Two new ornithurine birds from the Early Cretaceous of western Liaoning, China

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Abstract **We describe two new ornithurine birds from the Early Cretaceous Jiufotang Formation of western Liaoning, northeast China: *Yanornis martini* gen. et sp. nov. and *Yixianornis grabaui* gen. et sp. nov. They represent the best fossil record of ornithurine birds known from the Early Cretaceous. They are more advanced than the most primitive ornithurine *Liaoningornis*, and are more similar to the other two Chinese Early Cretaceous ornithurines *Chaoyangia* and *Songlingornis*. Compared with *Confuciusornis, Liaoxiornis* and *Eoenantiornis* from the same age, the two new birds show remarkable advanced characteristics and suggest the presence of powerful flight capability like modern birds. Compared with *Yixianornis* and *Chaoyangia*, *Yanornis* is larger, with a more elongated skull and relatively long wings. The new discoveries indicate that by the Early Cretaceous both enantiornithine and ornithurine birds had already radiated significantly. The flight structures of *Yanornis* and *Yixianornis* are hardly distinguishable from those of modern birds; however, both retain a few primitive traits such as teeth on the jaws, wing claws and pubic symphysis, which exclude them from being the most recent ancestor of all extant birds.**

Keywords: Ornithurae, origin, radiation, Jiufotang Formation, *Yanornis, Yixianornis*.

Enantiornithines have been generally known as the dominant terrestrial birds in the Mesozoic. Comparatively, few ornithurine birds have been described from the continental Early Cretaceous deposits. Here we report two new species of ornithurine birds that are represented by nearly complete materials from the Early Cretaceous of western Liaoning, northeast China. The study of these birds will shed new light not only on the radiation of early birds but also on the origin of birds with modern appearance.

1 Systematics

Class Aves Linnaeus, 1758

Subclass Ornithurae Haeckel, 1866

Order Yanornithiformes ord. nov.

Family Yanornithidae fam. nov.

Yanornis gen. nov.

Yanornis martini gen. et sp. nov.

(figs. 1 and 2)

Diagnosis. Dentary straight, about 2/3 the length of skull, with about 20 teeth. Cervicals long, hetercoelous. Synsacrum composed of 9 sacrals. Pygostyle short and less than 1/3 the length of tarsometatarsus. Sternum with a pair of posterior fenestra; distal end of the lateral process semicircular. Ratio of forelimb to hindlimb length about 1.1. Manus shorter than ulna and radius. Tarsometatarsus completely fused. Ratio of third pedal digit to tarsometatarsus length 1.1. Proximal pedal phalanges longer and more robust than distal ones.

Holotype. A complete individual without feather impressions (Institute of Vertebrate Paleontology and Paleoanthropology Collection V12558).

Referred material. an incomplete individual (Institute of Vertebrate Paleontology and Paleoanthropology Collection V10996).

Locality and horizon. Chaoyang City and Yixian County, Liaoning Province; Jiutotang Formations, Early Cretaceous.

Etymology. "Yan" is derived from the Chinese spelling of the ancient Chinese Yan Dynasty, the type locality Chaoyang City was its capital; the species name is dedicated to Larry D. Martin for his contribution to the study of Meosozoic birds.

Skull. The skull is elongated, the ratio of the skull length to height is 2.3. The premaxilla and the maxilla are relatively long. The premaxilla is pointed at the anterior end; the nasal process is flattened, and extends posteriorly to the lachrymal. The maxiallar process of the premaxilla is long and slender; it extends posteriorly to the anterior end of the nasal. The premaxilla contains 4—5 teeth of different size; the tooth is robust, conical in shape, and constricted at the base. The nasal is short. The premaxilla has at least 9 teeth; they are short and conical. The dentary is relatively straight with about 20 teeth; the dentary is about 2/3 the length of the skull. Compared with the teeth of the premaxilla, those of the dentary and the maxilla are relatively small and slightly curved posteriorly. The nasal opening is slender and large. The orbit is large. The antorbital is small. The jugal is rod-shaped with a low ascending process. The frontal is expanded. The squamosal has three small ventral processes with grooves in between. The quadrate has a well-developed postorbital process. The postorbital is probably reduced. The occipital condyle is posteriorly positioned.

