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A NEW ENANTIORNITHINE BIRD FROM THE EARLY CRETACEOUS OF WESTERN LIAONING, CHINA

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Abstract. We describe a new enantiornithine bird, *Huoshanornis huji* gen. et sp. nov., from the Early Cretaceous Jiufotang Formation in Chaoyang, western Liaoning Province, China. This new bird is distinguished from other known enantiornithines in possessing a considerably reduced alular digit, a broad intermetacarpal space, a relatively long phalanx of the minor digit of the manus, and a remarkable triangular expansion at the distal end of the lateral trabecula of the sternum. The morphology of the manus may also suggest that at low flight speeds the new bird's maneuverability was exceptional.

Key words: *Early Cretaceous,* Huoshanornis huji *gen. et sp. nov., enantiornithine, manus, sternum*.

Una Nueva Ave Enantiornitina del Cretácico Temprano del Oeste de Liaoning, China

Resumen. Describimos una nueva ave enantiornitina, *Huoshanornis huji* gen. et sp. nov., de la formación Jiufotang del Cretácico Temprano de Chaoyang, oeste de la Provincia de Liaoning, China. Esta nueva ave se distingue de otras enantiornitinas conocidas por poseer un dígito alular considerablemente reducido, un espacio intermetacarpal amplio, la falange del dígito menor relativamente larga y una notable expansión triangular en el extremo distal de la trabécula lateral del esternón. La morfología del manus también podría sugerir que, a velocidades de vuelo bajas, la maniobrabilidad de esta nueva ave era excepcional.

INTRODUCTION

The Enantiornithes were the most dominant and diverse group of Mesozoic birds and occurred nearly worldwide throughout the entire Cretaceous Period (Chiappe 1995, Feduccia 1996). Although the taxonomy of some taxa is uncertain, or debated, the abundance and absolute number of Enantiornithes excavated from China exceed those from all other countries. To date, more than 20 species have been reported from the Early Cretaceous deposits of Liaoning, Hebei, Inner Mongolia, and Gansu provinces alone (Table 1).

A good deal of research indicates that enantiornithines had undergone extensive differentiation and radiation in size, morphology, habit, diet, and flight capability by the Early Cretaceous. For example, one genus, *Dalingheornis*, is peculiar in possessing a heterodactyl foot (Zhang et al. 2006), the rostral morphology of *Longirostravis* suggests it fed by probing (Hou et al. 2004), and still another, *Pengornis*, the largest yet known, is approximately the same size of the basal bird *Confuciusornis sanctus* (Zhou et al. 2008). The long paired tail feathers reported in the enantiornithines *Protopteryx*, *Dapingfangornis*, *Paraprotopteryx*, and *Shanweiniao* may have had an important role in display as well as a possible aerodynamic function (Zhang and Zhou 2000, Li et al. 2006, Zheng et al. 2007, O'Connor et al. 2009).

In this paper, we describe yet another new specimen from Chaoyang in western Liaoning province. It adds new evidence that enhances our understanding of the morphological diversification of the manus and sternum of the Enantiornithes.

SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758
Enantiornithes Walker, 1981
***Huoshanornis* new genus**
***Huoshanornis huji* new species**

Holotype. An almost complete skeleton preserved in partial articulation (Fig. 1). The specimen is housed at Dalian Natural Museum, collection number D2126.

Locality and horizon. Dapingfang, Chaoyang County, western Liaoning, China. Jiufotang Formation, Early Cretaceous (~120 mya) (He et al. 2004, Zhou and Zhang 2006).

Etymology. From the Chinese pinyin *huoshan*, which means volcano, and *ornis*, from the Greek word for bird. This

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TABLE 1. Enantiornithine birds known from China.

