

PLEISTOCENE MAMMALS FROM
THE LIMESTONE FISSURES
OF SZECHWAN, CHINA

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INTRODUCTION

IN THE EARLY AUTUMN of 1921 Dr. Walter Granger, paleontologist of the Central Asiatic Expeditions of the American Museum of Natural History, made a journey into the province of Szechwan, China, to investigate the possibilities of collecting fossil mammals in that region. This trip was made at the suggestion of the Director and certain members of the Geological Survey of China, who had obtained information from Mr. J. Langford Smith, at that time British Consul at Ichang on the Yangtze River, as to the presence of fossil bones in the vicinity of Wanh sien on the upper Yangtze. The trip, when undertaken, was for the most part a "shot in the dark," since the information on the nature and location of the fossils was indeed meager. Fortunately the expedition proved to be a huge success, so much so that Granger stayed at Yen ching kou, the fossil locality, through the winter and spring of 1921-1922, and returned for two additional seasons of collecting in the winters of 1922-1923 and 1925-1926. A large collection of choice fossil mammals of Pleistocene age was brought out and shipped to the American Museum of Natural History, and for the first time definite information as to the age and locality of these fossils, which previously had been described in part by various authors on the basis of very fragmentary remains, was obtained. An account of the collecting trips in Szechwan can be found in Granger (1932).

The fossils from Szechwan came from limestone fissures or pits at the tops of high Palaeozoic ridges which parallel the Yangtze River. These pits have been worked for many years by Chinese farmers, who sell the bones they obtain to druggists in the belief that they are dragon bones and are therefore efficacious in the treatment of many human ills. It was through the channels of Chinese drug stores and traders that most of the earlier fossils came to the attention of trained paleontologists—notably Owen, Koken, Schlosser, and Matsumoto. Granger was the first paleontologist to succeed in reaching the source of supply for these fossils and to supervise personally their collection.

The results of the work at Yen ching kou have been summarized by Granger in the fol-

lowing words: "The collections of the three years give a very adequate representation of the animal life of early Pleistocene times in this region. It is a fauna of which previously we had just an inkling through the descriptions of fragmentary specimens by Owen, Koken, and Matsumoto, of specimens probably obtained from drug merchants and others along the upper Yangtze and the exact source of which was not known. The collection is important not only as giving a picture of the life of this particular region but, being midway between fossiliferous deposits of the same age in north China and northern India, it helps greatly in working out the general distribution and migrations of mammalian life in eastern Asia during the Pleistocene period" (Granger, 1932, p. 528).

Within the past two decades extensive collections and studies have been made in the Pleistocene of Asia, particularly in India, Burma, Java, Indo-China, and at various localities in South and North China. As the result of this work our knowledge of the Quaternary succession of faunas in eastern Asia and the Orient has been growing and taking shape, and consequently it has become increasingly apparent that the many discoveries in the various regions and localities can be integrated to form a unified and logical interpretation of the Pleistocene mammals of Asia and of the environment in which they lived. The mammalian faunas of southern China are especially important in the study of the Asiatic Pleistocene, because they are intermediate, geographically, between the famous Choukoutien fauna of North China and the Trinil fauna of Java, both of which are associated with remains of early man. Of the South Chinese faunas, none is so rich either in the number of forms represented or in material belonging to each species as the assemblage collected by Granger at Yen ching kou.

Because of the importance of this large collection and the additional knowledge regarding Asiatic Pleistocene faunas that has been obtained since the preliminary report by Matthew and Granger, it has been thought advisable to make a thorough study of the fossil mammals from Yen ching kou.

The results of this investigation are set down in the following pages. In doing this work the present authors are merely following the intentions of Matthew and Granger, which because of a varied set of circumstances were never carried to an actual realization.

HISTORICAL BACKGROUND

The first Chinese fossils known to be from Szechwan were described by Owen in 1870 and consisted of a series of teeth obtained by Mr. Robert Swinhoe, a British diplomatic official in the Orient. These were said to be "from a cave, near the city of Chung-king-foo, in the province of Sze-chuen" (Owen, 1870, p. 421). From the fossils thus obtained, Owen described several new forms: *Stegodon orientalis*, *Hyaena sinensis*, *Rhinoceros sinensis*, *Tapirus sinensis*, and *Chalicotherium sinense*.

Fossils from Szechwan were next described and discussed by Koken in 1885 and by Schlosser in 1903. Their work has been briefly summarized by Matthew and Granger as follows: "Koken in 1885 described a collection secured by von Richthofen, apparently from the trading junks of the Yang-tse-kiang and understood by him to have come from far up the river in 'caves in Yun-nan.' Whether this was the real locality remains to be verified; one has the impression from the reading of von Richthofen's letter, quoted by Koken, that the traveller himself suspected that the locality might not have been correctly stated. It is certain at all events that the major part of Koken's collections, like Owen's, represent substantially the same faunal facies, and they seem to agree as to species, in part at least, with our collections. Koken also distinguishes an older fauna of supposed Lower Pliocene age, including *Hipparion*, *Camelopardalis*, *Palaeomeryx*, etc., which is more extensively represented in Schlosser's later collections, and is probably substantially the same fauna as the fine collections secured recently by J. G. Andersson and now being studied by Professor Wiman.

"Schlosser in 1903 described a large collection secured by Dr. Haberer for the Munich museum, and revised the work of Owen, Koken and other previous writers. He concluded that Owen's fauna, except

Stegodon, and most of Koken's material, was of Pleistocene age. There is no doubt, however, that the *Stegodon* is coeval with the rest of the fauna in Granger's collection, and one may assume that it was probably so in the Owen and Koken collections. Schlosser's material belonged mostly to the older Pliocene fauna distinguished by Koken and came from localities farther to the north" (Matthew and Granger, 1923, p. 565).

Subsequently, in 1915, Matsumoto brought out a very carefully prepared paper, containing numerous fine plates, describing a collection of fossil mammals obtained by Mr. T. Sakawa "in a certain marly district of Sze-chuan, China." Matsumoto recognized two faunas in the material before him, according to the manner in which the fossils were preserved. The first, which he designated as the "*Stegodon* fauna" was found in a "brown clay, which is evidently a decomposed product of lime-stone." These fossils were supposed by Matsumoto to be of Upper Pliocene age. The other fauna, which according to this author was found in a cave loam, he regarded as of Lower Pleistocene affinities.

Such was our knowledge of the fossil mammals from Szechwan at the time Granger made his first trip to Yenchingkou. Fragmentary fossils had been described by various authors, who had secured their materials largely through the channels of the Chinese drug merchants. It was only after the American Museum collections had been gathered together that a truly definitive knowledge of the Szechwan fossil mammalian fauna could be obtained. In 1923 Matthew and Granger published a brief description of the American Museum collection, and this represents a great advance over any previously existing knowledge regarding the Szechwan fossil mammals. This paper was frankly of a preliminary nature and therefore presented an incomplete picture of the Yenchingkou fauna.

Since the publication of Matthew and Granger's paper of 1923, and up until the writing of the present contribution, a few additional papers have been published bearing upon this problem in a specific way.

In 1929 (pp. 16-17) Osborn described as a new subspecies the *Stegodon orientalis* material from Yenchingkou, collected by Granger.

er. In 1934 (pp. 384-385) Colbert described a chalicothere tooth from the Yen-chingkou collection in connection with a broad study of chalicotheres from China and Mongolia. Young in 1935 (1935a) described a mammalian microfauna from this locality, listing 10 species or examples of bats, insectivores, and rodents hitherto unknown as members of the Yen-chingkou fauna. This author admits, however, that his material was not collected *in situ* and that a majority of the forms recorded may very possibly be of post-Pleistocene age. A year later, Young described discoveries of fossil *Bubalus* in China and mentioned specimens from Yen-chingkou. He pointed out (1936, p. 511) the fact that *Bubalus* remains already had been collected at this locality by Granger but had not as yet been described. In 1939 Young described new materials from the Yen-chingkou sites collected by L. P. Chia. These fossils, though for the most part fragmentary, supplement and add to the materials described by Matthew and Granger.

In the meantime Granger (1938) published a semi-popular account of his discovery of a complete gaur skeleton at the Yen-chingkou pits and included a photograph of the specimen as it is now mounted at the American Museum of Natural History.

Finally, Hooijer has recently published two papers (1947a, 1951a) describing some tigers and two new deer in the American Museum collection from Yen-chingkou.

As a result of these several papers, together with the contributions made in the present work, the fossil fauna from Yen-chingkou is constituted as follows:

Primates

Cercopithecidae

Rhinopithecus roxellanae tingianus Matthew and Granger

Hylobatidae

Hylobates (Bunopithecus) sericus Matthew and Granger

Lagomorpha

Leporidae

Lepus sp.

Rodentia

Rhizomyidae

Rhizomys sinensis troglodytes Matthew and Granger

Hystricidae

Hystrix cf. *subcristata* Swinhoe

Carnivora

Canidae

Cuon javanicus antiquus Matthew and Granger

Ursidae

Euarctos kokeni (Matthew and Granger)

Procyonidae

Ailuropoda melanoleuca fovealis Matthew and Granger

Mustelidae

Charronia flavigula tyrannus, new subspecies
Arctonyx collaris rostratus Matthew and Granger

Arctonyx collaris collaris Cuvier

Viverridae

Viverra zibetha expectata, new subspecies

Hyaenidae

Crocuta crocuta sinensis (Owen)

Felidae

Felis tigris Linnaeus

Felis sp.

Proboscidea

Stegodontidae

Stegodon orientalis Owen

Elephantidae

Palaeoloxodon namadicus (Falconer and Cautley)

Perissodactyla

Chalicotheriidae

Nestoritherium sinense (Owen)

Tapiridae

Megatapirus augustus Matthew and Granger

Rhinocerotidae

Rhinoceros sinensis Owen

Artiodactyla

Suidae

Sus scrofa Linnaeus

Cervidae

Rusa unicolor (Kerr)

Moschus moschiferus plicodon, new subspecies

Muntiacus muntjak margae Hooijer

Elaphodus cephalophus megalodon Hooijer

Bovidae

Bubalus bubalis (Linnaeus)

Bibos gaurus grangeri, new subspecies

Capricornis sumatraensis kanjereus, new subspecies

Naemorhedus goral (Hardwicke)

OCCURRENCE OF THE YEN-CHINGKOU FAUNA

The little hamlet of Yen-chingkou is about 10 miles up the Yangtze River from the city of Wanhsien and about 10 miles inland from the south bank of the river. Granger has described its situation as follows: "Arriving at Yen-ching-kou, I found the village nestled at

the base of a great ridge of Palaeozoic limestone which had been thrust up in remote times through the Permo-Mesozoic red beds. The ridge rose abruptly nearly 2,000 feet above the valley and was nearly fifty miles long. It was the conspicuous feature of the landscape as one looked south from the Yangtze River which parallels the ridge ten miles away" (Granger, 1932, p. 513).

The Yenchingkou fossils came from the top of this ridge and their mode of occurrence is thus described by Granger: "Limestone is mildly soluble in rain water, especially water which has soaked through humus and decaying vegetation. Such water gathering in pools on top of the limestone ridge had in times past, when the region was forested, dissolved out shafts in the rock—sometimes to a depth of one hundred feet—often to fifty feet or more. The soluble parts of rock passed on down through cracks and the residue remained as mud in the bottom of the pit. These shafts were really vertical caves, and the action which produced them was similar to that which produces horizontal caves.

"The majority of the shafts or pits seem to have been of Pliocene or early Pleistocene origin, and they are for the most part filled to-day with yellowish or reddish mud which had flowed in from the surface or had been left as undissolved residue. There were times, however, when they were open and evidently acted as pitfalls for the various animals which inhabited the region. At any rate the fossil bones were being found in the mud filling of the pits—and usually at depths of twenty feet or more. It was quite evident that the bones got into the pits in two ways. When a complete skeleton was found in a pit it seemed almost certain that the animal had fallen in and either had been killed by the fall or had died of starvation. On the other hand, when single elephant teeth, sometimes considerably weathered, were found, it seemed obvious that the animal had died on the surface, its skeleton had become disorganized and parts of it had gradually drifted into the pit by gravitation.

"A few such pits as these are being formed to-day along the top of the ridge, and undoubtedly they still occasionally act as traps for unwary animals that stray too close to the edge, which is usually masked by a dense

undergrowth. Some of these open pits have diameters of fifty feet or more—real sink-holes—but more often they are smaller—eight or ten feet across. The pits as observed are rather unevenly distributed along the fifty miles of ridge top, although this may be simply because certain areas are more denuded than others and the pits consequently are more easily located" (p. 514).

It is from these pits that bones are procured for the Chinese drug trade. Most of the prospecting and digging of the pits is done by Chinese farmers in the fall and winter, after the summer crops are harvested and the winter crops are planted. The bones thus discovered are then sold to drug merchants by weight. In the digging out of the bones, crude mining methods are followed. One or two men may be lowered into the pit by means of a rope rigged on a pulley supported by poles directly over the center of the pit. The mud and residue in the bottom of the pit are dug out and shoveled into wicker baskets, which are raised to the surface by the winch. This deposit is searched for bones, and such bones as are found are scraped clean and piled up in some convenient farmhouse to dry.

Granger found that the most practicable way to procure fossils from the pits was to make frequent visits along the top of the limestone ridge and to purchase from the native diggers the best of the fossils procured by them. By spending three winters in the vicinity of Yenchingkou, by careful purchasing of the fossils on the spot, so that the exact pit for each specimen was known, and by paying bonuses to the diggers for unusually complete specimens, he obtained a collection of Pleistocene mammals that at the present time is quite unsurpassed.

Matsumoto considered the Szechwan fossils as belonging to two distinct faunas, an older or "*Stegodon* fauna" regarded as of upper Pliocene age, and a younger fauna from the "cave-loam" placed by him in the lower Pleistocene. The work of Granger at Yenchingkou does not bear out Matsumoto's supposition of two faunas of distinct and different ages. What Granger did determine, however, was the fact that there was an "ecologic stratification" of the Yenchingkou fauna, based on the altitude of the pits on

the top of the limestone ridge and on the assumption that the topography of the top of the ridge has not changed greatly since early Pleistocene times.

"It was interesting to note that the pits in the lower areas contained animals not frequently found in pits high up on the knolls. *Stegodon*, *Rhinoceros*, the giant tapir and the gaur were, as might be expected, confined pretty much to the lower pits, while the deer and goats were found more abundantly in the pits higher up. One would naturally expect large animals to keep more or less to the lower levels, while the deer and goats would frequent the hills" (Granger, 1932, p. 517).

