

# 河北阳原山神庙咀早更新世直隶狼(*Canis chihliensis*)新材料<sup>1)</sup>

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**摘要:** 于2006—2011期间的4次野外发掘中, 在泥河湾盆地的山神庙咀遗址发现了大量犬科化石, 材料包括残破颅骨、前颌骨、上颌骨、若干下颌骨及头后骨骼的主要部件, 其中的头后骨骼是迄今在中国发现的早期犬属化石中最为完整的。依据有关形态特征和测量数据, 将其归入直隶狼(*Canis chihliensis*)。具体特征如下: 体形较大, I3强大, P4窄长, 原尖发育, M1前后向变扁并具宽阔的齿带状次尖, m1具下后尖和下内尖, 相对其M1大小而言, 上、下第二臼齿较大, m2下跟座宽阔等。其头部骨骼及牙齿测量数据与现代灰狼的较为接近, 但头后骨骼数据较后者明显为小。该种的最大特征是其下臼齿舌侧齿尖的退化和P4窄长及M1前后方向变扁。但山神庙咀犬属材料的m1舌侧齿尖的发育程度变异较大, 因此, 仅仅依据m1的特征不足以区分直隶狼和拟豺(*Xenocyon dubius* (= *Cuon dubius*)), 尽管后者的鉴定与分类问题尚存争议, 但直隶狼与被归入拟豺的材料有更多相似之处, 它们与非洲野犬(*Lycan pictus*)差异很大。山神庙咀遗址化石层与邻近的小长梁遗址文化层时代相当或稍晚, 大约为1.3 Ma。

**关键词:** 河北阳原山神庙咀, 早更新世, 直隶狼, m1变异, 头后骨骼

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## NEW REMAINS OF *CANIS CHIHLENSIS* (MAMMALIA, CARNIVORA) FROM SHANSHENMIAOZUI, A LOWER PLEISTOCENE SITE IN YANGYUAN, HEBEI

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**Abstract** From 2006—2011, numerous *Canis* specimens were recovered from the newly

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discovered Shanshenmiaozui Locality in the Nihewan Basin. The material includes broken crania, premaxillae, maxillae, mandibles and postcranial skeleton with most of the elements preserved, and represents the most extensive and informative sample of early fossil *Canis* ever recovered in China. This material can be assigned to the species *Canis chihliensis* based on morphological and metric characters, including large size, robust I3, elongated P4 with anterior notch and well-developed protocone, M1 strongly mesiodistally compressed and with broad cingular hypocone, m1 with metaconid and entoconid (however small), M2 and m2 large relative to M1 and m1 respectively, and m2 with broad talonid. Measurements of the skulls and the teeth are similar to the equivalent measurements for *Canis lupus*, but those of the postcranial elements are smaller. *Canis chihliensis* is characterized by reduction of the lingual cuspids on the lower molars, an elongated P4, and a mesiodistally compressed M1. However, the first lower molars from Shanshenmiaozui are quite variable in the development of their lingual cuspids. This study shows that it is not easy to distinguish *Canis chihliensis* from *Xenocyon dubius* (= *Cuon dubius*) based exclusively on characters of the first lower molar, and the taxonomic status of the latter species is still open to question. Both of them differ greatly in morphology from the African hunting dog *Lycaon pictus*. Unlike in *Canis chihliensis*, the tooth dimensions of *Xenocyon dubius* are quite variable. The fossil bearing stratum at Shanshenmiaozui can be correlated with, but probably later than that at the neighboring Xiaochangliang Site, which has an age of ca. 1.36 Ma.

**Key words** Shanshenmiaozui, Yangyuan, Hebei; Early Pleistocene; *Canis chihliensis*; m1 variation; postcranial bones

Although occurrences of fossil canids in China are not rare, they still have not been well-studied (Qiu et al., 2004). To date, almost no papers focusing explicitly on the study of Chinese *Canis* fossils have been published. With regard to Chinese Quaternary canid taxa, the ongoing disputes always concern the nomenclature of the species *Cuon dubius* Teilhard de Chardin, 1940, *Xenocyon dubius*, or *Sinicuon dubius*. The fourth species, *Canis chihliensis* Zdansky, 1924, is intermediate between *Xenocyon dubius* and *Canis lupus*, but also differs from them in being characterized by the reduction of the lingual cuspids of the lower molars. In addition to the type locality in Huailai, Hebei (formerly known as Chihli), a few other localities have been reported to yield *Canis chihliensis* over the past several decades, including Nihewan (Teilhard de Chardin and Piveteau, 1930), Zhoukoudian Loc.18 (Teilhard de Chardin, 1940), Bajiazui (Wang, 2006) and Gengjiagou (Xie, 1983) in Gansu. Previous studies of this species, however, mainly paid attention to dental characters, which resulted in considerable taxonomic controversy and confusion as mentioned above. At present, it is still difficult to sum up the diagnostic characters of this species.

In recent years, a rich sample of large canid fossils has been recovered from the Shanshenmiaozui Site in the Nihewan Basin in North China. The sample includes maxillae, mandibles and most parts of the postcranial skeleton (Fig.1). In addition, some upper teeth

collected by Dr. A C Ma from Xiashagou were also included in this study. This material is very helpful in understanding the morphological characters of *Canis chihliensis*, and reveals that this species is much closer to *Canis* than to *Xenocyon* or *Cuon*.

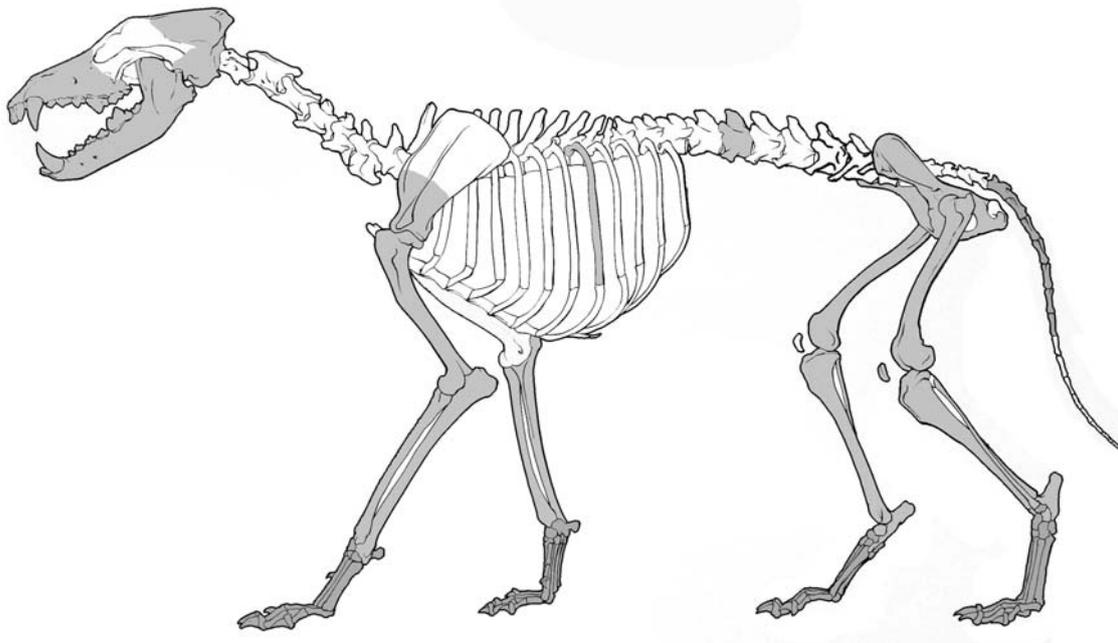


Fig. 1 Diagram of a *Canis* skeleton, the shaded parts represent the *Canis chihliensis* bones recovered from SSMZ in Nihewan

Furthermore, the canid fossils are associated with a rich mammalian assemblage, which is also very important from the perspectives of biostratigraphic correlation and paleoenvironmental reconstruction. All of the taxa present in the SSMZ fauna, such as *Pachycrocuta*, *Mammuthus trogontherii*, *Coelodonta nihowanensis*, *Elasmotherium*, *Proboscideipparion*, *Equus sanmeniensis*, *Eucladoceros* and *Spirocerus*, are also common elements of the classic Nihewan Fauna. This implies that the SSMZ and Nihewan faunas are probably of the same geological age (Tong et al., 2011b).

The geological age of the *Canis*-fossil bearing stratum at Shanshenmiaozui can also be evaluated by stratigraphic correlation in the field. SSMZ is adjacent to, and can be correlated with, the Xiaochangliang Site (Tong et al., 2011b), whose paleomagnetic age is ca. 1.36 Ma (Zhu et al., 2001).

**Terminology and methods** Anatomical terminology used in this paper follows Evans and Christensen (1979). Measurements were taken following the procedures used by Driesch (1976) and Tedford et al. (2009), and are given in millimeters. Dental terminology and character descriptions follow Butler (1939), Tedford et al. (1995, 2009), Qiu et al. (2004) and Bever (2005). In this paper, “cusp” is used for upper teeth, and “cuspid” for lower teeth. Terminology and measurements used for postcranial bones follow Munthe (1989).

A box plot illustrating variations in the length of the m1 was created in Excel, as was a bivariate scatter plot of width versus length for the lower molars. 3D images of various

specimens of this tooth were generated using a 3D laser scanner (3D scanner HD, Nextengine).

