

Chalicotheriidae (Mammalia, Perissodactyla) from the *Lufengpithecus* locality of Lufeng, Yunnan Province, China

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(Received 30 December 2014; accepted 20 April 2015)

Shihuiba in the Lufeng Basin, Yunnan Province, China, is a very important hominoid locality. Chalicotheriidae from this locality are referred to *Anisodon yuanmouensis* based on the size and morphology of the cheek teeth. This species has a variable protoloph on upper molars, a markedly ‘three-lophed’ structure on P4, longer M2 than M3 and narrower lower cheek teeth than other species in this genus. Including specimens described in this paper, this species has been found from the Yuanmou and Lufeng basins in Yunnan Province, China and the Irrawaddy Formation in Myanmar. Relationships within *Anisodon* are proposed wherein *Anisodon salinus* constitutes a sister group with *Anisodon yuanmouensis*. The absence of *Anisodon* to the north of the Tibetan Plateau likely indicates the uplift of the plateau to an elevation which prevented the free immigration of anisodonts during the Mid-Late Miocene. The appearance of *Anisodon* in the Lufeng hominoid fauna confirms a subtropical forest local environment.

Keywords: Chalicotheriidae; *Anisodon*; Lufeng; Late Miocene

Introduction

Chalicotheres are extinct peculiar perissodactyls. Their materials are very rare during the Late Cenozoic and all belong to the family Chalicotheriidae, which have clawed phalanges instead of hooves. There are two subfamilies in this family, Chalicotheriinae and Schizotheriinae. The former has lower crowned and quadrate upper molars, whereas the latter has higher crowned and elongated upper molars. Eurasia is the central zone for the evolution of Chalicotheriinae, but the relationships among chalicotheriines from the Indian Subcontinent, East Asia and Europe are still unclear. However, excavations during the 1970s–1980s in the Shihuiba locality of Lufeng County, Yunnan Province, China provide a valuable opportunity to understand them further.

The Shihuiba fauna in Lufeng County (Figure 1) is well known for the great number of *Lufengpithecus* fossils, but other mammalian species are also abundant. A list containing 34 mammalian species was given in the preliminary report (Qi 1979). Later, this number was increased to more than 100, including the chalicotheriines *Macrotherium salinum* and *Macrotherium* sp. (Qi 1985a; Qiu and Qiu 1995). The number of chalicothere fossil specimens from this locality is the richest among Neogene deposits of China. This locality is also significant for studying the evolution and dispersal of chalicotheres, because Yunnan Province is southeast of the Tibetan Plateau and northwest of the Bay of Bengal, on the only

path of intercommunication between the faunas of the Indian Subcontinent and the East Asia. Furthermore, the unique morphological structure and hypothesised diet of chalicotheres can give us some information about the palaeoenvironment in which the Lufeng hominoid lived.

Terminology and abbreviations

The dental terminology used in this paper is diagrammed in Figure 2. Abbreviations: IVPP Loc. and IVPP V, locality and fossil prefixes of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; *L*, length (for upper cheek teeth, it is the length of ectoloph); *W*, width; a*W*, width of trigonid; p*W*, width of talonid.

Systematic palaeontology

- Class MAMMALIA Linnaeus, 1875
- Order PERISSODACTYLA Owen, 1848
- Superfamily CHALICOTHERIOIDEA Gill, 1872
- Family CHALICOTHERIIDAE Gill, 1872
- Subfamily CHALICOTHERIINAE Gill, 1872
- Genus *Anisodon* Lartet, 1851
- Anisodon yuanmouensis* (Gao and Ma, 1997)
(Figures 3–6; Table 1)

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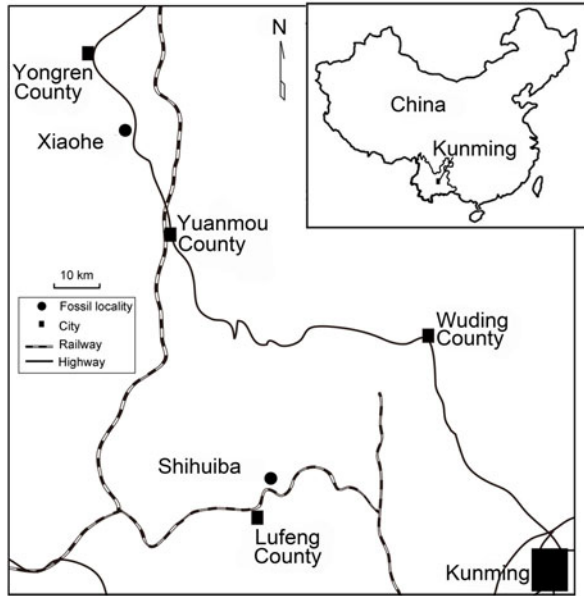


Figure 1. (Colour Online) Map of *Anisodon yuanmouensis* localities (black circle) in Yunnan Province, China.

- 1979 *Macrotherium salinus* – Qi, p. 19.
- 1985a *Macrotherium salinus* – Qi, p. 64.
- 1985a *Macrotherium* sp. – Qi, p. 64.
- 1995 *Macrotherium salinus* – Qiu and Qiu, p. 64.
- 2010 Chalicotheriinae gen. et sp. indet. – Chavasseau et al., pp. 13–22.

Referred materials

IVPP V 18546.1, right horizontal ramus with p3-m3; V 18546.2, left dp2; V 18546.3, right dp3; V 18546.4, right dp4; V 18546.5, left p4; V 18546.6, right p4; V 18546.7, right p4; V 18546.8, broken left m1; V 18546.9, left m1; V 18546.10, left m2; V 18546.11, left m2; V 18546.12, right m2; V 18546.13, right m2; V 18546.14, left m3; V

18546.15, right m3; V 18546.16, broken mandible with right m3; V 18546.17, left DP3; V 18546.18, left DP4; V 18546.19, left DP4; V 18546.20, left DP4; V 18546.21, right DP4; V 18546.22, right DP4; V 18546.23, right DP4; V 18546.24, left P3; V 18546.25, right P3; V 18546.26, left P3; V 18546.27, right P3; V 18546.28, right P3; V 18546.29, right P3; V 18546.30, right P4; V 18546.31, left P4; V 18546.32, left M1; V 18546.33, left M1; V 18546.34, right M1; V 18546.35, broken left M1; V 18546.36, left M2; V 18546.37, broken right M2; V 18546.38, left M3; V 18546.39, left M3; V 18546.40, left M3; V 18546.41, several tooth fragments.

