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Dongyu Hu^a; Li Li^a; Lianhaim Hou^{ab}; Xing Xu^{ab}

^a Paleontological Institute of Shenyang Normal University, Shenyang, China ^b Chinese Academy of Sciences, Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

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

DONGYU HU,^{*1} LI LI,¹ LIANHAIM HOU,^{1,2} and XING XU^{1,2}

¹Paleontological Institute of Shenyang Normal University, 253 North Huanghe Street, Shenyang 110034, China, hudongyu@synu.edu.cn; lilishenyang1978@163.com; lxgsw253@126.com;

²Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xiwai Street, Beijing 100044, China, xingxu@vip.sina.com

ABSTRACT—A new enantiornithine bird, *Bohaiornis guoi*, gen. et sp. nov., is described in this paper. The holotype, presumably a sub-adult, is a complete, fully articulated skeleton from the Lower Cretaceous Yixian Formation of western Liaoning, northeastern China. *Bohaiornis* exhibits some similarity in morphology to *Eoenantiornis*, but *Bohaiornis* is much larger than *Eoenantiornis* and differs from all previously known enantiornithine birds including *Eoenantiornis* in having the following features: caudal end of the articular pointed caudoventrally, sacral centra strongly compressed transversely, and clavicular ramus straight with a laterally expanded omal end. The almost perfectly preserved skeleton of this new specimen not only reveals many morphological features previously unknown in basal birds, but also clarifies many fine details of previously known features.

INTRODUCTION

The Early Cretaceous Jehol Group has produced spectacular fossil remains of enantiornithines. Reported taxa include *Eoenantiornis* (Hou et al., 1999), *Longirostravis* (Hou et al., 2004), and *Vescornis* (Zhang et al., 2004) from the lower Yixian Formation and *Cathayornis* (Zhou et al., 1992), *Sinornis* (Seren and Rao, 1992), *Boluochia* (Zhou, 1995), *Longipteryx* (Zhang et al., 2001), *Eocathayornis* (Zhou, 2002), and *Pengornis* (Zhou et al., 2008) from the upper Jiufotang Formation. These discoveries demonstrate a surprisingly high diversity of enantiornithine birds, in morphological and ecological terms as well as taxonomic ones (Zhou and Zhang, 2006). Here we report a new enantiornithine, based on a specimen collected from the lacustrine beds of Jianchang, western Liaoning. These beds have been previously considered to be part of, or laterally equivalent to, the Lower Cretaceous Yixian Formation, but more data are needed to confirm this (Hu et al., 2009). This new enantiornithine bird is larger than most other enantiornithines from the Jehol Group, though it is smaller than the newly discovered *Pengornis* (Zhou et al., 2008).

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

ENANTIORNITHES Walker, 1981

BOHAIORNIS GUOI, gen. et sp. nov. (Fig. 1, Table 1)

Etymology—The genus name *Bohaiornis* is derived from the name of the Bohai Sea, an inland sea close to the type locality, and ‘ornis,’ the Greek term for bird. The species name *guoi* is in honor of Mr. Guo Chen, who collected the holotype specimen.

Holotype—LPM B00167 (Liaoning Paleontology Museum, Shenyang Normal University), a nearly complete and fully articulated skeleton, presumably of a sub-adult, with feather impressions, only missing the posterior part of the skull.

Horizon and Locality—Yixian Formation, Lower Cretaceous; Lamadong Town, Jianchang County, Liaoning Province, Northeast China (Swisher, 1999, 2002).

Diagnosis—An enantiornithine bird having the following autapomorphies: caudal end of the articular pointed caudoventrally, sacral centra strongly compressed transversely to be crest-like, clavicular ramus straight with a laterally expanded omal end. It also differs from other enantiornithines in the following unique combination of characters: large size, thoracic vertebrae with anteroposteriorly strongly expanded neural spines, acromion process extremely elongated with expanded distal end, sternal third of coracoid with weakly convex lateral margin.

Institutional Abbreviation—LPM, Liaoning Paleontology Museum, Shenyang, Liaoning, China.

DESCRIPTION AND COMPARISON

The holotype of *Bohaiornis* has a total skeletal length of about 296 mm, and a total length of >357 mm including the tail feathers (Fig. 1, Table 1). Its skeletal length is approximately 165% of that of *Eoenantiornis* (Hou et al., 1999), which is itself relatively large among known Early Cretaceous enantiornithines. Although the forelimbs of *Bohaiornis* and *Longipteryx* are subequal in length, the hind limb of the latter taxon is only about 80% as long as that of the former (Zhang et al., 2001).

Skull

The cranial morphology of *Bohaiornis* closely resembles that of *Eoenantiornis* (Zhou et al., 2005). The skull is short and deep in lateral view (Fig. 2). The antorbital region accounts for less than 55% the length of the skull, whereas the corresponding ratio is approximately 65% in *Longipteryx*; the two values separately approach to two extremities of the mesorostrine range of known Early Cretaceous enantiornithines (O’Connor et al., 2009).

The right premaxilla is exposed in ventrolateral view and has a damaged ventral margin. This bone seems to have a more pointed rostral margin than in *Eoenantiornis* (Zhou et al., 2005).

