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Significance of Chinese tritylodonts (Synapsida, Cynodontia) for the systematic study of Japanese materials from the Lower Cretaceous Kuwajima Formation, Tetori Group of Shiramine, Ishikawa, Japan

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Introduction

In early October 1997, two fossil teeth found from "Kaseki-Kabe", which is known as the fossil bluff, an outcrop of the Lower Cretaceous Kuwajima Formation, Tetori Group at Kuwajima, Shiramine, Ishikawa were identified as the tritylodont lower cheek teeth. It was the first discovery of a mammal-like reptile from Japan.

The tritylodonts are herbivorous mammal-like reptiles belonging to Cynodontia. They have homodont cheek dentition and the tooth is multicusped, with crescentic cusps arranging in three rows on upper and two on lower jaws. They are advanced members of mammal-like reptiles shearing numerous synapomorphies with the Mammalia. The fossil records distribute in all continents except Australia.

The discovery of the tritylodonts from the Lower Cretaceous deposit surprised us. The fossil records of the tritylodonts have been thought to concentrate to the Upper Triassic to middle Jurassic formerly, and this family has been treated as the index fossil of these ages. On the contrary, the record from Kuwajima Formation, as well as the recent report from Kemerovo in the Western Siberia by Tatarinov and Matchenko (1999), revealed the survival of this group to the Early Cretaceous in the western part of the Asian continent on wide area.

For the taxonomical study of the Japanese tritylodont, we compared it to the Chinese members first, by the opportunity to attend the paleoprimatological field survey of Yunnan, China (1 Nov. 1997 - 25 Dec.) leaded by Prof. Nobuo Shigehara of Primate Research Institute, Kyoto University. Lufeng in Yunnan is the world's largest locality of the tritylodonts, and is the type locality of 9 species in 5 genera. We could examine the most of them including the world's famous *Bienotherium yunnanense* in IVPP (Institute of Vertebrate Paleontology and Paleoanthropology), the Chinese Academy of Science, Beijing. We also could examine *Bienotheroides* from Xinjiang in IVPP, and *Polistodon chuannanensis* in Zigong Dinosaur Museum, Sichuan. That means we could examine the most of the Chinese tritylodonts in the days while we were in China for two months. We brought the casts of four fossils from Shiramine that had been collected before the departure. The direct comparison between the Shiramine materials and Chinese fossils was truly purposeful.

Observation on the Chinese, mostly complete, tritylodont skulls also let us have an idea on the system of cheek teeth replacement unique in this group. It is very important for the taxonomical study of Shiramine fossils because they all have been found in isolated position, and so it is discussed in latter chapter.

Scope of this study

The main aim of this paper is to find the relatives of the Japanese tritylodont. Among the tritylodonts of the world, the Chinese members, which are classified to 12 species in 7 genera and amount to more than the half of the world's records, are the most important for the investigation of fossils from Japan, because of the following two, geographical and chronological, reasons.

Geographically, the fauna that must be closest to the Japanese one is of Asia, because it was before the Miocene opening of the Sea of Japan and the stage that proto-Japan was a part of Asian continent when the Tetori Group was formed. So the Japanese fossil is highly expected to be identical to, or at least to be the close relative of some Chinese members.

The early Late Jurassic species *Bienotheroides wansienensis* from China is the youngest member of the tritylodonts except the two present latest records, Japanese one and *Xenocretosuchus sibiricus* from Russia. Therefore, chronologically also, Chinese members are essential to studying the occurrence from Japan.

The other intention is to provide a model for the system of cheek teeth replacement in the tritylodonts. Because it is very important, for the taxonomical investigation of isolated fossils, to know how the teeth replaced, we would like to provide a base of discussion on the evolution of teeth replacement in the tritylodonts.

Therefore, the Chinese tritylodonts are the keys to promoting the study of this group in Japan. This paper reports "harvest" of observation on the Chinese tritylodonts, and it will provide the first step of activity for the mammal-like reptile paleontology in Japan.

Tritylodont occurrence from Japan

Materials-- Four lower cheek teeth, catalogued to Shiramine Board of Education, Ishikawa; SBEI-023, 024, 053, and 056. SBEI-024 and 056 are from right lower jaw, while SBEI-053 is from left. SBEI-023 is broken and the orientation is uncertain.

Locality— Kaseki-Kabe of Kuwajima, Shiramine Village, Ishikawa Prefecture, Ja-

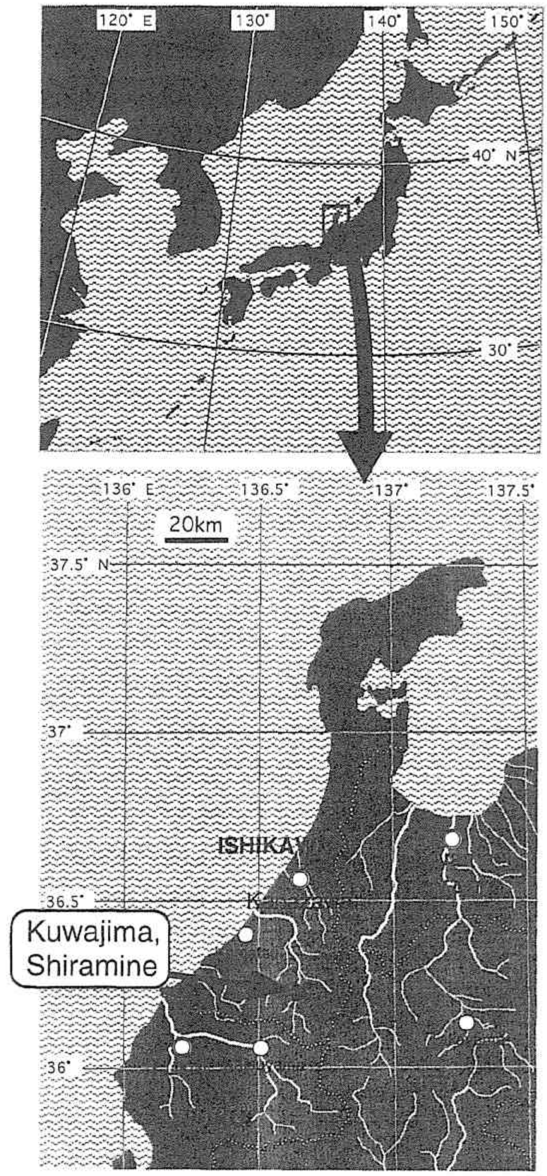

Figure 1. The locality map of tritylodont fossil from Kuwajima, Shiramine, Ishikawa.

