On fossil remains of Early Pleistocene tapir (Perissodactyla, Mammalia) from Fanchang, Anhui

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Abstract **The materials of *Tapirus* from Renzidong, Fanchang, Anhui Province, are the best ones among the early most Pleistocene findings in China up to now, not only in richness, but also in completeness. The fossils contain complete tooth rows of both the upper and the lower, as well as most parts of the postcranial skeletons. These materials are very helpful in understanding the evolutionary level of this kind of animal. In morphology, the materials from Fanchang appear to be very similar to *Tapirus sanyuanensis*, and can be placed within this species. The materials from Fanchang provided sound evidence to distinguish the Early Pleistocene tapirs and the living form *Tapirus indicus*. As to the geological distribution, it can be tentatively concluded that *Tapirus sanyuanensis* and *Tapirus sinensis* only appeared in Early Pleistocene, *Megatapirus* appeared after Early Pleistocene, and lasted until Holocene. The Early Pleistocene tapirs of South China resemble *Megatapirus* more closely than *Tapirus indicus.***

Keywords: Tapiridae, Mammalia, Early Pleistocene, Fanchang, Anhui.

Renzidong, located in Fanchang County, Anhui Province, is a very important locality found recently, it is under the organization of a big project aiming at searching for the earliest human remains and the studying of the related environmental background. Quite a lot of mammalian fossils have been found during excavation since 1998, and the most important finds include *Procynocephalus* and some almost complete skeletons of *Homotherium* and *Tapirus*. The geologic age of the new locality is between 2.4—2 Ma[1].

Tapir is among the most important members in the *Ailuropoda-Stegodon* fauna in South China, its latest record is around 5000 a BP. But because of the poor materials, the systematic studies on this group was not conducted in the past half century, and the relationships among *Tapirus sinensis, Megatapirus augustus* and *Tapirus indicus* remained uncertain for quite a long time.

1 Note on materials

(ⅰ) Materials. Almost all of the materials are from two individuals: V 12576 is an adult, the finds include complete premaxilla and upper tooth rows as well as almost complete mandibles. V 12578 is a sub-adult, the parts found include left mandible, major part of the right maxilla, supra-occipital bone, and fragment of right mandible. The majority of the postcranial skeletons are preserved, including vertebrae, scapular, ribs and limb bones. Very few materials from other individuals were also found.

(ⅱ) Skull. Most of the facial parts of the skull were preserved, including premaxilla, mandibular symphysis and complete tooth rows, nasal., etc., very few of the cranial part of the skull was preserved. Some fragments of other parts of the skull were found, including supraoccipital, parietal, zygomatic process of temporal, condyle of mandible, coronoid process, etc. The measurements of the skull are shown in table 1. The doubled sagittal crests form a flat table in the parietal and supraoccipital parts. The narrowest part of the table is 13 mm in width, but in the living form of Malay tapir, the narrowest

Table 1 Comparative measurements (in millimeters) of skull and teeth

Dimensions	*T. sanyuanensis* From Fanchang (V 12576)	*T. indicus* Living form (IVPP 1326)	*Megatapirus augustus* From Yanjinggou (Colbert et al., 1953)
Nasal breadth	>76	100	
Minimum width of the sagittal crest	13	37	
Upper premolar series, length	85	88	108—119
Upper molar series, length	79		89—101
Length of upper tooth row	164		
Maxillary diastema	47	52	
Lower premolar series, length	70—73	74	91—97
Lower molar series, length	85		104—111
Length of lower cheek tooth row	155		
Mandibular diastema	50	58	
Height of ramus in front of P_2	52	56	
Height of ramus behind P_4	63	66	
Length of mandibular symphysis	93	100	
Maximum width of mandibular symphysis	45	60	

part of the sagittal table is much wider, in a juvenile, it is 24 mm (IVPP 535), in a sub-adult, it is 37 mm (IVPP 1326). This bone fragment is supposedly from the sub-adult. Nasal is heart-shaped, the anterior tip bends downward slightly, the middle part is 11 mm thick, because both ends are broken, the maximum length of the nasal is uncertain, but definitely no less than 70 mm. The infraorbital foramen is located 30 mm in front of the orbit, corresponding with the vertical line between P^2 and P^3. The premaxilla is slightly compressed laterally during preservation, the frontal edge of the incisive foramen cannot be observable. The ascending process of the premaxilla has a sharp posterior projection ending about above the middle part of P^1. Anteriorly the zygomatic arch begins from above the anterior end of M^3. The anterior border of the orbit is above the middle part of P^4. The maxilla contracts sharply in front of P^1.