Vertebral column. there exist at least 10 hetercoelous cervical vertebrae; the length of the middle cervicals is about twice the width. The dorsal vertebrae have long and deep pleurocoels. The synsacrum is composed of 9 sacrals; among the transverse process of the sacrals, that of the 7th sacral is the longest, and those of the 8th and 9th sacrals are united at the distal end. The pygostyle is short and less than one third the length of the tarsometatarsus. The dorsal rib is slender; the gastralia is probably present.

Pectoral girdles and sternum. The characteristics of the sternum, coracoid and scapula are hardly distin

Fig. 1. *Yanornis martini* gen. et sp. nov., holotype (V12558).

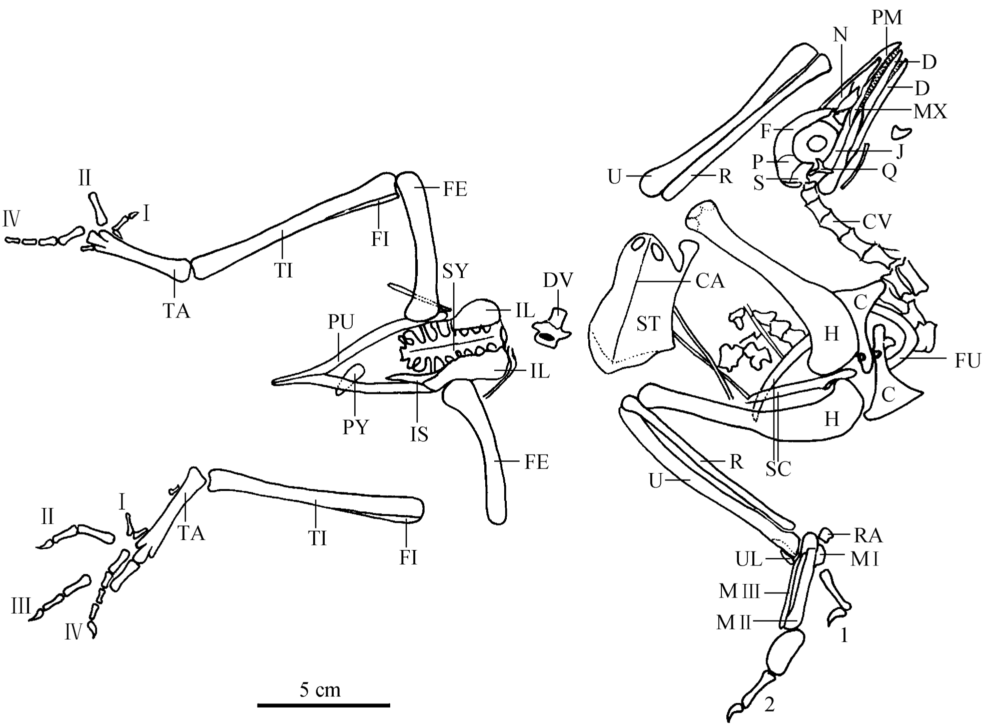

Fig. 2. Line drawing of *Yanornis martini* gen. et sp. nov. (V12558). C, Coracoid; CA, carina; CV, cervical vertebra; D, dentary; DV, dorsal vertebra; M Ⅰ—Ⅲ, Metacarpals Ⅰ—Ⅲ; F, frontal; FE, femur; FI, fibula; FU, furcula; H, humerus; IL, ilium; IS, ischium; J, jugal; MX, maxilla; N, nasal; P, parietal; PM, premaxilla; PU, pubis; PY, pygostyle; Q, quadrate; R, radius; RA, radiale; S, squamosal; SC, scapula; ST, sternum; SY, synsacrum; TA, tarsometatarsus; TI, tibiotarsus; U, ulna; UL, ulnare; 1 and 2, manual digits Ⅰ—Ⅱ; Ⅰ—Ⅳ, pedal digits Ⅰ—Ⅳ.