pan. (Figure 1)

Horizon and age— Dark green-gray colored mudstone in the upper part of Kuwajima Formation, which forms the upper part of Itoshiro Subgroup, Tetori Group. The age is estimated at earlymost Cretaceous, Berriasian or Valanginian.

Description of the lower cheek teeth— All specimens are similar in morphology. SBEI-056 (Figure 2), which is right lower cheek tooth, is the most complete one.

Two rows arranging buccolingually consist of two cusps in each, and totally four cusps are present on one tooth. All cusps show sharp crescentic outline. Each cusps are high, and groove between cusp rows is deep correspondingly. Crescentic ridges surrounding the posterior slope of cusp are sharp and the slopes concave vertically. In the lateral view, crescentic ridges go down vertically from the apex of cusp in the upper part and

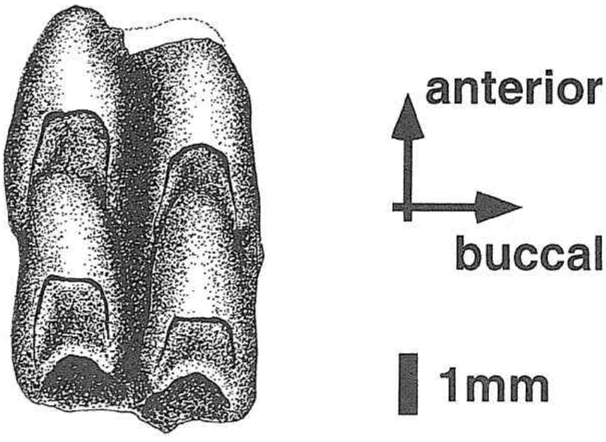

Figure 2. A tritylodont right lower cheek teeth, SBEI-056, from the Lower Cretaceous Kuwajima Formation, Tetori Group of Shiramine, Ishikawa. Occlusal view.

bent, with clear turning-point, to slanting on the lower margin of crown in about 20 degrees in the lower part. The covering for the anterior part of two posterior cusps by the posterior part of crescentic ridges of two anterior cusps are not deep and terminate with small expansion.

The measurements of anteroposterior and buccolingual length of SBEI-024, 053, and 056 are 4.5 mm/3.0 mm, 7.4 mm/5.2 mm, and 7.7 mm/4.7 mm respectively. SBEI-023 is a broken tooth on witch only one cusp row is preserved, but the size corresponds to those of SBEI-053 and SBEI-056. That means only SBEI-024 is apparently smaller than the rest, and four specimens can be divided into two groups by size. It is hard to tell any differences in cusp morphology between the SBEI-024 and others.

Tritylodont finds in China

Mainly three areas (Yunnan, Sichuan and Xinjiang; Figure 3) in China have been producing tritylodont fossils, that have been described as 12 species in 7 genera (Table 1). Even though some taxonomically doubtful members were removed, China is obviously one of the largest locality of the tritylodonts. Especially, the Lower Jurassic of Lufeng in Yunnan, yielding 9 species of 5 genera, is the world's largest locality. The other two genera are from the upper Middle (to the lower Upper) Jurassic formations in Sichuan and Xinjiang.

Lufeng, Yunnan

The Lower Lufeng Formation distributes widely with N-S direction in the east of Lufeng, about 60 km west from Kunming. Especially, the northeastern area in distance of some kilometers from Lufeng town is famous for its abundant fossil productivity. In addition to the early works by Bien and Young, subsequent studies have been carried out to

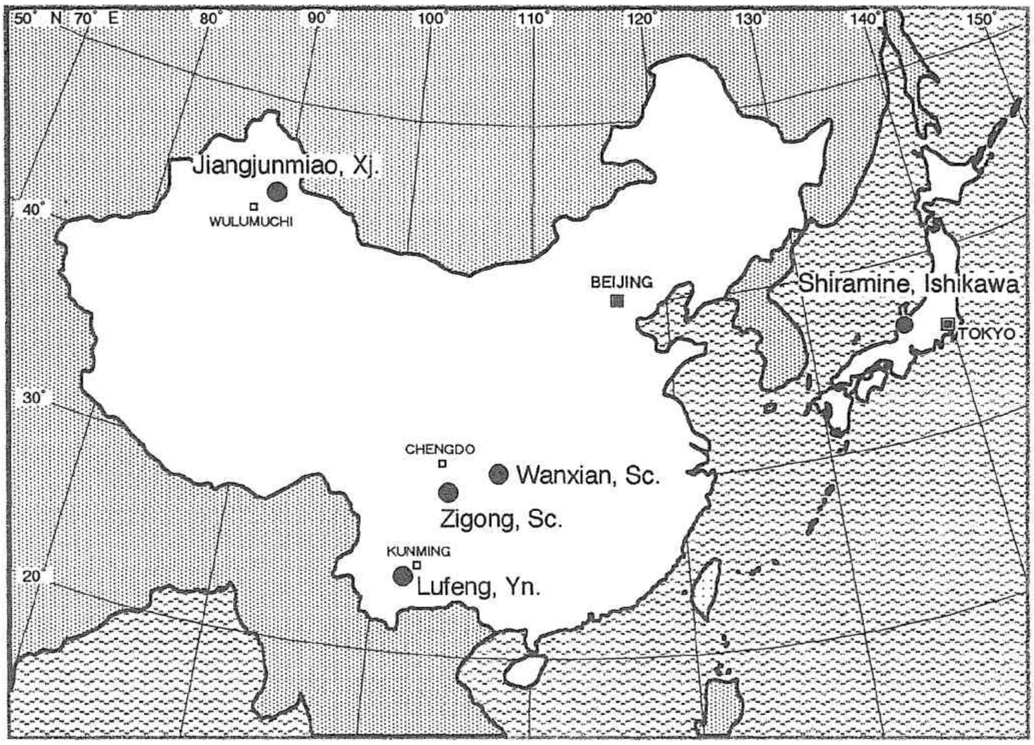

Figure 3. Localities of tritylodont find in China and Japan.

