

ON FOSSIL AND PREHISTORIC REMAINS OF TAPIRUS FROM JAVA, SUMATRA AND CHINA

by

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With plates I and II

The tapir is an extremely rare element in the fossil Mammalian fauna of Java. In the enormous collection of fossil teeth and bones brought together in this island by Eug. Dubois in the years 1890 to 1900, the tapir is represented only by six teeth, originating from three localities in the Kendeng Mts., viz., Kedoeng Broeboes, Kedoeng Loemboe, and Kebon Doeren. Previous to his researches in Java, Dubois collected teeth in a number of caves in the Padang Highlands. In this Sumatran collection *Tapirus* is not uncommon. We possess one hundred and twenty complete, and a still larger number of broken teeth. Half of this collection originates from three caves, viz., the Lida Ajer cave near Pajakombo, the Sibrambang cave, and the Djamboe cave near Tapisello. The exact localities of the other teeth unfortunately are not recorded; besides those given above in the reports of Dubois's paleontological researches in W. Sumatra (Anonymus, 1889-1890) mention is made of the following caves:

Sampit cave near Pajakombo;
Caves in the Ngalau Seriboe Mts., between Boea and Sidjoendjoeng;
Pandjang cave (no. 1) = Kepala Sawah Liat cave, near Sibalín;
Mansioe cave, in the Andjing Mt., near the Sinamar river;
Batang Pagian cave, near Boea;
Moeka Moeka cave, near Moeara;
Bandar cave = Batang Siparok cave, in the Andjing Mt.;
Boelan cave, near Sibalín;
Lebawah cave, near Lisawah;
Pandjang cave (no. 2) near Sisawak;
Caves on the western shore of lake Singkarah, near Paningahan.

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The examination of the *Tapirus* teeth in the Dubois collection (referred to below as Coll. Dub.) brought me to the following conclusions:

The teeth of *Tapirus* from the prehistoric Sumatran caves as a rule are larger than those in the recent skulls of *Tapirus indicus* Desmarest from the island, but otherwise their characters are similar. The dimensions of the prehistoric teeth are set in an entirely unexpected light when compared to those of the Pleistocene *Tapirus augustus* Matthew et Granger from China, Indo-China and (?) Java. They fill the gap that exists between the recent Malay tapir and the fossil Chinese form in such a remarkable way as to induce me to designate the subfossil teeth from Sumatra as *Tapirus indicus intermedius* nov. subsp. (p. 288).

The fossil *Tapirus* teeth from Java (on which Dubois (1908, p. 1265) based a new species, *Tapirus pandanicus* Dubois) are of the same size as the recent teeth from Sumatra, and present no characters by which they can be distinguished from those of the Malay tapir. The suggestion is given at the end of the present paper that they might belong to a distinct Javan subspecies; my material is not conclusive on this point.

Evidence is presented of the species still being in existence in the prehistoric fauna of Java; up to now it was believed to be extinct in this island since the middle Pleistocene.

Fossil teeth of the tapir from China have been described and figured as *Tapirus sinensis* Owen by Owen (1870) and Koken (1885). The study of the variation of the teeth of *Tapirus indicus* Desmarest showed me that the supposed differential characters of the former as compared with the latter do not exist. The Chinese teeth are doubtless specifically identical with the Malay tapir; they might, however, represent an extinct subspecies. To establish this more material is needed than is at present available.

The Chinese teeth of which Schlosser (1903, p. 74) has given the measurements, and which he ascribes to Owen's species must, however, as rightly remarked by Matthew and Granger (1923, p. 588) and Zdansky (1935, p. 14), be referred to the gigantic species *Tapirus augustus* Matthew et Granger from the early Pleistocene of China and Indo-China, which I have to say a few words about at the end of the present paper.

The recent material of *T. indicus* Desmarest I used for this study for the greater part belongs to the collection of the Leiden Museum; I am indebted to Prof. Dr. L. F. de Beaufort (Zoological Museum at Amsterdam), Prof. Dr. Chr. P. Raven (Zoological Laboratory of the University at Utrecht), and Dr. W. E. van Wijk ("Museum van het Onderwijs", The Hague) for the permission to examine the material in the institutions under their charge.

My thanks are due to Dr. C. de Jong who made the photographs.
The measurements in the present paper are given in mm.

Tapirus indicus Desmarest subsp.

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Recent material examined:

1. Skeleton of young individual. Leiden Museum, cat. c. Sumatra. From J. F. R. S. van den Bossche, 1870.

2. Young female skeleton. Leiden Museum, reg. no. 1378. Babat district, res. Palembang, Sumatra. From the Rotterdam Zoological Garden, 27-1-1925.

3. Young skull. Leiden Museum, reg. no. 4952. Boea, Padang Highlands, Sumatra. Ex coll. Dubois, 1941.

4. Idem. Museum van het Onderwijs, The Hague, no. 30423, no data.

5. Idem idem, U2, no data.

6. Young skeleton. Zoological Laboratory Utrecht, no data.

7. Young skull. Leiden Museum, cat. e. Sumatra. Coll. Van Lidth de Jeude, 1866.

8. Young male skeleton. Leiden Museum, reg. no. 2100. From the Rotterdam Zoological Garden, 13-8-1932, no data.

9. Young female skeleton. Leiden Museum, reg. no. 1014. Padang Highlands, Sumatra. E. Jacobson don., 2-9-1920.

10. Young male skeleton. Leiden Museum, reg. no. 1345. From the Rotterdam Zoological Garden, 22-9-1924, no data.

11. Young skull. Leiden Museum, cat. g. Coll. Van Lidth de Jeude, 1866, no data.

12. Idem. Leiden Museum, reg. no. 4949. Ex coll. Dubois, 1941, no data.

13. Idem. Amsterdam Museum. Moeara Laboe, Padang Highlands, Sumatra. From the Amsterdam Zoological Garden, 23-11-1927, Kessler don. The right P¹ is duplicated¹⁾.

14. Idem. Leiden Museum, cat. f. Coll. Van Lidth de Jeude 1866, no data.

15. Subadult skull. Leiden Museum, reg. no. 4950. Ex coll. Dubois, 1941, no data.

16. Subadult male skeleton. Leiden Museum, reg. no. 1384. Babat district,

1) Other dental variations were not found by me in *T. indicus* Desmarest. In *T. terrestris* (L.), however, I noticed anomalies in three skulls, viz.,

1. Leiden Museum, cat. h. There is an extra premolar internal to the left P², the latter is somewhat displaced outwards. In shape and size the extra tooth agrees with the P²; it is rotated, with the anterior surface facing outwards. The left P¹ is more forward than that of the right side. Noted by Jentink (1887, p. 169).

2. Leiden Museum, reg. no. 4951. The upper left C is duplicated.

3. In a skull in the Zoological Laboratory of the University at Utrecht the P⁴ is rotated on both sides.

res. Palembang, Sumatra. From the Rotterdam Zoological Garden, 20-3-1925.

17. Subadult female skeleton. Leiden Museum, reg. no. 1954. From the Rotterdam Zoological Garden, 6-5-1931, no data.

18. Skull of subadult individual. Leiden Museum, cat. d. Sumatra. From Reinwardt.

19. Adult female skeleton. Leiden Museum, reg. no. 1152. From the Rotterdam Zoological Garden, 7-7-1922, no data.

20. Adult skeleton. Leiden Museum, cat. b. Sumatra. From Reinwardt.

21. Adult skeleton of male. Leiden Museum, cat. a. Padang Besi, Sumatra. From S. Müller, 1835.

22. Adult female skeleton. Leiden Museum, reg. no. 1238. From the Rotterdam Zoological Garden, 28-6-1923, no data.

23. Adult skull. Amsterdam Museum, no. 497, no data.

24. *Idem idem*, no. 496, no data.

25. Fully adult skeleton. Amsterdam Museum, no. 505, no data.

The skins of all the specimens from the Rotterdam Zoological Garden in the Leiden Museum are preserved too. Reg. nos. 1384 and 1378 (nos. 16 and 2 of the above list) are the specimens described by Kuiper (1926) as *Tapirus indicus* var. *brevetianus*, a black variety. They are not different from the other specimens in any cranial or dental character. At Kuiper's remarks I have only to add, that of the skin of the almost adult male (Kuiper, l.c., pl. I fig. 1) the whole of the back is sparsely haired, with numerous bald spots (scabies?), and that the young specimen, which is a female (a post-mortem photograph of which has been given by Kuiper, l.c., pl. I fig. 2) has not yet completely lost its infantile colour pattern. There are still indications of the white spots on the legs. The "small grey stripe on the median line of its belly" (Kuiper, l.c., p. 425) in reality is not less than 22 cm broad! The hinder part of the body is not paler above and on the sides than the rest, as is the case already in younger normal specimens (Kerr, 1927). The white under part of the body is very peculiar, as in younger normal specimens this median stripe is much narrower, and in normal adults this part of the skin is black.

The measurements of the teeth of the twenty-five specimens enumerated above will be found in the tables I and II. The range of variation is given in the text when dealing with the separate teeth, and again, besides that observed in the prehistoric cave teeth from Sumatra, in the table on p. 291 to be compared with the dimensions of the teeth of *Tapirus augustus* Matthew et Granger, which I took from the literature.

The tapir is extinct now in Java ¹⁾, but still lives in Sumatra. The first European who observed it, at the mouth of one of the southern rivers, was an officer Whalfeldt, in the year 1772. He made a drawing of the animal, which was mistaken by Marsden (1811, p. 116) for that of a hippopotamus. On this evidence the latter author records *Hippopotamus* from Sumatra, which was doubted at by Cuvier (1821, p. 279). After the Malayan tapir had become known by the figures of F. Cuvier and of Farquhar, Horsfield (1821) was able to identify the animal of Whalfeldt's drawing as a tapir.

Müller (1839, p. 44) states that Diard had obtained a tapir in the interior of Borneo, near Pontianak. This statement was given without reserve, and so the opinion found its way in literature (I may mention Cantor, Flower, Gervais, Lydekker, Von Martens, Mohnike, Schinz, Sterndale, Tjeenk Willink, Wagner, and Weber), that the tapir is an inhabitant of Borneo. Everett (1893, p. 496) includes the tapir in his list of Mammals from the "Bornean group of islands", and Beccari (1904, p. 38) also records the tapir from Borneo, though he does not mention if he actually saw a specimen, or merely based his statement on the study of the literature, as the authors cited above apparently did. Neither Hose (1893), Gyldenstolpe (1919), nor Banks (1931) mention the tapir from Borneo; the latter author (l.c., p. 18) writes that the appearance of a tapir was described in correct detail to Everett by a Sadong Malay, who had killed it in Dutch Borneo, but that the teeth he produced in evidence were those of a rhinoceros!

The existence of the tapir in Borneo has never been proved by actual specimens, nevertheless Borneo is included in the geographical range of the tapir in some recent atlases (De Beaufort, in: Atlas Tropisch Nederland, 1938, pl. 7 b 3 II (this map was published separately in Van Steenis, 1935), and Joleaud, 1939, pl. LXXXVI).

