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THE TRIASSIC VERTEBRATE REMAINS OF CHINA

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CONTENTS

INTRODUCTION

The scientific study of vertebrate fossils in China began with those of the latest geological era, the Cenozoic. Remains of Cenozoic fossils, chiefly *Chilotherium* and *Hipparion*, with deer, pigs, etc., were for many centuries known to the Chinese, especially to the druggists, as "dragon bones," but not until recent years were the remains of extinct reptiles recognized in China. During the early years of the Chinese republic, dinosaurian remains were secured both by the members of the Geological Survey of China and their foreign advisors, and by the Central Asiatic Expeditions of the American Museum of Natural History of New York. The latter institution, especially, collected a large number of interesting specimens, not only of dinosaurs but also of other reptiles, from various horizons in the Cretaceous and Cenozoic.

Fossil reptiles were later collected from various places and various ages in China under the auspices of the Geological Survey and the Sino-Swedish Expedition to the northwest provinces. They covered an area from Peking to Kunming and from Tsingtao to Urumchi, with strata ranging in age from Devonian to Cenozoic. In the present notes I shall restrict myself to the Triassic.

In the section immediately following I shall discuss briefly the geographical distribution of the Triassic vertebrate localities, with an outline of geological occurrence, in sequence from old to young. The next two sections present a paleontological review of all the known vertebrates. A stratigraphical and paleontological comparison with those of the other parts of the world is particularly emphasized. In the last two sections, the most important and latest observations on some of the principal groups are given. A discussion of problems for future work is given as a general conclusion.

For a rather comprehensive review of Triassic faunas all over the world, a recent paper by von Huene (1940a) may prove useful to the reader. Young (1945) gives a recent review of the fossil fishes of China.

GEOLOGICAL OCCURRENCE OF FOSSIL VERTEBRATES IN THE TRIASSIC

Continental facies of the Triassic beds are most extensively developed in northern China, but are also partly represented in southern China. Both in Sinkiang and in Shansi and Shensi, the entire sequence of the Triassic formations is fairly well developed.

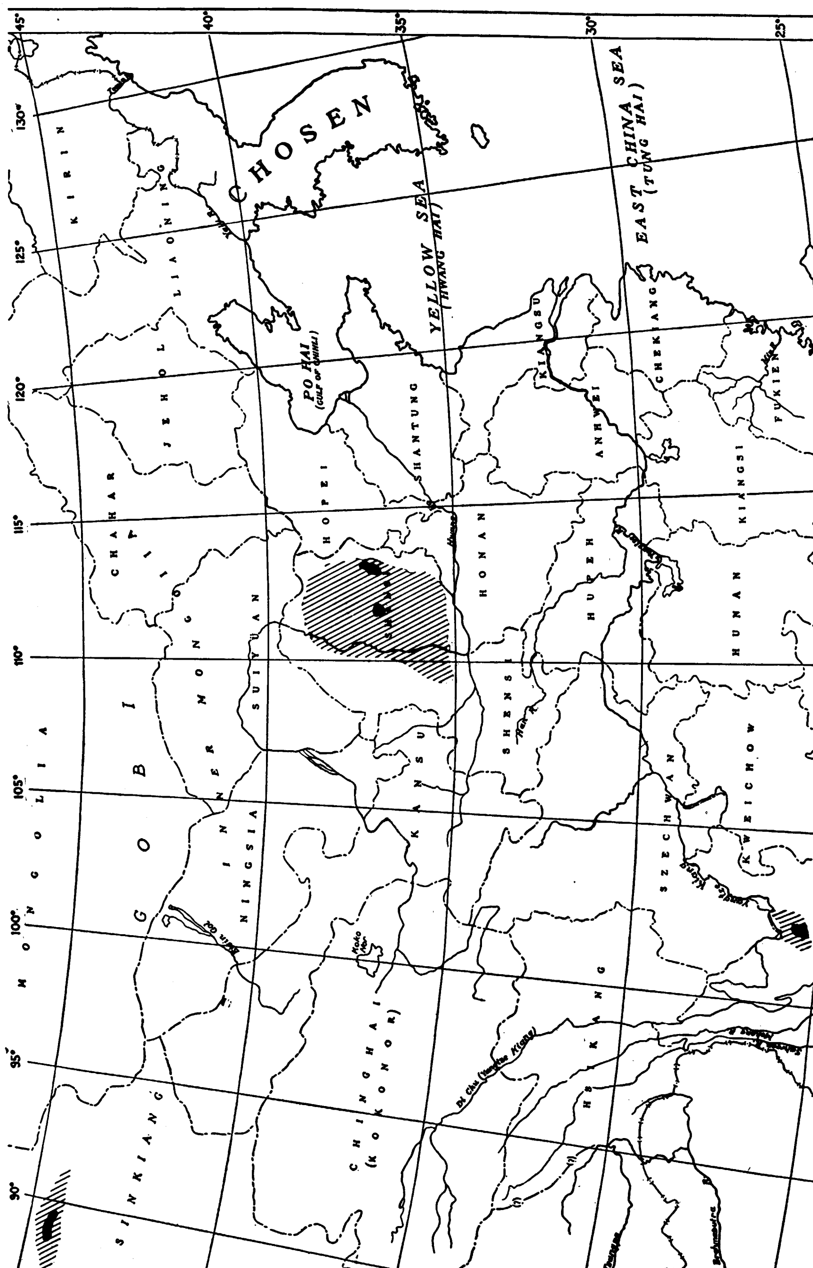

Fig. 1. Map of China showing exposures of vertebrate-bearing Triassic sediments in Sinkiang, Shansi, and Yunnan. The black areas show localities at which Triassic vertebrates have been discovered; the diagonally shaded areas show the general distribution of the Triassic vertebrate-bearing horizons.