Species	Locality	Horizon	Literature
Sinornis santensis	Chaoyang, Liaoning	Jiufotang Formation	Sereno and Rao 1992
Cathayornis yandica	Chaoyang, Liaoning	Jiufotang Formation	Zhou et al. 1992
Otogornis genghisi	Otog, Inner Mongolia	Yijinhuoluo Formation (corresponds to Jiufotang Formation in western Liaoning)	Hou 1994
Boluochia zhengi	Chaoyang, Liaoning	Jiufotang Formation	Zhou 1995
Longipteryx chaoyangensis	Chaoyang, Liaoning	Jiufotang Formation	Zhang et al. 2001
Eocathayornis walkeri	Chaoyang, Liaoning	Jiufotang Formation	Zhou 2002
Aberratiodontus wui	Chaoyang, Liaoning	Jiufotang Formation	Gong et al. 2004
Dapingfangornis sentisorhinus	Chaoyang, Liaoning	Jiufotang Formation	Li et al. 2006
Alethoalaornis agitornis	Chaoyang, Liaoning	Jiufotang Formation	Li et al. 2007
Pengornis houi	Chaoyang, Liaoning	Jiufotang Formation	Zhou et al. 2008
Cathayornis caudatus	Chaoyang, Liaoning	Jiufotang Formation	Hou 1997
Cathayornis aberransis	Chaoyang, Liaoning	Jiufotang Formation	Hou 1997
Longchengornis sanyanensis	Chaoyang, Liaoning	Jiufotang Formation	Hou 1997
Cuspirostriornis houi	Chaoyang, Liaoning	Jiufotang Formation	Hou 1997
Largirostrornis sexdentornis	Chaoyang, Liaoning	Jiufotang Formation	Hou 1997
Cathayornis chabuensis	Otog, Inner Mongolia	Jingchuan Formation (corresponds to Jiufotang Formation in western Liaoning)	Li et al. 2008
Jibeinia luanhera	Fengning, Hebei	Yixian Formation	Hou 1997
Liaoxiornis delicates	Lingyuan, Liaoning	Yixian Formation	Hou and Chen 1999
Protopteryx fengningensis	Fengning, Hebei	Dabeigou Formation (older than Yixian Formation in western Liaoning)	Zhang and Zhou 2000
Vescornis hebeiensis	Fengning, Hebei	Yixian Formation	Zhang et al. 2004
Longirostravis hani	Yixian, Liaoning	Yixian Formation	Hou et al. 2004
Eoenantiornis buhleri	Beipiao, Liaoning	Yixian Formation	Zhou et al. 2005
Dalingheornis liweii	Lingyuan, Liaoning	Yixian Formation	Zhang et al. 2006
Paraprotopteryx gracilis	Fengning, Hebei	Yixian Formation	Zheng et al. 2007
Shanweiniao cooperorum	Lingyuan, Liaoning	Yixian Formation	O'Connor et al. 2009
Undetermined, CAGS-IG-02-0901	Changma, Gansu	Xiagou Formation (corresponds to Jiufotang Formation in western Liaoning)	You et al. 2005
Undetermined, CAGS-IG-04-CM-007	Changma, Gansu	Xiagou Formation (corresponds to Jiufotang Formation in western Liaoning)	Lamanna et al. 2006
Undetermined, CAGS-IG-04-CM-023	Changma, Gansu	Xiagou Formation (corresponds to Jiufotang Formation in western Liaoning)	Harris et al.2006

generic name reflects the geoenvironmental background of the Early Cretaceous, which is characterized by high rates of volcanism. The species name *huji* represents an abbreviation in Chinese pinyin and refers to the lacustrine deposits characteristic of Jiufotang and Yixian formations in western Liaoning province.

Diagnosis. A bird of moderate size characterized by the following features: intermetacarpal space broad; first phalanx of alular digit greatly reduced, roughly one fourth the length of the carpometacarpus; the single (proximal) phalanx of the minor digit as long as and almost as wide as that of the major digit; lateral trabecula of the sternum slightly shorter than xiphoid process, with a remarkable triangular expansion at its distal end.

Measurements (in mm). Length of the coracoid, 14.1; length of the humerus, 21.3; length of the ulna, 24.5; length of the carpometacarpus, 13.9; length of the proximal phalanx of alular digit, 3.9; length of the femur, 20.8; length of the tibiotarsus, 27.5; length of the tarsometatarsus, 15.5; length of the pygostyle, 9.4.

Description. The skull of *Huoshanornis* is exposed mainly in right lateral view (Fig. 1). Modifications of the skull during preparation prevent a more definite anatomical description, other than to report that the beak is relatively short and straight.