RELATIONSHIPS OF THE YENCHINGKOU FAUNA TO RECENT FAUNAS OF CHINA

A list is given above of all the genera and species of mammals now known to be included in the extinct fauna from the fissure fills at Yenchingkou. In a general way this extinct fauna is compared here with the recent faunas of China, to see what resemblances and differences exist between the fossil and the recent assemblages, and to interpret, if possible, the significance of the comparisons.

It is obvious that the Yenchingkou fauna should resemble certain of the recent faunas of China more than others, since China and Mongolia cover a vast area in which are included several zoogeographic divisions of greater or lesser extent, and it is to be expected that the Yenchingkou fauna would be most closely related to the modern fauna living in a habitat most closely resembling that in which the Middle Pleistocene mammals of Szechwan lived.

Glover Allen in his monograph on the mammals of China and Mongolia (1938) lists seven faunal areas, some of which are in the great Palearctic zoogeographic realm while others are in the Oriental realm, as follows:

1. The Northern Forest, roughly north of the northern boundary of Mongolia, extending through Manchuria and into the northern part of Hopei Province east of the Khingan Range.
2. The Gobi, including Inner and Outer Mongolia and Sinkiang.
3. North China, composed of southern Hopei

Province, Shantung, Shansi, Shensi, Kansu, and the northern portion of Honan, bounded on the north by the Gobi and on the south by the Min Shan and Tsingling ranges.

4. South China, generally speaking the lowland area south of the thirty-fourth parallel and east of the Western Highlands; containing Kiangsu, Anhwei, Hupeh, Hunan, Kiangsi, Chekiang, and Fukien Provinces.

5. The Western Highlands, principally of Szechwan but including parts of Kweichow and Yunnan.

6. The Subtropical region, a northeastern extension through southern Yunnan, Kwangsi, and Kwangtung of conditions typical of Burma and Indo-China.

7. The Tibetan Plateau, the high land west of Szechwan and north of the Himalayas.

An examination of table 1 will show that numerically the extinct fauna of Yenchingkou is most closely related to the recent fauna of the Western Highlands of Szechwan. This is about as would be expected, since, as Granger pointed out, there is every reason to think that the topography of Szechwan was not much different in Pleistocene times than it is at present. Moreover, the climate, while not exactly the same, was similar enough to the present climate so that there is a strong resemblance between the fauna living in the region at that time and the present fauna in the same area. In addition to the general broad similarities thus indicated between the extinct and recent faunas of the Szechwan highlands, more definite relationships between the assemblages can be classified as follows:

1. Many mammals in the Yenchingkou fauna are very similar to their modern counterparts living in the same region or in nearby parts of China. These animals constitute the bulk of the fauna, and their general prevalence gives to the Yenchingkou assemblage its "modern look."

2. But a certain proportion of the Yenchingkou fauna consists of animals that no longer are found in this portion of Szechwan but that persist in modern times in more distant portions of China or of Asia, or in a few cases in other parts of the world.

3. Finally, a portion of the Yenchingkou fauna is made up of completely extinct genera and species. It is these animals that give to the fauna its "ancient look," and it

TABLE 1
COMPARISON OF THE YENCHINGKOU FAUNA WITH MODERN ASIATIC FAUNAS

	1. North- ern Forest	2. Gobi	3. North China	4. South China	5. West- ern High- lands	6. Sub- tropical	7. Tibet	Yenching- kou
<i>Rhinopithecus</i>					x			x
<i>Hylobates</i> " <i>Bunopithecus</i> "						x		x
<i>Lepus</i>		x	x	x	x		x	x
<i>Rhizomys</i>				x	x	x		x
<i>Hystrix</i>				x	x	x		x
<i>Cuon</i>	x	x	x	x	x	x		x
<i>Euarctos</i>			x	x	x	x		x
<i>Ailuropoda</i>					x			x
<i>Charronia</i>	x		x	x	x	x		x
<i>Arctonyx</i>	x		x	x	x	x		x
<i>Viverra</i>				x	x	x		x
<i>Crocuta</i>								x
<i>Felis</i>	x	x	x	x	x	x		x
<i>Stegodon</i>								x
<i>Palaeoloxodon</i>								x
<i>Nestoritherium</i>								x
<i>Megatapirus</i>								x
<i>Rhinoceros</i>								x
<i>Sus</i>	x		x	x	x	x		x
<i>Rusa</i>					x	x		x
<i>Moschus</i>	x		x	x	x			x
<i>Muntiacus</i>				x	x	x		x
<i>Elaphodus</i>				x	x			x
<i>Bubalus</i>								x
<i>Bibos</i>								x
<i>Naemorhedus</i>			x	x	x			x
<i>Capricornis</i>				x	x	x		x
Total number of genera	6	3	9	15	18	13	1	27

is the extinction of these forms that causes, for the most part, the real differences of the Yenchingkou mammalian assemblage from the modern mammalian fauna of western China.

What are the significant facts to be found in the extinction of certain members of the Yenchingkou fauna, and in the relationships that are shown between other elements in the assemblage and their modern counterparts? These are questions that deserve a certain amount of attention.

As mentioned above under 3, the outstanding difference between the Yenchingkou mammalian assemblage and the modern fauna from this part of China is the complete extinction of certain genera [(*Bunopithecus*), *Stegodon*, *Palaeoloxodon*, *Nestoritherium*, and

Megatapirus] during the transition from middle Pleistocene to Recent times.

Except for *Bunopithecus* (a subgenus of doubtful validity), these are large mammals and for that reason are particularly conspicuous in the Yenchingkou fauna. Since none has exact counterparts living at the present time it is difficult to attempt an interpretation of their extinction. Suffice it to say that they seem to have been the victims of a general world-wide trend marking the transition from Pleistocene to Recent times whereby certain large mammals ranging widely over the several continents were caught in a "wave of extinction" during the final phases of the glacial period.

Those forms that no longer are to be found in the western Szechwan highlands but that

still persist in other parts of the world (*Crocota*, *Rhinoceros*, *Bibos*, and *Bubalus*) combined with the extinct types contribute to the Yenchingkou fauna most of the differences distinguishing it from the recent fauna of western China. Of these forms all but the hyena (*Crocota*) are found in portions of Asia adjacent to or near Szechwan. *Crocota* is at the present time limited to the Ethiopian region.

This brings us to a consideration of the bulk of the Yenchingkou fauna, which consists of animals not so greatly different from their modern counterparts living in Szechwan. Generally speaking, it can be said that the Pleistocene mammals of Szechwan are very similar to the corresponding modern types in this region, except that in most cases the extinct animals are larger than their modern relatives.

This distinction occurs time and again in the comparisons between Pleistocene and prehistoric mammals and modern types. One of us (Hooijer, 1949, 1950) has cited several examples from the East Indies islands, and the phenomenon is apparently world-wide. Naturally, the supposition is that this decrease in general size during the Quaternary is correlated with the warming-up of the world's climates since the Ice Age (see Romer, 1949, pp. 111-112; and Simpson, 1949, p. 136). However, there are some exceptions to this "rule" (Hooijer, 1950, pp. 147-148), which seems to indicate that the general decrease in size in the course of time is not controlled by environmental factors exclusively.

In the case of the Yenchingkou mammals, it seems that most fossil mammals are the direct ancestors of the modern related types in this region of Asia. Thus we must assume that there has been a general decrease in size from Pleistocene ancestor to Recent descendant in this area as well as elsewhere. This change may have been brought about, as stated already several years ago by one of us (Colbert, 1949, p. 129), by the gradual transition from a generally cool climate in western China in middle Pleistocene times to a rather warm climate at the present time. Thus there may have been a working of Bergmann's principle through time: as the climate became increasingly warmer during

the passage from the middle Pleistocene to the Recent the succeeding generations of mammals became successively smaller.

In the present case, however, it seems that there may be still another explanation for the differences between the Szechwan fossil mammals and their recent counterparts. The province of Szechwan is at present a very hilly or mountainous region, and it is probable (as suggested above) that much the same geographic conditions as are now developed were characteristic of the region in middle and late Pleistocene times. If so, there is reason to believe that with the generally cooler temperatures supposedly prevailing in those days there was a certain disparity in temperatures between the lowlands and the uplands. Consequently, it is possible that the fossil fauna from the Szechwan pits, coming as it does from the tops of the peaks and ridges, was in reality a "cool-climate fauna" ecologically limited to the highlands, while there was a correlative fauna (not represented by fossil remains) of corresponding but smaller types living in the lowlands. Then with the general increase in the average temperature consequent upon the transition from the Pleistocene to Recent times, the upland fauna of large types may gradually have become extinct, to be succeeded by the lowland fauna or smaller types invading the upland regions as they followed the ascent of the isotherms up the mountainsides. This argument can be applied to many of the elements in the Yenchingkou fauna—elements that are found represented in this same region today by corresponding but smaller animals.

Yet there are certain members of the Yenchingkou fauna to which this explanation does not readily apply, since they are not represented at the present time by corresponding types in this portion of Szechwan. Therefore, as an alternative explanation, it is reasonable to suppose that some of the Yenchingkou Pleistocene mammals may have been forced out of this region as the climate became warmer, to seek elsewhere a refuge in cooler areas at higher altitudes. Such an emigration would be to the west, and it is in the extreme western portion of Szechwan, characterized by rugged topography running up to considerable heights, that the giant

panda, *Ailuropoda*, and the golden monkey, *Rhinopithecus*, animals formerly living at Yenchingkou, are now found.

None of the above explanations need apply exclusively to the entire fossil fauna of Szechwan. Indeed it is very likely that there was a combination of circumstances that led to the size differences that distinguish the modern Chinese fauna from its Pleistocene antecedent. There may have been a combination of regressive size growth, plus extinction and replacement, plus emigration. The purpose here is not to attempt any definite explanation for the phenomena observed but to suggest the possibilities that might variously explain them.

Other considerations besides those of size differences can be presented with regard to this comparison of the fossil and recent faunas of Szechwan in their relationships to past and present climates. For instance, some of the genera of mammals living in Szechwan during the Pleistocene which since have become entirely extinct, such as *Stegodon* and *Nestoritherium*, have no close modern relatives, so that speculation regarding them is of little avail. Others, however, particularly the genus *Megatapirus*, have closely related genera living at the present time outside China. *Megatapirus* lived in Szechwan; its modern relative, *Tapirus*, inhabits the Malay Peninsula and Sumatra. Why did not *Tapirus* succeed *Megatapirus* in Szechwan? In this case, it seems very probable that although there was a rising temperature accompanying the change from Pleistocene to Recent conditions in western China, the rise was not sufficient to permit certain tropical forms such as the modern tapir to replace its cool-climate predecessor. Of course this may not be the only factor involved in the case of the tapirs. The disadvantages of rough topography might also have been effectual in preventing the modern *Tapirus* from invading Szechwan subsequent to or during the extinction of *Megatapirus*. But it seems likely that climate was a more potent barrier in this case than were topographical conditions.

Certain elements in the fossil fauna of Szechwan are hard to explain on the basis of our knowledge of recent related animals. Such is the case of the gibbon (*Hyllobates* or *Bunopithecus*) at Yenchingkou, the hyena (*Crocuta*), the rhinoceros (*Rhinoceros*), and

the gaur (*Bibos*). At present these animals live in regions outside China and in habitats that are essentially hot or tropical. Why should such animals have lived in Szechwan in Pleistocene time when climatic conditions, so we think, were much cooler than they are now? If these animals were capable of living in the cool climate of the Pleistocene in Szechwan, why did they become completely extinct in this habitat, even though their closely related modern counterparts persist in distant, tropical regions? This case is somewhat different from that of the tapirs, discussed above. In the case of the tapirs, we are dealing with different genera, sufficiently distinct to presuppose ecological adjustments of such magnitude as to account for the one living in a cool climate and the other in a tropical region. But in the cases of the gibbon, the hyena, the rhinoceros, and the gaur, the fossils are so nearly like their modern representatives that it is difficult to understand why the fossil forms should have been supposedly cool-climate types and the modern ones warm-climate types. Or, rather, it is difficult to understand why, if these animals were able to live in Szechwan during the Pleistocene, they were unable to persist into a period of warmer temperatures when very closely related modern types are able to withstand tropical conditions.

Then the elements in the fossil fauna of Szechwan to which none of the above speculations need apply are the forms that are so nearly like the modern related types in size that it is not necessary to account for their presence in past and present faunas as the result of changing ecological conditions. In other words, some of the Yenchingkou mammals must have been directly ancestral to their modern counterparts in this region, surviving the climatic changes that took place with the passage of time without showing corresponding physical changes. In this category may be placed the civet (*Viverra*) of Yenchingkou, which shows certain minor qualitative differences but no essential quantitative differences from the modern *Viverra* in the same region.

Finally, there is the question of why certain elements which might logically be expected are absent from the Yenchingkou fossil fauna. In some cases these absences are undoubtedly due to the accidents of preser-

vation and collecting. Such an explanation is readily applicable to the small insectivores, of which a considerable number exist in the present fauna of Szechwan but which are virtually unrepresented in the fossil fauna. Because of their small size it is likely that the bones of these animals did not withstand the rather rigorous conditions of burial typical of the Yen-ching-kou sediments. The same is probably true with regard to the bats and to a lesser extent the rodents and hares. In this connection it is interesting to note that such rodents as are found in the Yen-ching-kou fauna are forms of rather large size, such as *Rhizomys* and *Hystrix*. Even with these two forms the implications are peculiar. Why should *Hystrix*, a very prominent member of Pleistocene faunas in other parts of eastern Asia, be so sparsely represented at Yen-ching-kou? Why should *Rhizomys* be so unusually abundant in this particular fossil fauna?

It may be that another factor of importance in an explanation of the lack of small mammals (except *Rhizomys*) in the Yen-ching-kou fauna is the relationship of climbing ability to body size and gravity. The occurrence of a great proportion of the fossil remains at Yen-ching-kou is probably due to animals' having inadvertently fallen into the pits when these pits were open and deep. Thus many large forms were trapped and killed. But small mammals like insectivores and rodents would in the first place be but slightly injured by falling into these pits, and in the second place would in many cases be able to climb out because of their ability to cling to the rough surface of the sides of the pits with sufficient effectiveness to overcome the downward pull of gravity. Moreover, it is likely that these small mammals would not blunder into the open pits as would large animals. The small forms would become aware of the danger in time to avoid it, and would be able to cling to vegetation growing around the pits and in this manner escape falling in.

