

A partial skeleton of an enantiornithine bird from the Early Cretaceous of northwestern China

MATTHEW C. LAMANNA, HAI-LU YOU, JERALD D. HARRIS, LUIS M. CHIAPPE, SHU-AN JI, JUN-CHANG LÜ, and QIANG JI



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Although recent discoveries from Lower Cretaceous sediments in northeastern China have greatly improved our understanding of the initial stages of avian diversification in eastern Asia, the early evolution of Aves elsewhere on the continent remains poorly understood. In 2004, a collaborative field effort directed by personnel from the Chinese Academy of Geological Sciences and Carnegie Museum of Natural History recovered multiple partial to nearly complete avian skeletons from outcrops of the Lower Cretaceous Xiangou Formation exposed in the Changma Basin of northwestern Gansu Province, China. Here we describe a thrush-sized partial skeleton comprised of a fragmentary pelvic girdle and largely complete hind limbs. A phylogenetic analysis of 20 avian ingroup taxa and 169 anatomical characters places the specimen in Enantiornithes, and within that clade, in Euenantiornithes. When coupled with additional recent discoveries from the Changma Basin, the new skeleton improves our understanding of early avian evolution and diversification in central Asia.

Key words: Aves, Enantiornithes, Cretaceous, Xinminpu Group, Xiangou Formation, China.

Matthew C. Lamanna [lamannam@carnegiemnh.org], Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, USA (corresponding author);

Hai-Lu You [youhailu@sinofossa.org], Shu-An Ji [jishu_an@sina.com], Jun-Chang Lü [tmcp168@yahoo.com], and Qiang Ji [jjirod@cags.net.cn], Institute of Geology, Chinese Academy of Geological Sciences, 26 Baiwanzhuang Road, Beijing 100037, P.R. China;

Jerald D. Harris [jharris@dixie.edu], Dixie State College, Science Building, 225 South 700 East, St. George, Utah 84770, USA;

Luis M. Chiappe [lchiappe@nhm.org], The Dinosaur Institute, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA.

Introduction

Spectacular recent discoveries from Early Cretaceous deposits in northeastern China, principally Liaoning and Hebei provinces, have provided important insight into the early stages of avian evolution and diversification in eastern Asia (Chiappe and Dyke 2002; Zhou and Hou 2002; Zhou 2004). In contrast, the record of Early Cretaceous birds from elsewhere on the continent, and most other areas of the world, remains sparse (Kurochkin 2000; You et al. 2005). In August of 1981, Lower Cretaceous sediments exposed in the Changma Basin, in the far northwest of northern China's Gansu Province (Fig. 1), produced the first Chinese Mesozoic avian remains to be discovered, a distal hind limb that became the holotype of the ornithuromorph *Gansus yumenensis* (Hou and Liu 1984; You et al. 2005). More than two decades later, in July–October of 2004, a collaborative expedition led by researchers from the Chinese Academy of Geological Sciences and Carnegie Museum of Natural History revisited these deposits and recovered multiple partial to nearly complete avian skeletons, several preserving feathers or soft-tissue impressions. Here we de-

scribe one of these specimens, a thrush-sized partial postcranial skeleton that consists of a fragmentary pelvic girdle and largely complete hind limbs (Fig. 2).

Institutional abbreviations.—BPV, Beijing Natural History Museum, Paleovertebrate Collection, Beijing, China; CAGS-IG, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LH, Las Hoyas Collection, Museo de Cuenca, Cuenca, Spain (provisionally housed in the Unidad de Paleontología of the Universidad Autónoma de Madrid); LPM, Liaoning Paleontological Museum, Beipiao, China; NIGPAS, Nanjing Institute of Geology and Paleontology, Nanjing, China.

Geological and paleoecological context

Mesozoic sediments outcropping in the Changma Basin are included within the Xinminpu (= "Xinminbao," e.g., Tang

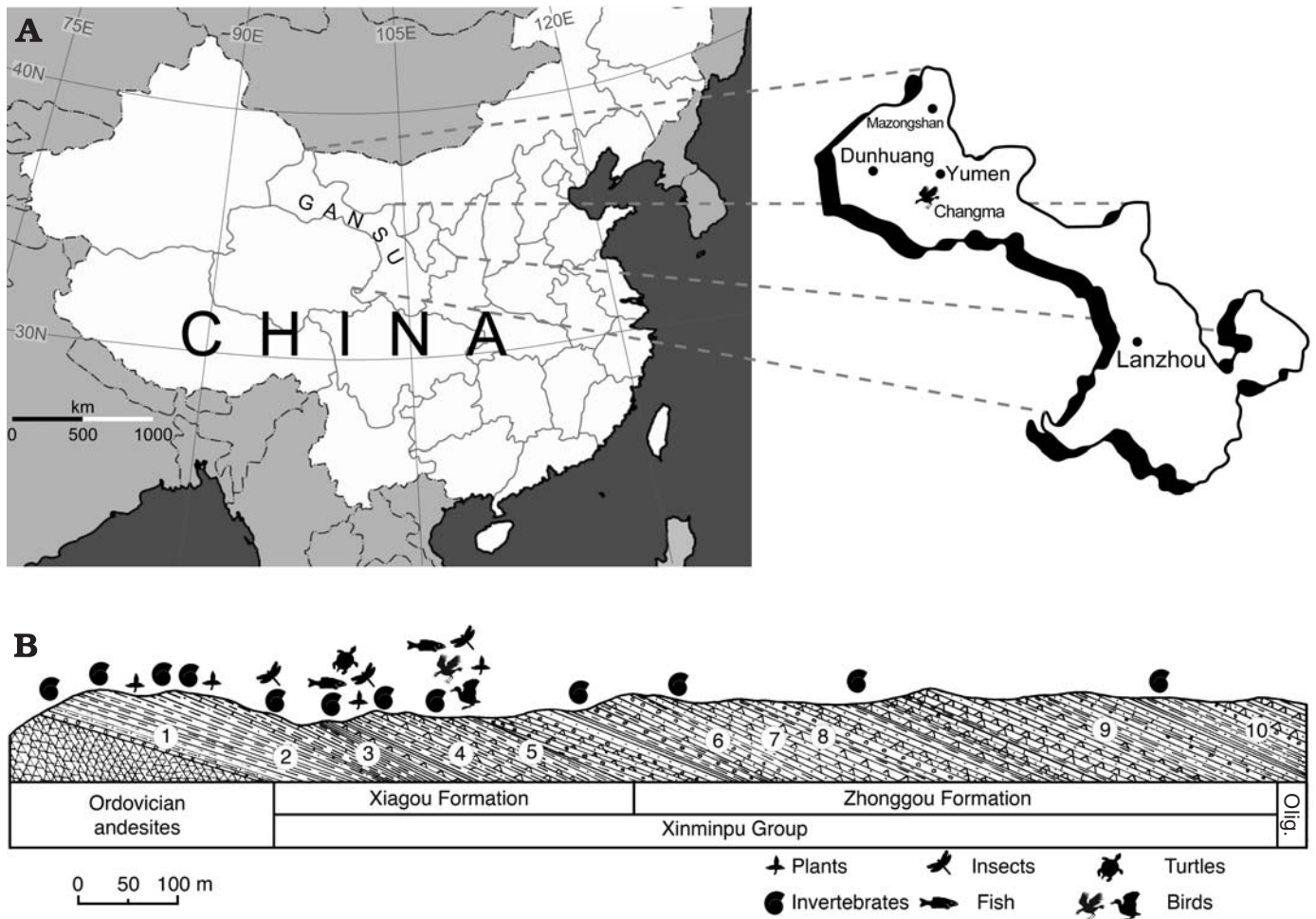


Fig. 1. A. Geographic location of the Changma Basin (indicated by avian silhouette) and the Mazongshan fossil locality in northwestern Gansu Province, China. B. Schematic stratigraphic section of the Xinminpu Group as exposed at Changma, modified from Niu (1987: fig. 7). Numerals correspond to stratigraphic levels recognized by Niu (1987). Abbreviation: Olig., Oligocene Huoshaogou Formation.

