

A mandible of *Leptobos* (Bovidae, Artiodactyla) from the Lower Pleistocene of Longdan, Gansu, China, and evidence of feline predatory strategy

—Addition to the Early Pleistocene Longdan Mammalian Fauna (4)

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Abstract A completely preserved mandible of *Leptobos* from the Early Pleistocene mammalian fauna of Longdan, Gansu Province, China, is described here. The mandible has a long thin mandibular body, and a long mandibular diastema. The premolar row is short. The mandibular body forms an obtuse angle of about 120° with the mandibular ramus, while the angle of the mandible is nearly 90°. The paraconid and parastylid are well developed, and the metaconid extends posteriorly, not connecting with the paraconid in p3 or p4. The main cusps of the molars are rounded, and ectostylids (basal pillars) present in m1-m3. The metastylid of m2 is weak, and the preprotocristids of m2-m3 and posthypocristid of m3 are anteroposteriorly constricted. Skulls of *Leptobos brevicornis* were previously discovered in the same area, and the new specimen is also attributable to this species. Wounds preserved in the anterior part of the mandible are interpreted as resulted from attack by a feline predator, indicating the predatory behavior similar to that of living big cats, using muzzle clamps to suffocate preys, may have already occurred in the Early Pleistocene.

Key words Longdan mammalian fauna, Early Pleistocene, *Leptobos*, feline, predatory behavior

1 Introduction

Leptobos is a primitive bovine genus that was widespread in Eurasia from the Middle Pliocene to the Early Pleistocene (Thenius, 1969; Hu and Qi, 1978). Rüttimeyer (1878) established the genus based on materials that he assigned to *Leptobos falconeri*. The first occurrence of *Leptobos*, thought to coincide with those of *Equus* and *Elephas*, was viewed as indication of the beginning of Quaternary (Wang and Xue, 2006). However, further studies proved that the first occurrences of these three genera were asynchronous (Kurtén, 1968; Deng and Xue, 1997; 1999). Fossils of *Leptobos* have been found in many localities in the Pleistocene of China from south to north (Chi, 1975; Hu and Qi, 1978; Jia and Wang, 1978;

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Tang, 1980; Zheng et al., 1985; Li and Feng, 2001; Fang et al., 2004; Qiu et al., 2004; Zheng, 2004; Dong, 2008). However, all previously reported specimens that retain mandibular teeth are poorly preserved and always have undergone diagenetic deformation. A new complete mandible of *Leptobos* from the Lower Pleistocene of Longdan in Gansu Province is more informative. A subround wound is preserved in the front part of the mandible, which is interpreted as the result of injury by a carnivore. Few fossil records provide evidence regarding the predatory behavior of extinct mammals (Antunes et al., 2006; Deng and Tseng, 2010). This paper described the new specimen and discussed the likely predatory behavior of the attacking predator based on the wound.

Tooth terms are according to Duvernois (1990), Gentry (1992) and Dong (2004), and measurements are taken according to the protocols of Ma and Hou (2007) and Shi (2012).

Institutional abbreviations HMV, Hezheng Paleontological Museum, Gansu Province, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; JNTZ, Nanjing Provincial Museum, Jiangsu Province, China; YNDM, Office of Cultural Relics, Diqing District, Yunnan Province, China.

2 Systematic paleontology

Order Artiodactyla Owen, 1848

Family Bovidae Gray, 1821

Subfamily Bovinae Gill, 1872

Genus *Leptobos* Rüttimeyer, 1878

Type species *Leptobos falconeri* Rüttimeyer, 1878.

Other included species *L. elatus* (Croizet & Pomel, 1853); *L. etruscus* (Falconer, 1859); *L. brevicornis* Hu & Qi in Chi, 1975; *L. crassus* Jia & Wang, 1978; *L. furtivus* Duvernois, 1989; *L. bravardi* Duvernois, 1989.

Subgenus *Smertiobos* Duvernois, 1990

Included species *L. etruscus* (Falconer, 1859); *L. brevicornis* Hu & Qi in Chi, 1975; *L. crassus* Jia & Wang, 1978; *L. bravardi* Duvernois, 1989.

Leptobos brevicornis Hu & Qi in Chi, 1975

1975 *Leptobos amplifrontalis* Chi, p. 173-174, Pl. IV 1

1975 *Leptobos laochihensis* Chi, p. 174-175, Pl. III 1

1985 *Leptobos vallisarni* Zheng et al., p. 119-120, Pl. VII 2, VIII 1-2

Holotype IVPP V 2946.1, a partial adult skull, with its left horn and posterior part of cranium missing, from the upper Lower Pleistocene of Gongwangling in Lantian County, Shaanxi Province.