In a preliminary paper on the fossil Vertebrate fauna of Java, which he regarded as a unit, and of Pleistocene age, Dubois (1891, p. 94) recorded the tapir as *Tapirus*, spec. indet.; in one of his reports published in the same year (Anonymus, 1891, p. 14) the fossil form is mentioned as in all probability identical with *Tapirus indicus* Desmarest. Trouessart (1898, p. 768, 1905, p. 634), with a reference to Dubois's paper, mentions '*Tapirus indicus* foss.' from the Pleistocene of Java and Sumatra. Dubois, however,

1) Sody (1936, pp. 46-47) mentions that a European hunter once told him that he had observed a wild tapir near Tjilatjap, on Java's S. coast. Sody finally believed the story, but states that the animal of course was not indigenous, and must have escaped from captivity.

recorded the fossil *Tapirus* from Java only, and had referred the Sumatran cave fauna to the Holocene (l.c., p. 93). The erroneous statement of Trouessart has been copied by Raven (1935, p. 261). In 1908 the specific name *pandanicus* was given to the fossil Javan form (Dubois, 1908, p. 1265), which is stated to differ from *indicus* by its smaller size, and by the wider entrance to the medisinus of the upper molars. The age of the fossil Javan Vertebrates is now considered as upper Pliocene (l.c., p. 1270).

Von Koenigswald (1934, p. 193) records an M³ of *Tapirus* from Djétis deposits at Sangiran (Java), and remarks that it is at least as large as, if not larger than the corresponding tooth in *indicus*, but probably belongs to Dubois's species. Afterwards he records *Tapirus* cf. *indicus* Desmarest both from the (lower Pleistocene) Djétis fauna, and the (middle Pleistocene) Trinil fauna (Von Koenigswald, 1939, pp. 35, 38; 1940, p. 60, pl. II fig. 14). Neither in the upper Pleistocene Ngandong fauna, nor in the prehistoric Sampoeng fauna of Java, remains of *Tapirus* have so far been met with.

It was, therefore, with great surprise that I discovered a complete unworn left M² of a tapir in a collection of bones and teeth of man, deer, swine, apes, and rodents from the Wadjak cave, res. Kediri, Java (Coll. Dub. no. 3808a, see p. 269). The tapir tooth has exactly the same state of preservation as the other remains from this locality, famous for the discovery of *Homo wadjakensis* Dubois. The base of the tooth is covered with a yellowishgrey calcareous concretion, identical with that found on the associated specimens, and the roots, which are only partially preserved, are not gnawed at by porcupines. This find forms the first proof of the occurrence of *Tapirus indicus* Desmarest in the prehistoric fauna of Java. It is not the only animal that has since disappeared from Java; *Elephas maximus* L. and *Cervus eldi* Güthrie have been recorded by Dammerman (1934) from the Sampoeng fauna, which is of about the same geological age.

The description of the teeth in the Dubois collection from Sumatra and Java is given in the following pages. Reference is made to the published figures and descriptions of *T. sinensis* Owen. The teeth described by Owen (1870) and Koken (1885) were obtained in drug-stores, and are of uncertain age and locality. The latter author regards them as of Pliocene (Koken, l.c., p. 34), Schlosser (1903, p. 73), however, as of Pleistocene age. The incomplete pd₂ figured by Young (1932, p. 389 fig. 6) was collected in a cave deposit in the Yunnan province in S. W. China; the age is considered by Young as lower Pleistocene (l.c., p. 392). The teeth of "*sinensis*" described by Koken (1885) have been supposed to originate from this, or other caves in the southern provinces. Patte (1928, p. 56) and Young (1932,

p. 389) state that *T. sinensis* Owen was found at Yen Ching Kao, Wanhsien, Eastern Szechuan, but this is not correct. In their preliminary paper on the early Pleistocene fauna from these deposits Matthew and Granger (1923, p. 573) indeed mention *T. sinensis* Owen, but remark that this species is absent in their collection. The gigantic tapir which is such a remarkable element in the Wanhsien fauna (see this paper, pp. 290-293) seems to have lived in Java too; Von Koenigswald (1940, p. 60/61) identifies a lower molar from the Trinil fauna of Patjitan as *Tapirus* cf. *augustus* Matthew et Granger. Unfortunately he neither describes nor figures this tooth.

In the descriptions I use a uniform nomenclature (cf. Osborn, 1907, pp. 180-181) for the cusps of the premolars, milk premolars and molars throughout, for the reasons given previously in my paper on the rhinoceroses (Hooijer, 1946a, pp. 3-6).

pd¹ or P¹

In the Malay tapir the first upper milk premolar and its successor so closely resemble each other, that a separate tooth cannot be referred with certainty either to the milk or to the permanent dentition. From the Sumatran caves we have four specimens, all of the right side, one of which (Coll. Dub. no. 1134d) originating from the Djamboe cave. Their measurements are given in the table below.

	Coll. Dub. nos.				" <i>T. sinensis</i> "	recent
	1134d	7002k	7002p	829c	Koken, 1885, p. 38.	(table I)
antero-posterior	23	22	22	23	19	19—22
postero-transverse	17	17	18	19	17.5	14—21

The basal plane is pear-shaped or almost oval-shaped in outline. On the outer wall of the tooth there are two vertical ridges, the paracone style and the metacone style, with a depression between, continued down to the base of the crown. They are more closely approximated in the first two, than in the other specimens. The posterior moiety of the teeth is much broader than the anterior, except in the first, and has a hypocone of rather different development. In the last two teeth the hypocone forms a distinct cusp, opposite to the depression between the two outer cusps, and connected by a low oblique ridge with the metacone. In no. 7002k the hypocone is smaller and in a more backward position. It is situated opposite to the metacone, from which it is completely isolated. And in no. 1134d the hypocone is no more than a slight elevation of the inner cingulum, this tooth is only slightly broader behind than in front. I figure this tooth (pl. I fig. 1) together with no. 829c (pl. I fig. 2) to show the difference in form. All

these variations are found in the recent pd^1 and P^1 of *T. indicus* too; in two skulls (Leiden Museum, cat. f and g) the P^1 even is more simply built than Coll. Dub. no. 1134d: the paracone has an almost central position, and the metacone style has not developed; the hypocone is rather small, though more developed than in the subfossil specimen. The outer cingulum is distinct only at the antero- and postero-external angle; in some recent specimens it has more developed than in the cave specimens. The left pd^1 or P^1 figured as *Tapirus sinensis* Owen by Koken (1885, pl. IV fig. 15) is indistinguishable in structure from that in recent *T. indicus*, and added to that it is not larger.

pd^2

This tooth, and its successor, differ from the following upper teeth of *Tapirus indicus* Desmarest in being narrower in front than behind. We possess four specimens, three of the left, and one of the right side; the first is from the Lida Ajer cave, and the third of the Sibrambang cave. Two specimens are figured on pl. I (figs. 3 and 4). Measurements:

pd^2	Coll. Dub. nos.				recent (table I)
	1820w	7002b	772Aa	7002f	
antero-posterior	25	—	29	28	23—25
antero-transverse	22	23	23	23	19—22
postero-transverse	24	24	26	26	22—25

The first specimen is unworn, the tip of the metacone is slightly damaged; of the second the inner cusps are touched by wear, and the parastyle is missing; the last two teeth are entire and little worn. At the base they are about three-fourths as long internally than externally. From the protocone, which is the lowest cusp, a descending ridge is continued outward and forward. In the labial half of the tooth it recurves backward and joins the paracone. This protoloph stands about at an angle of 68° on the ectoloph. The metaloph is higher lingually (the hypocone is the highest cusp); it descends to the outer side and abuts upon the ectoloph with a faint upturn, on the antero-internal side of the metacone. The ectoloph is straight, the paracone style and the metacone style have equally well developed. The medisinus remains of equal depth from its lingual entrance outwards. It forms a dividing line between the bases of proto- and metaloph, and gradually winds forwards. It is bisected by a prominence on the inner surface of the paracone (which is called the crista by Von Rautenfeld, 1928, p. 440).

The postsinus is as large antero-posteriorly as the medisinus, bounded

behind by a low cingulum between faint ascending ridges on the hypocone and the metacone. The horizontal cingulum is continued for a small space along the posterior surface of the hypocone, and also, but more distinct, on that of the metacone. There is no inner cingulum, except for a small tubercle at the entrance to the medisinus. Anteriorly the cingulum forms a horizontal ledge, at the antero-external angle it rises into a distinct parastyle, behind which it rapidly fades away.

Whereas the first two teeth fall within the range of variation of the recent specimens, the last two are larger, especially longer. But structural differences from the recent teeth cannot be found, except that in the first specimen the metaloph is seen to descend more steeply to the outer side than the protoloph, whereas in the few unworn recent pd^2 the reverse is the case, but this I regard as an individual variation only.

pd^3 or pd^4

In recent skulls of *T. indicus* the pd^4 differs from the pd^3 in its somewhat greater transverse diameter; the anterior cingulum with the parastyle, and the posterior with the ascending ridges are somewhat better developed, the "crista" often too. In our collection from Sumatra we have seven teeth which are referable either to pd^3 or to pd^4 , four of the left and three of the right side. Three of them (nos. 1820i and j, and 755a) are from the Lida Ajer cave. With the exception of the first, all specimens are unworn or nearly so. Two specimens are figured (pl. I figs. 5, 6).

pd^3 or pd^4	Coll. Dub. nos.							recent (table I)	
	1820j	7002d	7002r	644a	1820i	7002o	755a	pd^3	pd^4
antero-posterior	26	28	27	25	27	25	25	24-25	23-26
antero-transverse	27	29	27	24	28	26	26	23-26	25-27
postero-transverse	25	27	25	23	25	22	24	21-24	22-24

The metaloph is shorter transversely and antero-posteriorly and higher than the protoloph, both are less oblique than in pd^2 and about parallel. The antero-external angle is less prominent, and the cingula have heavier developed than in pd^2 . Except for their greater average size, the present specimens are not different from the posterior milk premolars in the recent Sumatran species.

P^2

Ten specimens of P^2 occur with the collection, four of the right, and six of the left side. They differ from pd^2 in their still greater postero-transverse as compared with the antero-transverse diameter; the former

measurement is greater than the length, instead of smaller as in P^2 . The cingulum has more developed too; on the posterior side it extends almost to the internal angle, and lingually, at the entrance to the medisinus, it most often forms a distinct ledge, a "pass" into the medisinus. It can be traced as a smooth swelling along the base of the outer surface, sometimes (Coll. Dub. nos. 770Ac, 7002q, 7002h) forming a tubercle in the depression between the para- and metacone style. The protocone is the lowest cusp, the hypocone the largest, the transverse ridges from these cusps descend steeply and diverge somewhat when passing outwards; they are separated by a deep cleft from the ectoloph.

P^2	Coll. Dub. nos.									
	770Ac	1820s	1134b	770Ah	7002q	7002e	11467a	815c	7002h	7002l
antero-posterior	26	26	26	24	26	24	25	24	26	25
antero-transverse	22	23	24	23	23	24	22	23	23	24
postero-transverse	29	28	29	—	29	29	28	—	29	29
	"T. sinensis"			recent						
	Koken, 1885, p.38			(table I)						
antero-posterior	21	22	21.5	22—24						
antero-transverse	—	—	—	17—23						
postero-transverse	22.5	25	25	24—27						

Koken (1885, pl. IV fig. 14) figures a left P^2 from China as *T. sinensis*; there is no development of the cingulum at the lingual entrance to the medisinus, nor is this the case with Coll. Dub. no. 1820s (pl. I fig. 9). The latter specimen agrees with that figured by Koken in every detail but it is larger, the Chinese teeth (Koken (l.c.) gives the measurements of three specimens) are of the same size as the recent specimens. I figure another specimen (Coll. Dub. no. 7002 l, pl. I fig. 8) to show the common development of the inner cingulum at the entrance to the medisinus.

