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Article original

Dental characters of the Quaternary tapirs in China, their significance in classification and phylogenetic assessment

Caractères dentaires des tapirs du Quaternaire de Chine : signification pour la classification et a la phylogénie

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Abstract

Most of the Quaternary tapir fossils from China are isolated teeth. The purpose of this paper is to identify them and to extract systematic and evolutionary information from them. Based on morphology and W/L ratio, isolated teeth can be identified successfully. On the whole, the identification of P^1, M^3 and P_2 is believed to be reliable, while it is difficult to distinguish P_3 from P_4, M_1 from M_2 etc. Concerning the variations of the teeth, P^1 is the most variable one in dimension. In the Quaternary tapirs in China, some dental characters can be used as reliable indicators to evaluate their evolutionary levels. The degree of the atrophy of the upper canine relative to the caniniform I^3 is reflected in the C/I^3 diameter ratio, which is decreasing during evolution. P^1 changes considerably in outline and strength of the hypocone. Some forms are without hypocone, such as *Tapirus sanyuanensis*, some have a very faint hypocone, such as *Tapirus indicus*; although most of them show a developed hypocone. For other cheek teeth, the W/L ratio is decreasing through geologic time. Two lineages can be tentatively proposed: one is the *Tapirus peii–Tapirus sinensis–Megatapirus augustus* progression; the other is the *T. sanyuanensis–T. indicus* lineage. *T. sanyuanensis* and *T. peii* stand on the base, and it is very probable that the latter is more primitive.

Résumé

La plupart des tapirs fossiles de Chine ne sont connus que par leurs dents isolées. Le but de ce travail est de les identifier et d'en extraire l'information systématique et évolutive. Globalement, l'identification de P^1, M^3 et P_2 est considérée comme fiable alors qu'il est plus difficile de distinguer P_3 et P_4, M_1 de M_2, etc. Concernant les variations des dents, P^1 est la plus variable en termes de dimension. Chez les tapirs du Quaternaire de Chine, quelques caractères dentaires peuvent être utilisés de façon fiable pour évaluer leur niveau évolutif. Le degré d'atrophie de la canine supérieure par rapport à la caniniforme I^3 est reflété par le rapport du diamètre de C/I^3 qui décroît au cours de l'évolution. P^1 change considérablement au niveau du contour et de la force de l'hypocône. Certaines formes n'ont pas d'hypocône telles que *Tapirus sanyuanensis* d'autres ont un hypocône très faiblement marqué comme *T. indicus*. Toutefois, la plupart des formes ont un hypocône développé. Pour les autres dents jugales, le rapport l/L décroît à travers le temps géologique. Deux lignées peuvent être proposées : l'une représentant la progression *Tapirus peii–Tapirus sinensis–Megatapirus augustus* l'autre étant la lignée *T. sanyuanensis–Tapirus indicus*. *T. sanyuanensis* et *T. peii* ont une position basale et il est très probable que cette dernière lignée soit plus primitive.

Keywords: Dental characters; Evolutionary degree; Tapir; Quaternary; China

Mots clés : Caractères dentaires ; Degré d'évolution ; Tapir ; Quaternaire ; Chine

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1. Introduction

Because practically all of the available Quaternary tapir fossils are teeth materials, most research work on tapirs has focused on dental characteristics. In fact, Schoch (1989) proposed that "if more than one genus were generally recognized among Pleistocene and recent tapirs, then most isolated tapir teeth would be generically indeterminant."

Concerning the dental characters of the Pleistocene and recent tapirs, Simpson (1945) once conducted some studies, especially paying attention to the variations of tooth dimensions. He pointed out that most of the characters of tapir dentitions that have been utilized in the separation of species are suspect. Lundelius and Slaughter's (1976) observations show that "such features as the presence, absence, or strength of basal tubercles between the lophs (both lingual and labial) of upper and lower teeth are extremely variable in all American species of *Tapirus*. The degree of molarization of P^1 and/or P^2 appears to be the most promising feature of the dentition to differentiate geographic populations but even this must be treated with caution."

The new research on the materials from South China (Fig. 1) shows that there have been certain evolutionary changes in dental characters for the Quaternary tapirs. In the dentition of *Tapirus*, there exist some special features, such as the caniniform I^3, the degree of molarization of P^1 and P^2, and the variation of W/L ratio of other cheek teeth. All these features might have evolutionary or/and taxonomic significance.

Abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology; L, length; W, width; Wa, width of anterior lobe; Wp, width of posterior lobe; W/L ratio, width/length ratio.

2. Summary of systematics

2.1. Tapirus indicus *Desmarest (1819)*

Distribution: Anyang, Henan. Holocene (Teilhard de Chardin and Young, 1936).

Characteristics: The largest species of living tapir, but smaller than *Tapirus sinensis* and *Megatapirus augustus*. The skull has a very high nasal opening and a prominent occipital ridge. The anterior teeth arrange loosely; lower canine and upper I^3 robust and directed outwardly. The upper canine and I^3 are compressed conical in shape. The inner cusp on P^1 is very weak.

2.2. Tapirus sanyuanensis *Huang (1991)*

Type specimen and type locality: Maxilla with P^4–M^3 (CV.858). Damiao, Wushan in Chongqing (Huang and Fang, 1991).

Distribution: Wushan in Chongqing; Fanchang in Anhui; Jianshi in Hubei. Early Pleistocene.

Characteristics: The most important character is the absence of inner cusps on P^1. Almost the same size as *T. indicus*, but much smaller than *M. augustus*. Nasal heart-shaped. The mandibular symphysis is relatively shorter and narrower, and the distal end is not expanded. Incisors arrange densely. The lingual tubercles in I^1 and I^2 are very developed. The caniniform I^3 and the lower canine are nearly circular in cross section. P^1 is sub-triangular in shape, with a wide ledge of internal cingulum. The cheek teeth are relatively lower-crowned than these of *T. indicus*. The medisinus is relatively more open on the upper molars. Hypoconulids on M_3 is prominent (Huang and Fang, 1991; Tong et al., 2002).

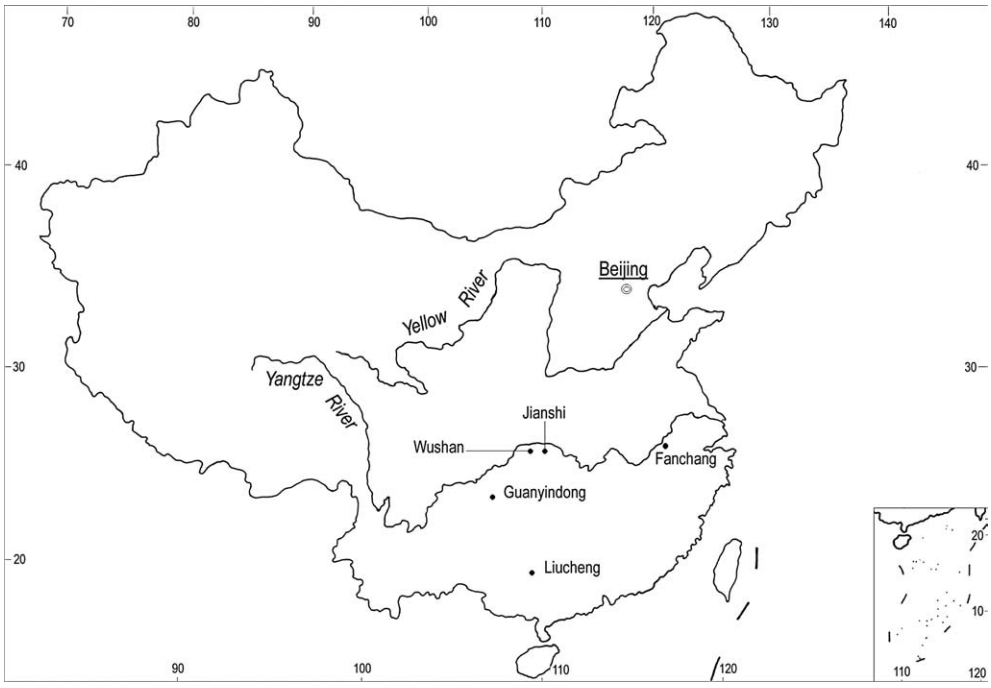

Fig. 1. Locations of the tapir localities of this study.
Fig. 1. Localisation des tapirs dans cette étude.

