

Discovery of an ornithurine bird and its implication for Early Cretaceous avian radiation

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Edited by David L. Dilcher, University of Florida, Gainesville, FL, and approved October 26, 2005 (received for review August 16, 2005)

An ornithurine bird, *Hongshanornis longicresta* gen. et sp. nov., represented by a nearly complete and articulated skeleton in full plumage, has been recovered from the lacustrine deposits of the Lower Cretaceous Jehol Group in Inner Mongolia, northeast China. The bird had completely reduced teeth and possessed a beak in both the upper and lower jaws, representing the earliest known beaked ornithurine. The preservation of a predentary bone confirms that this structure is not unique to ornithischian dinosaurs but was common in early ornithurine birds. This small bird had a strong flying capability with a low aspect ratio wing. It was probably a wader, feeding in shallow water or marshes. This find confirms that the aquatic environment had played a key role in the origin and early radiation of ornithurines, one branch of which eventually gave rise to extant birds near the Cretaceous/Tertiary boundary. This discovery provides important information not only for studying the origin and early evolution of ornithurines but also for understanding the differentiation in morphology, body size, and diet of the Early Cretaceous birds.

evolutionary radiation | fossil bird | Inner Mongolia | beak

Over 20 species of birds have been described from the Early Cretaceous Jehol Biota in western Liaoning Province and its neighboring areas since 1992, documenting the earliest known major avian radiation in its evolutionary history. Most of these birds are referable to the monophyletic and dominant Mesozoic avian group Enantiornithes, which became extinct by the end of the Late Cretaceous (1, 2). Some Jehol birds, however, belong to the more advanced Ornithurae, a branch of which had given rise to all extant birds (3, 4). In addition to enantiornithine and ornithurine birds, some more basal birds also existed in the Jehol Biota, such as the beaked bird *Confuciusornis* (5, 6); *Sapeornis*, the largest bird of the Early Cretaceous (7); and the long-tailed bird, *Jeholornis* (8).

The Chinese Early Cretaceous birds have shown not only a high taxonomic diversity but also a great degree of variation in skeletal morphology, body size, flight capability, diet, and habitat. Although most of these birds are toothed forms like other Mesozoic birds, several taxa showed independent reduction or loss of teeth, such as *Confuciusornis*, which was reported as the earliest bird with a horny beak, and *Jeholornis*, which only retained three small teeth on the lower jaw as a specialization for seed-eating adaptation (9).

Recently, a small bird with the unusual preservation of a nearly complete skeleton and plumage was discovered from the Lower Cretaceous of Inner Mongolia, bordering western Liaoning, northeast China. The fossil was from the lacustrine Yixian Formation, the lower part of the Jehol Group, representing one of the few complete skeletons of Mesozoic ornithurines. The bird featured unexpectedly preserved complete hyoid bones and a predentary bone in the lower jaws. Most of the known ornithurines from the Jehol Biota were from the Jiufotang Formation, the upper part of the Jehol Group, and only one genus, *Liaoningornis*, represented by an incomplete postcranial skeleton, has been discovered from the Yixian Formation (9). Therefore, the new bird represents only the second, but much more complete,

ornithurine from the Yixian Formation, shedding light on our understanding of the origin and early radiation of ornithurines. Because all known ornithurines from the Jehol Biota are toothed forms, the present bird also represents the earliest ornithurine known with a horny beak, adding much to our knowledge of the tooth reduction in early avian evolution.

Systematic Description of Aves Ornithurae *Hongshanornis longicresta* gen. et sp. nov.

Holotype, Etymology, Locality, and Horizon. The holotype for *H. longicresta* is held at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP; Beijing) under collection number IVPP V14533. The generic name is derived from the Hongshan culture, one of earliest Chinese cultures mainly recorded in this region; the specific name derived from the Latin word *cresta*, refers to the raised crest of this bird. The locality of the find was Shifo, Ningcheng, Inner Mongolia, China. The horizon of the find was the Yixian Formation, Early Cretaceous (Aptian).

