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New material of *Stephanorhinus* (Rhinocerotidae, Mammalia) from Jinyuan Cave, Luotuo Hill in Dalian, Northeast China

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ABSTRACT

Middle Pleistocene rhinocerotid material from the upper strata of Jinyuan Cave, Luotuo Hill, Dalian, is described in the present study. The specimens mainly consist of maxillary and mandible with dentition of juvenile and aged individuals, respectively. Based on comparison between the new discovery and known records of Pleistocene rhinocerotid, the Jinyuan Cave specimens are most similar to *Stephanorhinus kirchbergensis* and then have been identified as *Stephanorhinus* cf. *kirchbergensis*. Tooth loss has been present on the Jinyuan Cave rhinocerotid specimen, represented by a mandible without both p2s. This problem could be a result of heredity issues. This condition may be due to mechanical damage from a coarse diet, which can lead to tooth loss and alveolar remodelling, according to the findings from an environmental investigation.

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Introduction

The large two-horned rhinocerotid is a common representative in Pleistocene megaherbivores in Eurasia. Among these forms, two lineages are the most common in northern China: genera *Stephanorhinus* (forest rhino) and *Coelodonta* (woolly rhino). In comparison with *Coelodonta*, which has a clear evolutionary route (Deng et al. 2011), the research of *Stephanorhinus* in China is relatively poor. Even after the establishment of this genus, many species belong to it had still been attributed to other genera. Tong and Wu (2011) reviewed Pleistocene species which had been attributed to genera *Rhinoceros* and *Dicerorhinus* in China and figured out some forms belong to *Stephanorhinus*. They further attributed all forms in Middle–Late Pleistocene to species *Stephanorhinus kirchbergensis*. Dong et al. (2021) described Early Pleistocene rhinocerotid specimens from Tianzhen, Shanxi. They identified three species and ascribed one as *Stephanorhinus* cf. *kirchbergensis*. Wang (1931) erected a new species *Dicerorhinus choukoutienensis* based on cranial and dentition specimens from Zhoukoudian Locality 1. Black et al. (1933) and Teilhard de Chardin (1936) considered this species as a synonym of *Rhinoceros mercki*, which has been revised as *S. kirchbergensis*. Chow (1963) identified an almost complete skull from Zhoukoudian Locality 20 as *D. choukoutienensis* and argued that this species was valid based on the significantly different cranial and dentition morphology in comparison with '*Dicerorhinus mercki*'. Chow (1979) described cranial and plenty of dentition specimens from Zhoukoudian Locality 1 and identified them as *D. choukoutienensis*. It is no doubt that this species belongs to *Stephanorhinus*. Since Wang (1931) and Chow (1963, 1979), the known record of *S. choukoutienensis* is limited in Zhoukoudian, and other Middle Pleistocene forms of this genus have been almost attributed to *S. kirchbergensis* later. In their comprehensive review, Tong and Wu (2010) accepted that *S. choukoutienensis* should be a synonym of *S. kirchbergensis*. Based on the recent recognition, three species of *Stephanorhinus* are present in the fossil record in China: *S. kirchbergensis* (Early? to Late Pleistocene), *S. yunchuensis* (Early Pleistocene) and *S. lantianensis* (late stage of Early Pleistocene). Recently, a joint exploration team formed by IVPP, CAS, Administrative Committee of Dalian Jinpu New District and DNHM performed excavation work on the richly fossiliferous deposit of Jinyuan Cave in Luotuo Hill, which was found in at limestone quarry of Donghai Cement Factory in Dalian. Abundant rhinocerotid specimens were found throughout the Jinyuan Cave deposit. According to a preliminary examination, both *Stephanorhinus* and *Coelodonta* have been present in the fossil record of Jinyuan Cave deposit. Among which, the forms of *Stephanorhinus* from lower strata (Jinyuan upper and lower faunas) were identified as *S. yunchuensis*, and the forms from upper strata (Wanghai faunas) were identified as *S. kirchbergensis* (Jin et al., 2021). The specimens from the upper strata consisting of maxillary and complete mandible, both with dentition, are the best preserved material of Middle Pleistocene *Stephanorhinus* during the recent decade. The research on these new specimens would provide some new clue of evolution of *Stephanorhinus*.