**Institutional and locality abbreviations** AMNH, American Museum of Natural History; AZ, Iziko Museum, South Africa; BPI, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, South Africa; CKT, Chou-kou-tien (=Zhoukoudian) Locality, China; C/O, extant vertebrate specimens of the Cenozoic Laboratory of the Geological Survey of China; CP, fossils of the Cenozoic Laboratory, Peking (=Beijing); IOZ, Institute of Zoology, Chinese Academy of Sciences, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; Loc, Locality; MNHN, Muséum National d'Histoire Naturelle, Paris in France; OV, IVPP extant vertebrate specimens other than fish; RV, IVPP catalog number prefix denoting specimens retroactively catalogued after publication; SSMZ, Shanshenmiaozui locality; TM, Transvaal Museum, South Africa; TNP, Tianjin Natural History Museum, Tianjin, China; V, IVPP vertebrate fossil specimens.

## 1 Systematic paleontology

### **Class Mammalia Linnaeus, 1758**

#### **Order Carnivora Bowdich, 1821**

#### **Suborder Caniformia Kretzoi, 1943**

#### **Family Canidae Fischer de Waldheim, 1817**

#### **Subfamily Caninae Fischer de Waldheim, 1817**

#### **Genus *Canis* Linnaeus, 1758**

#### ***Canis chihliensis* Zdansky, 1924**

(Figs.2-3, 4A-E, 5A1-2, 5B, 6, 9)

1930 *Canis chihliensis chihliensis* Teilhard de Chardin and Piveteau, p.56

1975 *Canis chihliensis* (Zdansky, 1924) ATPML and IVPP, p.130-131, figs.11-12, pl.III-3

1983 *Canis chihliensis* (Zdansky, 1924) Xie, p.358, pl.I-1

1994 *Canis (Xenocyon) antonii* (in part)(Zdansky, 1924) Rook, p.76

2009 *Canis chihliensis* (Zdansky, 1924) Tedford et al., p.197

**Diagnosis (revised)** Large body size, sagittal crest high and long, I3 robust, P4 elongated and with well-developed protocone, M1 strongly mesiodistally compressed with broad cingular hypocone, m1 with metaconid and entoconid (however small), M2 and m2 large relative to M1 and m1 respectively.

**New fossil specimens** 1) Fossils from SSMZ: most skeletal elements are represented in the SSMZ fauna. Specimens include one broken cranium (Fig.2, IVPP V 18333.1), one broken cranium with P4-M2 (V 17755.1), 2 broken maxillae (V 17755.2, V 17755.9), 2 premaxillae (V 17755.7-8), 10 hemimandibles (V 17755.3-6, V 17755.10-13, V 18333.2a,b), 8 isolated teeth (V 17755.14-21), and 133 postcranial bones and fragments including vertebrae

(V 18139.1-14), a fragmentary rib (V 18139.15), a broken scapula (V 17755.22), humerii (V 18138.1-2, V 18333.3), radii (V 17755.23, V 18138.3-5), ulnae (V 17755.24, V 18138.6-8), carpals (V 18138.9-22), metacarpals (V 18138.23-31), phalanges (V 18138.32-45), a pelvic girdle (V 18139.17), femora (V 18139.18-19), tibiae (V 18139.20-21), a fibula (V 18139.22), a patella (V 18139.23), calcanea (V 18139.24, V 18139.74), astragali (V 18139.25, V 18139.75), other tarsals (V 18139.26-30, V 18139.53-57), metatarsals (V 18139.31-35, V 18139.49-52), phalanges (V 18139.36-48, V 18139.58-60), and sesamoids (V 18138.46-53, V 18139.61-73). In total, 154 teeth and pieces of bone have been catalogued.

2) Fossils from Xiashagou: an upper canine (IVPP V 17754.1), a fragment of lower canine (V 17754.2), 2 I3s (V 17754.9-10), 2 P2s (V 17754.3-4), a maxilla with P3-4 (V 17754.6), a P4 (V 17754.5), and 2 M1s (V 17754.7-8). All of these specimens (V 17754.1-10) appear to belong to one individual.

**Fossils restudied for comparison** *Canis chihliensis* from Xiashagou: crania (TNP 00162, 00198), mandibles (TNP 00161, 00163, RV 30019-21), maxillae (RV 30015-18); *Canis* cf. *C. chihliensis* from CKT Loc.18: cranium (CP.79 or RV 40005) and mandible (CP.88 or Loc.18: 11:5:37); *Xenocyon dubius* (= *Cuon dubius*): mandible (CP.82) from CKT Loc.18, mandibles and postcranial bones from Yunxian Man Site; *Cuon alpinus*: upper M1-2 and lower m1 from CKT Loc.1.

**Recent specimens used for comparison** *Canis lupus*: skulls and postcranial bones in IVPP (OV 454) and IOZ (IOZ 07872/76277); *Cuon alpinus*: skulls and postcranial bones in IVPP (OV 819 IVPP C/O.3) and IOZ (IOZ 26747); *Lycaon pictus*: skulls and postcranial bones in TM (T.M. No. 5560) and BPI (BPI/C 223).

**Locality** Shanshenmiaozui (40° 13'08"N, 114° 39'54"E), Yangyuan County, Hebei Province, China.

**Horizon** Lower Pleistocene, ca. 1.3 Ma, no more than 1.8 Ma (Qiu, 2000).

**Descriptions** Crania and maxillae: three partial skulls were recovered; one is seriously fragmented, in that only the parietal and supraoccipital areas and the teeth P4 and M1-2 are preserved (IVPP V 17755.1). In the second skull, only the maxilla and parts of the nasal bones are preserved, but almost all of the cheek teeth are in situ (V 17755.2). The third skull is a broken cranium with the facial region and all of the teeth except the left P2 preserved (V 18333.1). Cranium V 17755.1 with the sagittal crest and nuchal crest preserved. In this specimen the zygomatic process of the frontal is robust, as are the postglenoid process and the exoccipital protuberance. Specimen V 18333.1 provides more information about the facial region. The snout length (preorbital skull length) is 103 mm, the distance between the prosthion and the infraorbital foramen is 74 mm, and the palatal length exceeds 118 mm. All of these measurements indicate that the rostrum is quite long and slender.

The upper teeth (Figs.2-4; Table 1): examples of all permanent teeth were recovered during the excavations, and are described below.

I1: Although a few samples are available, all of them are too heavily worn for much detail

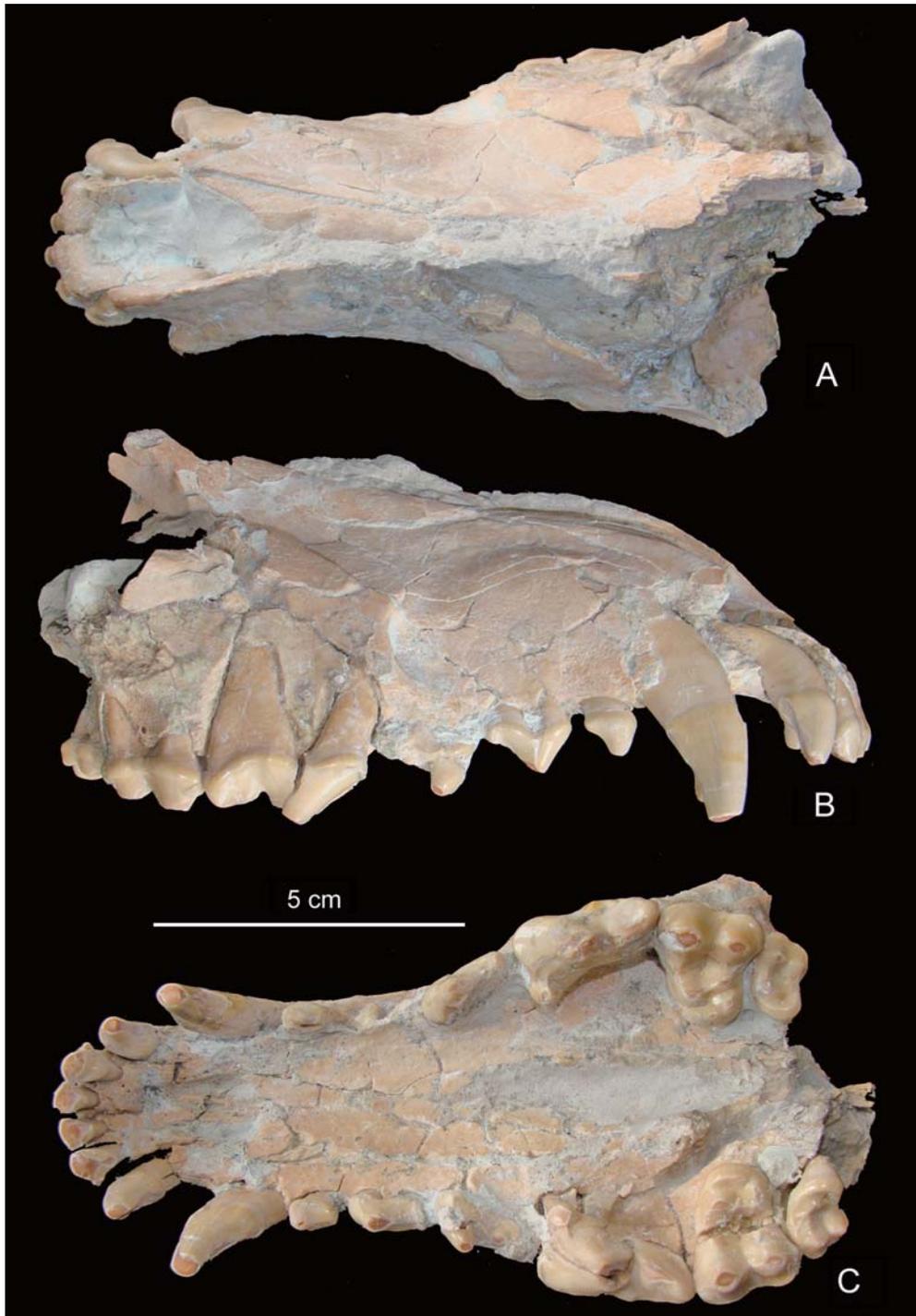


Fig. 2 Maxilla of *Canis chihliensis*, IVPP V 18333.1, from SSMZ in Nihewan  
A. in dorsal view; B. in lateral view; C. in ventral view

to be apparent. Because of the wear, the situations of the medial cusps are uncertain.