et al. 2001; "Xinmingu," O'Connor et al. 2004) Group (Fig. 1B), which is considered to be Early Cretaceous in age (Bureau of Geology and Mineral Resources of Gansu Province 1989, 1997; Editorial Committee of Chinese Stratigraphic Standard: Cretaceous 2000; Tang et al. 2001). The Xinminpu Group is subdivided into two lithostratigraphic units, in ascending order: the Xiagou and Zhonggou formations (Bureau of Geology and Mineral Resources of Gansu Province 1997; Editorial Committee of Chinese Stratigraphic Standard: Cretaceous 2000). In the Changma Basin, the Xiagou Formation, consisting of mudstones and siltstones interbedded with coarser clastics, unconformably overlies Ordovician-aged igneous deposits (Fig. 1B; Niu 1987). The Zhonggou Formation comprises purple-red and gray-green clastics (Bureau of Geology and Mineral Resources of Gansu Province 1989) and is also well-exposed at Changma (Fig. 1B; Niu 1987; Bureau of Geology and Mineral Resources of Gansu Province 1997). Oligocene sandstones and conglomerates pertaining to the Huoshaogou Formation unconformably overlie the Zhonggou Formation (Fig. 1B; Niu 1987).

The avian specimen described here was recovered from finely laminated (possibly varved) yellowish-brown mudstones belonging to the Xiagou Formation (Fig. 1B). Other vertebrate fossils thus far reported from this unit in the Changma Basin include the *Gansus yumenensis* holotype (Hou and Liu 1984), another bird specimen consisting of a nearly complete enantiornithine pectoral girdle and forelimb (O'Connor et al. 2004; You et al. 2005), as well as fishes and turtles (Niu 1987; Ma 1993). Niu (1987) also noted pterosaur remains from the Xiagou Formation, though not from the Changma Basin. Additional, as-yet undescribed fossil vertebrate material from the Xiagou Formation of Changma includes multiple fish specimens, a nearly complete salamander, a turtle, and approximately 50 fragmentary to nearly complete avian skeletons, several preserving feathers or soft-tissue impressions (H-LY, MCL, JDH, et al. unpublished research). Moreover, in the Changma Basin and at neighboring localities, the Xiagou Formation has yielded an abundance of fresh-water and terrestrial invertebrates and plants, including bivalves of the *Nakamuranaia*-*Margaritifera* (*Mengyinaia*)-*Neomiodonoides* assemblage of Ma (1994), gastropods (Edi-

torial Committee of Chinese Stratigraphic Standard: Cretaceous 2000), ostracodes (Hu 2004; Hu and Xu 2005), conchostracans (Shen 1981), insects (Hong 1982), charophytes (Fu and Lu 1997), a dominantly gymnospermous palynoflora (Liu 2000), and abundant and well-preserved plant megafossils (Niu 1987; H-LY, MCL personal observations).

The precise age of the Xiagou Formation within the Early Cretaceous remains uncertain. The Chijinpu Formation, which conformably underlies the Xiagou, contains elements of northeastern China's celebrated Jehol Biota, such as the conchostracan *Eosestheria middendorffii*, the insect *Ephemeroptera trisetalis*, and the fish *Lycoptera* sp. (Shen 1981; Editorial Committee of Chinese Stratigraphic Standard: Cretaceous 2000). The Xiagou Formation contains some, but not all, of the same taxa: in particular, it lacks *Lycoptera* (Ma 1993; Editorial Committee of Chinese Stratigraphic Standard: Cretaceous 2000). The Xiagou Formation may therefore be slightly younger than the Jehol Biota-bearing Yixian and Jiufotang formations of Liaoning Province and their equivalents elsewhere in northeastern China. Radiometric dates from the Yixian and Jiufotang formations typically place these units between approximately 125 and 120 million years ago (e.g., Swisher et al. 1999, 2002; He et al. 2004, 2006), corresponding to the latest Barremian–early Aptian (Gradstein et al. 2005); the Xiagou Formation may consequently be middle–late Aptian in age or marginally younger.

A diverse dinosaur fauna has been recovered from exposures referred to the Xinminpu Group in the Mazongshan area of northern Gansu (approximately 250 kilometers from the Changma Basin—Fig. 1A; see papers in Dong 1997; also Shapiro et al. 2003; You et al. 2003; You and Dodson 2003; You et al. 2005), but detailed correlation of these sediments with the Xinminpu Group of the Changma Basin has not yet been performed; accordingly, the stratigraphic relationship between these exposures is uncertain. Based primarily on palynological evidence, Tang et al. (2001) argued for an Albian age for the Xinminpu Group as exposed at Mazongshan.

Based on its fossil assemblage and lithologic character, the depositional environment of the Xiagou Formation has usually been interpreted as lacustrine (e.g., Ma 1993). Deposition of Xiagou Formation sediments has been interpreted as driven by lacustrine turbidites in a series of subaqueous fans as exemplified by repeating patterns of fining-upward, conglomerate to silty mudstone beds (Duanmu and Zhou 1990). Turbidity currents in the Xiagou lake(s) were ostensibly fault-driven by basin subsidence (Duanmu and Zhou 1990).

Systematic paleontology

Aves Linnaeus, 1758

Pygostylia Chatterjee, 1997 (*sensu* Chiappe, 2002)

Ornithothoraces Chiappe, 1996

Enantiornithes Walker, 1981

Euenantiornithes Chiappe, 2002

Gen. et sp. indet.

Referred specimen: CAGS-IG-04-CM-007, a partially articulated appendicular skeleton consisting of a fragmentary pelvic girdle and largely complete hind limbs (Fig. 2). The pelvic girdle is represented by the acetabular portion of the right ilium and ischium and nearly complete pubes; the left hind limb by the (tentatively identified) distal half of the femur, the nearly complete tibiotarsus, the proximal end of the fibula, and the complete tarsometatarsus and pes; and the right hind limb by the complete femur and the proximal half of the tibiotarsus. Possible feather impressions are preserved adjacent to the putative left femur.

Locality and horizon: Area surrounding the town of Changma in the Changma Basin of northwestern Gansu Province, China (Fig. 1A). More precise locality information is available to qualified researchers upon request. Lower Cretaceous (Aptian–?Albian) Xiagou Formation, lower unit of the Xinminpu Group (Fig. 1B).

Description

Ilium.—The acetabular portion of the right ilium is preserved and exposed in lateral view. The exposed portion of the acetabulum is subtriangular and deep. A low, dorsoventrally elongate prominence at the caudodorsal corner of the acetabulum probably represents the antitrochanter. The ventral end of the pubic peduncle possesses a small, cranially-projecting process.

Pubis.—Both pubes are preserved but broken proximally, precluding a definitive determination of their orientation relative to the remainder of the pelvis. The proximal half of the pubic shaft is straight and subcylindrical, while the distal half is mediolaterally compressed and curves caudodorsally. The distalmost ends of the pubes are slightly enlarged, but are not expanded dorsoventrally into a “boot”-like structure. The ends are closely appressed, but separated by a gap, indicating that they are not coossified.

Ischium.—A subtriangular process projecting from the caudoventral region of the acetabulum is identified as the mediolaterally thickened proximodorsal portion of the right ischium. It is fused to the ilium fragment, with no line of contact visible between these elements.