Materials and methods

All the newly described specimens were collected from Jinyuan Cave (Figures 2-3). The most substantial material for comparison includes the cranial and dentition specimens from Loc. 1 and Loc. 20 of Zhoukoudian, housed in IVPP, which had ever been identified as *S. choukoutienensis*. The specimens of *S. kirchbergensis* from Shennongjia, Hubei Province, housed in Shennongjia Museum of Natural History and the local government office for cultural relics administration at Shennongjia, described by Tong and Wu (2010); and other specimens identified as *S. kirchbergensis* from Liaoning and Shaanxi Provinces, respectively, housed in Liaoyang Museum and IVPP.

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Table 1. Upper deciduous cheek tooth measurements of *Stephanorhinus* cf. *kirchbergensis* in Jinyuan Cave, compared with important specimens of *Stephanorhinus kirchbergensis*, data after Tong and Wu (2010) (mm).

		DJPJ210814-266		Rhino Cave	Tangshan, Nanjing	CKT Loc.1	CKT Loc.13	West Europe
Teeth	Items	Left	Right	Mean	Mean	Mean		Mean
DP1	L	28	29.1	32.4	29.5	27.5	35	29
	W	24.9	22.4	27	28	24.5	32	25.3
DP2	L	38.5	40.8	45.7	38.5		41	36.7
	W	32.2	36	45.3	41		40	37.6
DP3	L	45	46.4	53.2	47.5		51	45.9
	W	42.5	42.5	50.1	51		53	46.9
DP4	L		53.9	58.3	50	48.3	53	52.8
	W	47	46.2	53.6	54	51	56	53.2

Table 2. Lower deciduous teeth measurements of *Stephanorhinus* cf. *kirchbergensis* in Jinyuan Cave, compared with important specimens of *Stephanorhinus kirchbergensis*, data after Tong and Wu (2010) (mm).

		DJPJ210721-122		Rhino Cave	West Europe	Taubach	
Teeth	Items	Left	Right	Mean	Mean	Mean	CTK Loc.13
dp1	L	20.7	21	23.2	20.3	19.8	21
	W	11.7	12	12.3	14	11.1	13
dp2	L	31	33.7	36.5	33.1	31	35
	W	14.6	16.1	18.4	19.3	18.1	21
dp3	L	43.2	42.9		42.2	42	44
	W	20.3	22		23.4	23	26
dp4	L	46.3	44.9		45.6	34.7	47
	W	22.4	22.3		26.6	26.7	29

Method

The terminology follows Qiu and Wang (2007). Measurements follow Guérin (1980) and all given in millimetres and rounded to 0.1 mm and can be seen in Tables 1–3.

Abbreviation

DNHM: Dalian Natural History Museum.
DJPJ: field specimen number of Jinyuan Cave collection in Dalian, China.
IVPP, CAS: Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences.
IVPP V: vertebrate fossil specimen number of IVPP.

Geological setting

Jinyuan Cave is located at Luotuo Hill in Fuzhouwan Town, Jinpu New District, Dalian, Liaoning Province, about 80 km north of the Dalian metropolitan area (Figure 1). The sedimentary deposits are mainly composed of clayey silt, sandy silt and clay, containing fossiliferous layers interbedded with calcareous lens, up to seven layers from top to bottom (Jin et al. 2021).

Jinyuan Cave is an extremely fossiliferous cave, with seven layers that produced fossils spanning from the Late Pliocene to the Middle Pleistocene (ca. 3.60–0.35 Ma) and can be divided into three successive faunas: the Wanghai fauna (Middle Pleistocene, 0.78–0.35 Ma), the Jinyuan fauna (Early Pleistocene, 2.60–0.78 Ma) and the Luotuoshan fauna (Late Pliocene, 3.6–2.6 Ma) (Jin et al. 2021).

The rhinocerotid specimens described in this study were unearthed from the upper layer (L 2) of the cave, with the age of Middle Pleistocene (0.78–0.35 Ma, Ge et al. 2021; Jin et al. 2021).

