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Enantiornithine Bird with Diapsidian Skull and Its Dental Development in the Early Cretaceous in Liaoning, China

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Abstract A large number of enantiornithine birds are discovered from the Early Cretaceous Jiufutang Formation in western Liaoning, China. They are all small-sized birds with a few small teeth. The enantiornithine bird from the Jiufutang Formation in the Shangheshou area, Chaoyang, Liaoning Province reported in this paper is the largest individual known in all enantiornithine birds of the Early Cretaceous. However, its teeth possess a feature of pseudoheterodont. Some different development stages of the new teeth substitute the earlier stages and the stages of development are preserved in this specimen. This development pattern is similar to that of *Archaeopteryx* and alligator but not dinosaur. A well-developed postorbital was also preserved in the skull, which was a diapsidian skull like that of *Confuciusornis*. Additionally, the distinctive preservation of its prefrontal distinguishes it from other enantiornithine birds of the Early Cretaceous.

Key words: Early Cretaceous, enantiornithine, dental development, *Aberratiodontus wui*

1 Introduction

Western Liaoning of China is an important locality of Mesozoic fossils (Ji et al., 2003; Xu et al., 2003; You et al., 2003a and b; You and Dong, 2003; Zhang, 2003). A large number of fossils of enantiornithine birds discovered in the Jiufutang Formation of the Early Cretaceous in western Liaoning, China (Sereno and Rao, 1992; Hou, 1994; Zhou, 1995; Hou, 1997; Hou et al., 1999a; Zhang et al., 2001) revealed small-size birds with a few small teeth. An enantiornithine bird discovered from the Jiufutang Formation in the Shangheshou area, Chaoyang, Liaoning Province is not only the largest individual bird among all known enantiornithine birds of the Early Cretaceous, but also have teeth possessing properties of pseudoheterodont. Additionally, evidence showing different stages of new teeth development and substituting the earlier ones is preserved in this specimen. The teeth pattern is very similar to that of *Archaeopteryx* and Alligator, but different from that of Dinosaurs (Martin, 1991; Martin and Stewart, 1977). Moreover, this bird has a diapsidian skull in which a well-developed postorbital is preserved. This feature is similar to that of *Confuciusornis*. The distinctive preservation of the prefrontal is also unique. It differs from any other enantiornithine birds of the Early Cretaceous period. These discoveries indicate that the diversification of the bodily form and ecological pattern of enantiornithine birds had completed before the Early Cretaceous.

2 Systematic Description

Aves Haeckel 1858

Enantiornithes Walker 1981

Aberratiodontuiformes ord. nov.

Aberratiodontuidae fam. nov.

Aberratiodontus gen. nov.

Aberratiodontus wui sp. nov.

Etymology: The species name is dedicated to Professor Wu Qicheng, who is devoted to the paleontological research of Liaoning Province and the genera name refers to the features of the teeth in this bird.

Holotype: A nearly completely articulated skeleton on the main part and counterpart slabs with feather impression; Collection Number of the Department of Land and Resources of Liaoning Province: LHV0001a, LHV0001b.

Horizon and locality: Jiufutang Formation (Early Cretaceous); Shangheshou, Chaoyang County, Liaoning Province, China.

Fig. 1. *Aberratiodontus wui* gen. et sp. nov, Photograph of the holotype, LHV0002.
Co – coracoid; Fu – furcula; Sc – scapula; Hu – humerus; Ra – radius; St – sternum; Ul – ulna

Fig. 2. The skull of *Aberratiodontus wui*.