Referred specimen IVPP V 18532 (Fig. 1), a nearly complete mandible, from the Lower Pleistocene of Longdan in Dongxiang Autonomous County, Gansu Province.

Description The specimen represents an adult individual, since the m3 is moderately worn and the occlusal surface of p2 is oblique due to wear. Measurements of the mandible and its cheek teeth are given in Tables 1–2.

Table 1 Measurements of the mandible (IVPP V 18532) of *Leptobos brevicornis* from Longdan (mm)

Measurement	Left	Right
Length from anterior margin of incisors to angle	416.5	417.0
Length from anterior margin of incisors to condyle	426.4	431.0
Length from anterior margin of p2 to condyle	74.4	73.7
Length from posterior margin of m3 to rear margin of mandibular ramus	128.8	131.0
Height of condyle	170.0	180.8
Height of mandibular notch	163.0	167.2
Height of coronoid process	206.5	203.4
Height of mandible at anterior margin of p2	39.42	48.30
Height of mandible at anterior margin of m1	48.90	57.74
Height of mandible at posterior margin of m3	81.28	79.14
Transverse width between lateral surfaces of left and right canines	64.24	
Length of mandibular symphysis	64.14	
Minimum width of mandibular symphysis	16.28	
Length of mandibular diastema	120.30	122.60
Length of cheek tooth row (buccal side)	145.86	144.16

The mandibular body of the mandible is long and thin. The diastema is long, as long as 85% of the cheek teeth row. The mental foramen is oval, located below the anterior part of the diastema. The dorsal border of the mandibular body is straight in lateral view, while the ventral border is convex. The most convex part of the ventral border is situated below the anterior margin of m3. The mandibular body forms an angle of about 120° with the mandibular ramus, while the angle of the mandible is nearly 90°. The coronoid process is thin and curved posteriorly. The tip of the coronoid process is missing, and the basal length of the coronoid process is nearly half the anteroposterior length of the mandibular ramus. The width of the condyloid process is approximately equal to the basal length of the coronoid process.

The incisors are procumbent and almost uniform in size, with shovel-shaped occlusal outlines. The canine is incisorized, and there is no diastema between the canine and i3.

The p2 is oblique in occlusal surface due to wear. The protoconid is higher than the entoconid and hypoconid. A groove occurs at the lingual part of the protoconid.

The p3 is rectangular in occlusal outline, and is longer than p2. The parastylid and paraconid are well developed, which are situated in an anteroposterior line with the metaconid and entoconid along the lingual margin of the tooth. The metaconid is narrow, and its collar is slightly swollen towards the lingual part of the teeth. The metaconid extends in a considerable distance posteriorly. The trigonid basin (the valley between the paraconid and metaconid) is open transversely. The entoflexid (the valley between the metaconid and the entoconid) is narrow and open posteriorly. The protoconid is located at the level of the metaconid transversely. The hypoconid extends towards the buccal margin of the tooth, and the hypoflexid (the valley between the protoconid and hypoconid) is narrow and open posteriorly.

