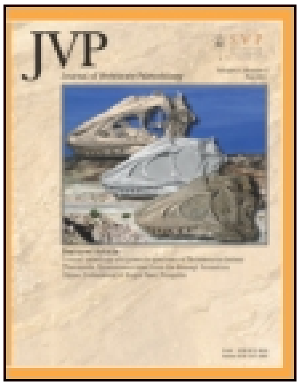

Journal of Vertebrate Paleontology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujvp20

A new and primitive enantiornithine bird from the Early Cretaceous of China

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Available online: 24 Aug 2010

To cite this article: Zhonghe Zhou (2002): A new and primitive enantiornithine bird from the Early Cretaceous of China, Journal of Vertebrate Paleontology, 22:1, 49-57

To link to this article: http://dx.doi.org/10.1671/0272-4634(2002)022[0049:ANAPEB]2.0.CO;2

Journal of Vertebrate Paleontology 22(1):49–57, March 2002

A NEW AND PRIMITIVE ENANTIORNITHINE BIRD FROM THE EARLY CRETACEOUS OF CHINA

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ABSTRACT—A new Early Cretaceous enantiornithine bird, *Eocathayornis walkeri*, gen. et sp. nov. is reported from Liaoning, northeast China. It is about the size of *Cathayornis* but is more primitive. Teeth are present on the jaws. Claws are retained on three wing digits, but that of the minor digit is reduced. The width of the radius is nearly three-fourths that of the ulna. The sternum is relatively short, with a pair of long caudo-lateral processes and a low and caudally distributed keel. The coracoid is strut-like and caudally concave, typical of enantiornithine birds. The advanced features of the scapula and the wing suggest a powerful flapping flight capability. This bird is referred to the family Cathayornidae based on a few shared derived characters with *Cathayornis*.

INTRODUCTION

The Early Cretaceous bird locality in Boluochi, Chaoyang, Liaoning Province, northeast China, was first discovered by the author in 1990. Three birds, namely *Cathayornis* (Zhou et al., 1992), *Chaoyangia* (Hou and Zhang, 1993), and *Boluochia* (Zhou, 1995a) have been described based on about 30 individuals collected from this locality. The new specimen *Eocathayornis walkeri*, gen. et sp. nov. was collected by the author in 1994, and initially identified as *Cathayornis*. However, recent preparation and study show that this is a new genus and species. Nearly all specimens from this locality (Boluochi) were collected from a layer of solid mudstone about 60 cm thick; however, the new specimen is an exception. It was collected from a layer of fragile shale lying about 50 cm above the solid mudstone layer. The new species is about the size of *Cathayornis*, but appears more primitive in many of its features.

Since 1992, seven genera from the Early Cretaceous of China have been referred to the group Enantiornithes: *Sinornis* (Sereno and Rao, 1992), *Cathayornis* (Zhou et al., 1992), *Otogornis* (Dong, 1993; Hou, 1994), *Boluochia* (Zhou, 1995a), *Eoenantiornis* (Hou et al., 1999), *Longipteryx* (Zhang et al., 2000), and *Protopteryx* (Zhang and Zhou, 2000). *Protopteryx* was found from Fengning, Hebei Province, and was recognized as the most primitive known enantiornithine bird. It is relatively more primitive than the rest of the enantiornithines from China. *Liaoxiornis* (Hou and Chen, 1999) was reported as the smallest Mesozoic bird, yet it is obviously a juvenile bird that can also be referred to Enantiornithes. So far, only three genera of ornithurine birds, *Gansus* (Hou and Liu, 1984), *Chaoyangia* (Hou and Zhang, 1993), and *Liaoningornis* (Hou et al., 1996) have been recognized from the Early Cretaceous of China. Therefore, the enantiornithine birds in the Early Cretaceous seem to have been not only more abundant, but also more diverse than ornithurine birds.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Infraclass ENANTIORNITHES Walker, 1981
Order CATHAYORNITHIFORMES Zhou et al., 1992
Family CATHAYORNITHIDAE Zhou et al., 1992
Eocathayornis walkeri, gen. et sp. nov.
(Figs. 1–9)

Etymology—Eo [Greek], dawn; cathay, old poetic name for China; ornithos [Greek], bird. The species name is dedicated to C. A. Walker, who first published and recognized the significance of the Enantiornithes.

Holotype—Skull, vertebrae, a pair of complete forelimbs and coracoids, scapulae, sternum and rib fragments. Institute of Vertebrate Paleontology and Paleoanthropology (Beijing) Collection V10916 (part and counterpart).

Horizon and Locality—Jiufotang Formation, Early Cretaceous; Boluochi, Chaoyang County, Liaoning Province, northeast China.

Diagnosis—Cranial cervical heterocoelous; length of coracoid about twice of the width; sternum with a pair of postero-lateral processes; length of ulna about 110% that of humerus; radius about three-fourths as wide as ulna; manus slightly shorter than forearm.

DESCRIPTION

Eocathayornis walkeri is a small bird (Figs. 1, 2; Table 1), its size is about typical of all other known Early Cretaceous enantiornithine birds. The holotype is split into two slabs, with only the impression of bones preserved on both the part and the counterpart.

Skull

The cranial part of the skull is to some extent separated from the caudal part. Most of the skull bones are disarticulated, thus the complete outline of some can be observed.

The premaxilla is similar to that of *Cathayornis* in having a long and slender nasal process (Zhou, 1995b). The same process is relatively short in *Archaeopteryx* (Wellnhofer, 1993). There are four teeth on the premaxilla. Each tooth is small and pointed with a constriction at the base of the crown typical of all toothed birds. The maxillary process of the premaxilla is straight, caudally pointed and overlapping the dorsal process of the maxilla. The cranial tip of the premaxilla is similar to those of *Archaeopteryx* and *Cathayornis* (Martin and Zhou, 1997), but different from that of *Boluochia*, in which it is hook-shaped and edentulous (Zhou, 1995a).