Femur.—The caudal surface of the nearly complete right femur is exposed, while an elongate fragment overlapping the left pubis is tentatively identified as the distal half of the left femur. If correctly identified, the latter is exposed in cranial view. The femoral head is spheroidal, slightly caudally projected, and bears a shallow fossa, presumably for the insertion of the capital ligament. A femoral neck (defined here as a constriction separating the femoral head from the remainder of the element) is absent. The proximolateral region of the femur bears a recess that is defined caudodistally by a prominent ridge [the caudal (= posterior) trochanter] for the insertion of the M. ischiofemoralis (Hutchinson 2001). The caudal surface of the right femoral shaft is crushed just distal to the caudal trochanter. Distal to this, the shaft is damaged laterally, but it appears to have been slender. As preserved, it is nearly straight in mediolateral view, curving only slightly caudally both proximally and

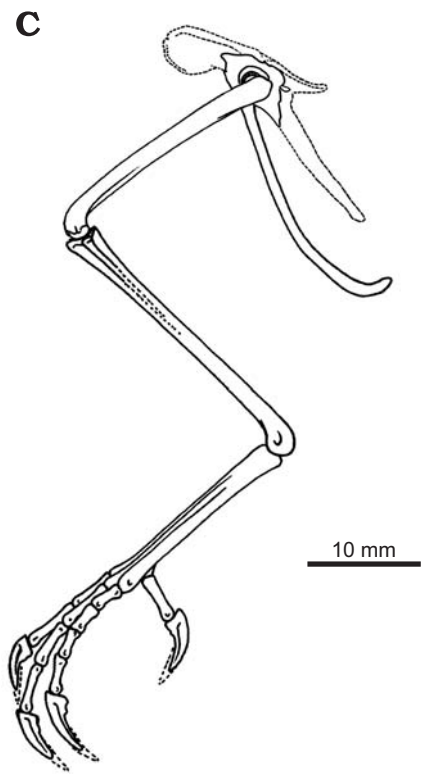
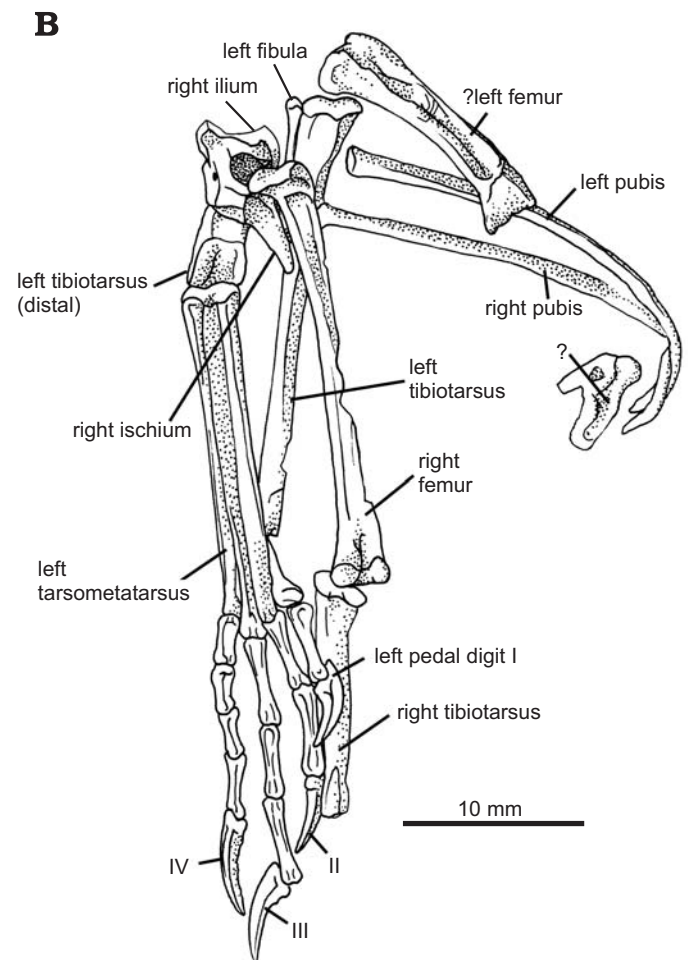


Fig. 2. *Euenantiornithes* gen. et sp. indet. (CAGS-IG-04-CM-007) from the Xiagou Formation (Lower Cretaceous) of the Changma Basin, Gansu Province, China: almost complete pelvic girdle and hind limbs. Stereopair (A), interpretive drawing (B), and reconstruction of articulated pelvic girdle and hind limb (C).

Table 1. Measurements (mm) of *Euenantiornithes* gen. et sp. indet., specimen CAGS-IG-04-CM-007. Parentheses indicate estimated measurement; asterisk denotes incomplete element.

Ilium (right)	
Acetabulum, craniocaudal diameter	1.6
Femur (right)	
Length	24.0
Proximal width	3.8
Distal width	3.1
Tibiotarsus (left)	
Length	(29.2)
Proximal width	3.4
Distal width	3.2
Tarsometatarsus (left)	
Lengths	
Metatarsal I	3.1*
Metatarsal II	19.6
Metatarsal III	20.3
Metatarsal IV	19.1
Proximal width	3.4
Pedal phalanges ¹ (left)	
I-1	4.3
I-ungual ²	(3.9)
II-1	3.6
II-2	4.9
II-ungual ²	4.4
III-1	4.8
III-2	4.0
III-3	5.0
III-ungual ²	4.4
IV-1	2.8
IV-2	2.0
IV-3	2.2
IV-4	3.7
IV-ungual ²	(4.7)

¹ Nonungual phalangeal length measured from the dorsoplantarily deepest part of the proximal articular cotyle to the apex of the furthest distal condyle.

² Ungual length measured as a chord from the extensor process of the proximal end to the distal tip of the ungual.

distally. Although much of the preserved portion of the putative left femur is badly crushed, there appears to be no patellar groove on its craniodistal surface. [Nevertheless, we deemed it most conservative to code this character (141) as indeterminate (“?”) in our phylogenetic analysis.] Caudally, a shallow popliteal fossa is developed near the distal end of the right femur. This fossa is open caudomedially, but bounded laterally by a small, poorly defined tubercle that occupies the caudolateral edge of the femur proximal to the lateral condyle. A similar tubercle is present, but better developed, in *Halimornis thompsoni*, a Late Cretaceous enantiornithine from Alabama, USA (Chiappe et al. 2002). Distally, the popliteal fossa is bounded by the two articular condyles and the intercondylar bridge. Both condyles pro-

ject well caudally. The medial condyle is nearly twice as mediolaterally broad as the lateral, and its caudal surface is rounded. The lateral condyle extends slightly farther caudally than its medial counterpart before terminating in a distinct apex that is confluent with the intercondylar bridge. The distal end of the lateral condyle defines the lateral border of a deep, broad, medially shallowing depression, possibly for the origin of the cranial cruciate ligament (Baumel and Witmer 1993).

Tibiotarsus.—Both tibiotarsi are exposed in caudal view. Only the proximal half of the right is present, while the left is broken into two portions. No significant quantity of bone seems to be missing between the two preserved portions of the left tibiotarsus, suggesting that, when complete, it was probably only slightly longer than the femur (Table 1). As in some other enantiornithines [e.g., *Gobipteryx minuta* (= “*Nanantius valifanovi*”; Kurochkin 1996: fig. 10D, F); *Soroavisaurus australis* (Chiappe and Walker 2002: fig. 11.13A)], the proximal articular surface is canted slightly distolaterally. It is ovoid in proximal view, slightly broader mediolaterally than craniocaudally. The proximolateral edge of the right tibiotarsus is damaged, while that of the left cannot be observed because it is covered by the right ischium and femur and the left fibula. The proximomedial edges of both tibiotarsi bear low, medially-projecting longitudinal crests. That of the left tibiotarsus appears damaged medially, while that of the right is largely obscured by pedal digit I. The tibiotarsal shaft is slender and straight.

The distal end of the left tibiotarsus is clearly exposed caudally and articulated with the corresponding tarsometatarsus. The tibia is probably coossified with the proximal tarsals because there is no evidence of a suture between these elements, and because no separate tarsals are present. Both tibiotarsal condyles expand much farther cranially than caudally, and are subcircular in mediolateral view. The lateral surface of the lateral condyle is excavated by a shallow, subcircular epicondylar depression; the medial surface lacks a comparable feature.

Fibula.—The proximal end of the left fibula is articulated and closely appressed to the tibiotarsus. As articulated, it projects slightly farther proximally than does the proximolateral margin of the tibiotarsus. The fibula is slender and mediolaterally compressed, with convex lateral and concave medial surfaces. It is slightly craniocaudally expanded proximally, more so cranially than caudally. The shaft is broken immediately distal to the proximal end. Nonetheless, the morphology of the tibiotarsus indicates that the fibula was reduced distally and probably did not extend to the proximal tarsals.

