Early diversification of birds: Evidence from a new opposite bird

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Abstract **A new enantiornithine bird *Longipteryx chaoyangensis* gen. et sp. nov. is described from the Early Cretaceous Jiufotang Formation in Chaoyang, western Liaoning Province. This new bird is distinguishable from other known enantiornithines in having uncinate processes in ribs, elongate jaws, relatively long wings and short hindlimbs, and metatarsal Ⅳ longer than metatarsals Ⅱ and Ⅲ. This new bird had probably possessed (ⅰ) modern bird-like thorax which provides firm attachment for muscles and indicates powerful and active respiratory ability; (ⅱ) powerful flying ability; (ⅲ) special adaptation for feeding on aquatic preys; and (ⅳ) trochleae of metatarsals Ⅰ—Ⅳ almost on the same level, an adaptation for perching. The new bird represents a new ecological type different from all known members of Enantiornithes. It shows that enantiornithines had probably originated earlier than the Early Cretaceous, or this group had experienced a rapid radiation right after it first occurred in the early Early Cretaceous.**

Keywords: Enantiornithes, Early Cretaceous, radiation.

Enantiornithine birds are the dominant avian group in the Mesozoic time. Although the Early Cretaceous enantiornithines have been reported from nearly around the world, most of them are similar in terms of feeding and ecological adaptation[1]. *Longipteryx* represents a new type distinctive from other known enantiornithines[1—7].

1 Systematics

Class Aves Linnaeus, 1758
Subclass Enantiornithes Walker, 1981
order Longipterygiformes ord. nov.
family Longipterygidae fam. nov
Genus *Longipteryx* gen. nov.
Species *Longipteryx chaoyangensis* sp. nov.

Diagnosis. Skull length at least 2.5 times of skull height. Tooth short and pointed. Middle cervical vertebrate heterocoelous. Distal region of sternum with well developed carina and lateral processes. Uncinate processes present but not fused with ribs. At least 6 rows of gastraliae present. Carpometacarpus not completely fused, minor metacarpal longer than major one; second phalanx of minor digit reduced to a small triangle. Pubis curved and with perpendicular pubic-foot. Tarsometatarsus fused proximally, metatarsal Ⅳ longer than other metatarsals; trochleae of metatarsals Ⅰ—Ⅳ almost on the same level. Phalanges of alular digit long. Wings remarkably longer than hindlimbs, ratio of wing to leg (femur+tibiotarsus+tarsometatarsus) length more than 1.5, tibiotarsus shorter than humerus and ulna (fig. 1).