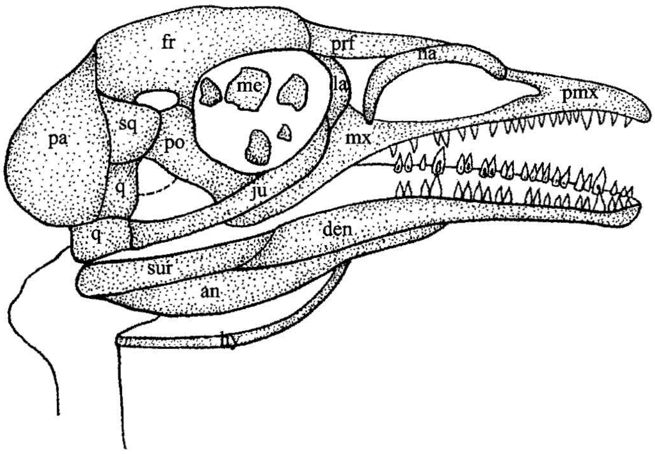

Fig. 3. The skull line drawing of *Aberratiodontus wui*.
Abbrreviations: an – angular; den – dentary; fr--frontal; hy – hyoid; ju – jugal; la – lacrimal; me–mesethmoid; mx – maxilla; na – nasal; pa – parietal; pmx – premaxillary; po – postorbital; prf--prefrontal; q – quadrate; qj – quadratojugal; sq – squamosal; sur – surangular

Diagnosis: The holotype is a primitive enantiornithine bird about twice as large as *Longipteryx* (Zhang et al., 2001). The skull is situated lower and has a well-developed postorbital. The quadrate is like a pillar at the lower region and expanded in the upper region. The furcula differs from that of any other known enantiornithine birds (Sanz et al., 1995; Sanz and Chiappe, 1996), and is similar to that of *Confuciusornis* (Hou et al., 1999b) or *Archaeopteryx* (Martin, 1995); but its clavicular branch is longer than those of other known enantiornithine birds. The lateral process of the coracoids is well-developed at the distal end and the scapula is curved externally at the distal end, which differs from that of *Confuciusornis* and *Archaeopteryx*. The fact that this bird has the largest number of teeth (up to 21 teeth on the lower jaw of each side) among all of the known early birds is significant. The rows of teeth show characteristics of pseudoheterodont and set it apart from those of the other early birds. The teeth on the rostral side are thin and fine, and the front cheek teeth are very large, like "dentes canini", and then like *Eoenantiornis* (Hou et al., 1999a), the middle cheek teeth become smaller, and the biggest teeth are in the back. Additionaly, on the rows of teeth there are some new teeth in different developmental stages. The new teeth grew out of the insides of the rows of teeth, which is similar to what was found in *Archaeopteryx* (Martin, 1991; Howgate, 1984) and crocodilian (Cong et al., 1998).

Measurements of holotype (mm): The skull length of *Aberratiodontus wui* 58.7; height 28.9; length of neck 88; length of the clavicular branch 27.5; length of coracoid 31; length of scapula 53; length of femur 55; length of tibiotarsus 66.7; length of tarsometatarsus 33; length of pygostyle 24.5; length of the pubic bone 43.

Description: *Aberratiodontus wui* is larger and stronger than any other known enantiornithine birds. Like other early enantiornithine birds, the proximal tarsometatarsus is fused but the carpometacarpus of the forelimb is not formed. Another unique feature is that the postorbital and prefrontal are well-developed in the skull and the large number of teeth with pseudoheterodont characteristics.

The skull of *Aberratiodontus wui* is nearly completely preserved. The nasal process of the premaxilla is long, and the damaged nasal is between the premaxila and the prefrontal, the external surface of which is spread to the front then downward. The lacrimal bone, an irregular sclerite, occurs in the posterolateral of the nasal. Another difference it bears from other known early enantiornithine birds is that *Aberratiodontus wui* has a pair of well-preserved prefrontals between the nasal and the frontal bone.