Tarsometatarsus.—The complete left tarsometatarsus is preserved and prepared in plantar view. The distal tarsals are fused together, forming a solid cap that is coossified with the proximal ends of metatarsals II–IV. However, the remainder of the metatarsus appears unfused. There is no evidence of a hypotarsus.

The shaft of metatarsal I is splint-shaped and appressed to the distalmost end of the plantaromedial surface of metatarsal II. This may represent its natural position; however, we suspect that it has been displaced plantarily, such that its condyle would have been situated more medially in life. Although the proximal end of metatarsal I is broken away, the element appears to have been very short. As in *Sinornis* (Serenó et al. 2002: fig. 8.5), angular dorsal and plantar processes occur immediately proximal to its bulbous and dorso-plantarily elliptical distal condyle.

Metatarsals II–IV are mediolaterally compressed, coplanar, and elongate, with the longest (metatarsal III) measuring 85% the length of the femur (Tables 1, 2). The three metatarsals are slightly plantarily expanded proximally; at least metatarsals II and IV are dorsally expanded as well. The proximal ends of the latter two elements are also moderately mediolaterally expanded, “pinching” metatarsal III between them. Both the proximomedial margin of metatarsal II and the proximolateral margin of metatarsal IV are attenuated into plantarily-projecting ridges (the medial and lateral plantar crests of Baumel and Witmer 1993) that persist for the proximal three-fourths of the metatarsus, tapering distally. Metatarsal II is only slightly shorter than metatarsal III, and appears dorsoplantarily compressed. Metatarsal IV, marginally the shortest of the three, is also the narrowest, especially at midlength, where its mediolateral diameter is approximately half that of the third metatarsal. Distally, a notch that probably corresponds to the distal vascular foramen (Baumel and Witmer 1993) is present between metatarsals III and IV. Because these metatarsals are distally unfused, we consider the distal vascular foramen to be only partially enclosed in CAGS-IG-04-CM-007.

Metatarsals II–IV are slightly mediolaterally expanded distally. The distal trochleae of metatarsals II and III possess defined medial and lateral rims separated by a shallow sulcus. The medial rim of the metatarsal II trochlea is partially covered by metatarsal I and phalanges I-1 and II-1. Both distal rims of the metatarsal III trochlea project plantarily roughly the same distance. The lateral rim is slightly wider than the medial. The trochlea of metatarsal IV, although partially obscured by phalanx IV-1, appears to be relatively small and plantarily undivided. Metatarsal V is absent.

Pes.—The left pes is complete, well preserved, and except for digit I and the ungual of digit III, exposed in plantar view. The pedal phalangeal formula is 2-3-4-5-x. All nonungual phalanges are expanded mediolaterally and dorsoplantarily at their proximal and distal ends. Digit I is exposed in lateral view, having rotated medially from a probably retroverted in vivo orientation. Its proximal phalanx is approximately the same length as its ungual (Table 1). The proximal phalanx of digit II is slightly shorter than both its penultimate phalanx and ungual. In digit III, the proximal phalanx is the most robust and about the same length as the penultimate phalanx, the second is the shortest, and the ungual is intermediate in length. The first three phalanges of digit IV are much shorter than the penultimate phalanx, which is in turn shorter than

the claw. The proximoplantar ends of phalanges II-1 and III-1 bear shallow sagittal sulci that are absent in phalanx IV-1. The nonungual phalanges of digits I and III and at least the distalmost three phalanges of digit IV bear collateral ligament pits; the relevant regions of digit II cannot be observed. The collateral ligament pits are best developed on the penultimate phalanges, where they are dorsally situated.

Pedal unguals II–IV are approximately the same length; ungual I is marginally shorter. None of the unguals are sharply recurved. Those of digits I–III exhibit grooves on their exposed medial and/or lateral surfaces; damage prevents a definitive assessment of this character in the digit IV ungual. Ungual I possesses a weak flexor tuberculum that is barely distinct from the proximoventral corner of the articular cotyle. In contrast, ungual III displays a better-developed, plantarily rounded flexor tuberculum that is situated distal to, and is distinctly separate from, the proximoventral end of the articular cotyle. All unguals are generally laterally compressed, but at least ungual III is slightly wider plantarily than dorsally. No keratinous ungual sheaths are preserved.

Integument.—Possible feather impressions are preserved adjacent to the putative left femur, but are too poorly preserved to be definitively identified.

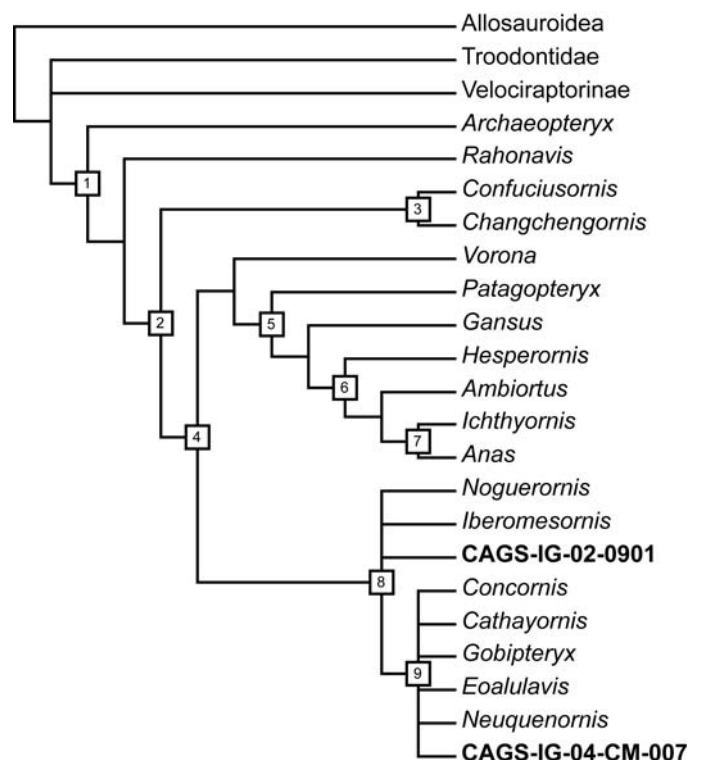


Fig. 3. Hypothesized phylogenetic position of CAGS-IG-04-CM-007, based on a parsimony analysis of three nonavian theropod outgroups and 20 avian ingroup taxa in PAUP* 4.0b10 (Swofford 2002). Numbered nodes are as follows: 1, Aves; 2, Pygostylia; 3, Confuciusornithidae; 4, Ornithothoraces; 5, Ornithomorpha; 6, Ornithurae; 7, Carinatae; 8, Enantiornithes; 9, Euenantiornithes. Note the position of CAGS-IG-04-CM-007 within Euenantiornithes, as opposed to that of another Changma specimen (CAGS-IG-02-0901; You et al. 2005), as a putative basal enantiornithine.

Phylogenetic relationships

To gain an understanding of the evolutionary affinities of CAGS-IG-04-CM-007, we performed a phylogenetic analysis. We added the new specimen to the character-taxon matrix presented by Chiappe (2002) and augmented by You et al. (2005) (see Appendix 1). We further modified this matrix by deleting representatives of Alvarezsauridae (*Alvarezsaurus*, *Patagonykus*, *Mononykus*, and *Shuvuuia*) because the majority of recent phylogenetic analyses (e.g., Norell et al. 2001; Sereno 2001; Chiappe 2002; Novas and Pol 2002; Makovicky et al. 2005) have recovered this clade outside of Aves (albeit in an unresolved position among nonavian coelurosaurs). The resulting matrix of 23 OTUs and 169 anatomical characters was subjected to parsimony analysis using the heuristic search option [random addition sequence (50 replicates), TBR swapping algorithm] of PAUP* 4.0b10 for Macintosh (Swofford 2002). Following You et al. (2005), characters 58, 96, and 154 were treated as additive (ordered), and Allosauroidea, Troodontidae, and Velociraptorinae were used as outgroups.