detailing the fossil assemblage. Now it is clear that Lufeng vertebrate fossil assemblage can be divided into two groups by stratigraphic sequence. The lower faunal assemblage from the Dull Purplish Beds is dominated by prosauropod dinosaurs and tritylodont *Bienotherium*, and the upper one from the Dark Red Beds has a much greater taxonomic diversity (Luo and Wu, 1994). Both assemblages are thought to be of the Lower Jurassic.

9 tritylodont species of 5 genera have been established from Lufeng. They are; *Bienotherium yunnanense* Young, 1940, *B. elegans* Young, 1940, *B. minor* Young, 1947, *B. magnum* Chow, 1962, *Lufengia delicata* Chow and Hu, 1959, *Yunnanodon brevirostre* Cui, 1976, *Dianzhongia longirostrata* Cui, 1981, *Oligokyphus sinensis* Young, 1974, and *O. lufengensis* Luo and Sun, 1993. However, *Bienotherium elegans* is now thought to be a junior synonym of *B. yunnanense* (Hopson and Kitching, 1972; Sun et al., 1992), and type specimen of *Oligokyphus sinensis* do not have cusp pattern unique to the genus and so the name *O. sinensis* should be deleted (Sues, 1985; Sun and Cui, 1986; Sun et al., 1992; Luo and Sun, 1993; Luo and Wu, 1994). Even after the two were removed, the high diversity of Tritylodontidae in this area is still solid.

On the other hand, the occurrence of tritylodonts from Lufeng, as well as the other tetrapods, is divided into two horizons, and each species are said to be unique in one horizon only (Luo and Wu, 1994). *Bienotherium yunnanense*, *B. minor* and *Oligokyphus lufengensis* are collected from the lower Dull Purplish Beds, and, *Bienotherium magnum*,

Table 1. List of Chinese tritylodonts. *1: Treated as a junior synonym of *B. yunnanense*. *2 The type specimen does not have the diagnostic character of *Oligokyphus*, and the specimen is now thought to be of an immature *B. yunnanense*.

	Jurassic				
	Early		Middle / Late		
	Dull Purplish Beds, Lower Lufeng Fm.; Lufeng, Yunnan.	Dark Red Beds, Lower Lufeng Fm.; Lufeng, Yunnan.	Xiashaximiao (=Lower Shaximiao) Fm.; Zigong, Sichuan.	Wucaiwan Fm.; Jiangjunmiao, Xinjiang.	Shangshaximiao (=Upper Shaximiao) Fm.; Wanxian, Sichuan.
Bienotherium Young, 1940					
· *B. yunnanense* Young, 1940	●				
· *B. elegans* Young, 1947	○*1				
· *B. minor* Young, 1947	●				
· *B. magnum* Chow, 1962		●			
Lufengia Chow and Hu, 1959					
· *L. delicata* Chow and Hu, 1959		●			
Bienotheroides Yang, 1982					
· *B. wansienensis* Yang, 1982					●
· *B. zigongensis* Sun, 1986			●	●	
Polistodon He and Caj, 1984					
· *P. chuannanensis* He and Cai, 1984			●		
Yunnanodon Cui, 1976					
· *Y. brevirostre* Cui, 1976		●			
Dianzhongia Cui, 1981					
· *D. longirostrata* Cui, 1981		●			
Oligokyphus Henning, 1922					
· *O. sinensis* Young, 1974		○*2			
· *O. lufengensis* Luo and Sun, 1993	●				

Lufengia delicata, *Yunnanodon brevirostre* and *Dianzhongia longirostrata* are from the upper Dark Red Beds. Generally speaking, tritylodont assemblage of the lower Dull Purplish Beds is characterized by *Bienotherium* solely, in contrast with the diversified small species from the upper Dark Red Beds.

Zigong and Wanxian etc., Sichuan

The Jurassic of Sichuan, which is famous for its huge Middle Jurassic dinosaur assemblage from Zigong especially, also yields the significant tritylodonts. The Xiashaximiao (=Lower Shaximiao) Formation of Dashanpu in Zigong, the great locality of dinosaurs, has yielded two species in two genera, *Polistodon chuannanensis* He and Cai, 1984 and *Bienotheroides zigongensis* Sun, 1986. They are large species, and represented by well-preserved skulls. The other species of *Bienotheroides*, *B. wansienensis* Young, 1982 is from the Shangshaximiao (=Upper Shaximiao) Formation, which is the upper next formation of Xiashaximiao, of Gaoling in Wanxian. Wanxian fossils include extremely well-preserved skull specimen, and the detailed description is by Sun (1984). In addition to these type specimens, the postcranial elements referred to *Bienotheroides* were reported from the localities in Sichuan (Sun and Li, 1985). They provide significant information on the life style of younger member of Tritylodontidae.

Ages of Xiashaximiao (=Lower Shaximiao) Formation and Shangshaximiao (=Upper Shaximiao) Formation are assumed to be the upper Middle Jurassic and the lower Upper Jurassic respectively.