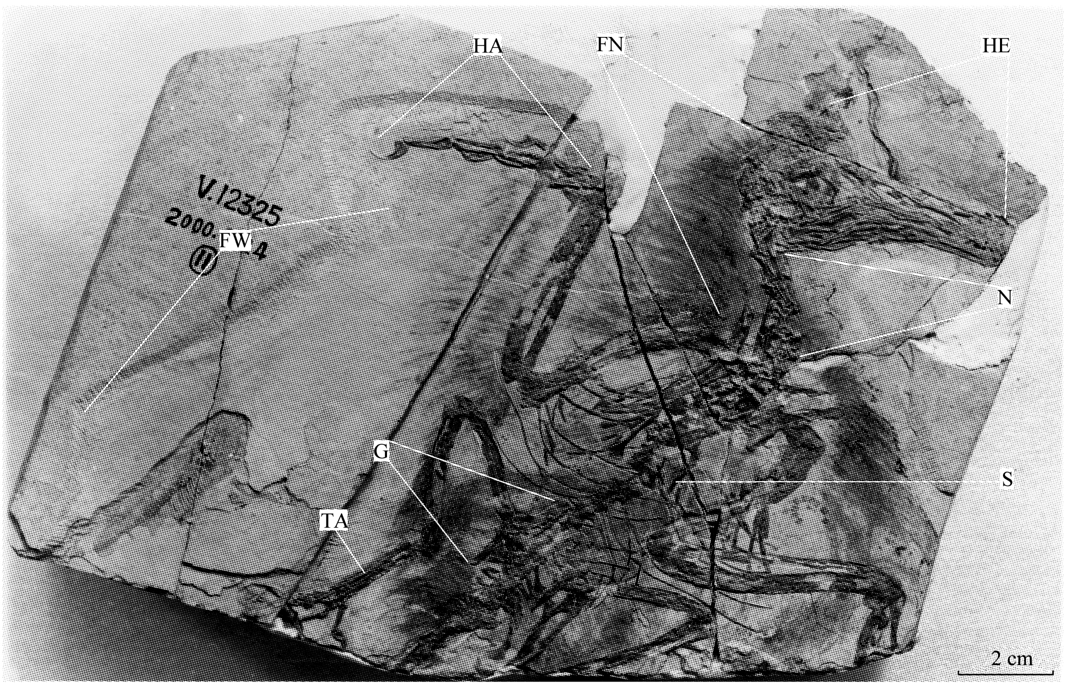

Fig. 1. *Longipteryx chaoyangensis*. Holotype (IVPP collection number V 12325). FN, Down feather prints at the neck region; FW, flight feather prints at the forelimb region; G, pelvic girdle; HA, hand; HE, head; N, neck; S, sternum; TA, tarsometatarsal.

Holotype. A nearly completely articulated skeleton with feather impressions. Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) collection number V 12325.

Other materials. A completely articulated skeleton (IVPP collection number V 12552); humerus and furcula (IVPP collection number V 12553), and ulna (IVPP collection number V 12554).

Horizon and locality. Jiufotang Formation, Early Cretaceous; Qidaoquanzi, Chaoyang City, Liaoning Province.

Etymology. The genus name "Longipteryx" means long-wing bird; the species name "chaoyangensis" is derived from Chaoyang City where the specimens were collected.

2 Description

Skull. The premaxilla is long, and about 70% of the total length of the skull. There are 6 teeth preserved in the upper jaw; they are short, conical and slightly caudally curved. Mandibular bones are not fused; the length of the dentary is about 57% that of the skull; the 3 preserved teeth are similar to that of the premaxilla; the angular is short; it is about 20% that of the skull. The quadrate is rectangle with well-developed jugal and otic processes; the orbital process is less well-developed; the mandible process is stout as in *Archaeopteryx*, *Confuciusornis* and *Protopteryx*[7]. There appears to exist an incomplete and thin interorbital septum. The sclerotic ring is composed of 9 bones near the thoracic girdle region.

Vertebral column. There are 7 preserved cervical vertebrae; the total number of the cervical vertebrae is estimated to be 9. The length of the cervical vertebra varies, the longest being about one and half of the shortest; the ratio of the longitudinal axis to the transverse axis is about 1.4 in the anterior vertebrae and only about 0.7 in the posterior vertebrae. Neural spines of dorsal vertebrae decrease posteriorly in length, but the neural spine of the last vertebra is more prominent than those of the two preceding ones. The costal processes are distinguishable in 4th and more posterior cervical vertebrae, and the length is half that of the vertebra. Both prezygapophyses and postzygapophyses are well-developed. The cervical vertebrae appear to be heterocoelous. The last three thoracic vertebrae are articulated with the synsacrum, the total number of the thoracic vertebrae is estimated to be more than 10. Synsacrum is composed of at least 8 vertebrae as indicated by the transverse processes; among the transverse processes of the synsacrum the last three are longer than the others; and the penultimate one is the longest. There are at least 4 unfused caudal vertebrae and the transverse processes are shorter than those of the last three sacral vertebrae. The pygostyle is completely coossified and longer than that of the total length of the free caudal vertebrae.

Thoracic girdle. The furcula is Y-shaped; the angle of the two clavicles is 50°; the ratio of the clavicle to the hypocleideum is 1.75. The clavicle is flat craniocaudally at the distal end; the sagittal and transverse axes are nearly of equal length (fig. 2(c)). The shaft of the scapula is straight and dorsoventrally flat; the neck is round and thin; the distal end is wide and obtuse. The glenoid facet is oval, its long axis is parallel to that of the scapula. The coracoid is shorter than the scapula; the proximal three fifths of the coracoid is cylinder-shaped, and its distal two fifths triangle-shaped. There is a marked dorsal process near the proximal end of the coracoid.