Like *Confuciusornis* and *Protopteryx* (Zhang and Zhou, 2000), *Aberratiodontus* has a well-developed postorbital. It is clear that the postorbital had contact with the squamosal. The relation between the jugal and postorbital is not clearly observed because the jugal bone was displaced and the descent branch of postorbital was not preserved completely. However, the postorbital appears to be connected with the jugal bone with a long and descent branch, therefore, it still can be concluded that *Aberratiodontus wui* has a diapsidian skull. The anterior extremity of the jugal bone, being relatively wide, connects to the posterior process of maxillary bone. The preorbital fossa of *Aberratiodontus wui* is quite large, and the inferior maxilla is strong. The dentary bone is straight, about 2/3 the length of the entire lower jaw. The posterior region of the dentary bone is curved ventrally, which is a general characteristic of birds (Fig. 2, 3).

The dentition of *Aberratiodontus wui* is the most representative among the early enantiornithine bird. There are no less than 21 teeth on each side of the maxilla. The diastema is small. From the rostral side to the end of the dentition, the sizes of teeth are greatly varied. The teeth on the rostral site are thin and fine, followed by a large dentes canini. The next 6 teeth are small, followed by larger teeth; and at the end there are 4 or 5 largest teeth. *Confuciusornis* and *Archaeopteryx* (Elzanowski and Wellnhofer, 1995) do not have these characteristics. Additionally, the radix clinica of the bird is thicker than corona dentis and twice as long as corona dentis. The cervix dentis is notably like that of *Archaeopteryx*, the apex corona dentis slopes posteriorly, and the teeth are tightly arranged. The radix clinica is a result of a broken bone exteriorly. The growth of the teeth is clearly observable. The process is surprisingly similar to that of *Alligator sinensis* teeth growth (Cong et al., 1998). There are some large and small punctum and impressions of the fenestra radicularis linguolis on the radicularis lingualis side of some teeth. The fenestra resulted from new teeth continually forming and growing, but no new teeth are found in the structure of the fenestra. The growth of new teeth can be observed from the fenestra radicularis lingualis. The corona dentis was formed first, and then, a new tooth (replacement tooth) appeared on the lingual side of the old radicis dentis. With its gradual growth, the new tooth eroded the wall of the lingual side of the old radicis dentis. The wall gradually thinned until it was perforated, after which the new tooth migrated to the cavitas radicis dentis from the fenestration, followed by the gradual growth of the new tooth corona dentis. After that, the cervix dentis began to appear during the formation of the base of corona dentis. Following the genesis of cervix dentisis, the old teeth were pushed out as the cervix dentis grew. Finally, the new teeth replaced the old ones in situ. In brief, the teeth growing period of *Aberratiodontus* can be divided into 4 stages which are the no fenestra period (embryo bud period), the perforation period (period of forming corona dentis), the fenestration period (period of forming tooth), and the replacement period (old teeth were replaced when new teeth matured).

The neck of the bird is longer than that of any other known birds of the Early Cretaceous (Feduccia, 1999). There are 11 cervical vertebrae and the vertebra is relatively long with well-developed pleurocoels. The neural spine is low, and the cervical vertebra becomes short and gradually grows toward the back. The thoracolumbar vertebrae are short but high with big and deep pleurocoels on the lateral side; its ventrolaternal is flat; and the middle part is narrow but wide at the two ends. The features mentioned above are similar to those of some modern raptorial birds. The pygostyle was formed like the other early enantiornithine birds. The sternum is rather developed, but similar to that of early enantiornithine birds, which is cake-shaped of nearly equal length and width with a pair of lateral processes. The keel is not well developed. There are costa ventralis.

Compared to other enantiornithine birds, *Aberratiodontus wui* has some special structures in the thoracic girdle, such as the furcula being of U-shape rather than V-shape (Hou, 1997), a long clavicular branch, and an unclear furcula process. These structures are similar to those of *Confuciusornis* and *Archaeopteryx*. The most obvious feature of the coracoid is its well-developed lateral process at the distal end. Only *Protopteryx fengningensis* (Zhang and Zhou, 2000) developed lateral process of coracoid in the early birds. Additionaly, the scapula of *Aberratiodontus wui* is long and wide and sharply curved externally from the middle to the end. This is an unusual feature in the early birds. *Aberratiodontus* sternum, like board, is similar to other early Cretaceous enantiornithine birds and has a well-developed lateral processes and a posterior process. The carina is not well developed. The sternum is in the ratio of approximately one to one in length to width with width even bigger than length.