Revised diagnosis

Size medium to small, upper molars quadrate or irregular trapezoidal with variable protolophs, ‘three-lophed’ structure on P4 present, M2 longer than M3, trigonid of lower molars V-shaped, lower cheek teeth narrower than other species in this genus.

Locality and horizon

Levels 3 and 5 of Section D at the hominoid fossil site (IVPP Loc. 75033) of Shihuiba in Lufeng County, Yunnan Province, China; Late Miocene at about 7 Ma (Deng and Qi 2009; Sun 2013). Detailed stratigraphic description can be found from Qi (1985a).

Description

Upper deciduous teeth

The DP3 is molariform. The paracone is lingually in line with the metacone; the protocone is conical and slightly posterior to the paracone and protoconule; the hypocone is triangular-conical and is as tall as the protocone; the conical protoconule is well developed. The parastyle is broken; the mesostyle is well developed; the metastyle is

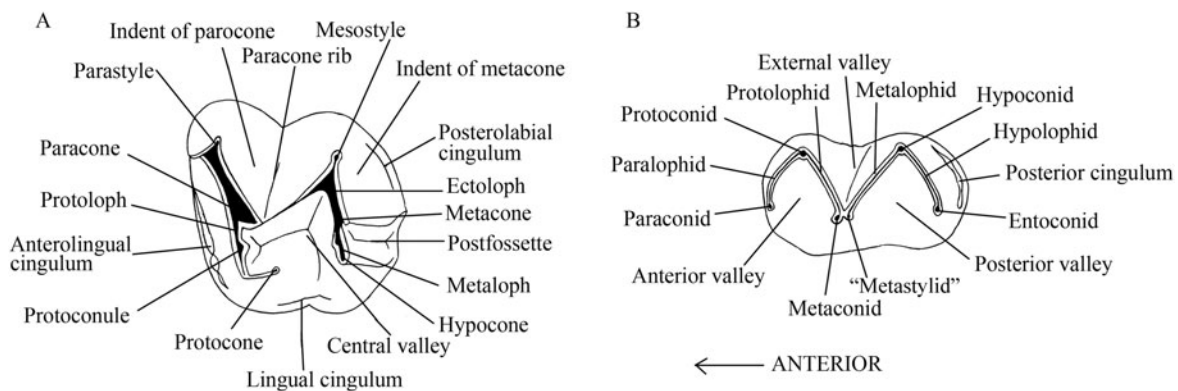


Figure 2. Dental structures and terminology of Chalicotheriidae. A, upper molar; B, lower molar. Modified from Zapfe (1979).

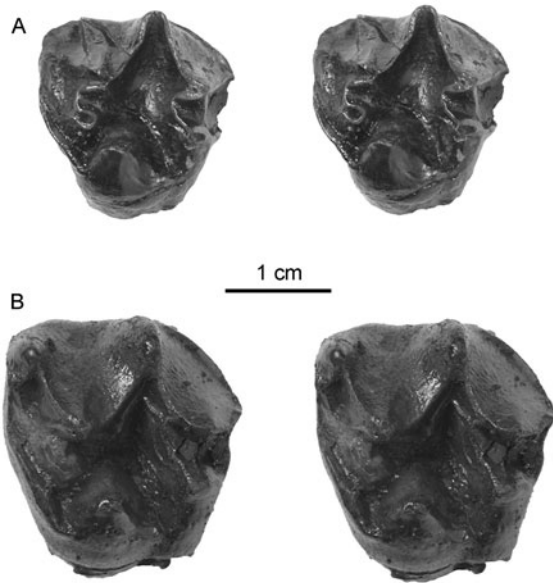


Figure 3. Crown view of upper deciduous teeth of *Anisodon yuanmouensis*. A, left DP3 (IVPP V 18546.17); B, left DP4 (V 18546.19).

almost reduced completely. The ectoloph is W-shaped; its anterior lobe is much longer than the posterior lobe. The protoloph is short, starting from the protoconule and just anterior to the paracone. The metaloph starts anterior to the metacone and extends posterolingually to the tip of the hypocone. The indent of the paracone is deep with an obvious paracone rib. The indent of the metacone is wide and shallow with a very weak metacone rib. The central valley is deep and its lingual opening is V-shaped. The postfossette is shallow and narrow. The cingulum only exists at the anterior and the posterolabial side; the former is well developed and the latter is weak. *L*: 16.6 mm; *W*: 17.5 mm.

The DP4 is similar to DP3 in morphology but larger. Its paracone is a little less lingual than that on DP3 and the protocone is more posterior. The outline of the tooth crown is more quadrate than DP3. *L*: 23.8–24.8 mm; *W*: 23.1–25.5 mm.

Upper premolars

The premolars are non-molariform, and they are much smaller than molars. Six specimens of P3 are preserved.