Again it is probable that the methods of collecting have had a considerable effect on the composition of the microfauna from the Yen-ching-kou pits. All the collecting to date has been done by natives, searching for "dragon bones." It is therefore quite probable that careful sieving would bring to light

from the Yen-ching-kou pits a microfauna that is still but little known.

However, these considerations do not apply to the larger forms that are present in the recent fauna of the Szechwan region but that are unknown from Yen-ching-kou. These are specifically certain carnivores and a few artiodactyls: *Ailurus*, *Ursus*, *Nyctereutes*, *Vulpes*, *Mustela*, *Lutra*, *Micraonyx*, *Viverricula*, *Paguma*, *Cervus*, and *Budorcas*.

The absence of some of these genera from the Yen-ching-kou fauna may be explained in several ways. The region of Yen-ching-kou and Wanhsien may have been too far east for *Ailurus* and *Ursus* during Pleistocene times, as today it is too far north for *Micraonyx*, and too far east or south for *Cervus*. Even so it is difficult to see why, if *Ailuropoda* and *Rhinopithecus* (now found to the west of Yen-ching-kou) could live in eastern Szechwan in Pleistocene times, the same should not apply to *Ailurus*. The same argument can be applied to some of the other forms here considered. The absence of *Lutra* from the Yen-ching-kou fauna may be explained by the aquatic habits of this animal, which would preclude its inclusion in an upland fauna.

But as for the other genera listed, their absence from the Yen-ching-kou fauna is indeed difficult to understand, especially since most of them are animals of considerable size, living at the present time in the vicinity of Wanhsien. The solution to this question must await further studies at a future date.

The absence from the Yen-ching-kou fauna of other genera now found in regions distant from the Western Highlands of China and not found in these highlands is so obvious as to need no comment. As is shown below, this geographic and regional separation explains many of the differences between the North Chinese fauna of Choukoutien and that of Yen-ching-kou, assemblages probably contemporaneous in time but quite different in habitat.

RELATIONSHIPS OF THE YEN-CHING-KOU FAUNA TO OTHER EXTINCT CAVE FAUNAS OF EAST ASIA

A number of cave faunas have been discovered in east Asia, principally in China and Indo-China, which compare very well with the characteristic fauna of Yen-ching-

TABLE 2
GENERAL COMPARISON OF CAVE FAUNAS OF EAST ASIA

	Yenching- kou	Hoshang- tung ^a	Tan- yang ^b	Mogok	Kweilin ^c	Lang Son ^d	Tam Nang ^e
<i>Rhinopithecus</i>	x						
<i>Hylobates</i>							
" <i>Bunopithecus</i> "	x						
<i>Lepus</i>	x						
<i>Rhizomys</i>	x						x
<i>Hystrix</i>	x	x	x	x	x	x	x
<i>Cuon</i>	x						x
<i>Euarctos</i>	x	x	x		x	?	?
<i>Ailuropoda</i>	x	x		x	x		x
<i>Charronia</i>	x						
<i>Arctonyx</i>	x	x	x		x		x
<i>Viverra</i>	x				(x)		
<i>Crocuta</i>	x	x	x		x		x
<i>Felis</i>	x	x			x	x	x
<i>Siegodon</i>	x	x		x	x	x	x
<i>Palaeoloxodon</i>	x	x	x	x	(x)	x	x
<i>Nestoritherium</i>	x						
<i>Megatapirus</i>	x	x	x			x	x
<i>Rhinoceros</i>	x	x	x	x	x	x	x
<i>Sus</i>	x	x	x	x	x	x	x
<i>Rusa</i>	x	x	x	x	x	x	x
<i>Moschus</i>	x				(x)		
<i>Muntiacus</i>	x	x	x				x
<i>Elaphodus</i>	x						
<i>Bubalus</i>	x					x or	x
<i>Bibos</i>	x					x	x
<i>Naemorhedus</i>	x						x
<i>Capricornis</i>	x						

^a Present at Hoshangtung, but not at Yenchingkou: *Macaca*, *Pongo*, *Ailurus*.

^b Present at Tanyang, but not at Yenchingkou: *Macaca*, *Rattus*, *Paguma*, and *Hydropotes* (?).

^c Present at Kweilin, but not at Yenchingkou: *Macaca* and *Pongo*. In parentheses are recorded the genera not found *in situ* in the cave but bought in drug stores.

^d Present at Lang Son, but not at Yenchingkou: *Nesokia* (?).

^e Present at Tam Nang, but not at Yenchingkou: *Macaca*, *Pongo*, *Canis*, *Paradoxurus*, *Cervus*, *Proboselaphus*, and *Spirocerus*.

kou. These faunas are those of:

Hoshangtung cave, Yunnan (Young, 1932b; Bien and Chia, 1938)

Tanyang cave, Kiangsu (Pei, 1940)

Mogok caves, Upper Burma (Colbert, 1943)

Kweilin cave, Kwangsi (Pei, 1935)

Lang Son, Tonkin, Indo-China (Mansuy, 1916; Patte, 1928)

Tam Nang, Indo-China (Arambourg and Fromaget, 1938)

From table 2 it is apparent that the several Middle Pleistocene faunas of southeastern Asia are very much alike, in fact almost identical, which is about what would be expected

on the basis of a study of the modern mammalian faunas of China. Here we see the differences between two zoogeographic areas. The Yenchingkou, Tanyang, Kweilin, Hoshangtung, and Mogok faunas are situated in what is now the Oriental zoogeographic realm. To the north is the Choukoutien fauna, situated in what is at the present time the Palearctic zoogeographic realm. The southern faunas are quite different from the northern fauna; therefore there is good reason to think that some sort of zoogeographic division, similar to that existing at the present time, caused the extinct faunas of North

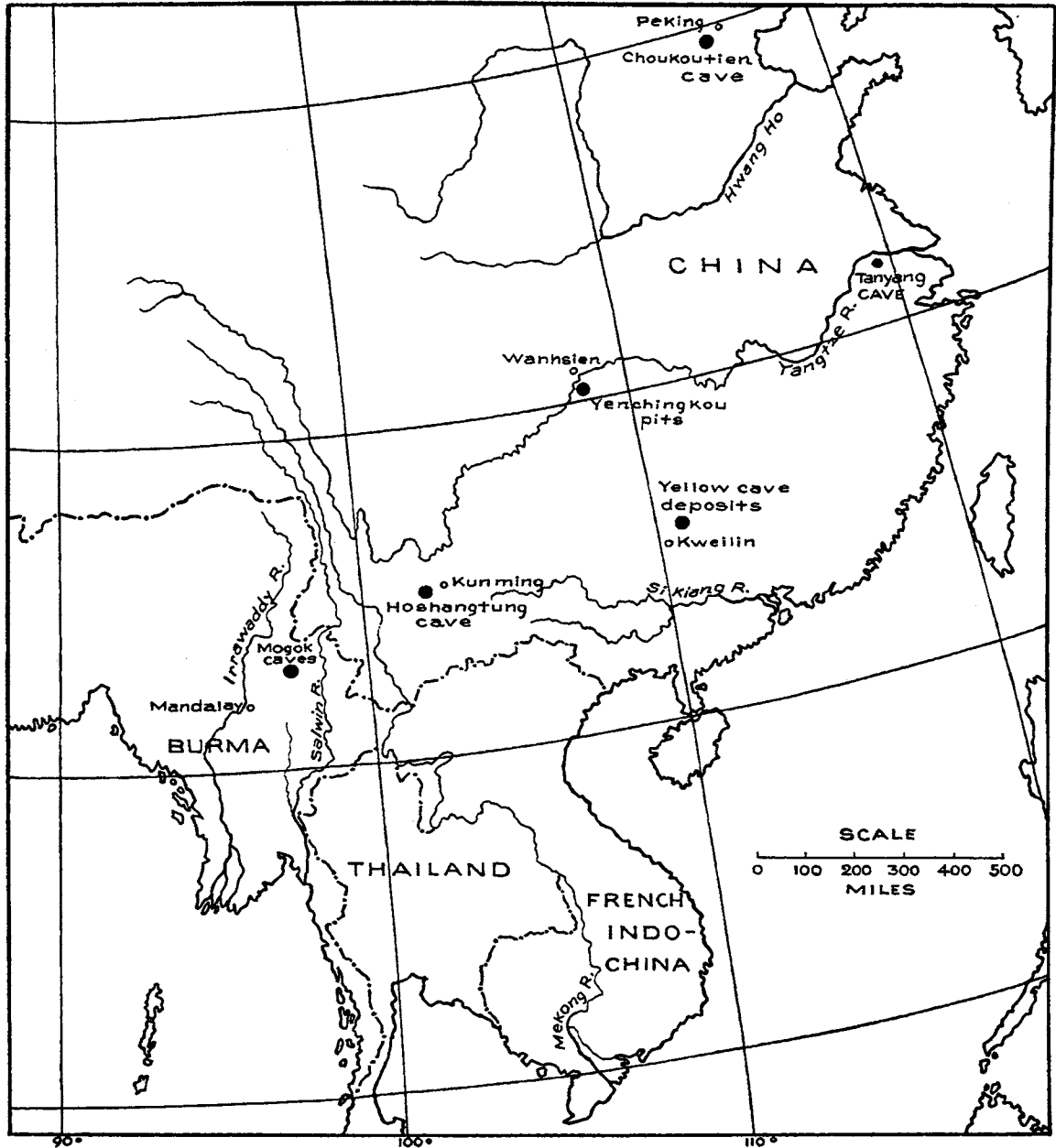


FIG. 1. Map of southeastern Asia showing Pleistocene fossil localities.

and South China to be distinct and different from each other, a fact that has been already pointed out by Teilhard, Pei, and others.

In discussing the characters of the fauna found in the Kwangsi caves, Pei wrote: "Most obviously the fauna found in Kwangsi associated with the Yellow cave-deposits

is the same as the Wanhstien fauna of Ssuchuan (see Matthew and Granger, 1923) and as the fauna of Yunnan recently described by Dr. C. C. Young from Yunnan.

"Thus it becomes clearer every day, that during the Lower Pleistocene times a single large faunistical unit of Indo-Malay-

sian affinities, characterized by *Stegodon*, *Tapir*, *Rhinoceros sinensis* (cf. *indicus*), *Hyaena ultima*, *Ailuropus* and (at least in the southernmost part of China) Orang, was largely spread over Southeastern China.

"Southward and westward, this faunistical block seems to fuse with the *Stegodon* fauna of Indo-China and Java, and to extend in the direction of India (Orang is known in the Siwalik deposits,¹ and *Ailuropus* has been described by Sir A. Smith Woodward from Burma).

"Northward, an abrupt change occurs at the latitude of the Tsinling range, north of which (for instance in Choukoutien) another, a widely different faunal assemblage, is found in the Lower Pleistocene, as characterized by the Euryceroid Deer, a special *Hyaena*, *Machairodus* and the *Dicerorhinus* types of *Rhinoceros* (*R. mercki* and *R. tichorhinus*).

"A few elements only of the southern block seem to have forced their way at that period, probably along the sea, up to the Huangho basin: the water Buffalo, *Hyaena ultima* (at the end of the period), and perhaps (unless he or his predecessor was already there) *Sinanthropus*" (Pei, 1935, p. 424).

It might be said here that the resemblances between the several southern faunas listed above go beyond generic relationships, so that there is a close specific identity between them. The conclusion following is that these faunas were contemporaneous, forming, as Pei has termed it, a "southern block" of Pleistocene mammals showing intergrading relationships much the same as are shown by modern mammals in this same general area.

AGE OF THE YENCHINGKOU FAUNA

In the original description of the fossils from Yenchingkou, Matthew and Granger designated them as of upper Pliocene age, a decision influenced largely by the presence of *Stegodon* and *Chalicotherium* (= *Nestoritherium*) in the fauna. At that time these two genera were considered as characteristic

¹ The alleged occurrence of "*Simia* cf. *satyrus*" in the Upper Siwaliks of India has found its way into the literature, but, as already stated by one of us (Hooijer, 1948, p. 290, footnote), the evidence is inconclusive, and it would seem best for the present to remove *Pongo* from the faunal list of the Siwaliks.

Upper Tertiary types, a view based in large part on the older theories regarding the correlation of the Siwalik series in India.

During the past two decades or so, however, there has been a considerable shift of opinion regarding the age of the Siwaliks, especially the upper portion of the series, so that now the persistence of *Stegodon* and *Nestoritherium* into the Pleistocene is generally recognized. Consequently there have been new evaluations of the Upper Cenozoic faunas of China, and although differences of opinion exist there is general agreement that the Yenchingkou fauna and similar cave faunas from other parts of southern China are of Pleistocene age.

This being the case, how is the Yenchingkou fauna to be correlated within the Pleistocene? What are the relationships of this and contemporaneous faunas to other Pleistocene faunas of southeastern Asia, and in what portion of the Pleistocene period are these several faunas to be placed?

To begin this consideration, it should be mentioned that the position of the Yenchingkou fauna and other mammalian assemblages within the Pleistocene depends, to some extent, on one's definition of the limits of this geological period. Teilhard de Chardin (1937) regards the Villafranchian of Asia as of upper Pliocene age, basing his conclusions largely on diastrophic evidence, the rejuvenation of the topography and the cutting of the Fenho gorges in post-Villafranchian times being regarded by him as the logical break between the Pliocene and the Pleistocene. On the other hand, it is the inclination of the present writers to regard the world-wide spread of certain new mammalian types, particularly *Equus*, *Archidiskodon*, and *Bos* (in the broad sense of the term), as indicative of the advent of Pleistocene times. Therefore we would regard the Villafranchian in Europe and Asia as of lower Pleistocene age, since here are found these new mammalian types, which would place the diastrophic movements in China resulting in the cutting of the Fenho gorges within the Pleistocene.

It is obvious therefore that certain formations or faunas designated by Teilhard as of upper Pliocene age are here regarded as being included within the lower portions of the Pleistocene, while the beds and their con-

tained faunas placed by Teilhard in the lower Pleistocene are here accorded a somewhat higher or later position.

