
A beaked basal ornithurine bird (Aves, Ornithurae) from the Lower Cretaceous of China

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Accepted: 23 January 2006
doi:10.1111/j.1463-6409.2006.00234.x

Zhou, Z. & Zhang, F. (2006). A beaked basal ornithurine bird (Aves, Ornithurae) from the Lower Cretaceous of China. — *Zoologica Scripta*, 35, 363–373.

We report here one of the earliest known beaked ornithurine birds from the Lower Cretaceous deposits in Liaoning, northeast China. The new basal ornithurine, *Archaeorhynchus spathula* gen. et sp. nov., has a rhynchokinetic skull with toothless jaws. It also contains over three dozen preserved gizzard stones, suggesting an herbivorous diet. The distal end of the tibiotarsus is unfused, enabling recognition of the astragalus with a broad ascending process, generally similar to that of *Archaeopteryx*. The new discovery sheds new light on our understanding of the early radiation and diet diversification of early birds in the Lower Cretaceous. *Zhonghe Zhou & Fucheng Zhang, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, China. E-mail: Zhonghe@yeah.net*

Most Mesozoic ornithurines are toothed birds (Zhou & Zhang 2001; Clarke & Norell 2002) with only a few exceptions (Zhou & Zhang 2005; Feduccia 2006). A recently discovered medium-sized basal ornithurine also lacks teeth in the jaws. The fossil was collected from the lacustrine Yixian Formation (125 Mya) of the famous Jehol Group (Swisher *et al.* 1999, 2002). It includes a skull containing much new information about the anatomy of a basal ornithurine. Phylogenetic analysis places the new bird at the base of the Ornithurae, which is consistent with the biostratigraphic sequences of the ornithurines in the Cretaceous.

Aves Linnaeus, 1758

Ornithurae Haeckel, 1866 (*sensu* Gauthier & de Queiroz 2001)
***Archaeorhynchus spathula* gen. et sp. nov. (Figs 1–4)**

Holotype. IVPP (Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China) collection number V14287; subadult individual, nearly complete skeleton with feather impressions.

Etymology. The generic name is derived from the Greek words *archae* and *rhynch*, meaning ‘ancient beak’. The specific epithet is derived from the Greek word *spatha*, indicating the spathulate dentary.

Locality and horizon. Yixian, Liaoning Province, China; Yixian Formation, Lower Cretaceous.

Diagnosis. A basal ornithurine bird distinguishable from other Mesozoic ornithurines by the following combination of

characters: beak present on both upper and lower jaws; premaxillae broad with slightly rounded tips; dentary spathulate, decorated with elongated foramina or grooves and a longitudinal ridge; sternum broad and strongly notched caudally with a pair of long lateral trabeculae; furcula with long and pointed acromion processes; metatarsals II and IV subequal in length; hindlimb shortened; ratio of femur to tibiotarsus 0.88; ratio of forelimb (humerus + ulna + major metacarpal) to hindlimb (femur + tibiotarsus + metatarsal III) about 1.35 (Figs 1–4).

Description and comparison

Archaeorhynchus is a medium-sized bird, represented by a partially articulated skull and nearly complete postcranial bones mainly preserved in ventral view, in association with feather impressions distributed on the whole body (Fig. 1). The holotype probably represents a subadult individual because the vertebrae and the extremities of many long bones are not well ossified (e.g. coracoid, humerus and femur) or fused (e.g. carpometacarpus and distal tibiotarsus).

The skull bones are mainly ventrally exposed and slightly dislocated due to some postmortem transportation. Such preservation, however, has made it possible to recognize many elements that are normally difficult to examine in a fossil bird. The bones of the lower mandibles are unfused. The left mandible is well articulated. The dentary is slender and its cranial half is spathulate, with elongated foramina or grooves on its medial surface. The caudal half of the dentary has a concave medial surface and tapers towards its caudal end without obvious forking. The articular is well developed, with a distinctive pneumatic foramen. The right mandible is

