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An extraordinary pattern of ruminant molars and associated cervids from the Pleistocene of Wushan, Central China

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Abstract Selenodont cheek teeth are diagnostic characteristics of ruminants, in which the upper molars are usually composed of four selenodont main cusps. During a local housing construction at Yantouxi near the Longgupo Site at Miaoyu Town of Wushan County in Chongqing Municipality of Central China, a mandibular fragment with extraordinary molars composed of five main selenodont cusps was uncovered with association of the Pleistocene *Muntiacus* sp. and *Cervus* (*Rusa*) *unicolor*. The morphological study shows that it is a new pattern of selenodont molars different from five-cusped upper molars of some tylopods such as anthracotheres and xiphodontids from the Paleogene as well as cainotheriids from the Oligocene to Miocene. The fifth selenodont cusp is interpreted as an overdevelopment of cingulum around the anterior lingual base of the protocone. The taxonomic status of the animal is placed temporarily in Muntiacinae as *Muntiacus* ? *huangi* sp. nov.

Key words Wushan, Chongqing, Pleistocene, ruminant, Artiodactyla, selenodont

1 Introduction

Miaoyu Town of Wushan County in Chongqing Municipality of Central China is noted for Longgupo Site. Locality 1 yielded the Early Pleistocene mammalian fauna and associated controversial hominins and Paleolithic artifacts (Huang et al., 1991, 1995, 1996; Schwartz and Tattersall, 1996; Boëda and Hou, 2011; Boëda et al., 2011). Locality 2, Longdong or Baotansi, about 162 m southwest of Locality 1 yielded the Late Pleistocene small mammal fauna (Zheng, 1993) and Locality 3, Shuimuoxi, yielded a mastodon. During a local housing construction at Yantouxi in 2008, some selenodont ruminant materials were uncovered from the deposits of the construction base. The locality is situated about 482 m east of Locality 1 of the Longgupo Site and about 620 m east of Locality 2. The deposits yielding fossils are mainly red clay, sometimes calcite cemented, with a thickness of 1-2 m and cover directly on the bedrock of the Triassic limestone. And the materials are uniquely ruminants in which there is a very peculiar

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specimen with five main cusps in the upper molars, or more precisely, three main selenodont cusps in the anterior lobe of the upper molars. The upper molars of ruminants are usually composed of four main selenodont cusps, two in anterior lobe and the other two in posterior lobe (Heintz, 1970; Janis and Scott, 1987; Gentry et al., 1999). The five cusped selenodont or selenobunodont upper molars are usually seen in some Tertiary tylopods, particularly in anthracotheres and xiphodontids from the Paleogene as well as cainotheriids from the Oligocene to Miocene (Viret, 1961). Here we describe the Pleistocene selenodont ruminant materials from Yantouxi locality and discuss their taxonomic status. The dental terminology follows that by Dong (2004) for cervids and that of Gentry and Hooker (1988) for artiodactyls. The studied specimens are housed in the Three Gorges Institute of Paleoanthropology, China Three Gorges Museum, Chongqing, China.

2 Systematic paleontology

Mammalia Linnaeus, 1758
Artiodactyla Owen, 1848
Ruminantia Scopoli, 1777
Cervoidea Gray, 1821
Cervidae Gray, 1821
Muntiacinae Pocock, 1923
***Muntiacus* Rafinesque, 1815**
***Muntiacus* ? *huangi* sp. nov.**

(Fig. 1)

Holotype A left maxillary fragment with P3-M3 (CPV 62), housed in the Three Gorges Institute of Paleoanthropology, China Three Gorges Museum, Chongqing, China.

Type locality Yantouxi, Xincheng Village, Miaoyu Town, Wushan County, Chongqing Municipality, China.

Type stratum Red clay of 1-2 m thick with occasional calcite cementation, Pleistocene.

Etymology The species is nominated in honor of Professor Huang Wanbo who worked a lot in the region and collected the specimen.

Diagnosis A small ruminant with a size slightly larger than a common muntjak. The upper molars are composed of five main selenodont cusps with three of them in the anterior lobe.

Description The type specimen CPV 62 (Fig. 1) is an adult maxillary fragment with two last premolars and complete three molars (see Table 1 for measurements). The cheek teeth are all brachyodont.