I2: All available examples of I2 are badly worn, but it can be observed that the crown is bifid (or possibly trifid) and obviously larger than that of I1.

I3: The I3 is shaped like a canine, but with a prominent posteromedial cingulum, and is

compressed mediolaterally. The I3 is obviously higher-crowned and much more robust than the I2. All of the available I3s are worn to varying degrees at the apex; additionally, one small facet resulting from occlusion with the lower canine can also be detected on the posterior surface of the crown.

Because all of the upper incisors are deeply worn, it is uncertain if they were bifid or trifid in their original form.

**Table 1** Upper tooth dimensions of Shanshenmiaozui specimens, compared with those of

			<i>Canis lupus</i> and <i>Cuon</i>									
			(mm)									
Taxa	Locality	Dimension	I1	I2	I3	C	P1	P2	P3	P4	M1	M2
<i>Canis chihliensis</i>	SSMZ (IVPP V 17755.1-2, V 18333.1)	L	4.8-6.3 (L-L)	5.8-7.4 (L-L)	5.6-8.6 (L-L)	11-12.5 (M-D)	7-8	13-13.3	14-16.4	21.8-24	16-17	8-9
		W	5.4 (M-D)	6.5 (M-D)	6.8-7.4 (M-D)	6.2-7.2 (B-L)	4.4-5.3	5-5.1	5.5-6.6	10-12	18-20	11-12
	Xiashagou IVPP V 17754.3-10	L	—	—	6.3-6.8(2)	13 (M-D)	—	13-13.1	15.8	24.7	15.7(2)	—
		W	—	—	7.9-8.6(2)	7.9 (B-L)	—	5.5-5.6	6.4	10.9	19.5(2)	—
<i>Canis lupus</i>	Extant IVPP C/O.3	L	4.99	6.42	6.64	13.54	7.56	13.35	15.75	24.26	14.47	8.72
		W	6.32	7.04	8.57	7.40	4.92	5.65	6.78	12.11	18.51	12.19
<i>Cuon alpinus</i>	Extant IVPP OV819	L	—	4.57	4.83	8.02	4.81	7.95	8.87	19.83	11.28	4.98
		W	—	4.68	5.72	5.29	4.41	4.14	4.77	10.02	14.35	5.60

Note: L-L. labial-lingual dimension; M-D. mesiodistal dimension; B-L. bucco-lingual dimension; numbers in parentheses represent sample sizes.

The upper canine is clearly distinguishable from the lower canine in being obviously compressed buccolingually, and having a crown that is quite straight. Occlusal facets are present at the apex and on the anterior face.

The P1 is single-cusped and single-rooted, without accessory cusps. The cusp is conical, with an anteriorly sloping anterior margin and a curved posterior one. The buccal surface is convex, and the lingual surface is nearly flat.

The principal cusp of the P2 is very well-developed and situated nearly in the middle of the tooth. There is also a tiny posterior accessory cusp. The anterior slope is straight, but the posterior one is curved.

The P3 is similar to the P2 in form. However, the P3 has both a posterior accessory cusp and a cingular cusp, the former being the larger of the two.

The P4 has very well-developed paracone and metastyle, as well as a fairly robust protocone, but lacks a parastyle. In crown view, a notch between the bases of the paracone and the protocone is visible at the anterior edge of the tooth. The sectorial part of the tooth is quite compressed buccolingually; the anterior blade of the paracone is nearly sectorial; a very narrow crest links the anterior blade of the paracone with the protocone; the protocone extends

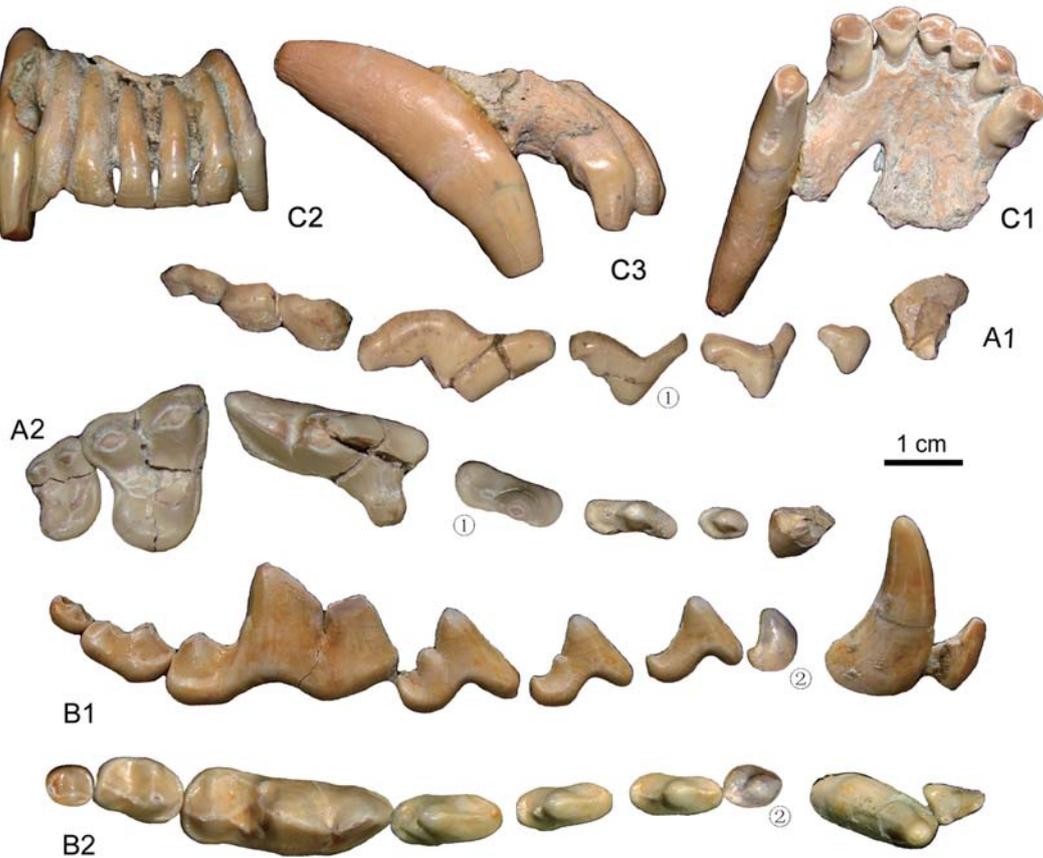


Fig. 3 Upper and lower dentition of *Canis chihliensis* from SSMZ in Nihewan  
 A. upper dentition (IVPP V 17755.2); B. lower dentition (V 17755.4); C. anterior teeth (V 17755.7); ① the P3 is from the left side of the same individual, and is shown reversed; ② the p1 is from V 17755.5; A1, B1, C3. in buccal views; A2, B2, C1. in occlusal views; C2. in anterior view

lingually but not beyond the anterior edge of the paracone; and the anterobuccal corner bulges prominently. The paracone and metastyle are not as close to each other as they are in *Canis lupus*. A slit-like carnassial notch can be seen in lingual view, and a moderately well-developed lingual cingulum extends along the crown base but is incomplete below the paracone and protocone. The anterior cingulum is faint. The P4 has three roots, of which the metastyle root is the most robust. The protocone root is slightly smaller than the paracone root.