Jiangjunmiao, Xinjiang

The Middle Jurassic Wucaiwan Formation which yields abundant fossil tetrapods such as dinosaurs, and that is a counterpart of Xiashaximiao Formation of Sichuan in Dzungar Basin, yielded *Bienotheroides zigongensis* which was originally described from Zigong in Sichuan (Sun and Cui, 1989). The locality is an area of about 120 km northwest from Wulumuchi, and about 30 km north from Jiangjunmiao. It is more than 2000 km far away from Zigong to Jiangjunmiao. Sharing fossil record of one species between these two points may suggest the wide distribution of Middle Jurassic tritylodont fauna.

Comparison between the chinese tritylodonts and fossils from Shiramine

While we were visiting China on November and December in 1997, we could examine all the genera of the Chinese tritylodonts in IVPP, Beijing and Zigong Dinosaur Museum, Sichuan, except for *Oligokyphus*. They are; the type specimen of *Bienotherium yunnanense* (IVPP-V1, an almost complete skull and lower jaw from Lufeng, Yunnan), the upper cheek teeth dentition of *B. yunnanense* prepared to showing root system (V8537 from Lufeng, Yunnan), a non-catalogued well preserved skull of *Bienotherium* sp., the specimens referred to *Lufengia delicata* prepared to showing root system (V8538-8542 from Lufeng, Yunnan), the Xinjiang materials of *Bienotheroides zigongensis* which are prepared to showing root system (V7911, 7912, 8545), the type specimen of *Yunnanodon brevirostre* (V5071, an almost complete skull from Lufeng, Yunnan) and the type specimen of *Dianzhongia longirostrata* (V5072, an almost complete skull from Lufeng, Yunnan), in the former institute, and the type specimen of *Polistodon chuannanensis* (ZDM8601, an almost complete skull and lower jaw in occluding position), in the latter museum.

We brought casts of four Shiramine fossils to China. All four fossils are of the lower

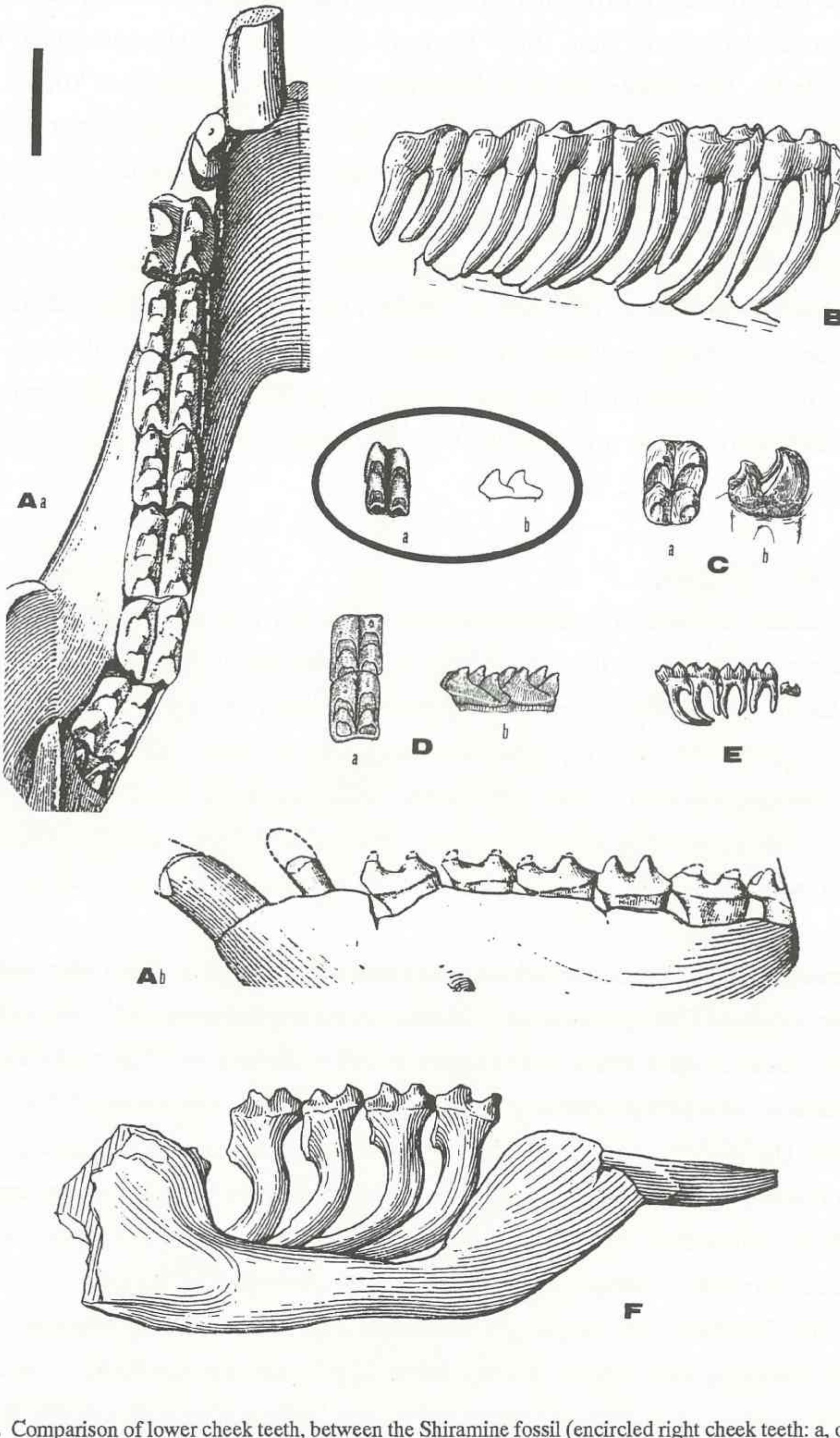

Figure 4. Comparison of lower cheek teeth, between the Shiramine fossil (encircled right cheek teeth: a, occlusal view; b, lingual view, anterior to the right) and Chinese members. A. *Bienotheroides wansienensis*: a, occlusal view; b, buccal view, anterior to the left; from Sun (1984). *B. Bienotherium yunnanense*: buccal view of the right dentition with root system, anterior to the right; from Cui and Sun (1987). C. *Bienotherium elegans*: a, occlusal view; b, lingual view, anterior to the left; from Young (1947). D. *Polistodon chuannanensis*: a, occlusal view; b, buccal view, anterior to the left; from He and Cai (1984). E. *Lufengia delicata*: buccal view of the left dentition with root system, anterior to the left; from Cui and Sun (1987). F. Right dentition of *Bienotheroides zigongensis*, with root system; anterior to the right; from Cui and Sun (1987). Scale bar is 1cm long.

cheek teeth. Direct comparison provided notable information on the taxonomical position of Shiramine fossils.