Table 1 Measurements of major skeletons of *Yanornis martini* gen. et sp. nov. (V12558) and *Yixianornis grabaui* gen. et sp. nov. (V12631) (mm)

	V12558	V12631		V12558	V12631
Skull length	65	39*	Pubis length	67*	35*
Skull height	28		Pubic symphysis length	20	7
Scapula length	55*	50	Hindlimb total length	209	153
Coracoid length	30	23	Femur length	52	41
Forelimb total length	235	153	Tibiotarsus length	78	52
Humerus length	79	48	Fibula length	32	15*
Ulna length	81	50	Tarsometatarsus length	38	26
Radius length	76	46	Metatarsal Ⅰ length	6	4
Manus total length	75	55	Pedal digit Ⅰ-1 length	8	7
Carpometacarpus length	35	25	Pedal digit Ⅰ-2 length	5	5
Metacarpal Ⅰ length	8	5	Pedal digit Ⅱ-1 length	13	11
Metacarpal Ⅰ width	3	2	Pedal digit Ⅱ-2 length	10	9
Metacarpal Ⅱ length	31	21	Pedal digit Ⅱ-3 length	6	6
Metacarpal Ⅱ width	4	2	Pedal digit Ⅲ-1 length	14	11
Metacarpal Ⅲ length	31	21	Pedal digit Ⅲ-2 length	11	9
Metacarpal Ⅲ width	2	0.5	Pedal digit Ⅲ-3 length	10	8
Manual digit Ⅰ-1 length	17	11	Pedal digit Ⅲ-4 length	6	6
Manual digit Ⅰ-2 length	10	5	Pedal digit Ⅳ-1 length	9	7
Manual digit Ⅱ-1 length	17	12	Pedal digit Ⅳ-2 length	6	5
Manual digit Ⅱ-2 length	16	11	Pedal digit Ⅳ-3 length	6	5
Manual digit Ⅱ-3 length	7	4	Pedal digit Ⅳ-4 length	6	6
Manual digit Ⅲ-1 length		6	Pedal digit Ⅳ-5 length	5	5
Synsacrum length	38				

* indicates estimated or approximate value; horny sheath not included in ungual length.

guishable from those of modern birds, but are significantly different from those of enantiornithines from the same deposits. The coracoid has a well-developed procoracoid and a round fossa for articulation with the scapula; distally it has a well-developed lateral process and a strape-shaped facet for articulation with the sternum; the distal coracoid is wide, the ratio of its length to width is about 1.4; the dorsal side of the coracoid is deeply concaved near the distal end. The scapular blade is flattened and curved; the acromion is long and pointed. The furcula is U-shaped and anteroposteriorly compressed; it also has a deep groove along the full length of the furcula anteriorly. The sternum is long and dorso-ventrally preserved; anteriorly the coracoidal articulation is well developed; the keel is long; posteriorly there exist a pair of elliptical fenestra and a pair of lateral processes with an expanded and semicircular distal end.