As is shown above, there can be but little doubt that the various cave faunas in southeastern Asia showing the association of *Stegodon*, *Ailuropoda*, and *Hystrix* are contemporaneous with one another. Thus we may regard the faunas of Tanyang, the Kwangsi caves, Hoshangtung, Yenchingkou, and Mogok as separated elements of a single southeastern fauna that lived in Pleistocene times across southern China, Burma, and the Malay region. Moreover there is good reason to regard the southeastern Asiatic fissure deposits containing these faunas as about the equivalent of the Boulder Conglomerate complex in the Siwalik series of India. This last statement is based on the observations by Teilhard and de Terra in Burma, whereby it seems evident that the Mogok fissure deposits are probably correlative with adjacent boulder fans, these latter seemingly equal in age to the Boulder Conglomerate deposits of India. Extended arguments have been presented (Colbert, 1942a, p. 1447) supporting the assignment of the Boulder Conglomerate to a position well up within the Pleistocene, possibly in the Middle Pleistocene, and above the Pinjor and Tatrot beds in which are found faunas of essential Villafranchian aspects. Therefore the Mogok fauna, and by implication the other cave and fissure faunas contemporaneous with it, takes a position considerably above the bottom of the Pleistocene, and it seems not unreasonable to regard this position as coming at about the middle of the Pleistocene period, stratigraphically and temporally.

Antecedent to the Mogok fauna in Burma is the Upper Irrawaddy fauna, which by its aspect is clearly contemporaneous with the Pinjor fauna of India. Thus the relationship in India of a Lower Pleistocene deposit containing a Villafranchian fauna, the Pinjor, and succeeded by a later series, the Boulder Conglomerate, is repeated in Burma by the Lower Pleistocene Irrawaddy sediments containing the Upper Irrawaddy fauna of Villafranchian age, succeeded by the later, possibly Middle Pleistocene Mogok fissure deposits with their contained fauna (Colbert, 1943).

Similarly the same general relationships seem to hold in Yunnan, where the Ma Kai Valley deposits, containing a fauna that seems to be more or less comparable with the Irrawaddy-Villafranchian assemblage, apparently is succeeded by the Hoshangtung cave deposits, the fauna of which is so clearly contemporaneous with that of Mogok (Colbert, 1940). In Kwangsi and in Szechwan, respectively, there are at the present time no faunas known that would correspond with the Pinjor-Irrawaddy-Ma Kai complex, but, as is mentioned above, the faunas of Kweilin and related caverns in Kwangsi and of the Yenchingkou pits in Szechwan are clearly correlative with Mogok and Hoshangtung, while the fauna of the Tanyang cave deposits in Kiangsu shows this same relationship.

Finally we come to a consideration of the deposits and faunas in North China, specifically the Nihowan or Sanmen fauna, the fauna from locality 18, near Peking, admittedly of Villafranchian relationships and placed by Teilhard in the Upper Pliocene, and the Choukoutien fauna, assigned by this author and his associates to the Lower Pleistocene. The Nihowan fauna, in which *Equus* makes its first appearance in China, is certainly correlative with the other Villafranchian faunas mentioned above, namely, Pinjor, Upper Irrawaddy, and Ma Kai, and in the scheme considered here is to be regarded as of lower Pleistocene age. The Choukoutien fauna, coming later than the Nihowan assemblage, would therefore be reasonably expected as about the equivalent in age of the cave faunas in southern China and Burma, even though because of zoogeographic differences its elements do not correspond closely to those of the southern cave faunas. Consequently, in the present correlation Choukoutien may be considered as well up in the Pleistocene, perhaps about middle Pleistocene in age.

The only other alternative in the present scheme of correlation would be to place all the southern cave faunas and the Choukoutien fauna to the north, seemingly correlative with them, in the upper portion of the Lower Pleistocene. This is a possibility to be considered, and may be adopted if the reader prefers to accord to these faunas this earlier relationship. The only arguments to

be brought against such a procedure are that it assigns to the lower Pleistocene deposits of India a very considerable thickness, while among the cave faunas of China it assigns to the Lower Pleistocene many types which by their relationships and preservation seem to be later than might be expected of early Pleistocene fossils. Thus among the mammals constituting the Yen-ching-kou fauna are many forms only subspecifically separable from their modern counterparts, and this in some cases on very small degrees of difference. Moreover the fossilization of these Yen-ching-kou types is not so great as might be expected in early Pleistocene fossils, although it is of appreciable extent. This is exclusive of the Yen-ching-kou forms of a date obviously more recent as shown by their relatively fresh condition. Perhaps this last argument is not very effective, but certainly that of the mere subspecific differentiation of cave forms from modern ones is to be carefully considered. Would a relationship as close as this be expected between early Pleistocene and recent types? Perhaps, but it is not nearly so likely as between Middle Pleistocene and recent forms.

The correlation of the Yen-ching-kou deposits and their contained fauna with related cave deposits and faunas and antecedent terrestrial flood plain deposits and their contained faunas in southeastern Asia can be represented as follows¹:

	INDIA	BURMA	YUNNAN	SOUTH CHINA	NORTH CHINA
Middle Pleistocene	Boulder Conglomerate	Mogok caves	Hoshantung cave	Kwangsi caves Yen-ching-kou pits Tanyang caves	Choukoutien fissures
Lower Pleistocene	Pinjor Tatrot	Upper Irrawaddy	Ma Kai Valley deposits		Nihowan (Sanmen)

NATURE OF THE MATERIAL COMPRISING THE YEN-CHING-KOU FAUNA

A very perplexing problem arises in connection with a considerable number of the

¹ The lower and middle Pleistocene stages here given are called the Siva-Malayan and Sino-Malayan faunas, respectively, by von Koenigswald (1939, 1940). Further correlations by genera with the Pleistocene faunas of Java will be found in Hooijer (1952).

species assigned to the Yen-ching-kou fauna. Do the bones from the pits invariably represent animals that were members of the Pleistocene fauna, or do some of them represent intrusions of a later age—animals that have fallen into the pits in subrecent or recent days? In some cases, such as those of the large *Stegodon orientalis* and the giant panda (*Ailuropoda melanoleuca fovealis*), there can be no doubt but that all the material is thoroughly fossil and that the species represented by this material are extinct members of a fauna having an appreciable geologic age. In other cases, however, the question as to whether or not the supposed fossils are actually representative of animals contemporaneous with the true Pleistocene Yen-ching-kou fauna cannot be so easily answered. Occasionally there seems to be a mixture of material, some thoroughly fossilized, some having the appearance of recent intrusions into the Yen-ching-kou mammalian assemblage. This is true, for instance, of the badger (*Arctonyx*). In still other cases, such as that of the golden monkey (*Rhinopithecus*), most if not all of the material has a suspiciously recent look. Thus, of the specimens listed as representing *Rhinopithecus roxellanae tingianus*, only one can be classified as showing evidence of having any appreciable geologic age. All the other specimens are of light weight, and the bone is hard and rath-

er elastic—evidences of the fact that there has been little replacement of the original bone. Therefore, it is possible that these specimens represent not animals contemporaneous with *Stegodon* and the other forms that we know are of Pleistocene age, but those of a much later age that fell into the pits, to become mixed in with the older fossils.

Indeed, from the nature of these pits, it

would be surprising if the remains found in them were limited to a single geologic horizon. Many of the pits were, over a considerable period of the Pleistocene, and still are, dangerous traps for unwary animals, so that the accumulation of bones found in them represents an accretion that has been built up from about the beginning of the Middle Pleistocene to the present day.

Of course the fact that some specimens may be more recent than those truly comprising the Yenchingkou fauna does not necessarily mean that they also were not members of that mammalian assemblage, for there is every reason to think that many of the Yenchingkou mammals persisted through the later phases of the Pleistocene and into Recent times. During that period of persistence there may have been changes of a subspecific nature, or it may be that little if any change was involved. That is why a real question is involved in the consideration of certain Yenchingkou forms concerning their specific identity with, and subspecific differentiation from, the corresponding recent animals from this section of China. Cases are individually discussed in the consideration of each form.

It will be noticed that the American Museum collection of Yenchingkou mammals is conspicuously lacking in very small forms, the microfauna. Young (1935a) gives a list of certain insectivores and small rodents, the remains of which had been found in an inspection of the rubbish left by the excavation of two fossiliferous pits at Yenchingkou. As remarked by Young, their age is not certain, since they were not collected *in situ*. However, mixed with the microfauna were a number of fragmentary bones belonging to the large mammals described by Matthew and Granger. Of the forms mentioned in the list below, only *Tamias* and *Pteromys* are stated to be thoroughly fossilized, while the others look rather fresh.

Chiroptera indet.
Sorex cylindrocauda
Anourosorex squamipes
Scaptochirus sp.
Tamias asiaticus
Pteromys cf. *xanthipus*
Eothenomys melanogaster
Apodemus sylvaticus
Rattus rattus

SPECIES AND SUBSPECIES IN FOSSIL MATERIALS

In the discussion of the general aspects of the Yenchingkou fauna presented above an attempt is made to show that the fauna can be divided into several categories, namely, completely extinct genera and species, species belonging to genera not now found in this portion of Asia, and finally forms closely related to the modern species now living in this portion of Szechwan or in closely adjacent regions. In a comparison of the fossil fauna of Szechwan with the recent fauna from the same region, it is obvious that the differences between the two assemblages will be apparent in the first two of the above-named categories, so that in these cases no particular difficulties are encountered during the course of the comparative study. It is in the comparison of fossils with their recent counterparts from the same region that the greatest perplexities connected with this study arise.

The question arises as to whether the supposedly extinct mammals of this category from Szechwan are truly specifically separable from the recent animals found in this region. Matthew and Granger in 1923 designated various fossil types as distinct, and from the very incomplete manuscript on this subject left by Matthew at the time of his death it is apparent that he regarded still other types, not described in the 1923 paper, as new forms specifically separable from their recent relatives.

But in reviewing the fauna, both described and undescribed material, the present writers have doubted whether such distinctions as indicated by Matthew and Granger can truly be drawn. Close morphologic study of the fossils supplemented by extensive comparative measurements have revealed that the bases for separating many of the fossil types from their recent counterparts are at best subtle and usually tenuous. Yet, even so, one gets the impression in working over the material that a difference does exist in most cases between the fossil and recent specimens, even though such a difference is hard to define. In most cases it is apparent that the fossil specimens are in general larger than similar recent types, and this is usually visible in a comparison of the respective

means and modes. But there are strong size overlaps when all the material available is taken into consideration, so that usually a sharp differentiation between the extinct and persisting forms cannot be made. Consequently the question of subspecific distinctions comes to mind—might it not be possible that we are dealing in this case with differences of less than specific magnitude but none the less real?

Subspecific differences among modern mammals are based of course on various criteria, among them morphological differences, differences in the distribution of populations, and the presence of isolating factors that tend to keep populations separated. When fossils are dealt with, however, such factors as range and isolating factors are difficult if not impossible to evaluate; therefore the paleontologist must depend on morphology as his basic criterion for taxonomic separations.

It was thought advisable to investigate briefly and at random, as a sort of sampling study, the problem of subspecific separations as they may be reflected in osteological characters among some modern mammals, to see if such a study would throw any light on the possible relationships of the fossil mammals from Yenchingkou. If subspecific differences

appear in the osteology of modern forms, and if such differences can be distinguished from specific differences as reflected by osteological characters, then perhaps some conclusions can be drawn as to the proper distinctions to be made between the fossils from Szechwan and their modern counterparts from the same region.

In these comparisons the method of ratio diagrams as recently developed by Simpson was utilized. This is a very convenient method of comparing closely related animals, particularly in that it shows the resemblances and differences of a combination of characters. As Simpson has pointed out, "The basic purpose of the diagram is to represent each of a number of analogous observations by a single entry and to plot them in such a way that the horizontal distance between any two of them will represent the ratio of either one of those two to the other" (Simpson, 1941, p. 23). The method is not discussed here; the reader is referred to Simpson's paper. Suffice it to say that various analogous measurements are made on a series of specimens representing two or more forms. The logarithms of the greatest dimension, the least dimension, and the mean for each mensuration category are plotted, and in this way the various measurements can be

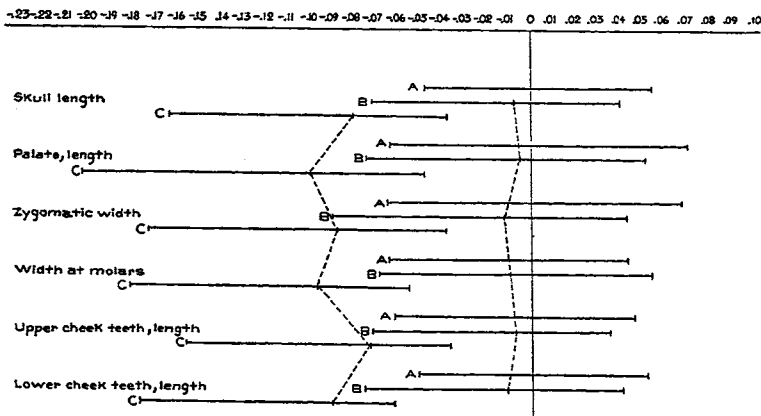


FIG. 2. Ratio diagram showing comparison of certain osteological characters in two species of *Mustela* and two subspecies of *Mustela sibirica*. The latter show a strong overlap of the characters measured, whereas the two species of *Mustela* show little overlap in these same characters. A. *Mustela sibirica fontanierii*, six males, four females. B. *Mustela sibirica davidiana*, six males, three females. C. *Mustela altaica kathiak*, four males, three females, one indeterminate. Data from Allen, 1938.

compared with one another and the forms being studied can also be compared one with another to great advantage.

The first comparison was made between two subspecies of *Mustela*, as based on material presented in Glover Allen's monograph on the recent mammals of China (Allen, 1938, pp. 371-381). The two forms, *Mustela sibirica fontanierii* and *Mustela sibirica davidiana*, the former based on a series of 10 individuals (six males and four females), the latter on nine individuals (six males and three females), were compared as shown in figure 2. The interesting fact, at once apparent in this comparison, is that there is a very strong overlap between the two subspecies in all the osteological characters considered—so much so that one might wonder on this basis alone as to the validity of any real subspecific separation between them. Yet their ranges are quite separate and do not overlap, the former being a North Chinese type of Palearctic distribution, the latter a southwestern Chinese type of Oriental distribution.

