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Tapirus yunnanensis from Shuitangba, a terminal Miocene hominoid site in Zhaotong, Yunnan Province of China

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Abstract The fossil tapirid records of Late Miocene and Early Pliocene were quite poor in China as before known. The recent excavations of the terminal Miocene hominoid site (between 6 and 6.5 Ma) at Shuitangba site, Zhaotong in Yunnan Province resulted in the discovery of rich tapir fossils, which include left maxilla with P2-M2 and mandibles with complete lower dentitions. The new fossil materials can be referred to *Tapirus yunnanensis*, which represents a quite small species of the genus *Tapirus*. But *T. yunnanensis* is slightly larger than another Late Miocene species *T. hezhengensis* from Gansu, northwest China, both of which are remarkably smaller than the Plio-Pleistocene *Tapirus* species in China. The new fossils provided more information to define the species *T. yunnanensis* more precisely. Yunnan can be regarded as one of the centers of tapir evolution during the Mid-Late Miocene period, as quite a number of Mid-Late Miocene tapir fossils have been recovered in several localities of Yunnan, which include Xiaolongtan, Yuanmou, Lufeng, Zhaotong and others. Based on the measurements of tooth size, the late Cenozoic tapirs were generally getting larger gradually through time in China, which means the tooth sizes coincide well with their geological ages, the later the larger, and all the Mid-Late Miocene tapirs are exclusively small-sized; thus, the tooth size of fossil tapirs in China is likely to have some significance in age estimation. By contrary, both the dwarf and the normal-sized or larger-sized tapirs were discovered from Mid-Late Miocene strata in Europe and North America.

Key words Shuitangba, Zhaotong, Yunnan; terminal Miocene; hominoid site; *Tapirus yunnanensis*

1 Introduction

A new, relatively complete and largely undistorted juvenile cranium of *Lufengpithecus* cf. *L. lufengensis*, which was recovered from a terminal Miocene locality of Shuitangba of

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Zhaotong in northeast Yunnan, was reported recently (Ji et al., 2013). The site is an open air pit of lignite mine located in the suburb of the city of Zhaotong (Fig. 1). Previous authors estimated that the vertebrate fauna from the Zhaotong Basin were of an Early Pleistocene age (Chow and Zhai, 1962) or from Pliocene to Early Pleistocene (Zhang et al., 1978; Shi et al., 1981); however, the results of the most recent biochronological and geochronological investigations indicate a terminal Miocene age, between 7.2 and 5.3 Ma, for the lignite layer (Zhu et al., 2008; Ji et al., 2013). In addition to the partial hominoid cranium, quite a number of other animal and plant fossils have also been recovered, the provisional list of fossil mammals is as follows: *Yunosaptor scalprum*, *Soriculus* sp., *Anourosorex* sp. nov., *Lantanoherium sanmigueli*, *Linomys* sp., *Yunomys* sp. nov., *Pliopetaurista* sp. nov., *Kowalskia hanae*, *Miorhizomys* sp., *Sinocastor zhaotungensis*, *Steneofiber* sp., *Alilepus longisinuosus*, *Lufengpithecus* cf. *L. lufengensis*, *Mesopithecus* sp. nov., *Martes* sp. nov., *Siamogale* sp. nov., Ursidae indet., Rhinocerotidae indet., *Tapirus yunnanensis*, *Muntiacus zhaotongensis* sp. nov., *Gazella* sp., *Propotamochoerus* sp., *Sinomastodon* sp., *Stegodon* cf. *S. zhaotongensis* (Jablonski et al., 2014; Dong et al., 2014; Ji et al., 2013). The most recent age determination for Shuitangba Fauna is 6.5-6 Ma (Jablonski et al., 2014).

Among the Shuitangba Fauna, the tapir specimens are more complete and better preserved than any of the ever reported specimens of Neogene *Tapirus* in China. The Zhaotong Basin is the type locality of the species *T. yunnanensis* which was established based on the specimens from the same locality. But the syntype specimens were poorly preserved and the

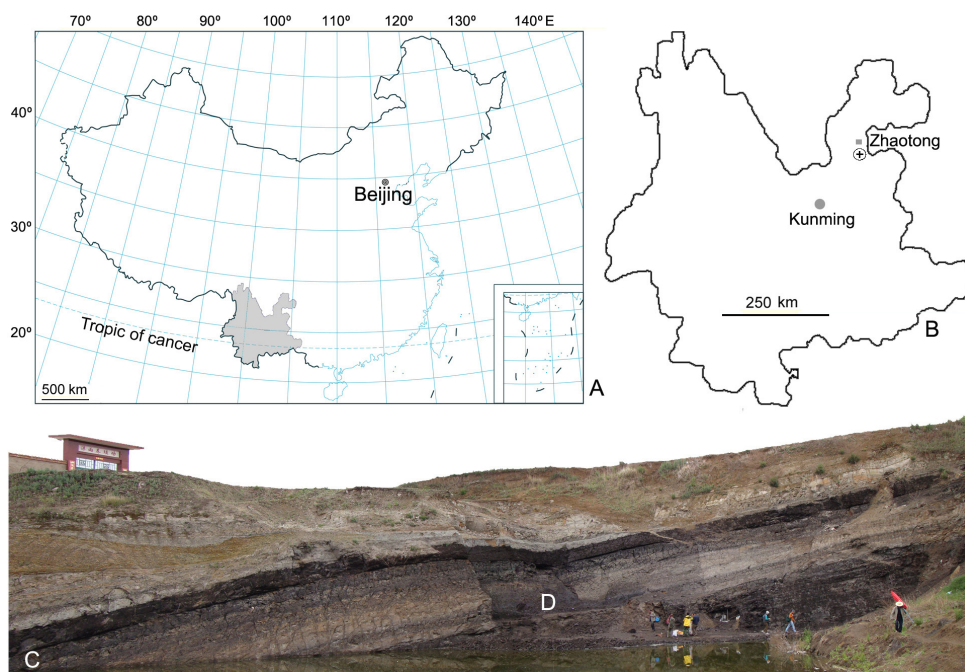


Fig. 1 Site location map

A. Map of China; B. Map of Yunnan Province showing the location of the site;
C. The Shuitangba fossil locality; D. Locus of tapir fossils

geological age was estimated to be Late Pliocene then (Shi et al., 1981).