The buccolingual width of M1 is much greater than the buccal length, and the buccal main cusps are quite well-developed. The paracone is markedly enlarged relative to the metacone; the protocone is moderately well-developed, whereas the metaconule is very weak and crest-like; there is no paraconule; the protocone and metaconule are very close together, which makes the postprotocrista very short; the hypocone forms a distinct tubercle on the lingual cingulum, and is obviously higher than the latter structure; a tiny tubercle lies adjacent to the hypocone on the lingual cingulum, and a narrow groove separates it from the hypocone. The parastyle is normally virtually indistinguishable from the cingulum that surrounds the mesiobuccal aspect of the paracone, and the metastyle is similarly indistinct relative to the

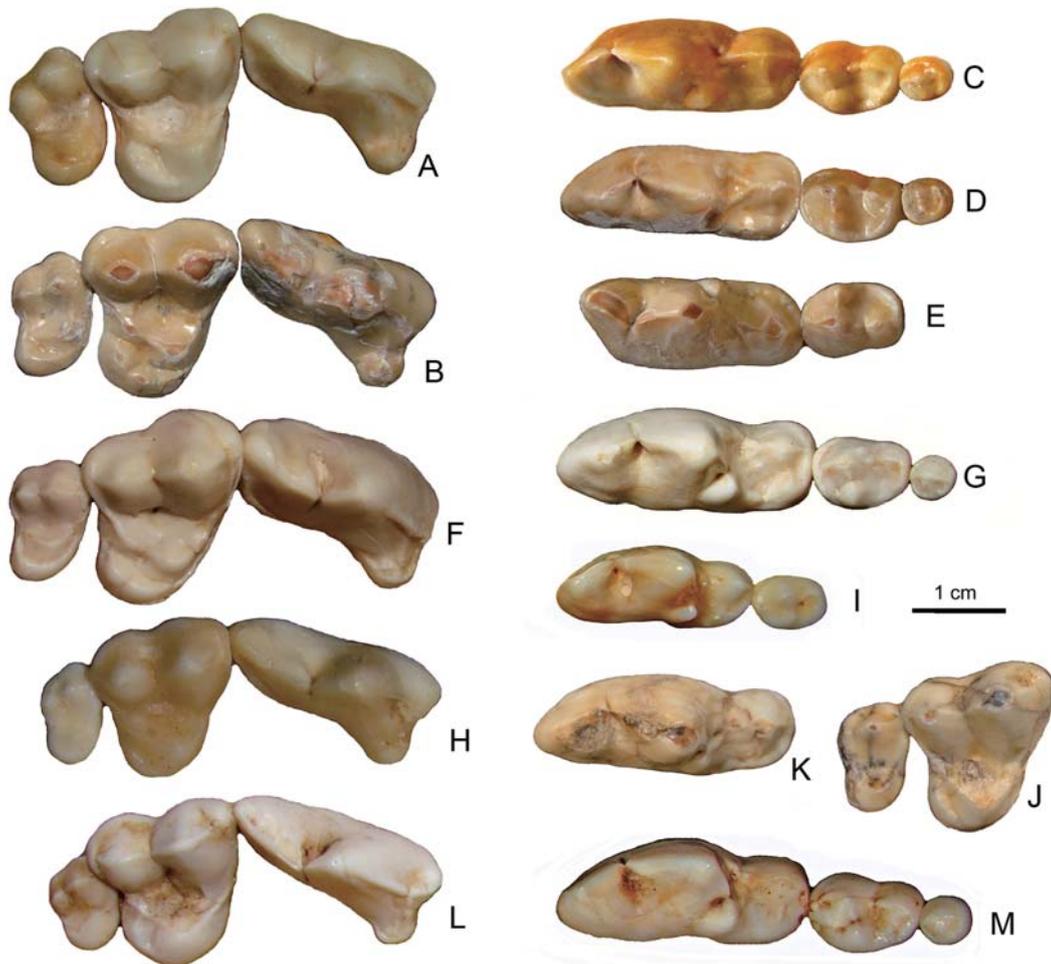


Fig. 4 P4 and molars of *Canis chihliensis* (A-E) from SSMZ in Nihewan, compared with those of *C. lupus* (F-G), *Cuon alpinus* (H-K) and *Lycaon pictus* (L-M), in occlusal views

A. P4-M2 (M 3496), Uppsala University, type specimen of *Canis chihliensis* from Huailai, China; B. P4-M2 (IVPP V 18333.1); C. m1-3 (V 17755.6); D. m1-3 (V 17755.4); E. m1-2 (V 17755.5); F-G. P4-M2 and m1-3 (IOZ no number, extant, China); H-I. P4-M2 and m1-2 (IOZ 26747, extant, China); J-K. M1-2 and m1 (Loc.1: 31:161, CKT Loc.1, Middle Pleistocene); L-M. P4-M2 and m1-3 (T.M. No. 5560 and BPI/C 223, extant, South Africa)

cingulum surrounding the distobuccal aspect of the metacone. In some specimens, however, the parastyle is distinct. A narrow crista extends along the lingual border of the trigon basin, and separates the trigon from the talon. The basin-like depression between the lingual cingulum and the protocone may be termed the hypocone basin, and surrounds the protocone and metaconule. The buccal cingulum is nearly continuous, but is especially pronounced at both the buccomesial and buccodistal corners. The distal cingulum meets the metaconule lingually. The mesial cingulum divides into two branches, of which the upper meets the preprotocrista and the lower continues to the mesiolingual corner.

The upper M2 is closely similar to the M1 in the structure of the main cusps, and is also buccolingually wide. The paracone and the metacone are well-developed. The protocone is

crest-like and quite prominent, but there is no postprotocrista. The hypocone is indistinct, having merged into the distolingual cingulum. There is a prominent metaconule. A continuous cingulum surrounds the lingual part of the trigon basin. The buccal cingulum is also very well-developed, and joins the anterior cingulum.

Mandible and lower teeth (Figs.3-8; Table 2): The mandibles are fairly well-preserved in specimens from SSMZ. In most respects the mandible resembles that of *Canis lupus*. The horizontal ramus is relatively deep and thick. There is no subangular lobe. The angular process is moderately well-developed, but is smaller than in *Canis lupus*. The lower cheek teeth are relatively low-crowned, and the tips of p2-4 are typically equal in height. The premolars are narrow and elongate, and a diastema is sometimes present. The anterior edges of the p2-4 are

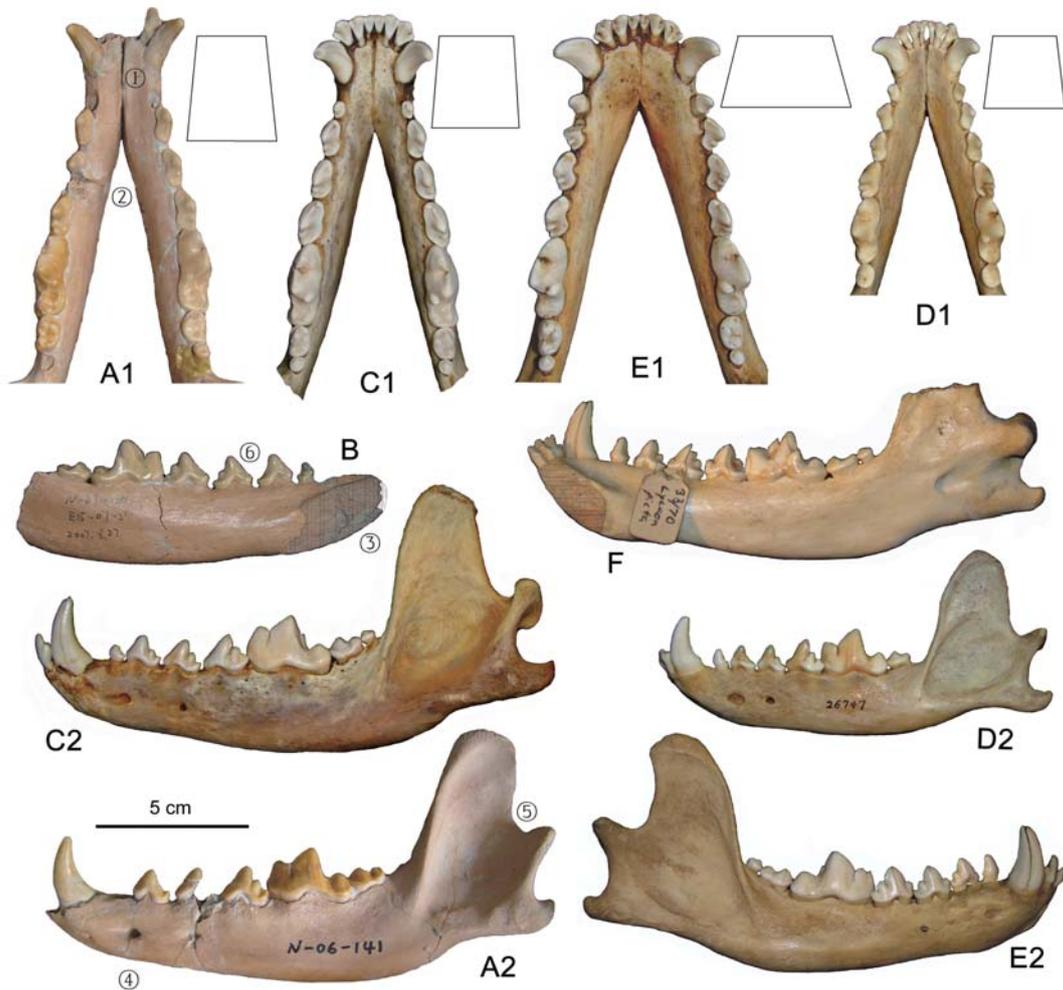


Fig.5 The symphyseal part of the mandible in *Canis chihliensis* (A1, A2, B), *C. lupus* (C1-C2), *Cuon alpinus* (D1-D2) and *Lycaon pictus* (E1, E2, F)

A1. IVPP V 17755.3; A2. V 17755.4; B. V 17755.5, SSMZ; C1-2. IOZ no number, extant, China; D1-2. IOZ 26747, extant, China; E1-2. BPI/C 223, extant, South Africa; F. BPI/C 33/70, extant, South Africa; A1, C1, D1, E1. in occlusal views; B, F. in lingual views; A2, C2, D2, E2. in buccal views; ① symphyseal length; ② angle of mandibular arch; ③ symphyseal facet; ④ mental foramen; ⑤ sigmoid notch; ⑥ accessory cusps on lower premolars; each trapezium represents the outline of the symphyseal part of the nearby mandible

blade-like in their unworn state. The apices of all the premolars are inclined posteriorly. The p1 is single-rooted, whereas the other premolars are double rooted.

