David's deer *Elaphurus davidianus* used to inhabit swampy areas and reed-covered marshlands in the lowlands of China (Nowak, 1999). It is generally assumed that the extinct giant deer *Sinomegaceros ordosianus* lived in areas with an open forest vegetation. The habitat of the aurochs *Bos primigenius* was most probably confined to open areas in marshlands along rivers in a forested area. Przewalski's gazelle *Procapra przewalskii* inhabit semi-arid steppes; it tolerates severely sub-freezing winters.

Summarizing it can be stated that the list of the Lingjing Middle Palaeolithic faunal assemblage indicates a grassland-dominated palaeoecological environment; a biome that was inhabited by *Crocota crocuta*, *Equus cf. przewalskii*, *E. hemionus*, *Coelodonta antiquitatis* and *Procapra przewalskii*. Other species (*Panthera tigris*, *Nyctereutes cf. procyonoides*, *Ursus sp.*, *Meles cf. meles*, *Palaeoloxodon sp.*, *Stephanorhinus kirchbergensis*, *Sus lydekkeri*, *Cervus elaphus*, *Cervus nippon* and *Sinomegaceros ordosianus*) prefer(ed) and indicate the occurrence of (open/semi-open) forest. The occurrence of swampy areas along rivers and lakes with tall reeds and rushes, is the preferred habitat of *Hydropotes pleistocenicus* and *Elaphurus davidianus*.

The grassland-dominated palaeoecological environment, with a mosaic of scattered forest and mixed forest vegetation as well as the occurrence of swampy areas and bushes along lakes and rivers, suggests temperate climatic conditions.

6. Discussion and conclusions

The Quaternary East Asian (palaeo)environment is characterised by the occurrence of two distinct biozones, the Palearctic biozone in the north and the Oriental biozone in the south (Fig. 1)(Norton et al., 2010; Dennell et al., 2020). The Palearctic Realm usually has sub-freezing winters, winter rainfall/precipitation and temperate flora whereas the Oriental Realm has above freezing winters, summer rainfall and a sub-tropical/tropical vegetation (Ficetola et al., 2017). The Himalayan Mountain Range in the west and the Qinling Mountain Range in the east form the barrier between the Palearctic and the Oriental biogeographic zones. The Palearctic Realm covers most part of the continental Eurasia, the Oriental Realm includes south-east and most of south Asia characterised by monsoonal climatic conditions. The mammalian faunas of the two biozones clearly differ. The Palearctic fauna is characterised by the occurrence of open-steppe species including *Equus przewalskii*, *Equus hemionus*, *Stephanorhinus kirchbergensis*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Bos primigenius* and *Procapra przewalskii*. The Oriental fauna is characterised by forest-dwelling, warm and humid adapted taxa. The Pleistocene South China Fauna is called the *Ailuropoda-Stegodon* fauna with the following elements: *Hystrix*, *Atherurus*, *Rhizomys*, *Ailuropoda* spp., *Stegodon*, *Megatapirus*, *Cervus unicolor*, *Capricornis*, *Bubalus*, etc. (Tong and Wu, 2010).

Although, there is a big contrast between the two faunas, there is, however, no strict barrier, not a strict division between the Palearctic and the Oriental biogeographic zones (Norton et al., 2010). *Stephanorhinus kirchbergensis* from the Rhino Cave in Shennongjia, Hubei is, for example, associated with the *Ailuropoda-Stegodon* fauna, the typical Pleistocene mammalian fauna in South China (Tong and Wu, 2010). Most of central-east China, the region east of the Qinling Mountain Range, is less than 1000 m above sea level and served as a continuous migration bi-directional corridor between the Palearctic and the Oriental biogeographic zones. This corridor offered open-steppe taxa (e.g. *Equus*) to migrate southward into SE Asia during glacial periods and warm-humid adapted taxa (e.g. *Ailuropoda*, *Macaca*, *Bubalus*) to expand their range to areas north of the Qinling Mountain Range (Tong, 2007, 2008; Norton et al., 2010).

The Lingjing Fauna is a typical Palearctic/Northern China fauna with boreal elements such as *Palaeoloxodon*, *Equus*, *Coelodonta*, *Cervus elaphus*, *Bos primigenius* and *Procapra*; Oriental/southern taxa i.e.,

Ailuropoda, *Stegodon* and *Tapirus* are not recovered in the Lingjing faunal assemblage. The Lingjing fauna shared many taxa with faunal assemblages such as those from the late Middle Pleistocene site Dingcun (Shanxi) (Pei et al., 1958), and the Late Pleistocene sites Salawusu (Inner Mongolia) and Xiaogushan (Liaoning) presented by Dong et al. (2010, 2014) and the late Middle Pleistocene site Xujiayao (Nihewan Basin, northern China) presented by Norton and Gao (2010) (Table 13). Sites that are located far to the north of Lingjing.