In Sinkiang, according to P. L. Yuan, the Triassic is represented by the Tunghunshan series, the Shoufangkou series, and the Kankou series. All the type sections were taken from Fuyuan about 100 km. east of Tihuan. The former two represent the lower Triassic, while the last one represents the upper portion of the middle Triassic and the lower part of the upper Triassic. It is the Tunghunshan series that yielded a rich vertebrate fauna. It is composed of alternating red sandstones and shales, lying unconformably on the upper Permian.

The Triassic sediments form the foothills of the northern slope of Tienshan east of Tihuan, but, according to recent observations, they also extend westward in Changtou and Usu, west of Tihuan in the southern slope of Tienshan. Outcrops of this age are scanty and poorly developed. We have observed good sections of red beds belonging to the Triassic about 60 km. south of Kusha. Because, however, of their more disturbed condition and the limited exposures of the strata, chances of finding rich vertebrate faunas in these beds are not promising, as compared with those of Fuyuan and Fukang, where the strata are only gently tilted and are well exposed as typical badlands.

In Shansi Province, the Triassic beds are widely distributed in several structural basins (C. C. Wang, 1926). We have evidence of the presence of vertebrate fossils both from the basin in southwestern Shansi and from southeastern Shansi. It was in the latter basin that we first found a determinable fossil (C. C. Young, 1937b, 1939). According to C. C. Wang, the continental facies of the Permian and Triassic sediments are conformable without a noticeable angular break. Owing to the scanty fossil evidence and the uniformity of the sediments, we still have not been able to classify these beds in a satisfactory way. However, the study of *Sinokannemeyeria*, found in a rather high level in the Triassic beds, leads us to feel that the whole age (as fixed by Wang) should be placed a little later. That is to say, the lower series of dark red shales, clays, and sandstones may be lower Triassic, and the upper series with green sandstones and red sandy clay and shales, middle and upper Triassic.

Triassic sediments are extensively developed in Shansi and northern Shensi. In many places the beds are beautifully exposed for fossil hunting. It is still premature to say that the Triassic of those places is either barren or rich in fossil remains, but it is clear that more detailed stratigraphic work with the object of finding additional fossils should be done immediately when conditions permit.

The Triassic beds of southern China are chiefly marine in facies. Some continental red beds of Triassic and later age are, however, found in Yunnan. Detailed stratigraphic studies of the I-Ping-Liang series (middle and upper Triassic), the Lufeng, and the Shihmen series were made by H. S. Wang and M. N. Bien. Fossil vertebrates have hitherto been found only in the Lufeng series. This series is particularly well exposed in the vicinity of the town of Lufeng, where it can be divided into lower and upper parts. The lower part is composed of dark purplish beds of shales, clays, and sandstones, while the upper series consists of bright red sandstones with shales and clays of various colors. The whole series lies unconformably on the metamorphosed early Paleozoic series and is capped by massive red sandstones known as the Shihmen series, of Jurassic or later age.

Sediments of similar character, with some evidence of fossils, are found in eastern Lufeng, northern Lufeng up to Yuanmo, and in Anning, while west of Kunming are beds of the same age as the Lufeng series. Extensive fossil hunting has not so far been undertaken. Detailed study of the red beds, which are extensively exposed in Yunnan, Kweichow, and southern Sinkiang and southern Szechwan, may result in new finds of the same fauna.

KNOWN TRIASSIC VERTEBRATES IN CHINA AND THEIR AFFINITIES WITH THE SOUTH AFRICAN FAUNA

The vertebrates so far known from the above-mentioned areas may be enumerated below. Some of the fragmentary, undeterminable finds are omitted.

Sinkiang

The vertebrate remains collected by P. L. Yuan with the Sino-Swedish Expedition have never been fully studied. Some of the specimens did not even reach Peking because of transportation difficulties. From the fossils brought to Peking, I had the opportunity of describing a number of well-preserved specimens, mostly Triassic, but the preparation and study of the whole collection was interrupted by the Japanese invasion in 1937. Some of the prepared specimens were left in Peking. Yuan moved a number of boxes of fossils to Yunnan, but has still had no chance to prepare and study them. An interesting prolacertiform was recently described by T. P. Koh (1941),[1] who had taken it to Germany for study. It is thus obvious that the following list does not contain the whole collection of Yuan, and it is hard to say just what proportion of the entire collection has been described. Nevertheless, it gives us an idea of the richness and significance of the fauna. The forms of vertebrate fossils from Sinkiang so far described are:

Order Eosuchia or Rhynchocephalia:
- *Santaisaurus yuani* Koh

Order Pseudosuchia:
- *Chasmatosaurus yuani* Young

Order Anomodontia:
- *Dicynodon sinkiangensis* Yuan and Young. At least two individuals
- *Lystrosaurus broomi* Young. One
- *Lystrosaurus hedini* Young. At least four individuals
- *Lystrosaurus weidenreichi* Young. At least three individuals
- *Lystrosaurus* sp. At least two individuals

Dicynodontia indet.