The analysis recovered 162 most parsimonious trees of 259 steps (CI = 0.641; RI = 0.782), the strict consensus of which is depicted in Fig. 3. CAGS-IG-04-CM-007 is resolved within Enantiornithes, a diverse and widespread clade of Cretaceous volant birds (Fig. 3). Phylogenetic relationships within the clade remain poorly resolved at present, despite recent efforts (e.g., Chiappe 2002; Chiappe and Walker 2002; Sereno et al. 2002; You et al. 2005, and references therein). This is due to at least two factors: the depauperate fossil record of the clade, and the remarkable similarity of the postcranial skeletons of at least the Early Cretaceous enantiornithine taxa (Sereno et al. 2002).

Chiappe (2002) subdivided Enantiornithes into two component clades: an unnamed clade including the Spanish Early Cretaceous forms *Iberomesornis* and *Noguerornis*, and another (Euenantiornithes) including all other taxa included in his analysis (*Concornis*, *Eoalulavis*, *Gobipteryx*, *Neuquenornis*, and *Sinornis*). Although Chiappe (2002) found only weak support for the former clade, the monophyly of euenantiornithines appears robust. CAGS-IG-04-CM-007 is here resolved within Euenantiornithes (Fig. 3).

Comparisons to other Early Cretaceous enantiornithines

Basal enantiornithines.—Two enantiornithines that purportedly reside outside Euenantiornithes are known from the Early Cretaceous of Spain: *Iberomesornis romerali* (Sanz and Bonaparte 1992) and *Noguerornis gonzalezi* (Lacasa-Ruiz 1989). In *Iberomesornis*, both the proximal and distal tarsals have been described as free, and the metatarsals appear to be unfused (Sanz and Bonaparte 1992; Sanz et al.

2002; but see Sereno 2000). Conversely, in CAGS-IG-04-CM-007, the proximal tarsals are fused to the distal tibia, and the distal tarsals to the proximal surfaces of the metatarsals. Elements in common between CAGS-IG-04-CM-007 and *Noguerornis gonzalezi* (Chiappe and Lacasa-Ruiz 2002) consist only of a partial, questionably identified tibia in the latter, obviating comparison between the two.

Zhang and Zhou (2000) reported *Protopteryx fengningensis* as a basal enantiornithine. Nevertheless, Chiappe and Walker (2002) questioned the placement of this taxon within Enantiornithes. Regardless of its precise affinities, the presence of free tarsals in *Protopteryx* differs from the condition in CAGS-IG-04-CM-007 and suggests a more basal phylogenetic position for the former taxon.

Euenantiornithines.—Two additional enantiornithine taxa, both considered to be representatives of Euenantiornithes, are known from the Spanish Early Cretaceous: *Concornis lacustris* (Sanz and Buscalioni 1992) and *Eoalulavis hoyasi* (Sanz et al. 1996). In *Concornis lacustris*, metatarsal I is straighter in mediolateral view than in CAGS-IG-04-CM-007 and many other enantiornithines (Sanz et al. 2002). The poorly known ilium and femur of *Eoalulavis hoyasi* (Sanz et al. 2002) do not allow for detailed comparisons to CAGS-IG-04-CM-007.

In their revision of the clade, Chiappe and Walker (2002) considered five previously described Chinese euenantiornithine species to be valid: *Sinornis santensis* [(Sereno and Rao 1992) = *Cathayornis yandica* (Zhou et al. 1992)], *Otogornis genghisi* (Hou 1994), *Boluochia zhengi* (Zhou 1995), *Eoenantiornis buhleri* (Hou et al. 1999), and *Longipteryx chaoyangensis* (Zhang et al. 2001). Chiappe and Walker (2002) were unable to evaluate several additional, more recently described Chinese Early Cretaceous enantiornithines: *Aberatiodontus wui* (Gong et al. 2004), *Dapingfangornis sentisorhinus* (Li et al. 2006), *Eocathayornis walkeri* (Zhou 2002), *Longirostravis hani* (Hou et al. 2004), and *Vescornis hebeiensis* (Zhang et al. 2004).

CAGS-IG-04-CM-007 differs from *Sinornis santensis* in several aspects of the hind limb. In *S. santensis*, the proximal articular surface of the tibiotarsus is oval, marginally longer craniocaudally than broad mediolaterally (Sereno et al. 2002); conversely, in CAGS-IG-04-CM-007, this surface is broader than long. Moreover, in *Sinornis*, the femur is approximately 1.5 times longer than metatarsal III, while in CAGS-IG-04-CM-007 metatarsal III approaches the femur in length (Table 2). Finally, although this is exaggerated by the preservation of keratinous claw sheaths in at least some specimens (e.g., BPV 538a; Sereno et al. 2002), the strongly recurved pedal unguis of *S. santensis* are much longer than their corresponding penultimate phalanges. In contrast, the pedal unguis of CAGS-IG-04-CM-007 are closer in length to their penultimate phalanges, and are less recurved than those of *S. santensis*.

CAGS-IG-04-CM-007 also differs from other Chinese enantiornithines. In the intriguing, possibly raptorial form

Table 2. Comparative ratios of hind limb element lengths in several Early Cretaceous enantiornithines. Parentheses indicate ratios based on one estimated length. Length of tarsometatarsus considered equivalent to length of metatarsal III in *Eoenantiornis* and *Longirostravis*. Abbreviations: CM-007, CAGS-IG-04-CM-007; f, femur; mt III, metatarsal III; tt, tibiotarsus. Sources: ¹Sereno 2000; ²Hou et al. 1999; ³Hou et al. 2004; ⁴Sereno et al. 2002.

Ratio	<i>Iberomesornis</i> LH-22 ¹	<i>Concornis</i> LH-2814 ¹	<i>Eoenantiornis</i> IVPP V11537 ²	<i>Longirostravis</i> IVPP V11309 ³	<i>Sinornis</i> BPV 538a ⁴	Gen. et sp. indet. CM-007
f/tt	0.82	0.69	0.86	0.78	(0.81)	(0.82)
f/mt III	1.39	1.20	1.19	1.43	(1.44)	1.18
tt/mt III	1.70	1.74	1.39	1.82	1.79	(1.44)

Boluochia zhengi, the trochleae of metatarsals II–IV lie in approximately the same proximodistal plane, and the pedal unguis are long and recurved (Zhou 1995; Zhou and Hou 2002). In *Longipteryx chaoyangensis*, the proximal tarsals are not completely fused with the tibia, and metatarsal IV is longer than metatarsals II and III (Zhang et al. 2001). In *Aberratiodontus wui* (Gong et al. 2004), *Dapingfangornis sentisorhinus* (Li et al. 2006), and *Longirostravis hani* (Hou et al. 2004), the metatarsus is short, only about half the length of the tibiotarsus (Table 2). All of these characters are absent in CAGS-IG-04-CM-007. Interestingly, as described by Hou et al. (1999) and Zhou et al. (2005), most aspects of the anatomy and proportions of the hind limb of *Eoenantiornis buhleri* appear closely similar to those of CAGS-IG-04-CM-007 (Table 2). However, in *E. buhleri*, the pubis is craniocaudally compressed and the femur strongly curved (Zhou et al. 2005), differing from the conditions preserved in the Changma specimen. The pelvic girdle and hind limb remain unknown for *Otogornis genghisi* and *Eocathayornis walkeri* (Hou 1994; Kurochkin 1999; Zhou 2002); as a result, these taxa cannot presently be compared with CAGS-IG-04-CM-007.