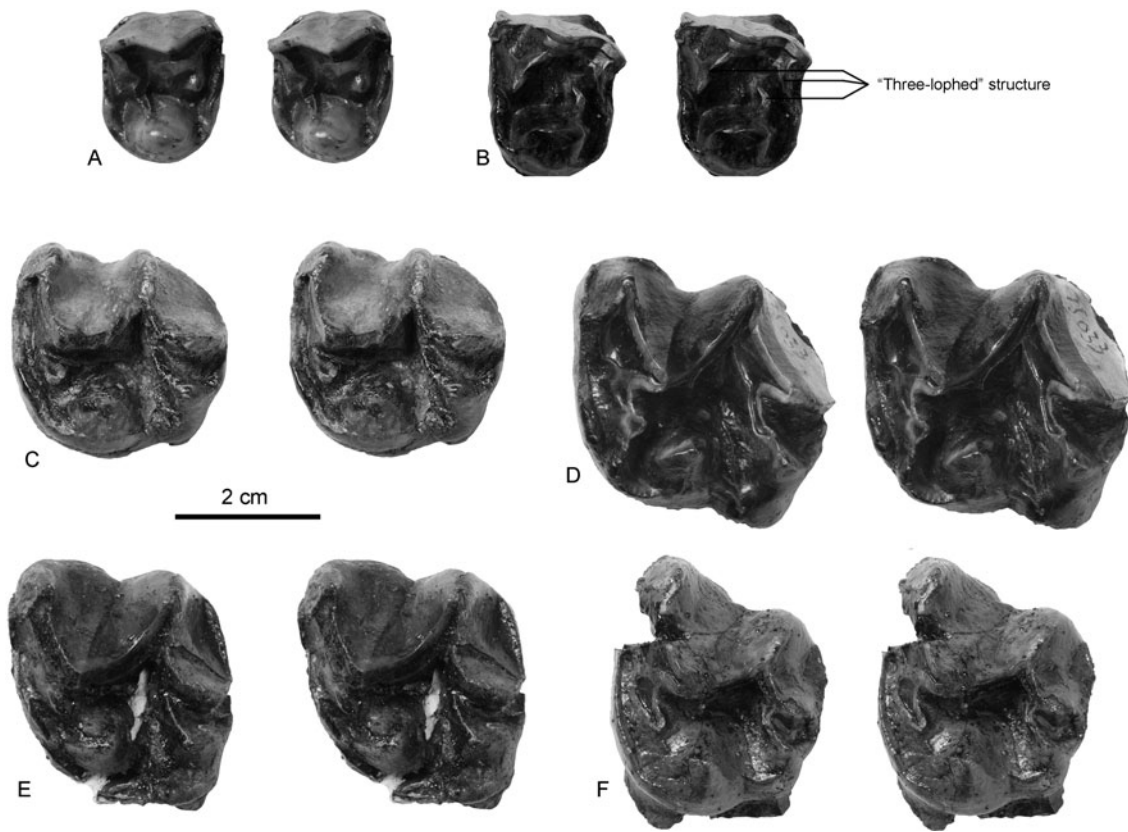


Figure 4. Crown view of upper cheek teeth of *Anisodon yuanmouensis*. A, right P3 (V 18546.28); B, left P4 (V 18546.31); C, left M1 (V 18546.33); D, left M2 (V 18546.36); E, left M3 (V 18546.38); F, left M3 (V 18546.40).



Figure 5. Crown view of lower deciduous teeth of *Anisodon yuanmouensis*. A, left dp2 (V 18546.2); B, right dp3 (V 18546.3); C, right dp4 (V 18546.4).

The parastyle is developed and the mesostyle is very weak. The paracone is as tall as the metacone on unworn specimens, but much taller or shorter than the metacone after wear. The paracone rib and the metacone rib are strong. The protocone is very large and conical, located at the central lingual side; its lingual wall is steep. The protoconule is low but obvious, which is isolated on three P3, but connects with protoloph on other P3s. The ectoloph is slightly W-shaped but with a flat labial wall. The protoloph starts from the protoconule and ends at the paracone. The metaloph starts from the metacone or the ectoloph anterior to the metacone and ends at the tip of the protocone. In the central valley, one crochet on the

metaloph of partial specimens and one crista on the ectoloph are clearly present. The anterior and the posterior cingula are well developed, and the latter connects with the ectoloph. The postfossette, surrounded by the posterior cingulum and the ectoloph, is small and shallow.

Two specimens of P4 are preserved. They are larger than P3. The most obvious difference between P4 and P3 is the ‘three-lophed’ structure, which means three transverse lophs are developed on the crown of P4 (the first loph is the protoloph which starts from the protoconule and ends at the paracone or protrudes to the anterolingual cingulum; the second loph is the metaloph which starts from the anterolingual side of the metacone and ends at the tip of

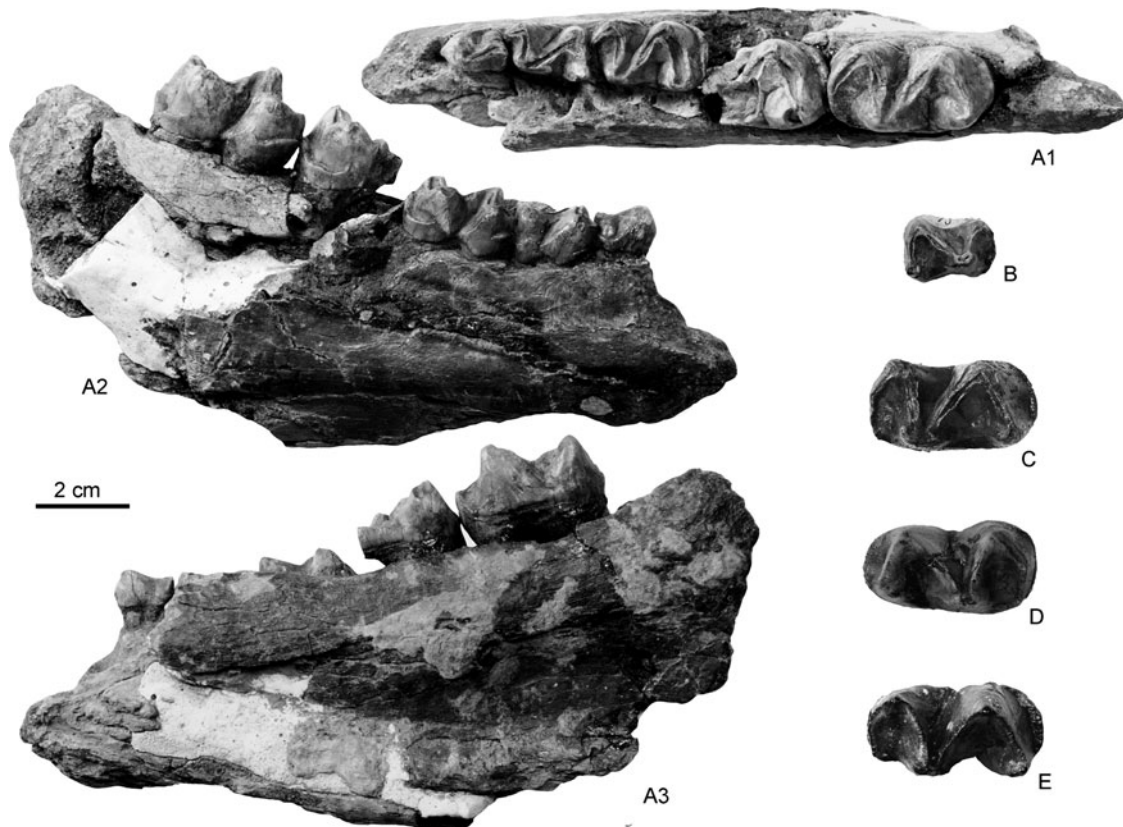


Figure 6. The mandible with p3-m3 and crown view of lower permanent cheek teeth of *Anisodon yuanmouensis*. A1 (crown view), A2 (labial view) and A3 (lingual view), right horizontal ramus (IVPP V 18546.1); B, left p4 (V 18546.5); C, right m2 (V 18546.13); D, left m3 (V 18546.14); E, right m3 (V 18546.15).