2.3. Tapirus peii Li, *MS, (1979)*

Lectotype and type locality: Incomplete skull with P^4, M^1 and M^2 (V 5780.428). Liucheng, Guangxi.

Distribution: Liucheng in Guangxi. Early Pleistocene.

Characteristics: It is a primitive form, characterized by small size and less molariformity of P^2. Otherwise it resembles *T. sinensis* more closely than does *T. sanyuanensis*. P^1 with developed inner cusp.

This species was named by Li Youheng in 1979, but this has not been formally published yet. It is really a pity that only parts of the fossil materials are available today (Fig. 2).

2.4. T. sinensis *Owen (1870)*

Lectotype and type locality: Right M^3. Yanjinggou, Sichuan (Owen, 1870).

Distribution: More than 10 localities in South China. Early to Middle Pleistocene.

Characteristics: Larger than *T. sanyuanensis*, smaller than *M. augustus*. The W/L ratio of cheek teeth is smaller than in *T. sanyuanensis*. P^1 with developed inner cusp (hypocone). In upper cheek teeth, outer cingulum is developed on the posterior lobe, anterior and posterior cingula very developed (Tong, 2004).

2.5. M. augustus *Matthew and Granger (1923)*

Type specimen and type locality: Number 18433, skull and jaws. Yanjinggou (= Yenchingkou), Sichuan (Matthew and Granger, 1923).

Distribution: More than twenty localities in south China. Middle to Late Pleistocene.

Characteristics: Teeth and skull about one-fourth larger lineally than *T. indicus* or *terrestris* and almost as much exceeding *T. sinensis* in size. Anterior premolars more molariform than in *T. indicus*, the inner cusp and cingulum much more developed, especially in P^1 which is wider than long. Skull very short and deep, the vomer higher and thicker than in *T. indicus*, much more so than in *Tapirus terrestris* (Matthew and Granger, 1923).

3. Identification of isolated teeth

The identification of tapir teeth in some previous publications are questionable. Colbert and Hooijer (1953) said that in *M. augustus*, there is no DP^4 in the upper tooth row. Shi et al. (1981) mistook P^1 for P^2 in their description of *Tapirus yunnanensis*. It is necessary therefore to stress that the dental formula for the Late Cenozoic tapirs in China should be as follows: 3·1·4·3/3·1·3·3 for permanent dentition and 3·1·4/3·1·3 for milk dentition.

Most of the tapir teeth are characteristic enough to be distinguished from those of other mammals. Only some lower tapir incisors resemble those of ape in its spatulate shape (Fig. 3).

Among the isolated tapir teeth, most of them are easily recognizable, such as DP^1, P^1, DP_2, P_2 and M3s, but the others are not so easy to be distinguished from each other. Among anterior teeth, the difficulties lie in the distinction between I1 and I2 for both upper and lower teeth, and between upper I^3 and lower canine. It is also very difficult to distinguish P_3 from P_4. Some studies have been conducted in order to distinguish the isolated teeth detailed below.

3.1. Tooth morphology

3.1.1. Between upper I^3 and the lower canine

In I^3, the wear surface of the crown is on the posterior side, and the root is much more robust and is curved. In the lower canine, the wear surface of the crown is on the anterior

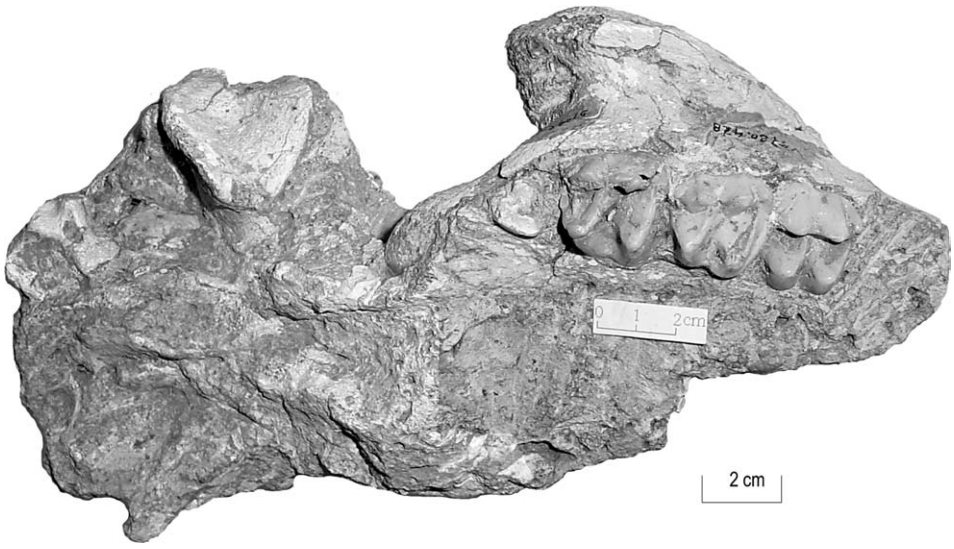

Fig. 2. V 5780.428, lectotype of *T. peii.* Incomplete skull with P^4, M^1 and M^2. Basal view.
Fig. 2. V 5780,428, lectotype du *T. peii.* Crâne incomplet avec P^4, M^1 et M^2. Vue basale.