To carry this study still further, a distinct species, *Mustela altaica kathiah*, represented by a series of eight individuals (four males, three females, and one of unknown sex),

was compared with the two subspecies just discussed. It can be seen from the ratio diagram (fig. 2) that the means of this form, which is supposedly specifically distinct from the two forms mentioned above, show a wide separation from the means of the two subspecies of *Mustela sibirica*, with a certain amount, but a relatively small proportion, of overlap. Consequently, if the specific and subspecific separations of these Chinese mustelids are correct, it would seem that, so far as morphology is concerned, subspecific distinctness, based as it is for the most part on external characters, shows little differentiation in the measurable osteological characters, while specific distinctness, being of a more deep-seated nature, is apparent in the osteological characters.

To check this general picture of the close osteological relationships between subspecies, a second ratio diagram (fig. 3) was drawn up for two subspecies of the big-eared rat of the Congo, as discussed by Hatt (Hatt, 1940, pp. 502-503). Here again, it can be seen that there is a strong overlap in osteological characters between two subspecies in all but one character, that of the size of the bullae. This diagram was based on relatively

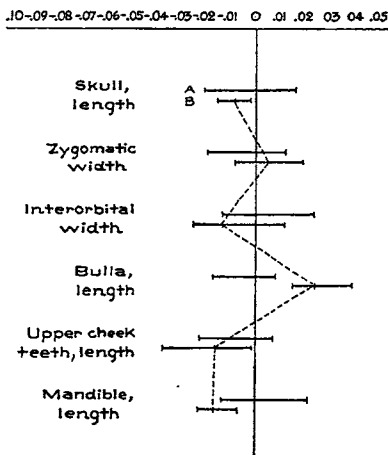


FIG. 3. Ratio diagram showing comparison of certain osteological characters in two subspecies of *Malacomys longipes*. This diagram shows a strong overlap of the characters measured, except for the length of the bulla. A. (Upper bar.) *Malacomys longipes centralis*, five males. B. (Lower bar.) *Malacomys longipes wilsoni*, five males. Data from Hatt, 1940.

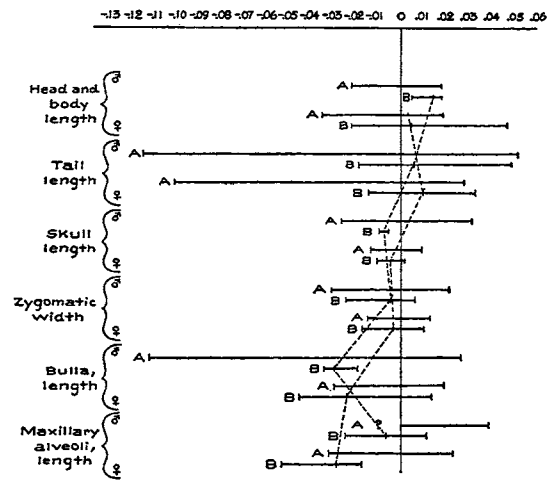


FIG. 4. Ratio diagram showing comparison of certain osteological characters in two subspecies of *Funisciurus congicus*. The sexes are separately plotted. A strong overlap in the measured characters is evident. A. *Funisciurus congicus flavinus*, nine males, 34 females. B. *Funisciurus congicus congicus*, four males, eight females. Data from Hill and Carter, 1941.

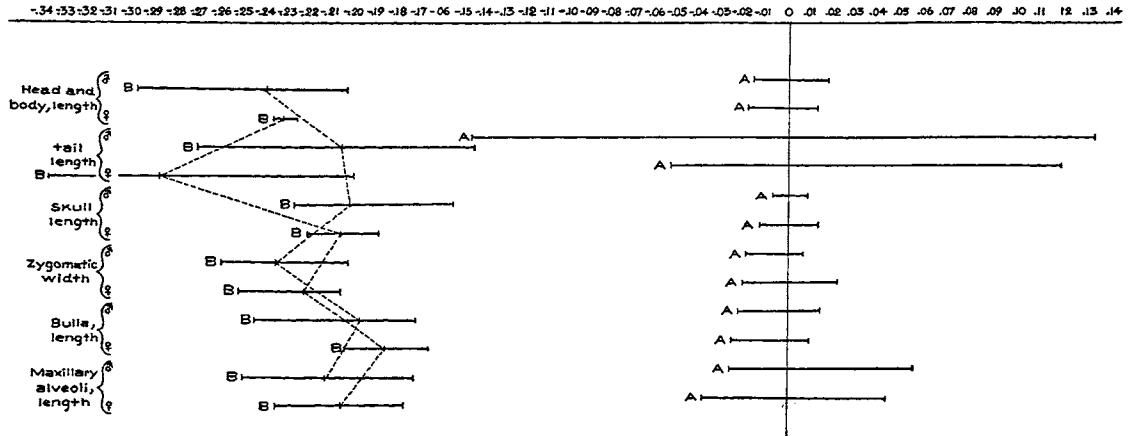


FIG. 5. Ratio diagram showing comparison of certain osteological characters in two species of *Cryptomys*. There is virtually no overlap in the characters measured. A. *Cryptomys mechowii*, six males, six females. B. *Cryptomys bocagei*, 10 males, five females. Data from Hill and Carter, 1941.

small suites of specimens, five males in each case, so a third check was deemed desirable.

This was found in a comparison of two subspecies of the genus *Funisciurus*, discussed by Hill and Carter in their monograph of the mammals of Angola (Hill and Carter, 1941, pp. 70-73). In this case fairly large suites were available—43 individuals of *Funisciurus congicus flavinus* and 12 of *Funisciurus congicus congicus*. The ratios between sexes are rather uneven; in the former of the above-mentioned types there were nine males and 34 females, while in the latter there were four males and eight females. In the ratio diagram the various osteological characters for the sexes were separately plotted. Again, the strong overlap in osteological characters between subspecies can be seen. The few apparent aberrations in this diagram are probably due to the disparities in the sizes of the samples compared, so it might be expected that with suites of more nearly equal size such divergences would tend to disappear. But with all these qualifications taken into account, it is still apparent that the overlap in these subspecies is very strong indeed.

After the very close osteological relationships between subspecies was checked, in several cases by an application of the ratio diagram method, an additional test was made of the seeming distinctness of osteological characters between truly recognizable species.

For this purpose the data published by Hill and Carter (Hill and Carter, 1941, p. 200) on the genus *Cryptomys* from Angola were utilized. In this case, two distinct species were compared, *Cryptomys mechowii* and *Cryptomys bocagei*, and, as may be seen in figure 5, they show virtually no overlap in osteological or proportional characters, the only overlap whatsoever in this case being in one highly variable character, namely, the length of the tail. Otherwise the two species are quite distinct and separate.

From the above considerations it seems evident that in many cases the differences between closely related species and subspecies can be detected by comparisons of osteological measurements, especially by an application of the ratio diagram method. Perhaps species and subspecies relationships can be expressed in a general way as follows.

Closely related species may show little overlap of quantitative osteological characters, for the differences between forms of this taxonomic rank are sufficiently deep-seated to be reflected in the size and proportions of the skeleton. Closely related subspecies, on the other hand, may show a very strong overlap of their quantitative osteological characters, since the differences between forms of this taxonomic rank are for the most part not sufficient to be strongly indicated by size differences in the skeletal parts. However, even where there is a strong overlap of quan-

titative osteological characters, there may be significant differences in the means of these characters.

ACKNOWLEDGMENTS AND ABBREVIATIONS

We wish to acknowledge the work done by several artists and photographers in making illustrations for this paper. Line drawings of specimens, except those of *Stegodon*, were made by Mr. John C. Germann. The drawings of proboscideans were taken from Osborn's monograph on the Proboscidea, published by the American Museum of Natural History. The map and the various diagrams and charts were made by Mrs. Elsa Arnoux. The photographs of specimens were made by the photographic division of the American Museum of Natural History.

The junior author wishes to express his sincere appreciation to the Director and staff of the American Museum of Natural History for the help and facilities given to him during his stay at the Museum, from the spring of 1950 to the fall of 1951.

The names of various institutions are ab-

breviated when used in connection with the official catalogues of those institutions, as follows:

A.M.N.H., the American Museum of Natural History, Department of Geology and Paleontology

A.M.N.H.(C.A.), the American Museum of Natural History, formerly Department of Comparative Anatomy, now under the jurisdiction of the Department of Mammals

A.M.N.H.(M), the American Museum of Natural History, Department of Mammals

B.M., British Museum (Natural History)

C.N.H.M., Chicago Natural History Museum

U.C.M.P., University of California, Museum of Paleontology, Berkeley

U.S.N.M., United States National Museum

The following abbreviations are used in the tables:

a, approximate measurement

e, estimated measurement

L, length

Los, length, outer surface

W, width

Wa, width, anterior diameter

Wp, width, posterior diameter

consequent lesser growth of individual parts. The upper canine in *Megatapirus* is relatively small and separated from the caniniform third incisor by a diastema.

There is little to be said about the postcranial skeleton in *Megatapirus*. Such bones as are preserved are similar to the same elements in *Tapirus* but are larger and heavier, as might be expected.

From the foregoing, it is apparent that *Megatapirus* might be said to represent the culmination of evolution in the tapirs, in that it is more specialized along those lines of adaptation that have characterized modern tapirid development than are any of the surviving forms. Although the specializations of *Megatapirus* over *Tapirus* are not large, they are nevertheless distinct and of such magnitude as to show the final trend of tapirid evolution.

In view of these considerations, what should be the generic position of the extinct tapir from Szechwan? Matthew and Granger regarded it as a subgenus of the genus *Tapirus*, and there is much to be said for this point of view. On the other hand, since distinct evolutionary trends are shown by the fossil over the recent form, and since it is a fact that the fossil is in certain respects more different from the recent tapirs than any of them are from one another, there is a good argument for regarding *Megatapirus* as a distinct genus. This latter viewpoint is adopted in the present work.

RHINOCEROTIDAE

RHINOCEROS LINNAEUS

Rhinoceros LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 56.

GENERIC TYPE: *Rhinoceros unicornis* Linnaeus.

DIAGNOSIS: Large rhinocerotids, with an elongate skull having a high occipital crest, and distinguished by a single dermal horn on the nose. Nasal bones arched. No post-orbital processes. Teeth moderately hypsodont.

Rhinoceros sinensis Owen

Rhinoceros sinensis OWEN, 1870, *Quart. Jour. Geol. Soc. London*, vol. 26, pp. 424-426, pl. 29, figs. 1-3.

Rhinoceros sinensis, KOKEN, 1885, *Palaeont. Abhandl.*, vol. 3, p. 52.

Rhinoceros sivalensis KOKEN, 1885, *ibid.*, p. 58 (in part).

Rhinoceros plicidens KOKEN, 1885, *ibid.*, p. 50.

Rhinoceros simplicidens KOKEN, 1885, *ibid.*, p. 60.

Rhinoceros sivalensis, LYDEKKER, 1886, *Catalogue of the fossil Mammalia in the British Museum*, pt. 3, p. 130, 131.

Rhinoceros sinensis, MATTHEW AND GRANGER, 1923, *Bull. Amer. Mus. Nat. Hist.*, vol. 48, pp. 567, 572-573, figs. 1, 2.

LECTOTYPE: B.M. No. 41935, third left upper molar, lacking the outer portion.

COTYPES: B.M. Nos. 41936, posterior portion of M¹; 41936a, ectoloph of left P⁴; 41941-41944, five lower cheek teeth.

REFERRED SPECIMENS: A.M.N.H. Nos. 18628, a crushed skull with left P²-M² and right DM¹, P²-M³ (this specimen was designated by Matthew and Granger as the neotype; also included under this number are various teeth, as follows: left DM³, right DM⁴, right M₂₋₃, left M₃, right P₂₋₃, left P₂₋₄, fragmentary right ramus with worn teeth, metapodials); 18470, right DM³ or DM⁴; 18471, left maxilla with DM⁴, M¹; 18486, right DM³, left DM⁴; 18511, fragmentary left ramus with cheek teeth; 18538, left lower cheek teeth; 18539, several lower cheek teeth; 18540, upper and lower incisors; 18547, right DM²; 18560, jaws; 18606, maxilla with right P²-M³, maxilla with left P³-M³; 18607, maxilla with right P²-M³, mandibular ramus with right P₂-M₃; 18609, fragment of an upper molar, right P₄, and a right femur; 18610, left maxilla with DM¹⁻⁴, M¹ in alveolus; 18611, fragmentary skull and jaw of a juvenile animal with right DM²⁻⁴ and right DM₂₋₄; 18612, right P⁴, M¹, M², left P³, DM⁴, M², M³, right ramus with DM₄, M₁₋₂ (in alveolus), metatarsal; 18613, right DM², DM³, DM⁴, P², DM₃, M₁ (?); 18614, patella; 18615, right P³ or P⁴, right lower cheek tooth, fragments of teeth; 18616, left P₃; 18617, right DM⁴, fragment of right DM⁴, left P₂, right astragalus; 18618, three lower molars; 18619, left P⁴, right DM₄, left lower cheek tooth; 18622, right P³⁻⁴, M¹, left M¹⁻³, right M₁₋₃; 18623, right M¹, mandible with right DM₂₋₄, M₁₋₂, left P₂₋₃ (in alveoli), DM₄, M₁₋₂, maxilla with left DM¹⁻³, mandible with left DM₂₋₄, mandible with right DM₄, left DM³⁻⁴, left

DM³, three right DM², right DM³ or DM⁴, maxilla with two molar fragments, right lower cheek tooth, atlas, axis, two cervicals, five dorsals, calcaneum, 11 metapodials; 18625, palate with right and left DM¹⁻⁴, M¹⁻², P²⁻⁴ (in alveoli), mandible with right and left DM¹⁻⁴, M¹⁻², premolars and M₃ (in alveoli); 18626, skull with right and left DM¹⁻⁴, M¹⁻², premolars and M³ (in alveoli), mandible with right and left DI, DM¹⁻⁴, M¹⁻², premolars and M₃ (in alveoli); 18626a, right P⁴, M², left M¹, M², right lower molar; 18627, right ramus with M₁₋₃, left ramus with M₃; 18758, maxilla with right DM¹⁻⁴, mandibular ramus with left DM¹⁻⁴, M₁ (in alveolus); 18780, right P², P⁴, DM⁴, M¹⁻², left P², P³⁻⁴, DM⁴, M¹, fragmentary ramus with left P₂₋₃, ramus with right P₂, ramus with right M₁₋₂, various lower cheek teeth and incisors; 18781, right M², left DM³, left DM₂ in fragmentary ramus; 18782, right DM¹⁻³, right and left DM¹, ramus with left DM₂₋₄, ramus with left DM₄, M₁, ramus with left M₁ or M₂; 18783, maxilla with left P^{3-M1}; 18784, left DM⁴, left M₂ or M₃; 18785, right P⁴, left M³, right M₃, fragment of upper molar; 18786, right P₂; 18787, right P₂, three right lower cheek teeth; 21790, right lower molar. C.N.H.M. No. P.14160, right P^{2-M3} and left P^{3-M3}, associated. Also a right mandibular ramus with P₂-M₃, and left M₁-M₃, associated.