Diagnosis. A small ornithurine. Upper and lower jaws toothless. Premaxilla with a slender and pointed rostral end. Dentary with a curved rostral end. Sternum with two pairs of excavations, and lateral trabecula medially inclined and tapering distally. Furcula “U”-shaped, with a short hypocleidum. Ratio of total wing to leg length about 0.84. First phalanx of major manual digit with a distinct lateral process and the second phalanx slightly curved.

Description and Comparison. The holotype of *Hongshanornis* is a small adult individual completely preserved as part and counterpart in full plumage (Fig. 1). It is approximately the average size of a contemporaneous enantiornithine bird and is smaller than other ornithurines and more basal birds from the Lower Cretaceous. The skull is laterally exposed, showing an expanded braincase and a large orbit (Fig. 2). The posterior portion of the skull is crushed. There appears to exist a large and elongated nostril. A C-shaped lachrymal borders a triangular antorbital fenestra anteriorly. The antorbital fenestra appears smaller than the nostril. The nasals are relatively short compared with basal birds, such as *Archaeopteryx*.

Both the upper and lower jaws are elongated and toothless, with a pointed rostral end. The premaxilla has a long and slender nasal process that nearly contacts the frontal posteriorly. The rostral end of the premaxilla is triangular with a straight ventral margin. The maxilla occupies the majority of the facial margin. The jugal appears to be slender and rod-shaped, lacking any ascending process. The dentary is more than half the length of the lower jaw and tapers posteriorly. The rostral end of the dentary is distinctly curved. A small crescent-shaped bone near

Conflict of interest statement: No conflicts declared.

This paper was submitted directly (Track II) to the PNAS office.

Abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology; Ma, million years ago.

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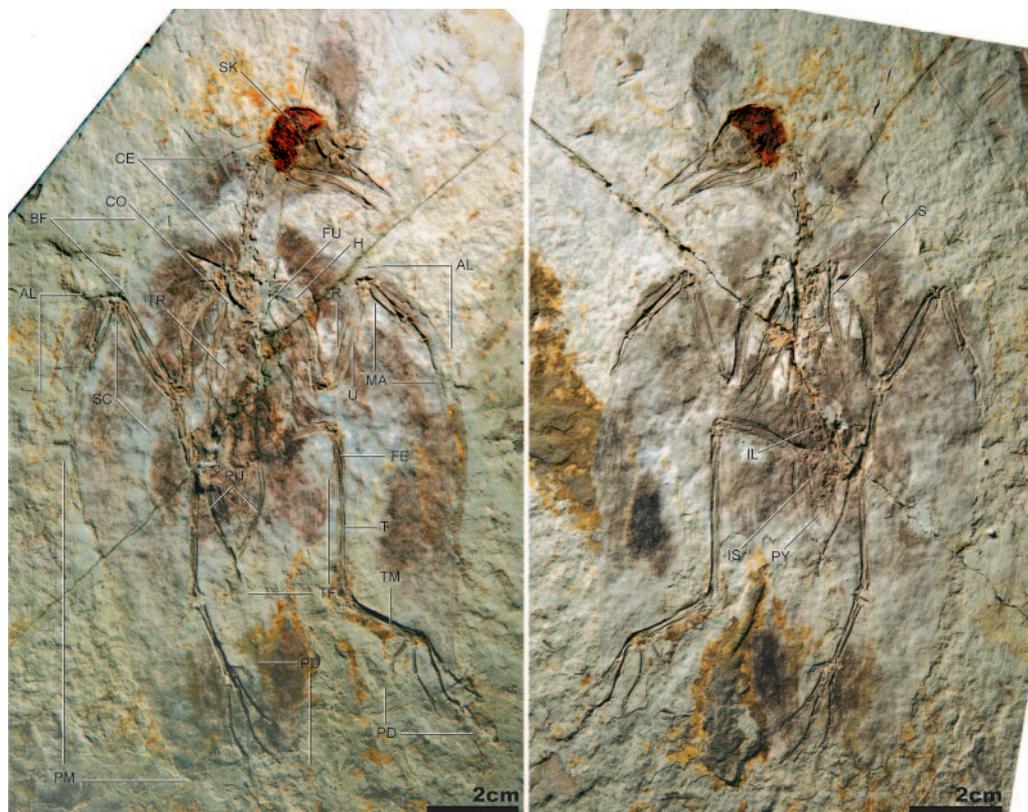