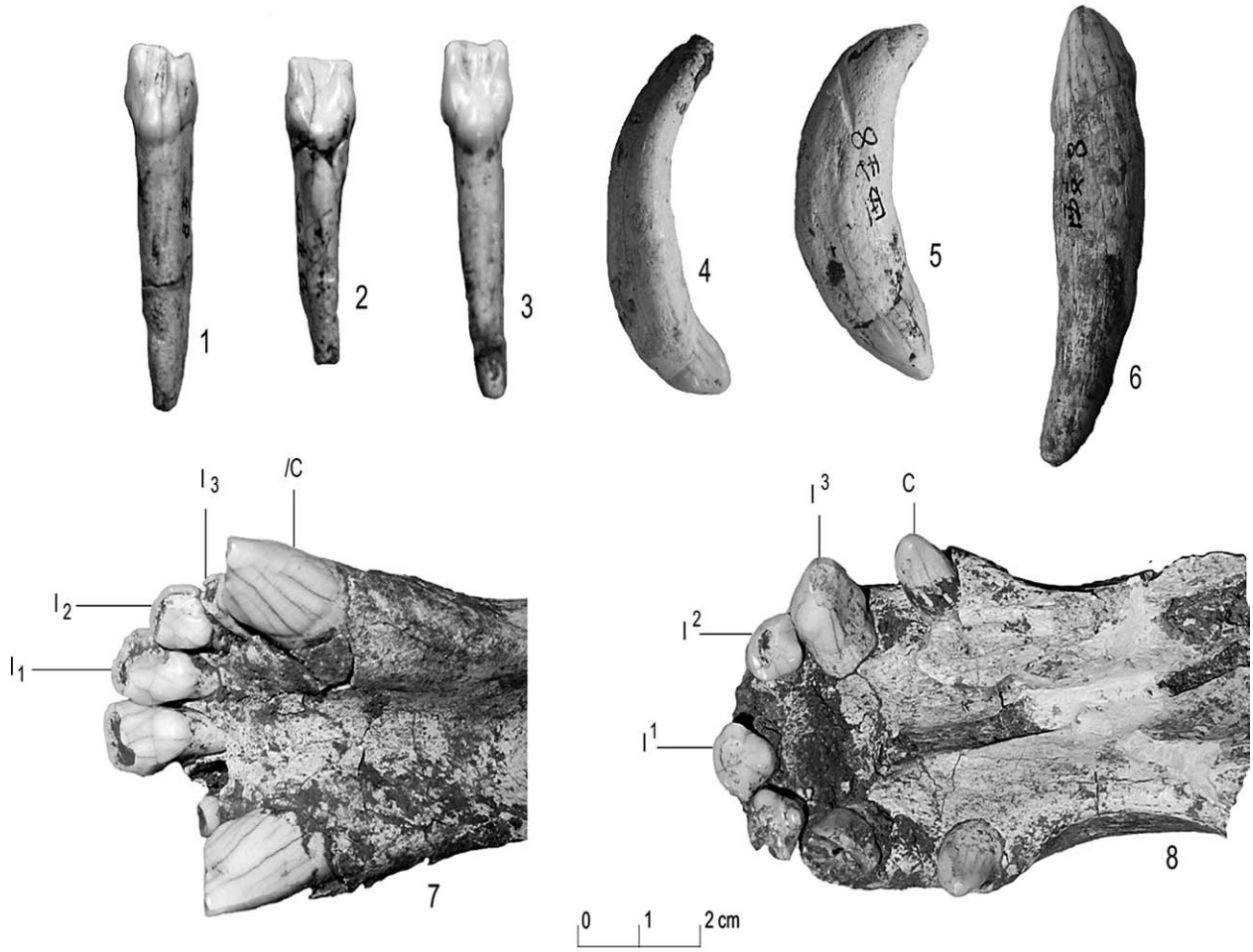

Fig. 3. **1**–**6**. Anterior teeth of *T. sinensis* from Jianshi. (1–3) I_1; (1) V 13588.306, labial view, (2–3) V 13588.393, V 13588.419, lingual view. (4) V 13588.293, upper canine. (5) V 13588.301, third upper incisor. (6) V 13588.611, lower canine. **7**, **8**. V 12576. 01, muzzle of *T. sanyuanensis* from Fanchang; (7) lower anterior teeth, superior view; (8) upper anterior teeth, basal view.
Fig. 3. **1**–**6**. Dents antérieures du *T. sinensis* de Jianshi. (1–3) I_1 ; (1) V 13588.306, vue labiale, (2–3) V 13588.393, V 13588.419, vue linguale. (4) V 13588.293, canine supérieure. (5) V 13588.301, troisième incisive supérieure. (6) V 13588.611, canine inférieure. **7**, **8**. V 12576. 01, museau du *T. sanyuanensis* de Fanchang ; (7) dent antérieure inférieure, vue supérieure ; (8) dent antérieure supérieure, vue basale.

side of the tip, and the root is slender than that of upper I^3 and is almost straight.

3.1.2. Between deciduous and permanent teeth

Simpson (1945) wrote that he could not distinguish all DM_2 (DP_2) from P_2, in upper teeth, while the same difficulty exists with regard to DP^1 and P^1.

Actually it is not very difficult to distinguish milk teeth from permanent ones, because milk teeth usually are lower-crowned. Milk teeth are larger than their successors (Figs. 4–6). On DP^1, there is a faint cingulum in front of the protocone; and the metaloph connects with the ectoloph, but on P^1, the metaloph is not developed, and the hypocone is almost isolated; it seems that DP^1 is more uniform in morphology than P^1 in all the four fossil forms (Fig. 4). DP^2 is typical of its great dimension of length relative to P^2; DP^3 and DP^4 are completely different from P^3 and P^4, respectively. Usually DP^4 resembles M^1 very much, except its relatively smaller size (Fig. 5).

For the lower cheek teeth, the deciduous ones are much longer than the permanent premolars. Additionally, DP_2 has greater transversely extended metalophid, and the anterior and posterior valleys are much broader (Fig. 6).

Furthermore, milk teeth usually have thinner enamel layer than their permanent counterparts.

3.1.3. Premolars and molars

Molars are quite distinct from the premolars. Premolars usually have a lower W/L ratio, with less developed parastyle, and a narrower medisinus. Molars usually have shorter metaloph and broader medisinus. Molars have much better developed accessory ridges than premolars, both on upper and lower teeth.

3.1.4. Among premolars

P^3 is rhomboid in outline, but P^4 usually has a much shorter metaloph compared with protoloph; P^3 has a much broader medisinus than P^4. Additionally, P^3 has a lower W/L ratio than P^4 (Fig. 7).

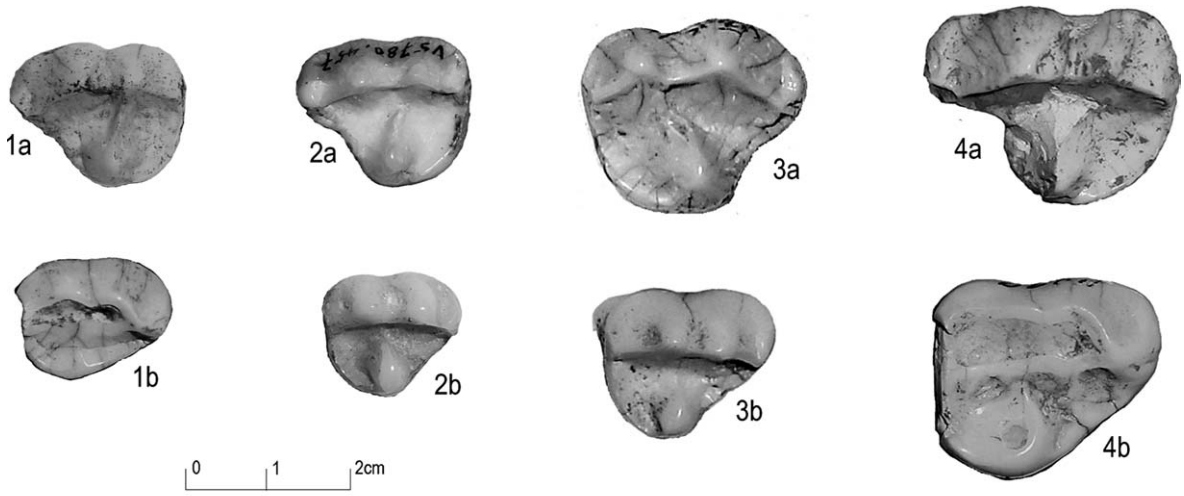

Fig. 4. Comparison between DP^1 and P^1. (a) deciduous teeth; (b) permanent teeth. **1**. *T. sanyuanensis* from Fanchang, (1a) V 12575.01; (1b) V 12576.01. **2**. *T. peii* from Liucheng, (2a) V 5780.457, (2b) V 5780.433. **3**. *T. sinensis* from Jianshi. (3a) V 13588.351, (3b) V 13588.66. **4**. V 5201, *M. augustus* from Guanyindong. Occlusal view.