Table 1. Measurements of permanent cheek teeth of *Anisodon* (mm).

		<i>Anisodon yuanmouensis</i>			<i>Anisodon salinum</i>	<i>Anisodon grande</i>	<i>Anisodon macedonicum</i>	<i>Anisodon</i> sp.
		Lufeng	Yuanmou	Myanmar	Siwalik	Neudorf	Macedonia	Dorn-Dürkheim
p3	L	12.8		12.7		15.0–17.5	14.3–14.5	12.1–15.6
	aW	7.1		7.8		9.6–11.8	11.1–11.2	9.3–10.8
	pW	8.1						9.0–12.7
p4	L	17.7–18.2		15.2		21.0–24.8	19.8–20.2	19.4–23.7
	aW	9.5–10.3		9.3		15.4–18.1	14.7–15.0	11.2–14.6
	pW	10.6–12.2		10.6				12.1–15.5
m1	L	22.6–22.7	20.3–25.5	22	22.0–28.7	28.1–33.2	26.7–26.8	26.6–30.7
	aW	a.12.0–13.7	14.4–14.8	11.4	15.0–18.0	16.8–21.6	16.9–17.4	14.9–18.0
	pW	a.13.5–14.5		13.2				17.0–19.7
m2	L	30.7–32.5	33.7		31	36.7–41.4	35.5–35.6	37.5
	aW	15.7–17.5	19		16.0–17.5	22.4–27.0	22.2–22.5	19.2–22.3
	pW	16.1–18.1						18.5–22.3
m3	L	30.4–32.2	35.5		40 +	40.3–46	40.0–40.8	38.4–44.3
	aW	15.2–17.6	19		20.5	22.0–26.3	23.2–23.3	19.8–23.6
	pW	15.8–16.9						21.0–23.3
P3	L	14.8–16.5			13.4	16.0–18.0	15.2–15.5	13.5–16.2
	W	17.1–21.6			14	18.0–19.7	20.0–20.1	17.2–21.6
P4	L	17.4–19.1	16.6		15.5–18.8	18.2–22.0	17.2	17.1–20.9
	W	21.9–22.4	21.6		20.5–25.7	22.5–25.0	23.3–24.0	23.5–25.8
M1	L	29.7–a.32	32.7		25.3–27.0	29.0–36.0	27.2–27.4	29.0–32.4
	W	27.4–a.31	36.7		27.7	26.3–34.0	31.0–31.1	29.8–33.9
M2	L	36.3–37.1	31.3		34–38.0	39.5–45.2	38.5–38.8	45.2
	W	31.7–34.7	31		32.5–37.8	37.7–43.0	37.5–39.4	41.7
M3	L	29.7–33.9			38.0–43.0	36.0–45.5	40.1–40.9	43.7
	W	31.3–33.5			39	41.4–48.0	40.0–40.4	45.0

protocone and a third loph is developed which starts from the metacone and ends at the middle part of the posterior cingulum). Another difference is in the central valley where the crochet is absent and two cristae exist on P4.

Upper molars

There are three specimens of M1. The outline of the crown is quadrate. The parastyle and the mesostyle are very well developed, and the metastyle is weak and does not protrude. The paracone is higher than the metacone; the paracone rib is weak and the metacone rib is absent. The protoconule is conical, small and low. The protocone is conical, large and isolated, standing at the middle part of the lingual side; the lingual wall of the protocone is steep; only the labial side of the protocone is worn. The hypocone is higher than the protocone, and this cone is triangular-conical and more posterior than metacone. The ectoloph is W-shaped and its anterior lobe is almost as long as the posterior lobe. The protoloph is short and low, starting from the protoconule and ending at the ectoloph at the anterior edge of the paracone. The metaloph is thin, starting from the middle point of the ectoloph between the mesostyle and the metacone and ending at the tip of the hypocone. The

central valley is deep and no crista exists; its opening between the protocone and the protoconule is V-shaped and between the protocone and hypocone is widely U-shaped. The postfossette is shallow, and its opening is V-shaped. The anterior cingulum is developed; the lingual cingulum is absent at the base of the protocone and the hypocone; the labial cingulum is very weak and only exists at the indent of the metacone; the cingulum at the posterior side is connected with the labial cingulum and protrudes at the base of the hypocone.

There are two specimens of M2; the protocone and the protoconule on one M2 are broken. Compared with M1, its size is larger; the protocone is more anterior; the metacone is more lingual than the paracone; the hypocone is more lingual. Two lophs protrude from the protoconule; one is the protoloph, ending at the protocone and another ends at the anterolingual corner of tooth, connecting with the anterior cingulum. In the central valley, the crista is present. Other structures are similar to M1.

Three specimens of M3 are preserved. The outline of the crown is irregularly trapezoidal because of its anterior part being clearly wider than the posterior part. The parastyle is anteriorly protruded. The mesostyles on two of the teeth are developed as well as the parastyle, but is much weaker on the third one because of the shrunken

posterior part of this tooth. The paracone is more labial than the metacone. The paracone rib is obvious, but the metacone rib is weak or absent. The protoconule is small and abuts against the paracone. The protocone is conical and a rib is clear on the anterior wall of this cone. The hypocone is triangular-conical, lower and more lingual than the protocone and as posterior as the metacone. The ectoloph is W-shaped and its posterior lobe shrinks markedly and is much shorter than the anterior lobe. The protoloph is short and another weak loph protrudes from the tip of the protoconule to the base of the protocone. The metaloph starts just anterior to the metacone. The central valley is similar to that of M1 and M2; a weak crista is present near the paracone. The postfossette is shallow and more reduced than on other upper molars. The anterior cingulum is developed; the posterior cingulum reaches the hypocone summit, and the posterolabial cingulum is weak; the labial and the lingual cingula are absent.