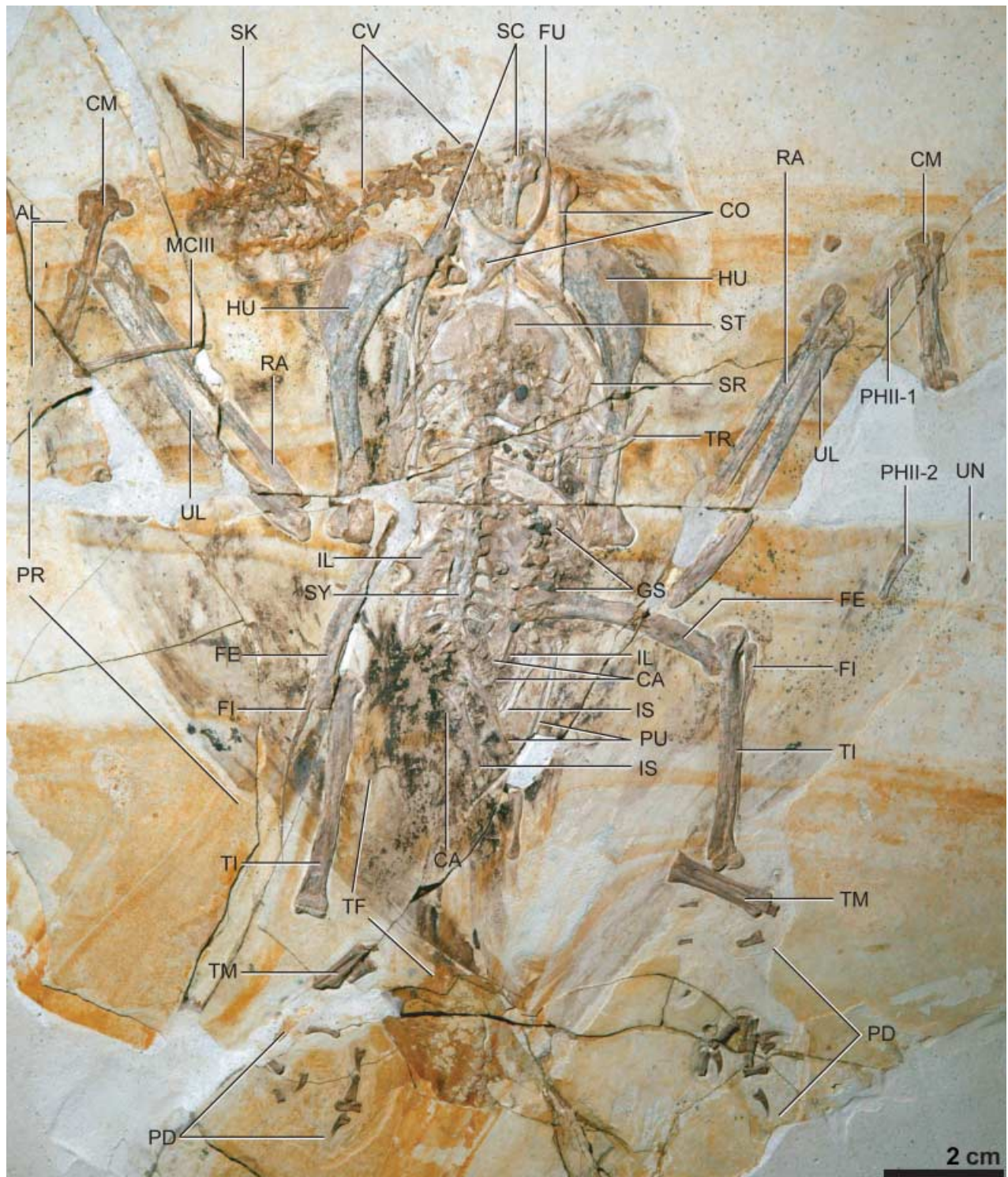


Fig. 1 A nearly complete skeleton of the holotype of *Archaeorhynchus spathula* gen. et sp. nov. (IVPP V14287). Abbreviations: AL, alula; CA, caudal vertebra; CM, carpometacarpus; CO, coracoid; CR, crest; CV, cervical vertebra; FE, femur; FI, fibula; FU, furcula; GA, gastralia; GS; gizzard stones; HU, humerus; IL, ilium; IS, ischium; MCIII, minor metacarpal; PD, pedal digits; PHII-1, first phalanx of major manual digit; PHII-2, second phalanx of major manual digit; PM, primaries; PU, pubis; RA, radius; SC, scapula; SK, skull; SR, sternal rib; ST, sternum; SY, synsacrum; TF, tail feathers; TI, tibia; TM, tarsometatarsus; TR, thoracic rib; UL, ulna; UN, ungual.