The humerus is strong and the sternum pectorale is extremely well developed; the proximatal end is curved towards the inside and the dorsal ankle of distal end is especially big like other early enantiornithine birds. The humerus is shorter than the ulna, which differs from that of *Confuciusornis* of the earlier period. The ulna and radius are also strong. The ulna is nearly twice as wide as the radius and there is a small olecranon at the proximal ulna. There are two lentiform carpals at the distal end of theulna and radius, which is an indication of primitive structure. The matacarpal and the digit were not completely preserved, but it is clear that the complete carpometacarpus was not formed in light of the two preserved claws of phalanx.

The pelvis is relatively small; the pubis is well preserved; the pubises are fused in the distal end without a long pubic foot, which differs from that of other enantiornithine birds (Zhou, 1995). Similar to other enantiornithine birds, however, *Aberratiodontus wui* is the shorter length of the femur in comparison to the tibiotarsus. Differing from other enantiornithine birds, the tarsometatarsus of *Aberratiodontus wui* is short, only half the length of the tibiotarsus. The phalanges of toes are long, but their claws are short and strong.

3 Comparison and Discussion

Since many small enantiornithine birds were discovered from the Early Cretaceous in China, it is believed that there is an evolutionary tendency in the size of an individual, i.e. transforming from big to small size in early birds (Hou et al., 1999b). However, all *Longipteryx* (Zhang et al., 2001) and *Aberratiodontus* discovered from the Chaoyang area in the same time period are larger than *Cathayornis*. The discovery of larger birds, such as *Aberratiodontus*, indicates that a diverse evolution of birds in terms of size took place in the Early Cretaceous. The diversification had surely been completed in the initial stages of the evolution of the bird. Therefore, the origin of enantiornithine bird should be earlier than what we previously had believed. The toe claws of *Aberratiodontus* are not well developed compared to that of *Longipteryx*. It shows that *Aberratiodontus* had little power to grip trees. It was therefore probably not a truly arboreal bird. The somatotype of birds, either big or small, is closely related to their ecological type. Based on its large body, *Aberratiodontus* should be a kind of bird with weak flying capability. *Longipteryx* was obviously a bird that ate aquatic creatures, especially fish, while *Aberratiodontus* held hunting behavior for terrestrial creatures based on the long proboscis. Both of the birds are very different from *Cathayornis*. It can be concluded that two ecological patterns of arboreal birds and terrestrial birds existed at least in the Early Cretaceous, and this ecological diversification of the structures of birds occurred in the Early Cretaceous.

Confuciusornis is the only one that had developed postorbital as well as a complete diapsidian skull in the birds from the Mesozoic (Hou et al., 1999b; Chiappe et al., 1999). *Protopteryx* (Zhang and Zhou, 2000) from the Yixian Formation in Fengning, Hebei Province, China, preserves a 'Y'-shaped postorbital as well. *Protopteryx* should be a bird in the lowest horizon of the Mesozoic in China. Based on the shape of postorbital, *Protopteryx* should have a diapsidian skull. Among all birds from the Early Cretaceous, only one skull specimen from El Montsee, Spain in addition to China, possesses a reduced postorbital without contacting with jugal bone (Sanz et al., 1997). This indicates that the bird, like the modern birds, did not possess diapsidian skull. The postorbital of *Aberratiodontus*, which clearly contacts with squamosal, is developed as *Confuciusornis*. Although the relation of postorbital to jugal bone is not observed for lacking of the posterior jugal, it is clear that the postorbital could contact with jugal bone as well by having a process bent down. Therefore, *Aberratiodontus* like *Confuciusornis* should also have diapsidian skull (Fig. 1). The enantiornithine birds from the Jiufutang Formation in the Early Cretaceous in China are earlier and with a more complex structure than the Spain birds (Sanz et al., 1997).