The horizontal ramus of mandible is robust, the inferior border is gently convex antero-posteriorly, and the buccal side is also convex, but the lingual side is flat. The mental foramen is located in front of the base of P_2. The ascending ramus is missing; the condyle of mandible is robust. The symphysis is long, and its distal end almost does not expand, the supra-symphyseal depression or groove is deep.

(iii) Dentition. Upper deciduous dentition: In the milk teeth, the most prominent character is that DP^1 and DP^2 are larger than their counterparts of the permanent teeth. The milk and permanent cheek teeth can be distinguished in the following aspects: milk teeth are more brachyodont and with a less developed enamel layer. The findings of upper milk teeth include DP^1, DP^3 and DP^4.

Upper permanent dentition: Incisors are small; there is a lingual tubercle in both I^1 and I^2 (see fig. 1, Plate Ⅰ), without diastema between incisors. I^1 is larger than I^2. All the upper incisors grow upright; the crowns are much wider than roots; there exists a shallow pit on the distal portion of the lingual side, it is very useful for the orientation of the anterior tooth; the crown surface is triangular, the labial wall is slightly convex. The mesiodistal length of the root is much less than its buccolingual width. I^3 is the largest and most developed upper incisor, which is of a caniniform, on its posterolingual corner, there is a worn surface which is the result of occlusion with the inferior canine.

The superior canine is vestigial and small, it is separated from I^3 by a short diastema of 10 mm, and is situated immediately behind the premaxillary-maxillary suture. It is peg-like in shape, but the lingual side is relatively flat, and the buccal side is convex (see fig. 1, Plate Ⅰ).

All the upper premolars, except P^1, are wider than the length, particularly for P^3 and P^4. The ectoloph is more

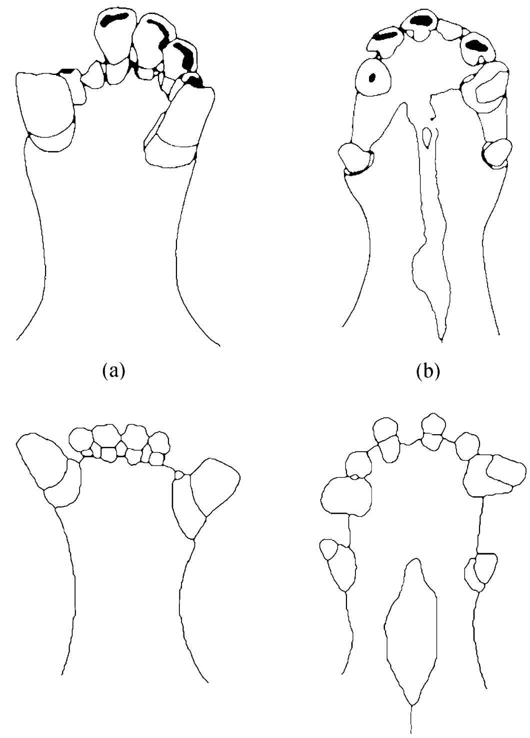

Fig. 1. Comparisons in the rostrum part between *Tapirus sanyuanensis* (a—b) and *Tapirus indicus* (c—d), (a) and (c): lower jaws; (b) and (d): upper jaws (not to scale).

developed than in molars. The paracone and metacone are also more developed than in molars. The antero-transverse diameter is a little larger or equals the postero-transverse diameter. The entrance of the medisinus is located much higher and less open than in molars. Parastyle is less developed than in molars.

In general, all the molars are very similar, except that M^1 is conspicuously smaller than others, they are wider than long, and distinctly wider in front than behind. The protolophs are very developed, but the ectolophs are less developed; the paracones and metacones shift toward the labial side; protocone, hypocone and parastyle are very developed. The anterior cingulum is prominent, Hooijer[2] thought the anterior cingulum forms the parastyle at the antero-external angle; the posterior cingulum is weak. From M^1 to M^3, the median valley is getting more open, and finally became U-shaped in M^3. There are three roots for each molar, one on the lingual side, two on the buccal side.

Lower permanent dentition: Like in some primates, the lower incisors and the canines are procumbent and form a "dental comb", they erupt upward only slightly, but mainly anteriorly, almost horizontally. The incisors are chisel-like, the lingual wall is like a slope. I_1 is the largest, I_2 is smaller, and I_3 is seriously diminutive. The roots of incisors are greatly elongated labio-lingually. The mesial part is more deeply worn than the distal part, it is a practical index for orientation determination (fig. 1, Plate Ⅰ-4).