The occlusal outline of P3 is nearly semi-circle. It is composed of two main selenodont cusps, the protocone on lingual side and the paracone on the buccal. The parastyle is very developed and metastyle is moderately developed, but the postparacrista is elongated that

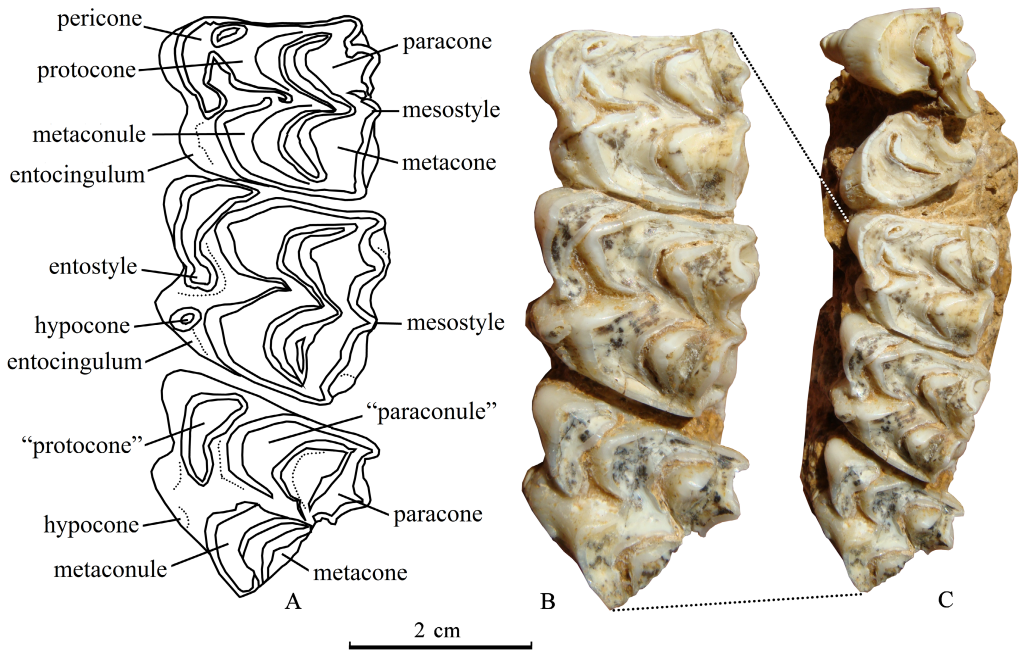

Fig. 1 Occlusal view of left upper cheek teeth of *Muntiacus* ? *huangi* sp. nov.
A. terminological illustration of the unusual molars from B; B. enlarged occlusal view of molar row from C; C. occlusal view of the holotype (CPV 62). Note that the anterior lingual cusp and the middle cusp of the molars are temporarily interpreted as pericone and protocone respectively which might also be regarded as "protocone" and "paraconule" accordingly as illustrated in fig. 9.1 by Gentry and Hooker (1988) for dental nomenclature of artiodactyls cheek teeth

the length of buccal side of the tooth is longer than that of the lingual one. A fold similar to neocrista is present on the buccal wall of the protocone. There are no cingula around the base of lingual cusp. The morphology of P4 is similar to but simpler than that of P3. It is also composed of two main cusps as in P3, but the protocone has no fold, parastyle is not very developed.

The most remarkable character of the specimen is the composition of the anterior lobe of upper molars, particularly an extra main cusp on the lingual side (Fig. 1). The lingual side of the anterior lobe is usually composed of a main cusp termed as protocone, but the twin cusped lingual side of the anterior lobe of the upper molars in Yantouxi specimen makes it difficult to term them. As a temporary way to describe the specimen in the present study, the one the closest to the tongue is called the presumed pericone and the one in the middle of the anterior lobe the purported protocone.

The M1 is composed of five main cusps and appears in two lobes. The anterior lobe is composed of three main selenodont cusps, with paracone on the buccal side, presumed pericone on the lingual side and purported protocone in the middle. The middle part of the lingual wall of purported protocone is somewhat fused with the middle part of the buccal wall of the presumed pericone in occlusal view. The precingulum and neocrista are absent.

The posterior crest of the presumed pericone is fused with the anterior part of the developed entostyle. The parastyle is developed, and the mesostyle less developed. The posterior lobe is composed of two main cusps, metacone and metaconule. The entocingulum is developed but the postcingulum is not evident. The metastyle is weak.

The morphology of M2 is similar to that of M1, three main cusps in the anterior lobe and two main cusps in the posterior one. But the purported protocone is not fused with presumed pericone in occlusal view, and a small, but evident hypocone is present on the entocingulum.

The morphology of M3 is similar to that of M2, but the entostyle is more developed and fused more with presumed pericone; and both entocingulum and hypocone are very weak. The buccal wall of metacone is partially broken.