The i1 is the smallest of the incisors, and its labiolingual width markedly exceeds its mesiodistal length. The labial face of this tooth is smooth and vertical, whereas the lingual face forms a slope. In anterior view, the top edge of the enamel is quite straight.

The i2 is slightly larger than the i1. The labiolingual width of the former tooth is only slightly greater than the mesiodistal length, and labiolingual width is the greatest at the mesial part of the tooth. The labial face of the i2 is slightly convex and nearly vertical, but the lingual face is sloping. In anterior view, the profile of the enamel edge is very straight.

The i3 is distinctly larger than the i2; the crown of the former tooth is chisel-like and bifid, but the distal cuspid is small and located in a low position; the labial face is vertical and mesiodistally convex.

The lower canine is much more robust than its upper counterpart, and is conical in form but slightly curved. Faint crests can be detected on both the mesial and distal aspects of the canine. A faint cingulum, connected to the anterior crest, also can be detected on the mesial aspect of the tooth.

The p1 is unicuspid and single rooted. The cuspid is well-developed and conical in form, but occupies only the mesial half of the tooth. A weak metastylid is present on the distal most part of the tooth.

The p2 is arrow-like in buccal view, the anterior slope being straight and the posterior slope concave. The principal cuspid is positioned almost at the middle of the tooth, with a tiny posterior cuspid next to it.

The p3 is very similar to the p2 in form, but is slightly larger. One well-developed posterior accessory cuspid and one tiny cingular cuspid are present on the p3.

The p4 is much larger than other premolars, and wider in its distal portion. The p4 has two posterior accessory cuspids, one mesial and one distal. The mesial accessory cuspid is the larger, and the distal one lies between the mesial one and the cingulid. The p4 also has a cingular cuspid. When unworn, the main cuspid is slightly lower than the paraconid of m1.

The m1, the lower carnassial tooth, consists of a carnassial blade and a talonid. The carnassial blade can be divided into a paraconid and a protoconid, and the cuspids on the talonid are quite variable (Fig.6). The m1 is the most variable of the lower cheek teeth, the variability lying mainly in the position of the hypoconid and the sizes of the metaconid and the entoconid. In most of the available examples of m1 the lingual cuspids, and particularly the entoconid, are very reduced. The entoconid is usually crest-like and is always present, however small it may be. The anterior edge of the paraconid is nearly straight and vertical. Almost all examples of m1 have a protostylid, albeit a tiny one. In some cases a blade-like crest across the hypoconid is also present. The distal cingulum is also variable, being present in some cases and completely absent in others.

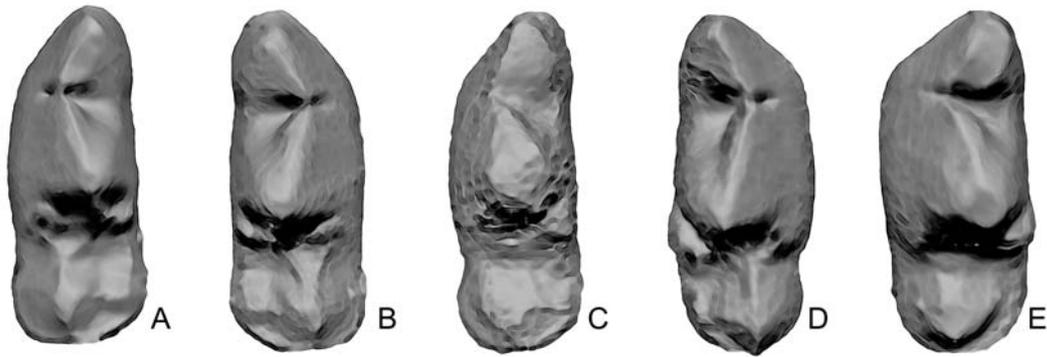


Fig. 6 3D laser scans showing variation in the lower m1 of *Canis chihliensis* with respect to development of the lingual cusps, in crown views

A, C, E. left m1s (IVPP V 17755.5, V 17755.21, V 17755.3); B, D. right m1s (V 17755.4, V 17755.6)

**Table 2** Lower tooth dimensions of *Canis chihliensis* from SSMZ, compared with those of *C. lupus* and *Cuon alpinus* (mm)

		<i>Canis chihliensis</i>								<i>C. lupus</i>	<i>Cuon alpinus</i>	
		V17755.3	V17755.4	V17755.5	V17755.6	V17755.10	V17755.11	V17755.12	V18333.2a	V18333.2b	IVPP C/O.3	IVPP OV.819
p1	L	—	—	5.19	—	—	5.21	5.21	6.3	—	5.59	4.44
	W	—	—	4.06	—	—	4.46	4.46	4.8	—	4.33	3.09
p2	L	11.79	11.83	12.07	—	12.06	12.43	12.43	11.3	11.8	12.09	6.91
	W	5.58	5.52	5.47	—	5.02	5.19	5.19	5	5.2	5.59	3.78
p3	L	—	12.76	13.54	—	13.49	13.40	13.40	13.3	14.1	13.41	8.80
	W	—	5.78	5.84	—	5.50	5.93	5.93	5.9	5.8	6.16	4.49
p4	L	14.08	14.45	15.77	14.95	14.97	15.32	15.32	15.6	15.9	14.91	11.14
	W	6.68	6.84	7.37	6.79	6.72	7.81	7.81	7.6	7.5	7.22	5.54
m1	L	24.81	25.46	24.93	25.27	24.74	23.75	23.75	26.5	26.5	27.11	20.46
	W	10.52	10.38	10.29	10.10	9.56	10.74	10.74	10.9	10.8	10.72	7.79
m2	L	11.54	11.17	11.34	10.93	—	—	—	10.8	10.6	10.92	6.30
	W	8.11	8.03	7.96	7.98	—	—	—	8.5	8.4	7.99	5.84
m3	L	—	5.69	—	5.78	—	—	—	5.5	—	5.66	—
	W	—	5.03	—	4.62	—	—	—	5.1	—	5.21	—

The m2 has an approximately oval outline, and is large in proportion to the m1. The best-developed cuspid on the m2 is the protoconid. The metaconid and hypoconid are also prominent, but no entoconid is present. A vestigial paraconid can be detected in some specimens (V 17755.5). Both mesial and distal cingula are present. The talonid is much shorter than the trigonid.

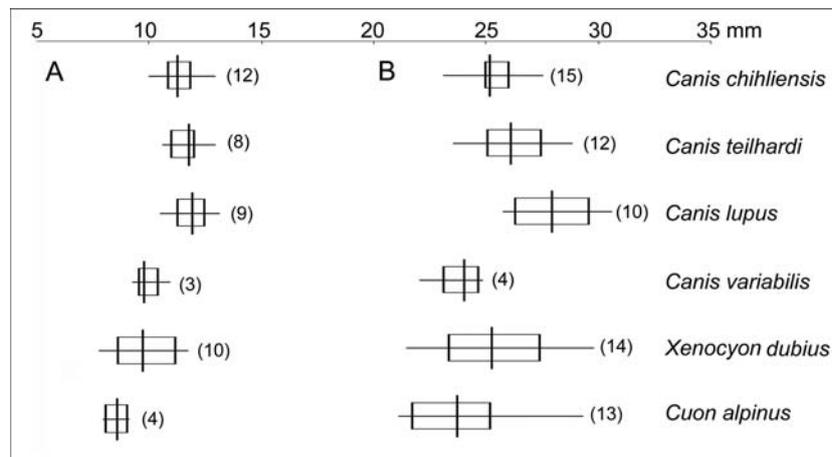


Fig.7 Box plot of the lengths of the m2 (A) and m1 (B) in the species *Canis chihliensis*, *C. teilhardi*, *C. lupus*, *C. variabilis*, *Xenocyon dubius* and *Cuon alpinus*

Horizontal bars represent ranges, boundaries of small rectangles represent upper and lower quartiles, the vertical lines represent the median values, and numbers in parentheses indicate sample sizes

Data sources: *Canis chihliensis* (Teilhard de Chardin and Piveteau, 1930; Teilhard de Chardin, 1940; Wang, 2006); *C. teilhardi* (Qiu et al., 2004); *C. lupus* (Teilhard de Chardin, 1940; Pei, 1934; Chi, 1974; Zong and Huang, 1985; Chow, 1959; HCCR et al., 1987; Zhou et al., 1990; Zong et al., 1996); *C. variabilis* (Teilhard de Chardin, 1940; Pei, 1934); *Xenocyon dubius* (Teilhard de Chardin, 1940; Wang, 2006; Echassoux et al., 2008; Wang and Zhao, 2006; Huang and Fang, 1991; Pei, 1987; Lu, 2010); *Cuon alpinus* (Pei, 1934; Teilhard de Chardin and Pei, 1941; Pei, 1940; Liu, 2002; Zheng and Han, 1993)

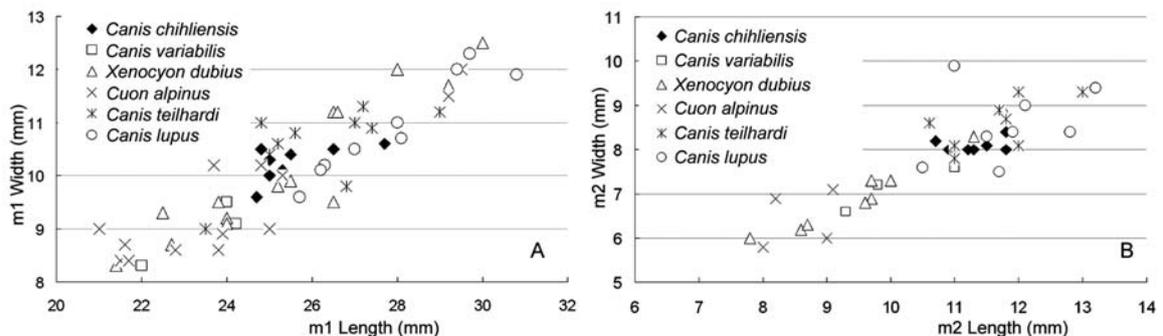


Fig.8 Bivariate scatter plot of measurements of m1 (A) and m2 (B) of *Canis chihliensis*, *C. teilhardi*, *C. lupus*, *C. variabilis*, *Xenocyon dubius* and *Cuon alpinus* (data sources as given in caption of Fig.7)

The m3 is quite small, and is nearly round in crown view but nevertheless not so round as in *Canis lupus*. The protoconid of the m3 is almost at the center of the tooth, and the metaconid and hypoconid are vestigial. A ridge extends along the distal edge of the tooth. The mesial cingulum is conspicuous.