Tapir used to be a very common mammalian taxon during the Quaternary Period in China, but the Neogene fossil record is quite rare. The Neogene species *Tapirus yunnanensis* Shi et al., 1981 was inferred as the direct ancestor for all of the late Cenozoic tapirs of the world (Van der Made and Stefanovic, 2006). Therefore, the tapir fossils from the Shuitangba site are of significant importance.

2 Materials and methods

The studied specimens were unearthed from the Shuitangba hominoid site between 2007 and 2014. In addition, the syntype specimens of *Tapirus yunnanensis* were also reexamined, and the mandible of *Tapirus teilhardi* from Shanxi and the dental specimens of *Plesiotapirus yagii* from Shanwang in Shandong were compared.

The terminology used in tooth descriptions is mainly after Tong et al. (2002), Scherler et al. (2011) (Fig. 2) and Hulbert (2005). Measurements and general methods are the same as described in Hulbert (2005, 2010) and Hulbert et al. (2009).

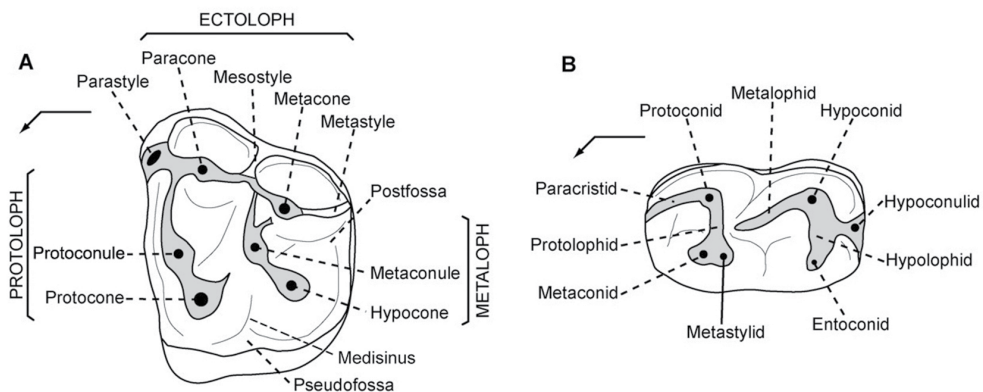


Fig. 2 Tooth terminology for perissodactyls (Modified from Scherler et al., 2011)

A. left upper second molar; B. right lower second molar. Arrows indicate the mesiolingual side of the teeth

Institutional abbreviations BNHM, Beijing Natural History Museum; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; PMU, Palaeontological collections, Museum of Evolution, Uppsala University, Uppsala, Sweden; YICRA, Yunnan Institute of Cultural Relics and Archaeology.

3 Systematic paleontology

Order Perissodactyla Owen, 1848

Family Tapiridae Gray, 1821

Genus *Tapirus* Brisson, 1762

Tapirus yunnanensis Shi et al., 1981

Emended diagnosis Small-sized but slightly larger than *Tapirus hezhengensis*. P1 has a robust hypocone and a still prominent protocone; P2 is variable in degrees of molarization; but the P3 and P4 are fully molarized. Upper molars with developed parastyle. Hypoconulid moderately developed in lower molars, with developed cingula. Symphysis begins posterior to p2. The lower cheek teeth have neither lingual nor buccal cingulid.

Plesiotype specimens Because no type specimen was selected in the original description of the species *Tapirus yunnanensis*, this paper regards the recently recovered specimens as plesiotypes of the species, which include a mandible with cheektooth rows and lower canines of both left and right sides (ZT-2007-03-184), a mandible with tooth rows of both left and right sides (except m3s) and the right lower canine (ZT-2010-03-063), a right semimandible with the symphysis and all the cheek teeth as well as the left i1 preserved in situ, also with the mandibular ramus preserved (ZT-2007-01-294), a mandible with p3-m3 (m3 not erupted yet) of both sides preserved (ZT-2014-0179), and a left maxilla with P2-M2 (ZT-2013-05-001). All the specimens are repositied in YICRA.

Referred specimens One partial mandible (YZ-003) and three isolated teeth also have been studied, which include upper left canine (YZ-006), left M1 (YZ-004) and right M3 (YZ-005). The aforementioned specimens are repositied in a private collection of a lignite mine owner at the site.

Reexamined specimens The syntype specimens (BPV 276) from the type locality currently repositied in the BNHM have been reexamined, which include the following specimens: left i1, upper canine, lower canine, a composed left upper dentition (P1-M2), right P1, right M2, left partial mandible with p4-m3, right partial mandible with p3-m1, and an isolated right p2.

Compared specimens Partial skull of *Tapirus hezhengensis* (IVPP V 15522) from Linxia, northwestern China. A right mandible with dp3-m1 of *Tapirus teilhardi* (PMU M 3832) from Wuxiang in Yushe Basin, Shanxi Province; it is currently repositied in PMU. Left P2-M3 of *Plesiotapirus yagii* from Shanwang in Shandong (IVPP RV 91002) repositied in the IVPP collection.

Location and horizon 27°19'41.9"N, 103°44'13.3"E, Shuitangba of Zhaotong, northeastern Yunnan Province, China; Terminal Miocene, between 6 and 6.5 Ma by paleomagnetic dating.

Descriptions Maxilla the left partial maxilla has partial jugal and partial premaxillary attached, and has P2-M2 preserved in situ. The canine-P1 diastema length should be longer than 30.7 mm. The infraorbital foramen is located over P2/P3. The anterior rim of the orbit is situated above the anterior border of P4. At the anterior end, the jugal mainly contacts the maxillary and only a little corner contacts the lacrimal. The root of the jugal process of maxilla is quite long, which arises from the level over P3 and stops at the level above M2, but not so much transversely extended (Fig. 3). According to the age estimation method proposed by previous authors (Tong and Qiu, 2009; Hulbert et al., 2009; Gibson, 2011), the maxilla represents a young adult individual, as the P4 has already fully erupted and is slightly worn, which means the M3 also should have erupted although it is missed on the specimen.