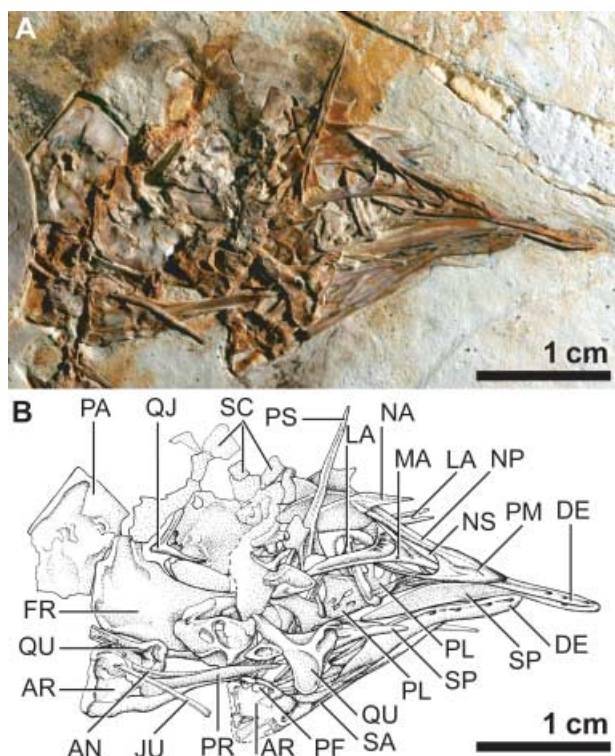


Fig. 2 A, B. Skull of *Archaeorhynchus spatbula* gen. et sp. nov. (IVPP V14287). —A. specimen. —B. line drawing. Abbreviations: AN, angular; AR, articular; DE, dentary; FR, frontal; JU, jugal; LA, lachrymal; MA, maxilla; NA, nasal; NP, nasal process of the premaxilla; NS, nostril; PA, parietal; PL, palatine; PF, pneumatic foramen; PR, prearticular; PS, parasphenoid; QJ, quadratojugal; QU, quadrate; SA, surangular; SC, sclerotic bones; SP, splenial. See Fig. 1 for other abbreviations.

disarticulated, with the dentary and splenial remarkably pushed forward. The right dentary not only shows elongated grooves or foramina but also a longitudinal ridge on its medial surface. The splenial is thin and tapers towards both cranial and caudal ends. The angular is small and slender. The surangular is long and tapers cranially towards a pointed end. The left quadrate retains a well-developed orbital process and a long otic process, but lacks any pneumatic foramen. The jugal is slender and rod-shaped. The quadratojugal is small and 'Y'-shaped.

Both the upper and lower jaws are toothless (Fig. 2A,B). The two premaxillae are fused at the cranial end. The right premaxilla is mainly laterally exposed with a slender maxillary process and a longer nasal process. The two nasal processes are dorsoventrally compressed and in very close contact along their full length, but are not fused. The rostral part of each premaxilla is broad with a slightly rounded margin, and there are some foramina or grooves on its external surface. The grooves or foramina on the dentary and the premaxilla



Fig. 3 Pectoral girdle and sternum of *Archaeorhynchus spatbula* gen. et sp. nov. (IVPP V14287). Abbreviations: LT, lateral trabecula of the sternum; SK, sternal keel; UP, uncinat process. See Fig. 1 for other abbreviations.

indicate that both the upper and lower jaws were equipped with a horny bill.

There appears to be an elliptical nostril. The maxilla is long and thin with a very slender dorsal process, defining a maxillary fossa in the cranial region of the antorbital fenestra. The lachrymal is large and its dorsal and ventral branches form a right angle. The nasal is short, compared to other early birds. It has two elongated cranial processes, forming the caudal margin of a large nostril. The parietal is square-shaped and the frontal is domed dorsally. Several square-shaped sclerotic ring bones are also preserved.

The parasphenoid is long and slender and tapers towards a pointed cranial end. A short palatal bone is preserved near the right maxilla and bears two small foramina (Fig. 2A,B). It has a hook-shaped choanal process, similar to that of *Archaeopteryx*, but which also appears to be triradiate, as in more derived birds.