The maxilla has a pointed dorsal process that is inclined caudally. The nasal has a notched cranial margin that forms the postero-dorsal border of the narial, a situation similar to that of *Archaeopteryx*. The lacrimal is slender and curved cranially. The jugal is rod-shaped, and overlaps the maxilla below the

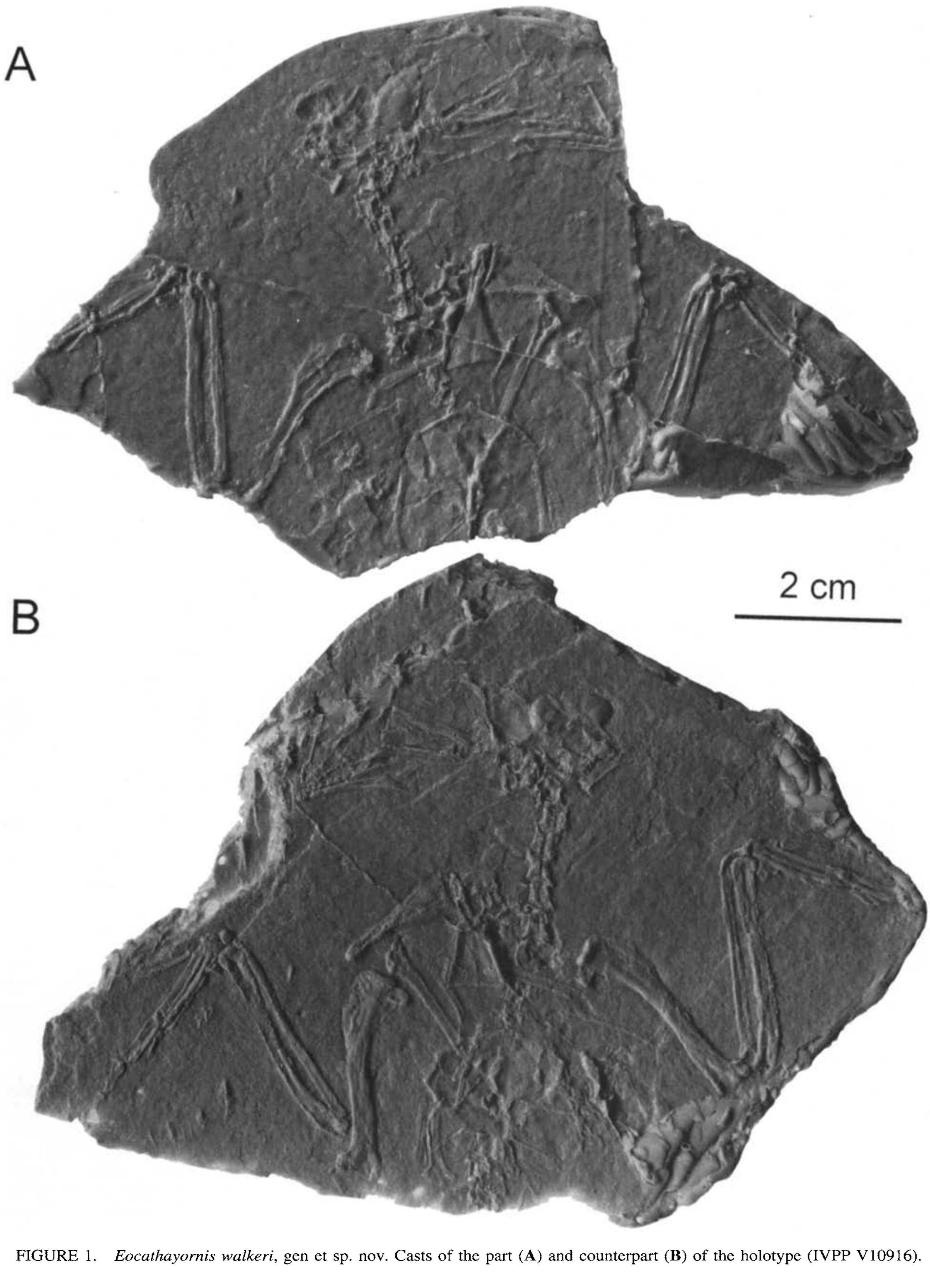

FIGURE 1. *Eocathayornis walkeri*, gen et sp. nov. Casts of the part (**A**) and counterpart (**B**) of the holotype (IVPP V10916).