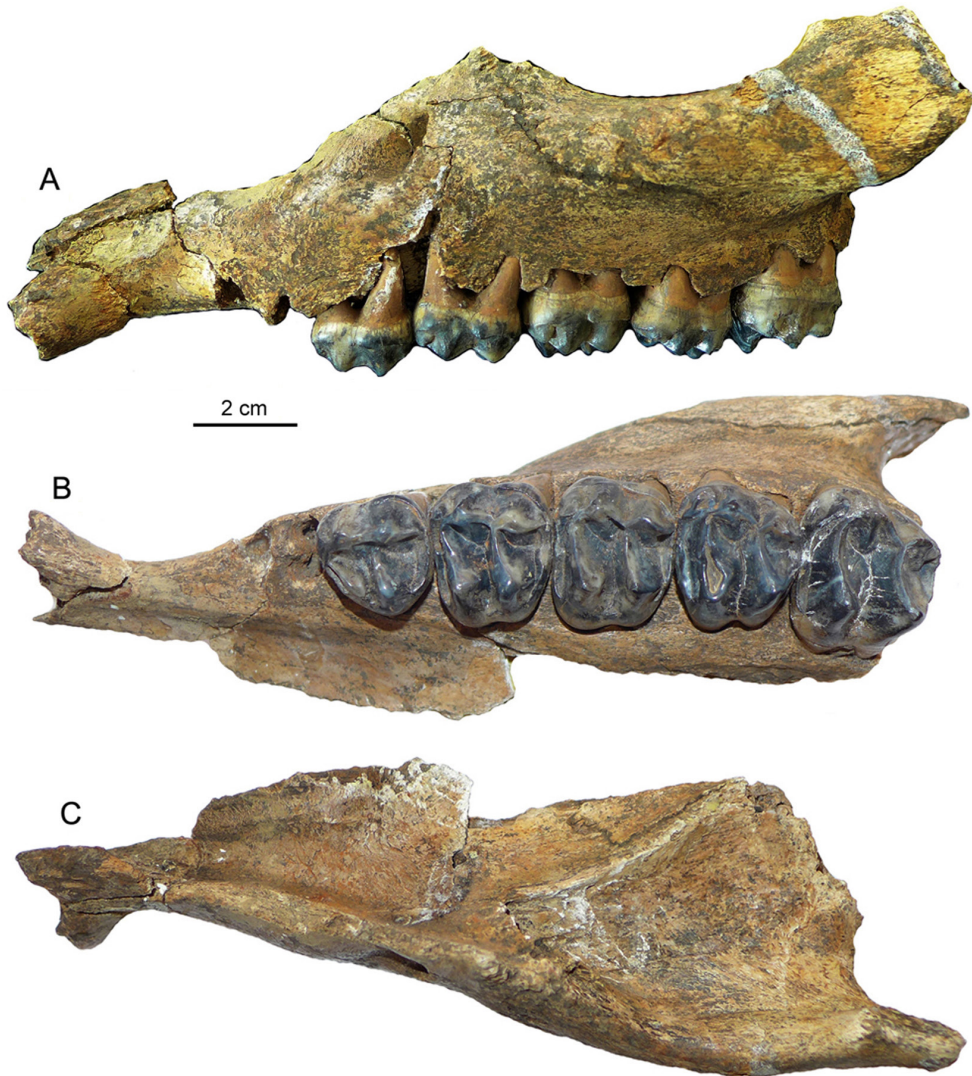


Fig. 3 Maxilla of *Tapirus yunnanensis* from Shuitangba, ZT-2013-05-001
A. buccal view; B. palatal view; C. dorsal view

Mandible The mandibular symphysis is narrow and has a deeply concave dorsal surface; the posterior edge of mandibular symphysis is slightly variable, corresponding with either the posterior border or the middle part of p2. The diastema length between lower canine and p2 is 39–44.7 mm (Table 1). The inferior border of the mandibular body is slightly convex. The depth of the mandibular body is moderate. The mental foramen is very large and located below p2. The masseteric fossa is large and covers almost the entire lateral surface of the angular process and most part of the ramus, and with its deepest part situated above the level of the alveolar border. The angular process is moderately developed. The posterior edge of the mandibular ramus strongly inclines forward whereas the situation of the anterior margin is not clear because of the poor preservation (Fig. 4). The mandibular foramen lies at a level slightly

Table 1 Mandible dimensions of *Tapirus yunnanensis* from Shuitangba (mm)

Dimensions	ZT-2007-03-184	ZT-2010-03-063	ZT-2007-01-294	YZ-003
Condylar length	–	–	230	–
Symphysis width	–	35	>30	–
Symphysis length	>64	70	>66	–
c-p2 diastema length	44	44.7	39	–
p2-m3 length	123	123 (alveolus)	113	–
p2-p4 length	59	58	52	–
m1-m3 length	64	65 (alveolus)	61	–
Depth of mandibular body between p3 and p4	53	48	40	44
Depth of mandibular body between m1 and m2	46	47	43	47
Depth of mandibular body between m2 and m3	43	41	44	48
Thickness of mandibular body below p3	22	21	20	24
Thickness of mandibular body below m1	27	25	25	29
Thickness of mandibular body below m3	28	30	25	30

higher than the alveolar border. The pterygoid fossa is not well defined but with a distinct pterygoid shelf.

Upper teeth P1 is described based on the syntype specimen, which is nearly roundish, with large width (Fig. 5; Table 2). Buccal cusps, paracone and metacone, are moderately developed and are close to each other to form a unique ectoloph. Hypocone is robust, and is separate from metacone. A minute and crest-like protocone is also prominent. It is double-rooted, the anterior one is small and the posterior one is bigger but antero-posteriorly compressed.