DIAGNOSIS: "Characters.—A large nasal horn. No clear indications of a second horn. Occiput apparently rather posterior in position. Teeth moderately hypsodont, slightly less so than in *R. indicus*. Premolars 130; length of molars, 160; p¹ small, deciduous. Both external ribs prominent on p²⁻⁴, posterior rib weak on m¹, wholly absent on m²⁻³, the anterior rib prominent on all three molars. Crochet prominent on p^{3-m3}, doubled on p^{4-m1}; crista rudimentary except on p², where it is prominent. No antecrochet save as an obscure swelling. Postfossette on p^{3-m1} only when considerably worn. The two inner cones of p² strongly twinned, slight twinning on p³⁻⁴" (Matthew and Granger, 1923, p. 572).

DISCUSSION

The relationships of *Rhinoceros sinensis* were ably discussed by Matthew and Granger

in 1923, and in the light of additional studies on the rhinoceroses from the Pleistocene of Szechwan there seems to be no reason for modifying the conclusions arrived at by those authors. However, it may be well to review the problem briefly.

Rhinoceros sinensis was described by Owen in 1870. Subsequent to Owen's original description of the species, various authors studied fossil rhinoceroses from China and came to diverse conclusions regarding their affinities. Koken, in 1885, recognized *Rhinoceros sinensis* among the materials he was studying from China, but in addition he also recognized *Rhinoceros sivalensis* and named two new species, *Rhinoceros simplicidens* and *Rhinoceros plicidens*, in the Chinese material at his disposal. This is an unnecessary complication of the matter, for comparison of Koken's plates with the large series of *Rhinoceros sinensis* teeth in the American Museum collection shows that without doubt all Koken's material belongs to the single species originally described by Owen. Koken was misled by the considerable variability in the dental characters of *Rhinoceros*, a subject elucidated at greater length below. The same is true of Schlosser, who recognized the several species designated by Koken and in addition designated another form, *Rhinoceros antiquitatus*, of probable Pleistocene age. These authors (working on mixed collections) between them also identified in the Chinese material *Rhinoceros brancoi*, *Aceratherium blanfordi*, *Aceratherium blanfordi hipparionum*, and *Aceratherium habereri*, forms of Pliocene age, the last three of which are now placed in the genus *Chilotherium*.

Lydekker in 1886 went to the other extreme by placing *Rhinoceros sinensis* in synonymy with *Rhinoceros sivalensis*. Finally Matsumoto in 1915, working with material from the Szechwan fissures but supposing he had two distinct faunas of different age, identified the rhinoceroses in his collection as *Aceratherium blanfordi hipparionum*, *Rhinoceros sinensis*, and *Rhinoceros plicidens*.

The solution of the problem, based on a study of variability of the teeth in the American Museum collection and a comparison of this known variability with the teeth of supposedly different species as figured by the earlier writers, is simple. All the

TABLE 34
MEASUREMENTS (IN MILLIMETERS) OF UNWORN CROWNS OF UPPER
PREMOLARS AND MOLARS IN *Rhinoceros*

	Greatest Width at Base	Greatest Height, Ectoloph	Ratio: Width/Height	Greatest Length, Ectoloph	Greatest Height, Ectoloph	Ratio: Length/Height
<i>R. sinensis</i>						
A.M.N.H. Nos.						
18615, P ³	55	69	0.80	47	69	0.68
18612, P ³	57	66	0.86	47	66	0.71
18626a, P ⁴	63	74	0.85	54	74	0.73
18780, P ⁴	58	64	0.91	50	64	0.78
<i>R. unicornis</i>						
Hooijer, 1946a, P ³	54-62	58-68	0.89-0.97	46-50	58-68	0.74-0.79
<i>R. sondaicus</i>						
Hooijer, 1946a, P ³	51	51	1.00	42	51	0.82
<i>R. sinensis</i>						
A.M.N.H. Nos.						
18623, M ¹	—	—	—	65	79	0.82
18612, M ²	—	—	—	63	75	0.84
18612, M ²	—	—	—	65	77	0.84
18625, M ²	—	—	—	75	84	0.89
<i>R. unicornis</i>						
A.M.N.H.(M.) No.						
54456, M ²	—	—	—	61	72	0.85
<i>R. sondaicus</i>						
A.M.N.H. (M.) No.						
146717, M ¹	—	—	—	49	53	0.93

rhinoceros material from the fissures of Szechwan belongs to a single species, *Rhinoceros sinensis* Owen. The relationships of this species are with the modern species representative of the genus *Rhinoceros*, particularly with *Rhinoceros unicornis*. With the above considerations in mind, it might be well at this place to include the remarks made by Matthew and Granger with regard to the affinities of *Rhinoceros sinensis*: "The characters of the teeth in the neotype are strongly suggestive of affinity to the Indian and Javan rhinoceroses, combining peculiarities of the two; the referred specimens bring it on the whole nearer to the Indian species . . . The neotype skull is too badly crushed to be decisive as to the characters of the occiput, and no other specimens show this region. The position of the horn, on the nasals but not quite terminal, is like *R. indicus* and unlike *Atelodus*" (Matthew and Granger, 1923, p. 572).

It is unfortunate that the skull of *Rhinoceros sinensis* is at present so imperfectly

known, with the result that most of our deductions as to the relationships of this species must of necessity be based on the structure of the dentition. It is possible, however, by combining our scanty knowledge of the skull (obtained largely from the single crushed specimen, A.M.N.H. No. 18626) with a rather abundant knowledge of the dentition (based in large part on the unusually fine series of teeth collected by Granger at Yenchingkou) to obtain a fair idea as to the zoologic position of the fossil rhinoceros from Szechwan.

So far as the skull is concerned, it would appear that *Rhinoceros sinensis* had but a slight development of the horn boss on the nasals, certainly much less than in *Rhinoceros unicornis* and very possibly less than in *Rhinoceros sondaicus*, although the crushing of the specimen makes this last point difficult to determine with certainty. However, it seems reasonably certain that the development of the nasal horn in the extinct species was no greater than in *Rhinoceros sondaicus*.

Except for this observation nothing more of importance can be said about the skull structure of the fossil.

Consequently it is necessary to turn to an examination of the dentition, and here we find the combination of the characters that Matthew mentioned but never elucidated.

There is a considerable amount of individual variation in the teeth of *Rhinoceros sinensis*, both in structural characters and in size, the latter much greater, in fact, than in either *R. sondaicus* or *R. unicornis*, both recent and fossil. Several years ago one of us (Hooijer, 1946a, 1946b) made a detailed study of the Dubois collection of prehistoric and fossil rhinoceroses from central Sumatra and Java, in which both of these species are abundantly represented by dental as well as skeletal material. *R. sondaicus* occurs in the Pleistocene fauna of Java as well as in the prehistoric fauna of Sumatra and Java; the fossil and prehistoric teeth differ from the recent mainly in their slightly superior size. *Rhinoceros unicornis* is also represented in the Pleistocene of Java. *Rhinoceros unicornis kendengindicus* Dubois, indistinguishable from the living Indian rhinoceros in cranial characters, differs from the recent form in being slightly less hypsodont, and in the fact that the posterior upper premolars have a more produced postero-internal angle, and the upper molars are comparatively narrower posteriorly. This material forms the base for the following comparison between the Yenchingkou rhinoceros and the Javan and Indian species.

The diagnostic characters of the teeth as quoted above from Matthew and Granger

are only a condensed description of A.M.N.H. No. 18628, one of the best-preserved upper dentitions of *R. sinensis* in the collection and selected as the neotype for the species. When all the rhinoceros material in the Yenchingkou collection is taken into account, this appears to be a medium-sized specimen of the dentition, with a relatively simple enamel pattern.

To begin with the upper dentition: Matthew and Granger (1923, p. 572) note that none of the specimens has the premaxilla preserved sufficiently to demonstrate the presence or absence of upper incisors. However, there is an upper incisor in the Yenchingkou collection (A.M.N.H. No. 18540). It belongs to the milk dentition, is unworn, and measures 31 mm. anteroposteriorly and 14 mm. transversely. No upper milk incisors of *R. unicornis* or of *R. sondaicus* are available for comparison; in these species the permanent upper incisor is over 50 mm. in length while the width of the crown is 15-19 mm. (Hooijer, 1946a, p. 55).

Matthew and Granger note in their diagnosis of *R. sinensis*: "p¹ small, deciduous." There is quite a variation in size in the anterior upper premolar, and some of the Yenchingkou specimens are definitely larger than their homologues in either of the recent species. Normally DM¹ has no successor in the permanent dentition of the recent species, but a skull of *Rhinoceros unicornis* [A.M.N.H. (M.) No. 54456, from Nepal, 1923] has a P¹ on the right side. The last molar in this skull has not yet erupted, but P² and P³ are already in place and worn, and DM⁴ is about to be shed. The left DM¹ is very much worn

TABLE 35

HEIGHTS (IN MILLIMETERS) OF UNWORN CROWNS OF P₃ AND M₃ IN *Rhinoceros*

	P ₃		M ₃	
	Metaconid	Entoconid	Metaconid	Entoconid
<i>R. sinensis</i>				
A.M.N.H. No. 18616	40	36	—	—
A.M.N.H. No. 18619	—	—	47	41
A.M.N.H. No. 18627	—	—	46	38
<i>R. unicornis</i>				
From Hooijer, 1946a	40-42	31-33	44-47	35-37
<i>R. sondaicus</i>				
From Hooijer, 1946a	32	25	34	25-29

TABLE 36

MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Rhinoceros sinensis*, *unicornis*, AND *sondaicus*

	<i>R. sinensis</i>											<i>R. unicornis</i> ^a	<i>R. sondaicus</i> ^a
	A.M.N.H. No. 18783	A.M.N.H. No. 18607	A.M.N.H. No. 18780	A.M.N.H. No. 18606	A.M.N.H. No. 18612	A.M.N.H. No. 18628	A.M.N.H. No. 18622	A.M.N.H. No. 18626a	A.M.N.H. Nos. 18613, 18612, 18781	A.M.N.H. No. 18625	C.N.H.M. No. P.14160		
P ²													
L	—	26a	28a	—	—	28a	—	—	33a	—	32a	26a-32a	27a-32a
Wa	—	41	36	—	—	45	—	—	43	—	42	40-47	34-45
Wp	—	43	41	—	—	50	—	—	—	—	46	40-49	39-45
P ³													
L	38a	32a	37a ^b	35a	38a	35a	42a	—	—	—	37a	35a-43a	34a-47a
Wa	51	52	55 ^b	54	57	59	63	—	—	—	58	53-62	48-57
Wp	49	51	50 ^b	50	54	58	56	—	—	—	55	51-56	45-53
P ⁴													
L	40a	35a	38a	37a	35a	39a	38a	44a	48a	—	42a	37a-39a	35a-42a
Wa	57	57	59	59	58	65	68	67	70	—	62	62-69	51-62
Wp	52	55	55	55	53	61	58	57	64	—	58	56-60	47-59
M ¹													
L	48a	41a	42a	45a	51a	46a	55a	50a	—	50a	49a	39a-44a	35a-45a
Wa	63	64	63	68	70	70	74	—	—	81	65	58-71	51-65
Wp	59	58	61	65	65	64	67	—	—	76	59	51-62	45-56
M ²													
L	—	45a	46a	50a	57a	49a	59a	55a	60a	57a	50a	42a-50a	37a-50a
Wa	—	64	63	72	71	73	75	75	80	82	69	59-68	53-64
Wp	—	56	56	64	60	63	65	67	72	75	58	52-61	44-54
M ³													
L	—	46	—	54	56	—	53	—	—	—	49	44-49	36-51
Wa	—	57	—	62	65	—	71	—	—	—	59	53-62	43-57
Los	—	54a	—	63	67	—	68	—	—	—	56	55-64	44-62

^a See Hooijer (1946a).^b A.M.N.H. No. 18615.

down, as usual in skulls of this age. The tooth in front of the right P², however, is only very slightly worn and is much larger than any DM¹ of *R. unicornis* or *R. sondaicus*, being 32 mm. anteroposteriorly and 30 mm. transversely. Only *R. sinensis* may have first milk molars that attain these dimensions, as shown in tables 38 and 39. Two of these are represented in figure 39 (A.M.N.H. Nos. 18782 and 18623), together with the small specimen (A.M.N.H. No. 18610).

Before entering into a discussion of the

specific characters of the premolars and molars of *R. sinensis*, we must enumerate the characters by which the dentition of *R. unicornis* differs from that of *R. sondaicus*:

1. The outer surface of the upper molars is approximately straight in *R. unicornis*, while in *R. sondaicus* there is a prominent paracone style and the outer surface is concave behind; the posterior moiety is more inclined inward and the metastyle is again raised, making the outer surface sinuate in its course.

2. In *R. unicornis* there is a vertical de-

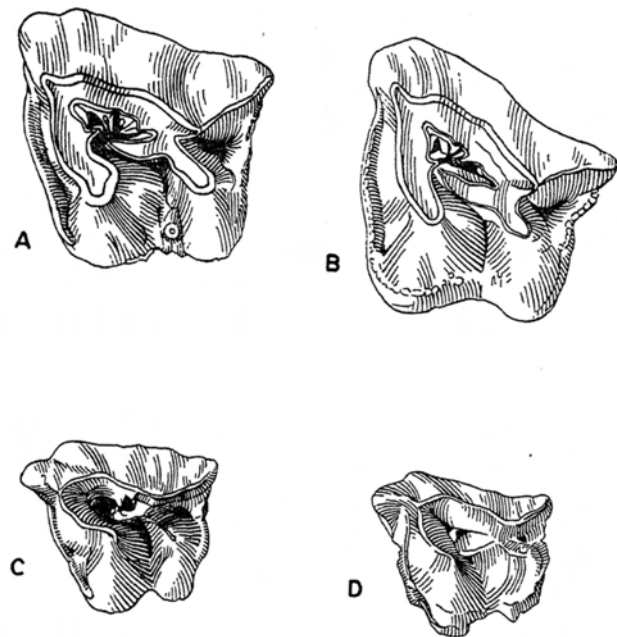


FIG. 35. A. *Rhinoceros sinensis* Owen, A.M.N.H. No. 18622, left M¹. B. *Rhinoceros plicidens* Koken (1885, pl. 6, fig. 6), M¹. C. *Rhinoceros sinensis* Owen, A.M.N.H. No. 18784, left DM⁴. D. *Rhinoceros simplicidens* Koken (1885, pl. 5, fig. 7), DM⁴. All figures three-fourths natural size.

pression in the anterior surface of the proto-loph, usually a pronounced vertical groove that is most distinct just above the anterior cingulum. This so-called protocone fold does not occur in *R. sondaicus*.