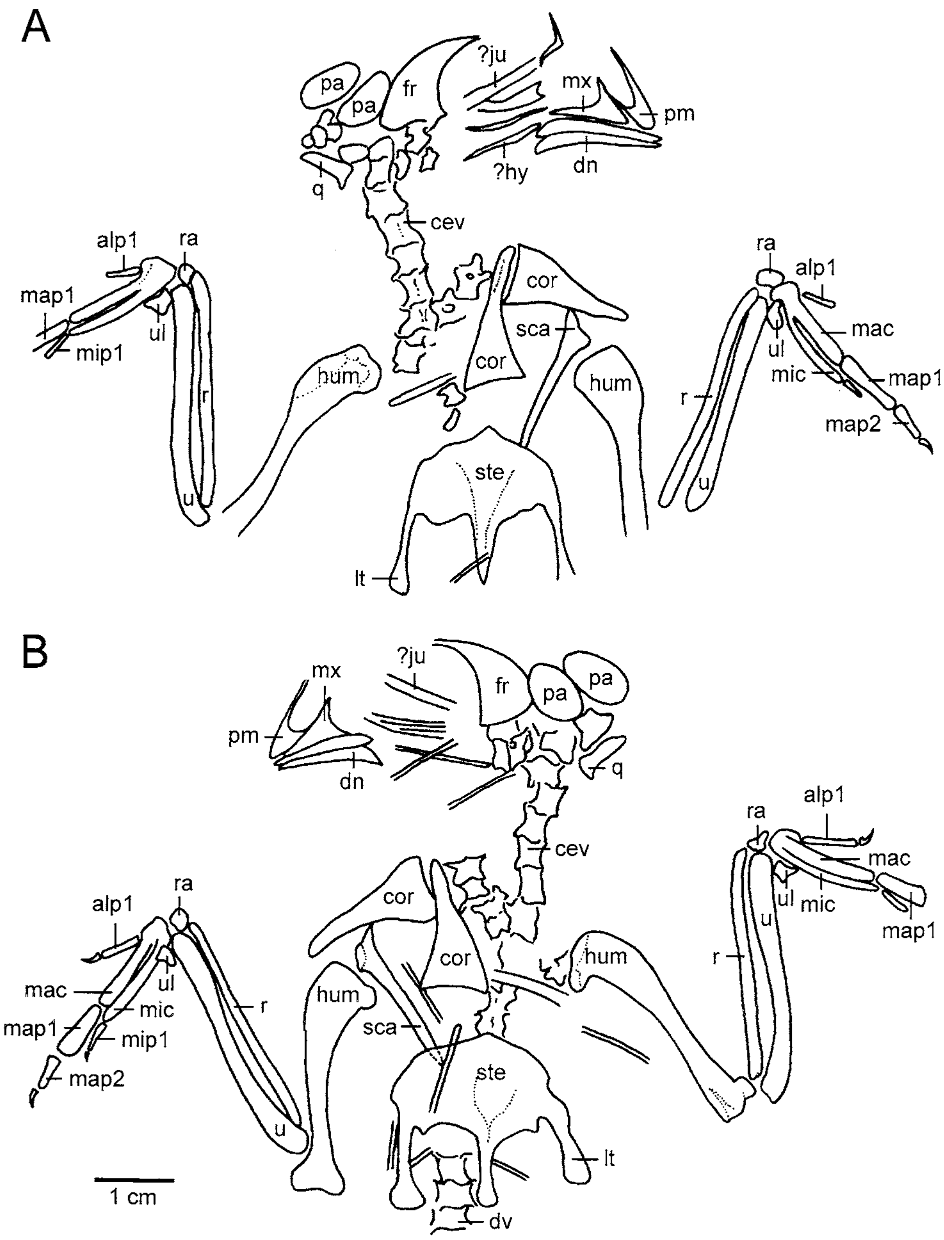

FIGURE 2. *Eocathayornis walkeri*, gen et sp. nov. Line drawing of the part (**A**) and the counterpart (**B**) of the holotype (IVPP V10916). **Abbreviations**: **alp1**, first phalanx of the alular digit; **cev**, cervical vertebra; **cor**, coracoid; **dn**, dentary; **dv**, dorsal vertebra; **fr**, frontal; **hum**, humerus; **?hy**, ?hyoid bone; **?ju**, ?jugal; **lt**, lateral trabeculum of the sternum; **mac**, major metacarpal; **map1**, first phalanx of the major digit; **map2**, second phalanx of the major digit; **mic**, minor metacarpal; **mip1**, first phalanx of the minor digit; **mx**, maxilla; **pa**, parietal; **pm**, premaxilla; **q**, quadrate; **r**, radius, **ra**, radiale; **sca**, scapula; **ste**, sternum; **u**, ulna; **ul**, ulnare.

lacrimal. The caudal end of the jugal is slightly expanded. A short bone behind the jugal might be the quadratojugal.

The frontal is similar to those of *Cathayornis* and *Archaeopteryx*. It is domed dorsally. The cranial process is pointed, and has an expanded caudal half. The outline of the ventral margin indicates the presence of a large orbit. A supraorbital rim is present, which is also similar to *Archaeopteryx*. The concave medial surface of the frontal shows the presence of an expanded brain.

The quadrate is also similar to that of *Archaeopteryx*. It is long and slender, and has a single head that articulates with the braincase. It has a straight caudal margin and is expanded cranially. As in *Archaeopteryx*, it lacks an orbital process and a bowl-shaped socket on the lateral side that is for the articulation of a ball-shaped process on the quadratojugal of modern birds (Fig. 3).

The two lower jaws are disarticulated. The dentary is about half the length of the skull. It is similar to those of *Archaeopteryx* and *Cathayornis* in being long and triangular (Fig. 1). The articular is wide and has a laterally expanded cotylus for articulation of the quadrate. No intercotylar crest seems to be present.

Axial Skeleton

Cervical vertebrae are relatively well preserved and most are articulated. Although the exact number of the cervical vertebrae is hard to count, I estimate a total of 11. The cervical vertebrae

TABLE 1. Measurements (mm) of the holotype of *Eocathayornis walkeri* (IVPP V10916).

Skull	
Dentary length	14.0
Frontal length	12.0
Quadrate height	6.0
Quadrate base width	3.0
Premaxilla length	10.0
Sternum	
Length	18.5
Maximum width	20.0
Latero-caudal process length	11.0
Coracoid	
Length	13.6
Base width	6.8
Humerus	
Length	23.5
Mid-shaft width	2.3
Radius and ulna	
Radius length	25.6
Radius mid-shaft width	1.3
Ulna length	26.0
Ulna mid-shaft width	1.8
Manus	
Total length	25.5
Carpometacarpus length	14.0
Alular metacarpal width	1.0
Major metacarpal width	1.2
Minor metacarpal width	1.1
Alular manual digit	
First phalanx length	6.0
Second (ungual) phalanx length	2.1
Major manual digit	
First phalanx length	7.0
Second phalanx length	4.3
Third (ungual) phalanx length	2.4
Minor manual digit	
First phalanx length	2.5
Second (ungual) phalanx length	1.3

are relatively wide, with a low ventral ridge as in *Cathayornis*. The articulations among the centra vary cranially to caudally. Heterocoelous articulations can be seen in the third, fourth and fifth cervical vertebrae. However, they are less obvious in the posterior cervical vertebrae, in which the central articulations are nearly flat.

One thoracic vertebra is well preserved. The vertebrate body is laterally compressed, but not excavated into a deep depression. This is similar in *Cathayornis* (Zhou, 1995b), but different from *Concornis* (Sanz et al., 1995) and other enantiornithines (Sanz et al., 1995). The parapophyses lie in the middle of the vertebra from top to bottom, but are located more caudally than in *Cathayornis*. The neural spine is nearly square, whereas in *Cathayornis* it is more elongated and more concave on both cranial and caudal margins. The neural spine is almost directly above the vertebral body, whereas in *Cathayornis* it is located more caudally (Zhou, 1995b).