Fig. 4. Comparaison entre DP1 et P1. a) dents déciduales ; b) dents définitives. **1.** *T. sanyuanensis* de Fanchang, (1a) V 12575.01 ; (1b) V 12576.01. **2.** *T. peii* de Liucheng, (2a) V 5780.457, (2b) V 5780.433. **3.** *T. sinensis* de Jianshi. (3a) V 13588.351, (3b) V 13588.66. **4.** V 5201, *M. augustus* de Guanyindong. Vue occlusale.

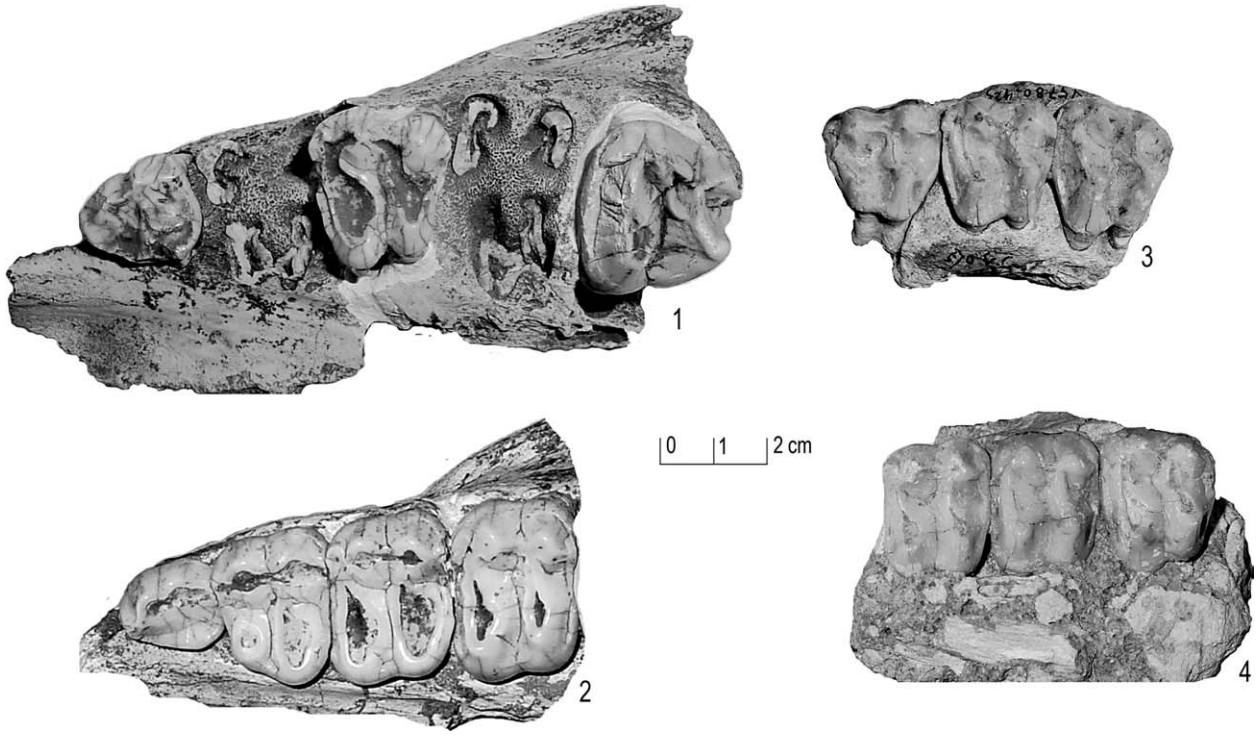

Fig. 5. Comparison between upper deciduous cheek teeth and their successors. **1**, **2**. *T. sanyuanensis* from Fanchang; (1) V 12573.01, left maxilla with DP^1, DP^3 and M^1. (2) V 12576.01, left maxilla with $P^{1–4}$. **3**, **4**. *T. peii* from Liucheng; (3) V 5780.425, upper $DP^{2–4}$; (4) V 5780.421, upper P^3-M^1. Occlusal view.

Fig. 5. Comparaison entre les dents jugales déciduales supérieures et leurs remplaçantes. **1**, **2**. *T. sanyuanensis* de Fanchang ; (1) V 12573.01, maxillaire gauche avec DP^1, DP^3 et M^1. (2) V 12576.01, maxillaire gauche avec $P^{1–4}$. **3**, **4**. *T. peii* de Liucheng ; (3) V 5780,425, $DP^{2–4}$; (4) V 5780,421, P^3-M^1. Vue occlusale.

In the lower tooth row, among the premolars, the length is decreasing from P_2 to P_3, P_2 is the longest, and P_3 is the shortest.

3.1.5. Among molars

In the upper tooth row, M^1 differs from the other two molars in its relatively smaller size. M^2 is very similar to M^3 when both teeth are newly erupted, but they can be distinguished in the following aspects: M^2 has a more developed parastyle and a narrower medisinus as well as a more developed metaloph than is found in M^3 (Fig. 8); when the neighboring M^3 is fully grown, M^2 has a vertical contact facet on the posterior side, which is absent from M^3. From M^1 to M^3, the postsinus is getting more developed.

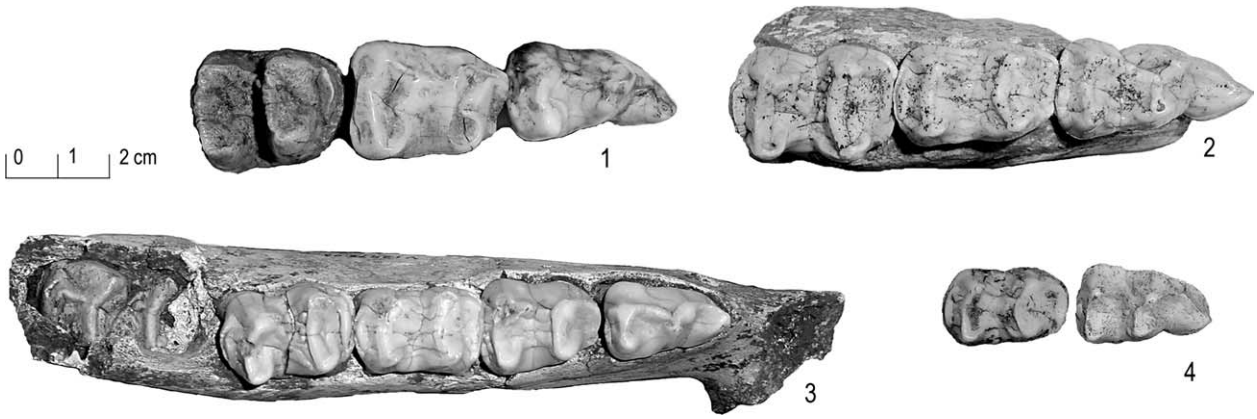

Fig. 6. Comparison between lower deciduous cheek teeth and their successors. **1**, **2**. V 5201, *M. augustus* from Guanyindong; (1) $P_{2–4}$; (2) DP_{2-4}. **3**, **4**. *T. sanyuanensis* from Fanchang; (3) V 12578.03, left mandible with $P_{2–3}$, DP_4, M_1; (4) V 12575.02, DP_2, and V 12575.03, DP_3.
Fig. 6. Comparaison entre les dents jugales déciduales inférieures et leurs remplaçantes. **1**, **2**. V 5201, *M. augustus* de Guanyindong ; (1) $P_{2–4}$; (2) $DP_{2–4}$. **3**, **4**. *T. sanyuanensis* de Fanchang ; (3) V 12578.03, mandibule gauche avec $P_{2–3}$, DP_4, M_1 ; (4) V 12575.02, DP_2, et V 12575.03, DP_3.