P2 is not completely molarized. The syntype specimen is more molarized. But the in situ P2 is roundish triangle in occlusal view. The buccal cusps, paracone and metacone, are quite robust; but the lingual cusps, protocone and hypocone, are only moderately expanded, especially the protocone is very tiny. The parastyle is observable, but the metastyle is

Table 2 Comparative tooth measurements of the small tapir species, compared with *T. sanyuanensis* (mm)

		<i>Tapirus yunnanensis</i>		<i>Tapirus hezhengensis</i>	<i>Tapiriscus pannonicus</i>	<i>Tapirus polkensis</i>	<i>Tapirus teilhardi</i>	<i>Tapirus sanyuanensis</i>
		Plesiotypes	Syntypes	Hezheng, China	Europe	Gray fossil site, USA	Wuxiang, China	Fanchang, China
		(This paper)	(This paper)	(Deng et al., 2008)	(van der Made & Stefanovic, 2006)	(Hulbert et al., 2009)	(Zdansky, 1935)	(Tong & Qiu, 2009)
P1	L	–	15.1–15.77 (15.44)	14.2	–	12.3–16.5 (14.39)	–	18.5
	W	–	13.99–14.38 (14.19)	12	–	11.5–16.2 (13.25)	–	16
P2	L	17.5	18.88	17.4	15–15.3	14–17 (15.39)	–	22–23 (22.5)
	Wa	16.74	18.68		13	15.1–19.1 (16.78)	–	22.5–23.5 (23)
	Wp	18.73	21.42	20	17.8–18.7	17.8–20.8 (18.98)	–	25.5–27.5 (26.5)
P3	L	18.57	19.42	17.2	15.3–15.4	14.5–17 (16.09)	–	22–24.5 (24)
	Wa	22.28	23.42	21.6	17.5–17.6	16.6–22 (20.36)	–	28–29 (28.5)
	Wp	21.92	23.31		19.8–19.9	18.5–21.9 (20.04)	–	28–28.5 (28.25)
P4	L	18.46	20.32	16.6	15.5	15–18.3 (16.78)	–	22.5
	Wa	24.04	–	21.2	18.9–19	19.4–23.4 (21.74)	–	32
	Wp	22.32	20.11	–	20.3–20.4	19–22.6 (20.57)	–	30

		Continued						
		<i>Tapirus yunnanensis</i>		<i>Tapirus hezhengensis</i>	<i>Tapirus pannonicus</i>	<i>Tapirus polkensis</i>	<i>Tapirus teilhardi</i>	<i>Tapirus sanyuanensis</i>
		Plesiotypes	Syntypes	Hezheng, China	Europe	Gray fossil site, USA	Wuxiang, China	Fanchang, China
		(This paper)	(This paper)	(Deng et al., 2008)	(van der Made & Stefanovic, 2006)	(Hulbert et al., 2009)	(Zdansky, 1935)	(Tong & Qiu, 2009)
M1	L	18.98–19 (18.99)	20.38–21.01 (20.7)	17.8	16.7–17	15.4–20.1 (17.94)	–	25–26 (25.5)
	Wa	22.54–23 (22.77)	22.56–23.93 (23.25)	21.4	19.6–19.7	19.4–22.9 (20.96)	–	29–32 (30.5)
	Wp	19.65–20 (19.83)	21.15–24.12 (22.64)	–	18.1–18.2	16.7–20.0 (18.30)	–	25–27 (26)
M2	L	22.26	23.33	21	18.5	17.9–21.7 (19.78)	–	27
	Wa	25.26	–	24.5	21.7	21.4–24.1 (22.84)	–	34.5
	Wp	22.3	22.66	–	19.7–19.8	17.4–21.3 (19.70)	–	29.5
M3	L	23	21	–	17.2–17.3	18.8–23.4 (20.19)	–	29.5–30 (29.75)
	Wa	26	23	–	21.5–21.6	21.4–24.2 (22.65)	–	31.5–33 (32.25)
	Wp	22	–	–	17–17.1	16.1–20.5 (18.36)	–	26.5–27 (26.75)
p2	L	20	20.64	–	17.1–17.3	16.9–19.9 (17.98)	25* (in alveolus)	25–26 (25.5)
	W	12–14 (12.7)	12.38	–	11–11.7	10.7–13.4 (11.89)	–	15.5–16 (15.75)
p3	L	18–20 (19.3)	18.71	–	15.6–16.3	14.4–18.2 (16.40)	23* (in alveolus)	23
	Wa	13–14 (13.3)	15.14	–	11.8–12.1	10.7–13.8 (12.24)	–	16.5–18 (17.25)
	Wp	15–16 (15.7)	16.03	–	13–13.3	11.7–15.3 (13.81)	–	19
p4	L	19–21 (19.3)	19.29–19.32 (19.31)	–	16.6–16.8	15.3–18.9 (17.16)	24* (in alveolus)	23
	Wa	16	–	–	13–13.7	12.2–15.5 (14.09)	–	20
	Wp	17–18 (17.3)	16.84–19.37 (18.11)	–	13–14	12.5–17.9 (14.82)	–	19.5
m1	L	19–20 (19.3)	20.62–22.16 (21.39)	–	15.8	16.2–21 (18.17)	26	25–27 (26)
	Wa	15	16.48–18.15 (17.32)	–	13	12.6–15.3 (14.02)	20.5	18–20 (19)
	Wp	14–15 (14.3)	16.34–17.62 (16.98)	–	11.2	11.9–15.1 (13.19)	19	17–18.5 (17.75)
m2	L	22–23 (22.3)	21.48	–	18.7–20.3	18.9–22 (20.40)	29.5	29–30 (29.5)
	Wa	17	18.31	–	14.8	13.7–16.2 (15.13)	22.4	20–21 (20.5)
	Wp	16	17.83	–	12.4–14.2	13.2–16.2 (14.58)	21	18–20 (19)
m3	L	22	23.35	–	19	19.7–24.7 (21.32)	–	30
	Wa	18	18.46	–	15	14.3–16.5 (15.37)	–	22
	Wp	15	15.89	–	12.8–12.9	12.6–15.2 (13.99)	–	19

Note: mean values are shown in the parentheses; * measured from CT image by the present authors. L. length; W. width; Wa. width of anterior lobe; Wp. width of posterior lobe.

undetectable. The protoloph is short and quite slanting. The metaloph is nearly straight and divides the crown into anterior and posterior parts equally. The medisinus is very narrow, with strong anterior and posterior cingula. The buccal cingulum is discontinued at the paracone, but its posterior part is fused with the posterior cingulum.