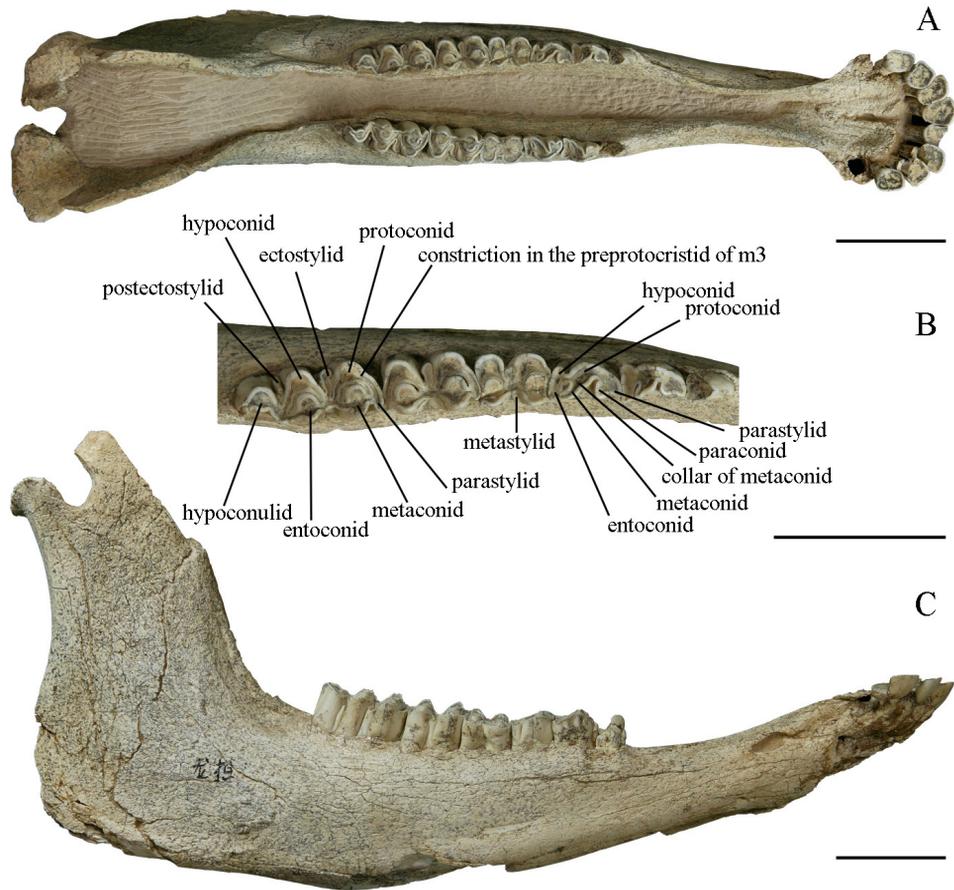


Fig. 1 Mandible (IVPP V 18532) of *Leptobos brevicornis* from Longdan
 A. occlusal view; B. occlusal view of dentition; C. buccal view. Scale bars=50 mm
 Terminology of B adapted from Duvernois (1990), Gentry (1992) and Dong (2004)

The p4 is longer than p3, but is narrower due to the smallness of the hypoconid. The occlusal surface of p4 resembles that of p3 in outline and topology. However, the parastylid and paraconid are better developed in p4, and the paraflexid (the valley between parastylid and paraconid) and trigonid basin are open wider. The collar of the metaconid is not swollen towards the lingual part of the teeth, and the metaconid nearly connects with the entoconid to enclose the entoflexid due to wear. The hypoflexid is wider than that in p3, and open transversely or anteriorly.

The m1 is rectangular in occlusal outline. The main cusps are sub-circular. The rib of the metaconid is strong and protruding lingually. The metastylid is weak. The trigonid basin (the valley between metaconid and protoconid) becomes a narrow line. There is no goat fold. The occlusal surfaces of the anterior and posterior lobes are similar. The ectostylid is relatively developed, extending in a distance towards the buccal margin of the teeth, which is at the level of half of the protoconid, and locates in the middle of two lobes.

The m2 is longer than m1 as the result of having well developed parastylid and entostylid. The m2 is similar to m1 in the outline and topology of the occlusal surface, but has wider trigonid and talonid basins (the valley between entoconid and hypoconid). The preprotocristid is anteroposteriorly constricted. The ectostylid is well developed, extending in a distance towards the buccal margin of the teeth, which is at the level of whole of the protoconid, and locates towards the posterior lobe.

The m3 is made up of three lobes, and the anterior two lobes are similar to those of m2 in the outline and topology of the occlusal surface. The trigonid and talonid basins are wider than those in m2. Weak folds towards the lingual side occur at the middle of the buccal margin of the trigonid and talonid basins. The preprotocristid and posthypocristid are anteroposteriorly constricted. The hypoconulid is rounded, and offset buccally relative to first two lobes. The ectostylid is similar to that of m2, and the postectostylid is small and conical.

3 Comparisons

The lower molars are selenodont with constant ectostylids (basal pillars), which show that the new specimen (IVPP V 18532) represents one kind of boodonts (Solounias, 2007). The parastylids and paraconids are well developed, and the paraconids do not connect with the metaconids (the trigonid basins are open) in p3 or p4. The metastylids are weak, and buccal main cusps are rounded in the lower molars. All these characters of the new specimen are typical of lower cheek teeth of the genus *Leptobos* (Duvernois, 1990). The talonid basin (the valley between entoconid and entostylid) is nearly closed due to heavy wear, which is not typical of the genus *Leptobos*. Two bovine species, *Leptobos brevicornis* and *Hemibos gracilis*, have been reported from the Longdan locality (Qiu et al., 2004). *L. brevicornis* may have a longer cheek tooth row and a smaller ratio between lower premolar and molar row than *H. gracilis*, which match the new specimen (V 18532) better (Geraads, 1992; Qiu et al., 2004). As a result, the new specimen can be attributed to *L. brevicornis*.