The above list includes at least 15 individuals of different reptiles, chiefly Anomodontia. As is c ear from previous publ:cations and by a glance at the faunal list, the fauna is of an interesting, cosmopolitan character. With the exception of the problematic eosuchian, all the other genera are known in the Karroo formations of South Africa. Although the presence of some uppermost Permian beds is not entirely excluded, it is obvious that most of the beds from which these fossils were obtained are of lower Triassic age, almost identical with the *Lystrosaurus* zone of the Karroo of South Africa, as shown by the large majority of specimens of *Lystrosaurus* and the presence of *Chasmatosaurus*. Comparison with the faunal list of the *Lystrosaurus*-zone of the Karroo series (von Huene, 1940a), suggests that a large number of forms are still to be expected from the Chinese locality.

[1] This paper is not available to the author at the present time, and therefore is not cited in the bibliography.

Shansi

Although at least seven localities in the Triassic beds of Shansi have yielded remains of reptilian bones, the only determinable fossil is from Shihpi. I have described this as *Sinokannemeyeria pearsoni* Young (1937b). The other bones are too fragmentary for any reliable conclusions. In spite of the promising future for vertebrate paleontology in Shansi Province, as indicated by these bone-bearing beds, we must confine ourselves at present to consideration of the only identifiable form, *S. pearsoni*.

The osteological features of *S. pearsoni* show close relationship with *Kannemeyeria*, a dicynodont from South Africa, as I made clear in the original description (Young, 1937b). *Kannemeyeria* was derived from the lower *Cynognathus*-zone. The *Cynognathus*-zone is regarded by Broom (1932) as belonging to the upper Triassic and by von Huene (1940a) as middle Triassic, according to the table given by von Huene. The Chinese beds with *Sinokannemeyeria* are, therefore, tentatively regarded as belonging in the lower part of the upper Triassic or the uppermost part of the middle Triassic.

It is, of course, not wise to draw a definite conclusion on the precise age from the evidence of a single form, but the presence of a good fossiliferous level in the middle part of the Triassic beds of Shansi is clear. We have evidence excluding a much younger age for the beds, because the *Sinokannemeyeria*-bearing horizon is overlaid in other places by a coal-bearing series which is Rhaetic. The thick series below it excludes the possibility of its being earlier than we now suppose it to be.

YUNNAN

Our knowledge of the Triassic beds in northern China is incomplete and scattered, but the fauna from those of Yunnan Province is much better known. We worked in Lufeng for two seasons, and all the specimens brought back were prepared. On account of the war, however, much of the material is still waiting for proper description. The following list (revised from that of 1940) is based on the forms already published and general observations on the undescribed materials.

UPPER LUFENG SERIES

Pisces
- *Hybodus houtrenensis* Young[1]. Variegated beds
- Ganoids, indet. .... Variegated beds

Chelonia, indet. .... Variegated beds

LOWER LUFENG SERIES

? Pseudosuchia
- *Platyognathus hsui* Young ..... Dark red beds

Saurischia
- *Lukousaurus yini* Young ...... Dark red beds
- *Sinosaurus triassicus* Young .... Dull purplish beds
- *Gyposaurus sinensis* Young .... Dark red beds
- *Yunnanosaurus huangi* Young. Dark red beds
- *Lufengosaurus huenei* Young ... Dark red beds
- *Lufengosaurus magnus* Young .. Dark red beds

Ictidosauria
- *Bienotherium yunnanense* Young .... Dull purplish beds
- *Bienotherium elegans* Young .... Dull purplish beds
- *Bienotherium* sp. .... Dull purplish beds
- A small ictidosaurian .... Dark red beds
- Ictidosauria gen. et sp. indet. .... Dull purplish beds

Forms from the variegated beds of the upper Lufeng series are scarce and fragmentary, often represented by isolated scutes and scales, and it is hard to draw definite conclusions therefrom. The fossils from the lower Lufeng series are characterized by the abundance of saurischians, of which one belongs to the Coelurosauria, one to the Carnosauria, and four belong to the Prosauropoda, and by at least three interesting genera of Ictidosauria. As we have made a rather extensive survey of the sites, the above list seems to be fairly reliable. This list, therefore, gives a fairly complete idea of the composition of the fauna.

[1] The type is from Anning.