Four caudal vertebrae are preserved. They are relatively wide, with slender and caudally directed transverse processes. The proximal end of the pygostyle is also present. Considering that the pygostyle usually becomes fused progressively from the distal to the proximal end, I estimate that *Eocathayornis* had a well-fused pygostyle, which is also true of *Cathayornis* and most other Early Cretaceous enantiornithine birds (Sanz et al., 1995). The fusion of the pygostyle is also apparent in *Confuciusornis* and newly discovered ornithurine birds of the same age (Zhou and Zhang, 2001).

Fragments of ribs are preserved. There are a few sternal ribs near the sternum. No gastralia are found. A dorsal rib is nearly completely preserved. It is thin and slender, with no evidence for the presence of an uncinate process.

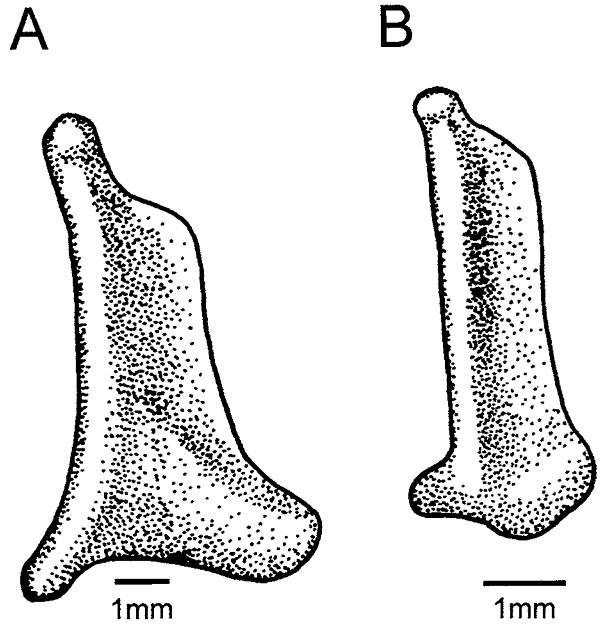

FIGURE 3. Comparison of quadrates of *Archaeopteryx* (**A**) and *Eocathayornis* (**B**).

Sternum

The sternum is more advanced than *Archaeopteryx* in having a low keel and a pair of caudo-lateral processes (lateral trabeculum; Fig. 4). The keel is low and distributed only in the caudal part of the sternum as is typical of enantiornithine birds; the early ornithurine birds such as *Liaoningornis*, *Chaoyangia*, and *Ambiortus* all have a long keel extending along the full length of the sternum (Kurochkin, 1985; Hou et al., 1996). The cranial margin of the sternum is rounded, and dorso-ventrally thin. The articulating surface for the coracoid is slightly convex and lacks the cranio-lateral process that is usually present in modern birds. The middle of the cranial margin extends further cranially as a small pointed process. Two pairs of notches are present on the caudal margin of the sternum. There is a pair of lateral expansions from the lateral margin of the sternum. The caudo-lateral processes are approximately parallel to each other. They have a foot-shaped expanded distal extremity similar to that of *Cathayornis* (Zhou, 1995b) and *Concornis* (Sanz et al., 1995). The keel also extends caudally to the caudo-lateral process. A pair of caudal processes lies between the lateral processes and the keel, they are short compared with that of *Cathayornis* or *Concornis*. The sternum of *Eocathayornis* is less elongated than that of *Cathayornis*; in the former it is wider than long whereas in the latter it is longer than wide. As in *Cathayornis*, a pair of low processes branch out from the cranial end of the keel, extending nearly to the cranial margin of the sternum. The dorsal surface of the sternum is obviously concave as in *Cathayornis* and all flying birds.

Scapula

The left scapula is well preserved, with only the caudal end missing. As in *Cathayornis*, it has a nearly straight, flat and thin scapular blade (Fig. 5). In modern birds the scapular blade is usually curved. The glenoid facet for the articulation of the humerus is elliptical and dorso-laterally directed as in modern birds. It lacks a coracoidal tuberculum that is typical of all modern birds. Instead, in *Eocathayornis*, the scapula has a facet that articulates with a process on the coracoid. This facet is

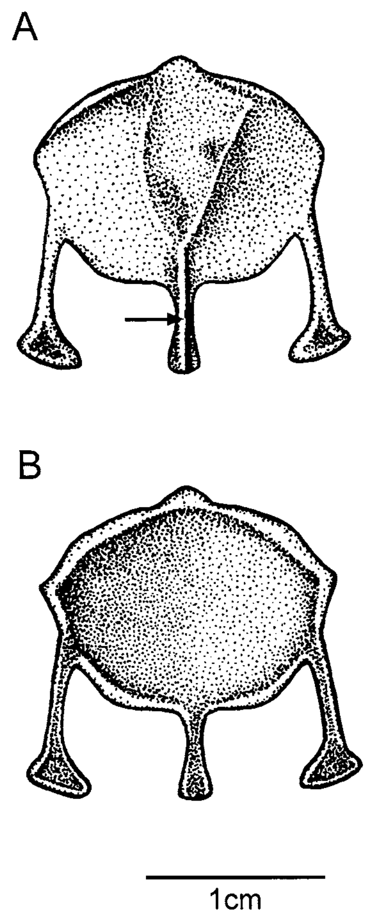

FIGURE 4. Sternum of *Eocathayornis*. **A**, ventral view; **B**, dorsal view. Arrow indicates keel.