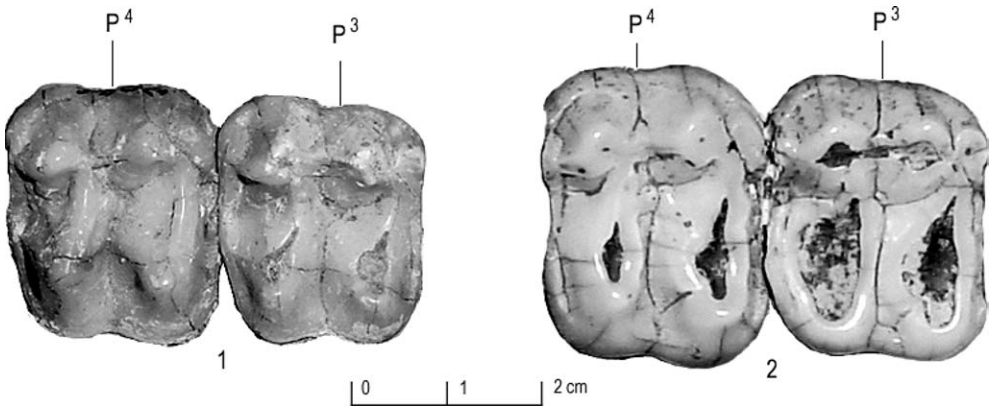

Fig. 7. Comparison between P^3 and P^4. **1**. V 5780.421, *T. peii* from Liucheng. **2**. V 12576.01, *T. sanyuanensis* from Fanchang. P^3 is rhombus in outline; P^4 has much shorter metaloph than the protoloph and is irregular in outline.
Fig. 7. Comparaison entre P^3 et P^4. **1**. V 5780,421, *T. peii* de Liucheng. **2**. V 12576.01, *T. sanyuanensis* de Fanchang. P^3 a un contour losangique ; P^4 présente un métalophe beaucoup plus court que le protolophe et a un contour irrégulier.

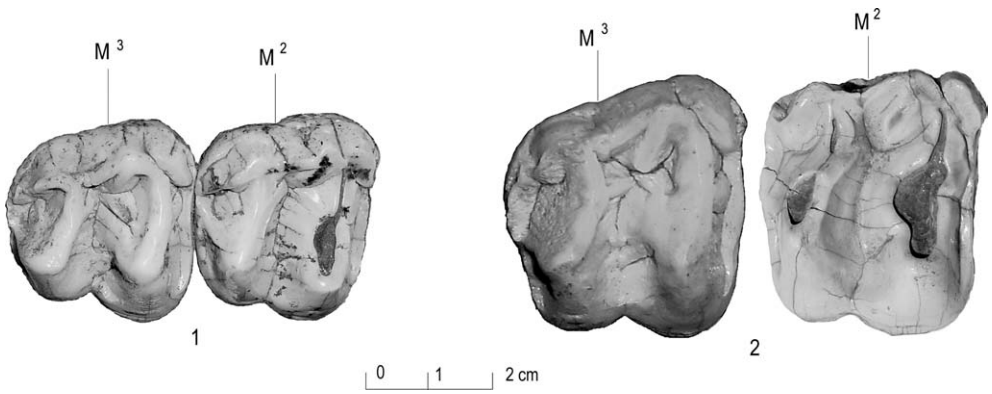

Fig. 8. Comparison between M^2 and M^3. **1**. V 12576.01, *T. sanyuanensis* from Fanchang. **2**. V 5201, *M. augustus* from Guanyindong.
Fig. 8. Comparaison entre M2 et M3. 1. V 12576.01, *T. sanyuanensis* de Fanchang. 2. V 5201, *M. augustus* de Guanyindong.

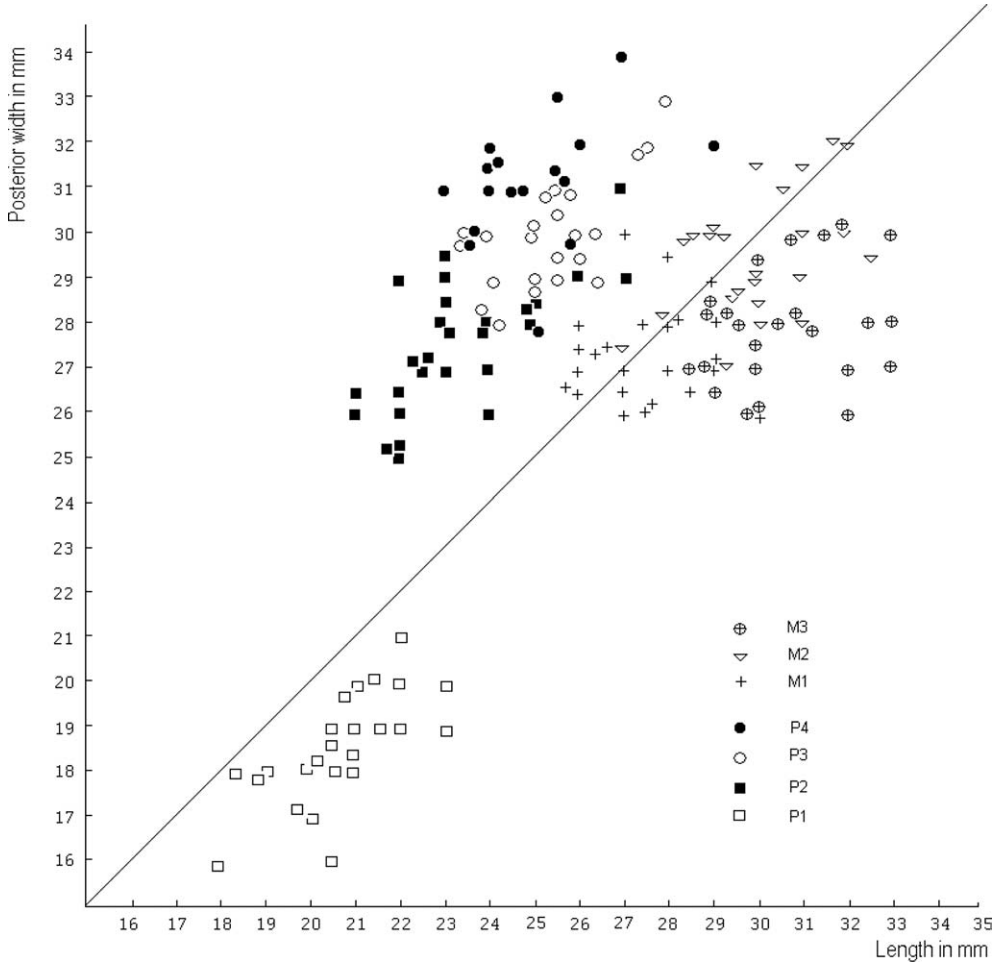

Fig. 9. Scatter diagram of length vs. posterior width of the upper cheek teeth of *T. sinensis* from Jianshi. In dimensions, P^1 and P^2 are the most variable teeth.
Fig. 9. Diagramme de dispersion des longueurs - largeurs postérieures des dents jugales supérieures de *T. sinensis* de Jianshi. P^1 et P^2 sont les dents les plus variables en dimension.

3.2. Tooth proportions

Besides the dental morphology, the proportions in dental dimensions also can be employed for taxonomic and phylogenetic usage.

3.2.1. Deciduous and permanent teeth

In the upper tooth row, milk teeth usually have a larger W/L ratio than permanent teeth.

3.2.2. Premolars and molars

Premolars usually have a larger W/L ratio than molars, and their W/L are above the average line. However, P^1 is always under the average line (Fig. 9).

3.2.3. Among premolars

From P^2 to P^4, the Wa/Wp ratio is increasing in the upper tooth row.