Close examination of the list reveals a surprisingly close resemblance between the Lufeng fauna and that of the red beds and cave sandstones of South Africa. The Lufeng fauna is characterized by the abundance of saurischians and ictidosaurians, including the *Tritylodon*-like *Bienothe ium*. Although there is no form in South Africa exactly identical with *Platyognathus*, this genus may be placed in the same general group as the South African *Sphenosuchus*. The faunas of both regions may thus be given below, side by side, for comparison:

CHINA	SOUTH AFRICA
Platyognathus hsui	? *Sphenosuchus acutus* or *Pedeticosaurus leviseuri*
Lukousaurus yini	*Gryponyx africanus*
Sinosaurus triassicus	?
Gyposaurus sinensis	*Gyposaurus capensis*
Yunnanosaurus huangi	Various species of *Plateosaurus*, and allied forms
Lufengosaurus hueni	
Lufengosaurus magnus	
Bienotherium yunnanense	
Bienotherium elegans	*Tritylodon longaevus*
Bienotherium sp.	

The above-mentioned three zones for Triassic vertebrates in China roughly indicate faunas of lower, middle, and upper Triassic age. Their close affinities with those of the South African Karroo formation have also been made clear.

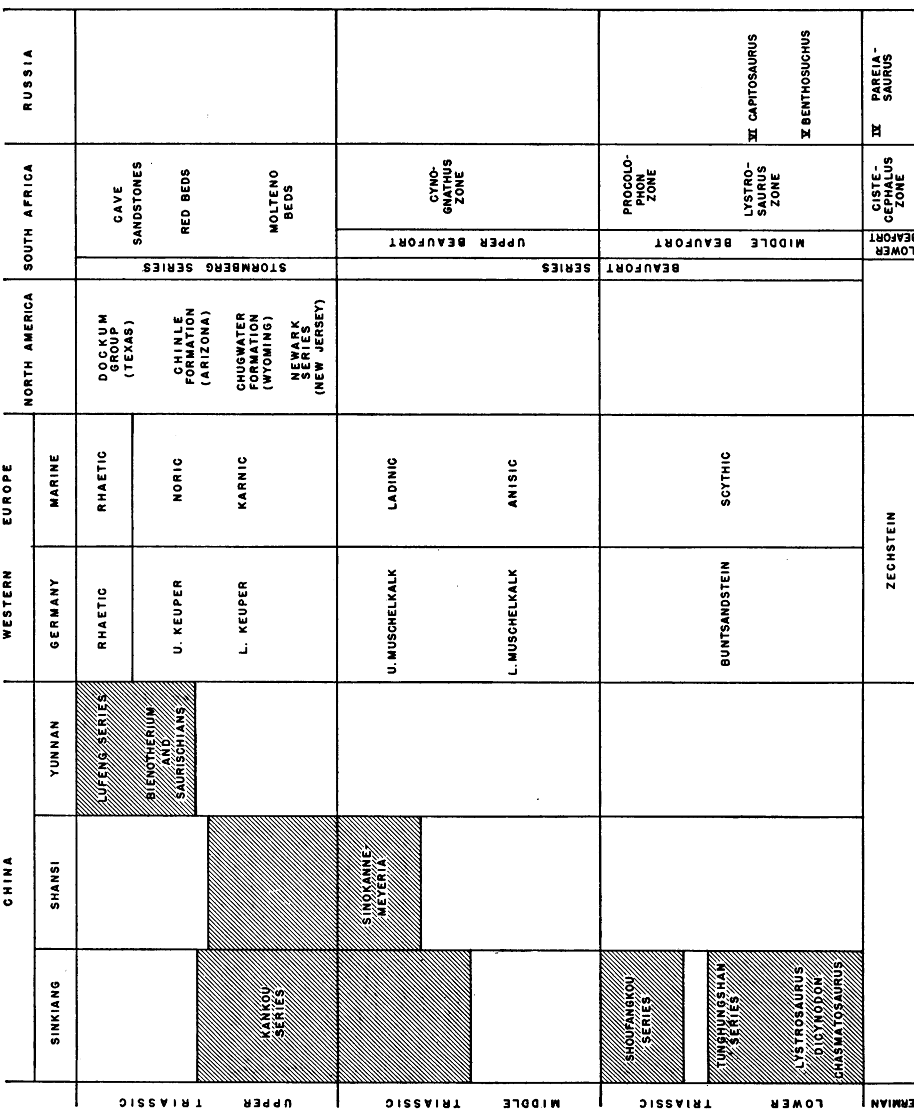

Fig. 2. Correlation of the Triassic vertebrate-bearing rocks of China with Triassic horizons in Europe, Africa, and North America.

COMPARISON OF THE CHINESE TRIASSIC VERTEBRATE FAUNAS WITH THOSE OF COUNTRIES OTHER THAN SOUTH AFRICA

First of all, in Asia, the three known areas that have closely related Triassic faunas are rather imperfectly known. In India, *Lystrosaurus orientalis* is found in the Panchut beds (lower Triassic), and a few saurischian forms are known from the Maleri beds (upper Triassic), which may serve as links with those of Sinkiang (lower Triassic) and Yunnan (upper Triassic). In Indo-China, *Dicynodon incisivum* is now considered to be from beds corresponding to the *Endothiodon*-zone of South Africa (Permian), and thus has nothing to do with our present discussion. It should be noted, however, that the locality of Luang Prabang is situated quite close to the Chinese frontier, and we may thus hope to find Permian anomodont-bearing beds in Yunnan. The lower Triassic beds of the Tour River in western Siberia has yielded so far only Labyrinthodontia, which are not yet recorded from Sinkiang.