P3 is molariform, with all the four main cusps equally developed, but the metacone is more lingually positioned. Protoloph and metaloph are of equal prominence and usually

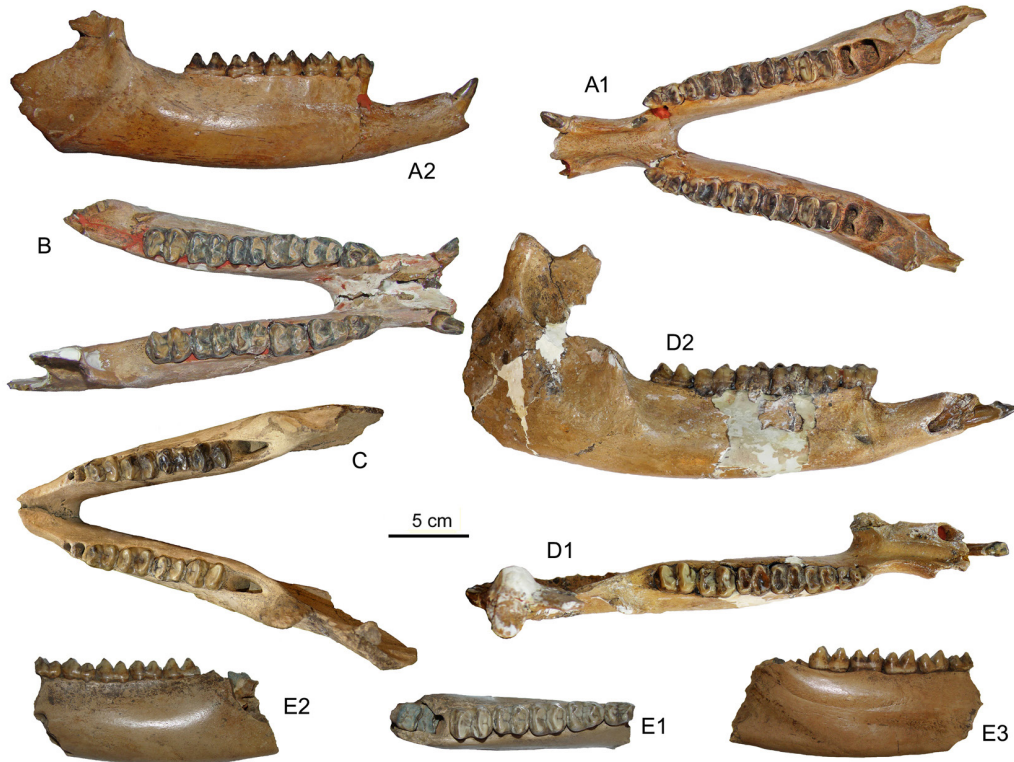


Fig. 4 Mandibles of *Tapirus yunnanensis* from Shuitangba

A. ZT-2010-03-063, mandible with p2-m2 of both sides and right lower canine; B. ZT-2007-03-184, mandible with p2-m3 and lower canines of both sides; C. ZT-2014-0179, mandible with p3-m3 of both sides (m3 in alveolus); D. T-2007-01-294, right semimandible with the symphysis and p2-m3 as well as left i1 preserved; E. left mandible with p2-m3 (m3 is still in alveolus) (private collection). A1, B, C, D1 and E1 in crown views; A2, D2 and E2 in buccal views; E3 in lingual view

of equal length. Metaloph meets the ectoloph between paracone and metacone. Parastyle is moderately developed. Anterior and lingual cingula are more prominent. Medisinus is becoming more open than that on P2.

P4 is larger than P3 and has an obviously shorter metaloph, and more open medisinus. Other characters are nearly the same as those in P3.

On M1 the four main cusps are nearly equally developed, but the protoloph is much stronger and longer than metaloph. The metacone is shortened, and is bounded by a prominent posterobuccal cingulum. The parastyle is robust, close to and slightly buccal to the paracone. The metastyle is prominent. The protoloph, paracone, and metaloph form a lingually open U-shaped wall. The anterior cingulum is very broad, but the posterior cingulum is reduced; the buccal cingulum is strengthened at the external syncline which may be regarded as the mesostyle by some authors.

M2 is similar to M1 in form but obviously larger, and with a more developed parastyle and more prominent posterobuccal cingulum.