3. The inner portion of the proto-loph has a greater backward extension in *R. unicornis* than in *R. sondaicus*.

4. In *R. unicornis* there is often a crista which joins with the crochet so as to form a medifossette. This is only very exceptionally found in *R. sondaicus*.

5. The premolars and molars are more hypsodont in *R. unicornis* than in *R. sondaicus*, as shown by the comparison of the unworn crowns of P³ (Hooijer, 1946a, p. 93), M³ (pp. 97-98), P₃ (p. 102), and M₃ (p. 100).

As far as point 1 is concerned, *R. sinensis* is definitely closer to *R. sondaicus* than to *R. unicornis*. As noted by Matthew and Granger, the posterior rib (metacone style) of the outer surface is weak on M¹ and absent on M²⁻³, while all upper molars have a promi-

nent anterior rib (paracone style). Actually, the paracone style is not so prominent on the upper molars of *R. sinensis* as is typical of *R. sondaicus*, although it is definitely more pronounced than in *R. unicornis*. Also the concavity of the posterior half of the ectoloph is not quite so marked in *R. sinensis* as in *R. sondaicus*, but more so than in *R. unicornis*, with its characteristically flat ectoloph. In *R. unicornis* the posterior moiety of the ectoloph is concave only in its upper part, and near the roots the metacone style may be as marked as the paracone style, flattening towards the top of the crown. In *R. sinensis* the metacone style is weak or absent, as in *R. sondaicus*, yet the incurving of the posterior half of the ectoloph is less than in the Javan species, which seems to be a function of the lesser prominence of the paracone style in front of it. *R. sinensis* is truly intermediate between *R. sondaicus* and *R. unicornis* in the shape of the ectoloph, but closer to *R. sondaicus* than to the Indian species.

TABLE 37

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Rhinoceros sinensis*, *unicornis*, AND *sondaicus*

	<i>R. sinensis</i>								<i>R. unicornis</i> ^a	<i>R. sondaicus</i> ^a
	A.M.N.H. No. 18607	A.M.N.H. No. 18623	A.M.N.H. No. 18627	A.M.N.H. No. 18628	A.M.N.H. No. 18625	A.M.N.H. No. 18626	A.M.N.H. No. 18780	A.M.N.H. No. 18787		
P ₂										
L	—	30	—	32	—	—	31	34	31-37	25-30
W	—	15	—	21	—	—	19	22	19-25	16-21
P ₃										
L	—	40	39 ^b	39	—	—	39	—	32-43	33-39
W	24	—	26 ^b	28	—	—	26	—	22-30	23-27
P ₄										
L	—	—	—	45	—	—	45	46	38	35-42
W	29	—	—	—	—	—	30	30	29-35	25-30
M ₁										
L	—	51	48	52	55	53	51	52	36-51	40-43
W	—	32	33	36	34	34	32	31	26-31	26-31
M ₂										
L	49	60	52	56	61	56	54	—	47-56	42-48
W	29	33 ^a	33	34	37	—	32	—	27-30	26-31
M ₃										
L	51	—	56	—	—	—	—	57 ^c	49-50	39-47
W	30	—	—	—	—	—	—	34 ^c	29-33	24-28

^a See Hooijer (1946a).^b A.M.N.H. No. 18616.^c A.M.N.H. No. 18619.

In most of the upper molars of *R. sinensis* there is a sharply defined protocone fold, a vertical groove in the anterior surface of the protoloph that is typical for *R. unicornis* but not shown in the upper molars of *R. sondaicus*. In molars with very sharp and deep protocone folds, such as in the large dentition, A.M.N.H. No. 18625, there is also a vertical groove in the anterior surface of the metaloph, and one in the posterior surface of the protoloph. In several last upper molars of *R. sinensis* the protocone fold is so weak as to be practically absent, as, for example, the M³ in A.M.N.H. Nos. 18606 and 18607. In the upper premolars the protocone fold does not show up so well as in *R. unicornis*, but in the DM³ and DM⁴ of *R. sinensis* the protocone fold is usually well defined. Consequently, in point 2, *R. sinensis* agrees very well with *R. unicornis*.

The protoloph of the upper molars in *R.*

sinensis is more produced backward and internally than in *R. sondaicus*, agreeing very well, again, with *R. unicornis* in this respect. In a number of fossil specimens the protoloph takes up about two-thirds of the inner surface of the crown, as in *R. unicornis*, while the metaloph is relatively stronger on the inside in *R. sondaicus*. Consequently, point 3 brings *R. sinensis* again closer to *R. unicornis*.

While in many upper molars and premolars of *R. sinensis* there are several irregularly shaped, small, enamel projections from the ectoloph into the mediusinus, there is never a well-defined crista that joins the crochet so as to enclose a medifossette. The latter condition is typical for *R. unicornis*, although in this species the crista may also be rudimentary. In *R. sondaicus* the crista is normally restricted to the upper milk molars and absent in the upper molars. There is very much individual variation in the development of minor

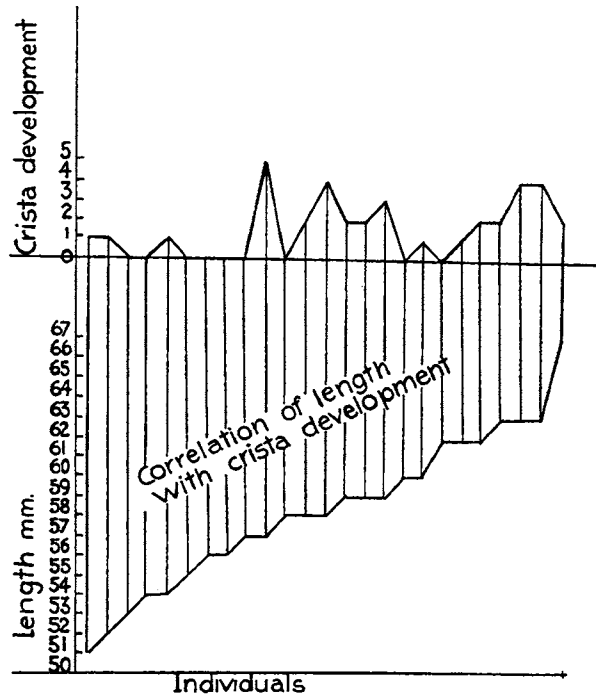


FIG. 36. Diagram illustrating correlation of length of M^1+M^2 with crista development in *Rhinoceros sinensis*.

enamel projections in the mediusinus, and the crochet may also bear several projections. In the dentition now in the Chicago Natural History Museum there is hardly any accessory enamel folding except for a duplicated crochet in the left P^4 . There is also a double crochet in both P^4 's and in the right M^1 , but not in the left M^1 , of A.M.N.H. No. 18628 (pl. 20). Cristae in the form of multiple enamel spurs are seen in the upper premolars and molars of A.M.H.N. Nos. 18606, 18622, 18626a, and 18780, and in the M^1 and M^2 of No. 18625, but in No. 18612 the two first molars show a junction of one of these small cristae with the crochet so that a medifossette will be formed upon wear. In M^2 of A.M.N.H. No. 18607 there is a distinctly developed single crista, not shown in the associated M^1 or M^2 . Some molars also have enamel projections into the post-sinus.

The cingulum is variable in development in *R. sinensis*, narrow or wide, with crenulated ledges on the anterior surface sometimes extending to the inner surface of the protoloph. There may be one to several tubercles devel-

oped in the entrance to the mediusinus, and the posterior cingulum often bears a distinct point labially to the V-shaped incision. Some upper premolars have a cingulum all along the inner surface, while others completely lack the cingulum on the inside.

All these variations are found in *R. unicornis* and *R. sondaicus*. In the rudimentary development of the crista and its general lack of juncture with the crochet, *R. sinensis* is somewhat closer to *R. sondaicus* than to the Indian rhinoceros. The heavier development of the crochet, however, brings *R. sinensis* again nearer to the Indian rhinoceros, in which the crochet is stronger than in *R. sondaicus*. In point 4, consequently, we see a condition in the fossil Chinese species that is intermediate between that in the two living species of *Rhinoceros*.

Matthew and Granger (1923, p. 572) remark that the teeth of *R. sinensis* are moderately hypsodont, slightly less so than in *R. unicornis*. The comparison between unworn crowns of homologous teeth in *R. sinensis*, *R. unicornis*, and *R. sondaicus* shows that the

TABLE 38

MEASUREMENTS (IN MILLIMETERS) OF THE UPPER MILK TEETH OF *Rhinoceros sinensis*, *unicornis*, AND *sondaicus*

	<i>R. sinensis</i>											<i>R. unicornis</i> ^a	<i>R. sondaicus</i> ^a
	A.M.N.H. No. 18610	A.M.N.H. No. 18758	A.M.N.H. Nos. 18581, 18623, 18613, 18612	A.M.N.H. Nos. 18623, 18628	A.M.N.H. Nos. 18547, 18623, 18780	A.M.N.H. Nos. 18613, 18617	A.M.N.H. Nos. 18782, 18623, 18470, 18626	A.M.N.H. Nos. 18782, 18628, 18626, 18613	A.M.N.H. No. 18782	A.M.N.H. No. 18623	A.M.N.H. No. 18625		
DM ¹													
L	25	26	30	—	—	—	32	34	32	33	—	22a-28a	20a-25
W	20	21	23	—	—	—	27	28	28	27	28	23-25	18a-24
DM ²													
L	28a	30a	29a	—	30a	33a	34a	34a	37a	36a	—	31a	26a-30a
Wa	32	34	36	38	39	39	41	43	43	40a	—	38a	33-36
Wp	36	37	37	37	39	40	43	45	45	46	47	38-39	32-37
DM ³													
L	35a	37a	37a	38a	40a	—	39a	37a	44a	45a	43a	36a-39a	33a-41a
Wa	45	46	49	50	51	—	52	55	54	57	—	46	40-46
Wp	44	43	46	46	47	—	47	50	53	51	54a	41-42	35-43
DM ⁴													
L	39a	—	40a	38a	41a	40a	44a	—	—	—	44a	38a-45a	34a-44a
Wa	49	—	50	51	52	52	59	—	—	—	61	49-56	41-51
Wp	46	—	47	49	49	50	54	57	—	—	58	48-50	38-50a

^a See Hooijer (1946a).

TABLE 39

MEASUREMENTS (IN MILLIMETERS) OF THE LOWER MILK TEETH OF *Rhinoceros sinensis*, *unicornis*, AND *sondaicus*

	<i>R. sinensis</i>					<i>R. unicornis</i> ^a	<i>R. sondaicus</i> ^a
	A.M.N.H. No. 18623	A.M.N.H. No. 18623	A.M.N.H. No. 18758	A.M.N.H. No. 18782	A.M.N.H. No. 18626		
DM ₁							
L	—	—	20	—	—	19-21	14-18
W	—	—	10	—	—	11	10-11
DM ₂							
L	30	31	30	31	—	31-33	25-29
W	15	17	17	16	18	18-19	14-16
DM ₃							
L	45	44	42	43	—	42-46	37-43
W	22	24	22	22	26	23-24	20-23
DM ₄							
L	—	—	43	43	—	43-45	38-42
W	26	—	23	23	29	23-25	22-24

^a See Hooijer (1946a).

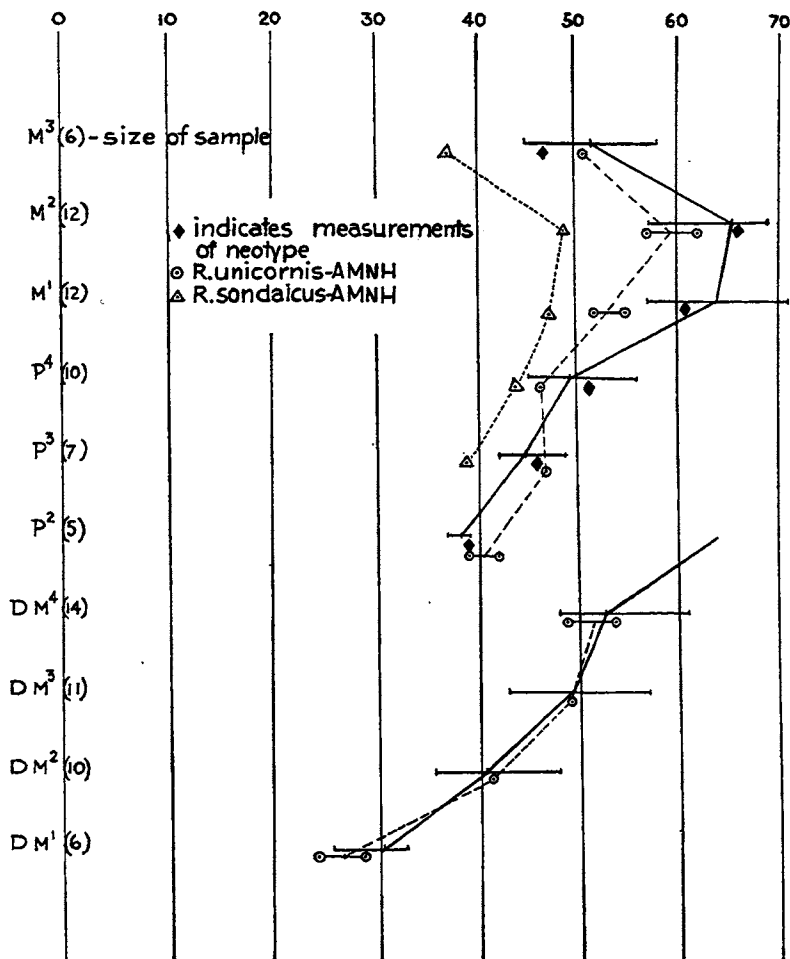


FIG. 37. Diagram comparing length of upper dentition in *Rhinoceros sinensis*, *R. unicornis*, and *R. sondaicus*. Horizontal lines represent observed ranges.

fossil Chinese species is more hypsodont than *R. sondaicus* but compares closely with *R. unicornis* in crown height, although some of the fossil teeth are even more hypsodont than their homologues in the Indian species, as far as the comparative material goes.