Shiramine fossils versus Chinese members (Figure 4)

Comparisons especially size examination in below based the larger specimens, SBEI-023, 053 and 056 at this stage, because the biological relationship between the two size groups should be made sure in future study.

Though we could not observe the original specimen of *Oligokyphus*, the unique cusp arrangement consisting of six or eight cusps distinguishes this genus from all other tritylodonts including Shiramine fossils, which have only four cusps fundamentally. And, *Oligokyphus* is a relatively small member. Therefore fossils from Shiramine are never identical with *Oligokyphus*.

Chinese tritylodonts can be classified into two groups by its size. The larger group, size of small dog to raccoon, includes *Bienotherium*, *Polistodon* and *Bienotheroides*. The smaller group, size of ferret to rat, includes *Lufengia*, *Yunnanodon*, *Dianzhongia* as well as *Oligokyphus*. The size distinguishes Shiramine tritylodont from the smaller members, and connects it to the larger members.

All the larger members, *Bienotherium*, *Polistodon* and *Bienotheroides* have four cusps, two in two rows, on the lower cheek teeth, same with Shiramine fossils. However, the detailed morphology may tell that the closest relative of Shiramine tritylodont is *Bienotheroides* among the three genera.

Bienotheroides has lower cheek teeth whose cusps are well expanded and the posterior slopes encircled by crescentic ridge are small. Anterior two cusps are much larger than the posterior ones. The lateral views of cusps show simple and high mountain shape.

The upper and lower dentition on type specimen of *Polistodon chuannanensis* have been glued in occluding position after the original description by He and Cai (1984), so we could not observe the occlusal surface of crown, but only the lingual and buccal are exposed. The posterior terminations of crescentic ridge of two anterior cusps extend far posterior, covering the most of the posterior cusp in the cingulum. Judging from the sketch by He and Cai (1984), in contrast that the anterior two cusps are buccolingually wide, posterior two cusps are smaller and surrounded by the posterior extension of crescentic ridge of anterior cusp, what are significant to *Polistodon chuannanensis*. On the other hand, some characters of *Polistodon chuannanensis*, such as the cusp heights not different between the anterior and posterior ones and the bent posterior margins of the crescentic ridges in the lateral view, may indicate that *Polistodon chuannanensis* is in the closer relationship to Shiramine fossils more than *Bienotherium*.