Comparison and discussion The dimensions of the described upper molars on CPV 62 are larger than those of *Muntiacus* sp. (CPV 63.1-2) from the same locality (Table 1), they are also larger than those of extant *Muntiacus* sp. specimen (OV 949) and those of *M. bohlini* (RV 40002) from the Lower Pleistocene at Locality 18 of Zhoukoudian Site (Teilhard de Chardin, 1940). They are smaller than those of *Dorcabune liuchengense* from Liucheng *Gigantopithecus* Cave (Han, 1974), close to those of *Dorcabune progressus* from the Upper Miocene of Lufeng *Lufengpithecus* Site (Han, 1986) and *Dorcabune* cf. *D. progressus* from the Upper Miocene of Yuanmou *Lufengpithecus* Site (Pan et al., 2006), slightly larger than those of *Dorcatherium naui* from the upper part of Lower Miocene of La Romieu in France (Ginsburg and Bulot, 1987), but much larger than those of *Dorcatherium orientale* from the Middle Miocene of Sihong (Qiu and Gu, 1991) and *Yunnanotherium simplex* from Lufeng *Lufengpithecus* Site (Han, 1986). The more selenodont and less bunodont main cusps on upper molars distinguish the Yantouxi specimen from those of *D. progressus* (Yan, 1978; Han, 1986) and *Dorcabune* cf. *D. progressus* (Pan et al., 2006) although their dimensions are close to each other.

As mentioned above, the morphology of the upper molars figures the most peculiar characters of the specimen. From the first to the last upper molars are all composed of five main crescent cusps in two lobes, three in the anterior lobe and two in the posterior. The presumed pericone is like an overdeveloped entocingulum in the anterior lobe, it is termed as “pericone” or “pericone shelf” for the upper molars in eutherians (Zhou et al., 1975) based on the “tubercular-sectorial theory” by Osborn (1907) and the crescent cusp between the paracone and presumed pericone should be consequently termed as “protocone”. The present authors have never seen such structure in cervids. It is somewhat close to a developed entocingulum on the upper molars of *Dorcatherium naui* from the upper part of Lower Miocene of La Romieu in France (Ginsburg and Bulot, 1987). The entocingulum around the protocone of the upper molars in genus *Dorcatherium* is well developed (Viret, 1961). The geological distribution of the *Dorcatherium* ranges from the Miocene to the Pleistocene (Han, 1986). The dimensions of the Yantouxi specimen are within the range of those of compared tragulids in Table 1, the Yantouxi specimen is therefore likely a derived tragulid from this perspective. Beside the extra cusp, the morphology of Yantouxi specimen is more close to that of Muntiacinae.

Table 1 Measurements of upper cheek teeth of *Muntiacus* ? *huangi* sp. nov. from Yantouxi and comparison with those of other related taxa (mm)

	Muntiacus ? *huangi* sp. nov.	*Dorcatherium orientale*	*Dorcatherium naui*	*Dorcabune progressus*	*Muntiacus* sp.	*Muntiacus* sp.	*Muntiacus* sp.	*M. bohlini*
	CPV 62	Qiu & Gu, 1991	Ginsburg & Bulot, 1987	Han, 1986	CPV 63.1	CPV 63.2	OV 949	RV 40002
P3 L	11.4	6.48-7.80	12.2	15.0	7.36		9.62-9.66	8.52-8.76
P3 W	13.8	3.77-5.80	8.2	11.0	8.2		11.56-11.72	9.84-10.18
P3 H	9.5			10.5	8.6		5.92-6.72	8.08-8.98
P4 L	10.5	5.85-7.10		12.0	7.96		8.24-8.54	9.02-10.02
P4 W	13.7	6.14-7.72		9.8-11.0			11.48-11.88	9.28-10.58
P4 H	5.9			8.0-8.4	8.8		5.38-6.3	9.66
M1 L	13.54	6.30-8.06	10.0-10.4	11.4	9.92	12.6	10.26-10.86	11.22-12.16
M1 W	11.96	7.70-10.24	11.4-11.5	11.8	12.2		11.94-11.96	11.02-11.28
M1 H	8.52			8.2	7.7	8.1	3.58-3.68	5.96-8.0
M2 L	14.54	7.20-9.60	10.6-12.1	14.5-15.0	11.1	11.2	11.96-12.02	11.98-12.44
M2 W	17.3	8.90-11.67	12.6-14.6	16.1-17.0	13.1	13.0	13.08-13.18	12.38-13.18
M2 H	9.52			9.0-12.0	8.62	9.1	3.72-4.84	10.36-10.42
M3 L	≥14.3	7.35-8.58	11.7-13.7				12.54-12.64	12.64-12.76
M3 W	17.1	9.56-11.12	13.0-15.0				13.06-13.5	11.82-12
M3 H	10.42						4.34-4.88	9.32-11.64
M1-3 L	43						33.82-34.28	36.2-36.18