Fig. 1. Holotype of ornithurine bird *Hongshanornis longicresta* gen. et sp. nov. from the Lower Cretaceous of Inner Mongolia, China (IVPP V14533). (Left) Part. (Right) Counterpart. AL, alula; BF, body feathers; C, coracoid; CE, cervical vertebrae; FE, femur; FU, furcula; H, humerus; IL, ilium; IS, ischium; MA, manus; PD, pedal digits; PM, primaries; PU, pubis; PY, pygostyle; R, radius; S, scapula; SC, secondaries; SK, skull; T, tibiotarsus; TF, tail feathers; TR, thoracic rib; U, ulna; TM, tarsometatarsus.

the tip of the dentaries is recognized as a prementary bone that has not been previously reported in any Lower Cretaceous birds. The hyoid bones are exceptionally well preserved, comprising a pair of short ceratobranchials, long and slender basibranchials, a small urohyal, and a large and triangular entoglossal, similar to those of a chicken (10), but the basihyal appears to be absent (Fig. 3).

The neck is moderately long. The cervical vertebrae appear to be amphicoelous and are slightly longer than wide. Cervical ribs are not observed. Thoracic ribs are slender, with short uncinat

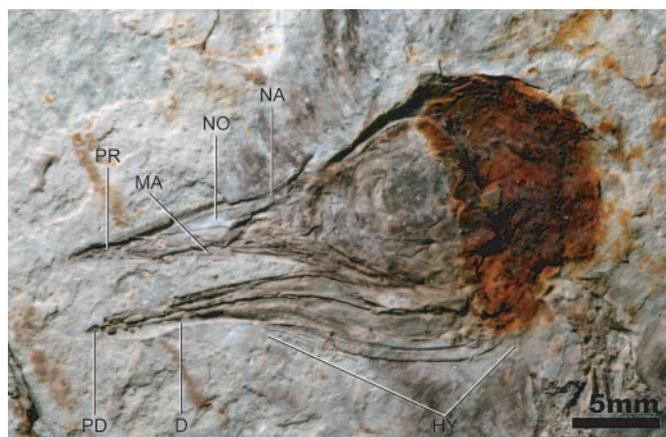


Fig. 2. Skull of the holotype of *Hongshanornis longicresta* gen. et sp. nov. (IVPP V14533). D, dentary; HY, hyoid bones; MA, maxilla; NA, nasal; NO, nostril; PD, prementary; PR, premaxilla.

processes that are probably unfused with the ribs. Gastralria are very slender. The synsacrum appears to be well fused, yet the exact number of sacral is difficult to determine. There is a very short pygostyle behind some short caudal vertebrae, similar to other ornithurine birds.

The scapula is long but slightly shorter than the humerus. Proximally, it has a short and pointed acromion process and a dorsolaterally exposed glenoid facet. The scapular shaft is laterally curved and tapers toward the distal end. The coracoid is strut-like and has a well developed procoracoid process; its length is more than twice the distal width. The coracoid has a convex lateral surface near the distal part. The furcula is U-shaped with a short hypocleidum. Two clavicles are slender with a tapering dorsal extremity. The sternum is more elongated than in enantiornithines and more basal birds, such as *Jeholornis*;

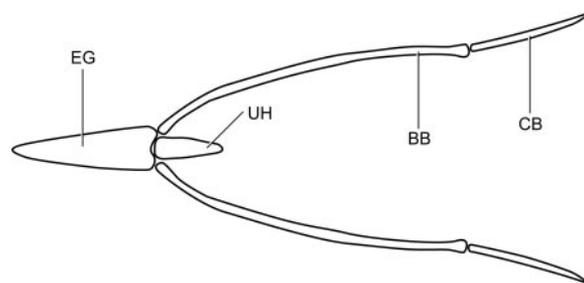


Fig. 3. Reconstruction of the hyoid bones of the holotype of *Hongshanornis longicresta* gen. et sp. nov. (IVPP V14533). BB, basibranchial; CB, ceratobranchial; EG, entoglossal; UH, Urohyal.