Postcranial skeleton (Fig.9; Table 3): The available postcranial material comes from several individuals, but most of the bones are from only two. The elements unearthed in 2007 are mainly from the forelimbs, whereas those unearthed in 2008 are mainly from the hind limbs. It is worth mentioning that the almost complete manus and pes represent the first discovery of these materials for the early *Canis* in China. Only the relatively complete and identifiable specimens are described below.

Scapula: Only the distal part of a single left scapula is available. Observable structures include the glenoid cavity, supraglenoid tubercle, coracoid process and scapular notch, as well as part of the spine. The glenoid cavity is kidney-shaped, with a rounded medial edge and a dorsal edge that bears a marked notch in lateral view. The coracoid process is poorly developed, to the point of being indistinguishable from the supraglenoid tubercle. The infraglenoid tubercle is just a rugose muscle scar and is triangular in caudal view. The scapular notch is deep. The length and width of the glenoid cavity (or fossa) are 26 and 17.8 mm respectively. The minimum diameter of the neck is 24.6 mm, much smaller than the corresponding value for the extant *Canis lupus*.

Humerus (Fig.9C1-2): The distal part of one left humerus is available. It is stout. In anterior view, the trochlea is slightly oblique to the shaft and asymmetrical, narrowing and heightening medially. The supratrochlear foramen is quite large, and occupies most of the coronoid fossa. The very deep olecranon fossa is visible in posterior view, and the medial epicondyle is markedly larger than the lateral epicondyle and has a pronounced tubercle on the medial side. The capitulum is quite pronounced in distal view. This humerus differs from that of *Canis lupus* in having a less well-developed lateral epicondyle, a narrow posterior humeral trochlea, a ridge-like medial edge on the trochlea, and a considerably smaller capitulum humeri.

Radius (Fig.9D1-2): In proximal view, the articular surface of this bone is dumb-bell shaped, with the medial portion much larger than the lateral portion. A prominent notch exists at the anterior edge of the proximal surface, whereas the lateral edge is tubercle-like. The radial shaft is quite straight in anterior view, but the anterior edge of the proximal end is wave-like. The medial side of the distal end bears a pronounced styloid process, and a weakly developed dorsal crest is present. The dorsal surface of the distal end presents only two grooves, rather than three. In lateral view, the distolateral surface bears a large, oval articular facet, the ulnar notch, for the ulna; the proximal part of the radial shaft becomes more flattened, and the lateral tubercle or radial tuberosity is small but distinct enough; the shaft looks slightly curved. In caudal view, the articular circumference of the radial head is prominent. A narrow rugose area, the interosseus border, extends along the lateral edge of the proximal two-fifths of the radial shaft. The anterolateral tubercle is less pronounced than in the radius of *Canis lupus*, the interosseus border extends farther distally, and the proximal anterior notch is more laterally located. Munthe (1989) thought that few morphological features of the radius, other than size, would be helpful in distinguishing different taxa.

Ulna: Although three ulnae were recovered, none of them includes a preserved distal end. In proximal view, the olecranon process is four-sided and laterally compressed. The proximal crest of the olecranon is grooved cranially, and enlarged and rounded caudally. The anconeal process is robust. The lateral portion of the coronoid process is pronounced. In cranial view, a groove can be seen at the proximal end, and the trochlear and radial notches show no unusual features. The proximal part of the shaft is laterally compressed and broad in lateral view, but



Fig. 9 Postcranial bones of *Canis chihliensis* from SSMZ in Nihewan

A. left and right manus, with most elements preserved (IVPP V 18138.9-45); B. complete left pes (V 18139.24-48); C. distal part of left humerus (V 18138.1); D. left radius (V 18138.3); E. left femur (V 18139.19); F. left tibia and fibula (V 18139.21); A1, B1, B3. in dorsal views; A2, B2, B4. in plantar views; C1, D1, E1, F1. in cranial views; C2, D2, E2, F2. in caudal views  
Abbreviations: 1st-3rd T. first to third tarsal bones第1-3跗骨; As. astragalus距骨; Ca. calcaneum跟骨; Cu. cuboid (=fourth tarsal bone)第4跗骨; Mc I-V. metacarpal I-V第1-5掌骨; Mt I, V. first and fifth metatarsals第1和5趾骨; Na. navicular (=central tarsal bone)中央跗骨

the distal part is narrower. The caudal border of the olecranon is much straighter than in *Canis lupus*.

Metacarpals (Fig.9A1-2): The manus has five metacarpal bones. Mc I is the smallest of the metacarpals, and bears a wide caudocranial groove at its proximal end and a proximolaterally situated facet for Mc II. Mc IV is the longest metacarpal, and Mc V is the

most robust (for dimensions see Table 3).

**Table 3** Dimensions of the postcranial bones of *Canis chihliensis* from SSMZ, compared with those of various *Canis* species and *Cuon alpinus* (mm)

Species		<i>C. chihliensis</i>	<i>C. variabilis</i>	<i>C. mosbachensis</i>	<i>C. lupus</i> (fossil)	<i>C. lupus</i> (extant)	<i>Cuon alpinus</i> (extant)
Locality		SSMZ	CKT Loc.13	Untermassfeld	Jurens	IOZ 07872/76277	IVPP OV 819
Sources		This paper	Teilhard and Pei, 1941	Sotnikova, 2001	Ballesio, 1979	This paper	This paper
Humerus	M.L	161	158–177(4)	169	225	205.10	128.35
	P.W	27	38–41(4)	—	—	54.23	28.87
	D.W	35–36.7(2)	32–34(4)	—	47	41.61	26.72
Radius	M.L	180.6	162–166(2)	163–169(4)	217–219(2)	208.84	109.90
	P.W	19.2–21.2(2)	18–19(2)	—	26.7–27(2)	22.44	14.40
	D.W	25.7	24(2)	—	37(2)	31.52	18.97
Ulna	M.L	>185.8	—	—	—	243.92	137.73
	P.W	11.7–13(2)	—	—	—	13.51	10.70
	D.W	—	—	—	—	—	7.88
Mc I	L	25–26(2)	—	—	—	—	17.50
Mc II	L	69	—	—	77–81(6)	—	43.15
Mc III	L	79(2)	—	72.5	90–95(4)	89.76	52.62
Mc IV	L	81	—	—	90–97(2)	—	51.34
Mc V	L	66	—	—	75–78(3)	—	43.50
Femur	M.L	182.4	181–192(3)	166–178(2)	—	220.98	148.32
	P.W	40	34–36(3)	—	—	46.78	33.39
	D.W	30.8–31(2)	21–23(3)	—	38–40(2)	41.11	28.43
Tibia	M.L	181.6	—	181–191(4)	245	229.94	140.09
	P.W	35.5–36.4(2)	—	—	51	49.27	29.37
	D.W	23.6–25.7(2)	—	—	33	21.02	21.58
Calcaneum	L	45.7–46.5	—	41.6–47.5(4)	—	48.50	38.63
Astragalus	L	26.8–27.3	—	25.5–28.5(4)	—	27.13	26.39
Mt II	L	67.6–68.4(2)	—	—	84–87(3)	—	52.65
Mt III	L	76.5–76.7(2)	—	73.9–81.1(3)	94.5–98(3)	95.61	62.20
Mt IV	L	76.5–77(2)	—	—	97–104(4)	96.81	61.13
Mt V	L	72–72.3(2)	—	—	86–90(3)	—	53.01

Abbreviations: M.L. maximum length; P.W. proximal width; D.W. distal width; L. length; numbers in parentheses represent sample sizes.

Femur (Fig.9E1-2): In proximal view, a groove can be seen between the greater trochanter of the femur and the ridge above the trochanteric fossa. The lateral and medial epicondyles of the trochlea are not pronounced. In caudal view, the greater trochanter is positioned slightly

below the head. The intertrochanteric crest (or trochanteric ridge) is quite vertical. The lateral side of the caput extends obliquely towards the trochanteric fossa. Below the prominent lesser trochanter is a sharp crest extending downward along the shaft. The rough surface for muscle attachment is not very rugose, and is limited to the lateral half of the rear surface of the shaft. The lateral epicondylar tuberosity is prominent. The lateral condyle is more robust than the medial one. Sesamoid facets can be detected on both the lateral and medial condyles. In medial view, the fovea capitis can be detected but is not particularly distinct, and the distal part of the femoral shaft is slightly curved. The greater and lesser trochanters are more pronounced than in *Canis lupus*, which also differs from *C. chihliensis* in that the two femoral condyles are almost equally developed and the trochlear surface is more upwardly directed.