In the south Ural area, the vertebrate-bearing formations are subdivided into six zones, according to the fossils. Of these the fifth and sixth belong to the lower Triassic. Again, they are characterized by the presence of Labyrinthodontia, with one anomodont, *Lystrosaurus klimovi*, and the pseudosuchians *Chasmatosuchus rossicus* and *C. parvus* from the sixth zone. The latter forms are comparable with *Chasmatosaurus yuani* from China (von Huene, 1940b).

The reptile-bearing beds of Elgin, in northern Scotland, are not closely comparable with those of China. The lower zone is a little older than the fossiliferous beds of Sinkiang, and the upper zone is older than our Yunnan beds.

The "Knollen Margel" facies of the German upper Triassic, however, show the same general fauna as that of Yunnan. *Sinosaurus triassicus*, *Yunnanosaurus huangi*, *Lufengosaurus hueni*, and *L. magnus* resemble the German *Teratosaurus*, *Pachysaurus*, and *Plateosaurus* even more closely than they do the corresponding forms of South Africa.

As regards North and South America, the affinities are less clear. Nevertheless, a saurischian recently found in Arizona by a University of California field party shows remarkable similarity to the Chinese *Yunnanosaurus*. The upper Newark series, in eastern United States, can be regarded as in part equivalent to, and in part later than, our Shansi beds.

In short, the Triassic development of reptilian faunas seems to be cosmopolitan. New finds of a *Tritylodon*-like animal in Somerset, England, is the latest addition to our knowledge of this group (Kühne, 1943).

PALEONTOLOGICAL CHARACTERS OF THE CHINESE TRIASSIC REPTILES

Since the descriptions of the fossil vertebrates from the Triassic beds of China are scattered and some of the specimens are not yet fully described, especially some of the saurischians and most of the ictidosaurians, a short summary of their principal characteristics and relationships is here given, based upon my latest observations.

Sinkiang Reptiles

As already made clear by von Huene (1940a), the Permo-Triassic reptiles may be divided into three groups, the old theromorph, the young theromorph, and the sauromorph. We have, so far, found no representatives of the old theromorphs in China. Both the lower Triassic fauna with *Dicynodon* and the middle Triassic or lowermost upper Triassic fauna with *Sinokannemeyeria* contain representatives of the young theromorph group. The upper Triassic saurischian fauna of Lufeng obviously represents the typical sauromorph group.

The prolacertiform described by Koh (1941) represents the only small protorosaurian reptile known from China. It may have some relationship to *Prolacerta*, recently discussed by C. L. Camp (1945).

The genus *Dicynodon* is represented in China by only one specimen. As I have pointed out (Young, 1937b), the nearly complete skeleton may belong with the type skull. It represents a rather primitive species of the genus, which raises some question as to its lower Triassic age. Among the three species of *Lystrosaurus* in Sinkiang, *L. hedini* is the most abundant, while *Chasmatosaurus yuani* shows a remarkable resemblance to the South African *Chasmatosaurus vanhoepeni*.

On the whole, the Sinkiang theromorph fauna seems to have a very close relationship with that of South Africa.

Shansi Reptiles

In Shansi, the middle Triassic anomodont *Sinokannemeyeria pearsoni* shows a close resemblance to the South African *Kannemeyeria*.

Yunnan Reptiles

?Pseudosuchia: The only known supposed pseudosuchian, described as *Platyognathus hsui* (Young, 1944), shows no close relationship with the South African forms, in part because of its much smaller size. Neither can it be closely compared with the American *Protosuchus richardsoni*. The systematic position and possible relationships with Pseudosuchia and Crocodilia are not clear.

Saurischia: *Lukousaurus yini*, not yet fully described, is represented by a fairly complete skull with well-preserved teeth. The teeth are sharply compressed, with gentle curvature and fine posterior serrations. It seems to be a member of the Coelurosauria rather than Carnosauria, as revealed by skull characters to be described later.

Sinosaurus triassicus material includes part of a left maxilla with teeth, many isolated teeth, and a number of articulated skeletons. The maxilla and the teeth seem to place it very close to *Teratosaurus*, both in osteological features and in size. Full description of the material awaits opportunity for further study.

One of the interesting members of the saurischian fauna in Yunnan is *Gyposaurus*, which is also known in the South African Stormberg series. The Chinese form, which I have described as *G. sinensis* (Young, 1941), is represented by two well-preserved individuals and many isolated bones. There are still a number of more or less well-preserved specimens awaiting full description. *G. sinensis* is characterized by its small size, general slenderness of limbs, and coarsely serrated teeth.

Yunnanosaurus huangi, of which we have about 20 individuals, is a medium-sized prosauropod, about the size of *Massospondylus*. At least one individual is represented by a well-preserved skull and skeleton. The structure of the skull is like that of *Plateosaurus*, but the anterior limb is unusually short as compared with most of the genera of Plateosauridae. A remarkable fact about this animal is that the sterna are well preserved and ossified. It is interesting to notice that the nearly complete dinosaur skeleton recently found in the Triassic beds of Arizona by the University of California seems to be of about the same size and has many of the same features as *Y. huangi*. It is the only specimen I have seen in the United States that so closely resembles this Chinese genus.