Although *Aberratiodontus* possesses a well-developed postorbital as *Confuciusornis* and preserves the ancestor features of the diapsid reptile, its skull shows the evolutionary features which exist only in birds, such as the frontal bone found in both *Aberratiodontus* and *Confuciusornis*. Its frontal bone has greatly expanded toward the brain case and holds the most portion of cerebral cranium. The parietal bone is restricted to the back, while the typical diapsid animals is different. In addition, for *Aberratiodontus* and other early birds, the nasal processes of the premaxillae extend posteriorly a lot and make up the inner wall of the anterior vacuity.

A pair of small prefrontal is preserved behind the nasal in the skull of *Aberratiodontus* and located above the orbit. The combined two pieces of prefrontal appear to be a rhombus. Until now, the prefrontal of any early birds, including *Archaeopteryx* (Martin and Zhou, 1997) and *Confuciusornis,* has never been described. The facts that the prefrontal of *Aberratiodontus* is back in position and simple in structure indicates that *Aberratiodontus* is primitive, and its frontal bone developed to be poorer than that of the modern birds. The skull of *Aberratiodontus* shows characteristics of combining the features of both evolutionary and primitive.

The teeth of *Archaeopteryx* and other Mesozoic birds have been studied by many scientists (Howgate, 1984; Martin, 1991, 1995), which show that the common features of the teeth are homodont and low tooth crown with a contractile tooth neck. The teeth of many Mesozoic birds in China are the same as those of *Archaeopteryx*. However, the teeth of *Aberratiodontus* differ from those of the earlier birds. First, the number of teeth of *Aberratiodontus* is greater, and also the teeth are arranged tightly. Secondly, the teeth are different in size and seem to be pseudoheterodont. Thirdly, because of the good preservation, the growth process of new teeth can be clearly observed. The development process of the teeth of *Aberratiodontus* is very similar to that of the teeth of *Alligator* (Cong et al., 1998). Up to now, no reliable evidence has been observed showing that dinosaurs have such teeth replacement pattern found in *Aberratiodontus* studies (Currie, 1987).

The furcula of enantiornithine birds is featured by a long furcular process and short clavicular branches with a 'V' shape. However, the furcula of *Aberratiodontus* is similar to that of *Archaeopteryx* or *Confuciusornis*; the furcular development is not obvious; clavicular branches are longer; and the furcula is a 'U' shape which is more primary than 'V'-shaped furcula. The shape of coracoid and scapula of *Aberratiodontus* is special among the enantiornithine birds (Fig. 2). The coracoid with a developed lateral process is similar to those of some modern raptorial birds, which shows an advanced feature of *Aberratiodontus*. The scapula is curved toward outside at the distal end, which is also the feature of modern birds and is different from that of any enantiornithine birds known. The sternum shape is the same as that of other enantiornithine birds with a low keel at posterior part of the sternum.

Aberratiodontus is similar in a few aspects to *Yanornis* and *Yixianornis* of Ornithurae which come from the Jiufutang Formation, such as greater number of teeth, furcula of "U" shape, similar proximal humeral (Zhou and Zhang, 2001). Because they belong to different subclasses, the differences of these birds are obvious in the following structure features.

The skull of *Yanornis* is comparatively advanced in that there is no prefrontal, and the skull is not diapsidian. These features are common to Ornithurae. The *Aberratiodontus*

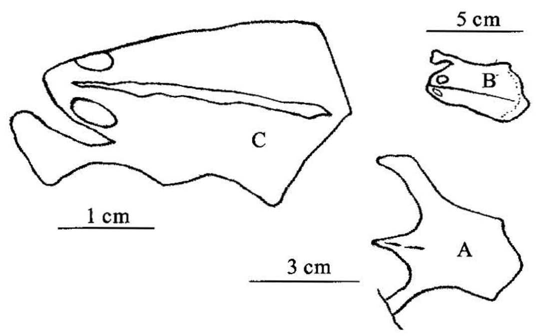

Fig. 4. Comparisons of the sternum in *Aberratiodontus* (A), *Yanornis* (B) and *Songlingornis* (C).

skull, however, is similar to that of *Confuciusornis*, which preserved the prefrontal and diapsidian skull, whereas the features occur in their reptile ancestors only.