P^3 and P^4

Owen (1870, p. 426/27, pl. XXVIII fig. 8) describes and figures a sub-fossil tooth from China as a P^3 of his *Tapirus sinensis*. It is said to differ from the corresponding premolar in the recent Sumatran species in its larger size, and proportionally greater transverse diameter, in the better development of the inner extension of the posterior cingulum, and in having a connecting ridge between the proto- and hypocone, obstructing the lingual entrance to the medisinus. Koken (1885, p. 35/6) redetermines Owen's tooth as a P^4 (he writes P^1 , for he numbers the premolars from back to front), but Schlosser (1903, p. 74) again follows Owen. I believe that Koken is right.

The P³ and P⁴ are distinguished from the other upper teeth of *T. indicus* at a glance by their rectangular outline, they most often only are very slightly greater transversely in front than behind, the proto- and metaloph stand about at right angles to the ectoloph. In recent skulls of *T. indicus* the P³ differs from P⁴ in its slightly smaller breadth; the length is equal in both teeth, and sometimes even a little less in P⁴, which gives this tooth a still greater proportional breadth as compared with that in P³. The unworn proto- and metaloph are somewhat lower, and slope to the inner side less steeply in P³ than in P⁴. In the latter the metacone is a little less developed as compared with the paracone than in P³, and the "crista" seems to be somewhat more prominent.

Owen (1870, p. 426) states that his tooth more resembles the P³ in the extension of the posterior cingulum to the inner end of the metaloph, "such rear portion of the cingulum not being bent up to the apex of that ridge as in the last premolar and the true molars of *Tapirus indicus*". But in the recent skulls I had for comparison the posterior cingulum may extend almost to the inner end of the metaloph also in P⁴, and the vertical ridge on the posterior surface of the hypocone may be practically absent (Leiden Museum, cat. b and reg. no. 1954). The statement of Koken (1885, p. 36), who writes that the outer border forms an acute angle with the posterior border in P¹-P³, a right angle in P⁴, and an obtuse angle in the molars, must not be taken too literally, but it is not without value, it results from the relative decrease of the protoloph and increase of the metaloph when passing from P² to M². The vertical posterior ridge descending from the apex of the hypocone gradually becomes more distinct and curved to the inner side from P² on backward; it may join the horizontal cingulum already in P³ (Leiden Museum, reg. no. 4950), and most often in P⁴, but also in M¹ (Leiden Museum, cat. f) this coalescence sometimes has not yet completely taken place. I noticed the same variations in *T. terrestris* (L.).

In our collection of teeth from the Sumatran caves there are seventeen specimens of P³ and P⁴ of *Tapirus*, which show a great variability in the development of the posterior cingulum and the vertical posterior ridge on the hypocone. The fact that the latter does not come into a contact with the former in the premolar described by Owen, as rightly remarked by Koken (1885, p. 36), is of no value for determining the serial position of the tooth. It was not easy to distribute our specimens over P³ and P⁴, because it is almost certain that there are no two specimens which belonged to one and the same individual, and even in recent skulls the differences are but slight. They present the dimensions as given in the table on p. 267.

The first five specimens, both of P³ and P⁴, are from the right side.

The teeth taken out of nos. 770A, 961 and 971 originate from the Sibrambang cave, those of no. 1820 from the Lida Ajer cave. The teeth I referred to P³ have a less broad appearance than the others. This is accompanied by

P ³	Coll. Dub. nos.								
	961p	770Ad	1820x	971b	829a	1820d	648Aa	1820t	7002j
antero-posterior	26	27	24	26	27	26	27	27	26
antero-transverse	29	30	29	30	29	32	31	33	31
postero-transverse	29	31	29	30	30	29	30	32	31

	"T. sinensis"			recent	
	Koken, 1885, p. 38.			(table I)	
antero-posterior	21.5	23.5	23	21.5	22—25
antero-transverse	22	27.5	28	28.5	26—29
postero-transverse	—	—	—	—	26—28

P ⁴	Coll. Dub. nos.							
	1820y	7002m	7002i	971c	1102a	1820h	1820c	1820r
antero-posterior	25	26	26	27	24	27	25	25
antero-transverse	31	32	32	33	30	33	33	33
postero-transverse	30	29	31	31	28	31	30	32

	"T. sinensis"		recent	
	Owen, Koken, 1870, 1885, p. 427. p. 38.		(table I)	
antero-posterior	25	26	22—23	
antero-transverse	31	30.5	28—31	
postero-transverse	—	—	26—29	

an increased size of the metacone, and an often more produced "crista" in the latter. The proto- and metaloph have a more gentle slope to the inner side in the first group than in most of the second. I noticed the following variations:

There is a basal antero-posterior ridge at the inner entrance to the medisinus (just as that in the P⁴ of "T. sinensis" figured by Owen, 1870, pl. XXVIII fig. 8): P³: nos. 971b, 829a, 648Aa; P⁴: nos. 7002i, 971c, 1820r (pl. I fig. 13). In the other teeth it is weakly indicated or absent.

The horizontal cingulum is absent on the posterior surface of the hypcone, the vertical ridge on that cone is a) weak; P³: nos. 971b, 7002j; P⁴: nos. 1102a, 1820r; b) moderately developed: P³: nos. 770Ad, 1820t, 829a; P⁴: nos. 7002m, 1820h; and c) strongly developed and in contact with the horizontal cingulum, from which it seems to be an upward prolongation: P³: no. 648Aa (pl. I fig. 11); P⁴: no. 971c.

The posterior cingulum is continued almost to the postero-internal angle, like in the premolar figured by Owen (l.c.): P³: no. 1820d (weakly

developed vertical ridge) and no. 1820x (too much worn); P⁴: nos. 1820c (pl. I fig. 12), 7002i (vertical ridge moderately developed).

Coll. Dub. nos. 961p (pl. I fig. 10) (P³) and 1820y (P⁴) are intermediate in this respect, the cingulum is continued on the posterior surface of the hypocone, but subsides some mm before reaching the internal angle; it extends a little less far inward than the anterior cingulum. The P³ and P⁴ from China figured by Koken (1885, pl. IV figs. 12-13) apparently belong to this intermediate type. From the table above it appears that the teeth of "*sinensis*" are not, or slightly, larger than the recent specimens; the subfossil Sumatran teeth almost invariably present greater dimensions.

M¹

This tooth is the smallest of the upper molars. The metaloph is shorter transversely than the protoloph, their inner slopes are more abrupt than in the posterior milk premolars, and they are higher. The well developed anterior cingulum descends from the strong and pointed parastyle to the inner side, and terminates at the antero-internal angle. On the posterior surface of the protoloph a ridge descends steeply from the top of the protocone to the inner side; a similar ridge as that on the posterior surface of the metaloph dealt with above (p. 266) which joins the posterior cingulum. This ridge has stronger developed in some specimens than in others, but always more than in the posterior milk premolars. The „crista" is always distinct. At the lingual entrance of the medisinus there often is a pointed tubercle, if it is absent, the entrance is narrower and V-shaped; the medisinus ascends gradually when passing outwards. In our collection from the Sumatran caves we have eight specimens of which the first still has its roots; they need no special remarks; the first five are of the right side. As usual, they are often larger than the recent teeth, as appears from the table of measurements below. Coll. Dub. nos. 1820n and v are from the Lida Ajer cave, and nos. 770Ae and i (pl. I fig. 14) from the Sibrambang cave. The length of the M¹ of "*T. sinensis*" figured by Koken (1885, pl. IV fig. 16) evidently

M ¹	Coll. Dub. nos.							" <i>T. sinensis</i> "		re- cent (ta- ble I)
	770Ae	1820n	1820v	790a	7002a	7002n	829b	770Ai	Koken, 1885, p. 38	
antero-posterior	28	27	27	25	26	28	27	28	21	24-27
antero-transverse	30	27	30	28	28	30	28	29	25.5	24-28
postero-transverse	26	25	27	25	25	27	26	26	—	22-25

is reduced by interproximal wear, the anterior breadth of this tooth, however,

I measure from the figure as 29 mm, which is also the value given for it by Schlosser (1903, p. 74).

M²

This molar is represented by eight specimens, three of the right and five of the left side. The measurements are given here together with those of the Wadjak tooth, mentioned on p. 261. Two teeth are incomplete, no. 18200 lacks the antero-internal portion of the cingulum and the portion at the base of the metacone, and of no. 733a the postero-internal angle is missing. No. 770Ak originates from the Sibrambang cave; nos. 18200 and 11 are from the Lida Ajer cave in Sumatra, no. 3808a is from the Wadjak cave in Java. It can be seen from the table that only three specimens fall

M ²	Coll. Dub. nos.								(Java)
	1820u	18200	770Ak	935a	7002c	7002g	733a	818a	3808a
antero-posterior	32	28	29	30	31	32	28	30	28
antero-transverse	32	31	33	33	34	33	31	33	30
postero-transverse	29	—	28	29	30	30	—	30	26
<i>“T. sinensis”</i>									
	Owen, 1870, p. 427.		Koken, 1885, p. 38					recent (table I)	
antero-postero	29		26	24.5	24			25—28	
antero-transverse	31		29.5	27	25.5			29—31	
postero-transverse	—		—	—	—			24—28	

within the range of variation of the recent M², the others being larger. But this is the only difference I can perceive. Nos. 1820u and 3808a are unworn, and of no. 7002g the protoloph has just been taken into use, but the dentine is not yet exposed. The proto- and metaloph are of the same height, their anterior surfaces are almost vertical and are somewhat grooved vertically. On their posterior surfaces, descending from the top of the protocone or hypocone respectively, there is a ridge running obliquely to the outer side, that on the metaloph joins the posterior cingulum. The “crista” is prominent, from its base the medisinus gradually slopes downward to the inner side. In its middle portion it is narrow and V-shaped, but the lingual part is somewhat wider. The metacone is less developed than the paracone, it has a vertical ridge posteriorly, which joins the cingulum. The anterior cingulum forms a strong ledge; it descends to the inner side and terminates at the antero-internal angle. At the antero-external angle it forms a large parastyle. On the outer surface it is distinct only at the base of the metacone, and at the postero-external angle.

In most of the specimens (only Coll. Dub. nos. 1820u and 818a excepted)

the horizontal cingulum is continued on the posterior surface of the hypocone as a weak but distinct ledge, descending to the postero-internal angle. In one of the subfossil specimens, but here partly worn away (Coll. Dub. no. 770Ak, pl. I fig. 15), and in some of the recent M² (Leiden Museum, cat. b and reg. no. 1954) there is a weak antero-posterior ridge at the inner entrance to the medisinus.

Owen (1870, p. 427) writes that in the M² of his *T. sinensis* the postero-internal portion of the cingulum is better developed than in *T. indicus*. He does not give a figure of this tooth, the measurements (see the table) are larger than those of the three specimens of M² from China which are given subsequently by Koken (1885, p. 38). Especially the breadth of the latter teeth is smaller than in the recent specimens. I figure here two of the cave specimens, one (Coll. Dub. no. 3808a, pl. I fig. 16) unworn, the other (no. 770Ak, pl. I fig. 15) worn and showing the development of the inner cingulum at the entrance of the medisinus.

M³

Two last upper molars of *Tapirus* are with the Sumatran collection. The first is a left specimen (Coll. Dub. no. 1134a, pl. I fig. 19), it is entire and unworn and originates from the Djamboe cave. The other is of the right side (Coll. Dub. no. 1820q, pl. I fig. 20), it lacks the internal portion of the protoloph, and is from the Lida Ajer cave. They differ from the penultimate molar in the greater transverse contraction of the posterior moiety, the descending posterior ridge of the hypocone has weaker developed than that of the protocone. In the first specimen the metaloph rises to a lesser height than the protoloph. In recent skulls we find the same characters for the M³, which also is always somewhat smaller than the M². The dimensions of the present subfossil teeth are distinctly greater than those of the recent M³.