The skull (IVPP V 2946.1) from Gongwangling in Shaanxi Province has been assigned as the holotype of *Leptobos brevicornis* (Hu and Qi, 1978). However, the name had already appeared in the paper of Chi (1975), to describe the materials attributed to the same species, and the date needs to be revised (Qiu et al., 2004). Except for skulls, the materials in the paper of Hu and Qi (1978) include more than ten fragmentary mandibular specimens. Actually, forty mandibular specimens are preserved in IVPP under one catalogue number (V 2946), which is unwise for further study. Considering the completeness of cheek teeth, accurate specimen numbers V 2946.10-49 following the numbers in the paper of Hu and Qi (1978) are given to the forty specimens, and their measurements are given in Table 2. The measurements of the materials from Gongwangling can be found in Dong (2008), however, no detailed informations of the average data are included in his paper. The materials IVPP V 14032.2-3 from Renzidong are remeasured to show the ranges of deviation by two independent measurements, and the

data in this paper are smaller than those in Dong (2008). Different ages of *L. brevicornis* are preserved at the locality Gongwangling, and the teeth eruption sequence of this species may be exposed by V 2946.30, 32–33, in which m3 erupts earlier than p4. The age of Longdan specimen V 18532 can be determined between V 2946.14 and V 2946.27. V 2946.14 is similar to V 18532 in the outline and topology of the occlusal surface, and different from V 18532 in having more developed metaconid with collars swollen deep towards the lingual part of the teeth in p4 and more constrictions along the buccal main cusps of lower molars, which occur at the preprotocristids of m1-m3, the postprotocristids of m2-m3, and the posthypocristids of m2-m3. V 2946.27 differs from V 18532 in having more developed metastylid of m1 and more constrictions, which occur at the preprotocristids of m1-m3, the postprotocristids of m2, and the pre- and posthypocristids of m1-m3. The place of constrictions along the buccal main cusps varies in *L. brevicornis* based on the observations of 32 specimens with lower molars. The preprotocristids of m1-m3, prehypocristids of m2-m3 and posthypocristid of m3 are constricted with high probabilities, which are larger than or nearly 90%; the postprotocristid of m1 is not constricted with the probability of 92%; the prehypocristid of m1 and posthypocristids of m1-m2 tend to be constricted with the probabilities larger than 50%; however, the postprotocristids of m2-m3 tend not to be constricted with the probabilities larger than 50%. Less constrictions of Longdan specimen are preserved due to heavy wear. Fourteen specimens with p4 are preserved in the materials from Gongwangling, and vary in the outline and topology of p4: strong metaconids developed in nine specimens, the collars of metaconids swollen deep towards the lingual part of the teeth in eleven specimens, and postmetacristids developed in four specimens. Measurement data of the materials from Longdan are in the range of those from Gongwangling except for the large size of m3.

Materials from Layihai in Qinghai Province are attributed to *Leptobos vallisarni* based on the shape of the back part of the skull (Zheng et al., 1985), and *L. vallisarni* was later assigned as a junior synonym of *L. brevicornis* (Qiu et al., 2004). IVPP V 6036.3 is different from V 18532 in having more developed metaconid in p4 and more constrictions in lower molars, and can be attributed to *L. brevicornis* based on the variation range of Gongwangling specimens.

Materials from Renzidong in Anhui Province are attributed to *Leptobos crassus* based on the horn cores (Dong, 2008; Dong et al., 2009). V 14032.2-3 are two half-mandibles from Renzidong, and different from V 18532 in having more developed metaconids in p4, more constrictions in lower molars, and less developed hypoflexid in p4. Former two differences can be viewed as intraspecific variation characters based on the observations of *L. brevicornis* from Gongwangling; however, all materials from Gongwangling and Longdan have deep hypoflexids in p4, and this character may be different between *L. brevicornis* and *L. crassus*.

Materials from Tuozidong in Jiangsu Province are attributed to *Leptobos* cf. *L. crassus* based on the size of the teeth and the presence of *Leptobos* at the nearby and contemporaneous Renzidong locality (Fang et al., 2004; Fang and Dong, 2007; Dong et al., 2013). JNTZ 22591 is also similar to *L. brevicornis* in size and topology.