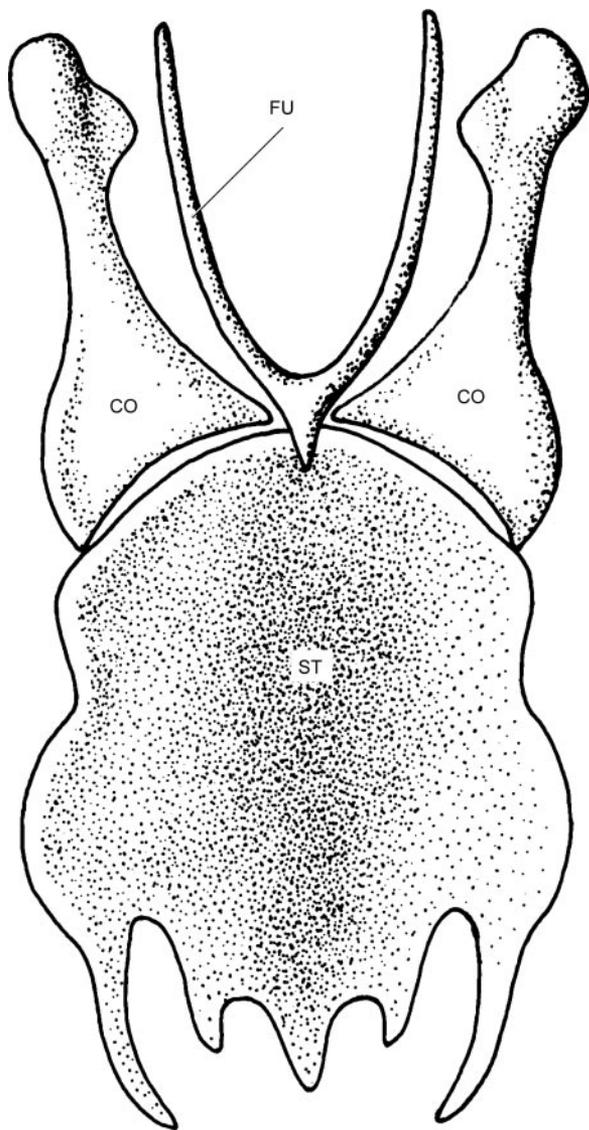


Fig. 4. Reconstruction of the sternum, coracoids, and furcula in dorsal view. CO, coracoid; FU, furcula; ST, sternum.

it has two pairs of posterior excavations. The lateral trabeculae is medially inclined and tapering distally; there are a pair of short posterior processes between the lateral trabeculae and the medial ridge of the sternum (Fig. 4).

The humerus is robust, with a large deltoid crest and a prominent head as in other ornithurines. The humerus is longer than the ulna as in basal birds, such as *Archaeopteryx* and *Confuciusornis*. Proximally, there appears to exist a well developed internal tuberosity and prominent bicapital crest. The ulna is bow-shaped and much wider than the radius, which is straight. The manus is longer than the humerus and ulna as in most basal birds. The carpometacarpus is well fused proximally with a well developed carpal trochlea. The radiale is heart-shaped. The major and minor metacarpals are nearly of the same length, unlike in enantiornithines (Fig. 5A). The minor metacarpal is approximately half the width of the major metacarpal. It remains unclear whether the major and minor metacarpals are fused distally. The intermetacarpal space is narrow and long. The alular metacarpal lacks an extensor process, as in most early birds. The first phalanx of the major digit is laterally expanded as in other ornithurine birds. The second phalanx of the major