The structure of Yantouxi specimen is also close to that of the upper molars of their chronologically and phylogenetically remote relatives, some tylopods from the Eocene to Oligocene, such as anthracotheres *Brachyodus*, *Parabrachyodus*, *Bothriodon* (Fig. 2A), and xiphodontids *Xiphodon* (Fig. 2B), etc. Their molars are also composed of five main selenodont cusps and three of them are in the anterior lobe (Fig. 2A-B). The anterior lingual and middle cusps are termed as protocone and protoconule respectively by Viret (1961) but as protocone and paraconule by Gentry and Hooker (1988). There are precingulum and entocingulum around the lingual cusp in the anthracotheres and xiphodontids but there is no cingulum around the lingual cusp in Yantouxi specimen. Furthermore, the premolars in Yantouxi specimen have almost semicircular occlusal outline and with no entocingulum, but those of the anthracotheres and xiphodontids have nearly triangular occlusal outline and with developed entocingulum. In addition, the dimensions of the upper molars of anthracotheres and xiphodontids are much larger than those of the Yantouxi specimen.

The molars with five main cusps are also seen in other tylopods such as rabbit-sized cainotheriids from the Eocene to Miocene, e.g. *Pleisiomeryx*, *Oxacron*, *Caenomeryx*, *Cainotherium*, etc. But the fifth cusp is in the posterior lobe rather than in the anterior lobe as in anthracotheres and xiphodontids (Fig. 2C). The anterior buccal cusp is still termed as paracone and the posterior buccal one metacone as usual, but the anterior lingual cusp is termed as protoconule, the posterior lingual one protocone and the posterior middle one metaconule (Viret, 1961). The protocone migrated from the anterior lobe to the posterior. The dimensions of the upper molars of cainotheriids are much smaller than those of the Yantouxi specimen.

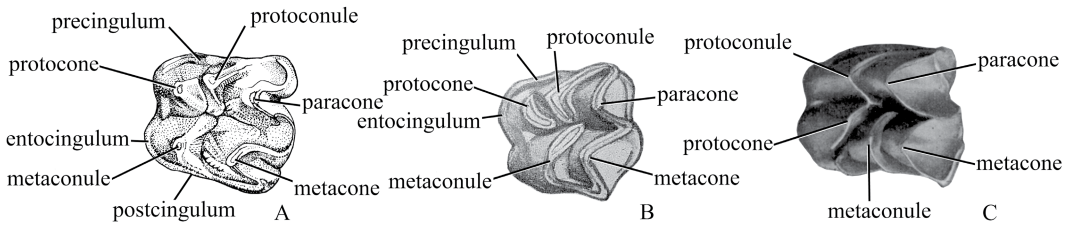

Fig. 2 Some upper molar patterns with five main cusps
A. *Bothriodon velaunum* from the Oligocene of France, the protoconule is smaller than protocone;
B. *Xiphodon gracile* from the Eocene of Europe, the protoconule is larger than protocone;
C. *Cainotherium* sp. from Oligocene of Europe. Based on left M2, not to scale (after Viret, 1961)

***Muntiacus* sp.**

(Fig. 3)

Materials A left maxillary fragment with P3-M2 (CPV 63.1), a right maxillary fragment with broken M1-M2 and complete M3 (CPV 63.2), a right mandibular fragment with m1-m3 (CPV 63.3), a left mandibular fragment with m1-m3 (CPV 63.4).

Remarks All available specimens are cheek teeth with P2 and p2-4 missing (Fig. 3). The cheek teeth are all brachyodont.

The available upper premolars are only a P3 and a P4 in the left maxillary fragment CPV 63.1. The P3 is composed of two equal sized main cusps on the lingual side and a third main