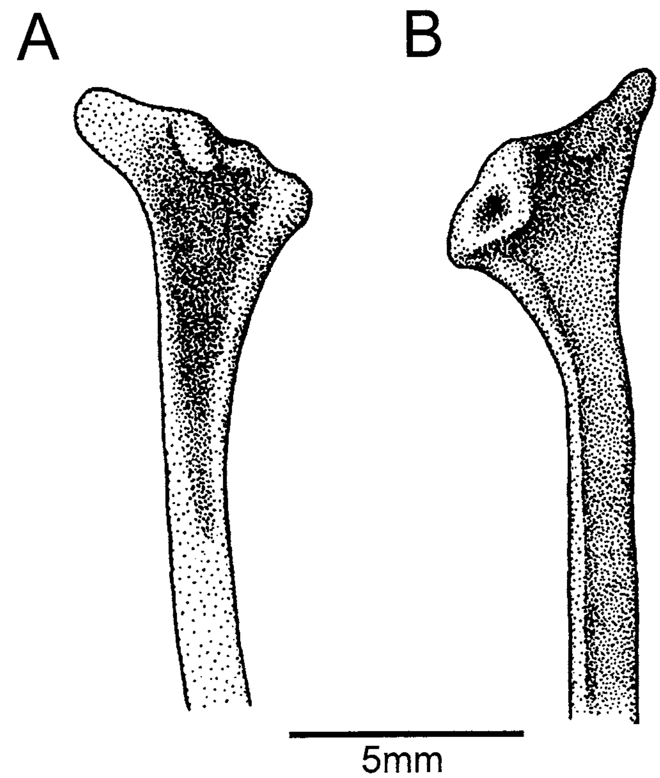

FIGURE 5. Left scapula of *Eocathayornis*, cranial end. **A**, ventral view; **B**, dorsal view.

cranio-ventral to the glenoid facet. This is characteristic of Enantiornithes. This coracoidal articulating facet is relatively shallow compared to that of *Enantiornis*.

The acromion of the scapula is slightly rounded, and has an articulating surface on its ventral side, also typical of enantiornithine birds. The articulating surface is regarded by Walker (1981) as for the furcular articulation.

Coracoid

The coracoid is blade-like (Fig. 6). As is typical of enantiornithine birds, it has a concave dorsal side (except the lateral margin, which is straight), a thin and concave articular surface for the sternum, and a scapular process at the proximal end. It lacks the procoracoid that is present in all modern birds. Also, the distal half of the coracoid has a convex lateral margin and a concave medial margin. However, in *Eocathayornis*, the coracoid is relatively shorter than in *Cathayornis* and *Enantiornis*. The scapular process on the coracoid is less rounded in *Eocathayornis* and *Cathayornis* than in *Enantiornis* (Walker, 1981). The depression on the dorsal side of the coracoid is also more shallow in *Eocathayornis* and *Cathayornis* than in *Enantiornis*.

Humerus

The humerus is shorter than the ulna. The head is typical of enantiornithine birds in having an internally slanting profile (Zhou, 1995b) (Fig. 7). The head is flat, cranially concave and caudally convex as in *Cathayornis* and *Concornis* (Sanz et al., 1995). At the proximal end, the ventral tubercle is developed, and the dorsal tubercle is not. The pectoral crest is similar to that of *Cathayornis*, and is moderately expanded externally. A pneumatic fossa is present below the ventral tubercle. The bicipital crest is bulbous as is typical of other enantiornithine birds, but is less expanded than in *Cathayornis*. An obvious depression is present below the head on the ventral side, which

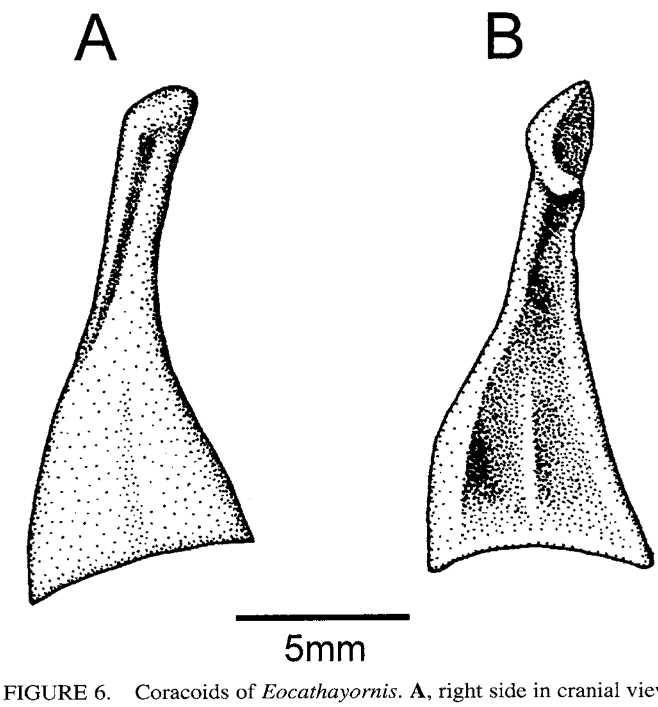

FIGURE 6. Coracoids of *Eocathayornis*. **A**, right side in cranial view; **B**, left side in caudal view.

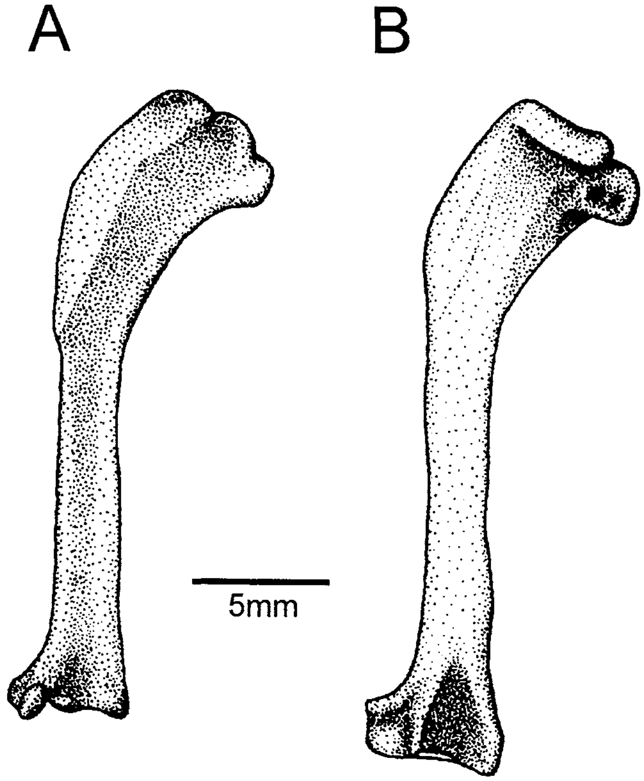

FIGURE 7. Humerus of *Eocathayornis*. **A**, right side in dorsal view; **B**, left side in ventral view.