Lower deciduous teeth

Three specimens of lower deciduous teeth are recognised among these isolated fossils, one dp2, one dp3 and one dp4, respectively. Their enamel is thinner than that of the permanent teeth, and the surface of the enamel is less smooth.

The dp2 is very small, slightly worn and molariform. The paraconid is the lowest cone on the crown surface, and it turns posteriorly, making its base lean against the base of the metaconid, but still keeping the anterior valley open. The 'metastylid' is against the metaconid and well developed. The paralophid and the protolophid are the shortest of the crests; the metalophid is the longest and the hypolophid is moderate. Both the anterior and the posterior valleys are V-shaped, but the latter is wider. The talonid is wider and longer than the trigonid. The cingulum is developed on the anterior and posterior sides. Double rooted. *L*: 15.3 mm; *aW*: 6.7 mm; *pW*: 8.7 mm.

The dp3 is moderately worn with broken paraconid; the dp4 is unworn. Overall, these two teeth are similar to dp2 in morphology, but obviously larger than the latter. However, there are still some differences between these two teeth and dp2. Their 'metastylids' are less developed than that of dp2. The paraconid of dp4 is less developed than that of dp2 and the trigonid is much smaller than the talonid. For dp3, *L*: ~16.3 mm; *aW*: ~7.8 mm; *pW*: 9.6 mm. For dp4, *L*: 21 mm; *aW*: 9.9 mm; *pW*: 10.7 mm.

Lower premolars

The p2 is double rooted as determined from its alveoli. The p3 is small and its two-lobed structure is subtle. The paraconid and the protoconid of p3 are almost reduced completely. The metaconid is the main cone; the hypoconid is relatively wide; the entoconid is weak.

Both the paralophid and the protolophid are very narrow and short; the metalophid is well developed; the hypolophid is short. The anterior valley is absent; the posterior valley is unclear; the external valley is weak. The cingulum is developed on the labial side.

The p4 is submolariform and markedly W-shaped. The paraconid is diminutive; the protoconid is weak; the metaconid and the hypoconid are developed to the same degree; the entoconid is triangular-conical and well developed. The paralophid is low and narrow, extending to the lingual side. The trigonid is taller and much shorter than the talonid. The anterior and the posterior valleys are shallow, and the external valley is V-shaped, leaning forward. The cingulum is weak on the anterior and posterior sides.

Lower molars

All lower molars have similar morphological characters. They are all typically W-shaped. The m1 is small; the m2 and m3 are similar in size. The paraconid is low; all the other cusps, except the 'metastylid', are developed to a similar degree; the 'metastylid' is clearly present on some specimens of m3, but not all. The paralophid parallels the metalophid and the protolophid parallels the hypolophid; the end of the hypolophid turns anteriorly. Both the anterior and the posterior valleys are V-shaped, but the former is not typical because its bottom is a little smooth; the external valley is very deep. The trigonid is narrower than the talonid on m1; they are of similar width on m2; the former is wider than the latter on m3. The anterior and the posterior cingula are developed, especially the posterior cingulum on m3, which is the strongly reduced hypoconulid.

Mandible

The only known mandible is poorly preserved. The preserved part is slender with a width of 23 mm at the level of m1. The lower border of the horizontal ramus is straight and the upper border is slightly curved. The height of the horizontal ramus is 38.4 mm at the anterior margin of p2, and 47.1 mm at the posterior margin of m1. The posterior margin of the mandibular symphysis is at the level between p2 and p3. The masseteric fossa is shallow with its anterior margin anterior to m3.

Comparison and identification

The chalicotherine materials from Lufeng can be identified as Chalicotheriinae by the low-crowned and quadrate upper molars. Classification in this subfamily is still controversial and several taxonomic interpretations have been proposed (Colbert 1935a; Butler 1965; Coombs 1989; de Bonis et al. 1995; Anquetin et al. 2007; Chen et al. 2012). In the recent

phylogenetic analysis by Chen et al. (2012), Chalicotheriinae was divided into six genera, *Butleria*, *Chalicotherium*, *Kalimantsia*, *Anisodon*, *Nestoritherium* and *Hesperotherium*. The Lufeng chalicotheres once were identified as *Macrotherium* (Qi 1979, 1985a), an abandoned *nomen nudum* (Anquetin et al. 2007). So, the position of the Lufeng materials in phylogeny should be reassessed.

Among the Chalicotheriinae, *Butleria*, '*Chalicotherium*' *pilgrimi* and *Kalimantsia* are very different from the Lufeng materials. *Butleria* is an Early Miocene African genus (Butler 1965; de Bonis et al. 1995; Coombs and Cote 2010), and there is only one species in this genus, *Butleria rusingense*. This species has lower incisors, as well as upper and lower canines; its length ratio of premolar row to molar row is bigger than other chalicotheriines. '*Chalicotherium*' *pilgrimi*, another Early Miocene species, is from the Bugti beds of Pakistan (Forster-Cooper 1920). It has a very labial paracone and metacone, which indicates the most primitive position of this species in the Chalicotheriinae. *Kalimantsia* is a Late Miocene genus from Bulgaria, also only including one species, *Kalimantsia bulgarica* (Geraads et al. 2001). Its size is much larger than the Lufeng materials; its upper premolars are wider than long and the upper molars are much longer than wide, which are also different from the Lufeng materials.

Chalicotherium, *Nestoritherium* and *Hesperotherium* have large body size and robust mandible (Chen et al. 2012). The upper cheek teeth of these three genera lack the crista and the crochet. *Nestoritherium* and *Hesperotherium* have a short premolar row, absent or weak protoconule on upper molars and strong posterior cingulum of m3. The Lufeng materials have moderate size, thin mandible, crista on M2/3 and 'three-lophed' structure on P4. These obvious divergences suggest the Lufeng materials cannot be identified as any of these three genera.

Anisodon, the genus which the Lufeng species can be included in, has four described species: *Anisodon grande*, *Anisodon macedonicus*, *Anisodon salinus* and *Anisodon yuanmouensis*. This genus shares the following characters with the Lufeng species: moderate size, thinner mandible than other late chalicotheriines, the shape and variation of the protoconule and the protoloph and V-shaped trigonid of lower molars.