6.1. The age of the lingjing faunal assemblage

The mammalian species of the Lingjing Layer 10 and 11 faunal assemblage represent a typical, Chinese Palearctic late Middle to Late Pleistocene fauna. The fauna does not include taxa with a limited biostratigraphical range that excludes a late Middle or a Later Pleistocene age. The OSL dates (Layer 10 between $\sim 96 \pm 6$ ka and $\sim 102 \pm 2$ ka; Layer 11 between ~ 105 ka and ~ 125 ka) give a more precise age indication. The dates correspond to the early Marine Isotope Stage 5 (MIS 5; MIS 5e to 5d) and to the last interglacial palaeosol S1 in the Loess Plateau of China (Nian et al., 2009; Li et al., 2017a). The dates and the assumed correlation with the last interglacial palaeosol strongly suggest that we are dealing with an interglacial fauna.

However, the Lingjing locality yielded the most southern distribution of *Procapra*, and the locality is located close to the most southern limit of the geographical distribution of *Coelodonta antiquitatis*. The Middle Pleistocene Nanzhao Man site (Henan) (Qiu et al., 1982) located just 100 km southwest of Lingjing site yielded southern taxa such as *Hystrix*, *Stegodon* and *Megatapirus* and the Xincui (Henan) fauna (Pei, 1956) which is located 200 km to the southeast of Lingjing includes Oriental taxa such as *Bubalus* and *Rusa unicolor*. These data suggests that the Lingjing fauna represents the southernmost occurrence of the boreal

Table 13

Lingjing larger mammal taxa represented in the faunal assemblages from Dingcun (Shanxi) (Pei et al., 1958), Salawusu (Inner Mongolia) and Xiaogushan (Liaoning) (Dong et al., 2010, 2014) and Xujiayao (Nihewan Basin, northern China) (Norton and Gao, 2010).

Taxa	Lingjing	Dingcun	Salawusu	Xiaogushan	Xujiayao
Carnivora					
<i>Panthera tigris</i>	X		X	X	X
<i>Crocota crocuta</i>	X		X	X	
<i>Canis cf. lupus</i>	X	X	X	X	X
<i>Nyctereutes cf. procyonoides</i>	X	X			
<i>Vulpes cf. vulpes</i>	X	X		X	
<i>Ursus sp.</i>	X	X		X	
<i>Meles cf. meles</i>	X	X	X	X	
Proboscidea					
<i>Palaeoloxodon sp.</i>	X	X	X		X
Perissodactyla					
<i>Equus cf. przewalskii</i>	X	X	X	X	X
<i>Equus hemionus</i>	X	X	X		X
<i>Stephanorhinus kirchbergensis</i>	X	X		X	
<i>Coelodonta antiquitatis</i>	X	X	X	X	X
Artiodactyla					
<i>Sus lydekkeri</i>	X	X	X	X	X
<i>Hydropotes pleistocenicus</i>	X	X		X	
<i>Cervus (E.) elaphus</i>	X	X	X	X	X
<i>Cervus nippon</i>	X	X		X	X
<i>Elaphurus davidianus</i>	X				
<i>Sinomegaceros ordosianus</i>	X	X	X	X	X
<i>Bos primigenius</i>	X	X	X	X	X
<i>Procapra przewalskii</i>	X	X	X	X	X

fauna in China during the Pleistocene Epoch. The site Lingjing is located east of the Qinling Mountain Range in the region that served as a corridor between the Palearctic and the Oriental biogeographic zones. Climatic fluctuations, characteristic for the late Middle and Late Pleistocene, result in migration of species and hence, changes in the faunal composition of a specific region as indicated by Li et al. (2012) for the Guanzhong area (Shaanxi Province, China). Taking these data, combined with the fact that the Lingjing assemblage represents the southernmost Palearctic fauna, into account, it is hard to believe that the Lingjing deposits that yielded the Middle Palaeolithic finds date from an interglacial. A late Middle Pleistocene (MIS 6) or Late Pleistocene glacial or stadial phase (MIS 4) seems more likely. This conclusion is, however, in conflict with the OSL-dates of Lingjing Layer 10 and 11. This is a contradiction that needs to be solved.

Summarizing, it can be stated that the Lingjing locality yielded an important Middle Palaeolithic assemblage that includes fragmented, incomplete human skulls, a large collection of stone artefacts, stone and bone tools as well as an extensive amount of mammalian remains from a large number of different taxa. The mammalian remains offers not only insight in human behaviour and human subsistence, but the faunal assemblage can also be used as a proxy to reconstruct the palaeoenvironmental conditions during the human occupation of the site. The mammalian fauna indicates that Xuchang man operated under temperate climatic conditions in a grassland-dominated environment, with a mosaic of scattered forest and mixed forest vegetation as well as the occurrence of swampy areas and open grasslands along lakes and rivers.

Author contributions

H.W. contributed the data acquisition, cataloguing of the specimens, analysis and interpretation, and authorship of the manuscript. Z.L. contributed as project leader to the fieldwork, data acquisition, analysis and interpretation, and authorship of the manuscript. H.T. and T.v.K. contributed to the analysis and interpretation, and authorship of the manuscript. All authors contributed to the development of the manuscript.

Data availability

Data used for the present research are detailed in the paper.

Declaration of competing interest

The authors declare that they 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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