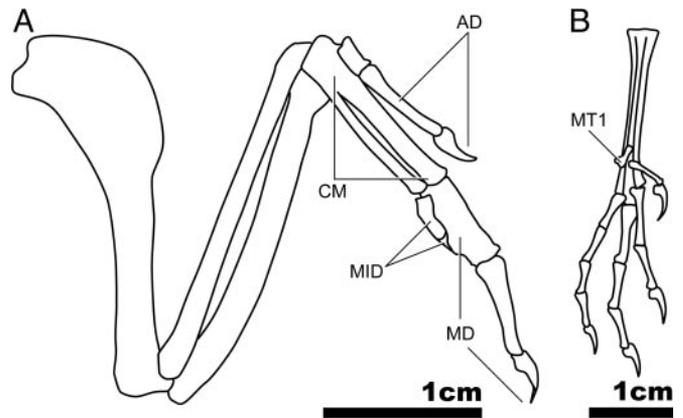


Fig. 5. Line drawing of the left wing (A) and left foot (B) of *Hongshanornis longicresta* gen. et sp. nov. (IVPP V14533). AD, alular digit; CM, carpometacarpus; MD, major digit; MID, minor digit; MT1, metatarsal I.

digit is approximately the same length as the first phalanx but is much more slender; it also has a slightly S-shaped curvature. The minor digit is very short and comprises two small phalanges, including a very small ungual; it tightly abuts the first phalanx of the major digit. The alular digit is slender but extends slightly past the distal end of the major metacarpal.

The pelvic bones are articulated, but it is unclear whether they are fused together. The pubis is slender and retroverted and appears to lack a distinctive pubic foot. The ischium lacks a proximal ascending process, unlike enantiornithines and more basal birds. The ilium does not approach the midline and is mainly dorsoventrally oriented.

The leg is much longer than the wing, which is different from other known Early Cretaceous birds. Leg bones are generally long and slender. The fibula is needle-shaped and short and does not reach the distal end of the tibiotarsus. The femur is slightly curved, and the ratio of the femur to tibiotarsus length is ≈ 0.58 , which is much smaller than in *Archaeopteryx* and known Early Cretaceous birds (see Table 1, which is published as supporting information on the PNAS web site). The tarsometatarsus is completely fused as in other ornithurines; it is approximately of half the length of the tibiotarsus. The fifth metatarsal is absent. The three major metatarsals (II–IV) are nearly of the same width. The hallux is short and in articulation with metatarsal II at a relatively high position as compared with arboreal birds. Toes are long and slender; the proximal phalanges are longer than distal phalanges, and the unguals are less curved, as is typical of terrestrial birds (Fig. 5B).

The holotype of *Hongshanornis* preserved a nearly complete plumage, with a very distinct raised crest for display. The primaries are particularly long, suggesting a low aspect wing and high wing loading. An alula is present. A slim and unslotted wing probably enabled a fast flight in open areas.

Discussion

Hongshanornis is easily distinguishable from other known Early Cretaceous birds in possessing a unique suite of characteristics, including small body size, a skull with slender and toothless jaws, a pointed snout and preentary bone, a sternum with two pairs of excavations, a lateral trabecula medially inclined with a tapering distal end, a U-shaped furcula with a short hypocleidum, a coracoid with a procoracoid process, a short wing compared to a long and slender leg, and the distinct shape of the major manual digit.

Phylogenetic analysis shows that *Hongshanornis* is more derived than enantiornithines and more basal birds and is most closely related to known ornithurine birds (see Fig. 6 and Data

Set 1, which are published as supporting information on the PNAS web site). *Hongshanornis* shares with other ornithurines a very short pygostyle, a strut-like coracoid with a well developed procoracoid process, a U-shaped furcula, a more elongated sternum, a significantly laterally expanded first phalanx of the major digit, a reduced minor digit tightly abutting this phalanx, and a completely fused tarsometatarsus. Therefore, it is regarded in this paper as the most basal member of the Ornithurae so far known. *Hongshanornis* also displays a combination of derived and primitive features. For instance, as in basal birds like *Archaeopteryx* (11), *Jeholornis*, and *Confuciusornis*, the humerus is longer than the ulna and the manus is longer than the humerus. It also resembles enantiornithines and *Sapeornis* in having a hypocleidum of the furcula, which is reduced in more advanced ornithurines, such as *Yixianornis* and *Yanornis* (12, 13). It is also more primitive than *Yanornis* and *Yixianornis* in the structure of the sternum. For instance, the posterior margin has two pairs of excavation and lacks a pair of closed fenestra.