At least seven cervical vertebrae, still articulated, are preserved on the specimen; these are exposed in ventral view. The prezygapophyses, postzygapophyses, and ventral processes are visible, and three dorsal vertebrae are preserved to the right of the proximal end of the synsacrum (Fig. 1). The articular facets of the dorsal vertebrae are flat, and their sides are deeply excavated by large longitudinal fossae. The synsacrum is preserved mainly as an impression, and seven sacral vertebrae can be discerned. At least four disarticulated free caudal vertebrae are present between the synsacrum and the pygostyle; the centra of these vertebrae are obviously shorter than those of the

FIGURE 1. Holotype of *Huoshanornis huji* gen. et sp. nov.

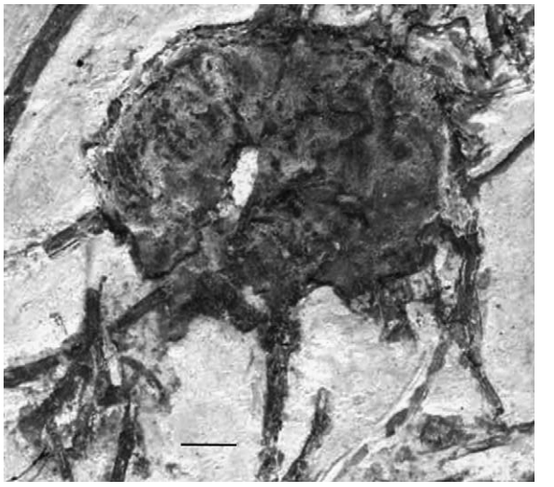

FIGURE 2. Close up of the sternum of *Huoshanornis huji* gen. et sp. nov., Scale bar, 2 mm.

cervical and dorsal vertebrae and possess long caudo-laterally directed transverse processes. The pygostyle is long and deepest proximally; its dorsal and ventral processes are well developed proximally.

The left coracoid is exposed in ventral view, while the right is seen in dorsal view (Fig. 1). This element is short, with a broad sternal articulation. The cranial half is cylindrical, but the omal end offers no detailed anatomical information because of poor preservation. As in other enantiornithines, the caudal half of the coracoid is expanded, with a convex lateral margin. The sternal end lacks a lateral process and is slightly concave, in concordance with the parabolic cranial edge of the sternum. The dorsal aspect of the caudal half of the coracoid is slightly concave.

The left scapula is poorly preserved; it is straight and longer than the coracoid, but the precise length and detailed morphology can not be ascertained.

The furcula is Y-shaped; most of the hypocleideum, the left clavicular ramus, and the lower part of the right ramus are preserved and exposed anteriorly (Fig. 1). As in the majority of enantiornithines (Chiappe and Walker 2002), the hypocleideum is long—nearly 60% the length of the ramus—and is compressed laterally. The cross-section of the left ramus, primarily on the distal half, is L-shaped and caudolaterally excavated. The interclavicular angle is about 60°, similar to that of *Concornis*, *Dalingheornis*, and *Alethoalaornis* (Sanz et al. 1995, Zhang et al. 2006, Li et al. 2007).

The main body of the sternum is nearly square and convex ventrally; there is no clear evidence for the presence of a carina. The cranial margin is parabolic, and the caudal margin is deeply notched, bearing the lateral trabeculae, medial trabeculae and xiphoid process (Fig. 2, 3). The xiphoid process is

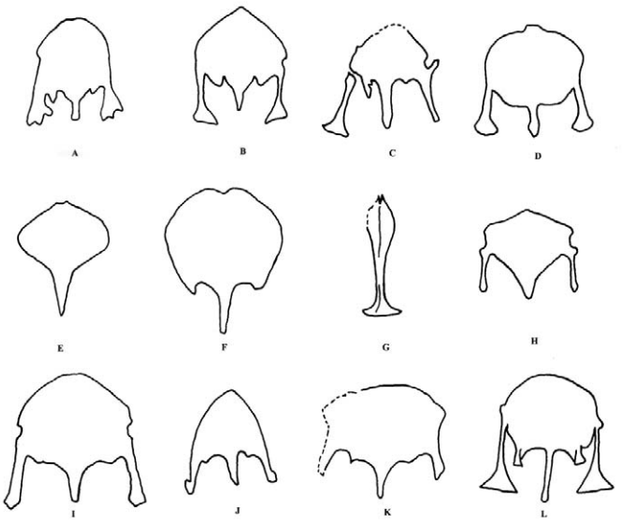

FIGURE 3. Comparison of the sternum of some enantiornithines (drawings not to scale): a, *Longirostravis*; b, *Cathayornis*; c, *Concornis*; d, *Eocathayornis*; e, *Liaoxiornis*; f, *Eoenantiornis*; g, *Eoalulavis*; h, *Protopteryx*; i, *Longipteryx*; j, *Dapingfangornis*; k, *Vescornis*; l, *Huoshanornis*.