Systematic palaeontology

Order Perissodactyla Owen 1848
Family Rhinocerotidae Owen, 1840
Subfamily Rhinocerotinae Owen, 1845
Genus *Stephanorhinus* Kretzoi, 1942

Revised diagnosis (modified after Tong et al., 2010): Skull is dolichocephalic; with nasal and frontal horns, and the nasal one relatively bigger; nasal septum partially ossified; the nasal notch and the orbit as well as the palatine notch moved back; vomer not sharply ridged; posterior margins of pterygoid plates sloped; mastoid developed, and the widest part of the occipital is at the level of the mastoid; subaural channel closed; occipital crest inclines backward slightly. Incisor less; premolar highly molarized; upper cheek tooth has flattened labial wall with a rib at the level of paracone, without anticrochet. Ascending ramus slopes backward. Labial wall of lower cheek teeth rounded. Radius quite long, which is more than 85% of that of humerus and even with the same length; great trochanter of the femur is robust; metacarpals long; head of the fibula is short.

Type species: *Stephanorhinus etruscus* (Falconer, 1859–1868)

Included species: *S. kirchbergensis* (Jäeger, 1839), *S. etruscus* (Falconer, 1859–1868), *S. hemitoechus* (Falconer, 1868), *S. hundsheimensis* (Toula, 1902), *S. yunchuchenensis* (Chow, 1963), *S. lantianensis* (Hu et Qi, 1978).

Stephanorhinus cf. *kirchbergensis* (Jäeger, 1839)

Referred material: DJPJ 210814-266, juvenile maxillary with DP1-DP4; DJPJ 210721-122, juvenile mandible with left dp1-dp4, right dp1-m1; DJPJ 210616-014, damaged mandible with both p3-m3s; DJPJ 210525-002, almost complete mandible with both cheek teeth rows. All fossils yielded from bottom part of second layers of Jinyuan Cave deposit.

Description

DP1 (Fig. 2): triangular in occlusal view. The ectoloph is strong and arc-shaped; the protoloph is relatively weak and strongly oblique, connecting with the ectoloph and the metaloph, respectively, making the valley closed and forming into large trigon basin; metaloph is moderately developed. Cingula are absent.

DP2 (Fig. 2): trapezoid in occlusal view. The labial length is larger than the lingual one; the maximum width lies at the level of metaloph. The protoloph and metaloph are both strong. Parastyle is strong. The crochet and crista are robust and meeting each other to form the medifossette. The tubercles are present on the anterior cingulum and the entrance of the medisinus; anterior and posterior cingula are strong; a faint lingual cingulum is present at the entrance of the medisinus.

DP3 (Fig. 2): trapezoid in occlusal view. The buccal length is larger than the lingual one; the maximum width lies at the level of protoloph. The parastyle and paracone ribs are strong. The protoloph and the metaloph are both strong, and the crochet and crista are both strong and meeting to each other. The postfossette is big. Anterior cingulum is strong but posterior one is shortened lingual cingulum is absent.

DP4 (Fig. 2): very similar to DP3 in morphology, but much larger in size. Parastyle and paracone rib developed. Crochet as well as the posterior cingulum are more developed; crochet almost

Figure 1. Geography of Jinyuan Cave, Luotuo Hill, Dalian.