Tibia (Fig.9F1-2): The proximal articular surface of the tibia is divided by a groove into medial and lateral condyles, and each bears an intercondyloid eminence. The medial condyle is kidney-shaped, whereas the lateral condyle is four-sided. In proximal view, two notches can be seen, the popliteal notch at the posterior edge and the cranio-lateral notch just in front of the fibular facet. A narrow, deep notch is also present at the distal end of the tibia, between the medial malleolus and the central ridge. The proximal half of the tibial shaft is triangular in cross section. In cranial view, the whole shaft forms a gentle S-shape. The most obvious structure on the cranial surface is the tibial tuberosity, whose lower part is referred to by different authors as the cranial border (Evans and Christensen, 1979) or the tibial/cnemial crest (Munthe, 1989). Only the upper portion of the blade-like crest bears a rugose surface. The medial malleolus is fairly well-developed. In caudal view, part of the lower portion of the tibia is fused with the fibula, but the distal ends of the two bones are separate. The popliteal fossa, which is located below the popliteal notch of the proximal extremity, is not very prominent; the popliteal line is quite prominent, but originates from the upper one-fifth of the tibia. The extremely small nutrient foramen is positioned on the lateral side of the upper two-fifths of the tibia, and a groove is present above this opening. In lateral view, the fibula and the two fibular facets can be seen; the upper part of the tibial tuberosity looks quite pronounced, and a broad, basin-like area lies lateral to this structure. The distal articular surface of the tibia is asymmetrically divided into two areas by a cranio-caudally aligned central ridge. The medial area is a narrow and deep depression that is anteroposteriorly longer than mediolaterally wide, but the lateral area is more broad and shallow.

Patella: This bone is oval in shape, and its caudal surface is transversely convex, but slightly concave along its long axis; its cranial surface is convex and rough proximally. The proximal end is relatively blunt, whereas the distal apex is slightly more pointed. The articular surface is generally convex, but in lateral or medial view this surface looks slightly concave along its long axis. The proximodistal length and mediolateral width of the patella are 14.8 and 11 mm respectively.

Calcaneum (Fig.9B3-4): In dorsal view, the body of the calcaneal tuber is quite mediolaterally compressed, but the proximal end is expanded to form lateral and medial

processes that are separated by a pronounced groove. Two major articular surfaces for the astragalus, one lateral and one medial, can be observed. The medial surface is oval in shape and directly anterior to the sustentaculum tali, whereas the lateral one is positioned in the middle part of the calcaneum's height. In plantar view, the lateral and medial sides of the calcaneal tuber are nearly parallel; the sustentaculum tali is quite robust and is lower positioned. The distal articular surface for the cuboid is very small. The total calcaneal length and the length of the calcaneal tuber are 46.5 and 33 mm respectively. All of the articular surfaces differ in shape from their counterparts in *Canis lupus*.

Astragalus (Fig.9B3-4): The lateral keel on the astragalar trochlea is broader and less steep than the medial one, and the neck of the astragalus is quite long. In lateral view, the body of the astragalus is ear-shaped, and the upper portion bears a facet for the lateral malleolus of the distal end of the fibula. In plantar view, curved lateral and medial articular surfaces can be seen, and the latter directly borders the distal articular surface. The head is transversely elongate in distal view, and the distal surface for articulation with the navicular is convex. The length of the astragalus and width of the astragalar trochlea are 27.3 and 14 mm respectively. The distal articular surface is smaller and tapers more strongly in the medial direction than its counterpart in *Canis lupus*, and the medial articular surface extends farther proximally but is proportionally narrower.

Metatarsals (Fig.9B1-2): The pes has five metatarsals, of which Mt III is the stoutest and the vestigial Mt I the smallest. Mt V has a curved shape and distinctively formed base (peroneus brevis insertion)(see Table 3 for measurements). The peroneus brevis insertion is positioned much higher on the metatarsal than in *Canis lupus*.

## 2 Comparisons and discussion

### 2.1 Comparisons with related species

#### 2.1.1 Comparisons with other species of *Canis*

Among all *Canis* species so far recovered from Chinese strata, the closest to the SSMZ canid in both morphology and geological age seems to be *Canis antonii* Zdansky, 1924. However, *C. antonii* differs from the SSMZ canid in having a less well-developed protocone on the P4 and an enlarged talon on the M1. Although *C. antonii* and *C. chihliensis* are comparable in size, Zdansky (1924) noted certain differences between the holotypes of the two species. In particular, *C. chihliensis* has a more robust P4 protocone and an M2 that is less reduced relative to M1, implying that this species is the more primitive form (Tedford et al., 2009).

*Canis teilhardi* Qiu et al., 2004, from the Lower Pleistocene Longdan locality in Gansu Province, bears some striking similarities to *C. chihliensis*: for example, the tooth dimensions (Fig.7) and length/width ratios (Fig.8) are similar, well-developed accessory cusps are present

on P2-P3 and p2-p4, the length of the P4 is nearly equal to the combined lengths of M1+M2, and the entoconid is markedly smaller and lower in position than the hypoconid on the m1. However, *C. teilhardi* differs from *C. chihliensis* in the following respects: the protocone on the P4 is less well-developed, the M2 and m2 are smaller relative to the sizes of the M1 and m1 respectively, and there is a very pronounced metaconule on the M1.

The Middle Pleistocene species *Canis variabilis* is markedly smaller than other Chinese *Canis* species with regard to the dimensions of the skull (Pei, 1934; Teilhard de Chardin and Pei, 1941) and teeth (Fig.7), but some of its postcranial bones are nearly the same size as those of *C. chihliensis* or in some cases even larger. This is true, for example, of the bones from CKT Loc.13 (Table 3).

The living species *Canis lupus* is much more larger than *C. chihliensis* (Fig.7; Table 3); the M1 is less compressed mesiodistally, with lower buccal cusps but a more hypertrophied paracone relative to the metacone, and has a more rounded anterobuccal corner; the P4 has a less well-developed protocone and a convex buccal surface, and a carnassial blade that is less compressed buccolingually; the lower molars have more pronounced lingual cuspids. Additionally, all of the limb bones of *Canis chihliensis* are less stout than those of the extant *Canis lupus* and the fossil species *Canis mosbachensis* from Untermassfeld (Table 3). According to Wang and Tedford (2010), canines (*Canis*, *Cuon* and *Lycaon*) tended to become larger and more hypercarnivorous over the course of their evolution, and from this perspective it can be assumed that *Canis chihliensis* is more primitive than *Canis lupus* and *Canis mosbachensis*.

### 2.1.2 Comparisons with material previously referred to *Canis chihliensis*

The fact that the length of P4 exceeds the combined lengths of M1 and M2 was once regarded as a crucial diagnostic feature of *Canis chihliensis* (IVPP, 1979). However, our study shows that, while this feature is most frequently seen in *C. chihliensis*, it also occurs in other *Canis* species.

Three morphotypes of the fossil *Canis* from Nihewan Basin, mainly from around the village of Xiashagou, were recognized by Teilhard de Chardin and Piveteau (1930) and were called *Canis chihliensis* forme typique, *Canis chihliensis* var. *palmidens* and *Canis chihliensis* var. *minor*. However, these designations were questioned by a number of subsequent authors. Some of the specimens have been transferred to a different genus (Tedford and Qiu, 1996), and “*Canis chihliensis* var. *palmidens*” has been elevated to the species level (Tedford et al., 2009). Our recent study shows that the dispute is far from settled. Our own examination reveals that some of the material once referred to *Canis chihliensis* var. *palmidens*, including the cranium TNP 00197 (Teilhard de Chardin and Piveteau, 1930:pl.XVIII, fig.4), appears to belong to *Nyctereutes*. Additionally, some maxillae and mandibles once referred to *Canis chihliensis* by Teilhard de Chardin and Piveteau (1930), and now housed in the IVPP collections, differ significantly from both the type specimen of *Canis chihliensis* and the SSMZ material in the

following characters: protocone on P4 poorly developed, M1 with prominent metaconule, hypocone on M1 strong and crest-like, M1 less strongly compressed mesiodistally, M2 quite small, lower m1 with developed lingual cuspids.

The *Canis* material from CKT Loc.18 was identified as *Canis* cf. *C. chihliensis* by Teilhard de Chardin (1940). The two skulls described by this author are quite close to that of the recent gray wolf in their proportions, apart from their considerably larger zygomatic width. However, it is apparent that the line drawings of the two skulls in Teilhard de Chardin's (1940) monograph were seriously distorted in width/length ratio. In recent years, specimens of *Canis* cf. *C. chihliensis* from CKT Loc.18 have been reassigned to a new species, *Canis teilhardi* (Qiu et al, 2004).

Two teeth from Danangou, a P4 (IVPP V 7252-1) and an M1 (V 7252-2), were originally identified as *Canis chihliensis minor* by Li (1984) but are too small to be included in this species. Additionally, the protocone on the P4 is too reduced and is located too far anteriorly, and the lingual portion of the M1 is very narrow. We think that these teeth probably belong to the genus *Vulpes*.