elongate, slightly surpassing the distal ends of the lateral trabeculae. The distal ends of the lateral trabeculae have remarkable triangular expansions. The medial trabeculae are short, robust, and nearly triangular. The ribs are preserved in disorder around the sternum, and there is no evidence for ossified uncinate processes.

The humerus is shorter than the ulna. The humeral head is flat proximally. The shaft of the humerus is nearly straight. The proximal end of the humerus is internally curved, with a well developed bicipital crest. The deltopectoral crest is relatively short, extending down just the proximal quarter of the bone. The ulna is more robust than the radius and is bowed for the proximal two-thirds of its length; its caudal margin shows no evidence of papillae for attachment of the secondary remiges. The ulna and radius are separated by a distinct spindle-shaped space. The radius is straight and about 2/3 of the ulna in diameter. The ulnare is nearly rectangular. The radiale and the alular metacarpal can not be discerned. The major and minor metacarpals are nearly the same width as one another and are separated by a broad intermetacarpal space. All manual phalanges are preserved and have a formula of 2-3-1. Compared to that of other enantiornithines, the alular digit of *Huoshanornis* is relatively short, nearly one fourth of the carpometacarpus in length. There are three phalanges in the major digit; the proximal phalanx is slightly longer than the intermediate one, and the claw is similar in size to that of the alular digit. The phalanx of the minor digit is as long as the first phalanx of major digit and only slightly thinner than the latter (Fig. 4).

The elements of the pelvic region, especially the ilium, are not well-preserved. The ischium is about 70% the length of the pubis; it is rodlike with an expanded proximal end and an obvious dorsal process. The pubis is slender and arches laterally. The distal end is not expanded to form a pubic spoon, as in other enantiornithines; there is no pubic symphysis.

The femur is slightly curved craniocaudally. The tibiotarsus is slender, straight, and 130% the length of the femur; development of a cnemial crest is minimal. The fibula can not be observed. Both tarsometatarsi are exposed in cranial view; they are straight and roughly half the length of tibiotarsus. Metatarsals II–IV are fully fused at their proximal ends, while the main body of the metatarsals remains separate. Metatarsal III is the most robust and longest; metatarsal IV is the narrowest, with the distal end curved laterally. Exposed in medial view, metatarsal I is short, J-shaped, and attaches to the distal end of metatarsal II. The distal trochleae of the metatarsals are not on the same level and are of different sizes.

The foot is anisodactyl. The phalangeal formula of the foot is that typical of birds, 2-3-4-5. The articulations of the pedal digits with the metatarsals are concave. All phalanges other than the claws are expanded mediolaterally and dorsoplantarly at their proximal and distal ends. The proximal phalanx of digit I is the most robust of all the phalanges, with an expanded proximal end and tapered distal end. Digit III is the longest; followed by digits IV and II. The distal phalanges of digits III and IV are longer than the proximal ones. The unguals are sharp and curved, typical of arboreal birds, with well-developed flexor tubercles at their proximal ends.