Forelimbs. the ratio of the forelimb to hindlimb length is 1.1 (table 1). The humerus and the ulna are relatively long while the manus is relatively short. The deltoid crest of the humerus is well developed and exceeds one-third the length of the humerus; the bicipital crest is ball-shaped; distally, both the ventral and dorsal condyles and the dorsal and ventral epicondyles are well developed. The dorsal condyle at the distal end of the ulna is semi-circular as in modern birds. The bicipital tubercle at the proximal radius is well developed; the distal end of the radius is spoon-shaped. The ulnare is rod-like. The radiale is square-shaped. The carpometacarpus is fused at both the proximal and the distal ends; the carpal trochlea is large. Metacarpals Ⅱ and Ⅲ are of nearly equal length. Metacarpal Ⅰ is short, the extensor tubercle is absent as in all early birds. Claws are retained in the first two digits. The first phalanx of the first digit is about half the length of the carpometacarpus. The first phalanx of the second digit is distinctively expanded antero-posteriorly, the second phalanx is slender and slightly shorter than the first phalanx. The third digit retains only the first phalanx, which is small and short.

Pelvis. The ilium is expanded medio-laterally and probably fused with the synsacrum. The pubis is slender and posteriorly directed; the pubic symphysis is about 30% of the total length of the pubis. The ischium is short and tapers posteriorly.

Hindlimbs. the femur is bow-shaped. The ratio of the tibiotarsus to femur length is 1.5. The fibula is reduced and less than half the length of the tibiotarsus. The tarsometatarsus is completely fused; it is about half the length of the tibiotarsus. Metatarsal Ⅰ articulates with metatarsal Ⅱ at the distal end. The trochlea for digit Ⅲ is wider and lower than those for digits Ⅱ and Ⅳ. The trochlea for digit Ⅱ is posteriorly shifted and is higher than those for Ⅲ and Ⅳ in position. The trochlea for digit Ⅳ is narrower than those for Ⅱ and Ⅲ; it also abuts the trochlea for digit Ⅲ. Digit Ⅲ is longer than other digits and the tarsometatarsus. Digit Ⅰ is short; digits Ⅱ—Ⅳ are relatively long. The first phalanx is more robust and longer than other phalanges in each digit. The unguals are relatively short.

Order Chaoyangornithiformes Hou, 1997.

Fam. indet.

Yixianornis gen. nov.

Yixianornis grabaui gen. et sp. nov.

(figs. 3 and 4)

Diagnosis. Ratio of skull length to width about 1.5. Postcranial long bones slender. Head of humerus protruding and elliptical. Metacarpal Ⅲ less than 1/3 the width of metacarpal Ⅱ. Pubic symphysis about 1/5 the length of pubis. Ratio of femur to tarsometatarsus length 1.6. Ratio of pedal digit Ⅲ to tarsometatarsus length 1.3.

Holotype. a nearly complete individual with feather impressions (Institute of Vertebrate Paleontology and Paleoanthropology Collection V12631).

Locality and horizon. Qianyang, Yixian County, Liaoning Province; Jiutotang Formation, Early Cretaceous.

Etymology. "Yixian" is derived from the Chinese spelling of the locality; the species name is dedicated to late American geologist Amadeus William Grabau, a pioneering geologist in Liaoning, for his contribution to the study of the Jehol Biota.

Skull. The skull is ventrally exposed; the ratio of its length to the width is 1.5. The dentary is about half the length of the skull; it also contains teeth. The teeth are small. The frontal is expanded. The orbit is large.

Vertebral column. There exist at least 9 heter-coelous cervical vertebrae. There are probably more than 11 dorsals. Five short free caudals are preserved. The pygostyle is short. Ribs are slender with uncinate processes. Gastralia are slender.

Pectoral girdles and sternum. The coracoid has a well-developed strut-like procoracoid process; distally it has a distinctive sternal articulating facet; the distal end of the coracoid is wide; the ratio of its length to width is 1.4; the dorsal coracoid is concave near the distal end. The scapula is slender and curved; it tapers distally; the glenoid is elliptical and laterally positioned. The furcula is U-shaped; the clavicle is rod-like and tapers dorsally. The sternum is laterally preserved; it is elongate with a deeply concave dorsal surface; the keel extends along the full length and is 7 mm in height.