Table 2 Measurements of the lower cheek teeth of some *Leptobos* species

Species	<i>L. brevicornis</i>		<i>L. brevicornis</i>		<i>L. brevicornis</i>	<i>L. crassus</i>		<i>L. cf. L. crassus</i>		<i>Leptobos</i> sp. 1		<i>Leptobos</i> sp. 2	
	Longdan IVPP V 18532	Gongwangling V 2946.10-46	Layihai V 6036.3	Renzidong V 14032.2-3		Tuozidong JNTZ 22591	Zheng, 2004	Longgudong V 13473.1-484	Zhongdian YNDM 98v-24-26	left	right	min-max	min-max
p2	Length	13.34	13.62	9.12-13.62	11.06 (n=7)	10.25-10.70 (n=2)	14.4 (n=1)						
	Width	9.82	4.82	6.28-9.6	7.25 (n=7)	8.40-8.70 (n=2)	11.5 (n=1)						
p3	Height	11.38	9.00	11.42-16.06	14.33 (n=7)	10.23-11.61 (n=2)							
	Length	19.24	18.80	17.89-21.25	19.45 (n=12)	19.75-20.10 (n=2)	18.6-23.0 (n=18)						19.0
p4	Width	13.34	11.74	9.2-11.81	10.34 (n=12)	9.64-10.24 (n=2)	10.8-13.7 (n=18)						10.2 (basal part)
	Height	12.36	13.14	11.56-21.46	17.77 (n=12)	13.18-15.49 (n=2)	15.5						
m1	Length	21.16	19.34	17.78-25.29	20.99 (n=15)	22.00-22.10 (n=2)	20.3-24.1 (n=17)						20.8
	Width	12.60	12.90	10.06-13.93	11.48 (n=14)	11.03-11.15 (n=2)	12.1-14.6 (n=17)						12.0 (basal part)
m2	Height	16.52	12.70	13.61-27.18	19.48 (n=13)	17.68-19.04 (n=2)	17.5						
	Length	22.04	21.64	19.44-28.62	23.66 (n=22)	22.22-23.30 (n=2)	21.3-26.0 (n=32)						20.6
m3	Width	16.98	15.54	11.9-17.06	13.70 (n=23)	15.48-15.76 (n=2)	15.5-19.0 (n=32)						15.6 (basal part)
	Height	11.12	8.64	10.06-42.62	22.33 (n=23)	20.32-20.86 (n=2)	19.96						17.5
m1-m3	Length	28.18	27.40	22.7-32.55	26.10 (n=26)	24.98-25.65 (n=2)	28.32						23.0
	Width	19.38	17.62	11.22-18.36	13.65 (n=25)	14.57-15.01 (n=2)	15.64						17.1 (basal part)
p2-p4	Height	16.24	18.84	15.53-36.71	24.31 (n=25)	28.62-30.15 (n=2)	21.32						24.8
	Length	42.66	42.34	27.27-38.97	34.65 (n=18)	35.18-35.55 (n=2)	39.25						32.0
m1-m3	Width	19.28	17.14	10.72-17.35	13.64 (n=19)	14.42-15.40 (n=2)	15.51						14.8 (basal part)
	Length	18.24	22.08	14.28-46.76	29.08 (n=17)	27.03-27.25 (n=2)	21.76						45.5
m1-m3	Length	52.36	52.64	44.42-55.96	49.73 (n=6)	52.26-55.06 (n=2)	94.61						
	Length	92.40	91.28	77.96-95.89	82.59 (n=12)	82.86-83.60 (n=2)	90						

Materials from the hominid site at Jianshi in Hubei Province are attributed to *Leptobos* sp. based on the cross section of horn core (Zheng, 2004). Figures presented by Zheng (2004:307, fig. 5.87 b–f) show that Jianshi materials are similar to *L. brevicornis* in having strong metaconid and deep hypoflexid in p4, and constrictions along the buccal main cusps of m3.

Materials from Zhongdian in Yunnan Province are attributed to *Leptobos* sp. based on the size of the teeth and occlusal surface morphology similar to the specimens of *L. brevicornis* (*L. vallisarni*) from Layihai (Ma et al., 2004). The description and illustrations (Ma et al., 2004:255, fig. 8A–B) show that paraconids and parastylids are developed, metaconids do not connect with paraconids in p3 or p4, basal pillars present in m1–m3, and buccal main cusps of m3 are rounded with constrictions at the preprotocristid and prehypocristid; however, more evidence is needed to determine what species the Zhongdian materials belong to.

Two species of the genus *Leptobos*, *L. brevicornis* and *L. crassus*, have been reported from China since Qiu (2004) revised the genus (Chi, 1975; Hu and Qi, 1978; Jia and Wang, 1978; Zheng et al., 1985; Li and Feng, 2001; Fang et al., 2004; Qiu et al., 2004; Zheng, 2004; Dong, 2008). Duvernois (1990) established the subgenera *Smertiobos* and *Leptobos* based on different curvatures of their horn cores. All of the *Leptobos* fossils previously reported from China belong to *Smertiobos* (Dong et al., 2009). *L. brevicornis* is similar to the subgenus *Smertiobos* and different from the subgenus *Leptobos* in having developed hypoconid and deep hypoflexid in p4, weak metastylid in m2 and constrictions along buccal main cusps of m2 and m3.