Putative enantiornithines.—Several works (e.g., Kurochkin 1991, 2000; Unwin 1993; Bakhurina and Unwin 1995) have commented on, but have not described in detail, a probable enantiornithine partial skeleton from Early Cretaceous (?Hauterivian–Aptian, see Kurochkin 1999) beds of Kholboot, south-central Mongolia. The specimen reportedly consists of an incomplete skull and pectoral, forelimb, and hind limb elements (Kurochkin 2000). As it is at least broadly similar in age and geographic provenance to CAGS-IG-04-CM-007, this bird is of considerable interest to the current study. Moreover, it apparently possesses a “very long tarsometatarsus” (Kurochkin 2000) and thus may be comparable to the Changma enantiornithine in this regard (see above, also Table 2). However, detailed comparisons of the two specimens will not be possible until the Mongolian form is fully described and illustrated.

Discussion

As demonstrated above, the preserved material of CAGS-IG-04-CM-007 exhibits anatomical distinctions from all

other presently recognized enantiornithine taxa to which it can be directly compared. Coupled with its geographic and probable temporal distance from these taxa, this suggests that the Changma skeleton may represent an as-yet unnamed euenantiornithine taxon. However, the incompleteness of the specimen, and its lack of definitive autapomorphies, prevents us from erecting a new taxon for CAGS-IG-04-CM-007 at this time.

You et al. (2005) described a nearly complete avian pectoral girdle and forelimb (CAGS-IG-02-0901) from the Xiagou Formation of the Changma Basin, from a locality only ~150 m from the discovery site of CAGS-IG-04-CM-007. They identified several synapomorphies of Enantiornithes displayed by CAGS-IG-02-0901, referring it to a generically indeterminate representative of this clade. As shown here, CAGS-IG-04-CM-007 also clearly pertains to Enantiornithes. Given the phylogenetic, stratigraphic, and geographic proximity of the two specimens, it is possible that they represent the same taxon. Regrettably, however, they preserve no overlapping elements and are thus not directly comparable.

CAGS-IG-02-0901 represents an avian individual approximately the size of a rock dove (You et al. 2005); CAGS-IG-04-CM-007 is considerably smaller, pertaining to a large sparrow or thrush-sized bird (Table 1). Nevertheless, the apparent fusion of most of its pelvic bones, as well as its tibiotarsal and tarsometatarsal elements, suggests that the latter individual was fully grown. Moreover, although this position is not strongly supported, our phylogenetic analysis recovers CAGS-IG-02-0901 as a basal enantiornithine, and CAGS-IG-04-CM-007 as a representative of Euenantiornithes (Fig. 3). Furthermore, the humerus of CAGS-IG-02-0901 measures 47.7 mm in length (You et al. 2005); the femur of CAGS-IG-04-CM-007 is 24.0 mm (Table 1), yielding a humerofemoral ratio of 1.99. This ratio varies between 0.94 and 1.56 in described enantiornithine specimens preserving both of these elements (Table 3). Consequently, if CAGS-IG-04-CM-007 is indeed an adult, it seems unlikely that this specimen and CAGS-IG-02-0901 could pertain to the same taxon. Multiple enantiornithine taxa may be present in the Xiagou Formation of the Changma Basin, as is definitively the case in several other Cretaceous units [e.g., Lecho Formation, Argentina (Walker 1981; Chiappe 1993); Calizas de la Huérguina Formation, Spain (Sanz et al. 2002); Yixian and Jiufotang formations, northeastern China (Zhou and Hou 2002)].

Table 3. Ratios of humeral to femoral length in selected enantiornithine specimens. Parentheses indicate ratios based on one estimated measurement. “*Liaoxiornis delicatus*” is here considered to be of doubtful validity following Chiappe and Walker (2002).

Taxon	Specimen	Ratio	Source
“ <i>Liaoxiornis delicatus</i> ”	NIGPAS 130723	0.94	Hou and Chen 1999
<i>Dapingfangornis sentisorhinus</i>	LPM 00039	0.96	Li et al. 2006
<i>Iberomesornis romerali</i>	LH-22	(1.07)	Sereno 2000
<i>Eoenantiornis buhleri</i>	IVPP V11537	1.11	Hou et al. 1999
<i>Sinornis santensis</i>	BPV 538a	(1.14)	Sereno et al. 2002
<i>Sinornis santensis</i>	IVPP V9769	1.17	Sereno et al. 2002
<i>Longirostravis hani</i>	IVPP V11309	1.20	Hou et al. 2004
<i>Concornis lacustris</i>	LH-2814	1.31	Sereno 2000
<i>Longipteryx chaoyangensis</i>	IVPP V12325	1.56	Zhang et al. 2001

Within the past decade, the Yixian and overlying Jiufotang formations of northeastern China’s Liaoning and Hebei provinces have produced hundreds of fossil bird specimens, pertaining to basal avians, confuciusornithids, enantiornithines, and basal ornithuromorphs (Zhang et al. 2003; Zhou and Zhang 2006). As noted by You et al. (2005), the avifauna preserved in the Xiagou Formation is generally similar to those of the Yixian and Jiufotang formations in that it includes both enantiornithines (e.g., CAGS-IG-02-0901, CAGS-IG-04-CM-007) and ornithuromorphs (*Gansus yumenensis*). However, more basal, non-ornithothoracine forms such as confuciusornithids, which are numerically dominant in the Yixian Formation (Zhou et al. 2003), and may also be present in the Jiufotang (Li et al. 2006; Zhou and Zhang 2006), and basal avians [e.g., *Jeholornis* (Zhou and Zhang 2002a), *Sapeornis* (Zhou and Zhang 2002b, 2003)], which are unequivocally known from the Jiufotang, have not yet been recovered from the Xiagou Formation. Moreover, based on our initial fossil collections from the Changma Basin, it preliminarily appears that ornithuromorph birds may be considerably more abundant than enantiornithines in the Xiagou Formation. Roughly four-fifths of the approximately 50 avian specimens thus far recovered from Changma appear to pertain to *Gansus yumenensis*; the remainder, including CAGS-IG-02-0901 and CAGS-IG-04-CM-007, appear referable to Enantiornithes (H-LY, MCL, JDH, et al. unpublished research). This contrasts sharply with the Yixian and Jiufotang avifaunas, in which enantiornithines greatly outnumber ornithuromorphs (Zhou et al. 2003).

If it is not an artifact of incomplete or biased sampling, this putative avifaunal distinction between the Xiagou and Yixian/Jiufotang formations could be due to one or more of several factors, including: (1) the geographic (and paleogeographic) distance (~2000 km) separating outcrops of the Xiagou Formation from those of the Yixian and Jiufotang formations; (2) potential differences in the paleoenvironments preserved in these units; and/or (3) the probable differing ages of the units. Preliminarily, we consider the latter factor to be the most important. As detailed above, biostratigraphic studies of nonavian fossils suggest that the Xiagou

Formation may be slightly younger than the Yixian and Jiufotang formations. As currently understood, the Xiagou avifauna appears to support this assertion, in that, like all known avifaunas younger than that of the Jiufotang Formation, it lacks basal, non-ornithothoracine birds. [The enigmatic theropod *Rahonavis*, from the latest Cretaceous (Maastrichtian), Maevarano Formation of Madagascar, was initially proposed as a basal avian (Forster et al. 1998); however, this taxon was recently reinterpreted as a member of the nonavian theropod clade Dromaosauridae (Makovicky et al. 2005)]. In any case, further insight into the temporal and paleoenvironmental context of the Xiagou Formation will be a prerequisite for a detailed understanding of the relationships of its emerging fossil biota to those of the Jehol Group and other Cretaceous bird-bearing units.

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References

- Bakhurina, N.N. and Unwin, D. 1995. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. *Historical Biology* 10: 197–245.