*Corresponding author

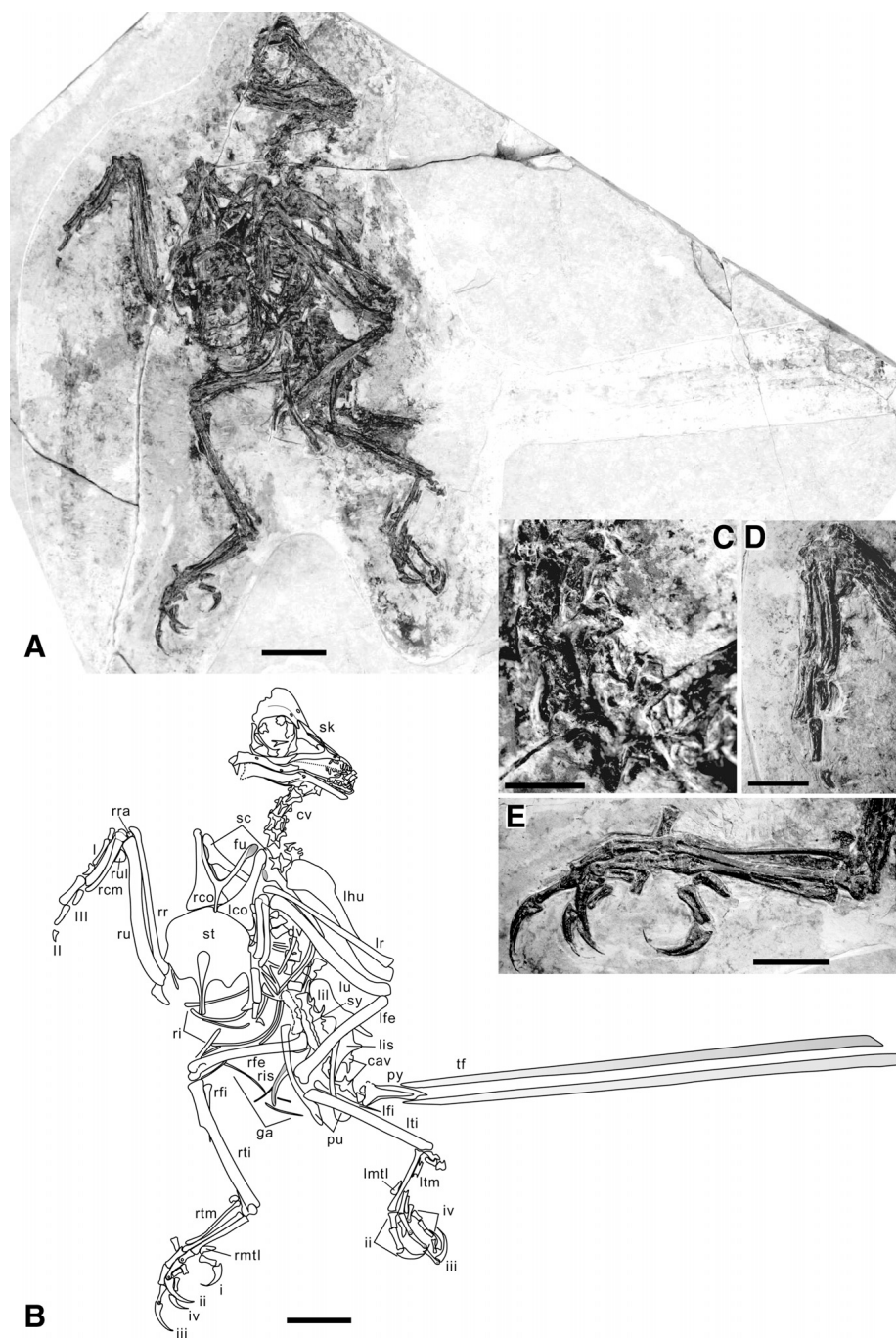


FIGURE 1. *Bohaiornis guoi* holotype (LPM B00167). **A**, photograph and **B**, line drawing. **Abbreviations:** **cav**, caudal vertebra; **cv**, cervical vertebra; **dv**, dorsal vertebra; **fu**, furcula; **ga**, gastralia; **lco**, left coracoid; **lfe**, left femur; **lfi**, left fibula; **lhu**, left humerus; **lil**, left ilium; **lis**, left ischium; **lr**, left radius; **ltm**, left tarsometatarsus; **lti**, left tibiotarsus; **lu**, left ulna; **pu**, pubis; **py**, pygostyle; **rcm**, right carpometa-carpus; **rco**, right coracoid; **rfe**, right femur; **rfi**, right fibula; **ri**, rib; **ris**, right ischium; **rmtl**, right first metatarsus; **rr**, right radius; **rra**, right radiale; **rtm**, right tarsometatarsus; **rti**, right tibiotarsus; **ru**, right ulna; **rul**, right ulnare; **sc**, scapula; **sk**, skull; **st**, sternum; **sy**, synsacrum; **tf**, tail feather; **I–III**, the first through third manual digits; **i–iv**, the first through fourth pedal digits. Scale bar equals 2 cm in **A** and **B**, 0.5 cm in **C**, 1 cm in **D** and **E**.

The nasal process is relatively short and only extends to the mid-length of the upper margin of the antorbital cavity, whereas it approaches the rostral margin of the orbit in *Eoenantiornis* (Zhou et al., 2005). Two rows of the nutrient foramina are visible in the lateral surface of the premaxilla. As in most toothed early birds, there are four premaxillary teeth. In contrast to *Eoenantiornis* (Zhou et al., 2005), the premaxillary teeth begin at the rostral-most part of the premaxilla. The maxilla forms most of the upper jaw; the rostral portion makes up less than one-third of the total length of the maxilla, the long strap-like caudal process forms the ventral border of the antorbital cavity, and the slender dorsal process forms the anterior border of the antorbital cavity. Several nutrient foramina also occur on

the lateral surface of the rostral part. Three maxillary teeth are implanted in the rostral part of the maxilla anterior to the dorsal process. In *Eoenantiornis*, the maxillary dentition extends posteriorly beyond the dorsal process (Zhou et al., 2005). The maxillary teeth are smaller than the premaxillary ones. The nasal is broad, and forms the posterior border of the external naris and the dorsal border of the antorbital cavity. The subtriangular antorbital cavity is separated by a slender lacrimal from the large and rounded orbit. The frontal is highly domed and forms the dorsal border of the orbit. The strap-like jugal forms the ventral border of the orbit and has a long dorsally directed posterodorsal process. The right quadrate is preserved in lateral view. It is long and robust with a short orbital process.