The type of *Lufengosaurus huenei* (Young, 1941a) is the most complete specimen in the collection from Lufeng. The nearly complete skull shows some interesting carnosaurian features, but the teeth are of prosauropod type. It is more closely related to *Plateosaurus fraasianus* of Germany. It is about one-third larger than *Yunnanosaurus* and, like it, has a pair of well-preserved sterna. Besides the type specimen, there are a large number of more or less well-articulated skeletons of this species.

A second species of the genus *Lufengosaurus*, based on isolated teeth, jaws, and a number of partly articulated limbs, was named *L. magnus* (Young, 1944), because of its enormous size. It is about one-third larger than *L. huenei* and looks much more robust in structure. Since, however, the limbs of Carnosauria and Prosauropoda are not easy to distinguish in the absence of associated teeth, and since members of both orders are present in the Lufeng collection, we cannot be absolutely confident in classifying the isolated bones.

Of the six genera named above, with seven species, one belongs to the ?Pseudosuchia, one to the Carnosauria, and four belong to the Prosauropoda. As already mentioned, some of the faunal relationships with South Africa and Germany are striking. The geological age of the lower Lufeng series is dated mainly on the basis of the saurischian remains, so well known from the Stormberg series of South Africa and the Knollen Margel facies of the Keuper of south Germany. According to Broom (1932), however, there remains the possibility that the upper part of the red beds of South Africa may belong to the Lias. This may also be true of our upper Lufeng series, or even of the Shihmen series, as already made clear by Bien (1940).

This leaves the Ictidosauria, of the Lufeng reptiles, still to be considered, and these are of such importance that they are discussed separately below.

PALEONTOLOGICAL CHARACTERS OF THE ICTIDOSAURIA

In 1940 I published a preliminary report on the supposed primitive mammals of Lufeng, with the proposal of a new genus, *Bienotherium*, including two species, *B. yunnanense* and *B. elegans*. Later, additional material of this genus was secured. There were, however, two reasons for the postponement of a final study of the material: some of the specimens needed delicate preparation, and I had no time for this, being occupied with other duties. Having a chance to come to the United States, I brought the material with me. Thanks to the kindness of the authorities in the American Museum of Natural History, preparation of the specimens has been skillfully completed.

In the meantime, a small skull with lower jaws was also prepared and made available for detailed study. There was also a lower jaw among the new material which seems to be a new type of ictidosaurian.

Since the full description of all of the Lufeng Triassic material is not yet completed and its publication may be delayed, I am using this opportunity to give preliminary descriptions of these forms, based on my latest observations. The final diagnostic characters, complete descriptions, and illustrations will, of course, have to be deferred for publication in a forthcoming paper. My thanks are due to many gentlemen in the United States for their kindly help and discussions, especially to Drs. W. K. Gregory, G. G. Simpson, E. H. Colbert, C. L. Camp, and A. S. Romer. To Mrs. Rachel H. Nichols I am deeply indebted for editorial work on my manuscript.

BIENOTHERIUM

SUMMARY OF MATERIAL

As mentioned above, new material was found after my descriptions of *Bienotherium yunnanense* and *B. elegans* had been published. In view of this and as the result of further preparation of all the material, I may summarize the remains of this genus as follows:

Bienotherium yunnanense Young

The type specimen (Cenozoic Lab. No. V-1) consists of a skull and lower jaws. Some isolated upper and lower jaws and some limb bones were also referred to this species. In addition we have found a fairly complete pair of lower jaws (Cenozoic Lab. No. V-65) in association with some limb bone fragments. A number of fragments of teeth, jaws, and limbs were also obtained from other localities during later excavations, made in 1939.

The type skull reveals many new points as the result of further preparation. The tooth formula is now definitely recognized as: $I^{?3}_{1}$ C^{0}_{0} $Pc_{6}\frac{7}{-}_{7}$. The presence of a first upper incisor is not clear. In any case, there is no indication of a definite alveolus clearly visible. The third incisor, on the contrary, is indicated by a rather large alveolus, but much inferior in size to that of I^2, being about 2 mm. in diameter. The last post-canine tooth is erupting much below the grinding surface. It was exposed during the later preparation by removing the thin coat of matrix. It is preserved only on the right side. As compared with the teeth of *Tritylodon*, the crescentic shape is rather less well developed. In many cases, the pattern is a little more complicated, but in some teeth, reduction of the cusps is observed. This cannot be explained simply by the advanced stage of wear, because some of the teeth are perfectly unworn; it may, however, not be considered as a diagnostic character. On the whole, however, the dentition has fundamentally the same pattern as *Tritylodon*, being composed of two external, three median, and three inner tubercles, or cusps. On the posterior teeth the number of tubercles of the middle and inner rows may be reduced. The lower teeth consist of one large incisor and six to seven post-canine teeth. The crown pattern of the latter is composed of two external and two internal cusps, separated by a deep groove, for reception of the middle cusps of the upper teeth.