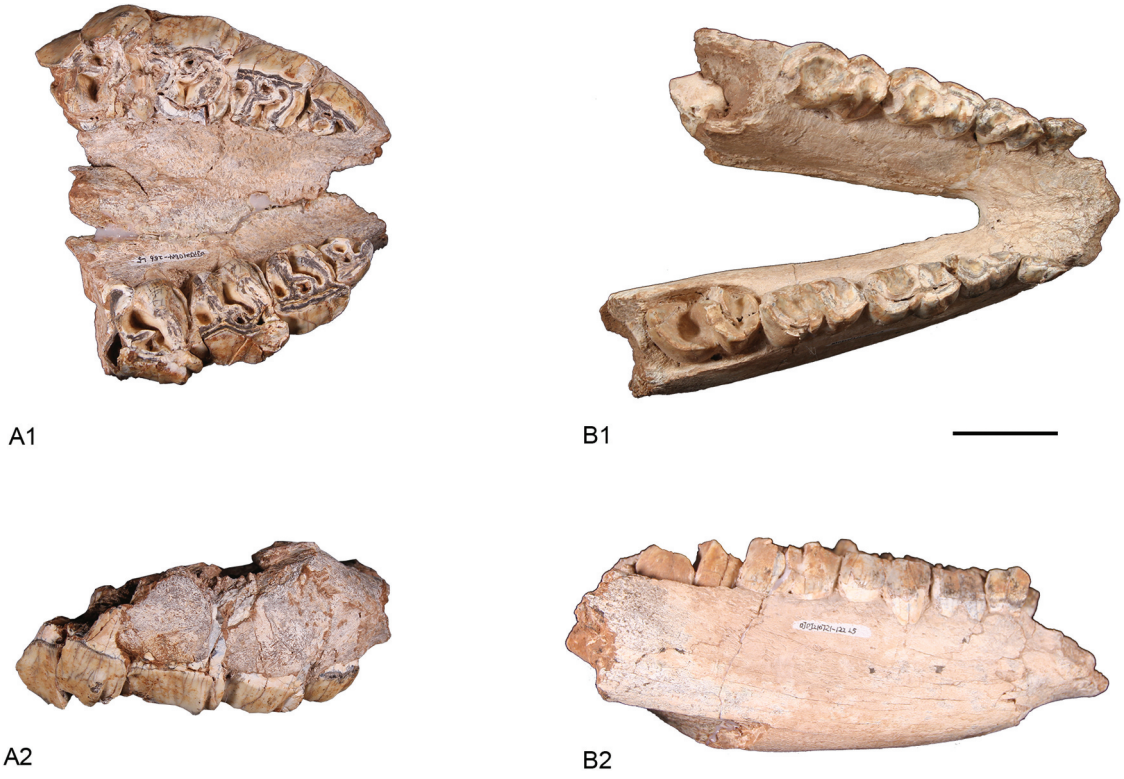

Figure 2. Juvenile individuals of *Stephanorhinus* cf. *kirchbergensis* from Jinyuan Cave: A. DJPJ 210814-266, maxillary; B. DJPJ 210721-122, mandible. 1. Occlusal view; 2. Right view. Scale bar = 5 cm.

connects to the protoloph; crista reduced. Protocone is seriously constricted. The medisinus is much broader.

The mandible is robust, the ascending rami is moderately oblique posteriorly (Fig. 2-3).

dp1: simply structured, posterior lobe is weak. Paraconid, protoconid and metaconid connected into a loph which is nearly straight. The anterior valley is not formed; posterior valley is narrow and shallow, and its orientation has a very small angle with the