	Coll. Dub. nos.		" <i>T. sinensis</i> "	recent
	1134a	1820q	Koken, 1885, p. 38	(table I)
antero-posterior	30	30	24	24—28
antero-transverse	32	—	29.5	27—30
postero-transverse	27	27	—	23—25

Owen (1870, pl. XXVIII fig. 9) figures a right M³ from China, but gives no measurements; another M³ of "*T. sinensis*" has been figured by Koken (1885, pl. IV fig. 19), the measurements of which are given in the above table. In both teeth the posterior cingulum is seen to extend to the internal angle, the antero-posterior ridge of the cingulum at the inner entrance to the medisinus is better developed in Owen's specimen than in that figured by Koken.

As remarked already when dealing with the penultimate molar, these variations in the development of the cingulum, to which Owen attached specific value, occur in the recent species too. In the M^3 the antero-posterior ridge at the entrance of the medisinus even may be more pronounced than in Owen's specimen (Leiden Museum, cat. b), but is not always present (Leiden Museum, reg. no. 1238). In the first of the present subfossil Sumatran M^3 the cingulum is not continued to the internal angle, just as in most of the recent teeth, but in the second it forms a ledge on the posterior surface of the hypocone, as is the case also in one recent M^3 (Leiden Museum, cat. b).

Teilhard de Chardin and Young (1936, pp. 16-18) have described and figured two incomplete subfossil lower jaws of a tapir from Anyang, near Changteho in N. China. They had no specimens of the Malay tapir for comparison, but state that the dimensions are approximately the same as in *T. indicus* Desmarest, and distinctly smaller than in the Pleistocene *Tapirus augustus* Matthew et Granger. The specimens are identified as "*Tapirus* cf. *indicus* Cuvier". I found the dimensions of the teeth to agree well with those of the corresponding subfossil teeth from Sumatra, they have the same disproportionate size, especially the molars, as compared with recent specimens from Sumatra. The dimensions of the subfossil Chinese teeth will be given in the tables below; they belong, without doubt, to the recent species, like the Sumatran cave teeth. I will deal with the dimensions of the jaws later on (p. 284).

pd²

There is only one specimen of the lower anterior milk premolar (Coll. Dub. no. 1820 a e); it originates from the Lida Ajer cave. It has a general resemblance to its successor, the P^2 , but differs in the curvature and greater transverse extension of the metalophid. The tooth (pl. II fig. 1), which is still in the germ stage, is of the left side, the hypolophid forms the broadest part of the crown, it stands at a little more than right angle to the outer border. The posterior surface is rather steep, and has a cingulum, which is confined to the middle portion of that surface and has a weak ridge ascending to the top of the hypoconid. The anterior surface of the hypolophid slopes down less abruptly. From the apex of the hypoconid a low but distinct ridge is continued forward and inward. It ascends on the posterior surface of the metalophid about half-way between the protoconid and the metaconid. The former cusp has a somewhat more anterior position than the latter, the interval between them is almost as great as that between hypo- and entoconid.

The connecting ridge between proto- and metaconid is a little higher than the hypolophid and is not straight; its inner portion runs parallel to the hypolophid, and the outer portion is curved forwards. It is continued over the apex of the protoconid, and forms the anterior half of the outer border of the tooth; finally it is recurved inwards and ends at the apex of the anterior cusp, the paraconid. The metalophid and its anterior prolongation thus form about a semi-circle, enclosing a valley, which opens to the inner side and which is shorter transversely but wider than the main transverse valley, which is that between meta- and hypolophid. On the anterior surface of the hypolophid there is also a ridge descending from the apex of the entoconid, but it does not extend downwards to the bottom of the valley, which, just as that of the anterior valley, deepens as it passes inwards. The cingulum is absent along the sides of the tooth; the almost imperceptible swelling along the base of the crown hardly deserves that name. The paraconid is the lowest cusp, but well distinct and pointed; it lies somewhat to the inner side of the median longitudinal line of the crown. The dimensions are given here; only the breadth falls a little outside the range of variation of the recent specimens.

The incomplete tooth from a cave deposit in the Yunnan province (S.W. China) described and figured by Young (1932, p. 388/89) as a ? P_2 of *Tapirus sinensis* Owen must be a right pd_2 , of which the outer surface in front of the hypoconid, and almost the whole of the paraconid are missing. In size and in all characteristic features it agrees with the present specimen;

pd_2	Coll. Dub. no. 1820ae	" <i>T. sinensis</i> " Young, 1932, p. 389	recent (table II)
antero-posterior	31	—	27—32
postero-transverse	18	18	13—16

the length, which Young gives as 24 mm, is not that of the complete tooth.

pd_3

Of this tooth we have eight specimens, five of the left, and three of the right side, with the following dimensions:

pd_3	Coll. Dub. nos.							
	745d	1820z	868Ba	7002z	7002ag	770Aj	1820aa	1820ab
antero-posterior	29	28	27	29	28	28	26	30
antero-transverse	16	17	17	18	17	17	16	17
postero-transverse	18	19	17	19	18	18	17	19

	Teilhard de Chardin and Young, 1936, p. 17		recent (table II)
antero-posterior	28		23—26
antero-transverse	—		15—16
postero-transverse	22		14—17

Nos. 1820 z, aa and ab, and no. 868Ba are from the Lida Ajer cave, and no. 770Aj is from the Sibrambang cave. One specimen only is seen to fall within the recent range of variation, the others are larger.

The hypolophid and the transverse valley are formed as in the preceding tooth, but the postero-internal angle is less acute; the metalophid is relatively broader and stands at a right angle to the outer border. Both protoconid and metaconid have descending ridges on the anterior surface, that of the latter cusp does not extend to the base of the metalophid, but that of the former is continued downward and forward to the anterior border and then inward, it terminates at the antero-internal angle on the level of the cingulum. The latter forms a ledge along the whole anterior border, is absent on the sides but has developed again posteriorly. In all specimens the posterior cingulum is "double". This convenient descriptive term is used by Koken (1885, p. 35); it means that above the basal ledge there is another one, which is shorter transversely, and as a rule more prominent. He gives it as a "sehr taugliches Merkmal" (very valid character) for the identification of *T. sinensis* Owen; as I shall show below, a double cingulum is found in almost every lower tooth of *T. indicus* Desmarest. I give here two views of one specimen (Coll. Dub. no. 745 d, pl. II figs. 2, 3) to show the general form, and the shape of the posterior cingulum.

pd₄

This tooth is broader than the pd₃, and especially differs in the shortening of the foremost portion, the anterior surface of the metalophid slopes down much more steeply. The ridges descending from the apices of the outer cusps on the anterior surface of metalophid and hypolophid again have better developed than those of the inner cusps. There are six specimens, four of the left, and two of the right side. No. 1134f is from the Djamboe cave, and no. 1820ac from the Lida Ajer cave.

pd ₄	Coll. Dub. nos.						Teilhard de Char- din and Young,	recent
	1102c	1102b	7002u	1134f	745c	1820ac	1936, p. 17.	(table II)
antero-posterior	29	29	27	28	29	26	29	24—27
antero-transverse	18	19	19	20	19	18	—	16—18
postero-transverse	20	19	18	20	18	17	21	15—18

In the last three specimens the ridge descending from the apex of the protoconid is continued, slightly above the anterior cingulum, to the antero-internal angle. In the first three the transverse portion of that ridge has

lost the contact with the descending portion, and so the double cingulum is formed (Coll. Dub. no. 1102c, pl. II figs. 4, 5). In three of the six specimens the anterior breadth exceeds the posterior; this we find in the recent teeth too.

P₂

Like its milk predecessor, the P₂ has a well developed paraconid, which has not developed in the other teeth. From the pd₂ it is easily distinguished by the shape of the metalophid, which is more oblique and shorter transversely, and in the better development of the ridge continued forward and inward from the apex of the hypoconid. On the posterior side a ridge descends from the hypoconid to the inner side.

Koken (1885, pl. V figs. 4-5) figures two specimens from China; the paraconid of the larger tooth is missing. The other tooth is rather short, but in the two views given of it by Koken I can see no differential characters as compared with recent P₂, they also are not mentioned by Koken.

Of the four specimens from the Sumatran caves the first is of the left side, and the others of the right. No. 7002ak has, an exceptional fact in the Sumatran caves, still preserved its roots, this is the smallest specimen

P ₂	Coll. Dub. nos.				"T. sinensis"		Teilhard de Chardin and Young,		recent (table II)
	7002ae	644b	7002ak	1134e	Koken, 1885, p. 38	1936, p. 17	1936, p. 17		
antero-posterior	30	27	27	30	24	22.5	30	30	25-28
postero-transverse	18	17	16	20	15	13	16	17	13-17

of the four, and falls within the recent range of variation. I figure it here (pl. II fig. 6) together with the largest specimen (pl. II fig. 7).

P₃

Owen (1870, pl. XXIX fig. 6) figures a left P₃ of his *T. sinensis*, and writes that there is a "marked superiority of development" of the ridge continued from the protoconid forward and inward, and also in the height of the corresponding ridge from the hypoconid, which extends forward to abut upon the back part of the metalophid, as compared with *T. indicus* Desmarest (l.c., p. 427). Judging by the figure the ridge descending from the protoconid is not especially large, but that continued forward from the hypoconid has strongly developed, indeed, as Owen (l.c., p. 428) remarks, like in a P₂. In none of my recent or subfossil specimens of P₃, though

different in the development of that ridge, it is so large as in the Chinese tooth. However, the left P₃ figured by Koken (1885, pl. V fig. 3) is not different in this respect from the corresponding tooth of *T. indicus* Desmarest.

The tooth is distinctly narrower in front than behind. Not only the meta-, but also the hypolophid is pinched in anteriorly; the ridge descending from the top of the protoconid is continued to the antero-internal angle, both in Koken's specimen as well as in mine. Koken (l.c., p. 35) states that the transverse valley is deeper in his specimen than in *T. indicus* Desmarest, this cannot be seen from the figure.

We have eight specimens of P₃ from the Sumatran caves, six of the left, and two of the right side. No. 770Ab is from the Sibrambang, and no. 1820l from the Lida Ajer cave. One specimen (no. 7002v) has a double cingulum both in front and behind; nos. 7002t, 7002am and 1820l have a double posterior cingulum, unfortunately largely cut out by the following tooth, so that a satisfactory figure cannot be given.

Dimensions are not given by Owen; those in the table below are taken from his figure, and agree with those recorded by Schlosser (1903, p. 74).

P ₃	Coll. Dub. nos.							
	745b	770Ab	7002t	7002v	7002w	7002am	1820l	917y
antero-posterior	27	29	28	27	27	27	28	28
antero-transverse	19	18	20	19	19	19	19	18
postero-transverse	21	22	23	21	21	21	23	22

	"T. sinensis"			Teilhard de Chardin and Young, recent		
	Owen, 1870, pl. 29-6	Koken, 1885, p. 38		1936, p.17	(table II)	
antero-posterior	25	24	24	24	29	23-27
postero-transverse	—	—	—	—	—	15-18
antero-transverse	18.5	17	19	16	20	17-20

It can be seen from the table that the Chinese teeth of Owen and Koken are of the same size as the recent, except one which is smaller; and that, as usually, the Anyang tooth is as large as the corresponding Sumatran cave teeth. Of the latter I figure a worn specimen (no. 745b, pl. II fig. 8) for comparison with the figure published by Koken (1885, pl. V fig. 3), and the rather large and almost unworn one (no 1820l (pl. II fig. 9) from the Lida Ajer cave.