The cervical vertebrae are less well ossified. At least ten are present. They are generally short, with well-developed costal

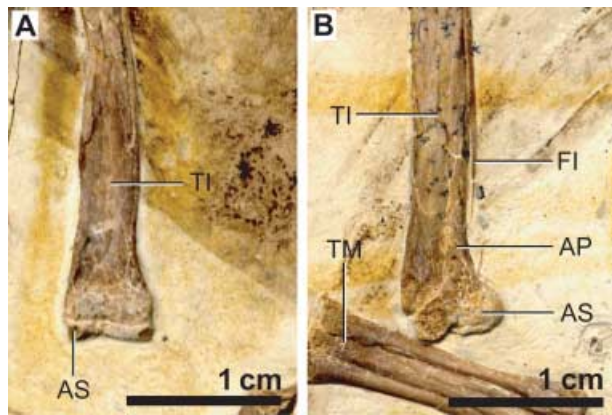


Fig. 4 A, B. Distal end of the tibiotarsus of *Archaeorhynchus spathula* gen. et sp. nov. (IVPP V14287). —A. right side in caudal view, showing the astragalus. —B. left side in cranial view, showing the broad ascending process of the astragalus. Abbreviations: AP, ascending process of the astragalus; AS, astragalus. See Fig. 1 for other abbreviations.

processes. The synsacrum comprises seven sacra, as in *Sapeornis* (Zhou & Zhang 2003), *Confuciusornis* (Chiappe *et al.* 1999) and *Protopteryx* (Zhang & Zhou 2000), compared with less than eight in *Cathayornis* and nine in *Yanornis* (Zhou & Zhang 2001). There are a few isolated caudal vertebrae with simple structure, but the distal caudals are not fused into a pygostyle, probably because it was a subadult individual. Thoracic ribs are relatively flat. Uncinate processes are short but robust. Sternal ribs are also well preserved. Several isolated gastralia are preserved near the pubes and other regions. They are small, short and curved, with one tapering end.

The scapula, coracoid and furcula are small in comparison with the wings. The scapula is only slightly curved and tapers towards the caudal end. It has a glenoid facet that is dorso-laterally directed. The coracoid is short and robust, although it is more elongated than in *Archaeopteryx* and *Sapeornis*. It has a large facet for articulation with the sternum, as in other ornithurines (Feduccia 1999). The furcula is 'U'-shaped and robust, with long and pointed acromion processes, but lacking any grooves or pitting on its cranial surface. The sternum is broad, with a keel extending along its full length as in other ornithurines, in contrast to more basal birds. The sternum has a strongly notched caudal margin and a pair of long lateral trabeculae, with its distal end only slightly expanded (Fig. 3).

The wing is significantly longer than the hindlimb. The ratio of humerus + ulna + major metacarpal to femur + tibiotarsus + metatarsal III is about 1.35 in *Archaeorhynchus*, which is most similar to that of the long-winged enantiornithine *Longipteryx* (Zhang *et al.* 2001) and the basal bird *Jeholornis* (Zhou & Zhang 2002); it is slightly smaller than that of the basal bird *Sapeornis*, but much larger than in other Lower

Cretaceous ornithurines such as *Yixianornis* and *Hongshanornis* (Table 1).

The humerus has a large deltoid crest, which is more than one third the length of the shaft; it also has a prominent head and ventral tubercle. Both the ulna and radius are slightly longer than the humerus. The ulna is only slightly bowed near the proximal end. The carpometacarpus has a prominent carpal trochlea, but lacks an extensor process or a pisiiform process. The alular metacarpal has a ginglymoid distal articulation with the first phalanx of the alular digit. The major metacarpal is robust and slightly longer than the minor metacarpal, contrary to the situation in enantiornithine birds. The manual digits are disarticulated. The first phalanx of the major digit is dorsoventrally compressed and posteriorly expanded, typical of ornithurine birds; the second phalanx is of nearly equal length but is much more slender. An ungual presumably belonging to the major digit is very small and not much curved.

The pelvis is preserved in ventral view. The ilium has a longer and larger preacetabular wing than the postacetabular wing. The retroverted pubis is slender and curved with a small pubic foot. The ischium is blade-shaped and much shorter than the pubis, lacking a strut-like proximal dorsal process that is often seen in enantiornithines and more basal birds.