Sternum, rib and gastralia. The medial process of the sternum gradually becomes the carina distally. The lateral process of the sternum is well developed with an expanded distal end; there is a short process between the lateral and the medial processes. The longitudinal axis of the sternum is longer than the transverse axis (fig. 2(a)). There are at least 9 pairs of vertebral ribs, they are thin and about 4—5 times as long as the sternal ribs. At least 4 uncinate processes on the left side of the body were preserved; they are unfused with the ribs and are slightly expanded distally; they are thinner than the ribs; the uncinate processes vary in length, with the longest one about 3 times that of the shortest one. There are at least 4 pairs of sternal ribs; the proximal end is slightly expanded; they decrease in length progressively toward the distal end, the last one is shorter than the lateral process of the sternum (fig. 2(e)). There are at least 6 rows of gastralia preserved.

Pelvic girdle. The ilium is long, with a round and stout preacetabular wing; the postacetabular wing is thin, short and rodlike. The ischium is long, the width of the iliac process is about half that of the ischiatic body; the width of the obturator process is about 150% that of the ischiatic body; the dorsal process of the ischium is similar to that of the ischiatic body in width. The pubis is thin, long, and curved caudally; the iliac process of the pubis is slightly wider than that of the pubic body. The pubic foot is perpendicular to the pubic body, and the width of the former is about twice that of the latter.

Forelimb. The wing is significantly longer than the hindlimb. The humerus is S-shaped; it is as long as the ulna but is slightly shorter than the hand. The humeral head is well developed; it is prominent in caudal view. The depression between the humeral head and the ventral tuberosity is about one fouth of the proximal humerus in width. The ventral condyle of the distal end of the humerus is craniocaudally positioned, the dorsal condyle is laterally and slightly craniocaudally positioned. The proximal three fifths of the ulna is straight while the distal two fifths is slightly curved. The ulna has a well-developed olecranon. The radius is straight and thin; it is about 63.2% of the ulna in diameter; its proximal end is slightly expanded. The radiale is smaller than the ulnare, both are triangle-shaped. The semilunate distal carpal is not completely fused with metacarpals. The alular metacarpal is short and about 26% as long as the major metacarpal; its diameter is similar to that of the minor metacarpal. The major and minor metacarpals are tightly attached but not fused; the major metacarpal is straight and about twice as wide as the minor metacarpal; the minor metacarpal is slightly curved and longer than the major metacarpal, its distal end is curved toward the major metacarpal. The alular digit is composed of two phalanges; the first phalanx is short and the ungual is curved with horny sheath preserved. There are three phalanges in the major digit, the first phalanx is wide and is about 109% of the second in length; the ungual is larger than the ungual of the alular digit. The minor digit is composed of two phalanges, the first phalanx is tightly attached to the first phalanx of the major digit and is about 54% as long as the latter; the second phalanx is triangle-shaped and is about 35.2% as long as the first phalanx (fig. 2(b)).

Hindlimb. The femur is short; its length is about 64.2% that of the humerus; it is craniocaudally curved. The distal three fifths of the tibiotarsus is slightly curved medially; it is slightly longer than the femur; its proximal articular facet is semicircular in caudal view; it has a well-developed fibular crest. The fibula is short and about 38.9% as long as the tibiotarsus; the proximal fibula is lateromedially flat; the fibula tapers toward the distal end; its proximal articular facet is slightly convex. The proximal tarsals are flat and not completely fused with the tibia. The distal tarsals are, however, fused with metatarsals Ⅱ—Ⅳ into a tarsometatarsus. The tarsometatarsus is about 65% as long as the tibia. Among the three major metatarsals, metatarsal Ⅳ is the longest, Ⅲ the second, and Ⅱ the shortest. The proximal metatarsal Ⅰ is flat and articulated to the distal end of metatarsal Ⅱ. The hallux is long and opposable to the other three digits. The trochleae for the pedal digits are almost on the same level (fig. 2(d)).