TABLE 1. Measurements (mm) of *Bohaiornis guoi* holotype (LPM B00167).

Skull length	38.5 (preserved part) 47 (estimated total length)
Height	30 (including lower jaw)
Mandible length	38
Scapula length	>36
Furcula length	24
Coracoid length	23
Base width	12.8
Sternum length	36.4
Max width	26
Humerus length	47
Ulna length	48
Mid-shaft width	3.7
Radius length	45.4
Mid-shaft width	2.2
Metacarpal I-III length	8, 21.3, 22.7
Manual digit length	
I-1, -ungula	9.5, 4.5
II-1, -2, -ungula	10.8, 7.5, 3.6
III-1	5.5
Ilium length	25.6
Pulvis length	33
Ischium length	21
Femur length	39
Tibia length	46
Fibula length	23
Metatarsus I-IV length	5.7, 20.8, 22.5, 21.8
Pedal digit length	
I-1, -ungula	6, 9
II-1, -2, -ungula	5, 7, 12
III-1, -2, -3, -ungula	7.6, 7.2, 6.5, 10.3
IV-1, -2, -3, -4, -ungula	4, 3.3, 3.5, 4.2, 7.5
Pygostyle length	>18.5
Tail feather length	>150

Three rows of nutrient foramina can be seen on the lateral surface of the dentary. Five teeth and two empty alveoli are observed on the left dentary, suggesting a total of seven dentary teeth. The rostral half of the postdentary part of the mandible is ventrally curved and laterally expanded. The caudal end of the articular is pointed caudoventrally, a condition not seen in other known enantiornithine birds.

Axial Skeleton

Ten cervical vertebrae are present, although the atlas is missing. The cervical vertebrae are axially longer than transversely wide, and their centra bear prominent ventral keels (Fig. 1C). Short cervical ribs are articulated with the vertebrae, but not fused to them. The heterocoelous posterior surface of one posterior cervical centrum is exposed. Seven scattered and poorly preserved thoracic vertebrae are visible. They are amphicoelous with lateral excavations, and their neural spines are expanded distally. Six or seven sacral vertebrae are co-ossified to form the synsacrum. The anterior articular surface of the synsacrum is significantly expanded. The sacral centra are strongly compressed transversely: their dorsoventral depth greatly exceeds their transverse width, and they form a prominent ventral keel (Fig. 3). In most other basal birds including enantiornithines, the sacral centra are either subequal in dorsoventral depth and transverse width or wider transversely than deep dorsoventrally (Zhang et al., 2001; Zhou and Zhang, 2003; Mayr et al., 2007). Six separate caudal vertebrae are discernible, each vertebra being amphicoelous with a pair of long, laterocaudally directed transverse processes. The pygostyle is sword-shaped in lateral view, and forked anteriorly as in other enantiornithines (Chiappe and Walker, 2002). The gastralia are present, but it is unclear whether the ribs bear uncinat processes.

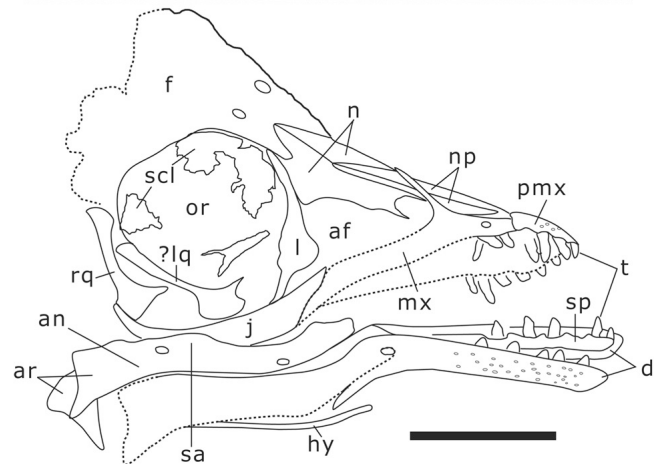
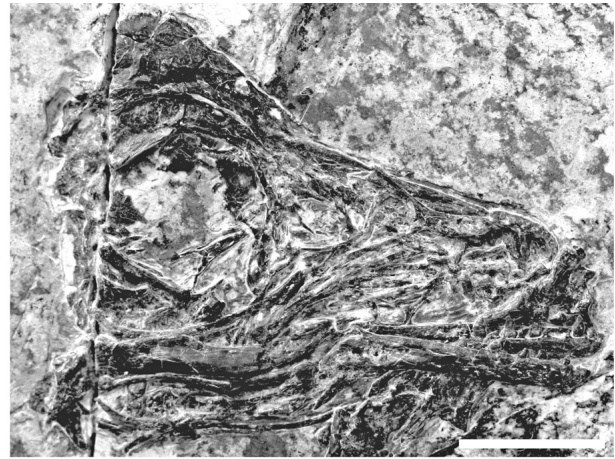


FIGURE 2. Close-up photograph and line drawing of the skull of *Bohaiornis guoi* holotype (LPM B00167). **Abbreviations:** af, antorbital fenestra; an, angular; ar, articular; d, dentary; f, frontal; hy, hyoid bone; j, jugal; l, lacrimal; ?lq, left quadrate; mx, maxilla; n, nasal; np, nasal process of the premaxilla; or, orbit; pmx, premaxilla; rq, right quadrate; sa, surangular; scl, scleral ossicle; sp, splenial; t, tooth. Scale bar equals 1 cm.