The leg is shortened but strong. The femur is robust and bowed. The tibiotarsus is only slightly longer than the femur. The astragalus is large and unfused with the tibia, probably due to its subadult status. It has a broad ascending process (Fig. 4) as in several other basal birds. The fibula is slender and long; its distal two thirds is needle-shaped, nearly extending to the distal end of the tibia.

Metatarsals II–IV are possibly partially fused along their full length. Metatarsal III is longer and wider than II and IV, but is not proximally displaced plantarly relative to II and IV. Trochleae of metatarsal II and IV are nearly on the same level. The pedal digits are preserved in partial articulation. Proximal phalanges are longer than distal ones, and the unguis are not much curved, precluding an arboreal habit.

Feathers are preserved in association with the skeleton, particularly in the skull, neck, wing and tail regions. The primaries are very long and asymmetric. An alula is also recognizable. The tail feathers are comparatively long compared to other more primitive birds (Zhang & Zhou 2004). It is notable that there is no feather attached to the tibiotarsus, unlike in *Archaeopteryx*, *Confuciusornis* and some enantiornithines (Zhang & Zhou 2004), probably indicating that the leg feathers, which had first occurred in nonavian theropods (Xu *et al.* 2003), had been lost in ornithurine birds that already possessed a powerful and skilful flight capability provided by both the wing and the tail feathers as in modern birds. The recently reported basal ornithurine *Hongshanornis* also lacks leg feathers (Zhou & Zhang 2005).

Table 1 Measurements (mm) and proportions of selected elements of *Archaeorhynchus spathula* gen. et sp. nov. (IVPP V14287) compared with those of some other early birds.

	<i>Archaeorhynchus spathula</i> (IVPP V14287)	<i>Sapeornis chaoyangensis</i> (IVPP V12698)	<i>Hongshanornis longicresta</i> (IVPP V14533)	<i>Archaeopteryx bavarica</i> (Solnhofen specimen)	<i>Yixianornis grabau</i> (IVPP V12631)	<i>Longipteryx chaoyangensis</i> (IVPP V12325)
Humerus	53 (l)	127 (l)	26 (l)	83	49 (r)	45 (r)
Ulna	56 (l)	133 (l)	24 (l)	72*	50 (r)	47 (r)
Major metacarpal	25 (l)	57 (l)	13 (l)	34+	21 (r)	19 (r)
Pubis	36 (l)	85 (l)	24 (l)	59	36* (r)	26 (r)
Femur	37 (l)	80 (l)	22 (l)	70*	42 (r)	31 (r)
Tibiotarsus	42 (l)	84 (l)	38 (l)	90	54 (r)	32 (r)
Metatarsal III	20 (l)	44 (l)	22 (l)	48	26 (r)	21 (r)
Femur/tibiotarsus	0.88	0.95	0.58	0.78	0.78	0.97
Hu + ul + mcll/fe + ti + mtll	1.35	1.52	0.79	0.91	0.98	1.32

*Estimation, + preserved length; l and r indicate left and right sides, respectively.

Approximately three dozen gizzard stones are preserved between the sternum and the pelvis (Figs 1 and 3). They vary in morphology, roundness and size.

Discussion

Although the holotype of *Archaeorhynchus* is a subadult individual, it can be easily distinguished from other early ornithurines due to a combination of features including toothless jaws, dentary spathulate with elongated foramen and a longitudinal ridge, furcula with long and pointed acromion processes, caudal margin of sternum with two pairs of notches, and a significantly shortened leg.