The new specimen from Longdan (V 18532) is preserved in a stratum within the Wucheng Loess whose geologic age is estimated to be 2.55–2.16 Ma based on paleomagnetic dating and 2.2 Ma based on mammalian biostratigraphy (Qiu et al., 2004). The Longdan strata are older than those at other known localities yielding *Leptobos brevicornis*, such as Gongwangling (1.15 Ma) and Yunxian (1–0.73 Ma) (An et al., 1990; Li and Feng, 2001). The Longdan fauna probably inhabited an environment resembling cold steppe (Qiu et al., 2004). Similar environments have been inferred for the Bajiazui fauna and Yunxian hominid site, whereas the Renzidong, Tuoqidong and Gongwangling strata were probably deposited in warmer paleoenvironments (Chi, 1975; Li and Feng, 2001; Fang et al., 2004; Wang and Xue, 2006; Dong et al., 2009).

4 Discussion of the wounds

A hole that appears to represent a wound pierces the anterior part of the mandible (V 18532), located close to the right canine (Fig. 2A). The hole is subround-shaped from occlusal view (length: 9.9 mm, width: 11.6 mm, length measured from the anteroposterior direction of cheek teeth), and the loss of bony matter is almost 7.7 mm thick at the interior lingual wall of the hole, which is measured from the left complete part. Along the labial rim of the hole, loss

of bony matter and cracks on the bone slice appear to be evident (Fig. 2B). Another hole is situated posteroventrally to the subround hole, which is oval-shaped (length: 5.3 mm, width: 7.2 mm). Two additional round pits are located in the ventral border of the mandible, below the posterior margin of the mental foramen, whose diameters are about 4.4 and 2.5 mm.

The curvature of the interior lingual wall of the subround hole indicates that a curved object is the wound maker. Bovids use horns as intraspecific weapons, and living bovids with horns shaped like those of *Leptobos* normally use them for wresting and head-on ramming in the context of fighting (Lundrigan, 1996). The horns would probably not have come into contact with the mandible during fighting, and it is unlikely for a horn to contact with the mandible at an angle that would result in a dorsoventral hole through the anterior part of the mandible. Furthermore, the dimension of the subround hole is too small to match those of bovid horns, even for those of small antelopes.

The subround hole may be interpreted as the result of stabbing by the conical canine, which would imply that one carnivore was the attacker on *Leptobos*. A rhinocerotid hemimandible, *Iberotherium rexmanueli zbyziewskii*, bitten by *Amphicyon giganteus* is found in the Middle Miocene of Portugal (Antunes et al., 2006). The round pits left on the ventral

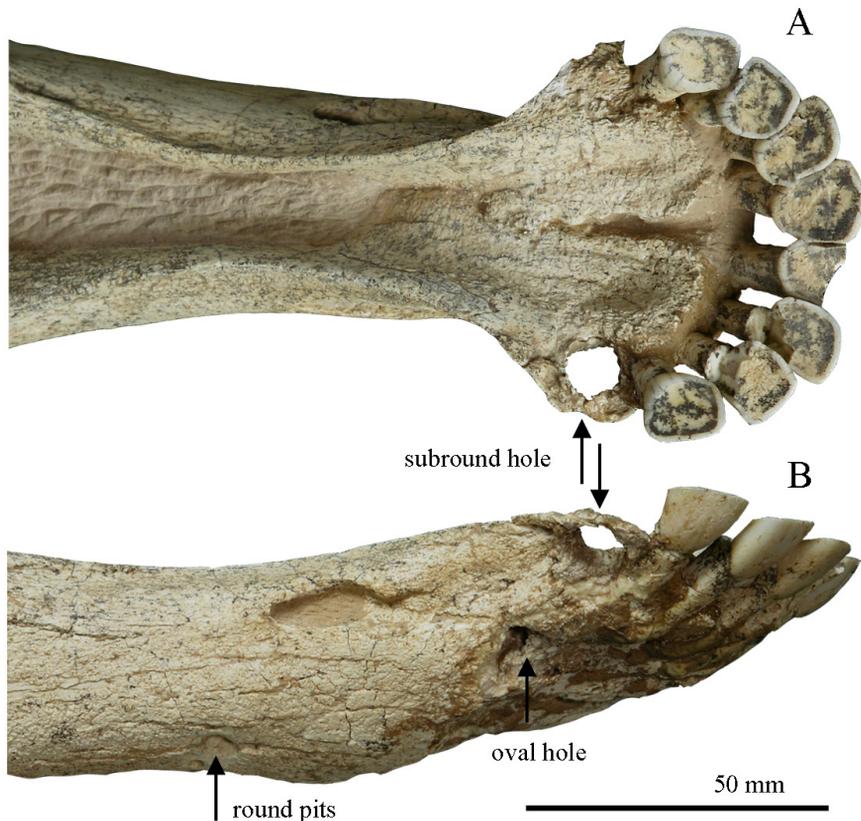


Fig. 2 Wounds in the mandible (IVPP V 18532) of *Leptobos brevicornis*
A. occlusal view; B. buccal view