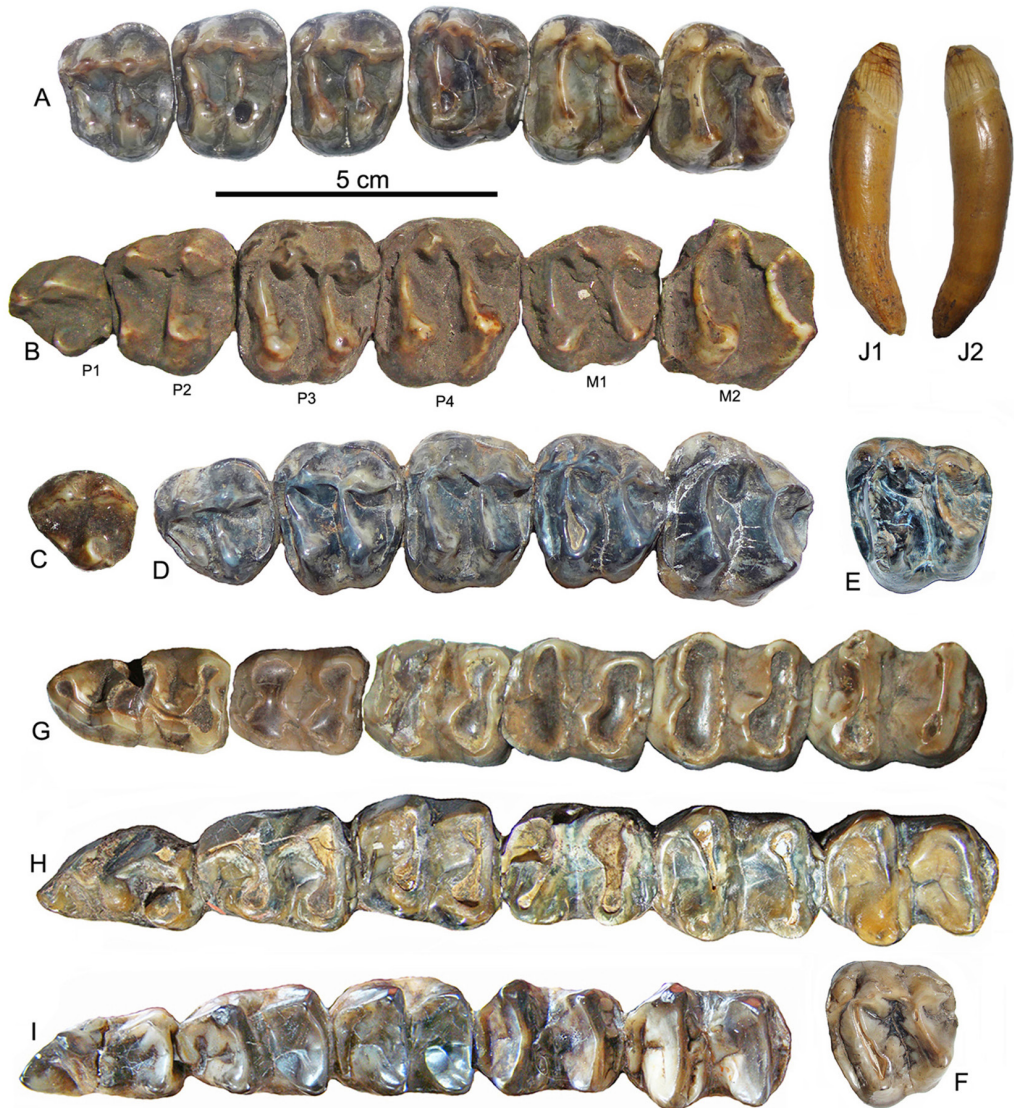


Fig. 5 Teeth of *Tapirus yunnanensis* (B-J), compared with that of *Plesiotapirus yagii* (A)
 A. IVPP RV 91002, P2-M3; B. BPV 276, syntype specimen, left P1-M2; C. BPV 276, right P1, flipped horizontally; D. ZT-2013-05-001, left P2-M2; E. YZ-005, right M3, horizontally flipped;
 F. YZ-004, left M1; G. BPV 276, composed lower dentition (left p4-m3, right p2 and p3), p2 and p3 reversed;
 H. ZT-2007-03-184, right p2-m3; I. ZT-2010-03-063, right p2-m2; J. YZ-006, upper canine
 A-I. occlusal views; J1. lingual view; J2. buccal view

M3 is similar to M2 in form but with more developed parastyle and metastyle; in addition, it has a prominently reduced metaloph and a greatly reduced posterior cingulum (Fig. 5).

From P3-M2, the parastyle is getting larger, the metaloph is getting reduced, and the medisinus is becoming more open.

Lower teeth The p1 is absent.

Although the general form of p2 is broadly triangular and with the five main cuspid

(paraconid, protoconid, metaconid, hypoconid and entoconid) quite developed, it is the most variable tooth; some of them with nearly straight outer wall, others with roundish or convex outer wall. Besides, paraconid is still differently developed in different individuals. It is different from other lower cheek teeth in having a developed paraconid and a paralophid (or paracristid).

The p3 is roughly rectangular in outline. It has a short and low paralophid bounding the trigonid buccally and anteriorly except the two parallel transverse lophids, protolophid and hypolophid, but the former is slightly shorter than the latter. In addition, a faint metalophid is also detectable at the buccoanterior aspect of the hypolophid. The posterior cingulid is less developed.

The p4 is like p3, but with paralophid more reduced, and the protolophid and hypolophid are equally developed and the anterior cingulid is strong.

The m1 and m2 are very similar in form, both of them with nearly equally developed protolophid and hypolophid. Anterior and posterior cingulids are moderately developed.

The m3 is different from m1-2 in having a more pronounced hypoconulid and a relatively more reduced hypolophid.

From p2 to m3, the paralophid is getting reduced gradually and the hypolophid is getting shorter than the protolophid.

4 Comparisons

Compared with *Plesiotapirus yagii* (Matsumoto, 1921) *P. yagii* is different from *Tapirus yunnanensis* in the following aspects: slightly smaller size, the protocone and hypocone are not completely separated on premolars, with quite developed cingula. This is the most primitive tapirid form in China. Its age is around the transition between Early and Middle Miocene (MN5) (Qiu et al., 1991), which was modified as MN4 later (Qiu et al., 2013) and is much earlier than that of *T. yunnanensis*.

Compared with *Tapirus polkensis* or *Tapiravus polkensis* Olsen, 1960 The American dwarf tapir species *Tapirus polkensis*, used to be *Tapiravus polkensis*, is different from *T. yunnanensis* in the following aspects: slightly smaller body size; lower positioned mental foramen; more developed cingula; thicker enamel layer; P1 has distinct protocone and more developed hypocone, some individuals even have fully developed metaloph; P2 is more molarized; each upper cheek tooth has weak links between buccal cusps and with the cross lophids more oblique; the inferior border of the mandibular body is more straight; lower cheek teeth have developed anterior arms on the cross lophids (or trigonid and talonid basins); m3 has more developed hypoconulid.

Tapirus polkensis is the smallest known North American *Tapirus*, and smaller than any of the extant species in the genus, with an estimated average body mass of 125 kg. The geological age of the species is significantly younger than previously thought, which should be

Hemphillian (10.3-4.9 Ma BP) rather than Barstovian (Hulbert et al., 2009:238).

Compared with *Tapiriscus pannonicus* Kretzoi, 1951 The European species *Tapiriscus pannonicus* is almost the smallest species of the late Cenozoic tapirs, and its diagnostic characters are as follows: “Small; cheek teeth brachyodont and relatively narrow; DP1 persistent; clearly smaller than *Tapirus priscus*” (Franzen, 2013). It is different from *T. yunnanensis* in the following aspects: parastyle strong; the medial portion of the lower molar constricts remarkably; the paracristid is undeveloped on the lower cheek teeth; without lingual cingulid, and the buccal cingulid only occurs at the buccal valley.

Compared with *Tapirus hezhengensis* Deng et al., 2008 *T. hezhengensis* is more advanced than *T. yunnanensis* in tooth morphology, such as the lingual cusps on P1 are reduced and the outline of P1 is more elongated, the protocone and hypocone are well separated on P2, all of which are very similar to that of the extant Malayan tapir. But *T. hezhengensis* is smaller than *T. yunnanensis*, the symphysis begins anterior to p2, and the inferior border of the mandibular body is nearly straight.

Compared with the syntype specimens of *Tapirus yunnanensis* Shi et al., 1981 The establishment of the species *T. yunnanensis* was based on poor specimens, some isolated teeth and partial mandibles (Shi et al., 1981). It is necessary to indicate that some of the syntype specimens were not correctly identified and the tooth row was not correctly composed. The reexamination shows that the recently recovered specimens resemble the syntypes very much. But some subtle differences can be detected, the latter has slightly larger upper cheek teeth and the P2 is more molarized than the recently recovered specimens. These differences can be regarded as individual variations.