In the further preparation of the skull, the piece of bone posterior to the last tooth of the right side was found and put in place. It reinforces Watson's ideas of the strong development of the transverse flange of the pterygoid. (See below.) The jugal is partly reconstructed. As already discussed in my previous paper, the skull is robust, with a general rodent-like appearance. Its resemblance to the Eocene multituberculate *Taeniolabis* is also remarkable. The peculiar shape of the pterygoid reveals reptilian features.

The lower jaws have also been reconstructed. On the right ramus, the so-called "boss" proved to be hollow when the matrix was removed from the top. The posterior construction is entirely hypothetical, especially the condyle. On the inner side, the depressed groove along the lower border and the sharp ridge resemble those features on the *Tritylodon* jaw from England described by Kühne (1943). It is therefore quite possible that there are some rudimentary elements such as the articular present in our form. The angular process is, however, well developed in the Chinese genus.

The limbs, especially the humerus and the femur, show some resemblances to those of the Theriodontia.

Bienotherium elegans Young

Materials assigned to this species consist of the type skull (Cenozoic Lab. No. V-2), several jaw fragments of other individuals, and some limb bones. The skull is crushed, especially the part along the cheek teeth, and the posterior part is damaged. It differs from *B. yunnanense* chiefly in its smaller size, rather long and constricted snout, and in the detailed structure of the teeth. In the cheek teeth, the three rows of tubercles are not so regularly arranged as in the preceding species. The median row tends to be more or less confluent with the inner row, which could not have been caused by crushing. The minute tubercles are more complicated, and the crescentic tooth form is still less clear.

It is possible that *B. elegans* represents merely a small form of *B. yunnanense*, the difference in size due to youth or sex. But the differences in shape of the snout and in the teeth seem to go beyond the limit of differences caused by age or sex. For the present, therefore, I keep it as a separate species.

Bienotherium sp.

In the additional collection, we have two upper jaws apparently associated with a right lower jaw (Cenozoic Lab. No. V-66) which I believe represent a third species of the genus *Bienotherium*. It is one-half smaller than *B. yunnanense*, and one-third smaller than *B. elegans*. The lower jaw is about the same size as the right dentary figured by Kühne as *Tritylodon*. The pattern of the upper teeth is fundamentally that of *B. yunnanense*. The lower jaw also differs remarkably from that of *B. yunnanense* in its low and straight appearance, being about the same shape as the British *Tritylodon*.

As with *B. elegans*, I believe the distinctions of this specimen are greater than could be due to age or sex differences and it may represent a third species of this genus.

Systematic Position of *Bienotherium*

Following the earlier system of classification of *Tritylodon longaevus*, I considered *Bienotherium* as also a member of the Multituberculata when I first described the material. The close relationship in the structure of the skull and teeth between *Tritylodon* and *Bienotherium* cannot be denied, and

Bienotherium certainly belongs to the same suborder, Tritylodontoidea, if not to the same family (Simpson, 1928). As I intended to discuss this subject more fully, I did not go into detail in my first report.

In the meantime, two interesting papers have been published regarding the systematic positions of these two genera. Watson (1942) compared my drawings of *Bienotherium* with those of *Diademodon* and shows that *Bienotherium* displays a series of cranial characters, such as the presence of the septomaxilla, shape of the pterygoid, possible articulation of the lower jaw with the quadrate, and so on, closely comparable with those of *Diademodon*. He also compares the lower jaw of *Bienotherium* with that of Broom's ictidosaurian, especially in the presence of the "boss." Basing his argument on the above characters, he prefers to classify both *Bienotherium* and *Tritylodon* as Ictidosauria rather than as Multituberculata.

The other paper, by Kühne (1943), is based on the new finds of *Tritylodon*-like material from east Somerset, England. On the basis of a composite lower jaw, he fails to find the real condyle of the jaw and thus assumes that it must have been situated on some accessory jaw element. This leads to the conclusion that *Tritylodon* must have had a compound lower jaw, the main reason for removing it from the Class Mammalia.

The facts presented in these two papers are fairly conclusive, and I shall take them into full consideration in describing my new material. For the present I wish only to mention the following points and some of my opinions.

First of all, I am in full agreement with Watson's interpretation that the skull of *Bienotherium* is closely comparable with that of *Diademodon*. The new facts set forth by Kühne are certainly also conclusive. The tiny tip of the articular process in *Tritylodon* seems too weak to perform the function of connecting the heavy lower jaw with the skull. But this is only negative proof, since he has not yet found any bone which belongs to the articular portion of the *Tritylodon* lower jaw.

The additional preparation on the type skull of *Bienotherium* disclosed an alveolus behind the canine-like incisors, and a newly erupted tooth behind the left cheek teeth, making the number of post-canine teeth seven instead of six. These facts bring *Bienotherium* even closer to *Tritylodon* than originally supposed.