border of the mandible of *Leptobos* are similar to those left on *Iberotherium*, which could be interpreted as the result of shallow bites that were cushioned by soft tissue overlying the bone. No healing marks, such as rough and granular surface textures or new bone formations near the border of the wound (Deng and Tseng, 2010), occur around the subround hole.

There are 17 species of carnivores in the Early Pleistocene mammalian fauna from Longdan (Qiu et al., 2004; 2009). Fig. 3 is drawn for comparison of the ratio between the upper canines of known carnivores from Longdan and the subround hole. The size of the upper canine of the attacker should be larger or close to that of the subround hole. Four carnivores meet the condition of the attacker, which are *Lynx shansius*, *Panthera palaeosinensis*, *Sivapanthera linxiaensis* and *Crocota honanensis* (Fig. 3). However, *L. shansius* can be excluded from the attacker due to the reason that *L. shansius*, with the body mass of 12.86 kg less than 21.5 kg, cannot feed on an adult *Leptobos*, whose body mass is about 304 kg, based on the energetic constrains (Carbone et al., 1999; Deng, 2009).

Because the measurements of the canine of carnivores are usually taken along the alveolus or the separation between the dentine and enamel, more detailed measurement is

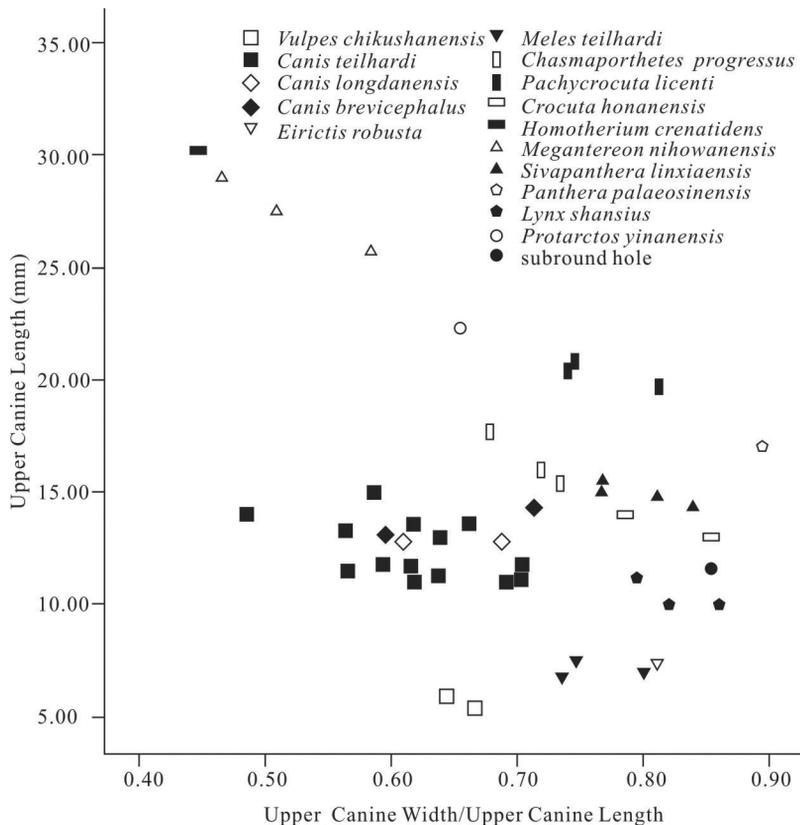


Fig. 3 Comparison of the width and length between upper canines of known carnivores from Longdan and subround hole
Data from Qiu et al. (2004, 2009)

taken, which is to measure the width of the canine when the length is nearly 11.60 mm. The data of *Sivapanthera* and *Panthera* seem to perfectly match the dimension of the subround hole, better than that of *Crocuta* (*Panthera palaeosinensis* (IVPP V 13538): Length 11.58 mm, Width 9.85 mm, Height 16.55 mm; *Sivapanthera linxiaensis* (V 13537): Length 11.60 mm, Width 9.88 mm, Height 12.70 mm; *Crocuta honanensis* (V 13535): Length 11.68 mm, Width 7.94 mm).