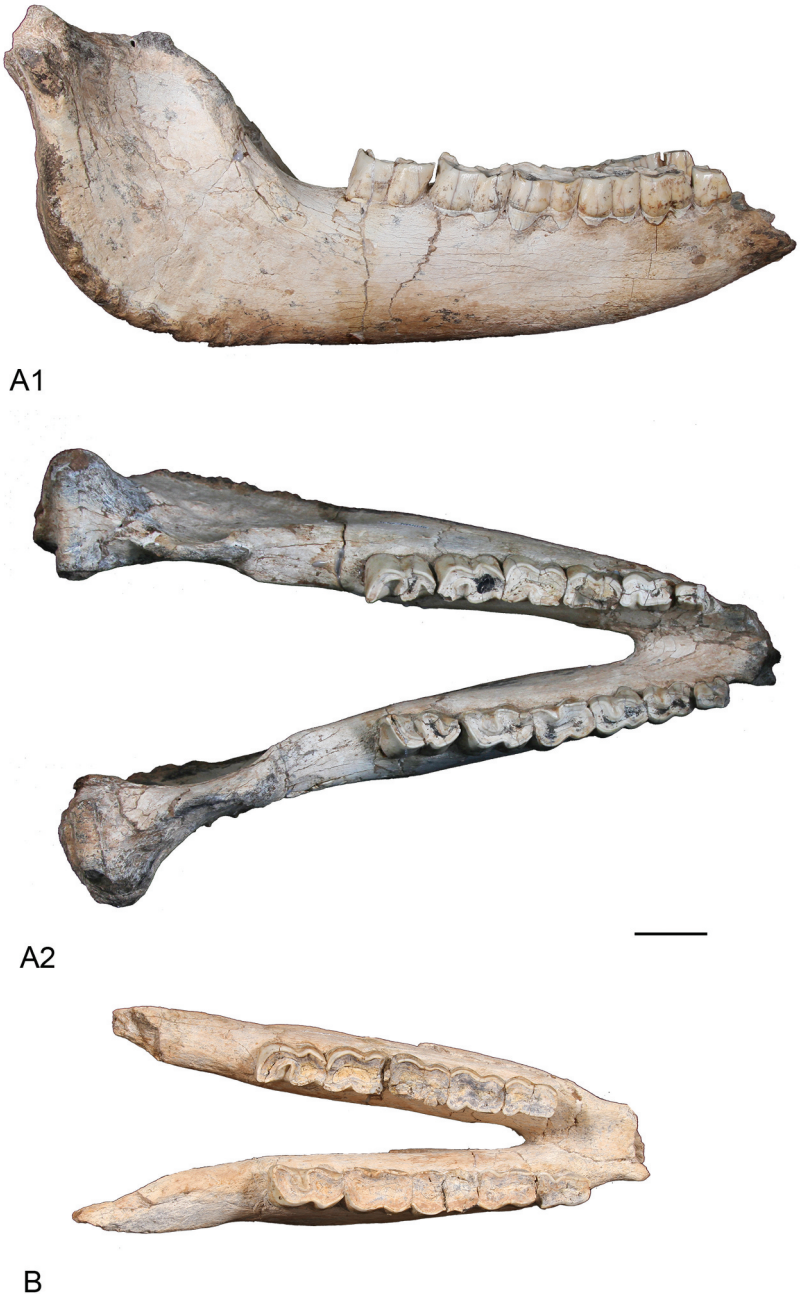

Figure 3. Mandible of *Stephanorhinus* cf. *kirchbergensis* from Jinyuan Cave: A. DJPJ 210525-002; B. DJPJ 210616-014. 1. Right view; 2. Occlusal view. Scale bar = 5 cm.

Table 3. Lower permanent teeth measurements of *Stephanorhinus* cf. *kirchbergensis* in Jinyuan Cave, compared with important specimens of *Stephanorhinus kirchbergensis*, data after Tong and Wu (2010) (mm)..

		DJPJ210721-122	DJPJ210525-002		DJPJ210616-014		Rhino Cave	Anping		CTK Loc.1	West Europe
Teeth	Items	Right	Left	Right	Left	Right	Mean	Min	Max	Mean	Mean
p2	L						32.1	29.1	32.7	29	32.1
	W		13.4	13.8			19.4	18.5	21.8	19.5	20.9
p3	L		36.3	35.2	33.9	34.1	35.6	32.6	41.1	36.4	40
	W		22.2	21.5	25.3	24.7	27.2	26.5	28.4	24.2	30.2
p4	L		42	37.1	39	38.1	42.6	37.9	42.8	43	44.8
	W			25.1	27.6	24.5	31.3	29.6	33.7	33.2	33.9
m1	L	50.5	43.6	42.7		43.4	45.3	44.1	51.1	42.5	51.2
	W	30.6	28.5	29.6	27.7	28.1	35	30.8	37.1	31.3	37.2
m2	L		47.4	47.1		45	54.2	49.5	54.7	44.2	57
	W		28.6	28.5	29.3	29	35.4	32.1	36.3	30.7	36.6
m3	L		49.4	52.3	48.3	48	55.8	52.1	55.8	53.4	58.4
	W		27.8	26.2	29.3	29.6	33.7	31.7	32.8	34	34.3

longitudinal axis; the entrance of the posterior valley is very backwardly located.

dp2: two-lobes shaped, the anterior valley is formed by paraconid, protoconid, metaconid, while the posterior one formed by the metaconid, hypoconid, entoconid. Some small tubercles are present at the level of the entrance of the anterior valley; the posterior valley is relatively narrow.

dp3: similar to dp2, obviously larger. On the lingual side of the parastylid, there exists a gulf or 'additional valley', but it's much smaller than in dp2; anterior and posterior valleys are broad.

dp4: two-lobes shaped. Anter- and posterior valleys are both broad. The labial wall of the whole tooth is very rounded.

p2 to p4: badly worn, morphology is difficult to distinguish.

m1 to m3: similar to dp4 but much larger and hypsodont.