3 Discussion

Longipteryx possesses several enantiornithine synapomorphies such as a Y-shaped furcula, a sternum similar to that of *Cathyornis* and *Eoalulavis*[8], and minor metacarpal longer than major metacarpal. It also preserved a few characteristics different from other known enantiornithine birds including: (ⅰ) lateromedially compressed proximal clavicles, (ⅱ) metatarsal Ⅳ longer

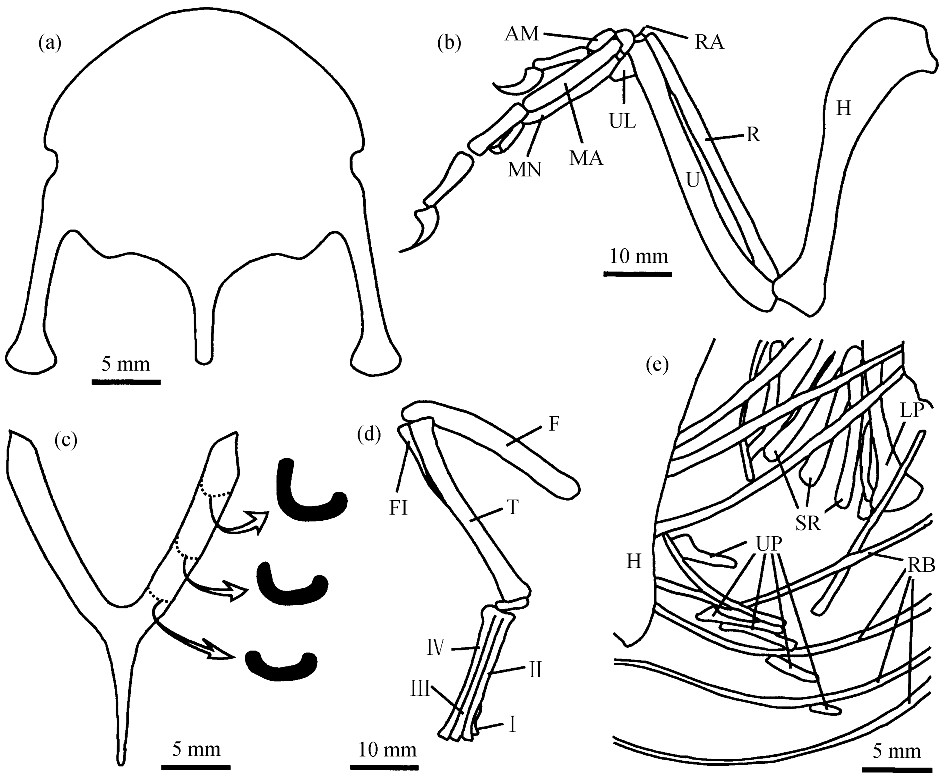

Fig. 2. *Longipteryx chaoyangensis* reconstructions. (a) Sternum; (b) wing, note that the second phalanx of the minor digit is small and triangle-shaped; (c) furcula; (d) femur, tibiotarsus, and tarsometatarsus, note that metatarsal Ⅳ is longer than Ⅱ and Ⅲ; (e) uncinate process and rib. AM, Alular metacarpal; F, femur; FI, fibula; H, humerus; Ⅰ-Ⅳ, metatarsals Ⅰ-Ⅳ; LP, lateral process of sternum; MA, major metacarpal; MN, minor metacarpal; R, radius; RA, radiale; RB, vertebral rib; SR, sternal rib; T, tibiotarsus; U, ulna; UL ulnare; UP, uncinate process