Thoracic Girdle and Sternum

The scapula is blade-shaped and straight. The acromion process is robust and extremely elongated (more than twice as long as the glenoid facet) with an expanded distal end (Fig. 4). A similarly long acromion process is seen in *Eoalulavis* (Sanz et al., 1996). The coracoid is strut-like and relatively short, with a length/width ratio of 1.8. The equivalent ratio is 2.2 in *Eoenantiornis* (Hou et al., 1999). The lateral margin of the coracoid is only slightly convex near the distal end, as in *Longipteryx* (Zhang et al., 2001) but in contrast to the strongly convex margin seen in many other enantiornithines including *Eoenantiornis* (Chiappe and Walker, 2002; Zhou et al., 2005). The furcula is Y-shaped, with a wide interclavicular angle of about 60° and a relatively short hypocleidum. The furcula of *Eoenantiornis* also has a short hypocleidum, but differs from that of *Bohaiornis* in having a smaller interclavicular angle (about 45°; Hou et al., 1999). The clavicular ramus is straight and has an L-shaped cross-section. The ventral surface of the clavicular ramus has a constant transverse width, whereas the lateral surface becomes wider towards the omal end and eventually comes to exceed the ventral surface in width. *Bohaiornis* differs from other enantiornithines in that the omal end of the clavicular ramus is blunt and laterally expanded.

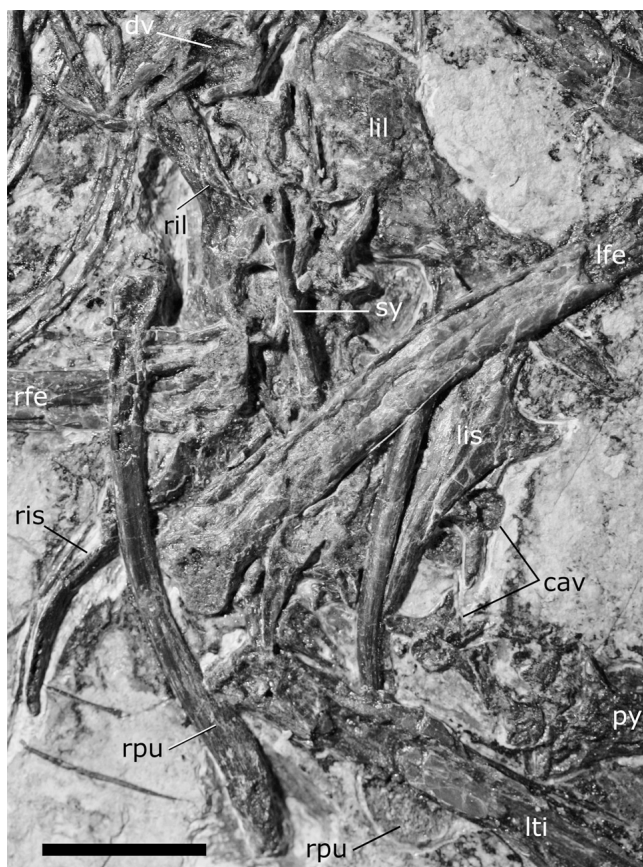


FIGURE 3. Close-up photographs of the synsacrum and pelvic girdle of *Bohaiornis guoi* holotype (LPM-B00167). **Abbreviations:** *dv*, dorsal vertebra; *lfe*, left femur; *lil*, left ilium; *lis*, left ischium; *lpu*, left pubis; *py*, pygostyle; *rfe*, right femur; *ril*, right ilium; *ris*, right ischium; *rpu*, right pubis. Scale bar equals 1 cm.

The sternum has a semicircular-shaped cranial outline. The sternal keel is low, and restricted to the posterior half of the sternum. The caudomedial processes are obtuse and short, and the caudolateral processes extend almost as far posteriorly as the distal end of the xiphoid process. The distal end of each caudolateral process expands mediolaterally in an asymmetric manner, taking on an arrow-shaped appearance as in *Cathayornis* (Zhou and Hou, 2002).

Forelimb

As in most known enantiornithines other than *Longipteryx* (Zhang et al., 2001) and *Pengornis* (Zhou et al., 2008), the forelimbs and hind limbs of *Bohaiornis* are subequal in length. Only the left humerus is exposed cranially, and its distal end is damaged. The central portion of the superior margin of the humeral head is slightly concave, and the ventral portion projects slightly further proximally than the dorsal portion. The bicipital crest is bulbous with a central fossa and the deltopectoral crest is relatively short and high.

The ulna is subequal in length to the humerus, with a caudally convex proximal half and a straight distal half. The radius is relatively straight and is more than half as wide as the ulna. It appears to bear a shallow groove along the interosseous surface. The ulnare and radiale respectively appear subtriangular and subrectangular, and are similar in morphology to the corresponding bones of *Eocathayornis* (Zhou, 2002).



FIGURE 4. Close-up photograph of the pectoral girdle of *Bohaiornis guoi* holotype (LPM B00167). **Abbreviations:** *fu*, furcula; *lco*, left coracoid; *lcm*, left carpometacarpus; *lsc*, left scapula; *rco*, right coracoid; *rsc*, right scapula; *st*, sternum; *II*, left second manual digit. Arrows indicate the distal boundary of the right caudolateral process of the sternum. Scale bar equals 1 cm.