Although teeth are present in most Early Cretaceous birds, there are a few exceptions. For instance, *Confuciusornis* was reported as the earliest known bird that had completely lost teeth and possessed a horny beak (5, 6), and it still represents the most primitive bird that had completely lost teeth. Some other Early Cretaceous birds had reduced the number and size of teeth. For instance, the seed-eating bird *Jeholornis* had only retained three small teeth in the lower jaw (8), and *Sapeornis* had lost the teeth in the lower jaw (7). Among enantiornithines, only the Late Cretaceous *Gobipteryx* (14) had completely lost teeth, and the Early Cretaceous *Longirostravis* (15) had teeth restricted to the rostral end of the upper and lower jaws. The Early Cretaceous ornithurine birds are usually equipped with many teeth. However, *Hongshanornis* had completely reduced the teeth in both the upper and lower jaws. Based on its phylogenetic position, the reduction of teeth in *Hongshanornis* must be regarded as independent of those in *Confuciusornis*, *Gobipteryx*, and extant birds, indicating that teeth had been lost many times in early avian evolution.

The prementary is a small single cap-like bone at the tip of the lower jaw of many ornithischian dinosaurs. Such a structure has also been reported in *Ichthyornis*, *Hesperornis*, and *Parahesperornis* (16). It is interesting that *Hongshanornis* also preserved a distinctive prementary in front of the dentaries. To our knowledge, a prementary bone has not been reported from any Early Cretaceous bird. Because of this feature's limited distribution in birds, it was suggested that a prementary bone might be primitive for the Class Aves or a derived feature for the Ornithurae and was lost in all modern birds, or it could be a feature to associate the Ichthyornithiforms with the Hesperornithiforms (16). The recognition of a prementary in the most basal ornithurine bird indicates that it might have been a common feature of early ornithurines and had subsequently become lost in extant birds.

The toe proportions and relatively short and less curved unguals in *Hongshanornis* preclude it from being an arboreal bird (17). The long and slender legs (compared with relatively short forelimbs) as well as the presence of an elongated tibiotarsus lend further evidence for its possible shore-dwelling habitat (Table 1). It is also noteworthy that the fossil was preserved in fine sandstones, unlike most other birds from the Jehol Biota that were mainly preserved in fine shales or mudstones. Such preservation may reflect the actual environment where *Hongshanornis* was living. The slender and pointed beak may further indicate that it fed on fish or invertebrates while it was wading in shallow water or marshes.

Recent isotope datings have provided a precise geochronological framework for understanding the evolutionary radiations of vertebrates in the Jehol Biota. The evolution of the Jehol Biota can be roughly divided into three stages represented by the Dabeigou, Yixian, and Jiufotang Formations and corresponding

to an age of 130 million years ago (Ma), 125 Ma, and 120 Ma, respectively (18–21). The only bird known from the Dabeigou Formation is the enantiornithine *Protopteryx* (22). Over 20 different species of the other birds have been described from the Yixian and Jiufotang Formations; therefore, the major radiations of birds in the Jehol Biota had occurred approximately during the temporal interval of 125–120 Ma. *Hongshanornis* and *Liaoningornis* (23), the two most basal ornithurines, are from the Yixian Formation, whereas more derived ornithurines such as *Yixianornis*, *Yanornis*, and *Gansus* are from the Jiufotang Formation or equivalent deposits. Although the absence of teeth in the new bird appears to hint a closer relationship to modern birds than toothed ornithurines, our phylogenetic analysis does not support this hypothesis (see Fig. 6 and Data Set 1). It is more likely that teeth were reduced several times in Cretaceous ornithurines, and, although the late Early Cretaceous represents a critical time for the evolution of ornithurine birds, the earliest radiation of extant birds probably only occurred shortly either before or after the Cretaceous/Tertiary boundary (24–26).