Yanornis possesses more advanced features that belong to Ornithurae, for example the coracoid with developed processus precoracoideus, the rotundity and evident cotyla jointed with scapular. Meanwhile the articular surface of coracoid distal end jointed with sternum is very noticeable. To compare the enantiornithine sternal structure with that of early birds of Ornithurae, it is necessary to compare the sternum shapes in detail between *Yanornis* and *Aberratiodontus*. The sternum shape of *Yanornis* is completely the same as that of *Songlingornis* discovered in Bolouci, Chaoyang (Hou, 1997). The sternum of *Yanornis*, with a long, well-developed carina, is bigger in length than in width and the anterior coraco-articular surface is also well developed. There are two circular fenestrae in the posterior sternum. The posterior margin is semicircular with lateral process developed. On the other side, *Aberratiodontus* possesses typical sternum features of early enantiornithine birds. The anterior margin of sternum is semicircular and the coraco-articular surface is not evident. The sternum, shaped like a board, is nearly the same in length to width with the width even bigger than length. The carina almost does not develop but a lower carina occurs in the back sternum with a well-developed posterior lateral process. It is also remarkable that there are differences between the *Aberratiodontus* and *Yanornis* according to the contrast of their sternum. *Aberratiodontus* is completely different in the evolution level although it and Yanornis occur in the same area and at the same time (Fig. 4).

The forelimb of *Yanornis* has developed some features similar to those of recent birds. For examples, the crests of triceps brachii and bicitibal are well developed. Not only are the ventral condylus and dorsal condylus on the distal end of humerus developed well, but also the epicondylus ventralis and epicondylus dorsalis are well developed. In addition, *Yanornis* has developed typical lune dorsal condylus at the distal end of ulna, and the proximate of radius has developed bicipital tubercle. Especially, *Yanornis* has typical carpometacarpus. All the evolutionary features mentioned above do not occur in the forelimb of *Aberratiodontus* and even do not occur in all of early enantiornithine known. On the other hand, the difference of *Yanornis* from *Aberratiodontus* about the posterior limb is that the former has tarsometatarsus developed well and all the metatarsal bones are completely fused each other. Nevertheless, the metatarsal bone of *Aberratiodontus* fuses in the proximate only.

Yanornis possesses comparatively big pelvic girdle with a long pubic foot. *Aberratiodontus* possesses comparatively small pelvic girdle with a short pubic foot.

Yanornis, like *Songlingornis* in teeth, has small and dense teeth as compared with *Aberratiodontus*. Meanwhile, its maxillary teeth are less than the mandible teeth showing a tendency of regression. *Aberratiodontus*, like its name, has many teeth with different sizes. The features of its maxillary teeth and mandible teeth do not show the tendency of regression. As the description mentioned above, all of the growth stages of *Aberratiodontus* teeth are shown above. Therefore the features of the bird tooth are the best displayed of all previous research except *Archaeopteryx*. It is so obvious that *Aberratiodontus* is sharply different from *Yanornis*. After comparing the contracts of their features, it is confirmed that *Aberratiodontus* and *Yanornis* are not the same kind of bird. In fact, *Yanornis* should be the synonym with *Songlingornis* because they are completely the same in tooth and shoulder girdle, especially in sternum.

The information on the missing link of the bird origin, which has never been reported before, has been obtained from studying a large number of Mesozoic birds with complex shapes in various horizons in China, which provides much material for researching in the evolution of the early birds. The discovery of *Aberratiodontus* and *Longipteryx,* one after another, reveals a new ecological type of the Early Cretaceous birds that were considered to be mainly small perching birds.

It would be a new question about the dinosaurian hypothesis of bird origins accepted widely that meet a new challenge.

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