P₄

This tooth differs from the penultimate premolar in the same points as do their respective milk predecessors; it is broader at the base, especially

the metalophid, which is as broad as, or only slightly less so than the hypolophid. The metalophid slopes down more abruptly on the anterior side, which makes the tooth decidedly shorter; it is the shortest of all lower teeth, the milk dentition included.

Koken (1885, p. 35) made a very evident mistake when determining the tooth, which is figured on his pl. V fig. 1, as a P_4 . It has all the characters of an M_2 or M_3 , I will return to this specimen later on.

Of the present last premolar we possess nine specimens, seven of the left, and two of the right side, their dimensions are given below. Three are from the Sibrambang cave, viz., nos. 770Af, 772Ab, and 815a. Most of the

P_4	Coll. Dub. nos.							
	745a	770Af	772Ab	7002y	7002aa	7002aj	7002al	815a
antero-posterior	28	27	26	26	27	27	27	27
antero-transverse	22	22	22	21	21	20	21	—
postero-transverse	24	22	22	22	22	22	22	22

	Teilhard de Chardin and Young,		
	7002ai	1936, p. 17	recent (table II)
antero-posterior	26	29	23—25
antero-transverse	21	—	18—20
postero-transverse	22	23	19—22

specimens show the double cingulum, as it is named by Koken, though, of course, the best in unworn teeth (no. 745a, pl. II figs. 10, 11). See also no. 772Ab (pl. II fig. 12) for a characteristic specimen. As in the case of the P_3 , all subfossil specimens are larger than the recent.

M_1

From the pd_4 the first molar differs in its proportionally greater breadth, and in the thicker layer of enamel on the crown; most often the tooth is broader in front than behind. In one skull (Leiden Museum, cat. e) the breadths in front and behind are the same, and equal to those in the pd_4 ; in this case the length is 1 mm less in the M_1 .

From the caves in Sumatra there are ten specimens, five of the left and five of the right side. The specimens of no. 1820 are from the Lida Ajer cave, no. 771Aa and 815b from the Sibrambang, and no. 959f from the Djamboe cave. Three of the cave teeth only fall within the recent range of variation; the Anyang teeth agree in size with the subfossil teeth from Sumatra, whereas there is almost no difference in size between the recent teeth and those of "*T. sinensis*". Of the latter one is described by Owen (1870, p. 428) as being "one line" longer both transversely and antero-posteriorly, and as having thicker enamel than the corresponding molar in

T. indicus Desmarest. In the latter remark, which is repeated by Koken (1885, p. 35), as judged by his figure (Owen, l.c., pl. XXIX fig. 5). Owen may be right, as far as concerns the recent specimens of *T. indicus* Desmarest. I figure (pl. II fig. 13) a cave specimen (Coll. Dub. no. 7002ab)

M ₁	Coll. Dub. nos.								
	771Aa	1820ad	815b	7002ab	7992a	1820k	1820f	1820m	959f
antero-posterior	27	29	28	30	27	28	31	27	29
antero-transverse	20	20	21	22	20	22	21	19	21
postero-transverse	19	20	19	20	19	20	20	19	20

	"T. sinensis"				recent (table II)
	7002ah	Owen, Koken, 1870, 1885, pl. 29—3 p. 38	Teilhard de Chardin and Young, 1936, p. 17		
antero-posterior	30	27	25	29	24—27
antero-transverse	21	20.5	19	23	17—20
postero-transverse	19	—	—	—	17—19

in about the same stage of wear, in which the layer of enamel at least has the same thickness as in the Chinese tooth. The characters of the accessory ridges Owen states to be less marked than in the P₃. Koken (1885, p. 35) also speaks of a more developed anterior cingulum, and a strong vertical depression anteriorly at the base of the metalophid in the Chinese tooth as compared with *T. indicus* Desmarst. He does not figure his specimen, but figures an M₂ which he says to have the same characters, to which I shall return below. It remains only to state that all my specimens have a "double" anterior cingulum, and some (e.g., no. 1820f, pl. II figs. 15, 16) a double posterior cingulum too.

M₂ and M₃

The recent jaws of *T. indicus* Desmarest at my disposal show no constant differences between the M₂ and M₃. In one skull (Leiden Museum, cat. a) they even are of exactly the same dimensions. The length of M₃ may be greater or smaller than that of the M₂, the anterior breadth greater or smaller, the posterior breadth is mostly smaller than in M₂. Added to that there is no reliable structural difference, neither in the obliqueness of the hypolophid, nor in the development of the cingulum, of the accessory ridges, etc.

It is only possible to distinguish between the M₂ and the M₃ in the case of specimens which are worn to a certain extent. The M₃ is not fully in place until M₂ is worn over the whole breadth; in this stage the M₂ has a vertical mark of compression on the posterior side, which is absent in the M₃. Of the seventeen teeth from the Sumatran caves which are referable

to either M_2 or M_3 only seven are worn to a degree sufficient to show a posterior compression-mark if any. Five of them (Coll. Dub. nos. 770Aa, 1113a, 1820e, 7002x, and 7002af) indeed present a vertical facet on the posterior cingulum, but the two others (nos. 959e and 1820a) do not possess it; it is, therefore, certain that the former are penultimate, and the latter ultimate molars. The serial position of the bulk of the molars thus remains uncertain, their dimensions are given below. The first eight are of the

M ₂ and M ₃	Coll. Dub. nos.									
	755c	829d	959d	959e M ₃	1820b	1820g	7002s	7002ac		
antero-posterior	31	31	32	32	31	32	30	31		
antero-transverse	23	23	23	24	23	23	22	23		
postero-transverse	22	20	22	22	21	20	20	22		
	770Aa M ₂	770Ag	959g	1113a M ₂	1820a M ₃	1820e M ₂	1820p	7002x M ₂	7002af M ₂	
antero-posterior	30	33	31	30	34	31	32	31	30	
antero-transverse	24	24	23	23	25	24	22	23	23	
postero-transverse	22	21	21	—	22	22	22	23	22	
"T. sinensis"										
	Owen, 1870, pl. 29-4	Koken, 1885, p. 38	Teilhard de Chardin and Young, 1936, p. 17			recent (table II)				
			M ₂			M ₂	M ₃			
antero-posterior	30	30	30	34			26-28	24-29		
antero-transverse	22	20	21	23			20-22	19-21		
postero-transverse	—	—	—	—			18-21	18-19		

left, the others of the right side. The teeth of no. 959 are from the Djamboe cave, those of no. 1820 from the Lida Ajer cave, and those of no. 770A from the Sibrambang cave.

Both Owen (1870) and Koken (1885) figure a tooth as an M_2 of "*T. sinensis*". Both teeth are, however, too little worn to determine whether it is not perhaps an M_3 . Owen (l.c., p. 428) states that the M_2 of his *T. sinensis* repeats the differential characters of the M_1 as compared with the corresponding molar in *T. indicus* Desmarest. These characters are the excess in length of both the transverse and the antero-posterior diameter by "one line", the thicker enamel, and, though less marked, the better developed accessory ridges. He gives two figures of the tooth (l.c., pl. XXIX figs. 4, 4a), but no measurements. Koken (1885, pl. V fig. 2) figures another specimen, of the left side, and unworn. The hypolophid is stated to be more directed backward than in the M_2 of *T. indicus* Desmarest; the second cingulum is especially strong anteriorly. Distinct vertical folds arise from the transverse valley on both metalophid and hypolophid; the metalophid has a deep depression anteriorly.

The remarks of Koken are invalidated by the comparison of his figures with those of one of my specimens from the Sibrambang cave in Sumatra (no. 770Ag, pl. II figs. 19, 20), which is also unworn. It is of the right side, and has all the characters of Koken's tooth. The tooth he determines as a P_4 (Koken, l.c., pl. V fig. 1) is of the right side too; the elongated form of the crown, wider in front than behind, together with its size, show it to be an M_2 or M_3 .

The measurements in the table above (those of Owen's tooth have been taken from the figures, and agree with those given by Schlosser, 1903, p. 74) show that there is an excess in length, but not in breadth, of the molars of "*T. sinensis*" over recent *T. indicus* Desmarest. The M_2 of the Anyang jaw is as long as the largest of our cave specimens, viz., the ascertained M_3 (no. 1820a, pl. II fig. 18), but is narrower; all subfossil specimens exceed the recent in size.

TAPIRUS INDICUS DESMAREST SUBSP. FROM THE PLEISTOCENE OF JAVA

The fossil *Tapirus*-teeth from Java do not show an excess in size over the corresponding teeth in the recent Malay tapir, and as structural differences of any value could not be found, they must be referred to the present species. Their age is certainly Pleistocene, most probably the middle division of that period, for, as judged by Van Es's maps (Van Es, 1931) the localities (Kedoeng Broeboes, Kedoeng Loemboe, and Kebon Doeren) are situated on the outcrop of the Trinil beds (Kaboeh layers: Duyfjes, 1936, p. 146).

Coll. Dub. no. 1458b (pl. I fig. 7), Kedoeng Broeboes.

pd³ or pd⁴ dext., almost unworn. The antero-internal angle with part of the protocone, and also part of the posterior cingulum, are missing. Consequently the length and the anterior breadth cannot be given; the postero-transverse diameter is 20 mm, which is 1 or 2 mm less than in the smallest corresponding recent or subfossil teeth. But structurally there are no differences. The protoloph is lower, longer transversely, and parallel to the metaloph. The metacone is less extended at the base than the paracone. The parastyle is comparatively large, there are no traces of an outer or inner cingulum. On the anterior aspect it forms a horizontal ledge. The mediusinus is not wider than in the recent specimens.

The small difference in size alone is without importance for specific distinction from *Tapirus indicus* Desmarest.

Coll. Dub. no. 3808b, Kedoeng Broeboes.

pd³ or pd⁴ sin., well worn. The anterior and the inner surface have broken

off, consequently no measurements can be given. The tooth, however, as judged from the rather closely approximated para- and metacone, seems to have been rather small, like the foregoing specimen.

In the Dubois collection from Java there are two upper molars of *Tapirus*; the most important specimens. One is complete except for the roots and for the tip of the metacone, which have broken off; of the other the antero-internal and postero-external angles are missing, this specimen still has its confluent pair of inner roots. The first tooth is an M², and must be considered as the type of *Tapirus pandanicus* Dubois. The second is an M³, notwithstanding its incomplete state of preservation it forms an extremely welcome addition, as will appear below.

Coll. Dub. no. 1458a (pl. I figs. 17, 18), Kedoeng Loemboe.

M² dext. Proto- and metaloph are taken into use, but the dentine is only exposed at the inner half of the protoloph. The tip of the metacone has broken off. The outer surface is only slightly depressed at the base between para- and metacone, and runs obliquely backwards and inward, the anterior and posterior borders are very little convex from side to side. The protoloph stands at right angles to the inner border of the tooth; the metaloph, in its present almost unworn state, runs from the antero-internal side of the metacone inwards and also a little backwards. Their inner and anterior slopes are very steep, on the outer surface the slope of the metacone is more abrupt than that of the paracone, the former cusp also is distinctly smaller than the latter.

The protoloph, on its posterior side, has the usual oblique ridge running downward and outward from the apex of the protocone; lingually of this ridge (indicated by the posterior angle of the triangular worn surface) the slope of the protoloph is more steep than that of the labial part of the posterior surface. From the top of the paracone there is a ridge descending into the medisinus, which is partly worn away, the "crista".