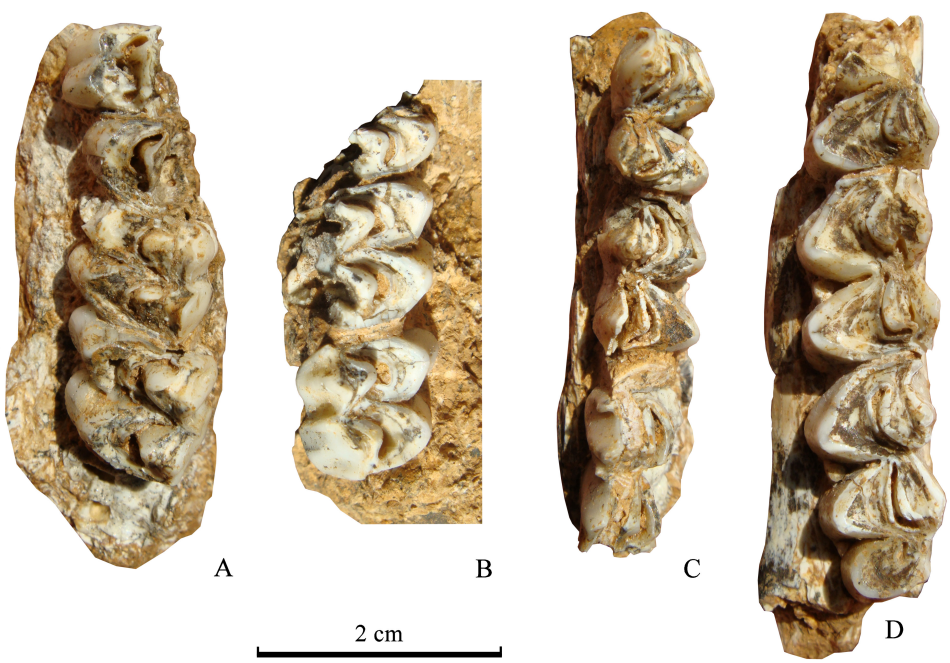

Fig. 3 Occlusal view of cheek teeth of *Muntiacus* sp. from Yantouxi
A. left maxillary fragment with P3-M2 (CPV 63.1); B. right maxillary fragment with broken M1-M2 and complete M3 (CPV 63.2); C. right mandibular fragment with m1-m3 (CPV 63.3);
D. left mandibular fragment with m1-m3 (CPV 63.4)

cusp on the buccal side, and some moderate enamel folds are present on the buccal wall of lingual main cusps. The P4 is composed of two main cusps, one on the lingual side and another on the buccal, and a weak enamel fold is present on the buccal wall of lingual main cusp.

The available upper molars are a nearly complete M1 and a complete M2 in the left maxillary fragment CPV 63.1, and a broken posterior lobe of M1, an incomplete M2 and a complete M3 in the right maxillary fragment CPV 63.2. The M1 is composed of four main cusps, the accessory elements such as cingula, neocrista and entostyle are absent. The morphology of M2 is nearly the same as M1, but the size is larger. The morphology of M3 is similar to that of M2, but the neocrista is present and moderately developed and the size of the tooth is between that of M1 and M2. The measurements of the upper cheek teeth are in Table 1.

The available lower cheek teeth are a nearly complete m1, a complete m2 and a broken m3 in CPV 63.3, and a posterior lobe of m1, a complete m2 and a complete m3 in CPV 63.4. The m1 is composed of four main cusps, the precingulid and ectostylid are present but *Palaeomeryx* fold, ectocingulid and postcingulid are absent. The m2 is nearly the same as m1 except its larger size. The m3 is composed of three lobes, the anterior and middle ones are similar to m2, the posterior lobe is much smaller. The measurements of the lower cheek teeth are in Table 2.

The dimensions of the upper cheek teeth of the described specimens are evidently smaller than those of *Muntiacus* ? *huangi* sp. nov. from the same locality, slightly smaller than those of extant *Muntiacus* sp. (OV 949) and those of *M. bohlini* (RV 40002) from the Lower Pleistocene at Locality 18 of Zhoukoudian Site (Table 1). Table 2 shows that the dimensions of the lower cheek teeth of the described specimens are close to those of *Muntiacus* sp. from the Late Pleistocene cave deposits of Gongjishan in Chongzuo (Dong et al., 2014b), slightly larger than those of *Muntiacus* sp. from the Early Pleistocene cave deposits of Longgupo Locality 1 (Huang et al., 1991) and Longgudong (Chen, 2004).

Table 2 Measurements of the lower cheek teeth of *Muntiacus* sp. from Yantouxi and comparison (mm)

	CPV 63.3	CPV 63.4	Longgupo Loc. 1 [1)]	Longgudong[2)]	Gongjishan[3)]
m1 L	13.1		12.0	10.1-11.5	13.3
m1 W	8.82	9.6	7.2	6.9-7.9	9.59
m1 H	8.8	8.6			10.64
m2 L	13.8	13.4	12.1	11.0-13.2	13.83-15.1
m2 W	10.1	10.2	7.8	7.7-8.2	9.62-10.85
m2 H	10	8.6			12.15-13.46
m3 L		17.7	18.0	14.2-17.5	16.72-18.38
m3 W		9.8	7.3	7.2-8.5	9.02-9.19
m3 H		9.9			9.91-11.25

1) Huang et al., 1991; 2) Chen, 2004; 3) Dong et al., 2014b.