The lower canines are very developed, and the root is more robust than the crown. There is no diatema between I_3 and canine. The occlusion surface with the superior third incisor is on the anterior side (fig. 1, Plate Ⅰ).

In all the premolars, the posterior moiety is much broader than the anterior, but the trigonid is more developed. The main transverse valley opens mainly to the lingual side. Except P_2, all other premolars have parallel hypolophid and metalophid.

M_1 is conspicuously smaller than M_2, sometimes even smaller than P_4. In morphology, all molars are exceptionally rectangular in occlusion section, but the anterior breadth is slightly larger than that of the posterior. Both of the transverse crests, i.e. hypolophid and metalophid, are very developed, but the hypolophid is slightly lower than metalophid before wear. On M_3, the hypolophid is reduced and became more oblique. The main transverse valley is open internally and externally. The talonid is more developed than in premolars. Paralophid diminished into a cingulum. Anterior cingulum is weak; metaconid is developed. Metalophid is getting more developed from M_1 to M_3 (Plate Ⅰ). Hypoconulid is very marked; in Quaternary tapirs, only the Chinese forms and few North American forms have hypoconulid [3].

(iv) Postcranial skeletons. Most of the parts of the postcranial skeleton were preserved (figs. 2 and 3), but the ulna and the fibula are missing. For the long bones, the epiphyses are not fused with the shaft yet, and most of them were detached from the shaft, it means that the

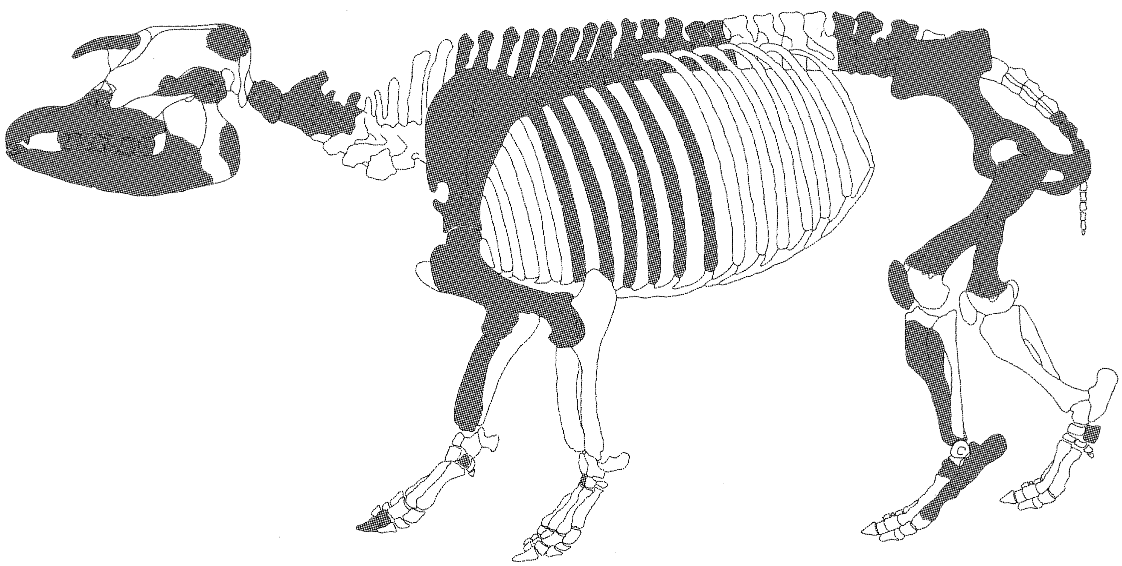

Fig. 2. Restoration of the skeleton of *Tapirus sanyuanensis*, the shadowed areas represent the parts actually preserved.