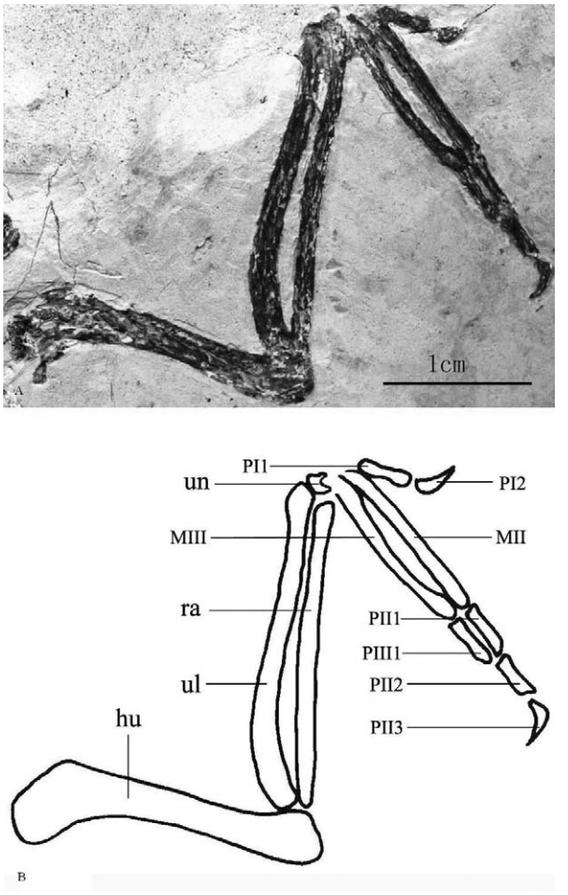

FIGURE 4. Forelimb of *Huoshanornis huji* gen. et sp. nov. Abbreviations: hu, humerus; MII, major metacarpal; MIII, minor metacarpal; PI1, first phalanx of digit I; PI2, second phalanx of digit I; PII1, first phalanx of digit II; PII2, second phalanx of digit II; PII3, third phalanx of digit II; PIII1, first (only) phalanx of digit III; ra, radius; ul, ulna; un, ulnare.

COMPARISON AND DISCUSSION

The identification of *Huoshanornis* as an enantiornithine is established by its V-shaped furcula with a long hypocleidum, coracoid with a convex lateral margin, sternum with a parabolic cranial margin, and a slender metatarsal IV (Chiappe and Walker 2002, O'Connor et al. 2009). Compared with other known enantiornithines, however, *Huoshanornis* is peculiar in the morphology of the manus and the sternum. The morphology of the sternum of enantiornithines is highly variable (Fig. 3); usually, the main body of the sternum is nearly rectangular transversely, and its cranial margin is parabolic.

In addition, in most enantiornithines in which the sternum has been preserved, the caudal margin is deeply notched with several processes. The sternum of *Huoshanornis* is similar to that of *Concornis*, *Sinornis*, *Cathayornis*, *Vescornis*, *Dapingfangornis*, and *Longirostravis* in bearing lateral trabeculae, medial trabeculae, and the xiphoid process but differs from those in that the distal ends of the lateral trabeculae are remarkably expanded and do not surpass the end of the xiphoid process.

An unreduced alular digit represented by the long proximal phalanx is a primitive character, persisting in more basal birds such as *Archaeopteryx*, *Confuciusornis* (Martin et al. 1998, Zhang et al. 2009), and the primitive enantiornithines *Protopteryx* and *Eoenantiornis* (Zhang and Zhou 2000, Zhou et al. 2005). In most of the enantiornithines, such as *Longipteryx*, *Cathayornis*, *Sinornis*, *Vescornis*, *Paraprotopteryx*, and *Eocathyornis*, the first phalanx of the alular digit is nearly or less than half the length of the carpometacarpus and may represent an intermediate stage in the evolution of the manus. In *Huoshanornis*, however, the alular digit is greatly reduced, due to the exceptionally short first phalanx, which is one fourth the length of the major metacarpal. The minor digit of *Huoshanornis* bears one phalanx; it is as long as and almost the same width of that of the major digit. By contrast, in other enantiornithines it is compressed and shorter than the first phalanx of the major digit.

In modern birds, the intermetacarpal space provides attachment and accommodation for the *M. interosseus dorsalis* and *M. interosseus palmaris*, which insert on the anterodorsal corner and the posterior surface of the distal phalanx of the major digit, respectively, to extend and flex the distal extremity of the wing (George and Berger 1966). In contrast to that of other known enantiornithines, the intermetacarpal space of *Huoshanornis* is broad. This character may indicate that *Huoshanornis* possessed strong capability for controlling the primaries and the shape of the wing tip, a potential advantage in maneuverability during low-speed flight.

The discovery of *Huoshanornis* adds to our knowledge of the morphological and taxonomic diversification of the Enantiornithes, and it highlights once again the rapid evolution the avian manus had undergone by the Early Cretaceous.

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