3.2.4. Among molars

From M^1 to M^3, the Wa/Wp ratio is increasing.

4. Caniniform I^3

A specialized feature of *Tapirus* is the atrophy of the upper canine and the enlargement of the third upper incisor into a caniniform tooth (Radinsky, 1965). This feature becomes increasingly clear in the later forms of tapirs (Figs. 9 and 10).

C/I^3 diameter ratio: Now that it is definite that the upper canine shrinks through time, we can use the C/I^3 diameter ratio as an index to estimate the evolutionary levels of the fossil tapirs. The larger the value of the index, the more primitive the animal.

For *T. sanyuanensis*, the C/I^3 ratio (vestibulo-lingual diameter) = 0.82; the C/I^3 ratio (Mesio-distal diameter) = 0.69.

For *T. sinensis*, the C/I^3 ratio (vestibulo-lingual diameter) = 0.6; the C/I^3 ratio (Mesio-distal diameter) = 0.57.

For *T. indicus*, the C/I^3 ratio (vestibulo-lingual diameter) = 0.5; the C/I^3 ratio (Mesio-distal diameter) = 0.57.

It can be seen from the measurements (Table 1) that the indices are decreasing from *T. sanyuanensis* via *T. sinensis* to *T. indicus*.

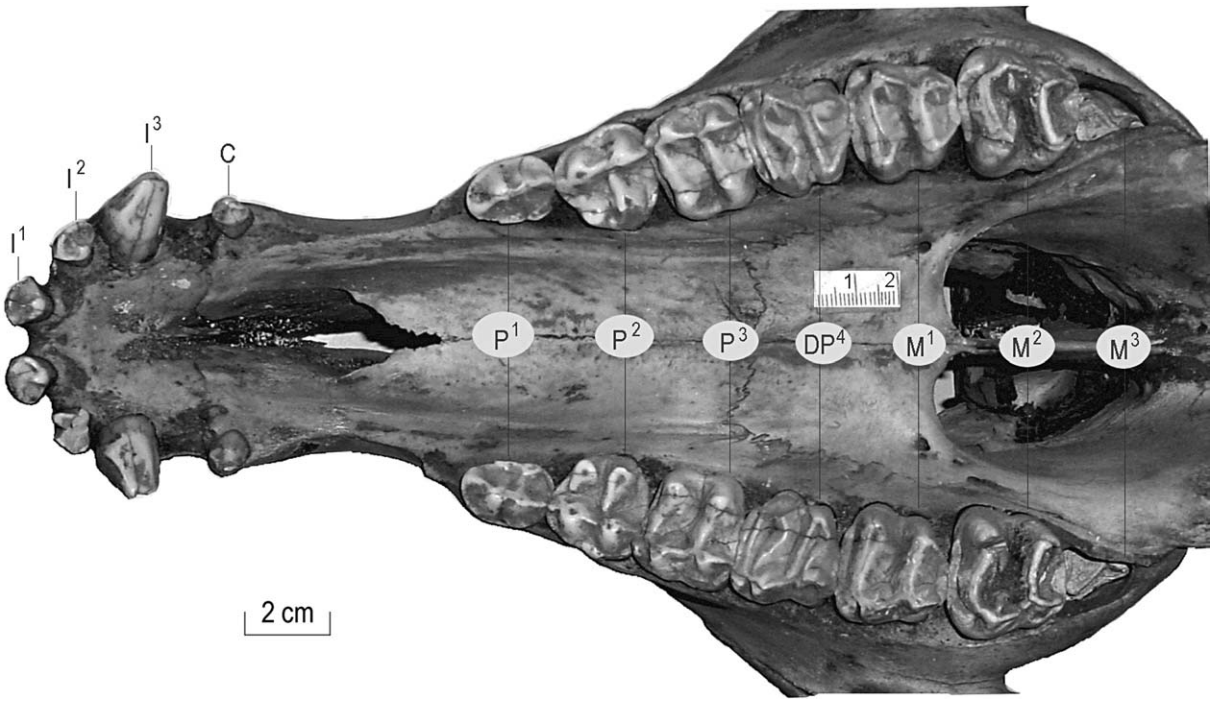

Fig. 10. V 1325, recent *T. indicus*, skull, basal view. It shows that the canines are greatly reduced and much smaller than I^3; It also shows that M^2 erupts later than P^{2-3}, because P^{2-3} are in wear, whereas M^2 is still very fresh and unworn.
Fig. 10. V 1325, *T. indicus* actuel, crâne, vue basale. Les canines sont fortement réduite et bien plus petite que I^3 ; l'éruption de P^{2-3} précède celle de M^2, parce que P^{2-3} est fonctionnelle avec des facettes d'usure, alors que M^2 est fraîche, non usée.

Table 1
Measurements of the anterior teeth (in mm)
Mesures des dents antérieures (en mm)

		T. sanyuanensis V 12576.01 (Tong et al., 2002)	*T. sinensis* Jianshi	*T. indicus* IVPP. 1326
I^3	Height of the crown	15	17	24
	Vestibulo-lingual diameter	11	13.5	14
	Mesio-distal diameter	13	14	15
C/	Height of the crown	10	10.5	11
	Vestibulo-lingual diameter	9	8	7
	Mesio-distal diameter	9	8	8.5

5. Variations of teeth

With regard to the variation of tapir teeth, the work should be conducted in two aspects: morphological and dimensional. Simpson (1945) provided an excellent dimensional study of tapir teeth, fossil and recent. In Europe, Eisenmann and Guérin (1992) also studied the variation of Miocene tapir fossils, in which they reached similar conclusions to some extent.

It should be indicated that in the present statistical work only the teeth that can be determined without doubt were taken into consideration, such as those listed in Table 2.

In the present sample, most of the results agree with those of Simpson and Eisenmann and Guérin, but some differences occurred. It seems that the situation for deciduous dentition is the most complicated; in morphology, they are less variable than their successors (Fig. 4); but in dimensions, they are more variable (Table 2). For the Chinese materials, dimensional variation is more detectable than morphological one. Through the dimensional studies, it appears that DP^1, P^1 and P^2 as well P_2 are among the most variable teeth (Fig. 11).

The study of tooth variation is not the final purpose, it is only a way to provide information for classification and phylogenetic evaluation. Through this kind of study, we can know which kind of features can be used as reliable indicators of evolutionary level, which kind of characters can only be used for intra-specific distinction, and which kind of feature can be used for inter-specific distinction. In the case of P^1, its morphology is really very useful for species recognition. Morphologically, they are quite stable within a species. Among 35 P^1 specimens of *T. sinensis*, the structure of the tooth crown is very uniform (Fig. 11), the hypocone always being present. In contrast to this, however, the size and dimensions vary markedly (Table 2). It shows that the presence or absence and the strength of hypocone on P^1 can be used to distinguish different species, though P^1 is among the most variable teeth in dimensions as has been mentioned above. Another useful parameter found as a result of the study of variation is the W/L ratio of the cheek teeth, showing that the W/L ratio of upper cheek teeth of the four Chinese Quaternary tapir species decreases with time (Fig. 12).