Forelimbs. The forelimb is as long as the hindlimb (table 1). The manus is slightly longer than the ulna. The deltoid crest of the humerus is well developed and more than 1/3 the length of the humerus; the humeral head is large and elliptical. The ratio of the ulna to radius width is 1.5. The ulna has a semicircular dorsal condyle at the distal end. The ulnare has a distinctive metacarpal incision. The radiale is semicircular and slightly shorter than the ulnare. The carpometacarpus is fused at the proximal end; the carpal trochlea is large. Metacarpal Ⅰ is short and unfused with the carpometacarpus. Metacarpals Ⅱ and Ⅲ are straight and of equal length; they are probably only fused at the proximal end. Metacarpal Ⅲ is extremely slender; it is less than 1/3 the width of metacarpal Ⅱ. Digit Ⅰ is slender, its ungual is slightly longer than that of digit Ⅱ. The first phalanx of digit Ⅱ is expanded antero-posteriorly, the second phalanx is slender, and the ungual is small. Digit Ⅲ only comprises one phalanx, which is small and tightly attached to the posterior margin of the first phalanx of digit Ⅱ.

Pelvis. The anterior and posterior portions of the ilium are similar in height. The pubis is curved and slender; the pubic symphysis is short and about one fifth of the length of the pubis.

Hindlimbs. The hindlimb bones are slender. The ratio of the femur to tarsometatarsus length is 1.6. The tibiotarsus is twice as long as the tarsometatarsus. The lateral condyle of the distal tibiotarsus is well developed; the intercondylar groove is narrow; the supratendinal bridge is absent. The fibula is short and only about 1/3 the length of the tibiotarsus. The tarsometatarsus is completely fused; the middle shaft is strongly latero-medially compressed. The trochlea for digit III is wider and lower than those for the other digits. The trochlea for digit IV is slender. The digits are slender and long; among the four digits, III is the longest, the ratio of digit III to tarsometatarsus length is 1.3. The first phalanx is the longest among all pedal digits. The unguals are relatively short.

Feathers. The alula is not preserved. The primary feathers are long and distinctively asymmetrical; the rachis is extremely slender; the barbs are slender and densely distributed. The tail feathers are short.

2 Discussions

Among the known Mesozoic birds from China, all but *Confuciusornis* can be referred to either Enantiornithes or Ornithurae. The former comprises more individuals and species, they include *Sinornis*[1], *Cathayornis*[2], *Boluochia*[3], *Liaoxiornis*[4], *Eoenantiornis*[5], *Protopteryx*[6], and *Longipteryx*[7]. Ornithurae from the Mesozoic of China comprise *Gansus*[8], *Chaoyangia*[9], *Liaoningornis*[10] and *Songlingornis*[11], which are represented by a total of only 5 specimens. *Songlingornis* and

Chaoyangia are from the same locality and are of nearly equal body size, it is uncertain if they belong to the same species as the known materials of both can not be directly compared with each other.

Chaoyangia is close to *Yixianornis* in size. The main differences between the two are: *Chaoyangia* has a long pubic symphysis (30% of the total length of the pubis compared to 20% in *Yixianornis*), a relatively long fibula and more robust long bones. *Songlingornis* only preserved the coracoid, sternum, dentary and premaxilla. In

Fig. 3. *Yixianornis grabaui* gen. et sp. nov., holotype (V12631).