Comparison

The Jinyuan Cave specimens are large-sized. The upper cheek teeth have relatively flattened labial wall with a rib at the level of paracone. The lower cheek teeth have rounded labial wall. This combination of characters is most identical to genus *Stephanorhinus*.

Chow (1963) listed differences of cranial and dentition morphology between *S. choukoutienensis* (*Dicerorhinus choukoutienensis*) and *S. kirchbergensis* (*Dicerorhinus mercki*) including *S. choukoutienensis* has obviously large body size (length from tip of nasal to posterior edge of condyle 750 mm, distance from condyle to anterior margin of orbit 410 mm, maximum widths of frontal and nasal 335 mm and 147 mm, respectively, height from dorsal margin of foramen magnum to occipital crest 160 mm, height from lowest points of condyle to median point of occipital crest 410 mm), shallower nasal notch (length from anterior margin of orbit to posterior margin of nasal notch 140 mm), small angle of occipital crest (65°) and more developed anterior and lingual cingulum and very broad entrance to medisinus on molar. In contrast to the data of Billia (2010), however, the measurements above are all due to individual variation. Two European skulls of *S. kirchbergensis* described by Billia are similar to Chow's Zhoukoudian skull in size. Another skull of Billia is even much larger than Zhoukoudian form. The characters of dentition Chow (1963) listed are influenced by abrasion of cheek teeth. *S. choukoutienensis* should be considered as a synonym of *S. kirchbergensis* indeed, as Tong and Wu (2010) argued.

Based on the further observation in this study, *S. kirchbergensis* shows an ontogenetical change on dentition. In the early wear stage, protocone and hypocone of the cheek tooth both extend posterolingually. But from the middle wear stage, the protocone of molar begins to extend lingually, and a constricted neck appears near the tip of protocone. This feature has been present on specimens from Shennongjia (Tong and Wu 2010), Zhoukoudian Loc. 1 (Chow 1979) and Loc. 20 (Chow 1963), Liaoyang (Xu, 1986), Yingkou (Jinniushan Joint Excavation Team 1976), Lantian (Chi 1974), China and Zagreb, Croatia (Billia 2010). This feature sometimes even appears on hypocone, represented by some dentition specimens from Zhoukoudian Loc. 1 (personal observation). Consequently, this character should be treated as a stable diagnostic one for identification of *S. kirchbergensis*.

Jinyuan Cave specimens include a juvenile maxillary with DP1–DP4 (Fig. 2), which can be directly compared with the same element of *S. kirchbergensis* in Shennongjia, Hubei. Most of the features of Jinyuan Cave specimen are identical to the Shennongjia ones, such as generally flatten labial wall with a rib at the level of paracone, strong crochet and crista which can be prominent but always weaker than crochet. The only difference is that the constricted neck on protocone of Jinyuan Cave specimen is obviously weaker than that of Shennongjia specimen. This could be led by the younger geohistorical age of Jinyuan Cave specimen. The morphology of mandible and lower dentition of Jinyuan Cave specimens are identical to those of Shennongjia and Zhoukoudian specimens. According to the difference discussed above, however, Jinyuan Cave specimens are identified as *Stephanorhinus* cf. *kirchbergensis* for prudent.