On account of the slight crushing of the skull, it is not possible to fit the lower jaw to the skull in an absolutely natural position, but it cannot be far off, since all parts of the skull and jaws are well preserved with little distortion. If the lower tooth row is placed in proper contact with the upper one, the prolongation of the articular process does not point to the supposed quadrate, as expected by Watson, but points at least 5 mm. external to this supposed quadrate. It is impossible to move the jaw inwards to this supposed quadrate because of the transverse flange of the pterygoid bone behind the tooth row. The reconstruction of the posterior part of the lower jaw is based upon this idea, and it is likely that the space between the posterior top of the lower jaw, presumably with an articular, and the quadrate surface has to be connected by the real quadrate bone which is missing. The angular is apparently lost, because the real angular process is well formed in *Bienotherium* and represents a part of the dentary.

From the above-mentioned facts, it is clear that our skull and jaws (the latter being very similar to the English *Tritylodon* jaw except for the angular process) have certain reptilian characters. As in many other classifications among main biological groups, it is always a question for debate to try to draw an exact boundary line between two closely related groups. It is difficult to say which of the basic characters should be used as a decisive one in separating primitive mammals from advanced reptiles. It seems quite reasonable that we cannot expect to have here the first mammal in geological history to have lost *all* reptilian characters and to be the perfect mammal, according to diagnosis and definition! On the other hand, it is generally accepted that many advanced reptiles may be allowed to possess basic mammalian characters. We have to draw an artificial line somewhere.

Obviously, *Bienotherium* and *Tritylodon* represent the closest approach yet found in the direction of mammals. There is even a small part of an articular beside the dentary. The dentary reaches an enormous size, comparatively speaking, and it includes both the ascending process and the angular process. In spite of some reptilian characters, revealed in the posterior region of the skull, the skull of *Bienotherium* looks more like a mammal skull than that of any mammal-like reptiles so far known.

On the other hand, as emphasized by many authorities, *Tritylodon*, and consequently *Bienotherium*, cannot be the real ancestor of any modern mammals. They represent a very specialized line of cynodonts progressing towards the goal of being mammals. But, during the course of evolution, they became so specialized that they went beyond the point of being possible ancestors of later mammals. This was probably correlated with the diet, which may have consisted of roots, a very hard diet which forced development of the jaw muscles and reduced the possibilities of progressive development of the brain. All these facts are also responsible for the peculiar shape of the skull and the teeth.

Considered broadly, the Tritylodontoidea and the Mesozoic mammals, and also many advanced cynodonts, were all "defeatists" that were constantly struggling towards better modifications in the direction of modern mammals. We know too little about the ancestral types of these groups. It seems clear, however, that the evolutionary history of the early mammals was polyphyletic and, as has already been suggested by Olson (1944), we should not expect to have only one ancestral type for all mammals. *Tritylodon* is one of the defeatists that achieved the most mammalian characters, as compared with the other advanced reptiles, but that failed to go further because of its too high degree of specialization.

Ictidosauria gen. and sp. indet.

This new form is represented only by the anterior part of a right lower jaw, with the anterior tip broken and the surface of the crowns of the teeth damaged. The outline of the jaw differs from that of *Bienotherium* in its increase in height posteriorly, in the prominent coronoid ridge with a depression below it, and in the much fainter longitudinal groove on the inner side of the jaw. The teeth are too much damaged for a detailed description. Roots are distinctly divided.

The systematic position of the specimen is not quite clear, but from the outline of the jaw and teeth, it shows some similarities with *Pachygenelus* (Watson, 1913). This genus has some incisors besides the canine-like tooth. The anterior portion of our specimen is broken, so it is impossible to tell whether there were incisors, but the cross section of a canine-like tooth remains. The relationship with *Pachygenelus* is therefore not certain, but the characters possessed by our specimen indicate that we are dealing possibly with another reptile, probably also a member of Ictidosauria.

A Small Ictidosaurian

A tiny skull with pair of lower jaws represents another interesting fossil from Lufeng. Both ends of the specimen are damaged, and it is so small and delicate that we have not risked removing the lower jaws from the skull in order to see the crowns of the teeth. The outline of the skull is in general mammal-like, with a very stout snout and comparatively heavy braincase. There is no trace of the postorbital element, which excludes the skull from most of the mammal-like groups and suggests an ictidosaurian. On the other hand, the lower jaw is low and slender with the anterior border sharply bent and with a straight lower border. There are indications that the jaw is composed of other elements besides the dentary. The upper teeth are clearly heterodont, the tooth formula probably being

$$\frac{?\ 1.6.2}{?\ ?\ ?\ ?}$$

There is an indication of the separation of the roots. The last two teeth, as shown clearly at the left side, have a broad crown surface with a number of tubercles.

The systematic position of this animal is still very obscure. Tentatively, I regard it as also belonging to the most advanced mammal-like reptiles, in the Order Ictidosauria.

CONCLUSIONS

From the point of view of vertebrate paleontology, the continental Triassic beds of China are very interesting not only because of the present knowledge, as summarized above, but also because of their extensive development in China, as repeatedly revealed by geological mapping work. It will be surprising if many new fossil fields are not discovered in the future. What we now know is only the beginning of the beginning.

Since the continental Triassic is represented only by the uppermost part in South China and a complete section of the red beds would include even part of the Permian and post-Triassic beds, a comprehensive view of the whole history of Permo-Triassic and later times is more likely to be obtained by future detailed research in North China. The Lufeng field, however, will remain a good one for Triassic-Jurassic fossils, and further work should be carried on there.

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