Cervinae Goldfuss, 1820

***Cervus* Linnaeus, 1758**

***Cervus* (*Rusa*) Smith, 1827**

***Cervus* (*Rusa*) *unicolor* (Kerr, 1792)**

(Fig. 4)

Materials A left broken antler base (CPV 64.1), a left maxillary fragment with broken P4-M3 (CPV 64.2), a right maxillary fragment with P4-M3 (CPV 64.3), a right incomplete mandible with p3-m3 (CPV 64.4), a right mandibular fragment with p4-m3 (CPV 64.5), and a right mandibular fragment with p3-m3 (CPV 64.6).

Remarks The specimen CPV 64.1 (Fig. 4A) is a left shed adult antler base. The burr is broken, but the medial part is preserved. It shows that its cross section is oval when complete, and its thickness measures 9 mm, its maximal and minimal diameters on the preserved part measures 66 and 52 mm respectively, the values should be a little greater when the specimen is complete. The length from the burr to the distal margin of the first bifurcation is 90.8 mm, the angle of the first bifurcation more than 80°, similar to that of *Cervus* (*Rusa*) *unicolor* from Yanjinggou (formerly spelled as Yenchingkou) described by Colbert and Hooijer (1953) but larger than that of *C.* (*R.*) *yunnanensis* from the Early Pleistocene of Yuanmou Formation described by Lin et al. (1978), the maximal and minimal diameters of antler base above the burr measure 56.6 and 38.3 mm respectively, similar to that of Yanjinggou specimens; the maximal and minimal diameters of the main beam above the first bifurcation are 43.8 and 30.6 mm respectively, also similar to that of Yanjinggou specimens. The cross sections of the main beam are somewhat fan-shaped above the bifurcation with round edge on the medial side and roughly oval at distal part. The ornamentation is mainly developed furrows and ridges along the growth direction of the antler. The general appearance of the specimen CPV 64.1 is closer to Yanjinggou specimens than to Yuanmou specimen.

The P4 is composed of two main cusps, one on the lingual side and another on the buccal. The accessory elements such as cingula and enamel folds are absent (Fig. 4B-C).

The M1 is heavily worn on both specimens and only the outlines of the crown can be observed which indicate the M1 is composed of four main cusps. The M2 is clearly composed of four main cusps, and the accessory elements such as cingula and enamel folds are absent. The morphology of M3 is similar to that of M2, the only difference is that the M3 has a weak entocingulum (Fig. 4B-C).

The p3 is composed of five cusps, with paraconid, metaconid and entoconid on the lingual side, protoconid and hypoconid on the buccal side; paraflexid is absent, trigonid basin is widely open, entoflexid and talonid basin are moderately open; entoflexid is present but moderately developed. The p4 is also composed of five cusps, but the metaconid extends so forward that premetacristid completely closed the trigonid basin to make the anterior lobe molarized; the hypoflexid and entoflexid are developed and they divided the tooth into two lobes; the posterior lobe is much less developed than the anterior (Fig. 4D-F). The morphology of Yantouxi lower premolars is similar to both *Cervus* (*Rusa*) cf. *C.* (*R.*) *unicolor* and *C.* (*R.*) *yunnanensis* from the Early Pleistocene of Longgudong of Jianshi (Chen, 2004).

The m1 is composed of four main cusps in two lobes; the accessory elements such as precingulid, ectocingulid and ectostylid are weak, and postcingulid and *Palaeomeryx* fold are absent. The morphology of m2 is very similar to that of m1, but size is larger. The m3 is

composed of three lobes, the anterior and middle ones are similar to m2, but the posterior one is much smaller; in addition, the precingulid is very weak on CPV 64.4, weak on CPV 64.5 and well developed on CPV 64.6 (Fig. 4D-F).

Table 3 shows that the dimensions of the cheek teeth of Yantouxi specimens are close to those of *C.* (*R.*) *yunnanensis* from the Early Pleistocene of Longgudong of Jianshi (Chen, 2004), slightly smaller than those of the Pleistocene Yanjinggou *C.* (*R.*) *unicolor* specimens and extant *C.* (*R.*) *unicolor* specimens from Yunnan (Colbert and Hooijer, 1953), as well as *Cervus* (*Rusa*) cf. *C.* (*R.*) *unicolor* from the Early Pleistocene of Longgudong of Jianshi (Chen, 2004).