### 2.1.3 Comparison with *Cuon* and *Xenocyon*

Ripoll et al. (2010) have conducted a thorough comparison between *Cuon* and *Canis*, and the two genera definitely differ in many anatomical characteristics and metric traits. *Cuon* is much smaller, lacks an m3, and differs from *Canis* in other obvious features such as the buccolingually narrower proportions of the M1 and the complete lack of an entoconid on the m1. Additionally, we think that a markedly reduced talonid on the m1 and well-developed posterior accessory cusps on the p4 are also crucial characteristics of the genus *Cuon*. *Cuon* is not well represented in the Chinese fossil record, but one partial mandible (IVPP V 1667) from the Changyang Man site in Hubei Province can be readily referred to the genus based on its lack of an m3, high-crowned teeth, distinct posterior accessory cuspids on p4, and reduced talonid on m1.

However, some large canids have reduced lingual cuspids on the m1 but also have an m3, further complicating the situation. They were once directly referred to the genus *Cuon* under the separate specific name *Cuon dubius* (Teilhard de Chardin, 1940). Other student has proposed new generic names, *Xenocyon* (Kretzoi, 1938) or *Sinicuon* (Kretzoi, 1941), for them. *Cuon* actually shares few characters with these specimens, apart from the reduced lingual cuspids of the lower molars.

All of the characteristics of the Shanshenmiaozui canid materials fall well within the range of the genus *Canis*, except the reduced entoconid. However, the entoconid has been shown to be quite variable in *Canis* (Qiu et al., 2004; Tedford et al., 2009). It is therefore reasonable to refer the Shanshenmiaozui canid materials to *Canis*.

Large canid fossils from the Yunxian Man site have been referred to the species *Xenocyon dubius* by Echassoux et al. (2008), but these materials are characterized by the following traits: relatively smaller dental and osteological dimensions, no diastema between premolars,

both posterior accessory cusps on p4 quite well-developed, metaconid on m1 consistently well-developed, and hypsodont. They are quite different from northern Chinese specimens of *Xenocyon dubius*. The type specimens of *Xenocyon dubius* (Teilhard de Chardin, 1940) from CKT Loc.18 is much bigger, but has a rather shallow mandibular body, a diastema between the lower premolars, and uniformly lower-crowned lower cheek teeth.

*Xenocyon dubius* should be considered closely related to *Canis*, rather than *Cuon*, because of the characteristics such as the following: larger size compared to *Cuon*, M1 with well-developed cingular hypocone, m3 and m1 with both metaconid and entoconid (however small), m2 double-rooted and with well-developed talonid. Other authors have regarded *Xenocyon* as a subgenus of *Canis* (Rook, 1994; Stiner et al., 2001; Sotnikova, 2001; Sotnikova and Rook, 2010), but we think our solution is more reasonable and practical.

The species *Xenocyon lycaonoides* was originally established by Kretzoi (1938) based on a large canid with a trenchant talonid but no entoconid on m1, but a recent study (Sotnikova, 2001) showed that the m1 has a minute entoconid in some cases. This indicates that the absence or presence of an entoconid on the m1 is not a very stable character. Sotnikova (2001) referred the Pliocene-Early Pleistocene species *Canis falconeri* from Europe, *C. antonii* from Asia and *C. africanus* from Africa to the supraspecific group *Canis (Xenocyon) ex gr. falconeri*, following Rook (1994).

#### 2.1.4 Comparison with *Lycaon*

In recent years, some authors have linked the large Eurasian canids with reduced lingual cuspids to the African hunting dog *Lycaon pictus*, hypothesizing that the recent African hunting dog was derived from the Eurasian *Lycaon lycaonoides* (Martínez-Navarro and Rook, 2003). However, this hypothesis was cast into doubt by the more recent discovery in South Africa of the much earlier fossil species *Lycaon sekowei*, which is as old as 1.9 Ma and was regarded by Hartstone-Rose et al. (2010) as the most likely ancestor of the living species *Lycaon pictus*. This new hypothesis also envisions a scenario of dietary specialization in the genus *Lycaon* (acquisition of characters related to hypercarnivory) prior to cursorial adaptation (loss of metacarpal I). The well-preserved specimens of metacarpal I among the SSMZ material (Fig.9) adds critical data to this debate.

On the other hand, the Eurasian *Xenocyon* and its close relatives, including *Canis chihliensis*, are quite different from the African wild dog in a number of features including the following: elongate skull, narrow palate, different mandibular morphology, vestigial entoconid on m1, less developed accessory cuspids (apart from the anterior cuspids) on the lower cheek teeth, less hypsodont, longer mandibular symphysis, pentadactyl forelimb (Tong et al., 2011a). In *Lycaon pictus*, by contrast, the choanal fossa is broader, the teeth are more hypsodont, the metacone on the M1 is nearly as well-developed as the paracone, and the I3 is more caniniform.

## 2.2 Taxonomic identification of the canid material from Shanshenmiaozui

Considering its large size, long symphyseal suture, robust canines, large M2 and m2 relative to the M1 and m1 respectively, and well-developed hypocone and lingual cingulum on the M1-2, as well as the presence of an m3, the taxon represented by the SSMZ canid material can be assigned to the genus *Canis*.

Although Hartstone-Rose et al. (2010) concluded that "... the M1 is not particularly useful for separating the large-bodied canids (Tedford et al., 1995)", we still think that the upper M1 is of particular significance in distinguishing among large Pleistocene canids from China. The examples of M1 from SSMZ are remarkably compressed mesiodistally with a well-developed cingular hypocone (Figs.3-4), characters that are typical of *Canis chihliensis* Zdansky, 1924. Additionally, the upper P4 of the holotype has a well-developed protocone, but its carnassial blade is markedly compressed buccolingually, and its buccal surface is quite flat and nearly vertical; the M2 and m2 are large relative to the M1 and m1 respectively, but the lingual cuspids on m1-2 are poorly developed. All these characters are mainly seen in *Canis chihliensis*. In the bivariate scatter plot, the points representing the data of *C. chihliensis* are tightly grouped (Fig.8).

## 2.3 Discussion

As early as 1942, Huxley (pp.280-281) related differences in predator size to differences in prey size, suggesting that animals using similar resources should evolve towards different sizes in order to reduce the effects of competition for the same foods. As a result, related animals with the same body size and same diet are unlikely to coexist. The idea of character displacement has also been applied to five sympatric canid species from Israel (Dayan et al., 1989, 1992), which have carnassial length ratios varying from 1.18 to 1.34. From this point of view, the coexistence of three large canine taxa (*Canis chihliensis*, *Canis chihliensis* var. *palmidens* and *Canis chihliensis* var. *minor*=*Eucyon minor*) of very similar body sizes in the Nihewan fauna should be questioned. In such a situation, it is necessary to take individual variation into consideration.

Our study shows that the degree of development of the lingual cuspids on the lower molars is not particularly stable (Figs.4, 6). This makes it necessary to reexamine the taxonomic identifications of the large canids from the Nihewan beds. One of them, previously called *Canis chihliensis* var. *minor*, has in fact already been reassigned to *Eucyon* as *E. minor* by Tedford and Qiu (1996).

Previous studies of early *Canis* relied too much on the upper and lower molars, which have proven to be quite variable and difficult to use as a basis for taxonomic identifications. A reliable classification should take as many characters as possible into consideration. It is unfortunate that the postcranial material known today is so limited. Although some skeletons were included in our study, the data available for comparison are still insufficient. The radius/

tibia ratio (radius length/tibia length) is nearly 100% in the SSMZ *Canis* material, which would identify this material as belonging to quite a derived member of the genus according to Tedford et al. (2009).

The dimensions of m1 and m2 in specimens assigned to *Xenocyon dubius* are variable enough to show that this species is not well-defined (Figs.7-8).

The species *Canis variabilis* is very strange in the context of the evolution of the *Canis* lineage in China, because it is strikingly smaller than both earlier and later species of *Canis* in cranial and dental dimensions. It is very likely that this species is the ancestor of the domestic dog *Canis familiaris*, a hypothesis that has been proposed by previous authors (Pei, 1934; Olsen et al., 1982; Olsen, 1985).

An evolutionary trend toward increased body size was evident in the *Canis* lineage in Europe, and all known Early Pleistocene *Canis* species have considerably smaller dental dimensions than the extant *Canis lupus* (Brugal and Boudadi-Maligne, 2011). In China, it is not yet clear whether a comparable evolutionary tendency existed within the canini lineage. However, the present study shows that all Chinese fossil species of *Canis* except *Canis variabilis* are quite close to *Canis lupus* in both dental and postcranial dimensions.

### 3 Conclusions

The sample of canid material from SSMZ is among the best available for *Canis chihliensis*, and includes maxillae, mandibles and postcranial bones. Based on measurements and such morphological characters as large size, P4 elongated with well-developed protocone and anterior notch, M1 strongly mesiodistally compressed and with broad cingular hypocone, long mandibular symphysis, m1 with metaconid and entoconid (however small), and m2 with well-developed talonid, this material can be assigned to the species *Canis chihliensis*. This species is characterized by reduction of the lingual cuspids of the lower molars, which links *Canis chihliensis* with the controversial *Xenocyon dubius*. Our study also shows that the first lower molars from Shanshenmiaozui are fairly variable in the development of the lingual cuspids. The teeth of *Canis chihliensis* are slightly smaller than those of *C. teilhardi* and *C. lupus*. However, the postcranial bones of *C. chihliensis* are remarkably smaller than those of the recent *Canis lupus*, and such bones as the calcaneum, astragalus and Mt V are quite different in form between the two species.

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