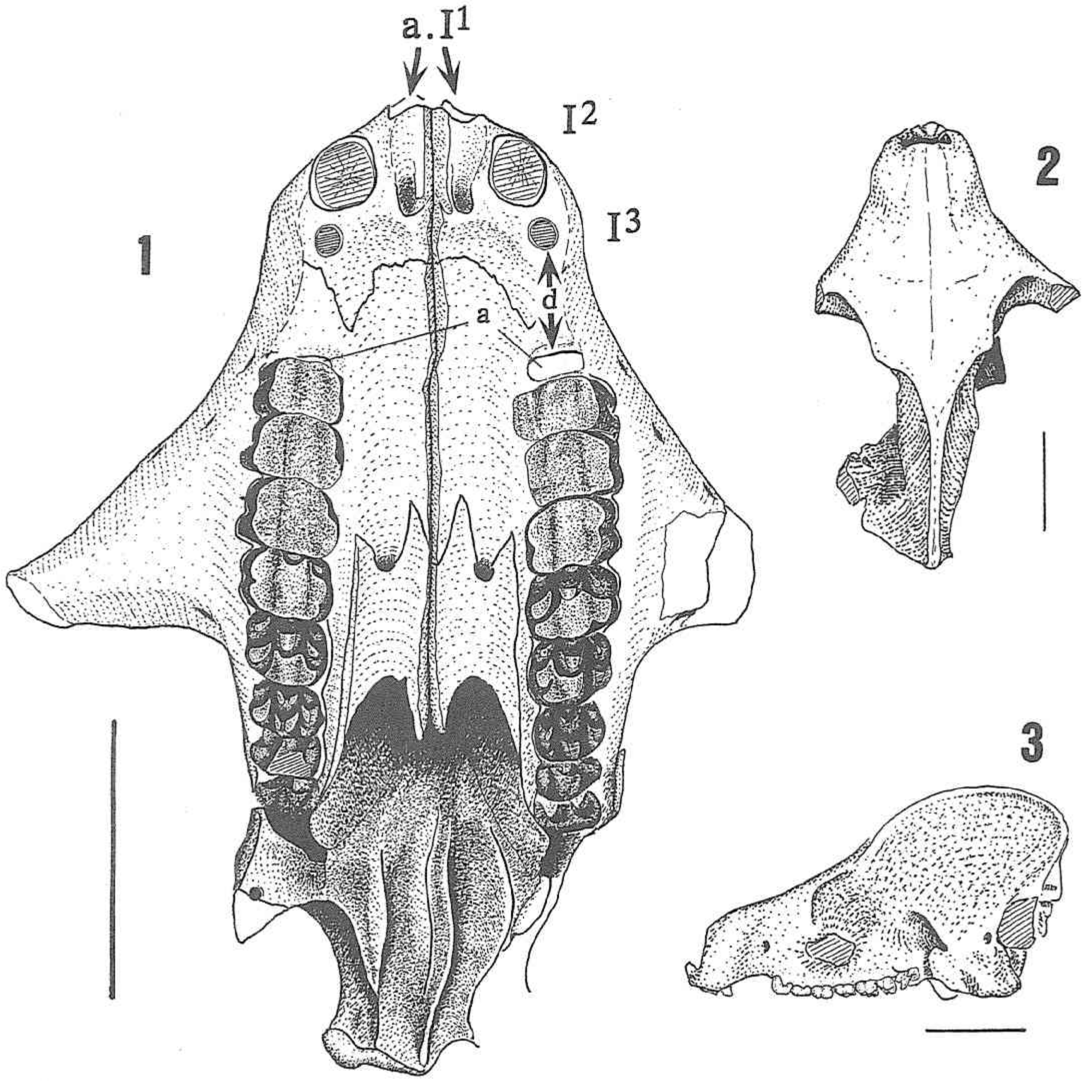

Figure 5. An undescribed specimen of *Bienotherium* sp. housed in IVPP, Beijing. 1, ventral view; 2, dorsal view; 3, left lateral view. Abbreviations are; a, alveoli; a.I1, alveoli for the first incisors; d, diastema; I2 and I3, the second and third incisors. Scale bar is 3 cm long.

It is *Bienotheroides* that was assumed to be the closest relative of Shiramine tritylodont among the Chinese members. The lower cheek teeth of *Bienotheroides* have four cusps of the same size, and the cusps are buccolingually flattish and antero-posterior connection of cusps in a cusp row is straight. Groove between cusp rows is V-shaped and deep correspondingly. Crescentic ridges are sharp and the encircled posterior slope of cusps is concave. On the other hand, though Shiramine fossils have small expansion in the termination of crescentic ridges of anterior cusps in the anterior side of posterior cusps, *Bienotheroides* do not have such structure. In *Bienotheroides*, the lateral view of cusps is rather simple mountain shape, different from Shiramine fossils.

Bienotheroides has formerly been the youngest member among the Tritylodontidae, so it is reasonable to assume that the Shiramine fossils are almost identical to this genus. Continuous investigation is requested to reach the taxonomical question whether the miner differences between the two are big enough to establish a new genus for Shiramine fossils independent from *Bienotheroides* or not.

A perspective on the evolution of cheek teeth replacement in tritylodont

One of the synapomorphies shared by advanced cynodonts including Mammalia is the reduced rate of tooth replacement (Kemp, 1983). In mammals, molars are monophyodont, and premolars are diphyodont. In the case of the tritylodonts, *Oligokyphus*, at least, seems that it did not have endless polyphyodont system because the younger tooth in posterior end of the cheek teeth dentition is clearly smaller than the anterior teeth (Kuhne, 1956).

However, in the collection of IVPP, Beijing, we recognized a specimen of *Bienotherium* that indicates a unique polyphyodont system in that animal. It is very important to understand the system of teeth replacement for the purpose of taxonomy because Shiramine fossils are isolated single teeth. So, though we still have many problems to solve, we note the observations and expected model primary.

An non-cataloged specimen of IVPP (Figure 5)

The specimen figured in Figure 5 is a specimen housed in IVPP, which do not have any information except the rough identification saying "*Bienotherium* sp." Even the locality is uncertain.

This "*Bienotherium* sp." specimen is slightly larger than the type specimen of *B. yunnanense*. Also the color of specimen, in contrast to the pale brown type specimen of *B. yunnanense*, the "*Bienotherium* sp." specimen is reddish, and the tendency is similar to the type specimens of *Yunnanodon brevirostre* and *Dianzhongia longirostrata*. Because fossil assemblage of Lufeng originate from two horizons, the coloring of the specimen might be useful for taxonomical purpose. Luo and Wu (1994) reported that only *B. magnum* occur from the upper Dark Red Bets as well as the small members including *Yunnanodon brevirostre* and *Dianzhongia longirostrata*, though the other *Bienotherium* species are known the lower Dull Purplish Beds. Therefore, we assume that this specimen is of *Bienotherium magnum* Chow, 1962.

Even though the zygomatic arches are missing and the basal part of the buck of skull is crushed, this specimen is of very well preserved, with no transformation by diagenetic pressure, especially in the sagittal crest to snout and palate.