The middle portion of the medisinus is narrow, the bases of the proto- and metaloph meet in a line, but near its lingual entrance the medisinus is partially obstructed by a development of the cingulum. It makes a faint ridge which runs from the antero-internal angle of the metaloph on forward for a length of 3 mm, then it turns outward along the base of the protoloph and into the medisinus, also for about 3 mm. In the anterior surface of the metaloph, near its inner end, there is a vertical groove, especially distinct below; its presence increases the width of the entrance to the medisinus. Due to the development of the cingulum the lingual entrance of the

medisinus is not only wide, but also high, it lies 7 mm above the lower margin of the enamel.

The cingulum forms a distinct parastyle at the antero-external angle of the crown, behind which it fades away and begins weakly again at the base of the metacone. On the anterior surface it descends to the inner side, but is not continued along the inner border, except, as said above, at the entrance to the medisinus.

The postsinus is closed behind by a thick ledge, which is turned up and ends at the posterior surface of the hypocone, 6 mm from the inner end of the metaloph. This upturned part is separated from the apex of the hypocone by a small vertical groove from the descending ridge. The latter ridge has weakly developed, but extends more downward than the cingulum. The descending ridge on the metacone is prominent and joins the posterior cingulum.

The present tooth is of exactly the same dimensions as the M² in some of the recent skulls of *T. indicus* Desm., and I cannot find a single difference in structure which would justify the specific distinction from that recent species. Dubois (1908, p. 1265) especially paid attention to the entrance to the medisinus, which he states to be wider than in *T. indicus* Desm. But in some skulls (Leiden Museum, cat. b and reg. no. 1954) the entrance is almost as high and wide as in the fossil M², whereas in others the development of the cingulum at the entrance is less and even almost absent, so that the medisinus remains V-shaped and opens to the internal side somewhat lower, ca. 5 mm above the lower margin of the enamel (Leiden Museum, cat. a and reg. no. 1152). The same variation is to be found in every upper tooth of *T. indicus* Desm.

M ²	Coll. Dub. no. 1458a	subfossil, Java	recent (table I)	subfossil, Sumatra (table on p. 269)
antero-posterior	27	28	25—28	28—32
antero-transverse	30	30	29—31	31—34
postero-transverse	26	26	24—28	28—30

Two other points still deserve special attention: First the presence of a vertical groove in the anterior surface of the metaloph. In the M² of a recent skull (Leiden Museum, cat. d) we find a similar groove in the same position, it even extends upwards to the top of the hypocone. Usually it has only weakly developed or is totally absent. And secondly the peculiarity, that the ridge on the posterior surface of the metaloph, descending from the apex of the hypocone, is not in contact with the posterior cingulum. As I stated before (p. 266) this coalescence usually takes place already in P⁴, but there is one skull (Leiden Museum, cat. f) in which the posterior hypocone ridge does not join the cingulum in a tooth anteriorly to the M².

In the present case the ridge descending from the apex of the hypocone extends downward to below the level of the posterior cingulum. The latter, however, so to speak, is too short. It does not extend sufficiently far inward to meet the descending ridge. This very feature I did not meet with in my recent material. The posterior cingulum in the recent teeth is so variable in development, however, that I do not regard the development in the fossil tooth as affording proof of its specific distinctness. The fossil tooth presents more peculiarities, viz., the wide entrance to the medisinus and the vertical groove in the anterior surface of the metaloph, which have been noticed in the description. That they are not constant in the Pleistocene form is fortunately shown by the second specimen of an upper molar we possess from Java:

Coll. Dub. no. 3802a (pl. II figs. 21, 22), Kedoeng Broeboes.

The present molar is of the right side, the protoloph is two-thirds, and the metaloph about one-third worn down. It lacks the innermost part of the protoloph; the postero-external angle is incomplete too, but here it is no more than the enamel layer that is lost. The posterior breadth thus can be estimated with sufficient certainty, and this, compared with the length, together with the absence of a mark of compression on the posterior side, enables us to determine the tooth as the last upper molar, M^3 .

The dimensions agree with those of one recent specimen, also the M^3

M^3	Coll. Dub. Von Koenigs-			
	no. 3802a	wald, 1934, p.	recent	subfossil
		193	(table I)	(table on p. 270)
antero-posterior	28	26	24—28	30
antero-transverse	—	29	27—30	32
postero-transverse	ca. 25	—	23—25	27

from the Djetis deposits at Sangiran, of which Von Koenigswald (1934, p. 193) gives the measurements¹⁾, is of the same size as the recent M^3 .

As shown by the figure (pl. II fig. 21) there is no obstruction of the cingulum at the entrance to the medisinus, which remains V-shaped down to the inner border of the tooth, where it opens only 4 mm above the lower margin of the enamel. Also there is no trace of a vertical groove in the anterior surface of the metaloph, which shows these characters to be variable in the fossil Javan form as well as in the recent Sumatran species. Finally in the present molar the cingulum is not continued along the whole of the posterior surface, but subsides suddenly 8 mm from the internal end of the metaloph.

1) The upper molar which he figures afterwards (Von Koenigswald, 1940, pl. II fig. 14) is 1 mm shorter and 2 mm narrower. If the figure is exactly on natural size it represents another specimen of M^3 ; the posterior breadth is only 23 mm.

Coll. Dub. no. 1458c (pl. II fig. 14), Kebon Doeren.

P₄ sin. The greater part of the confluent pair of posterior roots is present, the anterior roots have broken off. The specimen is little worn, only at the metaconid the dentine is exposed. The cingulum forms a ledge along the whole of the anterior surface, and fades away at the angles of the crown. The crown remains of equal breadth at the base throughout the length, except for a slight constriction at the labial entrance to the transverse valley. The latter entrance lies higher than that to the inner side. Both meta- and hypolophid have concave anterior surfaces due to the presence of ridges descending from the inner and outer ends forward and to the axis of the crown. Those descending from the outer cusps are the most prominent, that of the protoconid is continued inward to the antero-internal angle, and forms what Koken calls the second cingulum, above, but in this case not well distinct from the true cingulum.

The ridge descending from the hypoconid abuts against the metalophid, somewhat to the lateral side of the axis of the crown, and thus obstructs the transverse valley, the bottom of which slopes downward to either side, but more steeply so to the outer side.

The posterior surface of the crown is less convex from side to side than the anterior, and has a double cingulum too. This is very distinct, but it is not so much extended transversely as the anterior cingulum. The lower part remains 4 mm distant from the edges of the hypolophid, and the upper portion is still narrower, only 6 mm in breadth; it also has a central position. The total height of the cingulum is 8 mm above the base of the crown; it has not developed on the sides.

P ₄	Coll. Dub. no. 1458c	recent (table II)	subfossil (table on p. 276)
antero-posterior	24	23—25	26—29
antero-transverse	18	18—20	20—22
posterior-transverse	18	19—22	22—24

From the above table it appears that there is no difference in size between the present and the recent specimens. Of structural differences I only found one, which is of little importance, viz., the lesser breadth of the upper portion of the posterior cingulum; it ranges in width from 7 tot 9 mm in my recent specimens.

Coll. Dub. no. 1458d (pl. II fig. 17), Kebon Doeren.

M₁ dext. The anterior cingulum is largely cut out by the tooth in advance, and on the posterior side there is also a mark of compression. The roots have completely broken off. Both on the meta- and the hypolophid the dentine is exposed by wear over the whole breadth.

The crown is entire, and narrows distinctly backward. The antero-posterior diameter of the transverse ridges is the greatest at the outer side (to the right in the figure). The metalophid is depressed in the middle of its anterior surface, on the hypolophid the depression is found more to the inner side, as the ridge descending forward from the apex of the hypoconid is somewhat directed inwards. From this ridge the transverse valley gradually slopes down to the inner side, and opens U-shaped 4 mm above the base of the crown. The outer entrance to the median sinus is somewhat narrower, but is as high above the base. The inner and outer sides of the metalophid stand vertically, those of the hypolophid have a slight inward inclination. The posterior cingulum is highest in the middle, and has a breadth of 11 mm.

I cannot find any differential character, neither in structure nor in size (see the table below), as compared with recent *M*₁ of *T. indicus* Desmarest; the cingula also have not less strongly developed.

<i>M</i> ₁	Coll. Dub. no. 1458d	recent (table II)	subfossil (table on p. 277)
antero-posterior	25	24—27	27—31
antero-transverse	19	17—20	19—23
postero-transverse	17	17—19	19—20

DISCUSSION OF COMPARATIVE DIMENSIONS OF PREHISTORIC, FOSSIL, AND RECENT TEETH OF *TAPIRUS INDICUS* DESMAREST

We thus have seen that in prehistoric times there lived a tapir in Sumatra, of larger size than, but indistinguishable in the structure of its teeth from the recent Sumatran species. The teeth of the subfossil *Tapirus* jaws from Anyang in the N. of China figured by Teilhard de Chardin and Young (1936, pp. 16-18, figs. 4-5) agree in size with the subfossil Sumatran teeth, and it is, therefore, not surprising to find the Chinese jaws to be also larger than the recent.

The first lower jaw figured by Teilhard de Chardin and Young (1936, p. 16 fig. 4) consists of the symphysis, the left horizontal ramus and the ascending portion, of which the posterior border is incomplete; the extremity of the coronoid process, and the condyle have broken off. The teeth present are: *P*₂ (erupting), *pd*₃, *pd*₄, and *M*₁; the *M*₂ has not yet erupted but is visible in its alveolus. I have a recent mandible of *T. indicus* Desmarest (Leiden Museum, reg. no. 1345), which is in almost exactly the same stage of growth, in this jaw also *P*₂ is not yet fully in place, and *pd*₃ and *pd*₄ are still present, though the former is about to be shed; *M*₁ is but little touched by wear, and *M*₂ still buried in the bone. In side view, the contour of the jaw is different, the lower border being more convex

in its middle portion, and more gradually curved upwards anteriorly. But there is some variation in this respect, a somewhat younger mandible (Leiden Museum, reg. no. 1014, pd_2 not yet shed) agrees with the Chinese jaw in the slightly curved lower border from the angle on forward, and in the degree of the slope of the symphyseal portion. The length especially is the largest in the subfossil jaw.

	Teilhard de Chardin	Leiden Museum,	
	and Young, 1936, p. 17.	reg. nos.	
Length from the anterior border to the condyle	330	1345	1014
Height of ramus in front of M_1	62	295	305
		61	54

The second specimen (l.c., p. 18 fig. 5) consists of the right half of a lower jaw, the angle is damaged, the symphysis is not preserved. It has the permanent dentition, but M_3 has not yet erupted. Again the dimensions

	Teilhard de Chardin	Leiden Museum,		
	and Young, 1936, p. 17.	reg. nos.		
Height of ascending ramus (coronoid)	250	4950	1384	1954
Height of ramus in front of M_1	71	—	195	184
		57	66	60

exceed those of the recent jaws of *T. indicus* Desmarest of the same age, but the contour of the jaw, and the shape of the masseteric fossa are exactly the same.

The age of the subfossil jaws described by Teilhard de Chardin and Young (1936, pp. 16-18) is well settled: Anyang was the capital of the Shang dynasty, ca. 1400 B.C.-1100 B.C. (l.c., p. 5). How can we explain the occurrence of the tapir so far in the N. of China? Teilhard de Chardin and Young (l.c., p. 18) write as follows:

“First it might be supposed that a special form of Tapir (*T. sinensis*) [which they, with Matthew and Granger (1923, p. 573), regard as doubtfully distinct from *T. indicus* Desmarest] has been living all across the Pleistocene and protohistorical times along the sea-plain of China, much more to the north than we thought, and that some individuals could still have been killed by the Anyang hunters. The little excess in size observed in *T. sinensis* and the Anyang Tapir over *T. indicus* (or *malayanus* Raffles) would support this idea.