Discussion

Palaeoenvironment

Tong and Wu (2010) pointed out that *S. kirchbergensis* has slender limb, high head posture, ectolophodont dentition, hypsodont premolar and sub-hypsodont molar. Some authors considered the features above suggested a predominantly browsing diet for *S. kirchbergensis*. Tong and Wu (2010) also proposed that the strongly concave limb joints indicate that *S. kirchbergensis* shows a graviportal locomotion mode in closed forests, and the forest environment around the Rhino Cave in Shennongjia was consistent with this hypothesis. However, they tend to accept that *S. kirchbergensis* is a mixed feeder based on its premolars are hypsodont but molars not high enough. A recent analysis suggested that *S. kirchbergensis* was mostly a mix-feeder incorporating of leaf and grass, and its selection of foraging areas was also influent by season (Stefaniak et al. 2021). Tong and Wu (2010) pointed out that *S. kirchbergensis* could be accompanied with either Palearctic fauna assemblage in northern China or the typical Pleistocene mammalian fauna '*Ailuropoda-Stegodon* fauna' in southern China. Jin et al. (2021) proposed that Wanghai fauna, which contains *S. kirchbergensis*, is characterised by the first appearance typical Middle Pleistocene forms, and the faunal composition is mostly similar to those of Zhoukoudian Loc.1. Based on the pollen analysis performed by Shen et al. (2021), steppes had developed, climate was cold and arid in Luotuo Hill area during 0.59–0.41 Ma. In around 1.5 Ma, the habitat type of Luotuo Hill area shifted from mixed forest into woody grassland. Since 0.59 Ma, the habitat type of this area became shrub grassland.

Pathology

There is a very interesting specimen among the Jinyuan Cave specimens. On the mandible DJPJ 210616-014, the left and right p2s are both lost (Fig 3).

Chen et al. (2011) described a mandible of *Chilotherium wimani* with dental pathological deformity. They suggested that tooth deformity would be led by diverse causes, which should be divided into internal factors such as heredity, mutation and other congenital elements and external factors such as habits, environment and other postnatal condition. They considered that their specimen would experience both of the internal and external factors. They hypothesised that retention of left dp4 of their specimen was induced by abnormal growth of left p4 germ; the deformity of both p4s could due to hereditary factors or malnutrition. This sample would be a good reference for the discussion on the pathology of the Jinyuan Cave specimen.

The heredity and mutation could be the very important factor for the tooth loss. Tiffee et al. (1999) found that mice with relevant mutant would assume dental abnormality, and their incisors would not erupt. So the tooth loss of Jinyuan Cave specimen was likely relative to the heredity issues, and the p2s even dp2s might never

erupt since this individual's birth. Another probability could also exist, on the other hand, that this individual ever had p2, later it lost them and then the alveolar coalesced. This phenomenon of alveolar remodelling is common in mammalian, especially in primates (Miles and Grigson 1990; Stoner 1995; Cuozzo and Sauther 2004, 2006), and even present in giant fossil reptile (Xing et al. 2013). Xing et al. (2013) pointed out that tooth loss of animal would be led by a traumatic factor, likely a result of feeding behaviour. As discussed above, the habitat of *Stephanorhinus* cf. *kirchbergensis* in Jinyuan Cave was dominated by grassland, the climate was also cold and arid. So the food of rhinos would be coarse and harmful for their teeth. Another sample of tooth loss of rhinocerotid had recorded. Deng et al. (2011) described a new species of wooly rhino *Coelodonta thibetana*, holotype mandible of which lost the left p2. The geochemistrical analysis of Deng et al. (2011) indicated that enamel $\delta^{18}O$ values of herbivores are in the locality where *C. thibetana* lived was significantly lower than those of modern counterpart, which indicated a climate shift into much drier conditions in Middle Pliocene. They also pointed out that $\delta^{18}O$ values of fossil gastropods in Mio-Pliocene Zanda Basin, habitat of *C. thibetana*, suggested a palaeoelevation at least as high as and/or even up to 1500 m higher than current level, which indicated a cold climate with lengthy subfreezing temperatures during winter. Consequently, feed on very coarse vegetation for very long time would cause the significant mechanical damage for the teeth of rhinos, eventually led to the tooth loss and alveolar remodelling.

In discussion on the *C. wimani* from Linxia Basin with dental pathological deformity, Chen et al. (2011) proposed that occlusion would be compromised by anomaly, and this functional disadvantage would be fatal under the harsh condition in Late Miocene in Linxia Bain, Gansu. The abnormal individual was a relatively young one, with cheek teeth in early wear stage. So this individual had a short life indeed, supporting the hypothesis of Chen et al. (2011). In the reptile example of Xing et al. (2013), injury and tooth loss were non-fatal in their individual. The Jinyuan Cave mandible without p2s belongs to a very old individual. It seems that tooth loss does not strongly influence rhinos' feed or endanger the animal's normal life.

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