Comparison with *Anisodon grande*

Anisodon grande, the best known chalicotheriine and the generic type, is a Middle Miocene species from Europe. Its lectotype is a right maxilla from Sansan of France selected by Anquetin et al. (2007). Neudorf of Slovak Republic is another locality where at least 60 individuals of *Anisodon grande* have been unearthed (Zapfe 1979). There are some differences between the materials from these two localities, but which does not affect the comparison between *Anisodon grande* and the Lufeng

species. The Lufeng species is a little smaller than *Anisodon grande*; the entoconid of p4 is more developed on the Lufeng species than on *Anisodon grande*; some m3s of the Lufeng species have well-developed 'metastyloid', but this conid is weak on *Anisodon grande*; P3 and P4 are more molariform on the Lufeng species than on *Anisodon grande*; the crista and the crochet are more developed on the Lufeng species than on *Anisodon grande*; the protoloph of the Lufeng species is variable, but stable on *Anisodon grande*.

Comparison with *Anisodon macedonicus*

Anisodon macedonicus was established based on a skull with its articulated mandibles from the Late Miocene (Turolian) of Macedonia (de Bonis et al. 1995). This species is similar to *Anisodon grande*, especially the morphology of teeth except the shrink of M3. Compared with the Lufeng species, the size of M3 is much longer than M2 on *Anisodon macedonicus* but shorter on the Lufeng species, which means that the M3 is more reduced on the Lufeng species than on *Anisodon macedonicus*; the width of lower cheek teeth is wider on *Anisodon macedonicus* than on the Lufeng species; the entoconid of p4 is isolated on *Anisodon macedonicus*, but this conid connects with the hypoconid on the Lufeng species.

Comparison with *Anisodon salinus*

Anisodon salinus is a Mid-Late Miocene (Astaracian–early Turolian) species from South Asia, and was established based on the materials from the Siwaliks (Forster-Cooper 1922; Colbert 1935b; Pickford 1982; Khan et al. 2009). This species has a wide range from the Chinji Formation to the Dhok Pathan Formation and has many variations on cheek teeth. Due to the time scale and the variations, some palaeontologists have wondered whether the known material might represent more than a single species. Actually, the same variation can be observed on the Lufeng species. The Lufeng species and *Anisodon salinus* share the following characters: the similar degree of molariform premolars, the 'three-lophed' structure on P4, the similar crista on M2/3 and the same variation of protoloph. Other obvious differences can also be observed, including the more posterior protocone of upper molars, narrower width of the lower cheek teeth and more developed 'metastyloid' on some of the Lufeng specimens than in *Anisodon salinus*.

Comparison with *Anisodon yuanmouensis* from Yuanmou

Anisodon yuanmouensis was established based on isolated teeth from the Xiaohe locality in the Yuanmou Basin,

Table 2. Dental comparisons of species in the genus *Anisodon*.

	<i>Anisodon yuannouensis</i> Late Miocene	<i>Anisodon salinum</i> Mid-Late Miocene	<i>Anisodon grande</i> Middle Miocene	<i>Anisodon macedonicum</i> Late Miocene	<i>Anisodon</i> sp. (Dorn-Dürkheim 1) Late Miocene
Age	Yes	No	No	No	No
Length of M2 > M3	2	?	1/2	2	1
Roots of p2	Developed, unisolated	?	Weak, unisolated	Developed, isolated	Developed, isolated
Entoconid of p4	Developed on partial m3s	?	Weak	Weak	Weak
'Metastylid' of m3	Present	Present	Absent	Absent	Absent
'Three-lophed' structure on P4	Subcentral	Slightly posterior	Slightly posterior	Subcentral	Slightly posterior
Protocone of upper molars	Present	Present	Absent	Absent	Absent
Crista of M2/3	Variable	Variable	Stop at the protoconule	Stop at the protoconule	Stop at the protoconule
Protoloph of molars					

another hominoid site near Lufeng (Zong 1991; Gao and Ma 1997). The age of the Xiaohe fauna is close to or a little later than the Lufeng fauna (Deng 2006). Materials of this species are rare, especially the upper molars. Gao and Ma (1997) distinguished this species from *Anisodon salinus* based on the 'three-lophed' structure of P4, but this character can also be observed in *Anisodon salinus*.

In addition, one p3 and one p4 in the original paper (Gao and Ma 1997) are identified as two m1s herein. *Anisodon yuannouensis* is similar to some specimens of the Lufeng species on morphology, e.g. the obvious 'three-lophed' structure on P4, the short and low protoloph of upper molars, the developed 'metastylid' on some of m3s. No obvious difference can be observed between the chalicothere fossils from the Xiaohe locality and the Lufeng specimens described herein.

Comparison with *Anisodon* from Dorn-Dürkheim 1 of Germany

Recently, many isolated teeth of chalicotheriine were reported from Dorn-Dürkheim 1 of Germany and identified as *Anisodon* sp. by Fahlke et al. (2013). These materials resemble the Lufeng species in several characters, such as conspicuous entoconid of p4, moderately strong lingual cingulum and lower protoconule of upper molars. Meanwhile, the Lufeng species differs from *Anisodon* sp. from Dorn-Dürkheim 1 in having the characteristic 'three-lophed' structure of P4, smaller cheek teeth, thinner mandible, molariform dp2, less-developed paraconid of p4, more opened central valley of upper molars and more pinched postfossette of M3.

Comparison with *Anisodon* from Myanmar

A mandible was described from the Irrawaddy Formation of Myanmar and identified it as Chalicotheriinae gen. et sp. indet. (Chavasseau et al. 2010). This mandible was distinguished from other chalicotheriines by its double roots of p2. But this character can also be observed on other *Anisodon* species and some other chalicotheriines. Considering the lower crowned teeth, moderate size, thin mandible and V-shaped trigonid of m1, this mandible should be included in *Anisodon*. The posterior margin of the mandibular symphysis is more anterior on the Myanmar mandible than the Lufeng species, a unique main difference between them.

Via the comparisons, the Lufeng chalicothere fossils are the most similar to *Anisodon yuannouensis* from Yuanmou Basin and the mandible of *Anisodon* from Myanmar. They have close chronological and geographical distributions. Therefore, both the Lufeng chalicothere fossils and the Myanmar mandible should be identified as *Anisodon yuannouensis*.