Compared with the *Tapirus* fossils from other Miocene localities in Yunnan In China, the most productive area of Miocene *Tapirus* is Yunnan Province. Besides Zhaotong, such localities as Kaiyuan (Xiaolongtan), Yuanmou (Xiaohe, Zhupeng and Leilao), Lufeng (Shihuiba) and other localities also bear *Tapirus* fossils. The Kaiyuan hominoid fossil site is the earliest one among the *Lufengpithecus* sites in Yunnan, which bears some isolated teeth of *Tapirus*, including a partial p2, m2 and m3 (Yang, 1983; Dong, 1987) and a partial mandible with p3-m3 (Zhang, 1984). Unfortunately, all of the specimens were not described except the partial p2, which is smaller than the Zhaotong specimens.

At Xiaohe locality (8801) in Yuanmou, one m2 (YV 1820) was identified as *Tapirus* sp. (Gao and Ma, 1997) whose length and width are 21.4 and 15.5 mm respectively, which is slightly smaller than the Zhaotong specimens.

Shihuiba at Lufeng, the type locality of *Lufengpithecus*, also bears tapir fossils, but it was only mentioned in the fossil checklist by Qi (1979).

Because of the rareness of fossil specimens, most of the tapir fossils recovered from the aforementioned localities were identified as *Tapirus* sp. Therefore, their taxonomic position is still open to questions.

Compared with the Plio-Pleistocene *Tapirus* species Among the Pliocene *Tapirus* fossils,

the species *Tapirus teilhardi* is represented by the most complete specimen, although it is only a partial semimandible and without definite provenance. The mandible and teeth are remarkably larger than those of *T. yunnanensis*. It is worth mentioning that all the deciduous teeth, from dp2 to dp4, were mistaken for permanent teeth in Zdansky's paper of 1935. The recent CT scan reveals that all the permanent premolars are still in the alveoli and not erupted yet (Fig. 6).

Other localities such as Yangjiawan in southern Shaanxi (Tang and Zong, 1987) and Yongren in Yunnan (Zong et al., 1996) only bear a few isolated teeth (one m2 and one m1), all of which are larger than those of *T. yunnanensis*.

In China, the fossil records of Quaternary tapir are exclusively occur in South China except two sites, the Early Pleistocene Gongwangling hominid site in Shaanxi Province (Hu and Qi, 1978) and the historical site at Anyang in Henan Province (Teilhard de Chardin and Young, 1936). The Quaternary tapir fossils were referred to the following species: *Tapirus peii*,

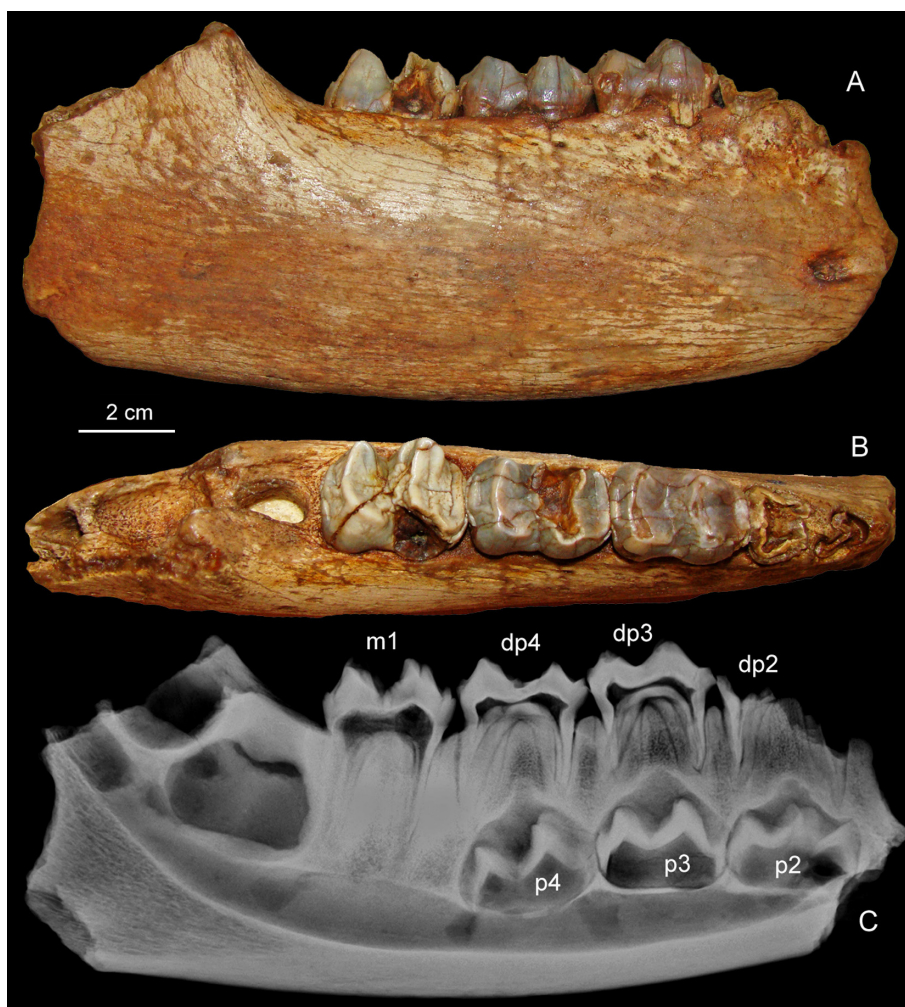


Fig. 6 Mandible of *Tapirus teilhardi*, PMU M3832
A. buccal view; B. crown view; C. CT image

T. sanyuanensis, *T. sinensis*, *T. indicus* and *Megatapirus augustus* respectively (Tong, 2005), all of which are remarkably larger than *T. yunnanensis*. The Plio-Pleistocene tapir species are distinguishable not only by their larger sizes, but also by the following morphologic characters: more molarized premolars except P1, reduced cingula, more buccally positioned metacone on upper premolars, and more developed parastyle and more opened medisinus on upper cheek teeth. In tooth dimension, *T. yunnanensis* is relatively closer to *T. peii* than to any other Plio-Pleistocene tapir species in China.