“But in opposition to these views, the impressive fact still holds strong that no trace of Tapir has ever been recovered so far from any *not artificial* Pleistocene or Holocene site in North China, and that this absence is in accord with definite climatic conditions. More positively, we shall give

below, further evidences pointing to the fact that the Anyang people had some kind of trade, furnishing them with foreign living or dead animals.

"It therefore seems that while waiting for more facts the most conservative opinion would be to regard the here described specimens as belonging to a *Tapirus indicus*, brought to Anyang from the South, possibly in the same way as the ingots of tin found by Dr. C. Li in the course of his excavations. We shall adopt below the same solution for the Elephant.

"N.B. The discovery of an "imported" Tapir in Anyang somewhat brings the real age and origin of *T. sinensis* described by Koken in doubt. For years, the Anyang site has been known for the bones it contains (see below the case of *Bubalus mephistopheles*, of *Elaphurus*, etc.). Koken's types most probably are from the same source. And this would be in full accord with the observations made by Schlosser (1903) concerning the characters of these specimens: slight fossilisation, colour, loamy matrix."

From my tables it is clear that there is no "excess in size" of "*T. sinensis*" over *T. indicus* Desmarest; the P⁴, pd₂ and M₁-M₃ may be a little larger than the corresponding recent, but not as compared with the subfossil teeth. More often the Chinese teeth are somewhat smaller, especially shorter, than the recent specimens. The Anyang tapir I have shown to be as large as the, likewise prehistoric, tapir of Sumatra. This fact strongly supports the second supposition of Teilhard de Chardin and Young quoted above, and which I adopt here for the present, viz., that the Anyang tapir has been imported from the South.

The recent distribution of the Malay tapir, according to the latest records (Harper, 1945, pp. 372-375), is Sumatra and the Malay Peninsula and adjacent region as far N. as Lower Burma. Its existence in Borneo has never been proven by actual specimens (see above, p. 260). We must accept on the evidence of the teeth which until now went under the names *Tapirus sinensis* Owen and *T. pandanicus* Dubois respectively, that the Pleistocene range of the Malay tapir extended to S. China and Java. This is by no means peculiar; the orang-utan represents a parallel case. The Malay tapir was larger in prehistoric times in Sumatra (and in the North of China, if the second supposition of Teilhard de Chardin and Young quoted above is not accepted) 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 form represent different subspecies. But the scanty fossil material at hand unfortunately is not conclusive.

It is interesting to draw a comparison between the Malay tapir and *Rhinoceros sondaicus* Desmarest. The latter species still has a wider recent

geographical range on the Asiatic continent than the tapir (see the excellent paper on the present and late historic distribution of the Javan rhinoceros by Loch (1937)). Like the tapir, it is absent in Borneo, occurs in the prehistoric and recent fauna of Sumatra, and is known in the fossil and prehistoric state from Java; in the latter island it still exists, though in small numbers only. In the following table, which is compiled from my paper on the fossil and prehistoric rhinoceroses from the Malay Archipelago (Hooijer, 1946a) we find the range of variation in size of the upper teeth of *Rhinoceros sondaicus* Desmarest. Not only the subfossil Sumatran teeth, but, as to be expected, also the fossil Javanese teeth often show an excess in size over the recent specimens. But it is seen, that the dimensions of many of the fossil teeth still fall within the recent range of variation, and that in some cases the prehistoric teeth are larger than the corresponding fossil specimens. It can only be said that the average size of the teeth was greater in Pleistocene and prehistoric times than it is at present.

	<i>Rhinoceros sondaicus</i> Desmarest		
	recent (Java and Sumatra)	subfossil (Sumatra)	fossil (Java)
pd ³ antero-posterior	ca. 36—ca. 37	ca. 40—ca. 41	ca. 34—ca. 38
antero-transverse	40—44	43—46	42
postero-transverse	35—41	40—43	ca. 37—39
pd ⁴ antero-posterior	ca. 34—ca. 39	ca. 43—ca. 44	—
antero-transverse	42—46	50—51	
postero-transverse	38—42	47—ca. 50	
P ² antero-posterior	ca. 27—ca. 32	ca. 28	28—ca. 32
antero-transverse	34—44	37	39—45
postero-transverse	39—44	40	41—45
P ³ antero-posterior	ca. 34—ca. 38	—	ca. 32—ca. 47
antero-transverse	47—57	—	48—57
postero-transverse	45—51	—	ca. 45—53
P ⁴ antero-posterior	ca. 36—ca. 42	ca. 35	ca. 37—ca. 42
antero-transverse	51—60	51—52	51—62
postero-transverse	47—54	ca. 48	48—59
M ¹ antero-posterior	ca. 35—ca. 43	—	ca. 38—ca. 45
antero-transverse	51—60	—	54—65
postero-transverse	45—52	—	48—56
M ² antero-posterior	ca. 37—ca. 47	ca. 48—ca. 50	ca. 43—ca. 47
antero-transverse	53—60	57—64	55—62
postero-transverse	45—52	44—51	47—54
M ³ antero-posterior	36—46	51	43—48
antero-transverse	43—55	57	48—56
length outer surface	44—58	58	50—62

The fossil tapir is known by much less abundant material than the rhinoceros, and the possibility must not be excluded that larger fossil teeth still await discovery.

I should not be surprised, however, if subsequent examination of more material, especially of the skull, will show the Chinese and the Javan tapir to possess differences of a true racial character from the typical and Sumatran form. The study of other mammals which are represented by one and the same species in the Pleistocene and the recent fauna of Java and in the Pleistocene and/or the recent fauna on the Asiatic continent has convinced me that the process of raiation was already evident in the Pleistocene. In other words: it is possible to distinguish fossil subspecies. The recent races must have descended from the racially distinct populations which existed already in the Pleistocene.

Is it mere coincidence that the only subfossil tooth of the tapir from Java, viz., the M² found in the Wadjak cave (see p. 269, and pl. I fig. 16) is smaller than the bulk of the corresponding teeth from the Sumatran caves? In fact it precisely has the dimensions we could expect in an animal that must have descended from comparatively small-sized individuals like those to which the six Pleistocene teeth from the same island must have belonged.

Not unlikely more teeth of the tapir will be found in Java some time, and it would be of great interest to ascertain whether they keep in size with the Pleistocene teeth described in the present paper or not. If the fossil Javan tapir in the future will be shown to represent a distinct subspecies of the Malay tapir, there is already a name available for it, viz., *Tapirus indicus pandanicus* Dubois.

The same holds for the Chinese tapir. The teeth described up to now present no characters to distinguish them from those of the recent Malay tapir, but should a fossil race for China be distinguished, it must be named *Tapirus indicus sinensis* Owen.

And now for the Sumatran cave teeth. Here the material is certainly sufficient for taxonomic purposes. The definition must necessarily be limited to the teeth:

***Tapirus indicus intermedius* nov. subsp.**

Diagnosis: Teeth identical in structure with those of recent *Tapirus indicus indicus* Desmarest from Sumatra. The dimensions of the teeth are intermediate between those of the latter and those of the Pleistocene *Tapirus augustus* Matthew et Granger, typically from Wanhsien, province of Szechuan, China.

Locality: Prehistoric caves in the Padang Highlands, Central Sumatra.

Material: The molars, premolars and milk premolars described in the present paper. As holotype I select the right upper second molar, Coll. Dub. no. 770Ak (pl. I fig. 15), from the Sibrambang cave.

Discussion: As has become evident from the description and figures given in the present paper, tooth for tooth the prehistoric Sumatran race is indistinguishable in structure, but is larger than the recent form of that island. From the table given under the head *Tapirus augustus* Mathew et Granger (below, p. 291) it clearly results that the dentition of the prehistoric Sumatran tapir presents smaller dimensions than that of the Pleistocene species. With the exception of the ultimate molars, each of the subfossil upper or lower premolars and molars is represented in the Sumatran collection by four to ten specimens. This material is sufficient to fill completely the gap that exists between the variation limits of the recent and that of the Pleistocene form. The transition in size is as complete as one could only wish; there remains a hiatus only in the intergradation between the breadth measurements of the upper molars. I shall return to this question below.

In contradistinction to what we observed in the case of fossil, subfossil and recent *Rhinoceros sondaicus* Desmarest (table on p. 287) there is hardly any overlap in the dimensions of the fossil, subfossil and recent teeth. In the example of the rhinoceros, however, I had fossil material of the postcranial skeleton too, and this made it evident to me that the general diminution in size of the species is accompanied by a fundamental change in the structure of the limbs. The Pleistocene form (Hooijer, 1946b) is of a mediportal type, like the recent *Dicerorhinus sumatrensis* (Fischer), whereas the recent *sondaicus* is graviportal, like *Rhinoceros unicornis* L. In the Sumatran caves we find almost invariably only the teeth of the species, which learn us but little of the amount of differentiation which the species underwent in the course of time. They only show us the tendency to develop smaller forms; a widespread phenomenon, as it seems.

The case of the tapir presented here offers an interesting analogon to that of, e.g., the porcupine I have already published upon (Hooijer, 1946c). *Acanthion brachyurus* (L.) is known also from rather scanty material (six teeth) from the Pleistocene of Java, and it is represented by abundant material from the prehistoric caves of Sumatra. In this case I had a series of teeth from the prehistoric Goea Djimbe cave in Java, and I could partially substantiate the case (cf. Hall, 1943, p. 143) of a species dating from the Pleistocene with at least two, but most probably three subspecies which has come down to the present by means of each of the subspecies having gradually changed its characters into those of one of the subspecies existing today. Similar vertical clines have been called chronoclines by Simpson (1943, p. 174). He gives an excellent example in the North American condylarth species *Ectocion osbornianus* Granger.

There can be no doubt that the cave teeth from Sumatra belonged to prehistoric populations which are ancestral to those of the species today inhabiting the same island. And we may postulate their Pleistocene ancestors to have possessed still greater dimensions. In the cases of the rhino and of the porcupine referred to above none of the known forms can be decidedly fixed upon as being the immediate ancestor. There is a species of tapir, however, which possesses the dimensions we should expect to find for the form from which *Tapirus indicus* Desmarest with its Pleistocene races in China and Java may have descended:

Tapirus augustus Matthew et Granger

- Tapirus sinensis* Schlosser, Abh. K. Bayer. Akad. Wiss., Math.-Phys. Kl., vol. 22, 1903, p. 72, pl. III figs. 13, 15.
Tapirus sp.? Mansuy, Mem. Serv. Geol. Indochine, vol. 5, fasc. 2, 1916, p. 13, pl. I figs. 5—8.
Tapirus (Megatapirus) augustus Matthew et Granger, Bull. Am. Mus. Nat. Hist., vol. 48, 1923, p. 588, figs. 21—24; Von Rautenfeld, Acta Zoologica, vol. 9, 1928, p. 425; Young, Bull. Geol. Soc. China, vol. 11, no. 4, 1932, p. 389; Von Koenigswald, Proc. Kon. Akad. Wet. Amst., vol. 38, 1935, p. 876.
T[apirus] (Megatapirus) augustus, Zdansky, Pal. Sinica, ser. C, vol. 6, fasc. 5, 1935, p. 14.
Tapirus augustus, Patte, Bull. Soc. Géol. France, ser. 4, vol. 28, 1928, p. 57 figs. 1—3.
Megatapirus augustus, Teilhard de Chardin and Young, Pal. Sinica, ser. C, vol. 12, fasc. 1, 1936, p. 17.
Tapirus (Megatapirus) cf. *augustus*, Bien and Chia, Bull. Geol. Soc. China, vol. 18, 1938, p. 336, fig. 8.
 ? *Tapirus* cf. *augustus*, Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Ind., no. 28, 1940, p. 60.