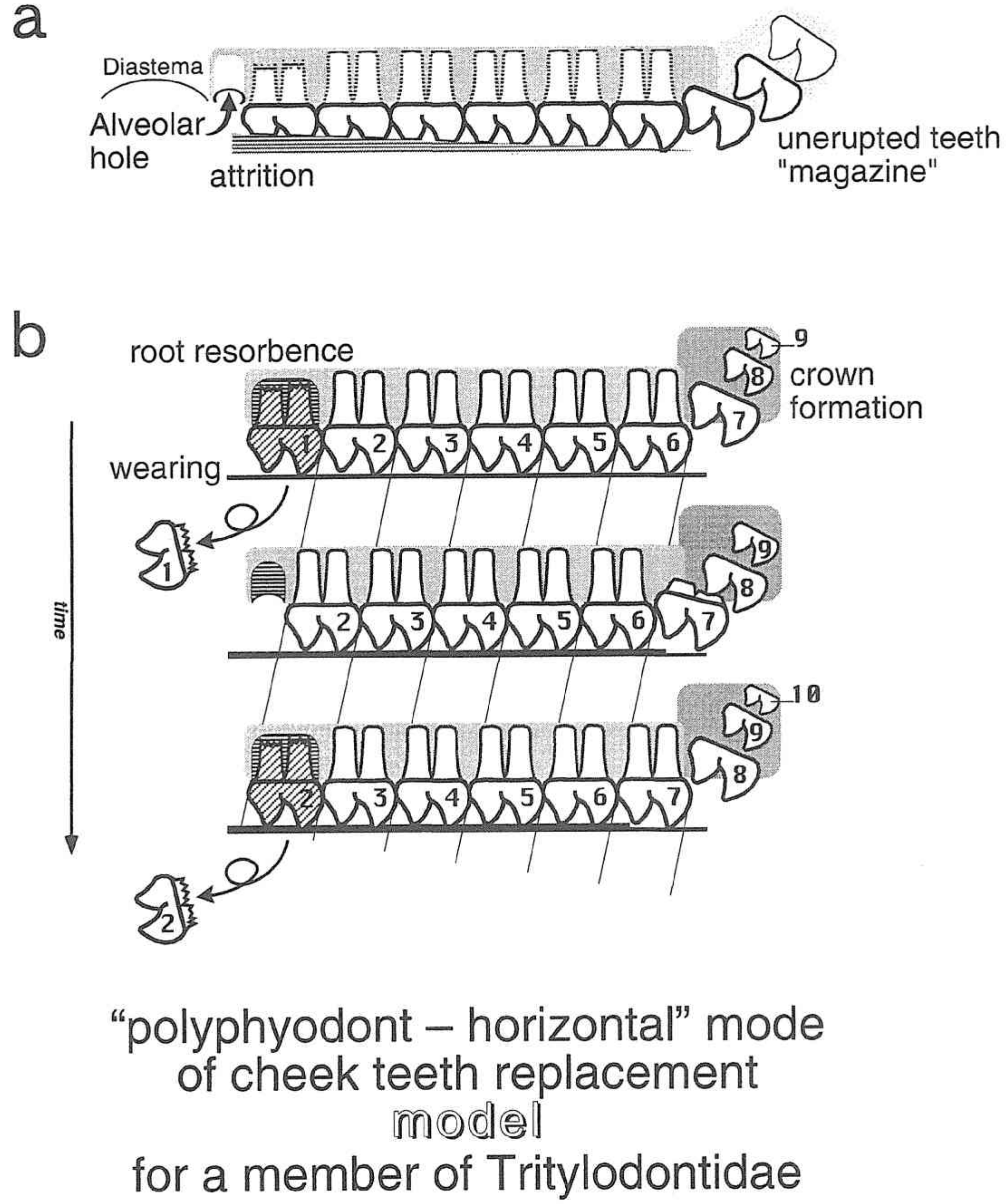

Figure 6. Schema of the Figure 5 undescribed specimen of *Bienotherium* sp. (a), and model for the "polyphyodont – horizontal" mode of cheek teeth replacement provided from the specimen (b).

There are evidences of three incisors in one side, but all are missing or broken and so the morphology in not observable. The first proximal incisors had come out before the deposition, but the sockets indicate that they were facing anterior strongly. The second incisors are extremely larger than the other two and canine-like.

Both right and left dentition consists of eight cheek teeth. In contrast the heavily worn teeth in anterior, posterior teeth gradually have lower degree of wear, and the most posterior two do not have any wear facets. The posterior cheek teeth that have low degree of wear show that a tooth begins to be worn from the groove side of the apex of posterior cusps, that means a tooth joins the occlusion from the posterior part. The attrition surface, even in the posterior teeth whose cusps are all worn away, has significant two grooves that are the vestiges of two grooves in between the three cusp rows, and was carved by the two cusp rows of the lower cheek teeth. The alveoli, that are in the anterior of cheek teeth dentitions and must be the sockets for cheek teeth coming out, have different sizes between the right and left; the one in the right dentition is very short and mere a slit, the left one has about a half length of antero-posterior diameter of one cheek teeth that are in line posterior. Correspondingly, the left cheek teeth dentition locates more posteriorly than the right one, with the length of half of one tooth. But diastemata, when they are measured between the posterior margin of socket of the third incisor and anterior margin of cheek tooth alveolus, have little differences. In the anterior teeth, the cervical lines as well as the continuative vast attrition surface are in a horizontal plain, but the posterior teeth imbricate with appearance that the anterior margin going to the posterior part of the neck of anterior next tooth. Gradually the teeth pile up posteriorly in the skull, and finally, the dentition has a magazine of unerupted teeth in the posterior-most part.

Propositional model for teeth replacement system of a tritylodont (Figure 6)

The specimen of *Bienotherium* sp. aff. *B. magnum* shown in Figure 5 provides a model for the system of teeth replacement. The anteriorly well-worn dentition means the posterior attendance of younger tooth. Unerupted teeth are piling up like bullets in magazine in the posterior-most part of the dentition, and subsequently attend occlusion. Because the antero-posterior diameters of cheek teeth alveoli are different between the right and left, and, even though the animal is homodont, the alveoli are too small to be the sockets of one cheek teeth, it is possible to assume that the cheek teeth dentition moved anteriorly to reclaim the alveolar hole. It seems that the reclamation of alveolar progress chiefly from the cheek teeth dentition side and diastema side act little, because diastemata are almost equal in length.

This animal had, it seems, "polyphyodont – horizontal" mode of cheek teeth replacement with the sequence of;

1. The continuous production of cheek teeth in the posterior-most part of dentition.
2. Attend occlusion from the "magazine of unerupted teeth".
3. With the falling off of the anterior-most cheek tooth, dentition shifts anteriorly while wear is going on, to reclaim the alveolus.

Posterior addition of younger cheek teeth is widely seen in advanced cynodonts. *Oligokyphus*, a primitive (Clark and Hopson, 1985) tritylodont, also shows the addition of younger cheek teeth in the posterior, but do not have endless polyphyodont system. *Bienotherium* sp. aff. *B. magnum* might have evolved the polyphyodont system secondary.