The manus is slightly shorter than the humerus (about 95% of the humeral length). The metacarpals are not proximally co-ossified with each other or with the semilunate carpal, as a suture is visible between all these bones (Fig. 1D). The alular metacarpal is rod-shaped, and measures about 20% of the length of the major metacarpal. The major and minor metacarpals both curve distally to some extent, and the minor metacarpal extends distally past the major metacarpal. There is a very narrow intermetacarpal space. As in *Eoenantiornis* (Hou et al., 1999), the alular digit bears a robust and curved ungual that extends as far distally as the major metacarpal (Fig. 1D). The proximal phalanx of the major digit is nearly as robust as the major metacarpal, and its diameter remains constant throughout its length. The intermediate phalanx of this digit is shorter and more slender than the proximal one, and tapers distally to a slight degree. The ungual phalanx of the major digit is smaller than that of the alular digit. The minor digit consists of a single phalanx, which is much shorter than the other non-ungual manual phalanges. This digit does not carry an ungual, and the phalangeal formula is probably 2–3–1.

Pelvic Girdle

The preacetabular portion of the ilium is expanded, cranially lobe-shaped, and apparently longer than the postacetabular portion, which is sharply constricted and tapers caudally (Fig. 3). The right ilium is exposed ventrally, revealing that the pubic peduncle is much more expanded than the ischiadic peduncle. The pubis is about 125% as long as the ilium and is slender and posteriorly curved, with a well-developed pubic boot. The mediolaterally compressed ischium is about two-thirds the length of the pubis (Fig. 3). The proximal part of this bone is broad and bears a large dorsal process, whereas the distal part tapers gradually and curves caudally.

Hind Limb

The femur is slightly bowed anteriorly. The femoral head seems to be small. Distally, the medial and lateral condyles are separated by a narrow and deep intercondylar groove, which joins the popliteal fossa proximoventrally.

The tibiotarsus measures slightly less than 120% of the femoral length. This bone bears a prominent fibular crest, which appears to be perforated by a foramen. The proximal tarsals are completely fused to each other, but incompletely fused to the tibia—the right proximal tarsals display an ascending process that is detached from the tibia and slightly displaced laterally from its natural position (Fig. 1E). The medial condyle is slightly wider than the lateral condyle, and the two condyles are separated by a wide intercondylar groove. The preserved length of the fibula is about 50% of that of the tibiotarsus, but the actual length of the intact fibula may have been considerably greater.

The metatarsals are not fused to each other proximally. Metatarsal I is J-shaped, and slightly twisted. Metatarsal II is clearly the widest of the metatarsals, whereas metatarsal IV is the narrowest and metatarsal III the longest (Fig. 1E). The hallux and digit II, including their respective unguis, are more robust than other digits. The penultimate phalanges of digits II–IV are longer than the corresponding proximal phalanges, whereas the unguis including their well-preserved horny sheaths are much longer than the penultimate phalanges. Except in the case of the hallux, the unguis are not as strongly curved as in *Eoenantiornis* (Zhou et al., 2005).

Plumage

Feather and soft tissue impressions are preserved around the skeleton, including several primaries on the right manus and a pair of long tail feathers missing their distal ends. The preserved impressions suggest that the longest of the primaries was about equal in length to the humerus and ulna combined, and the proximal parts of tail feather are scale-like, without rachis and barbs as in *Protopteryx* (Zhang and Zhou, 2000). Further details cannot be discerned due to the poor preservation of the plumage.

DISCUSSION

Bohaiornis displays the following enantiornithine synapomorphies: Y-shaped furcula with distinct hypocleideum; clavicular rami with L-shaped cross-section; sternum with parabolic anterior margin, keel limited to posterior half of bone, and paired caudolateral processes; radius with longitudinal groove along interosseous surface; minor metacarpal extending distally beyond major metacarpal; metatarsal II considerably wider transversely than metatarsals III and IV; and metatarsal IV more slender than metatarsals II and III (Chiappe, 2002; Chiappe and Walker, 2002). These features strongly support the enantiornithine affinity of *Bohaiornis*.

In order to further determine the systematic position of *Bohaiornis*, we ran a numerical phylogenetic analysis on a dataset specifically designed to illuminate enantiornithine interrelation-

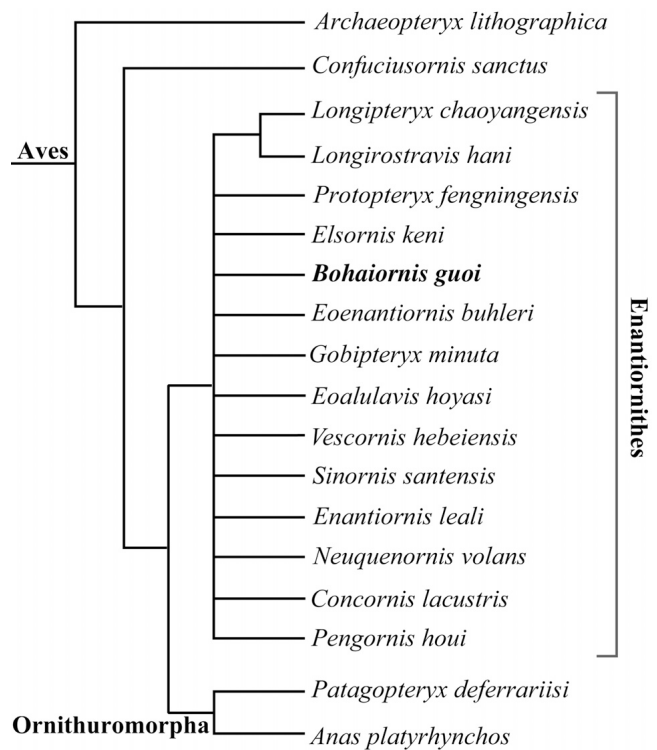


FIGURE 5. Strict consensus cladogram illustrating the systematic position of *Bohaiornis guoi* holotype (LPM B00167). Phylogenetic analysis on a dataset composed of 54 characters and 18 taxa was conducted using NONA 2.0 and WinClada (see Appendices 1 and 2), and produced 162 most parsimonious trees (tree length = 110; CI = 0.56; RI = 0.66).