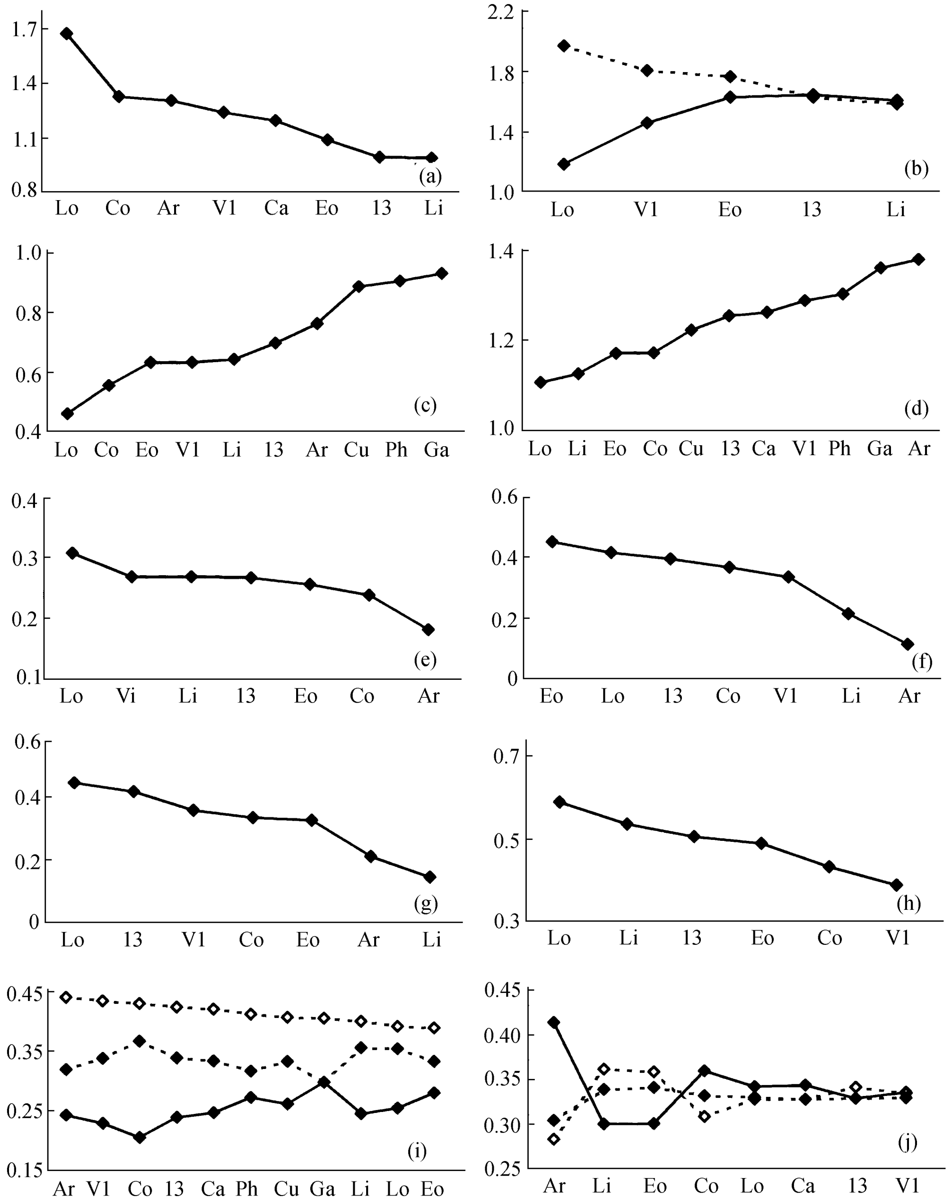

Fig. 3. Some ratios of skeletal elements of *Longipteryx chaoyangensis* and other birds. (a) The ratio of wing length to hindlimb (femur+tibiotarsus+tarsometatarsus) length; (b) the ratio of wing length to trunk length (◆---), and hindlimb (femur+ tibiotarsus+ tarsometatarsus) length to trunk length (◆—); (c) the ratio of tibiotarsus length to trunk length; (d) the ratio of tibiotarsus length to humerus length; (e) the ratio of coracoid length to trunk length; (f) the ratio of sternum length to trunk length; (g) the ratio of sternum width to trunk length; (h) the ratio of neck length to trunk length; (i) the ratio of humerus (◆---), ulna (◇---) and hand (◆—) length to wing length; (j) the ratio of femur (◆---), tibiotarsus (◇---) and tarsometatarsus (◆—) length. 13, An unnamed enantiornithine bird，Nanjing Institute of Geology and Paleontology (CAS) Specimen Collection Number, 130722；Ar, *Archaeopteryx*[16]; Ca, *Cathyornis*, Cu, *Caudipteryx*[16]; Co, *Confuciusornis*; Eo, *Eoenantiornis*; Ga, *Gallus*[16]; Li, *Liaoxiornis*; Lo, *Longipteryx*; Ph, *Phasianus*[16]; V1, *Protopteryx*.

than Ⅱ and Ⅲ, and (iii) presence of uncinate processes.

In living vertebrates, the uncinate process of the rib is unique to birds although cartilaginous uncinate processes are present in crocodiles. In fossil vertebrates, the uncinate process has been reported in *Sphenodon*, *Caudipteryx*[9,10], oviraptorids, *Confuciusornis*[11] and *Chaoyangia*[12]; however, it is absent in the oldest bird *Archaeopteryx*. *Longipteryx* is the first enantiornithine bird with such a structure. Uncinate processes strength the thorax. In some diving birds long uncinate processes cross two ribs, which help resist against water pressure. Uncinate processes also provide attachment for such muscles as the external intercostal muscles related to respiration[13,14]. Uncinate processes also provide attachment for scapular muscles[15]. The presence of uncinate processes in *Longipteryx* suggests a strong thorax and respiration capability similar to modern birds.