This is the first known example that a reptile has horizontal mode of cheek teeth replacement, if the model is correct. Some herbivorous mammalian members such as elephants, manatees and extinct desmostylians have horizontal mode of teeth replacement. Tritylodonts and herbivorous mammals converged in the mode of teeth replacement, as well as the gigantism that provide effective digestion, on the process to promoting herbivory.

The cheek dentition of tritylodont is homodont, so it is essentially difficult to estimate the phylogenetic changes in it. But, at least, it is highly probable that the matured individual of advanced tritylodont was sending its life with frequent opportunities losing the cheek teeth of same shape and same size. The fact is very suggestive for the taxonomical and paleoecological investigation of Shiramine fossils that are teeth, which have been found isolatedly.

Conclusions

The following two points must be mentioned as the conclusions of our discussions.

1. After the comparison between the most of the Chinese tritylodonts, the fossils from the Lower Cretaceous Kuwajima Formation, Tetori Group of Shiramine, Ishikawa, Japan were identified to *Bienotheroides* or the close relative. *Bienotheroides* is the middle (late Middle - early Late) Jurassic member having the fossil occurrence from Sichuan and Xinjiang.
2. At least a member of the tritylodonts (*Bienotherium* sp. aff. *B. magnum*) was suggested that it had "polyphyodont – horizontal" mode of cheek teeth replacement. Convergence on the post-canine teeth replacement between the herbivorous mammals and tritylodonts is probable.

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References

Chow, M. C., 1962: A Tritylodont specimen from Lufeng, Yunnan. Vertebrata PalAsiatica, vol. 6, p. 365-367.

Chou, M. and Hu, C., 1959: A new tritylodontid from Lufeng, Yunnan. Vertebrata PalAsiatica, vol. 3, p. 9-12.

Clark, J. M. and Hopson, J. A., 1985: Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of Tritylodontidae. Nature, vol. 315, p. 398-400.

Cui, G., 1976: *Yunnania*, a new tritylodont genus from Lufeng, Yunnan. Vertebrata PalAsiatica, vol. 14, p. 85-90, with 1 plate.

Cui, G., 1981: A new genus of Tritylodontoidea. Vertebrata PalAsiatica, vol. 19, p. 5-10, with 1 plate.

Cui, G. H., 1986: *Yunnanodon*, a replacement name for Yunnania, Cui, 1976. Vertebrata PalAsiatica, vol. 24, p. 9.

Cui, G. and Sun, A., 1987: Postcanine root system in tritylodonts. Vertebrata PalAsiatica, vol. 25, p. 245-259, with 2 plates.

He, X. and Cai, K., 1984: The tritylodont remains from Dashanpu, Zigong. Journal of Chengdo College of Geology, Supplement 2, Special paper on dinosaurian remains of Dashanpu, Zigong, Sichuan (II), p. 33-45, with 2 plates.

Hopson, J. A. and Kitching, J. W., 1972: A revised classification of cynodonts (Reptilia, Therapsida). Palaeontologia Africana, vol. 14, p. 71-85.

Kemp, T. S., 1983: The relationship of mammals. Zoological Journal of the Linnean Society, vol. 77, p. 358-384.

Kuhne, W. G., 1956. The Liassic Therapshid *Oligokyphus*. British museum (Natural History). London, 149p.

Luo, Z. and Sun, A., 1993: *Oligokyphus* (Cynodontia: Tritylodontidae) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China. Journal
of Vertebrate Paleontology, vol. 13, p. 477-482.

Luo, Z. and Wu, X., 1994: The small tetrapods of the Lower Lufeng Formation, Yunnan, China. In Fraser, N. C. and Sues, H-D. eds., In the shadow of the dinosaurs, p. 251-270. Cambridge.

Setoguchi, T., Matsuoka, H. and Manabe, M., 1998; "A mammal-like reptile discovered from the Lower Cretaceous of Tetori Group." Abstract of the 1998 Annual Meeting, p. 53. The Palaeontological Society of Japan.

Sues, H-D., 1985: The relationship of the Tritylodontidae (Synapsida). Zoological Journal of the Linnean Society, vol. 85, p. 205-217.

Sun, A., 1984: Skull morphology of the tritylodont Genus *Bienotheroides* of Sichuan. Scientia Sinica (Series B), vol. 27, p. 970-984.

Sun, A. and Cui, G., 1986: A brief introduction to the Lower Lufeng saurischian fauna (Lower Jurassic: Lufeng, Yunnan, People's Republic of China). In Padian, K. ed., The beginning of the age of the dinosaurs: Faunal change across the Triassic-Jurassic Boundary, p. 275-278. Cambridge.

Sun, A. and Cui, G., 1989: Tritylodont reptile from Xinjiang. Vertebrata PalAsiatica, vol. 27, p. 1-8.

Sun, A. and Li, Y., 1985: The postcranial skeleton of the late tritylodont *Bienotheroides*. Vertebrata PalAsiatica, vol. 23, p. 135-151.

Sun, A., Li, J., Ye, X., Dong, Z. and Hou, L., 1992: The Chinese fossil reptiles and their kins, 260 p. Science Press, Beijing.

Tatarinov, L. P. and Matchenko, E. N., 1999: A find of an aberrant tritylodont (Reptilia, Cynodontia) in the

Lower Cretaceous of the Kemerovo region. Paleontological Journal, vol. 33 (4), p. 422-428.
Young, C., 1940: Preliminary notes on the Mesozoic mammals of Lufeng, Yunnan, China. Bulletin of the Geological Society, China, vol. 20, p. 93-111.
Young, C., 1947: Mammal-like reptiles from Lufeng, Yunnan, China. Proceedings of Zoological Society, London, vol. 117, p. 537-597.
Young, C., 1974: "New material of therapsids from Lufeng, Yunnan. Vertebrata PalAsiatica, vol. 12, p. 111-114.
Yang, Z., 1982: On a *Bienotherium*-like tritylodont from Szechuan, China. Selected works of Yang Zhongjian, p. 10-13. Science Press, Beijing.