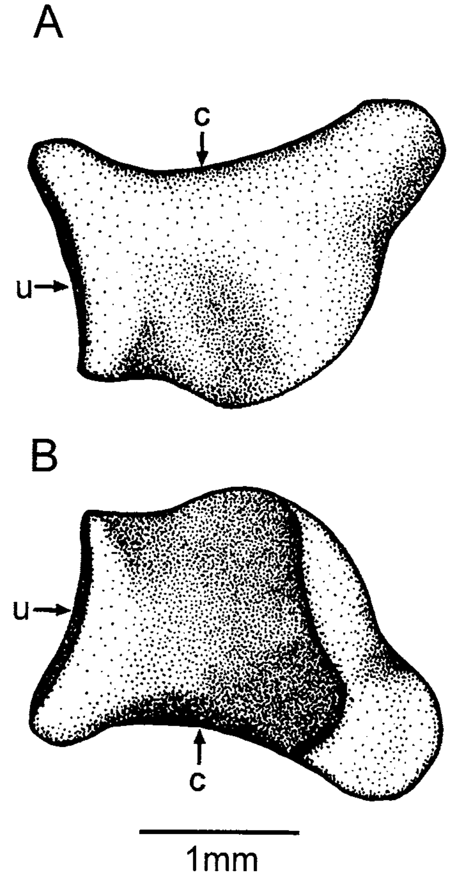

FIGURE 8. Right ulnare of *Eocathayornis*. **A**, ventral view; **B**, dorsal view. **Abbreviations**: **c**, articulation for the carpometacarpus; **u**, articulation for the ulna.

is typical of enantiornithine birds, but is not as deep as in *Enantiornis*.

At the distal end, the dorsal condyle is developed, but extends less far more proximally on the dorsal side than in *Cathayornis*. Similar to *Cathayornis*, the ventral condyle is small and barely seen on the dorsal side, and a dorsal epicondyle is only weakly developed and is situated near the dorsal condyle. The ventral epicondyle is not developed. The olecranon fossa is deep. The sulcus for the scapuloticipital muscle is narrow. The distal end of the humerus is expanded externally into a short strut-like process, which appears flat dorsally. This character is also seen in *Cathayornis* and *Enantiornis*. *Eocathayornis* also shares with *Cathayornis* a narrow flexor process.

Radius and ulna

Both the radius and the ulna are obviously longer than the humerus, and the ulna is only slightly longer than the radius. The radius is nearly three-fourths as wide as the ulna whereas in *Cathayornis* it is less than two-thirds of the width of the ulna. The radius is relatively straight. The proximal end is less expanded than in *Cathayornis* and has a deep humeral cotylus. The distal end is curved, with a narrow radiocarpal articulating face. The ligamental sulcus is deep. The ulna is bow-shaped. At the proximal end, the olecranon is pointed, and the dorsal cotylar process is not developed as in *Cathayornis*. The distal end of the ulna is only slightly wider than the shaft. The carpal tubercle is flat. As in *Cathayornis*, there is a long and deep groove at the distal end on the cranial side. The condylar labium is narrow and less rounded than in *Cathayornis*.

Carpals and carpometacarpus

The ulnare has a concave surface for the articulation with the ulna (Fig. 8). It has a shallow and curved metacarpal incision that articulates with the carpometacarpus. The radiale is smaller than the ulnare, and nearly square as in *Cathayornis* (Fig. 9). The carpometacarpus is fused only proximally. The numbering of the metacarpal and manual digits is controversial (Burke and Feduccia, 1997; Wagner and Gauthier, 1999). This paper will follow Baumel and Witmer (1993) in the following description. The minor metacarpal obviously extends past the major metacarpal distally, as is typical of all enantiornithine birds. The minor metacarpal is curved and extends more ventrally than the major one, especially toward the proximal end. This character is seen in all birds and unknown in any related taxon. The carpal trochlea is small and rounded, but less de-

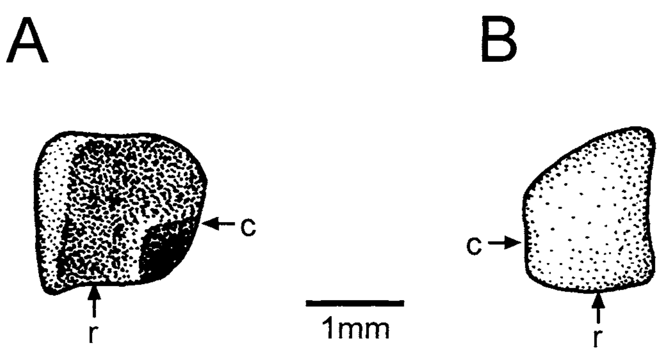

FIGURE 9. Left radiale of *Eocathayornis*. **A**, ventral view; **B**, dorsal view. **Abbreviations**: **c**, articulation for the carpometacarpus; **r**, articulation for the radius.

veloped than in *Cathayornis*. The extensor process is absent as in *Cathayornis*. Also similar to *Cathayornis*, *Eocathayornis* has a more or less rounded ulnocarpal articular face. The major metacarpal is obviously wider than the minor metacarpal. Ventrally, the minor metacarpal is deeply grooved along the majority of the middle line. This character is also seen in *Cathayornis*. As in *Cathayornis*, there is hardly any space between the major and minor metacarpals.

Manual Phalanges

The phalangeal formula is 2–3–2, significantly different from the 2–3–4 in both *Archaeopteryx*, *Confuciusornis*, and nearly all theropods and other archosaurs. *Cathayornis* has a 2–3–1 formula, as it has lost the claw of the minor digit. The alular digit is slender and relatively short as in *Cathayornis*; it is less than half the length of the carpometacarpus. The claw is small.

The major digit is both longer and more robust than the other two. The first phalanx is about as wide as the major metacarpal. It has a convex caudal margin and a concave cranial one. As in *Cathayornis*, the distal end of the first phalanx is slightly wider than the proximal end. However, the proximal end of the alular phalanx is much wider than the distal end. The first and second phalanges of the major digit altogether form a big bow-shaped supporting structure for the primary feathers. This character is more developed in *Cathayornis*, and only slightly developed in *Confuciusornis* and *Archaeopteryx* (Zhou and Martin, 1999). The claw is only slightly larger than the claw on the alular digit.