The Early Cretaceous bird evolution highlights a distinctive dichotomy between enantiornithines and ornithurines, the two major avian groups in the Mesozoic. These two groups differ significantly in morphology, flight, habitat, and physiology. Enantiornithines were mainly arboreal and had limited flight capability compared with ornithurines, and ornithurines were mainly terrestrial and possessed sophisticated flight skill nearly identical to modern birds. It is notable that studies on bone histology of these two groups indicated that enantiornithines and more basal birds still retained growth rings and grew slowly and were probably ectothermic. In contrast, the bone histology of Cretaceous ornithurines is similar to that of modern birds (27), showing that they were probably the only endothermic avian group in the Mesozoic. Although the new ornithurine already showed many typical ornithurine features, its occurrence from the Yixian Formation and more primitive appearance as compared with the ornithurines from the Jiufotang Formation indicate that it bears some implications for understanding the early diversification between enantiornithines and ornithurines.

During the Early Cretaceous, birds had already shown considerable variation in body size. The most basal birds, such as *Archaeopteryx*, *Jeholornis*, and *Sapeornis*, are generally large. Comparatively, contemporaneous enantiornithines were small and had not become much larger until the Late Cretaceous. The ornithurine birds appeared to have experienced a size increase during the Early Cretaceous. It is notable that ornithurines from the Yixian Formation (125 Ma), e.g., *Hongshanornis* and *Liaoningornis*, are approximately the size of an Early Cretaceous enantiornithine, and more derived ornithurines, such as *Yixianornis* and *Yanornis* from the Jiufotang Formation (120 Ma), are significantly larger. Other ornithurines, such as *Gansus* (28) and *Ambiortus* (29) from the deposits comparable with that of the Jiufotang Formation, are of similar size. The size increase in ornithurine birds during the Early Cretaceous must predate and be independent of the enantiornithines during the Late Cretaceous, given that the ancestors of both groups were small compared with most basal birds. The size increase in ornithurines may also reflect the increased flight capability that could afford a large body size during powerful flapping flight. The increased body size might also be an adaptation to more efficient fish catching that was common in early ornithurines.

By the Early Cretaceous, early birds had probably adapted to nearly all continental habitats that are currently dwelled by extant birds. Most early birds were arboreal, and only some ornithurines had become secondarily terrestrial and lived near the water. The paleoenvironment of the Early Cretaceous northeast China was characterized by the flourishing of forests and extensive distribution of fresh water lakes (30, 31). As a result, early birds in the Jehol Biota had differentiated signifi-

cantly not only in morphology and size but also in diet. For instance, the enantiornithine *Longipteryx* was believed to be piscivorous (32), which distinguishes it from most other enantiornithines that were probably mainly insectivorous. Another enantiornithine with specialized diet is *Longirostravis*, which probably had a probing feeding adaptation (15). The basal bird *Jeholornis* is a specialized seedeater with a very robust jaws adapted for crushing (8). *Sapeornis* is another herbivorous bird as evidenced by the preservation of gizzard stones and the reduction of teeth in the lower jaw (7). The basal ornithurine *Liaoningornis* was possibly an arboreal form, whereas other more derived early ornithurines had shifted their niche to the shore. *Hongshanornis* represents the earliest ornithurine with an obvious aquatic adaptation. *Yanornis* from the Jiufotang Formation

was mainly a fish eater; however, there also existed evidence showing that it could seasonally switch its diet from piscivorous to herbivorous (13). Other Early Cretaceous ornithurine, such as *Yixianornis* and *Gansus*, were also wading birds living in and near water. Therefore, this discovery confirms that the aquatic environment had clearly played a key role in the origin and early radiation of ornithurines (3, 9, 17).

We thank Drs. Xiaolin Wang and Desui Miao for reading the manuscript and Ms. Mingwan Yang for illustration. We also thank Larry D. Martin for discussions about the predeontary bone. This work was supported by Chinese Academy of Sciences Grant KZCX3-SW-142, National Natural Science Foundation of China Grants 40121202 and 40472018, and Major State Basic Research Projects of China Special Fund TG2000077700.

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