Fig. 3. Measurements (in milimeters) of the postcranial skeletons of *Tapirus sanyuanensis*, compared with the living *Tapirus indicus*. BA, Breadth of acetabulum; BBI, Breadth of body of ischium; BC, Breadth of calcaneum; BCT, Breadth of calcaneum tubercle; BDEH, Breadth of the distal end of humerus; BDMtIV, Breadth of the distal end of Mt IV; BPMtIV, Breadth of the proximal end of Mt IV; BSF, Breadth of the shaft of femur; BSH, Breadth of the shaft of humerus; BSI, Breadth of the shaft of ilium; BST, Breadth of the sacral tuberosity; BTI, Breadth of tuberosity of ischium; DC, Depth of calcaneum; DCF, Depth of the caput of femur; DCT, Depth of calcaneum tubercle; LA, Length of acetabulum; LC, Length of calcaneum; LH, Length of humerus; LMtIV, Length of Metatarsal IV; LR, Length of radius; LSF, Length of the shaft of femur; LT, Length of tibia; MBMtIV, Minimum breadth of Mt IV.

skeleton represents a non-adult individual. But the distal ends of humerus, radius and tibia have fused with the shafts, additionally, in the permanent dentitions, P2s, P3s and M1s have fully erupted, according to Simpson[4], this should be a sub-adult which reached almost the same size as an adult. The specimen (IVPP 535) used for comparison in fig. 3 is a juvenile, its permanent teeth have not erupted yet, and all the epiphyses are separated from the shafts.

2 Comparison and discussion

(i) Revised diagnosis. Almost the same size as the living *Tapirus indicus*, but much smaller than *Megatapirus augustus*. Nasal heart-shaped. The mandibular symphysis is relatively shorter and narrower, and the distal end is not expanded. There is no diastema between incisors in both upper and lower dentitions. The lingual tubercles in I^1 and I^2 are very developed. The caniniformed I^3 and the lower canine are more nearly circular in cross section. P^1 is sub-triangular in form, there exists a wide ledge of internal cingulum. The cheek teeth are relatively lower-crowned than that of *Tapirus indicus*, but with larger width/length ratio, the lingual wall is inclined, not so steep as in *Tapirus indicus*. In upper molars, protolophs and metalophs are usually crossed with the median sagittal plane in oblique angle. The medisinus is relatively more open in the upper molars. Hypoconulids are conspicuous.

(ii) Compared with *Megatapirus*. Except the finds in Java and Tonkin[2], *Megatapirus* almost is a native member in South China. Though we lack the data on the postcranial skeleton for comparison, in teeth morphology, *Tapirus sanyuanensis* is very similar with *Megatapirus*, particularly in having the crista-like structures in the upper molars, and hypoconulid in the lower molars, but *Tapirus sanyuanensis* is much smaller than *Megatapirus*. The systematic relationship between the Early Pleistocene tapir and *Megatapirus* still remains uncertain.

(iii) Compared with the living Malay tapir. As this study shows, in body size, *Tapirus sanyuanensis* is very similar to *Tapirus indicus*, but slightly smaller (table 1); in the antero-posterior length of cheek teeth, these two species are very similar, but *Tapirus sanyuanensis* has a wider anterior breadth (fig. 4). In the rostrum part, there is no diastema between incisors nor between lower incisors and lower canines, the symphysis is relatively shorter, narrower and not expanded at the distal end (fig. 1). P^1 in *Tapirus sanyuanensis* is sub-triangular, with developed internal cingulum; P^1 in *Tapirus indicus* is oval-shaped or sub-triangular, the internal cingulum is reduced. The premaxilla in *Tapirus sanyuanensis* is more convex, but in *Tapirus indicus*, it is more compressed. The canines and I^3 in *Tapirus sanyuanensis* are conical, but they are compressed conical in *Tapirus indicus*. *Tapirus sanyuanensis* has lower-crowned cheek teeth, and the internal wall has an inclination; The crown in *Tapirus indicus* is much higher and the internal wall stands vertically. The cheek teeth have weak external cingulum and posterior cingulum in *Tapirus sanyuanensis*, but have very developed posterior cingulum which extends upward to the apex of metacone in *Tapirus indicus*. In the lower cheek teeth, the paralophid is still obvious in *Tapirus sanyuanensis*, which continued from the outer angle of the anterior lobe forward and inward, circumscribing a cavity in front of the metalophid, but it is diminished into a cingulum and formed the double cingula in *Tapirus indicus*. In *Tapirus sanyuanensis*, the hypoconulid is prominent, but nearly disappeared in *Tapirus indicus*. In the postcranial skeletons, *Tapirus sanyuanensis* has more constricted ends in long bones than *Tapirus indicus*, particularly the femora head is much smaller in *Tapirus sanyuanensis*. The Tuberosity of the ischium is marked in *Tapirus sanyuanensis*, but in *Tapirus indicus* it extends toward the symphysis pubis in a more rounded outline.