Table 3 Measurements of the cheek teeth of *Cervus* (*Rusa*) *unicolor* from Yantouxi and comparison (mm)

	Cervus (*Rusa*) *unicolor*			*Cervus* (*R.*) *unicolor*	*C.* (*R.*) cf. *C.* (*R.*) *unicolor*	*Cervus* (*R.*) *yunnanensis*
	CPV 64.2	CPV 64.3		AMNH 43061/2[2)]	V 13469[3)]	V 13468[3)]
P4 L	10.9	12.1			13.9-16.4	12.1-15.5
P4 W	17.7	17.7			17.4-21.9	16.6-20.0
P4 H	7.8	10				
M1 L	15.1	15.3			17.4-24.4	17.0-21.0
M1 W	23.2	25			20.1-25.5	16.9-21.4
M1 H	9.6	7.3				
M2 L	20.9	19.1			23.2-26.7	20.0-24.3
M2 W	23.2	22.1			21.0-27.0	20.0-25.6
M2 H	10.9	9				
M3 L	19.2	20			24.0-28.6	18.9-23.9
M3 W	21.8	20.9			24.2-29.0	18.2-26.5
M3 H	12.2	16.2				
M1-3 L	55.5	52.3		68-69		
	CPV 64.4	CPV 64.5	CPV 64.6	AMNH 18799[2)]	V 13469[3)]	V 13468[3)]
p3 L	14.9		18.5		17.8-19.7	16.1-20.0
p3 W	9.1		12.1		9.8-12.0	10.2-12.0
p3 H	8.7		10.6			
p4 L	16.4	15.9	17.5		18.3-21.0	16.6-18.2
p4 W	10.2	9.3	12.6		11.1-14.0	9.2-11.8
p4 H	12.5	7	14.2			
m1 L	17.5	17.6	19.1	21.5[1)]	17.9-23.9	17.8-23.4
m1 W	13.6	13.8	16.2		12.2-16.4	10.7-13.3
m1 H	9.2	5.6	12.6			
m2 L	22.8	19.7	27	25.2[1)]	22.7-28.3	20.5-25.8
m2 W	14.4	15.7	19.9		15.3-18.7	12.9-16.3
m2 H	11.3	8.6	16.5			
m3 L	31.2	28	35.2	32.0[1)]	32.9-37.8	26.7-30.8
m3 W	13.6	14.4	18.1		16.0-18.5	12.0-15.8
m3 H	14.7	8.8	17.2			
m1–3 L	69.8	70.5	84.7	76	80.6	70.1

Note: 1) The length of the molars was obtained by calculating the pixels on pl. 27 by Colbert and Hooijer (1953) because they provided only the length of m1-3 in their table 43; 2) Colbert and Hooijer, 1953; 3) Chen, 2004.