Discussion

Relationships within the genus *Anisodon*

Anquetin et al. (2007) summarised a variety of chalicotheriines from Europe and conducted a phylogenetic analysis. In their analysis, the generic name *Anisodon* was revalidated, and its diagnosis revised. But their analysis, lacking some Asian species, is unstable. Chen et al. (2012) conducted a more detailed cladistic analysis including more taxa and more characters and divided the *Anisodon* clade of Anquetin et al. (2007) into two clades and three genera, *Anisodon*, *Nestoritherium* and *Hesperotherium*. Fahlke et al. (2013) made an analysis on the basis of dental characters of chalicotheriines and updated the relationships in the *Anisodon* clade. However, none of these analyses included *Anisodon yuanmouensis*. The new materials of *Anisodon yuanmouensis* from Lufeng give us a better chance to understand the relationships within *Anisodon*.

The sizes of Europe *Anisodon grande*, *Anisodon macedonicus* and *Anisodon* sp. from Dorn-Dürkheim 1 are relatively larger than Asian *Anisodon salinus* and *Anisodon yuanmouensis*. The upper premolars of the Asia species are more complex than the Europe species, especially on their P4s. Table 2 shows the detailed dental comparisons within the genus *Anisodon*. Via these comparisons, it is assumed that *Anisodon salinus* and *Anisodon yuanmouensis* constitute a sister taxon, and the relationship among Europe species are closer than with the Asian species.

In the genus, *Anisodon salinus* and *Anisodon yuanmouensis* retain some plesiomorphic characters, e.g. the complex structure of upper premolars and the connection of the protocone and the paracone by protoloph on partial M3s. Meanwhile, some apomorphic characters can also be found on *Anisodon yuanmouensis*, e.g. the highest degree of M3 reduction in *Anisodon*.

In consideration of the variation of *Anisodon salinus* and *Anisodon yuanmouensis* and their primitive characters, South Asia or the borderland of the Tibetan Plateau is more likely the originated place of *Anisodon*. Two species of Early Miocene chalicotheriines have been described from this area, '*Chalicotherium pilgrimi*' from the Bugti beds of Pakistan (Forster-Cooper 1920) and Chalicotheriinae gen. et sp. indet. from the Lanzhou Basin of China (Qiu et al. 1998). Both of these two species are fragmentary materials and cannot be regarded as the common ancestor of *Anisodon* based on current materials. More works and discoveries are still needed to resolve this question.

Palaeoenvironment

Anisodon yuanmouensis is morphologically different from other Mid-Late Miocene chalicotheriines from northern

China, which are all identified as *Chalicotherium* or *Nestoritherium*. If so, there is no direct relationship between *Anisodon yuanmouensis* and other chalicotheriines from northern China. *Anisodon yuanmouensis* may derive from its South Asian relative, *Anisodon salinus*. The early anisodonts existed in South Asia, and immigrated eastward to Myanmar and then northwards to Yunnan. This migration route happens to parallel the southern foot of Tibetan Plateau. It likely indicates that the Tibetan Plateau had uplifted to an elevation what prevented the free immigration of anisodonts during the Mid-Late Miocene.

Chalicotheres were apparently adapted to wooded environments. Chalicotheriinae, in particular, have generally been considered as typical browsers (Coombs 1983, 1989), but the dental micro- and mesowear analyses showed that bark, twigs and fruits also played an important role in their palaeodiet (Schulz et al. 2007; Semperebon et al. 2011). An isotopic study of the Siwalik fauna revealed that chalicotheres might have moved to open regions for drinking and feeding (Nelson 2007). The presence of chalicotheres, with other co-occurring taxa, such as *Dorcabune*, *Dorcatherium* and *Muntiacus*, suggests that the Lufeng Basin was a subtropical forest environment during the Late Miocene. This result is consistent with that of other palaeontologists (Qi 1985b; Qiu et al. 1985; Chen 1986; Chen et al. 1986; Badgley et al. 1988; Ni and Qiu 2002). It should be noticed that the absence of giraffid fossils in the Lufeng and Yuanmou faunas represents some differences from the Myanmar and South Asia hominoid faunas.

In addition, most anisodonts are paragenetic with hominoids in Asia, which may indicate an analogical living environment but different ecological niches between anisodonts and hominoids. For instance, majority *Anisodon salinus* from Siwalik were excavated with hominoids (Pickford 1982), but the dental carbon and oxygen stable isotopic values of these two animals are distinct (Nelson 2007).

Acknowledgements

The first author wants to show his special thanks to Dr Margery C. Coombs (University of Massachusetts, USA) for her kindly help on studying chalicotheres. We thank Dr Zhijie Jack Tseng (American Museum of Natural History, New York, USA) for his improvement in English. Dr Martin Pickford (Muséum National d'Histoire Naturelle, Paris, France) provided important references and Dr Olivier Chavasseau (Université de Poitiers, Poitiers, France) supplied the photos of the *Anisodon* mandible from Myanmar. The two reviewers' comments greatly improved the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the National Natural Science Foundation of China [grant number 41430102]; the Strategic Priority Research Program of the Chinese Academy of Sciences [grant number XDB03020104] the National Basic Research Program of China [grant number 2012CB821906] and the National Commission on Stratigraphy of China.