- Baumel, J.J. and Witmer, L.M. 1993. Osteologia. In: J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (eds.), *Handbook of Avian Anatomy: Nomina Anatomica Avium* (second edition), 45–132. Nuttall Ornithological Club, Cambridge.
- Bureau of Geology and Mineral Resources of Gansu Province. 1989. *Regional Geology of Gansu Province* [in Chinese with English summary]. 692 pp. Geological Publishing House, Beijing.
- Bureau of Geology and Mineral Resources of Gansu Province. 1997. *Stratigraphy (Lithostratigraphic) of Gansu Province* [in Chinese]. 314 pp. China University of Geosciences Press, Beijing.
- Chatterjee, S. 1997. *The Rise of Birds*. 312 pp. The Johns Hopkins University Press, Baltimore.
- Chiappe, L.M. 1993. Enantiornithine (Aves) tarsometatarsi from the Cretaceous Lecho Formation of northwestern Argentina. *American Museum Novitates* 3083: 1–27.
- Chiappe, L.M. 1996. Late Cretaceous birds of southern South America: anatomy and systematics of Enantiornithes and *Patagopteryx deferrariisi*. *Münchener Geowissenschaftliche Abhandlungen* 30: 203–244.
- Chiappe, L.M. 2002. Basal bird phylogeny: problems and solutions. In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 448–472. University of California Press, Berkeley.
- Chiappe, L.M. and Dyke, G.J. 2002. The Mesozoic radiation of birds. *Annual Review of Ecology and Systematics* 33: 91–124.
- Chiappe, L.M., and Lacasa-Ruiz, A. 2002. *Noguerornis gonzalezi* (Aves: Ornithothoraces) from the Early Cretaceous of Spain. In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 230–239. University of California Press, Berkeley.
- Chiappe, L.M., Lamb, J.P., and Ericson, P.G.P. 2002. New enantiornithine bird from the marine Upper Cretaceous of Alabama. *Journal of Vertebrate Paleontology* 22: 170–174.
- Chiappe, L.M. and Walker, C.A. 2002. Skeletal morphology and systematics of the Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes). In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 240–267. University of California Press, Berkeley.
- Dong, Z.-M. 1997. *Sino-Japanese Silk Road Dinosaur Expedition*. 114 pp. China Ocean Press, Beijing.
- Duanmu, H.-S. and Zhou, L.-F. 1990. Gravity-flow-submerged-fan deposits of Lower Cretaceous Xiagou Formation, Jiuxi Basin, Gansu [in Chinese with English summary]. *Acta Sedimentologica Sinica* 8: 75–85.
- Editorial Committee of Chinese Stratigraphic Standard: Cretaceous. 2000. *Chinese Stratigraphic Standard: Cretaceous* [in Chinese]. 124 pp. Geological Publishing House, Beijing.
- Forster, C.A., Sampson, S.D., Chiappe, L.M., and Krause, D.W. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279: 1915–1919.
- Fu, J.-H. and Lu, H.-N. 1997. Early Cretaceous fossil charophytes from Xiagou Formation at Jiedabangou, Huahui Basin, Gansu [in Chinese with English summary]. *Acta Palaeontologica Sinica* 36: 350–357.
- Gong, E.-P., Hou, L.-H., and Wang, L.-X. 2004. Enantiornithine bird with diapsidian skull and its dental development in the Early Cretaceous in Liaoning, China. *Acta Geologica Sinica* 78: 1–7.
- Gradstein, F.M., Ogg, J.G., and Smith, A.G. (eds.) 2005. *A Geologic Time Scale 2004*. 610 pp. Cambridge University Press, Cambridge.
- He, H.-Y., Wang, X.-L., Zhou, Z.-H., Wang, F., Boven, A., Shi, G.-H., and Zhu, R.-X. 2004. Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern China, and its implications. *Geophysical Research Letters* 31: L12605.
- He, H.-Y., Wang, X.-L., Zhou, Z.-H., Jin, F., Wang, F., Yang, L. K., Ding, X., Boven, A., and Zhu, R.-X. 2004. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Lujiatun Bed (Jehol Group) in Liaoning, northeastern China. *Geophysical Research Letters* 33: L04303.
- Hong, Y.-C. 1982. *Mesozoic Fossil Insects of Jiuquan Basin in Gansu Province* [in Chinese]. 187 pp. Geological Publishing House, Beijing.
- Hou, L.-H. 1994. A late Mesozoic bird from Inner Mongolia [in Chinese with English summary]. *Vertebrata Palasiatica* 32: 258–266.
- Hou, L.-H. and Chen, P.-J. 1999. *Liaoxiornis delicatus* gen. et sp. nov., the smallest Mesozoic bird. *Chinese Science Bulletin* 44: 834–838.
- Hou, L.-H., Chiappe, L.M., Zhang, F.-C., and Chuong, C.-M. 2004. New Early Cretaceous fossil from China documents a novel trophic specialization for Mesozoic birds. *Naturwissenschaften* 91: 22–25.
- Hou, L.-H. and Liu, Z.-C. 1984. A new fossil bird from Lower Cretaceous of Gansu and early evolution of birds. *Scientia Sinica (Series B)* 27: 1296–1301.
- Hou, L.-H., Martin, L.D., Zhou, Z.-H., and Feduccia, A. 1999. *Archaeopteryx* to opposite birds—missing link from the Mesozoic of China. *Vertebrata Palasiatica* 37: 88–95.
- Hu, Y.-X. 2004. Early Cretaceous ostracods from the Xiagou Formation of Hongliuxia in the Yumen area, Gansu of NW China [in Chinese with English summary]. *Acta Micropalaeontologica Sinica* 21: 439–451.
- Hu, Y.-X. and Xu, D.-L. 2005. Early Cretaceous ostracods from the Xiagou Formation in Xiagou, Gansu Province [in Chinese with English summary]. *Acta Micropalaeontologica Sinica* 22: 173–184.
- Hutchinson, J.R. 2001. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131: 169–197.
- Kurochkin, E.N. 1991. *Protoavis*, *Ambiortus*, and other palaeornithological rarities [in Russian]. *Priroda* 12: 43–53.
- Kurochkin, E.N. 1996. A new enantiornithid of the Mongolian Late Cretaceous, and a general appraisal of the Infraclass Enantiornithes (Aves). *Russian Academy of Sciences, Palaeontological Institute Special Issue*: 1–50.
- Kurochkin, E.N. 1999. The relationships of the Early Cretaceous *Ambiortus* and *Otogornis* (Aves: Ambiortiformes). In: S.L. Olson, P. Wellnhofer, C. Mourer-Chauviré, D.W. Steadman, and L.D. Martin (eds.), *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996*, 275–284. Smithsonian Institution Press, Washington, D.C.
- Kurochkin, E.N. 2000. Mesozoic birds of Mongolia and the former USSR. In: M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, 533–559. Cambridge University Press, Cambridge.
- Lacasa-Ruiz, A. 1989. Nuevo genero de ave fosil del Yacimiento Neocomiense del Montsec (Provincia de Lerida, España). *Estudios Geológicos* 45: 417–425.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, reformata*. 824 pp. Laurentii Salvii, Stockholm.
- Li, L., Duan, Y., Hu, D.-Y., Wang, L., Cheng, S.-L., and Hou, L.-H. 2006. New enantiornithid bird from the Early Cretaceous Jiufotang Formation of western Liaoning, China. *Acta Geologica Sinica* 80: 38–41.
- Liu, Z.-S. 2000. Early Cretaceous sporopollen assemblage from the Hanxia of Yumen in Gansu, NW China [in Chinese with English summary]. *Acta Micropalaeontologica Sinica* 17: 73–84.
- Ma, F. 1993. *Late Mesozoic Fossil Fishes from the Jiuquan Basin of Gansu Province, China* [in Chinese with English summary]. 118 pp. China Ocean Press, Beijing.
- Ma, Q.-H. 1994. Nonmarine Cretaceous bivalve assemblages in China. *Cretaceous Research* 15: 271–284.
- Makovicky, P.J., Apesteguía, S., and Agnolin, F.L. 2005. The earliest dromaeosaurid theropod from South America. *Nature* 437: 1007–1011.
- Niu, S.-W. 1987. Late Mesozoic strata of the Jiuquan in Gansu [in Chinese]. *Journal of Stratigraphy* 11: 1–22.
- Norell, M.A., Clark, J.M., and Makovicky, P.J. 2001. Phylogenetic relationships among coelurosaurian theropods. In: J. Gauthier and L.F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds*, 49–67. Peabody Museum of Natural History, New Haven.
- Novas, F. and Pol, D. 2002. Alvarezsaurid relationships reconsidered. In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 121–125. University of California Press, Berkeley.