Phylogenetic analysis indicates that *Archaeorhynchus* is more derived than enantiornithines and is most closely related to known ornithurines (Fig. 5). Ornithurae Haeckel, 1866 is a clade including comparatively close relatives of extant birds (Gauthier & de Queiroz 2001; Clarke & Norell 2002). Since Ornithurae is an apomorphy-based name (i.e. ornithurine birds possess a tail shorter than the femur, with a pygostyle of modern aspect), it should comprise not only the last common ancestor of *Apsaravis ukhaana* and extant birds, and all of its descendants (Gauthier & Queiroz 2001) but also some other basal ornithurines. *Yanornis*, *Yixianornis* and *Hongshanornis* all share a tail shorter than the femur, together with a pygostyle of modern aspect, and should thus be included in the Ornithurae. *Archaeorhynchus* has a tail shorter than the femur, and very likely has a pygostyle in an adult individual. Furthermore, it shares with other ornithurines a combination of 'U'-shaped furcula, a keel extending along the full length of the sternum, a prominent humeral head and a dorsoventrally compressed and posteriorly expanded first phalanx of the major manual digit, which clearly distinguish it from enantiornithines and more basal birds. In addition to these derived features, *Archaeorhynchus* also possesses a well-developed carpal trochlea of the carpometacarpus, a large wing and an alula, which suggest a powerful flight capability

similar to that of extant birds. Therefore, in this paper we refer *Archaeorhynchus* to the Ornithurae, as one of the basal-most members of the clade. Since *Archaeorhynchus*, *Hongshanornis* and *Liaoningornis*, the three most basal ornithurines according to the current phylogenetic analysis, are the only three genera known from the Yixian Formation of 125 Mya (Swisher *et al.* 2002), and most other known ornithurines are either from the overlying Jiufotang Formation of 120 Mya (He *et al.* 2004) or equivalent or younger deposits, the phylogenetic result is generally consistent with the stratigraphic distribution of the early ornithurines.

As one of the most basal ornithurines, *Archaeorhynchus* has retained several primitive features reminiscent of enantiornithines or more basal birds. For instance, the dentary is not strongly forked posteriorly as in *Apsaravis*; the sternum is broad but not as elongated as in *Ambiortus* (Kurochkin 1985) and *Yanornis*. The synsacrum comprises only seven sacra, similar to *Confuciusornis* and the primitive enantiornithine *Protopteryx*, while both *Yanornis* and *Yixianornis* have nine and *Apsaravis* has ten. The fibula is long and nearly extends to the distal end of the tibiotarsus while it is much more reduced in both *Yanornis* and *Yixianornis*. The tarsometatarsus lacks a distinctive vascular foramen, which is present in *Yixianornis*, *Yanornis* and *Apsaravis*.

Archaeorhynchus is larger than most enantiornithines from the Lower Cretaceous, but smaller than more basal birds such as *Archaeopteryx*, *Jeholornis*, and *Sapeornis*. It has greatly shortened legs compared to the wings, a feature which bears some resemblance to the enantiornithine *Longipteryx* and the largest Lower Cretaceous bird *Sapeornis*, but is different from *Archaeopteryx* and other ornithurines such as *Yixianornis* (Table 1). The shortening of the leg in the basal ornithurine *Archaeorhynchus* obviously represents a parallel evolution independent of enantiornithines or more basal birds. Furthermore, the most basal ornithurines *Archaeorhynchus*, *Hongshanornis* (Zhou & Zhang 2005) and *Liaoningornis* (Hou *et al.* 1996) are smaller than more derived ornithurines such as