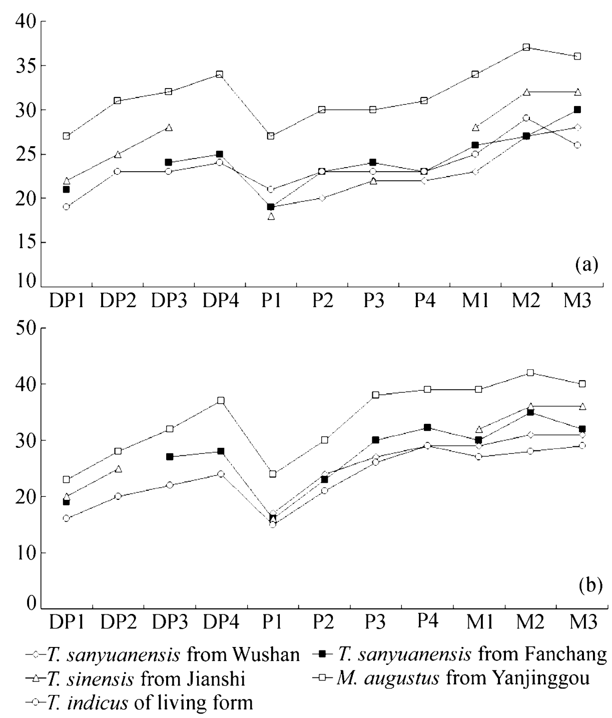

Fig. 4. Comparisons in length (a) and anterior breadth (b) of cheek teeth among *Tapirus sanyuanensis, Tapirus indicus* and *Megatapirus augustus*.

(iv) Compared with other tapir fossils of Late Cenozoic found in China. The first true tapir fossil record was described by Owen[5] who established a species, *Ta-*

pirus sinensis, which was based on some isolated teeth without certain locality and horizon, that's why this species was open to question for such a long time after him. Hooijer[2] once pointed out that there is no character to distinguish *Tapirus sinensis* from *Tapirus indicus*, and regarded the species *Tapirus sinensis* Owen as a race under the species *Tapirus indicus*, but later on Colbert and Hooijer[6] treated *Tapirus sinensis* as synonym of *Tapirus indicus*, anyway for many years in China, people used to adapt Owen's designation. In 1991, Huang et al.[7] named another species, *Tapirus sanyuanensis*, based on the materials of the Early most Pleistocene from Wushan near Chongqing. Additionally, we also have some other finds of Early Pleistocene tapirs, such as Liucheng and Liuzhou in Guangxi, Jianshi in Hubei. The relationships between the Early Pleistocene records and *Tapirus indicus* as well as *Tapirus sinensis* are open to debate.

When Owen erected the species *Tapirus sinensis*, he compared it with *Tapirus indicus.* The differences between the two species lie in the following aspects: The posterior cingulum extends horizontally toward the postero-internal corner of the metaloph in *Tapirus sinensis*, but it extends upward to the apex of the hypocone in *Tapirus indicus*. *Tapirus sinensis* has a much larger breadth/length ratio of cheek teeth and more prominent paralophid than *Tapirus indicus*. The materials from Fanchang share some similarities with the previous records, but different in the following aspects: teeth size, cingulum and parastyle character. The materials from Jianshi correspond to the materials described by Owen, it can be included into the species *Tapirus sinensis* which can be treated as a link between *Tapirus sanyuanensis* and *Megatapirus* (fig. 4).

Wushan is a very important locality for tapir fossils, Huang et al. established the species *Tapirus sanyuanensis* based on the materials including broken maxilla, mandible and isolated teeth[7]. The materials from Fanchang correspond to *Tapirus sanyuanensis* in the following character: size, not so compressed parastyle, not developed external cingulum in upper cheek teeth, diminished or disappeared internal cusps in P^1. But there exists also some small differences, such as the relatively small-sized, more developed parastyle and crista-like structures, much narrower medisinus and more developed paralophid in the materials from Wushan. Anyway, it is more suitable to place the materials from Fanchang within the species *Tapirus sanyuanensis*.

At the evolutionary level, mainly according to the body size and the development of the internal cusps on P^1, *Tapirus sanyuanensis* from Wushan and Fanchang represent the type of early most Pleistocene. *Tapirus sinensis* from Jianshi represents the transitional form between Early Pleistocene tapirs and the later gigantic tapir, i.e. *Megatapirus*[8].

Among the Neogene tapirs, the materials of Pliocene from Wuxiang, Shanxi[9], are the closest in both morphology and size, but other materials of Neogene from Yunnan and Shandong are very different[10,11].

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