6. Character changes among the Quaternary tapirs in China

Colbert and Schoch (1998) indicated that "the evolution of the tapirids is largely a story of the refinement of the pro-

Table 2
Cheek tooth dimensions of *T. sinensis* from Jianshi (in mm)
Dimensions des dents jugales du *T. sinensis* de Jianshi (en mm)

Tooth		Number of specimen	Mean	Minimum value	Maximum value	Standard deviation	Coefficient of variation
DP^1	L	7	21.5	20	24	1.68	7.8
	Wp		19.3	17.5	21	1.52	7.9
DP^2	L	7	25.6	25	27	0.80	3.1
	Wp		24.3	23	25	1.6	6.4
DP^3	L	11	26.2	25	28	0.9	3.5
	Wa		27.2	25	29	1.3	4.8
DP^4	L	13	26.8	25.5	28	0.83	3.1
	Wa		29.1	27.5	30.5	1.2	4.0
P^1	L	35	20.3	18	24	1.3	6.2
	Wp		18.7	16	21	1.3	6.8
P^2	L	34	24	21	27	1.6	6.8
	Wp		27.5	25	31	1.4	5.0
M^3	L	29	30.5	28	33	1.5	4.9
	Wa		34.2	32	38	1.4	4.1
DP_2	L	3	29.8	29	31	1.0	3.4
	Wp		16.2	15.5	17	0.76	4.7
DP_3	L	6	25.6	25	26.5	0.58	2.3
	Wp		16.5	15.5	17	0.6	3.6
DP_4	L	5	28.2	27.5	29	0.7	2.5
	Wa		18.5	17.5	19	1.0	5.4
P_2	L	32	26.3	23	30	1.6	6.1
	Wp		16.2	14.5	20	1.2	7.4
M_3	L	30	32.8	30	35	1.5	4.6
	Wp		22.9	20	25	1.2	5.2

boscis, molarization of the premolars, and a general increase in size."

Up to now, five species of Quaternary tapir have been noted in China. As few skulls and post-cranial materials have been discovered so far, we have to exploit more information from the teeth.

As to the lingual cusps on P^1, Albright (1998) proposed that the more the form is advanced, the more it will be developed. But it seems that this law does not work well when applied to the Chinese material. Since the Late Cenozoic, the evolutionary tendency of tapir is punctuated, because the Miocene (Qiu et al., 1991) and Pliocene (Shi et al., 1981) tapirs have much more developed lingual cusps than some Early Quaternary forms do. For the Chinese Quaternary tapirs, P^1 changes markedly in outline and in the strength of hypocone, some of them without inner cusp, such as in *T. sanyuanensis*, some of them with the weakest development of hypocone, such as in *T. indicus*; the others with developed inner cusp. Based on the foregoing, it seems reasonable to use the feature of P^1 to distinguish different species, but one has to be cautious to use it to evaluate the degree of evolution.

Concerning the evolution of tapirs in Southeast Asia, Hooijer (1947) proposed: "The Chinese teeth are doubtless specifically identical with the Malay tapir; they might, however, represent an extinct subspecies", and "The Malay tapir was larger in prehistoric times in Sumatra than it is at the present day. The fact that it was smaller again, of its recent dimensions, in the lower and middle Pleistocene of Java, and in the Pleistocene of southern China strongly suggests that the Chinese and the Javan forms represent different subspecies." Because Hooijer's hypothesis was based on very little Chinese materials, the present author does not agree with him concerning the systematical relationships among the Asian Quaternary tapirs. According to the current study, the evolutionary tendency for the Quaternary tapirs in China is quite clear, and some tendencies of character changes can be detected as follows.

6.1. Increasing body size

According to tooth and body size, from *T. sanyuanensis*, via *T. sinensis* to *M. augustus*, the body size is increasing (Figs. 13 and 14). In body size and P^1 shape, it seems that *T. indicus* is very close to *T. sanyuanensis*. The similarity in size between *T. sanyuanensis* and *T. indicus* lies not only in tooth dimensions, but also in skeletal measurements (Tong et al., 2002). *T. peii* is a primitive form, not only because of its small size, but also its less molariformity of P^2.

6.2. Decreasing width/length ratio of the cheek teeth

The W/L ratio of upper cheek teeth of the four Chinese Quaternary tapir species is decreasing with time. The difference between *M. augustus* and the living form was confirmed by Colbert and Hooijer (1953). In Fig. 12, it is shown

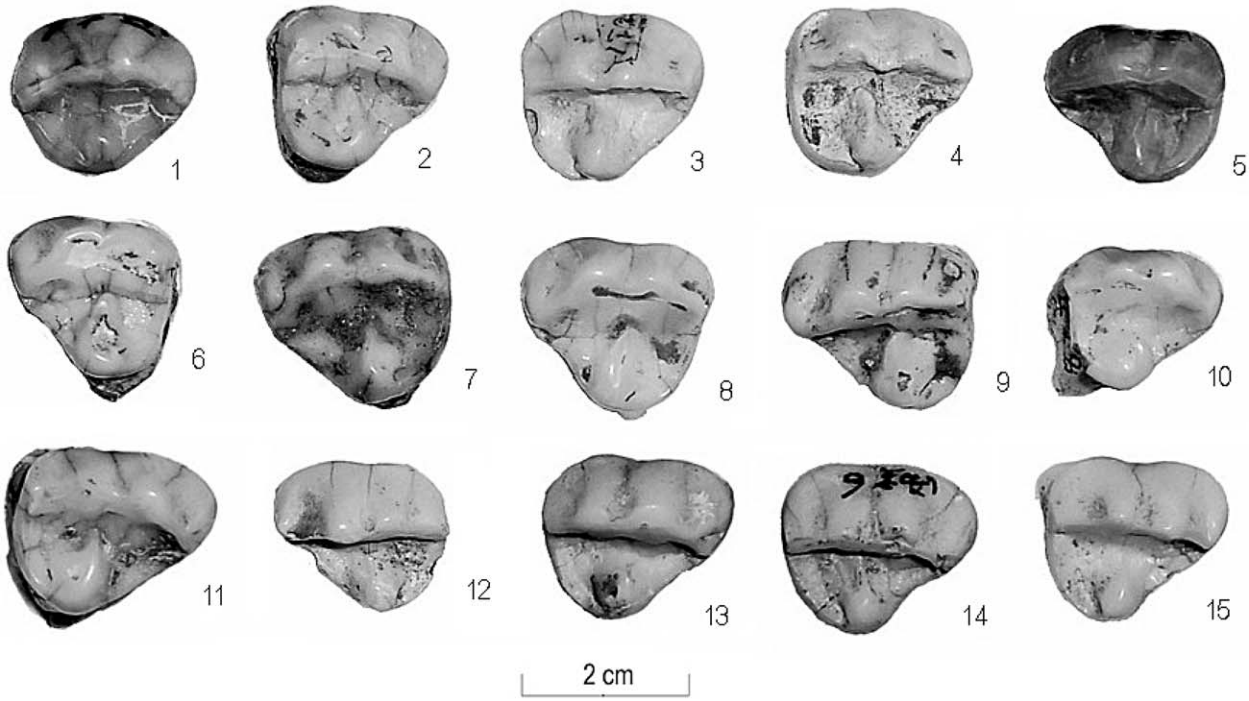

Fig. 11. Variation of P^1 of *T. sinensis* from Jianshi, in size they are very diversified (see Table 2); but in structure, except some few exclusions, it is almost uniform, the only notable change is the variations in W/L ratio. **1**. V 13588.293. **2.** V 13588.225. **3.** V 13588.169. **4.** V 13588.226. **5.** V 13588.170. **6.** V 13588.64. **7.** V 13588.457. **8.** V 13588.227. **9.** V 13588.229. **10.** V 13588.65. **11.** V 13588.66. **12.** V 13588.458. **13.** V 13588.230. **14**. V 13588.114. **15**. V 13588.113.