5 Discussions

The fossil records of tapirids in China are nearly continued from Middle Miocene onward. The evolution of tapirids since Neogene in China shows that the body size was increasing gradually through time. The Pliocene tapirids had reached a body size as the normal extant tapir does, but the pre-Pliocene species of *Tapirus* are obviously smaller (Fig. 7). On the other hand, the other prominent change occurred to P1, the lingual cusps weakened during evolution; but the length/width ratio is very variable and cannot be used as reliable index for evolutionary evaluation (Tong, 2005).

The Miocene tapirid fossil localities in China are limited to the following regions: Shanwang in Shandong, Hezheng in Gansu, and Yunnan, among which Yunnan is the most productive region. Based on the fossil records ever recovered, Yunnan could be regarded as the center of origin for the late Cenozoic tapir in East Asia. The provenance of the isolated *Tapirus* mandible from Pliocene strata in Shanxi still needs further verification.

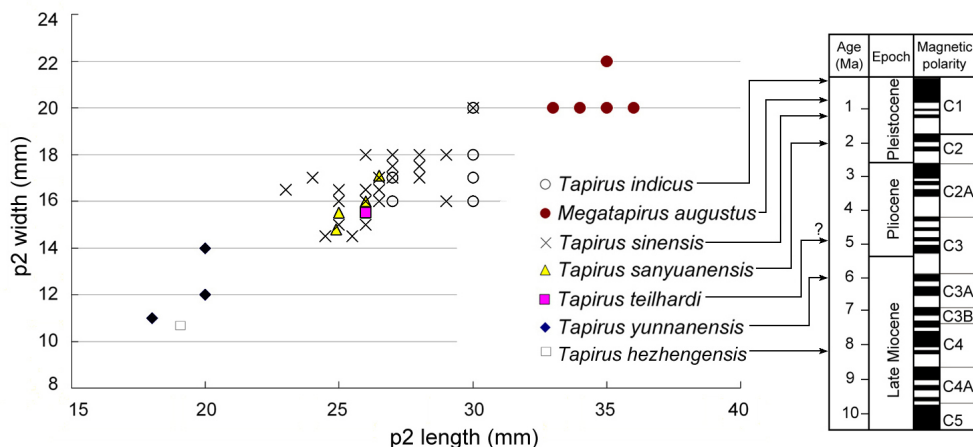


Fig.7 Bivariate scatter plot of measurements of the lower p2s of different tapir genera and species in China, correlated to the geological time scale

Data sources: *Tapirus yunnanensis* (this study); *T. hezhengensis* (Deng et al., 2008); *T. teilhardi* (Zdansky, 1935; this study); *T. sanyuanensis* (Huang and Fang, 1991; Tong et al., 2002); *T. sinensis* (Tong, 2004; this study); *T. indicus* (Hooijer, 1947; Teilhard and Young, 1936); *Megatapirus augustus* (Colbert and Hooijer, 1953; this study)

It is worth mentioning that around the Early-Middle Miocene transition, *Plesiotapirus yagii* was the only tapirid taxon on the earth. Therefore, what role the species *P. yagii* actually played in the phylogeny reconstruction for tapirids should be reconsidered.

During Middle Miocene, the tapirid in China was mainly limited to the north, but since the Late Miocene onward, the evolutionary center of tapirs moved to the south.

All the Chinese Mid-Late Miocene tapirs are exclusively small-sized, which is different from the situations in Europe and North America where both the dwarf and the normal-sized or larger-sized tapirs were discovered from Mid-Late Miocene strata. *Tapirus priscus*, *T. antiquus* and possibly *T. pannonicus* were present in Europe in MN9. During the latest Miocene the small tapirs became extinct everywhere except Shuitangba at Zhaotong in China. *Tapiriscus* became extinct in Europe, and *Tapiravus* in North America (van der Made and Stefanovic, 2006). But the recent study shows that the dwarf tapir *Tapiravus* survived into Pliocene in North America (Hulbert et al., 2009)

6 Conclusions

Shuitangba is the richest fossil site of Late Miocene tapir ever known in China. The new specimens include a maxilla with P2-M2, four mandibles with nearly complete tooth rows as well as some isolated teeth. The tapir fossils were discovered in the peaty clay layers which were interbedded with lignite layers, whose geological age is terminal Miocene (between 6 and 6.5 Ma). Based on the morphological characters and dimensions, the new specimens can be included in the species *Tapirus yunnanensis*. The new specimens expanded the knowledge of the species *T. yunnanensis*, which is small in size, but slightly larger than *T. hezhengensis*; P1 with two labial cusps and one robust lingual cusp (hypocone); P3 and P4 are fully molarized; upper molars with developed parastyle; hypoconulid moderately developed in lower molars; with reduced cingula; symphysis begins posterior to p2. Both *T. yunnanensis* and *T. hezhengensis* are obviously smaller than the Plio-Pleistocene tapir species in China. All the Mid-Late Miocene tapirs in China are exclusively small-sized, which is different from the situations in Europe and North America where both the dwarf and the normal-sized or larger-sized tapirs were discovered from Mid-Late Miocene strata.

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云南昭通水塘坝中新世末期古猿化石点的云南獬化石

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摘要: 此前, 中国晚中新世到早上新世的獬化石发现较为稀少。最近几年, 在云南省昭通市水塘坝禄丰古猿化石点发现了数量可观的中新世晚期獬化石, 其时代为6~6.5 Ma。新发现材料包括左上颌骨带P2-M2、4件下颌骨带基本完整颊齿列、若干零散牙齿。新材料可归入先前报道的小型獬类——云南獬*Tapirus yunnanensis*。云南獬比甘肃的和政獬*Tapirus hezhengensis*时代较晚, 体形也稍大; 两者都比上新世—更新世的獬类明显较小。新发现的化石材料对更全面认识云南獬的特征提供了新信息。在中—晚中新世期间, 云南是我国獬类动物的演化中心, 先后发现的化石点有开远(小龙潭)、禄丰(石灰坝)、元谋(小河、竹棚、雷老)、昭通(水塘坝)及其他地点。在晚新生代期间, 我国獬类动物演化的主要变化趋势是体形逐渐增大, 这一特点或许具有时代意义。在中国发现的中新世獬类毫无例外都是体形较小的类型, 这与欧洲及北美的情况迥异。

关键词: 云南昭通水塘坝, 中新世末, 古猿化石点, 云南獬

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