The minor digit is much smaller than those of *Archaeopteryx* and *Confuciusornis*. It is also relatively shorter than the other two digits. The first phalanx is wider proximally than distally. The ungual phalanx is lost in *Cathayornis*, but still retained in *Protopteryx* and *Eocathayornis*. This claw is very reduced, and is much shorter than the other two claws on the wing.

DISCUSSION

Eocathayornis can be referred to Enantiornithes by many enantiornithine synapomorphies such as a typical enantiornithine "opposite" articulation between the scapula and the coracoid, the coracoid with a convex lateral margin and a concave medial surface, and major metacarpal obviously extending past minor metacarpal distally. Among the known enantiornithines from the Early Cretaceous of China, *Eocathayornis* is more derived than *Protopteryx* (Zhang and Zhou, 2000) in having a reduced alular digit. It can also be easily distinguished from *Eoenantiornis* (Hou et al., 1999) by having a sternum with a pair of caudo-lateral processes. In most characters *Eocathayornis* is most similar to *Cathayornis*, another enantiornithine that was discovered from the same locality.

Comparison to *Cathayornis*

Cathayornis has been widely accepted as an Early Cretaceous enantiornithine bird, although its relationship to other enantiornithine birds remains unclear (Chiappe 1995; Martin, 1995; Zhou, 1995b). *Eocathayornis* is about the size of *Cathayornis*, and is most similar to *Cathayornis* in nearly all the main aspects that have been preserved in both genera. The characters uniquely shared by *Eocathayornis* and *Cathayornis* include: (1) teeth on premaxilla are inclined cranially; (2) dentary is about half of the length of the skull, with a straight and pointed caudal end; (3) The peculiar outline of the latero-caudal process of the sternum, which is strongly constricted in the middle and expanded into a foot-shaped distal end, which is expanded more medially than laterally; (4) the shape of the pectoral crest of the humerus; (5) a long and deep groove on the distal ulna along the cranial side; and (6) middle elongate groove on the major and minor metacarpals on the ventral side.

Eocathayornis is, however, also relatively more primitive than *Cathayornis* in many structures. The width of the sternum is greater than the length in *Eocathayornis* as in *Archaeopteryx* and the most primitive enantiornithine *Protopteryx*; however, in *Cathayornis* the length is much greater than the width. The caudal processes of the sternum are shorter and less pointed than in *Cathayornis*. The coracoid is also relatively shorter than in *Cathayornis*. Even though greatly reduced, the claw on the minor manual digit is still present in *Eocathayornis* as in *Archaeopteryx* and *Confuciusornis*, but is lost in *Cathayornis* and modern birds. The bicipital crest of the humerus is less bulbous in *Eocathayornis* than in *Cathayornis*. The phalanges of the major digit are less bow-shaped than in *Cathayornis*. The width of the radius is about three fourths of that of the ulna in *Eocathayornis*; however, it is less than two thirds of the length of the ulna in *Cathayornis*. In addition, the humerus in *Eocathayornis* is also less twisted than in *Cathayornis*. In both *Cathayornis* and *Eocathayornis*, the ulna is slightly longer than the humerus, a derived situation unknown in *Archaeopteryx* and *Confuciusornis*. The length of the ulna in *Eocathayornis* is about 110% of that of the humerus, however, the length of the ulna in *Cathayornis* is less than 105% of that of the humerus, indicating that *Eocathayornis* is not more primitive than *Cathayornis* in all features.

Coracoid

Cathayornis has a typical enantiornithine coracoid (Fig. 6). The coracoid in *Eocathayornis* is blade-like, obviously more derived than in *Archaeopteryx* and *Confuciusornis*, but more primitive than in all the other known Early Cretaceous enantiornithine birds. *Eocathayornis* has a relatively short coracoid, the length of which is about twice the width. In *Cathayornis* (IVPP V10896), the length of the coracoid is about 2.5 times the width. The same ratio in the Late Cretaceous *Enantiornis* is about 3 (Walker, 1981). The ventral halves of the coracoids in *Eocathayornis* and *Cathayornis* are very similar. However, the latter has an elongated dorsal neck: it is shorter than the rest of the coracoid in *Eocathayornis*, but is longer in *Cathayornis*. The Early Cretaceous Spanish enantiornithine bird *Concornis* also has a relatively long neck. This difference probably reflects the general evolutionary trend of the coracoid in the enantiornithine birds.

Sternum

Archaeopteryx bavarica has the oldest known type of sternum in birds (Wellnhofer, 1993). A distinct feature of this sternum is that it is significantly wider than long (Fig. 4). No modern birds has such a shape. *Cathayornis* has a relatively elongated sternum; its length is slightly greater than the width. As in *Protopteryx*, *Eocathayornis* has a relatively short sternum that is wider than long. Therefore, in this aspect *Eocathayornis* is also evolutionarily intermediate between *Archaeopteryx* and *Cathayornis*. Early Cretaceous ornithurine birds such as *Chaoyangia*, *Liaoningornis* and *Ambiortus* have evolved an even more elongated sternum that has a deep keel along its full length. Besides, these early ornithurine birds have also evolved a "modern" coracoidal articulation that is caudally butted on the cranio-lateral process. This "modern" articulation has never been observed in enantiornithine birds. *Eocathayornis* has a typical enantiornithine sternum that is rounded cranially and has a shallow keel distributed only along the caudal part of the sternum. It is also caudally notched as in other enantiornithine birds, and has a pair of long caudo-lateral processes.

The caudal processes between the latero-caudal processes and the keel in *Eocathayornis* are shorter than in *Cathayornis* and *Concornis* (Sanz et al., 1995). The sternum of the most primitive known enantiornithine *Protopteryx* lacks the caudal process (Zhang and Zhou, 2000). It can therefore be concluded that the caudal process evolved after the evolution of the caudo-lateral process in enantiornithine birds. *Eocathayornis* also has a relatively short caudo-lateral process compared to the total length of the sternum. The keel in *Eocathayornis* extends caudally nearly to the caudo-lateral process; however, it extends less far caudally than in *Cathayornis* and *Concornis*.