- O'Connor, J., Chiappe, L.M., Ji, Q., and You, H.-L. 2004. New enantiornithine bird from the Early Cretaceous of Gansu Province, northwestern China. *Journal of Vertebrate Paleontology* 24: 99A.
- Sanz, J.L. and Bonaparte, J.F. 1992. A new order of birds (Class Aves) from the Lower Cretaceous of Spain. In: K.C. Campbell (ed.), *Papers in Avian Paleontology Honoring Pierce Brodkorb*, 39–49. Natural History Museum of Los Angeles County, Los Angeles.
- Sanz, J.L. and Buscalioni, A.D. 1992. A new bird from the Early Cretaceous of Las Hoyas, Spain, and the early radiation of birds. *Palaeontology* 35: 829–845.
- Sanz, J.L., Chiappe, L.M., Pérez-Moreno, B.P., Buscalioni, A.D., Moratalla, J.J., Ortega, F., and Poyato-Ariza, F.J. 1996. An Early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature* 382: 442–445.
- Sanz, J.L., Pérez-Moreno, B.P., Chiappe, L.M., and Buscalioni, A.D. 2002. The birds from the Lower Cretaceous of Las Hoyas (province of Cuenca, Spain). In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 209–229. University of California Press, Berkeley.
- Sereno, P.C. 2000. *Iberomesornis romerali* (Aves, Ornithothoraces) reevaluated as an Early Cretaceous enantiornithine. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 215: 365–395.
- Sereno, P.C. 2001. Alvarezsaurids: birds or ornithomimosaur? In: J. Gauthier and L.F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds*, 69–98. Peabody Museum of Natural History, New Haven.
- Sereno, P.C. and Rao, C.-G. 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. *Science* 255: 845–848.
- Sereno, P.C., Rao, C.-G., and Li, J.-J. 2002. *Sinornis santensis* (Aves: Enantiornithes) from the Early Cretaceous of northeastern China. In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 184–208. University of California Press, Berkeley.
- Shapiro, M.D., You, H.-L., Shubin, N.H., Luo, Z.-X., and Downs, J.P. 2003. A large ornithomimid pes from the Lower Cretaceous of the Mazongshan area, northern Gansu Province, People's Republic of China. *Journal of Vertebrate Paleontology* 23: 695–698.
- Shen, Y.-B. 1981. Fossil conchostracans from the Chijinpu Formation (Upper Jurassic) and the Xinminpu Group (Lower Cretaceous) in Hexi Corridor, Gansu [in Chinese with English summary]. *Acta Palaeontologica Sinica* 20: 266–272.
- Swisher, C.C., Wang, Y.-Q., Wang, X.-L., Xu, X., and Wang, Y. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* 400: 58–61.
- Swisher, C.C., Wang, X.-L., Zhou, Z.-H., Wang, Y.-Q., Jin, F., Zhang, J.-Y., Xu, X., Zhang, F.-C., and Wang, Y. 2002. Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: new $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Yixian and Tuchengzi formations. *Chinese Science Bulletin* 47: 135–138.
- Swofford, D.L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Sunderland, Massachusetts.
- Tang, F., Luo, Z.-X., Zhou, Z.-H., You, H.-L., Georgi, J.A., Tang, Z.-L., and Wang, X.-Z. 2001. Biostratigraphy and palaeoenvironment of the dinosaur-bearing sediments in Lower Cretaceous of Mazongshan area, Gansu Province, China. *Cretaceous Research* 22: 115–129.
- Unwin, D.M. 1993. Aves. In M. J. Benton (ed.), *The Fossil Record* 2, 717–738. Chapman and Hall, London.
- Walker, C.A. 1981. New subclass of birds from the Cretaceous of South America. *Nature* 292: 51–53.
- You, H.-L. and Dodson, P. 2003. Redescription of neoceratopsian dinosaur *Archaeoceratops* and early evolution of Neoceratopsia. *Acta Palaeontologica Polonica* 48: 261–272.
- You, H.-L., Li, D.-Q., Ji, Q., Lamanna, M.C., and Dodson, P. 2005. On a new genus of basal neoceratopsian dinosaur from the Early Cretaceous of Gansu Province, China. *Acta Geologica Sinica* 79: 593–597.
- You, H.-L., O'Connor, J., Chiappe, L.M., and Ji, Q. 2005. A new fossil bird from the Early Cretaceous of Gansu Province, northwestern China. *Historical Biology* 17: 7–14.
- You, H.-L., Tang, F., and Luo, Z.-X. 2003. A new basal titanosaur (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Acta Geologica Sinica* 77: 424–429.
- Zhang, F.-C., Ericson, P.G.P., and Zhou, Z.-H. 2004. Description of a new enantiornithine bird from the Early Cretaceous of Hebei, northern China. *Canadian Journal of Earth Sciences* 41: 1097–1107.
- Zhang, F.-C. and Zhou, Z.-H. 2000. A primitive enantiornithine bird and the origin of feathers. *Science* 290: 1955–1960.
- Zhang, F.-C., Zhou, Z.-H., and Hou, L.-H. 2003. Birds. In: M.-M. Chang (ed.), *The Jehol Biota: the Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants*, 129–150. Shanghai Scientific and Technical Publishers, Shanghai.
- Zhang, F.-C., Zhou, Z.-H., Hou, L.-H., and Gu, G. 2001. Early diversification of birds: evidence from a new opposite bird. *Chinese Science Bulletin* 46: 945–949.
- Zhou, Z.-H. 1995. Discovery of a new enantiornithine bird from the Early Cretaceous of Liaoning, China [in Chinese with English summary]. *Vertebrata Palasiatica* 33: 99–113.
- Zhou, Z.-H. 2002. A new and primitive enantiornithine bird from the Early Cretaceous of China. *Journal of Vertebrate Paleontology* 22: 49–57.
- Zhou, Z.-H. 2004. The origin and early evolution of birds: discoveries, disputes, and perspectives from fossil evidence. *Naturwissenschaften* 91: 455–471.
- Zhou, Z.-H., Barrett, P.M., and Hilton, J. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421: 807–814.
- Zhou, Z.-H., Chiappe, L.M., and Zhang, F.-C. 2005. Anatomy of the Early Cretaceous bird *Eoenantiornis buhleri* (Aves: Enantiornithes) from China. *Canadian Journal of Earth Sciences* 42: 1331–1338.
- Zhou, Z.-H. and Hou, L.-H. 2002. The discovery and study of Mesozoic birds in China. In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 160–183. University of California Press, Berkeley.
- Zhou, Z.-H., Jin, F., and Zhang, J.-Y. 1992. Preliminary report on a Mesozoic bird from Liaoning, China. *Chinese Science Bulletin* 37: 1365–1368.
- Zhou, Z.-H. and Zhang, F.-C. 2002a. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* 418: 405–409.
- Zhou, Z.-H. and Zhang, F.-C. 2002b. Largest bird from the Early Cretaceous and its implications for the earliest avian ecological diversification. *Naturwissenschaften* 89: 34–38.
- Zhou, Z.-H. and Zhang, F.-C. 2003. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Canadian Journal of Earth Sciences* 40: 731–747.
- Zhou, Z.-H. and Zhang, F.-C. 2006. Mesozoic birds of China—a synoptic review. *Vertebrata Palasiatica* 44: 74–98.

Appendix 1

Determinate anatomical character states in CAGS-IG-04-CM-007. Character definitions, states, and numbers follow Chiappe (2002). The state of character 132 was treated as uncertain in our phylogenetic analysis. All other characters in Chiappe (2002) were coded as missing (“?”) in CAGS-IG-04-CM-007.

Character number	118	132	133	136	137	139	140	142	143	145	146	148	149	153	157	158	159	161	163	164	165	167
State	1	1/2	0	1	1	1	0	1	0	1	1	1	0	0	1	1	0	0	1	1	1	0