The most unique feature of *Longipteryx* is that its wing is longer than the hindlimb (fig. 3(a)). Comparisons of the limb elements with the trunk length indicate that the hindlimb is short (fig. 3(b)) and the tibiotarsus is relatively short compared to the femur (fig. 3(c),(d)). Because *Longipteryx* has a relatively short tibiotarsus, the femur, tibiotarsus and tarsometatarsus contribute more equally to the total length of the hindlimb than in other birds (fig. 3(i)). The proportions of the forelimb elements are similar to that of other primitive birds (fig. 3(j)).

The coracoid of *Longipteryx* is relatively long; a long coracoid increases the coelomic volume (fig. 3(e)). A relatively big sternum (fig. 3(f),(g)) also increases the coelomic volume. As in modern birds the proximal ends of the clavicles are flattened lateromedially, suggesting the presence of similar function of this structure as in modern birds [1].

The powerful wing, big sternum with well-developed carina, lateromedially flattened furcula, firm thorax, and shortened trunk indicate that *Longipteryx* possesses more powerful flight capability than other primitive birds; it probably has *Confuciusornis*-like, or higher metabolism[17,18]. In addition to powerful wings and short hindlimbs, *Longipteryx* also has a relatively long neck and heterocoelous cervical vertebrae (fig. 3(h)); both characters may indicate that the head and neck rather than the wing were predatory tools in this bird.

Longipteryx has relatively reduced hindlimbs, the tibiotarsus is especially shortened as opposed to walking birds which have relatively long tibiotarsus (fig. 3(c)), therefore the hindlimb of *Longipteryx* probably plays a less important locomotive than weight-supporting role. *Longipteryx* also has strong perching capability as the four metatarsal trochleae are almost on the same level; ungual phalanges are well developed as in modern perching birds[19—21]. *Longipteryx* is most similar to Coraciiform birds such as the kingfisher in having powerful wings and perching capability and relatively short hindlimbs.

The discovery of *Longipteryx* also suggests that, at least by the Early Cretaceous, there already existed an extensive ecological diversifications of birds: enantiornithine birds had either originated before the Early Cretaceous or experienced a rapid radiation at the beginning of the Early Cretaceous, and evolved into lots of ecospecies. The presence of many of the previously unoccupied niches could have provided more and better resources and refuges for the fast growing Early Cretaceous avian populations.

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