Fig. 11. Variation de P^1 du *T. sinensis* de Jianshi, en taille, elle est très diversifiée (voir Tableau 2) ; mais en structure, à part quelques cas, elle est pratiquement uniforme, le seul changement notable étant le rapprochement largeur/longueur. **1**. V 13588.293. **2**. V 13588.225. **3**. V 13588.169. **4**. V 13588.226. **5**. V 13588.170. **6**. V 13588.64. **7**. V 13588.457. **8**. V 13588.227. **9**. V 13588.229. **10**. V 13588.65. **11**. V 13588.66. **12**. V 13588.458. **13**. V 13588.230. **14**. V 13588.114. **15**. V 13588.113.

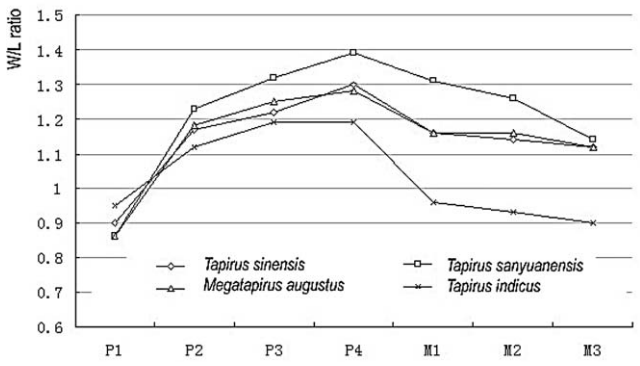

Fig. 12. W/L ratio of upper cheek teeth of the four Quaternary tapir species in China.

Fig. 12. Rapport de W/L des dents supérieures jugales des quatre espèces quaternaires de tapir en Chine.

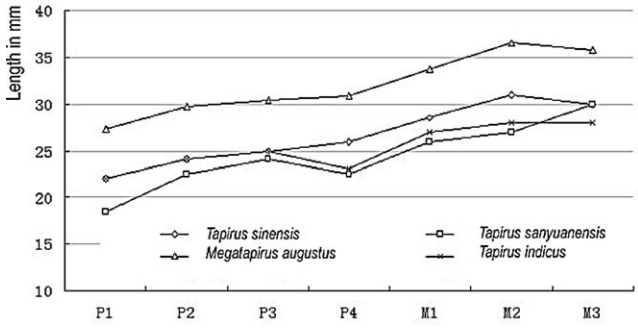

Fig. 13. Showing the size increase of cheek teeth through evolution from *T. sanyuanensis*, via *T. sinensis* to *M. augustus*.

Fig. 13. Augmentation de la taille des dents jugales de *T. sanyuanensis* à *M. augustus* via *T. sinensis*.

that *T. sinensis* is much closer to *M. augustus* than to other forms, as the two are also very close in body size. *T. peii* has a very low W/L ratio. It is very probable, therefore, that *M. augustus* derived from *T. sinensis* as was proposed by the author earlier (Tong and Xu, 2001), and that *T. sinensis* originated from *T. sanyuanensis* or *T. peii*. In conclusion, among all these tapir species, *T. peii*, *T. sinensis* and *M. augustus* are of close affinity, which shows in the well-developed inner cusps on P^1 and the lower W/L ratio of cheek teeth (Fig. 14).

6.3. C/I^3 diameter ratio

From the foregoing, it is apparent that the more advanced the form, the lower the ratio of C/I^3 diameter is, the living species has the lowest ratio (Fig. 15).

7. Conclusions

Among all the isolated teeth, DP^1, P^1, P^2, DP_2, P_2 are among the easiest ones to be identified; upper P^3 and P^4, lower P_3 and P_4, M_1 and M_2 are difficult to be distinguished.

Fig. 14. Comparison of P^1 (upper row) and M^3 (lower row) among the Quaternary tapirs in China and the Asian living form, they are quite different in size and morphology. All are in occlusal view. **1**. V 1325, *T. indicus*, living form. **2a**, **b**. V 12576.01, *T. sanyuanensis* from Fanchang. **3**. *T. peii* from Liucheng, (3a) V 5780.433, (3b) V 5780.760. **4**. *T. sinensis* from Jianshi, (4a) V 13588.113, (4b) V 13588.409. **5a, b**. V 5201, *M. augustus* from Guanyindong.
Fig. 14. Comparaison des P^1 (en haut) et M^3 (en bas) entre les tapirs quaternaires de Chine et les actuels d'Asie ; ils diffèrent tant en taille qu'en morphologie. Vue occlusale. **1**. V 1325, *T. indicus*, actuel. **2a**, **b**. V 12576.01, *T. sanyuanensis* de Fanchang. **3**. *T. peii* de Liucheng, (3a) V 5780,433, (3b) V 5780,760. **4**. *T. sinensis* de Jianshi, (4a) V 13588.113, (4b) V 13588.409. **5a**, **b**. V 5201, *M. augustus* de Guanyindong.

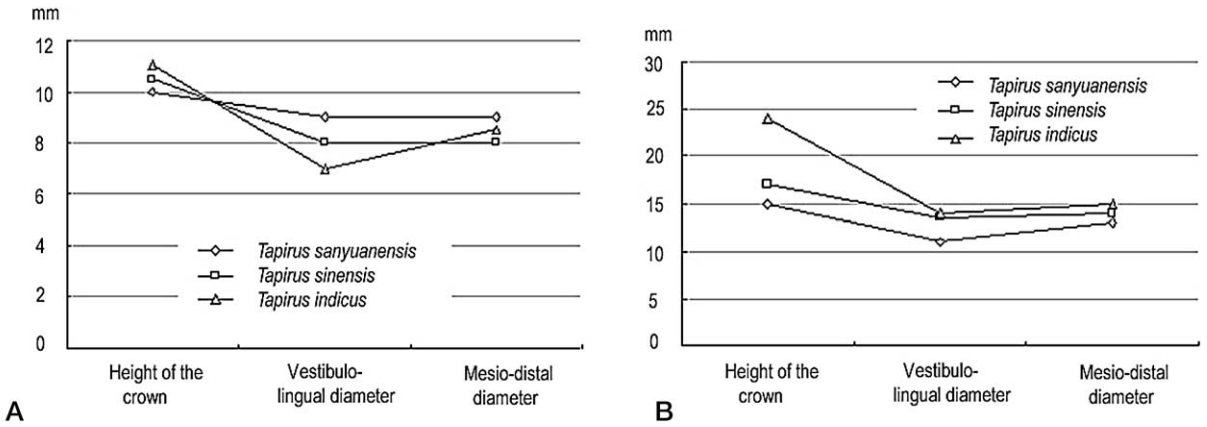

Fig. 15. Size comparison of upper canines (a) and I^3 (b) among recent *T. indicus*, *T. sanyuanensis* and *T. sinensis*. The figures show that the I^3 in *T. indicus* is much higher than in *T. sanyuanensis*, but *T. indicus* has much smaller upper canines, and *T. sinensis* stands between them.
Fig. 15. Comparaison des canines supérieures (a) et I^3 (b) de *T. indicus* actuel, *T. sanyuanensis* et *T. sinensis*. I^3 de *T. indicus* est nettement plus haute que celle de *T. sanyuanensis*, mais *T. indicus* a des canines supérieures beaucoup plus petites, *T. sinensis* se situant en position intermédiaire.

The W/L ratio of cheek teeth and C/I^3 diameter ratio decrease through time.

The character of P^1 and the W/L ratio of upper cheek teeth can be used as reliable evidence of identifying and/or evaluating evolutionary level of Quaternary tapirs.

In the Chinese Quaternary tapirs, two lineages can be recognized: one is the *T. peii–T. sinensis–M. augustus* progression; the other is the *T. sanyuanensis–T. indicus* lineage. *T. sanyuanensis* and *T. peii* stand on the base, and it is very probable that the latter is more primitive.

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