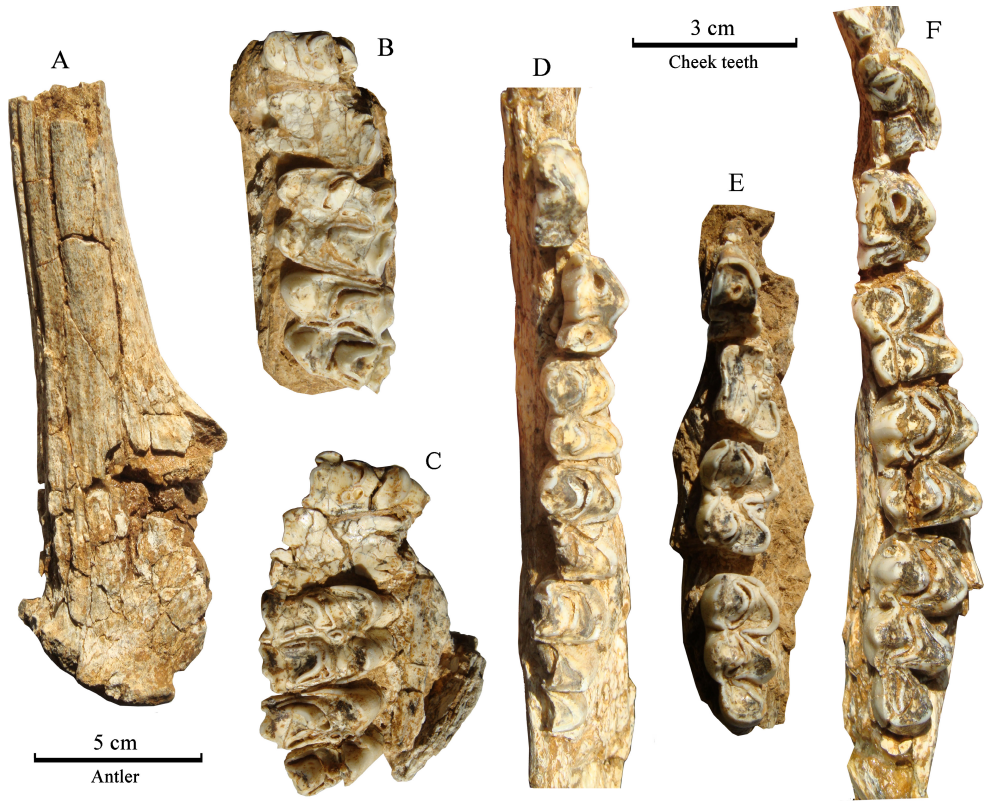

Fig. 4 *Cervus* (*Rusa*) *unicolor* from Yantouxi
A. antler base (CPV 64.1), medial view; B. left maxillary fragment with broken P4-M3 (CPV 64.2); C. right maxillary fragment with P4-M3 (CPV 64.3); D. right incomplete mandible with p3-m3 (CPV 64.4); E. right mandibular fragment with p4-m3 (CPV 64.5); F. right mandibular fragment with p3-m3 (CPV 64.6) All teeth are in occlusal view

3 Discussion and conclusion

Selenodont or selenobunodont upper molars can be grouped into two main categories according to the number of main cusps forming the molar crown: the four-cusped one as in most ruminants and five-cusped one as in some tylopods (Fig. 2). The latter category can be further divided into two types based on the position of the fifth cusp: the extra cusp located in the anterior lobe as one type and its location within the posterior lobe as another. The first type is mostly seen in anthracotheres and xiphodontids from the Paleogene, as well as in the Yantouxi specimen, and the second type in cainotheriids from the Oligocene to Miocene. The three cusps in the first type were termed from the lingual side to buccal side as protocone, protoconule and paracone respectively by Viret (1961). The protoconule of Viret was termed as paraconule by Gentry and Hooker (1988). And the first type can be further distinguished into two traditional patterns based on the size of the extra cusp: smaller protoconule or paraconule than protocone as one pattern and the inverse as another (Fig. 2A-B). Both patterns have cingulum or cingula around the base of the protocone. The Yantouxi specimen is similar to but

different from these patterns. The lingual cusp in the anterior lobe of Yantouxi specimen is more likely an overdeveloped entocingulum around the base of the protocone that explains the absence of normal cingulum around the lingual base of the anterior lobe in the traditional patterns (Fig. 1).

The earliest *Muntiacus* appeared in the Late Miocene (Dong, 2007; Dong et al., 2004, 2014a), the presence of *Muntiacus* sp. limits the Yantouxi deposits later than the Late Miocene. *Cervus* (*Rusa*) *yunnanensis* is limited in the Early Pleistocene, and *C.* (*R.*) *unicolor* ranges from the Early Pleistocene to the present. The presence of *C.* (*R.*) *unicolor* limits the Yantouxi deposits no older than the Early Pleistocene.

It is not impossible that the Yantouxi molars with five cusps are a pathological result or an atavism of a common ancestor of the early tylopods and ruminants. But the case of all three molars with the same pathological change is really rare, and it is even rare to be preserved as fossil and uncovered. The possibility of pathological variation is therefore very small.

To conclude, the Yantouxi five-cusped molar represent a new pattern of selenodont molars, whether it is a systematic pattern or pathologic one. The taxonomic status of the Yantouxi specimen with five-cusped molars is likely within Muntiacinae, probably *Muntiacus*. The geological age of the deposits is surely within the Pleistocene, and probably Early Pleistocene, based on the available evidences.

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重庆巫山更新世反刍类臼齿的新类型及伴生的鹿化石

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摘要：新月形颊齿是反刍类的鉴定特征之一，而反刍类的上臼齿通常由4个新月形主尖组成。2008年在重庆市巫山县庙宇镇新城村堰头溪地点的一建筑项目中从黏土质地基中挖掘出一件带有上颊齿的反刍类上颌骨残段，标本上的上臼齿由5个新月形主尖组成。伴生的其他动物有更新世麂属未定种(*Muntiacus* sp.)和黑鹿(*Cervus* (*Rusa*) *unicolor*)。形态学研究显示堰头溪标本的上臼齿代表一种新的新月形上臼齿类型，它不同于见于部分胼足类(tylopods)的5尖型上臼齿，例如古近纪的石炭兽类和xiphodontids以及分布于渐新世和中新世的真兽类。堰头溪标本上臼齿中的第五个主尖被诠释为原尖基部舌侧的齿带过度发育而成，与胼足类的舌侧主尖非同源关系。堰头溪标本代表一个新的种类，其分类位置暂定为麂亚科的麂属，即黄氏麂*Muntiacus* ? *huangi* sp. nov.。

关键词：重庆巫山，更新世，偶蹄目，反刍类，新月形齿

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