ships (Chiappe, Suzuki, et al., 2007; Appendices 1 and 2). The phylogenetic analysis was conducted using the NONA (version 2.0) software package (Goloboff, 1993), and matrix formatting and character exploration were performed in WinClada (Nixon, 1999). The analysis was run using Heuristic Search with the following search parameters: 1000 replications, 10 starting trees per replication, and Multiple TBR+TBR (mult*max*) search strategy. A strict consensus tree was generated from the resulting 162 most parsimonious trees. The analysis places *Bohaiornis* within Enantiornithines, but interrelationships within this group are not resolved (Fig. 5). This is partially caused by large numbers of missing data, but the problem of homoplasy within Enantiornithines probably also contributes to the low resolution of enantiornithine phylogeny.

Nevertheless, some morphological features might be informative in inferring the systematic position of *Bohaiornis*. *Bohaiornis* possesses several derived features that are present in derived enantiornithines but not seen in basal members of the group such as *Protopteryx* (Zhang and Zhou, 2000). For example, the sternum has distally strongly expanded caudolateral processes, the humerus has a centrally concave humeral head, and the manus is short relative to the humerus and has a major digit with a proximal phalanx that is longer than the penultimate one. These features suggest that *Bohaiornis* is a relatively derived enantiornithine bird.

Among the known enantiornithines, *Bohaiornis* is most similar to *Eoenantiornis* (Zhou et al., 2005). For example, the skulls of both taxa are short and deep, the proportions of their limb segments are similar, and in both cases the alular digit extends distally to the same level as the major metacarpal. However, *Bohaiornis* is clearly different from *Eoenantiornis* in a number of

respects. Firstly, several features seen in *Bohaiornis*, including a caudoventrally directed caudal end of the articular, a strongly keeled ventral surface of the synsacrum, and a straight clavicular ramus with a laterally expanded omal end, have not been previously reported in *Eoenantiornis* or any other basal bird. Other features of *Bohaiornis* that distinguish this taxon from *Eoenantiornis* include large size, maxillary dentition not extending posteriorly beyond dorsal process, acromion process extremely elongated with expanded distal end, lateral margin of coracoid weakly convex, caudolateral process of sternum extending posteriorly approximately as far as xiphoid process, and distal end of caudolateral process of sternum asymmetrically expanded mediolaterally.

The pattern of skeletal fusion seen in *Bohaiornis* deserves particular mention. All vertebral neural arches are fused to their corresponding centra and the sacral vertebrae are ossified into a synsacrum, suggesting that the holotype specimen represents an adult individual. Fusion features of many other elements indicate, however, that the holotype individual might not have been fully grown. For example, the semilunate carpal and proximal tarsals are only partially fused to the metacarpals and tibia, respectively, and there is no mutual fusion among either the metacarpals or the metatarsals. Collectively, these features suggest that (1) the holotype specimen is a sub-adult or young adult individual; and (2) the compound bones of the limbs ossify and fuse later in ontogeny than the vertebral segments. The postponement of complete fusion of limb elements until relatively late ontogeny suggests a developmental strategy different from modern birds but more similar to non-avian theropods (Chiappe, Ji, et al., 2007).