The material of Schlosser (1903) consisted of loose teeth only, and formed part of a collection of mammalian fossils from Chinese drug stores. Notwithstanding the considerable excess in size, Schlosser identified them as *T. sinensis* Owen, considering it premature to erect a new species of tapir on teeth alone. They were secured at I Chang, a hundred miles downriver from the type locality of the species, viz., Yen Ching Kao, Wanhsien, Eastern Szechuan. Matthew and Granger (1923, p. 588) recorded four skulls, three of them with lower jaws. From the same locality Von Rautenfeld (1928) subsequently described a partial, deformed calvarium.

The present species has been recorded from Tonkin, Indo-China, by Patte (1928) on the evidence of certain large teeth from an ossiferous breccia at Lang-Son, which were figured by Mansuy (1916, pl. I figs. 5-8) but left specifically undetermined by the lack of literature. Bien and Chia (1938) figured four teeth from the Hoshangtung cave in the province of Yunnan. An undescribed molar from the middle Pleistocene Trinil fauna of Patjitan in Java is tentatively referred to the present species by Von

Koenigswald (1940, p. 60/61). This find is highly significant, since it reinforces the similarity between the Javan and the southern Chinese, Burmese, and Indo-Chinese early Pleistocene assemblage known as *Stegodon-Ailuropoda* fauna (Bien and Chia, 1938, p. 343), the Sino-Malayan fauna of Von Koenigswald (1940, p. 72).

In the accompanying table I give the range of variation in size of the teeth, after the measurements published by the different authors (Schlosser, 1903, p. 74; Mansuy, 1916, pl. I, vide Patte, 1928, p. 57; Matthew and Granger, 1923, p. 593; Von Rautenfeld, 1928, p. 436; Bien and Chia, 1938,

	<i>Tapirus indicus</i>		<i>Tapirus augustus</i>
	<i>indicus</i> Desmarest	<i>intermedius</i> nov. subsp.	Matthew et Granger
P ¹ antero-posterior	19—22	22—23	23—27
postero-transverse	14—21	17—19	21—25
P ² antero-posterior	22—24	24—26	27—28
postero-transverse	24—27	28—29	30—34
P ³ antero-posterior	22—25	24—27	27—30
antero-transverse	26—29	29—33	33—38
P ⁴ antero-posterior	22—23	24—27	29—31
antero-transverse	28—31	30—33	34—39
M ¹ antero-posterior	24—27	25—28	29—33
antero-transverse	24—28	27—30	36—40
M ² antero-posterior	25—28	28—32	33—36
antero-transverse	29—31	31—34 ¹⁾	38—43
M ³ antero-posterior	24—28	30	34
antero-transverse	27—30	32	38—40
P ₂ antero-posterior	25—28	27—30	30—34
postero-transverse	13—17	16—20	17—20
P ₃ antero-posterior	23—27	27—29	30 ²⁾ —31
postero-transverse	17—20	21—23	22—24
P ₄ antero-posterior	23—25	26—29	31
postero-transverse	19—22	22—24	25—26
M ₁ antero-posterior	24—27	27—31	32—34
antero-transverse	17—20	19—23	24—25
M ₂ antero-posterior	26—28	30—34	34—38
antero-transverse	20—22	(22)23—24	25—28
M ₃ antero-posterior	24—29	(30)32—34	36—38
antero-transverse	19—21	(22)24—25	27—28

p. 337). It will be seen that the subfossil teeth of *Tapirus indicus* Desmarest in a very remarkable way fill the gap that exists between recent *T. indicus* Desmarest and *T. augustus* Matthew et Granger; in fact, it is only in the breadths of the upper molars that there remains an important hiatus. This is not mere coincidence; of the M¹ and M² we have eight

1) 30 mm in the subfossil specimen from Java.

2) Matthew and Granger (1923, p. 593) give the length of the P₃ in one of their specimens as 20 mm, which is apparently (judged by the figure) a misprint for 30 mm.

samples, a number which otherwise is sufficient to give a complete inter-gradation from the Pleistocene to the recent form. The Wanhsien tapir had the tendency to develop broader molars than *T. indicus* Desmarest. In the latter species the length of the upper molars is equal to the breadth, or the latter measurement exceeds the former. In *T. augustus* Matthew et Granger the breadth is always greater than the length, and there is no overlap between the range of the length and that of the breadth for the same tooth.

In their preliminary note on the species Matthew and Granger (1923, p. 588) write that the anterior premolars are more molariform than those in *T. indicus* Desmarest, "the inner cusp and cingulum much more developed, especially in p^1 which in *T. augustus* is wider than long (?)". The published measurements on the contrary show that the P^1 in *T. augustus* is longer than wide, as is the case in *T. indicus* too. Dr. E. H. Colbert kindly informed me that the P^1 of *T. augustus* is distinguished by the large size of its internal cusp, making the transverse diameter of the tooth almost equal to the antero-posterior diameter. I have referred to the variability in development of the hypocone of the P^1 in *T. indicus* above (p. 262, pl. I, figs. 1-2). In one recent tooth (no. 17 in table I) the width is only 1 mm less than the length.

A more important difference is found in the second premolar. From the figures of Matthew and Granger (1923, p. 590) and Rautenfeld (1928, p. 439) it is evident that the antero-transverse diameter of the P^2 is not much shorter than its postero-transverse diameter. In *T. indicus* the P^2 is always distinctly narrower in front than behind. The P^2 in *T. augustus* has a much greater resemblance to the posterior premolars than the corresponding tooth in *T. indicus*; in this respect *T. augustus* is more advanced than the recent species.

Skull differences, apart from size, apparently are of little importance. Matthew and Granger (1923, p. 588) write that "it appears in the skull to be an exaggerated type of *T. indicus*, deeper and shorter with more massive vomer, high-set nasals, etc.", but this is not apparent from their figures. In his description of the skull Von Rautenfeld (1928, p. 441/42) notes many close resemblances to *T. indicus* Desmarest; the mesethmoid, however, is stated to be very strongly developed and to extend as a bony plate beyond the nasals, as is the case in *Tapirella bairdii* (Gill). From the figures (l.c., p. 432 and 433) it can be seen that the extremity of the nasals is missing, so that there is no certainty on this point.

The present species, however, is certainly distinct from *Tapirus indicus* Desmarest, and it cannot be placed in the ancestral line of the latter. Colbert (in litt.) regards *T. augustus* Matthew et Granger as representing the

culmination of evolution in the tapirs. The purpose of the present note is only to call the attention to the now discovered almost complete intergradation in size between the teeth of the two species as represented by the subfossil Sumatran cave specimens.

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EXPLANATION OF THE PLATES

Plate I

- Figs. 1-6, 8-15, 19 and 20, *Tapirus indicus intermedius* nov. subsp. Crown views of upper teeth from cave deposits in the Padang Highlands, Sumatra.
- Figs. 1-2, pd¹ or P¹ dext.; fig. 1, Djamboe cave, Coll. Dub. no. 1134d; fig. 2, Coll. Dub. no. 829c.
- Fig. 3, pd² sin., Lida Ajer cave, Coll. Dub. no. 1820w.
- Fig. 4, pd² dext., Coll. Dub. no. 7002f.
- Fig. 5, pd³ or pd⁴ dext., Coll. Dub. no. 755a.
- Fig. 6, pd³ or pd⁴ sin., Coll. Dub. no. 7002r.
- Fig. 7, *Tapirus indicus* Desmarest subsp., pd³ or pd⁴ dext., Kedoeng Broe-boes, Java, Coll. Dub. no. 1458b, crown view.
- Fig. 8, P² sin., Coll. Dub. no. 7002l.
- Fig. 9, P² dext., Lida Ajer cave, Coll. Dub. no. 1820s.
- Fig. 10, P³ dext., Sibrambang cave, Coll. Dub. no. 961p.
- Fig. 11, P³ sin., Coll. Dub. no. 648Aa.
- Figs. 12-13, P⁴ sin.; fig. 12, Lida Ajer cave, Coll. Dub. no. 1820c; fig. 13, Lida Ajer cave, Coll. Dub. no. 1820r.
- Fig. 14, M¹ sin., Sibrambang cave, Coll. Dub. no. 770Ai.
- Fig. 15, M² dext., Sibrambang cave, Coll. Dub. no. 770Ak (holotype).
- Fig. 16, *Tapirus indicus* Desmarest subsp., M² sin., Wadjak cave, Java, Coll. Dub. no. 3808a, crown view.
- Figs. 17-18, *Tapirus indicus* Desmarest subsp., M² dext., Kedoeng Loemboe, Java, Coll. Dub. no. 1458a; fig. 17, crown view; fig. 18, posterior view.
- Fig. 19, M³ sin., Djamboe cave, Coll. Dub. no. 1134a.
- Fig. 20, M³ dext., Lida Ajer cave, Coll. Dub. no. 1820q.
- All figures natural size.

Plate II

- Figs. 1-13, 15-16, and 18-20, *Tapirus indicus intermedius* nov. subsp.
- Figs. 1-2, 4, 6-10, 12-13, 15, 18-19, crown views of lower teeth from cave deposits in the Padang Highlands, Sumatra.
- Fig. 1, pd₂ sin., Lida Ajer cave, Coll. Dub. no. 1820ae.
- Figs. 2-3, pd₃ sin., Coll. Dub. no. 745d; fig. 2, crown view; fig. 3, posterior view.

- Figs. 4-5, pd_4 sin., Coll. Dub. no. 1102c; fig. 4, crown view; fig. 5, anterior view.
- Figs. 6-7, P_2 dext.; fig. 6, Coll. Dub. no. 7002ak; fig. 7, Djamboe cave, Coll. Dub. no. 1134e.
- Fig. 8, P_3 sin., Coll. Dub. no. 745b.
- Fig. 9, P_3 dext., Lida Ajer cave, Coll. Dub. no. 1820l.
- Figs. 10-11, P_4 sin., Coll. Dub. no. 745a; fig. 10, crown view; fig. 11, anterior view.
- Fig. 12, P_4 sin., Sibrambang cave, Coll. Dub. no. 772Ab.
- Fig. 13, M_1 sin., Coll. Dub. no. 7002ab.
- Fig. 14, *Tapirus indicus* Desmarest subsp., P_4 sin., Kebon Doeren, Java, Coll. Dub. no. 1458c, crown view.
- Figs. 15-16, M_1 dext., Lida Ajer cave, Coll. Dub. no. 1820f; fig. 15, crown view; fig. 16, posterior view.
- Fig. 17, *Tapirus indicus* Desmarest subsp., M_1 dext., Kebon Doeren, Java, Coll. Dub. no. 1458d, crown view.
- Fig. 18, M_3 dext., Lida Ajer cave, Coll. Dub. no. 1820a.
- Figs. 19-20, M_2 or M_3 dext., Sibrambang cave, Coll. Dub. no. 770Ag; fig. 19, crown view; fig. 20, anterior view.
- Figs. 21-22, *Tapirus indicus* Desmarest subsp., M^3 dext., Kedoeng Broe-boes, Java, Coll. Dub. no. 3802a; fig. 21, inner view; fig. 22, crown view.
- All figures natural size.
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