The position of the wound brings to mind the predatory behavior of modern big cats (Kruuk, 1972; Turner and Antón, 1997). Big cats can tackle large animals by wrestling with them, seizing any chance to suffocate them with throat bites or muzzle clamps, and subsequently feeding after a prey animal has been choked to death; however, for dogs and hyenas, the only feasible method of killing large prey is to attack on the abdomen or anus, to attempt to bite on the muscles of abdomen and feet, and to kill the prey by eating it (Kruuk and Turner, 1967; Kruuk, 1972; Turner and Antón, 1997). In contrast to fatal suffocation in big cats, a wounding and weakening strategy is adopted by dogs. Eating the viscera of the prey is to get the flesh of high energy immediately, whereas biting on the feet is to reduce the locomotive ability of the prey efficiently. This type of predatory behavior would be unlikely to target the anterior part of the mandible or involve enough force to pierce the bone. The behavior of scavenging may be excluded, considering that small numbers of tooth imprints are kept on *Leptobos* and only the anterior part of the right mandibular body preserves them. Consequently, *Crocuta honanensis* can be excluded from the predator.

Nothing indicates that there are more than one individual or more than one single species biting on *Leptobos*. The predator is probably an individual of either *Sivapanthera* or *Panthera*. *Panthera leo* is known to feed on African buffalo (*Syncerus caffer*) in Serengeti (Kruuk and Turner, 1967; Sinclair et al., 2003), and a recent study showed that the hunting strategy of the giant Plio-Pleistocene cheetah, *Acinonyx pardinensis* was probably more similar to that of pantherine cats than that of the living cheetah based on cranial musculoskeletal anatomy and average body mass (Cherin et al., 2014). Carnivores are dominant over herbivores in the Early Pleistocene of Longdan (Qiu et al., 2004), and thus *Leptobos brevicornis* may have suffered a heightened predation rate.

5 Conclusion

The new specimen from Longdan (V 18532) is attributed to *Leptobos* based on the following characters: in p3 and p4, parastylids and paraconids are developed, and metaconids do not connect with paraconids; in lower molars, metastylids are weak, and buccal main cusps are rounded. The new specimen can be more specifically identified as *Leptobos brevicornis* because the skulls of this species have previously been found at the same locality. Within the classification of Duvernois (1990), *L. brevicornis* can be attributed to the subgenus *Smertiobos* based on the morphology of the lower cheek teeth. *L. brevicornis* is similar to *L.*

crassus in the size and topology of lower cheek teeth, and may be different from *L. crassus* in having deep hypoflexid in p4.

The wounds preserved in the anterior part of the mandible (V 18532) are interpreted as resulting from predatory behaviors by a carnivore. The subround hole is caused by a stab from a canine. The predator is probably one individual of *Sivapanthera linxiaensis* or *Panthera palaeosinensis* based on the size of upper canine. The interpretation of the wound indicates that the predatory behavior, using muzzle clamps to suffocate preys, may have already occurred in large felines during the Early Pleistocene.

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甘肃龙担早更新世丽牛下颌骨新材料及其对虎亚科捕食策略的证据

——龙担哺乳动物群补充报道之四

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摘要: 记述了甘肃龙担早更新世哺乳动物群中首次发现的一件丽牛(*Leptobos*)下颌骨, 这是我国目前发现的保存最为完整的丽牛下颌骨材料。依据p3、p4的下前尖与下前附尖分离, 下后尖向后延伸不与下前尖愈合, m1-m3的下后尖和下内尖冠面形状近于圆形, 连续发育有下外附尖, m2的下后附尖弱, m2和m3的下原尖和下次尖有前后向收缩等特征, 以及相同地点产出的短角丽牛头骨, 将新材料归为*Leptobos brevicornis*。新材料补充了丽牛的下颌形态特征: 下颌骨水平支窄长, 齿槽间隙对颊齿齿列的比例大, 前臼齿列短, 水平支与垂直支之间的夹角约为120°, 下颌角约呈90°。这件下颌骨的前端保留有食肉动物袭击的痕迹, 该伤痕可以被解释为由大型虎亚科动物攻击丽牛时犬齿刺穿形成。这样的骨骼证据表明, 攻击猎物口鼻部而使猎物窒息死亡, 这种与现生大型猫科动物类似的捕食行为在早更新世的虎亚科动物中已经出现。

关键词: 龙担哺乳动物群, 早更新世, 丽牛, 虎亚科, 捕食行为

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