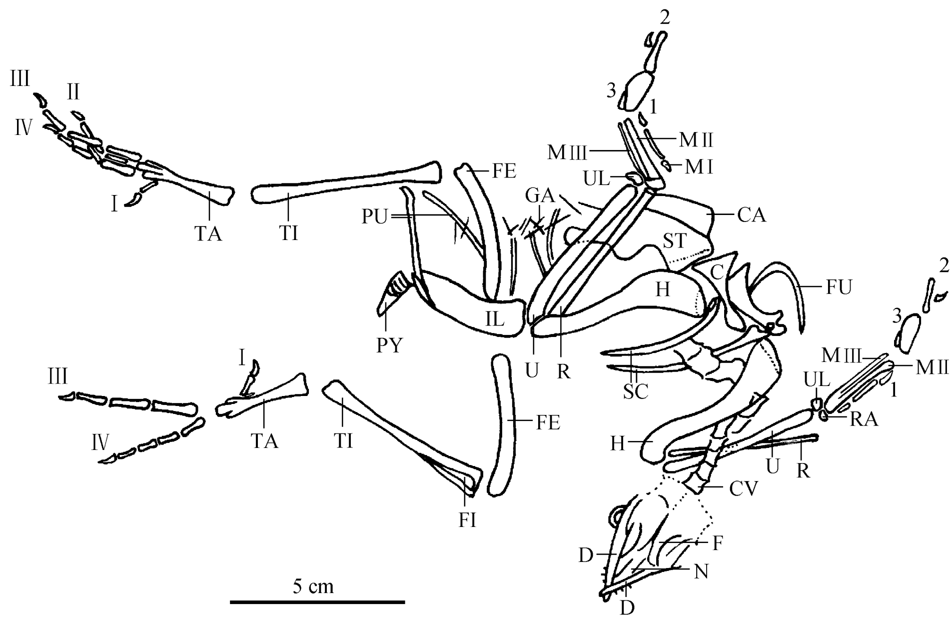

Fig. 4. Line drawing of *Yixianornis grabaui* gen. et sp. nov. (V12631). GA, Gastralia; 3, manual digit Ⅲ; for other abbreviations see fig. 2.

Table 2 Comparisons of some skeletal length ratios between *Yanornis martini* gen. et sp. nov. (V12558) and *Yixianornis grabaui* gen. et sp. nov. (V12631)

	Forelimb /hindlimb	Manus /ulna	Manual digit Ⅱ /ulna	Skull /femur	Tarsometatarsus /femur	Pubic symphysis /pubis	Pedal digit Ⅲ /tarsometatarsus
V12558	1.12	0.93	0.49	1.25	0.73	0.3	1.08
V12631	1.0	1.1	0.54	0.95	0.63	0.2	1.31

Songlingornis the two clavicles of the furcula form a flatter bottom while in *Yixianornis* the two clavicles form a more curved bottom. The characteristics of the premaxilla indicate that *Songlingornis* is probably close to *Yixianornis* in having a less elongated skull than *Yanornis*.

Compared with *Yanornis* and *Yixianornis*, *Liaoningornis* is smaller in size; its sternum is not posteriorly notched and lacks lateral processes. *Gansus* only preserved an incomplete left hindlimb; it is similar to *Yanornis* in size. Its tarsometatarsus is completely fused as in both *Yanornis* and *Yixianornis*, but its digits are more slender with shorter unguals, which have well-developed extensor tubercles. Pedal digit Ⅳ is longer than Ⅲ in *Gansus*, but digit Ⅲ is longer than Ⅳ in both *Yixianornis* and *Yanornis*. The extensor tubercles are absent in the pedal claws of *Yixianornis* and *Yanornis*.

Enantiornithine birds are more common than ornithurine birds in the Early Cretaceous[12]. *Ambiortus* is probably the only known ornithurine from the continental Early Cretaceous deposits outside China[13]. This bird is similar to *Yanornis* in size. Compared with *Yixianornis* and *Yanornis* its second digit appears to have a more slender first phalanx. It also has a U-shaped furcula, and appears less robust than that of *Yanornis*. The sternum of *Ambiortus* is also laterally preserved; the height of the keel is similar to that of *Yixianornis*.