Manus

Complete wing claws have been retained in *Archaeopteryx*, *Confuciusornis*, *Eoenantiornis*, *Protopteryx* and *Eocathayornis*. However, in both *Cathayornis* and *Sinornis*, in which the manual phalanges were completely preserved, only the claws on the alular and major digits have been found. The claw on the minor digit is probably also lost in *Concornis* (Sanz and Buscalioni, 1992; Sanz et al., 1995). The rest of the known Early Cretaceous birds have not preserved a complete manus. It is interesting to note that in modern birds such as the hoatzin, which have retained two wing claws at their juvenile stage, the claws are also restricted in the alular and major digits. *Eocathayornis* can be distinguished from *Archaeopteryx*, *Confuciusornis* (Hou et al., 1995), and *Protopteryx* by the small size of the wing claws (Fig. 2). It is also noteworthy that the claw on the minor digit is much more reduced than the other two in *Eocathayornis*. This observation may suggest that the claw on the minor manual digit was lost in *Concornis* and later enantiornithine birds. Several newly discovered materials of Early Cretaceous ornithurine birds from Liaoning, northeast China all preserved claws on the alular and major digits but lost the claw on the minor digit (Zhou and Zhang, 2001), suggesting that the reduction of the claw on the minor digit represents a trend in the evolution of the manus in both Enantiornithes and Ornithurae. It seems that the minor digit in *Cathayornis* is already hardly different from that of modern birds. When the manus of the avian ancestor was modified into the wing of birds, the major digit was emphasized because it provides the main support for the attachment of the primary flight feather, and the alular digit is modified into the structure supporting the alula (bastard wing). However, the minor digit has virtually lost its ancestral grasping function. Therefore, *Eocathayornis* represents a functionally intermediate type from the primitive hand used in both flight and other functions (such as climbing?) as represented by *Archaeopteryx* and *Confuciusornis* to the more advanced exclusively flight-oriented manus of birds beginning with *Cathayornis* and *Sinornis*.

The manus in both *Archaeopteryx* and *Confuciusornis* is remarkably longer than the forearm. However, in *Eocathayornis*, the total length of the manus is slightly longer than the ulna, a situation that also occurred in *Cathayornis*. The long manus in *Archaeopteryx* and *Confuciusornis* might be useful in the gliding stage of flight, but obviously less efficient in flapping flight. The major digit is more robust than the other two, and the distally expanded first phalanx and the proximally expanded second phalanx form a bow-shaped caudally convex margin that is typical of modern birds. This character is more developed in *Cathayornis* than in *Eocathayornis*.

Flight capability

Eocathayornis possesses a wing fundamentally adapted for flapping flight and more advanced than those of *Archaeopteryx* and *Confuciusornis* (Hou et al., 1995). The alular and minor digits are reduced, the wing claws become smaller, the major digit more robust, and the carpometacarpus fused proximally. The ulnare and radiale of *Eocathayornis* have nearly all the key features of modern birds necessary for powerful flapping flight (Vazquez, 1992). As in *Cathayornis* and other Early Cretaceous birds, the scapula of *Eocathayornis* is unfused to the coracoid, and has a latero-dorsally directed glenoid facet for the articulation of the humerus, further showing the capability of lifting the wing well above the body. The scapula and coracoid are still fused in *Confuciusornis*, as in modern flightless birds. *Eocathayornis* probably also has a pygostyle similar to *Cathayornis* or *Confuciusornis*.

Although the sternum is relatively short compared to those of more advanced birds, it does have a sternal keel. The sternum is also notched caudally, another adaptation for flight. It should also be noted that the body size of *Eocathayornis* is similar to *Cathayornis* and nearly all the other Early Cretaceous birds. The change in body size is probably one of the most important features in the early avian evolution (Sanz and Buscalioni, 1992; Zhou and Hou, 1998).

The alula has been reported in the Early Cretaceous Spanish enantiornithine *Eoalulavis* (Sanz et al., 1996). The same structure has also been preserved in more primitive enantiornithine birds *Protopteryx* and *Eoenantiornis*. The alular digit of *Eocathayornis* is similar to those of *Cathayornis* and most Early Cretaceous enantiornithine birds, but is more reduced than in *Protopteryx* (Zhang and Zhou, 2000) and *Eoenantiornis* (Hou et al., 1999). Therefore, it seems reasonable to conclude that the alula was also present in *Eocathayornis*. The alula has not been found in either *Archaeopteryx* or *Confuciusornis*, both of which have a long alular digit with a well-developed claw. None of *Confuciusornis* has shown any evidence of an alula. The alula is most useful in slow flight in taking off or landing in modern birds. *Archaeopteryx* and *Confuciusornis* probably could not take off directly from level ground (see Burger and Chiappe, 1999 for a different view) and lack the skill of smooth landing as a modern bird. It is interesting to note that the appearance of the alula associated with an unreduced alular digit in the most primitive enantiornithine *Protopteryx* (Zhang and Zhou, 2000) indicates that sophisticated flight capability of early birds had appeared even before the alular digit was reduced. With a more reduced alular digit than in *Protopteryx*, *Eocathayornis* can be viewed as a bird capable of powerful sustained flight similar to modern birds.

ACKNOWLEDGMENTS

I would like to thank Joel Cracraft, Jose L. Sanz and an anonymous reviewer for their critical reviews, Lianhai Hou, Fan Jin, Jiangyong Zhang, Yucai Gu, Yutie Sun, and Fengxue Wang for their assistance in the field. L. D. Martin, Desui Miao and Townsend Peterson read the manuscript. David Burnham prepared the cast of *Eocathayornis*, Jie Zhang the photos. The research was supported by the National Science Fund for Distinguished Young Scholars of China (40025208), the Special Funds for Major State Basic Research Projects of China (G2000077700), the Chinese Academy of Sciences (KZ951-B1-410 and KZCX3-J-03), and the National Geographic Society of the United States.

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Received 15 January 2000; accepted 25 January 2001.