References

- Anquetin J, Antoine P-O, Tassy P. 2007. Middle Miocene Chalicotheriinae (Mammalia, Perissodactyla) from France, with a discussion on Chalicotheriine phylogeny. *Zool J Linn Soc.* 151(3):577–608. doi:10.1111/j.1096-3642.2007.00327.x.
- Badgley C, Qi GQ, Chen WY, Han DF. 1988. Paleoeology of a Miocene, tropical, upland fauna: Lufeng, China. *Nati Geogr Res.* 4:178–195.
- Butler PM. 1965. Fossil mammals of Africa. No. 18: East African Miocene and Pleistocene Chalicotheres. *Bull Brit Mus Nat Hist (Geol).* 10:163–237.
- Chavasseau O, Chaimanee Y, Coster P, Emonet EG, Soe AN, Kyaw AA, Maung A, Rugbunrung M, Shwe H, Jaeger JJ. 2010. First record of a chalicothere from the Miocene of Myanmar. *Acta Palaeont Pol.* 55(1):13–22. doi:10.4202/app.2009.0033.
- Chen SK, Deng T, He W, Chen SQ. 2012. A new species of Chalicotheriinae (Perissodactyla, Mammalia) from the Late Miocene in the Linxia Basin of Gansu, China. *Vert Palasiat.* 50(1):53–73. (in Chinese with English summary).
- Chen WY. 1986. Preliminary studies of sedimental environment and taphonomy in the Hominoid fossil site of Lufeng. *Acta Anthropol Sin.* 5(1):89–100. (in Chinese with English summary).
- Chen WY, Lin YF, Yu QL. 1986. On the paleoclimate during the period of Ramapithecus in Lufeng County, Yunnan Province. *Acta Anthropol Sin.* 5(1):79–80. (in Chinese with English summary).
- Colbert EH. 1935a. Distributional and phylogenetic studies on Indian fossil mammals. III. A classification of the Chalicotherioidea. *Am Mus Novit.* 798:1–16.
- Colbert EH. 1935b. Siwalik mammals in the American Museum of Natural History. *Trans Am Phys Soc.* 26:1–401.
- Coombs MC. 1983. Large mammalian clawed herbivores: a comparative study. *Trans Am Phil Soc.* 73(7):1–96. doi:10.2307/3137420.
- Coombs MC. 1989. Interrelationships and diversity in the Chalicotheriidae. In: Prothero DR, Schoch RM, editors. *The evolution of Perissodactyls*. New York, NY: Oxford University Press.
- Coombs MC, Cote SM. 2010. Chalicotheriidae. In: Sanders WJ, Werdelin L, editors. *Cenozoic mammals of Africa*. Berkeley, CA: University of California Press; p. 659–667.
- de Bonis L, Bouvrain G, Koufos G, Tassy P. 1995. A skull of Chalicothere (Mammalia, Perissodactyla) from the Late Miocene of Macedonia (Greece): remarks on the phylogeny of the Chalicotheriinae. *Palaeovertebrata.* 24:135–176.
- Deng T. 2006. Chinese Neogene mammal biochronology. *Vert Palasiat.* 44(2):143–163.
- Deng T, Qi GQ. 2009. Rhinocerotids (Mammalia, Perissodactyla) from Lufengpithecus site, Lufeng, Yunnan. *Vert Palasiat.* 47(2):135–152. (in Chinese with English summary).
- Forster-Cooper C. 1920. Chalicotherioidea from Baluchistan. *Proc Zool Soc Lond.* 3:357–366.
- Forster-Cooper C. 1922. *Macrotherium salinum*, sp. n., a new chalicothere from India. *Ann Mag Nat Hist (Ser 9).* 10:542–544.
- Gao F, Ma B. 1997. Perissodactyla. In: He ZQ, editor. *Yuanmou hominoid fauna*. Kunming. (in Chinese with English summary) Yunnan Science and Technology Publish House; p. 94–113.
- Geraads D, Spassov N, Kovachev D. 2001. New Chalicotheriidae (Perissodactyla, Mammalia) from the Late Miocene of Bulgaria. *J Vertebr Paleontol.* 21(3):596–606. doi:10.1671/0272-4634(2001)021[0596:NCPMFT]2.0.CO;2.
- Khan MA, Iqbal M, Akhtar M, Hassan M. 2009. Chalicotheres in the Siwaliks of Pakistan. *Pak J Zool.* 41(6):429–435.
- Nelson SV. 2007. Isotopic reconstructions of habitat change surrounding the extinction of Sivapithecus, a Miocene hominoid, in the Siwalik Group of Pakistan. *Palaeogeogr Palaeoclimatol Palaeoecol.* 243(1–2):204–222.
- Pickford M. 1982. Miocene Chalicotheriidae of the Potwar Plateau, Pakistan. *Tert Res.* 4(1):13–29.
- Qi GQ. 1979. Pliocene mammalian fauna of Lufeng, Yunnan. *Vert Palasiat.* 17(1):14–22. (in Chinese with English summary).
- Qi GQ. 1985a. Stratigraphic summarization of Ramapithecus fossil locality, Lufeng, Yunnan. *Acta Anthropol Sin.* 4(1):55–69. (in Chinese with English summary).
- Qi GQ. 1985b. A preliminary report on Carnivora from the Ramapithecus fossil locality, Lufeng, Yunnan. *Acta Anthropol Sin.* 4(1):33–43. (in Chinese with English summary).
- Qiu ZD, Han DF, Qi GQ, Lin YF. 1985. A preliminary report on a micromammalian assemblage from the Hominoid locality of Lufeng, Yunnan. *Acta Anthropol Sin.* 4(1):13–32. (in Chinese with English summary).
- Qiu ZX, Qiu ZD. 1995. Chronological sequence and subdivision of Chinese Neogene mammalian fauna. *Palaeogeogr Palaeoclimatol Palaeoecol.* 116(1–2):41–70.
- Qiu ZX, Wang BY, Xie JY. 1998. Mid-Tertiary chalicothere (Perissodactyla) fossils from Lanzhou, Gansu, China. *Vert Palasiat.* 36(4):297–318. (in Chinese and English).
- Schulz E, Fahlke JM, Merceron G, Kaiser T. 2007. Feeding ecology of Chalicotheriidae (Mammalia, Perissodactyla, Ancylopoda). Result from dental micro- and mesowear analysis. *Verh Natur Ver Hamburg.* 43:5–31.
- Semperebon GM, Sise PJ, Coombs MC. 2011. Potential bark and fruit browsing as revealed by stereomicroscopic analysis of the peculiar clawed herbivores known as Chalicotheres (Perissodactyla, Chalicotherioidea). *J Mamm Evol.* 18(1):33–55. doi:10.1007/s10914-010-9149-3.
- Sun BY. 2013. The Miocene Hipparion (Equidae, Perissodactyla) from Shihuiba locality, Lufeng, Yunnan. *Vert Palasiat.* 51(2):141–161. (in Chinese with English summary).
- Ni XJ, Qiu ZD. 2002. The micromammalian fauna from the Leilao Yuanmou hominoid locality: implications for biochronology and paleoecology. *J Hum Evol.* 42(5):535–546. doi:10.1006/jhev.2001.0540.
- Zapfe H. 1979. *Chalicotherium grande* (Blainv.) from a Miocene fissure of Neudorf on the March River (Devinská Nová Ves), Czechoslovakia. *N DenkSch Natur hist Mus Wien.* 2:1–282.
- Zong GF. 1991. On age of the strata with Hominoid fossils in Yuanmou Basin. In: Institute of Vertebrate Paleontology and Paleoanthropology, editor. *Contributions to the XIII INQUA*. Beijing: Beijing Science and Technology Publish House. (in Chinese) p. 55–60.

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