In three unworn M³'s of *R. sinensis* the ectoloph is either slightly shorter or slightly longer than high:

	LENGTH	HEIGHT
A.M.N.H. No. 18606	63 mm.	68 mm.
A.M.N.H. No. 18785	66	70
A.M.N.H. No. 18612	67	64

In summary, *Rhinoceros sinensis* agrees with *R. unicornis* in having a protocone fold

in the upper molars; in the fact that the inner portion of the protoloph is much expanded posteriorly, and in the degree of hypsodonty of the upper and lower premolars and molars. On the other hand, *R. sinensis* is closer to *R. sondaicus* in the shape of the ectoloph, although this is not quite so sinuate as it is in the Javan species, and in the rudimentary development of the crista, although the crochet is stronger than it is in *R. sondaicus* and more like that in *R. unicornis*.

The measurements of the upper and lower permanent and milk teeth of *R. sinensis* are presented in tables 34 to 39. The ranges of variation of the measurements in the two

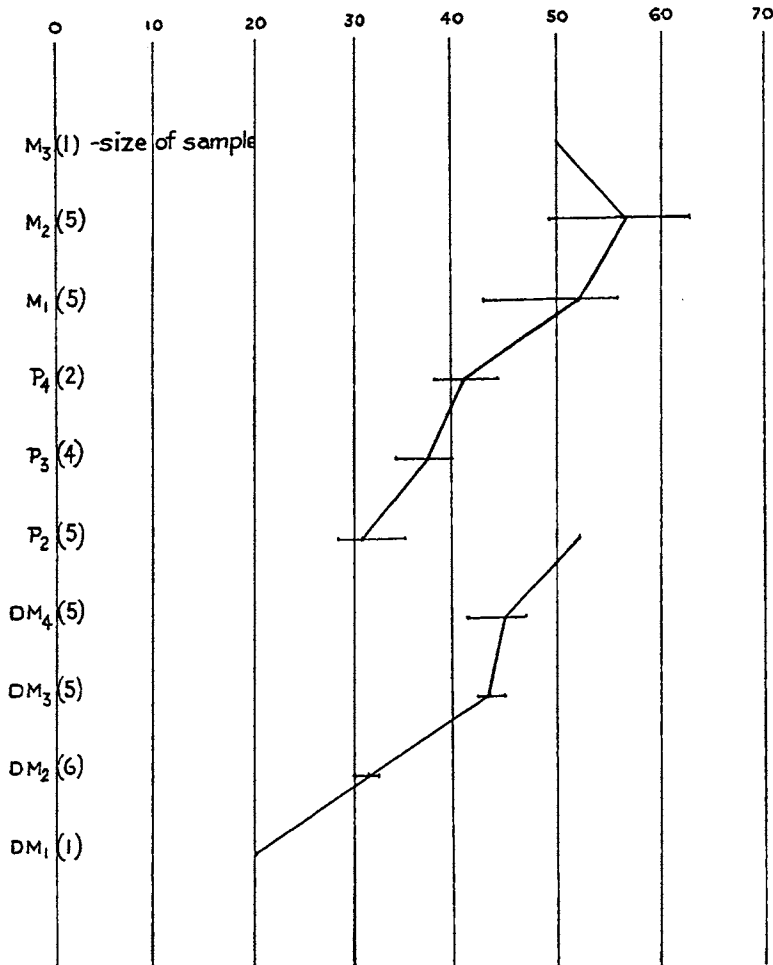


FIG. 38. Diagram of length of lower dentition in *Rhinoceros sinensis*. Horizontal lines represent observed ranges.

recent species, *R. unicornis* and *R. sondaicus*, are taken from Hooijer (1946a) and include both the recent and the fossil teeth, while some measurements were added from the recent *R. unicornis* skulls [A.M.N.H. (M.) Nos. 54454, 54456, and 70445]. The anteroposterior diameters of the teeth are taken at the base of the crown; in the upper teeth, at the base of the ectoloph except for M³ where this measurement was taken on the inner surface. The transverse diameters are also taken at the base of the crown, and the ratio given for the upper molars is that between the posterior width and the anterior width. It will be seen that the range of variation in *R. sinensis* often is greater than in the recent teeth, and that many Chinese teeth exceed

those of the two recent species in size. There is, however, a gradation in size from the smallest to the largest teeth in the Yenchingkou series, and it seems unnecessary to accept the presence of more than one species of *Rhinoceros* at this site. The text figures (figs. 35, 39, 40) and the various photographs (pls. 20-22) of more or less complete dentitions show the variability in these teeth from relatively simple to relatively complex enamel patterns.

The lower dentition of *R. sinensis* needs little comment. There is a lower incisor in this species, as shown by milk teeth *in situ* in the mandible of A.M.N.H. No. 18626 and several isolated milk incisors in Nos. 18540 and 18780. They measure about 20 mm. by

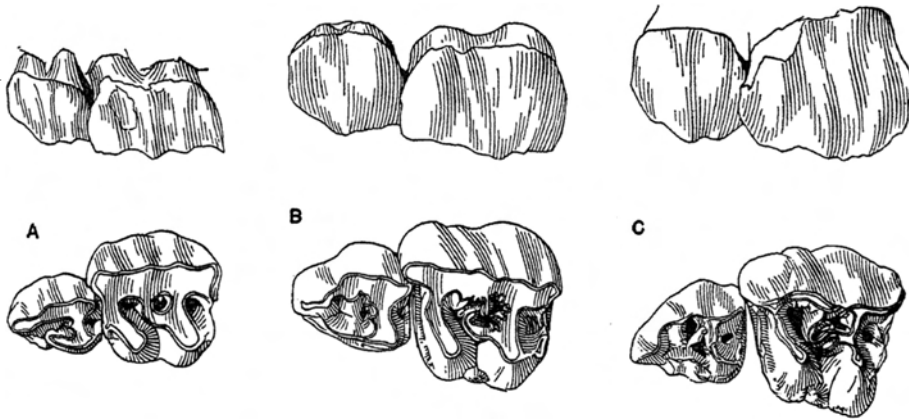


FIG. 39. *Rhinoceros sinensis* Owen. Three left DM^{1-2} , to show variability. Lateral and crown views. A. A.M.N.H. No. 18610. B. A.M.N.H. No. 18782. C. A.M.N.H. No. 18623. One-half natural size.

15 mm. in cross section; the alveoli of the deciduous lower incisors in a specimen of *R. sondaicus* measure 17 mm. by 13 mm. (Hooijer, 1946a, p. 62). One permanent lower incisor in the Yenchingkou collection (A.M.N.H. No. 18780, of the left side) measures 29 mm. by 21 mm. in cross section.

Some of the teeth show interesting variations. The posterior valley of DM^2 is either open or closed on the inside (A.M.N.H. Nos. 18781 and 18623, respectively), while intermediate conditions also occur (A.M.N.H. No. 18539, where the lingual wall to the posterior valley is only partially formed). This type of variation is known from the recent species as well (Hooijer, 1946a, p. 32). DM_4 in a left mandibular ramus (A.M.N.H. No. 18757) has the anterior valley closed on

the inside by an enamel wall that swings inward and backward from the protoconid, thus forming an isolated pit. Similar extra formations are seen both in the right and in the left P_2 of the mandible A.M.N.H. No. 18623 (fig. 40). In this case the posterior valley is closed on the inside by an enamel wall, which is more complete in the left than in the right specimen. The right and left P_3 of A.M.N.H. No. 18780 are peculiar in having the metaconid constricted so as to form an isolated cusp. A normal P_3 (A.M.N.H. No. 18616) is figured beside the anomalous specimen for comparison. The crowns of the lower premolars and molars, as already stated above, are as high as, if not even higher than, those of *R. unicornis* when unworn.

It seems evident from the above discussion

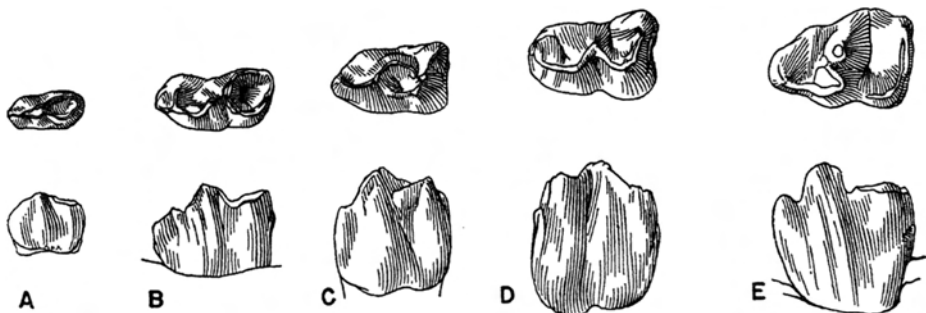


FIG. 40. *Rhinoceros sinensis* Owen. A. A.M.N.H. No. 18758, left DM_1 . B. A.M.N.H. No. 18623, left DM_2 . C-E. A.M.N.H. Nos. 18623, 18787, and 18780, respectively, left P_2 , to show variability. Crown and lateral views. One-half natural size.

of its characters that *R. sinensis* occupies a more or less intermediate position between the Javan and the Indian species. One of us (Colbert, 1942b) has expressed the view that *R. sondaicus* may be considered a persistent primitive species from which, as a structural ancestor, *R. sinensis* arose. Further evolutionary development, from either *R. sinensis* or a closely related form descendent from the *R. sondaicus* type, led to the separation probably through *R. sivalensis* or *R. unicornis*.

In the skeleton of *R. sondaicus* there is seen a progression into the present graviportal type. In the Pleistocene of Java the humerus and femur were shorter, but the radius, tibia, and metapodials were longer, than in the recent animals. The Pleistocene type is mediportal as is the recent Sumatran rhinoceros (Hooijer, 1946b). The single preserved femur in the Yenckingou collection (A.M.N.H. No. 18609) is strikingly small, being 397 mm. long from caput to medial condyle against 438–495 mm. in eight specimens of *R. sondaicus*, and with a proximal width of 142 mm. against 171–219 mm. in 10 specimens of *R. sondaicus* (Hooijer, *ibid.*, p. 72), and two third metatarsals (A.M.N.H. No. 18623) measure 175 and 176 mm. in median length against 150–155 mm. in four recent, and 165 mm. in a fossil third metatarsal of *R. sondaicus* (Hooijer, *ibid.*, p. 81).

ARTIODACTYLA

SUIDAE

SUS LINNAEUS

Sus LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 49.

GENERIC TYPE: *Sus scrofa* Linnaeus.

DIAGNOSIS: Skull long, high, and narrow, without osseous tuberosities above or on sheaths of upper canines; full dentition may be present, or there may be a reduction by suppression of I3 and P1; canines directed outward, cheek teeth brachyodont. Four complete toes in both fore and hind feet, glenoids raised and paroccipital processes very long.

Sus scrofa Linnaeus

Sus scrofa LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 49.

Sus scrofa, LYDEKKER, 1915, *Catalogue of the ungulate mammals in the British Museum*, vol. 4,

p. 308. (This source gives the full history of the synonymy of the species, which is long and involved and need not be repeated here.)

REFERRED SPECIMENS: A.M.N.H. Nos. 18437, a left fourth metacarpal; 18438, skull and jaw, lacking the zygomatic arches and the tip of the snout, but with deciduous molars and first permanent molars, above and below, erupting; 18441, lower canine; 18442, right and left radius, right third metacarpal, left third metatarsal, M₁; 18443, left maxilla with DM²⁻⁴, M¹, right mandibular ramus with DM₄, M₁; 18444, skull, lacking the arches, bullae, and paroccipital processes but possessing the right P²-M¹, and the left P⁴-M², and the broken bases of other teeth; 18445, skull and jaw, lacking portions of the snout, the bullae, the paroccipital processes, and the lower borders and angles of the jaws; the teeth present are the left canine, P¹-M², right P²-M², broken incisors and canines in the lower jaw, and P₂-M₃ on both sides; 18447, fragments of right maxilla with P⁴-M², left maxilla with P⁴-M² and M² loose, right mandibular ramus with P₂₋₃ erupting and M₁₋₂; 18463, back of right mandibular ramus with M₂₋₃; 18555d, symphysis with deciduous and permanent incisors; 18581, lower incisors, upper canine; 18582, left half of symphysis with I₂ and canine; 18759, skull and jaw, the skull lacking the tips of the nasals, the left zygomatic arch and the left paroccipital process, and the jaw the right ascending ramus; teeth present are the first upper incisors, right canine, right and left P¹-M², all lower teeth except right P₁; 18760, skull and jaw of a juvenile, the skull lacking the right zygomatic arch, the basicranium, and the front of the snout, the jaw lacking the ascending rami; the following teeth are present on both sides, DM²⁻⁴, M¹ in alveolus, DM₃₋₄, M₁ in alveolus; 18761, front of skull with right canine in alveolus, DM¹⁻³, and left DM¹⁻⁴, M¹; 18762, left premaxilla with I²⁻³, left maxilla with P¹⁻²; mandible lacking the ascending rami, but with canines, right P¹-M² and left P²-M²; 18788, left ramus fragment with canine, P₂-M₂; 18789, right and left rami with DM₂₋₄, M₁; 18790, palate and mandible of juvenile with right DM²⁻⁴, left DM²⁻⁴, right and left DM₃₋₄; 18791, right ramus with P₄-M₃; 18792, right ramus fragment with

especially the lower series, are probably slightly longer in the fossil than in the recent forms. However, there is very much age variation in this kind of measurement, with the result that old skulls have shorter tooth rows than young adult ones, and the fossil specimen belongs to the latter group. If there is a difference in tooth size between the fossil and the recent forms it must be an "average" difference only, and the available single fossil specimen is not conclusive. Although the teeth of the fossil goral of

Szechwan seem to differ from their recent homologues in the same point in which those of most of the Yenchingkou mammals differ from the corresponding recent mammals, we feel that in the present case there is no justification for the erection of a new subspecific name. It can be added that there seems to be no reliable difference between the north-eastern and the western recent race of *Naeomorhedus goral* so far as the length of the tooth series is concerned.

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