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LITERATURE CITED

- Chiappe, L. M. 2002. Early bird phylogeny: problems and solutions; pp. 448–472 in L. M. Chiappe and L. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, California.
- Chiappe, L. M., and C. Walker. 2002. Skeletal morphology and systematic of the Cretaceous Enantiornithes; pp. 240–267 in L. M. Chiappe and L. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, California.
- Chiappe, L. M., S. Ji, and Q. Ji. 2007. Juvenile birds from the Early Cretaceous of China: implications for Enantiornithine ontogeny. *American Museum Novitates* 3594:1–46.
- Chiappe, L. M., S. Suzuki, G. J. Dyke, M. Watabe, K. Tsogtbaatar, R. Barsbold. 2007. A new Enantiornithine bird from the Late Cretaceous of the Gobi desert. *Journal of Systematic Palaeontology* 5:193–208.
- Goloboff P. A. 1993. NOVA, ver. 2.0. Published by the author, S. M. de Tucuman, Argentina.
- Hou, L., L. M. Chiappe, F. Zhang, and C. Chuong. 2004. New Early Cretaceous fossil from China documents a novel trophic specialization for Mesozoic birds. *Naturwissenschaften* 91:22–25.
- Hou, L., L. D. Martin, Z. Zhou, and A. Feduccia. 1999. *Archaeopteryx* to opposite birds—missing link from the Mesozoic of China. *Vertebrata Palasiatica* 37:88–95.
- Hu, D., L. Hou, L. Zhang and X. Xu. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461:640–643.
- Linnaeus, C. 1758. *Caroli Linnaei Systema naturae: a photographic facsimile of the first volume of the tenth edition (1758): Regnum animale*. British Museum (Natural History), London, 823. pp.
- Mayr, G., B. Pohl, S. Hartman, and D. S. Peters. 2007. The tenth skeletal specimen of *Archaeopteryx*. *Zoological Journal of the Linnean Society* 149:97–116.
- Nixon, K. C. 1999. Winclada (BETA), ver. 0.9.9. Published by the author, Ithaca, New York.
- O'Connor, J. K., X. Wang, L. M. Chiappe, C. Gao, Q. Meng, X. Cheng, and J. Liu. 2009. Phylogenetic support for a specialized clade of Cretaceous enantiornithine birds with information from a new species. *Journal of Vertebrate Paleontology* 29:188–204.
- Sanz, J. L., L. M. Chiappe, B. P. Pérez-Moreno, A. D. Buscalioni, J. Moratalla, F. Ortega, and F. J. Poyato-Ariza. 1996. A new Lower Cretaceous bird from Spain: implications for the evolution of flight. *Nature* 382:442–445.
- Sereno, P. C., and C. Rao. 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. *Science* 255:845–848.
- Swisher, C. C., Y. Wang, X. Wang, X. Xu, and Y. Wang. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* 400:58–61.
- Swisher, C. C., X. L. Wang, Z. H. Zhou, Y. Q. Wang, F. Jin, J. Zhang, X. Xu, F. Zhang, and Y. Wang. 2002. Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: new ⁴⁰Ar/³⁹Ar dating of the Yixian and Tuchengzi Formations. *Chinese Science Bulletin* 47:135–138.
- Walker, C. A. 1981. New subclass of birds from the Cretaceous of South America. *Nature* 292:51–53.
- Zhang, F., and Z. Zhou. 2000. A primitive Enantiornithine bird and the origin of feathers. *Science* 290:1955–1959.
- Zhang, F., P. G. P. Ericson, and Z. Zhou. 2004. Description of a new Enantiornithine bird from the Early Cretaceous of Hebei, northern China. *Canadian Journal of Earth Science* 41:1097–1107.
- Zhang, F., Z. Zhou, L. Hou, and G. Gu. 2001. Early diversification of birds: evidence from a new opposite bird. *Chinese Science Bulletin* 46:945–949.
- Zhou, Z. 1995. Discovery of a new enantiornithine bird from the Early Cretaceous of Liaoning, China. *Vertebrata Palasiatica* 33:99–113.
- Zhou, Z. 2002. A new and primitive enantiornithine bird from the Early Cretaceous of China. *Journal of Vertebrate Paleontology* 22:49–57.
- Zhou, Z., and L. Hou. 2002. The discovery and study of Mesozoic birds in China; pp. 160–183 in L. M. Chiappe and L. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, California.
- Zhou, Z., and F. Zhang. 2003. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Canadian Journal of Earth Science* 40:731–747.
- Zhou, Z., and F. Zhang. 2006. Mesozoic birds of China—a synoptic review. *Vertebrata Palasiatica* 44:74–98.
- Zhou, Z., L. M. Chiappe, and F. Zhang. 2005. Anatomy of the Early Cretaceous bird *Eoenantiornis buhleri* (Aves: Enantiornithes) from China. *Canadian Journal of Earth Science* 42:1331–1338.
- Zhou, Z., J. Clarke, and F. Zhang. 2008. Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird. *Journal of Anatomy* 212:565–577.
- Zhou, Z., F. Jin, and J. Zhang. 1992. Preliminary report on a Mesozoic bird from Liaoning, China. *Chinese Science Bulletin* 37:1365–1368.

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APPENDIX 1. Character list and states used in phylogenetic analysis. The character list and states employed for the cladistic analysis of enantiornithine taxa (Chiappe, Suzuki, et al. 2007) are modified from those of Chiappe and Walker (2002) and Chiappe (2002).

- (1) Upper dentition: teeth present in the premaxilla and maxilla (0); present only in premaxilla (1); absent (2). (Ordered).
- (2) Length of rostrum: brevirostral (0); longirostral (1).
- (3) Keel-like ventral surface of cervical centra: absent (0); present (1).
- (4) Parapophyses located in cranial (0) or central (1) portion of thoracic centra.