Yanornis is distinguishable from *Yixianornis* by an elongate skull. Among other known Early Cretaceous birds, the skull of *Longipteryx*[7] bears a lot resemblance to that of *Yanornis*. They are similar in having an elongated skull, densely arranged teeth, and relatively long forelimbs. Since *Longipteryx* is referred to the Enantiornithes, therefore these two birds lack a close phylogenetic relationship. They probably independently adapted to the fish-predating life in the water. *Longipteryx* has relatively short hindlimbs, but has strong perching capability, it probably spent most of the life in the trees when resting; however, *Yanornis* has a less arboreal foot as indicated by the relatively long basal toes and short unguals, it probably spent more time walking on the shore.

Yanornis can also be well distinguished from *Yixianornis* by the following characters: relatively long cervicals, antero-posteriorly compressed furcula (more or less latero-medially compressed in *Yixianornis*), limb bones more robust, forelimbs relatively long, manus and pedal digits relatively short and pubic symphysis long. Besides, metacarpal Ⅲ is extremely slender in *Yixianornis* (table 2).

Although *Yixianornis* possesses strong flying capability, it still retains such primitive features as the gastralia. This represents the first occurrence of such structures in ornithurine birds. Further examination of the type of *Chaoyangia* shows that it probably also retains gastralia. The gastralia has been reported in *Archaeopteryx*, *Confuciusornis*, *Sinornis* and *Longipteryx*. We believe that it was probably present in all early birds.

In contrast to the fast growing knowledge about enantiornithines and the most primitive birds *Archaeopteryx* and *Confuciusornis* over the past decade, little progress has been made for our understanding of the ornithurine birds. The discovery of *Yixianornis* and *Yanornis* provides a lot more new information about the anatomy of ornithurine birds. Ornithurine birds appear to share at least the following synapomorphies: pygostyle short, heterocoelous cervicals, synsacrum composed of 9 or more sacrals, scapula curved, coracoid with a well-developed procoracoid and a round scapular articulating fossa, sternum elongate with antero-lateral processes, keel high and extending along the full length of the sternum, ulna with a semicircular dorsal condyle; first phalanx of second manual digit antero-posterioly expanded, and tarsometatarsus completely fused.

It is interesting to note that all ornithurine birds are larger than the enantiornithines in the Early Cretaceous. Size matters not only during the transition from dinosaurian ancestors to birds but also at the early evolution of birds. For the purpose of tree-climbing, the body size had decreased from dinosaurs to birds [14], this process had continued through the early stage of avian evolution[15]. *Archaeopteryx* and *Confuciusornis* remain the most primitive and the largest birds from the Late Jurassic to the Early Cretaceous. Enantiornithines reduced their body size in order to obtain the flapping power with yet less perfect flight apparatus. Ornithurine birds are different, most Early Cretaceous forms almost had the flight structure as perfect as in modern birds, but the oldest ornithurine *Liaoningornis* is a lot smaller. Therefore, body size reduction had independently occurred in enantiornithines and ornithurines; however, ornithurine birds began to increase their body size in the Early Cretaceous while enantiornithines probably started this process in the Late Cretaceous.

The discovery of the two new ornithurine birds also indicates that by the Early Cretaceous both enantiornithines and ornithurines had experienced remarkable radiation and differentiation. It is still a mystery when ornithurines began to split from their common ancestors with enantiornithines.

It is also noteworthy that although Early Cretaceous ornithurines birds had possessed the flight structures hardly distinguishable from those of modern birds, they also retained several primitive characteristics that have been well known in enantiornithines and more primitive birds. Among these characteristics are teeth on the upper and lower jaws, antero-posteriorly compressed furcula with deep anterior groove, presence of gastralia, first manual digit long, wing claws on manual digits Ⅰ and Ⅱ, absence of extensor tubercle on metacarpal Ⅰ, pubic symphysis present, supratendinal bridge absent at the distal tibiotarsus, etc. These characteristics show that Early Cretaceous ornithurine birds are still significantly different from modern birds. Because none of the Late Cretaceous birds has been commonly accepted as being related to a special group of modern taxa with solid evidence, we believe that the origin and radiation of modern birds had most likely begun in the Paleocene.

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