- (5) Cranial end of pygostyle dorsally forked: absent (0); present (1).
- (6) Laterally compressed shoulder end of coracoid, with nearly aligned acroracoid process, humeral articular surface and scapular facet, in dorsal view: absent (0); present (1).
- (7) Strongly convex lateral margin of the sternal third of the coracoid: absent (0); present (1).
- (8) Supracoracoid nerve piercing the coracoid through large foramen separated by a thick bar from medial margin: absent (0); present (1).
- (9) Broad, deep fossa on dorsal surface of the coracoid: absent (0); present (1).
- (10) Scapular acromion costolaterally much wider than deeper: absent (0); present (1).
- (11) Costal surface of scapular blade with prominent longitudinal furrow: absent (0); present (1).
- (12) Dorsal and ventral margins of furcula: subequal in width (0); ventral margin clearly wider than dorsal margin (1).
- (13) Hypocleideum: absent or poorly developed (0); well developed (1).
- (14) Distinctly keeled ventral surface of hypocleideum: absent (0); present (1).
- (15) Ossified sternal keel: absent or incipient (0); present and not reaching the cranial border of sternum (1); present and near to or projecting cranially from the cranial border of sternum (2). (Ordered).
- (16) Semicircular-shaped cranial end of the sternum: absent (0); present (1).
- (17) Sternal xiphoid process: absent (0); present (1).
- (18) Lateral process of sternum: absent (0); present (1).
- (19) Medial process of sternum: absent (0); present (1).
- (20) Superior margin of the humeral head: flat (0); concave in its central portion, rising ventrally and dorsally (1); domed proximally (2).
- (21) Prominent bicipital crest of the humerus, cranioventrally projecting: absent (0); present (1).
- (22) Distal end of humerus very compressed craniocaudally: absent (0); present (1).
- (23) Dorsal cotyle of ulna separated from the olecranon by a groove or distinct depression: absent (0); present (1).
- (24) Shaft of radius with longitudinal groove on its caudoventral surface: absent (0); present (1).
- (25) Shape of alular metacarpal: subrectangular (0); subcircular (1).
- (26) Combined lengths of the alular metacarpal and its digit longer (0), subequal (1), or shorter (2) than the major metacarpal. (Ordered).
- (27) Length of manus (semilunate carpal + major metacarpal and digit) relative to humerus: longer (0); shorter (1).
- (28) Minor metacarpal projecting distally more than the major metacarpal: absent (0); present (1).
- (29) Relative lengths of the non-ungual phalanges of the manual major digit: proximal phalanx shorter (0) or longer (1) than the intermediate phalanx.
- (30) Pubic pedicel of ilium caudally hooked and very compressed transversally: absent (0); present (1).
- (31) Pubic foot: present (0); absent (1).
- (32) Hypertrophied femoral posterior trochanter: absent (0); present (1).
- (33) Caudal projection of lateral border of the distal end of the femur: absent (0); present (1).
- (34) Trochlea of metatarsal II much broader than the trochlea of metatarsal III: absent (0); present (1).
- (35) Distal end of metatarsal II strongly curved medially: absent (0); present (1).
- (36) Metatarsal IV significantly thinner than metatarsals II and III: absent (0); present (1).
- (37) Medial rim of the trochlea of metatarsal III with strong plantar projection: absent (0); present (1).
- (38) Strong transverse convexity of the dorsal surface of the mid-shaft of metatarsal III: absent (0); present (1).
- (39) Ungual phalanx of pedal digit I longer, more robust and larger than other pedal claws: absent (0); present (1).
- (40) Scapular shaft: straight (0); sagittally curved (1).
- (41) Distal end of metacarpals in adults: unfused (0); partially or completely fused (1).
- (42) Metatarsal II–IV fusion in adults: largely unfused (0); completely to nearly completely fused (1).
- (43) Pygostyle: absent (0); present (1).
- (44) Orientation of the proximal portion of the pubis: cranially to subvertically orientated (0); retroverted, separated from the main synsacral axis by an angle ranging between 65° and 45° (1).
- (45) Scapula articulated at the shoulder (proximal) end of the coracoid (0); or well below it (1).
- (46) Ungual phalanx of minor digit (manual digit III): present (0); absent (1).
- Characters newly added:
- (47) Lower dentition, number: more than 10 (0); 5 to 10 (1); less than 5 (2). (Ordered).
- (48) Thoracic vertebrae, strong neural spine craniocaudal expansion: absent (0); present (1).
- (49) Synsacrum, ventral surface, prominent longitudinal groove: absent (0); present (1).
- (50) Sternum, length relative to width: longer (0); subequal (1); shorter (2).
- (51) Sternum, lateral process, length relative to that of xiphoid process: shorter (0); subequal (1); longer (2). (Ordered).
- (52) Sternum, lateral process, distal expansion: weak (0); strong (1).
- (53) Sternum, lateral process, distal expansion: symmetrical (0); asymmetrical (1).
- (54) Ulna, length relative to humerus: shorter (0); subequal (1); longer (2).

APPENDIX 2. Character matrix of phylogenetic analysis. This character matrix was employed for the cladistic analysis of enantiornithine taxa, (Chiappe, Suzuki, et al. 2007). ?, indeterminate; n, not comparable.

Taxon/Character	10	20	30	40	50	
<i>Archaeopteryx lithographica</i>	0000n00000	000n0mnn0	0000000000	0000000000	000000000?	???
<i>Confuciusornis sanctus</i>	2000000000	000n000000	0000000000	1000000000	0011002000	00-0
<i>Patagopteryx deferrariisi</i>	??00?00000	?nnn?????0	0000??1???	1000000001	11?10??01?	????
<i>Anas platyrhynchos</i>	n100000000	000n200100	0000021010	1000100001	1111112100	10-2
<i>Gobipteryx minuta</i>	201??1??10	?111??????	??1?1??1?0	1??11100??	001?1??01?	???
<i>Elsornis keni</i>	??10?01011	0110111101	0001??????	??????????0	1??11??0?0	???
<i>Enantiornis leali</i>	?????11111	1????????1	10111?????	??????????0	0??1??????	????
<i>Neuquenornis volans</i>	??1?1111?	110n2??1??	?1?11??1??	?111?11110	00??1?????	?112
<i>Sinornis santensis</i>	00?1111111	0?1111?111	1??1?21110	010?011?00	00111111?1	2111
<i>Eoenantiornis buhleri</i>	00??11111?	?111?1111?	??1011111?	01?1010?00	0011111??1	0102
<i>Longipteryx chaoyangensis</i>	111?11011?	?1????1111	1??0011111	01?0010?00	0011112??2	2101
<i>Protopteryx fengningensis</i>	00?01?00??	?111?????0	?0??00010?	?1?1?1??00	001?1120?2	10-1
<i>Longirostravis hani</i>	11??1?0?11	?11??11111	??????1111	??001??0?	001?112??1	1112
<i>Concornis lacustris</i>	??1?11111	?110111111	111??21?1?	111101?11?	00?11??0?	2101
<i>Eoalulavis hoyasi</i>	??1??11110	?11100n001	11?1?2111?	?1??????0?	0??11?0??	???
<i>Vescornis hebeiensis</i>	0/101??1???	0?11111111	1??112111?	??0111?000	001?111??1	00-2
<i>Pengornis houi</i>	0010??0???	?110?????2	0??????11?	0??111?0??	?011??0???	???
<i>Bohaiornis guoi</i>	00111?0???	1111111111	111101111?	0??111?000	0011?11101	1111

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