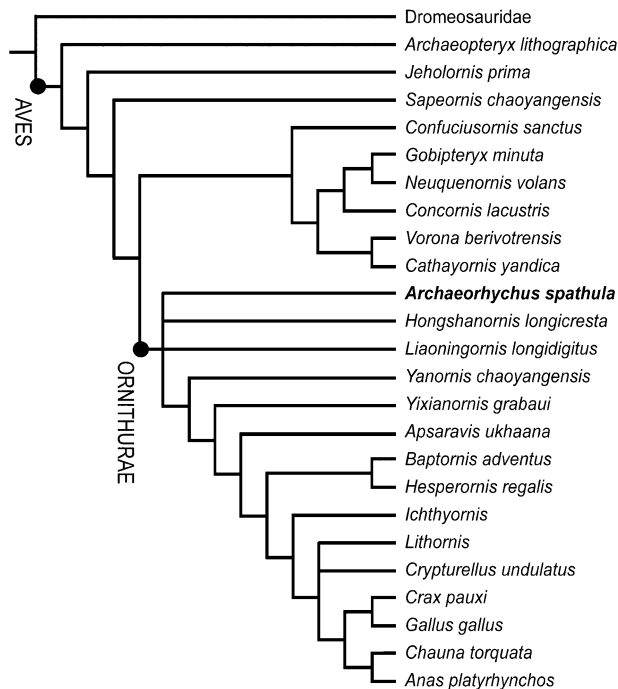


Fig. 5 Phylogenetic relationship of *Archaeorhynchus spathula* and other birds (strict consensus cladogram obtained from four equally parsimonious trees). Phylogenetic analysis was conducted using PAUP * Version 4.0b10. A total of 202 morphological characters was used, following Clarke & Norell (2002). The data matrix is based on Clarke & Norell (2002) and Zhou & Zhang (2005) (see Appendix), and *Patagopteryx deferrariisi* is excluded from the analysis. All characters are unordered except the following 36: 1, 8, 11, 23, 31, 52, 54, 61, 62, 66, 68, 69, 71, 76, 80, 105, 113, 117, 139, 142, 149, 153, 159, 170, 175, 177, 180, 182, 185, 188, 192, 193, 194, 195, 196, and 202. All characters have equal weight. The optimality criterion is parsimony. Branch-and-bound searching method was adopted. Accelerated transformation (ACCTRAN) was used for character-state optimization. Tree length = 678; consistency index (CI) = 0.58; homoplasy index (HI) = 0.42; CI excluding uninformative characters = 0.58; HI excluding uninformative characters = 0.42; retention index (RI) = 0.73; rescaled consistency index (RC) = 0.42.

Yanornis and *Yixianornis*, showing a trend of increasing body size among ornithurines in the Cretaceous. In contrast to the shorter legs in *Archaeorhynchus*, *Hongshanornis* had significantly elongated legs (Table 1).

Archaeorhynchus has preserved much new information about the skull among Mesozoic ornithurine birds (Fig. 2A,B). It represents the second Mesozoic ornithurine bird to have completely lost its teeth and to have possessed a horny bill in both the upper and lower mandibles. *Hongshanornis* was another toothless ornithurine. Other known Lower Cretaceous ornithurines such as *Yixianornis* and *Yanornis* are all equipped with many teeth. The loss of teeth must have

appeared several times in the evolutionary history of birds because it has independently occurred in extant birds as well as more basal birds such as *Confuciusornis* and *Gobipteryx* (Elzanowski 1995). The nasal process of the premaxilla is very thin and dorsoventrally compressed, with the middle portion particularly narrow and depressed, possibly indicating a rhynchokinetic skull (Gussekkloo *et al.* 2001). Unlike extant birds, the maxilla occupies most of the facial margin, with an antorbital fossa in the maxilla, similar to more basal birds. The preservation of some palatal bones and the parasphenoid provides new information for the discussion of palatal evolution in early birds.

Archaeorhynchus has preserved an astragalus with a prominent ascending process (Fig. 4), very similar to those of *Archaeopteryx* (Wellnhofer 1992; Mayr *et al.* 2005), *Rabonavis* (Forster *et al.* 1998) and *Jeholornis* (Zhou & Zhang 2002), but it lacks a high narrow pretibial bone associated primarily with the calcaneum as in neognathous birds (Martin *et al.* 1980; McGowan 1984). The new bird may further indicate that the pretibial bone represents a novel structure in late ornithurine evolution.

The habit and possible diet of *Archaeorhynchus* are difficult to ascertain. Although the bill of *Archaeorhynchus* has some ostensible similarities to that of a duck, it lacks the characteristic latter's horny lamellae on the interior of the beak near the cutting edge. The bill of a bird is a key adaptation for feeding. The tip of the moderately long and flat bill of the new bird is not pointed; thus it was probably not suitable for grabbing fish or insects. The predatory bone, which is clearly present in *Hongshanornis* and in several other presumably fish-eating ornithurine birds (Zhou & Zhang 2005), is absent in *Archaeorhynchus*. Since the specimen of *Archaeorhynchus* contains over three dozen preserved gizzard stones, it probably fed mainly on plants.

Our understanding of the morphological diversification and early radiation of birds has improved significantly thanks to the extraordinary discoveries from the Lower Cretaceous Jehol Group in Liaoning, north-east China. Over 20 species of birds have been described; however, there has been comparatively less discussion about the diversification of their diet. The basal bird *Confuciusornis* represents the most primitive bird with a horny beak (Hou *et al.* 1995; Chiappe *et al.* 1999), yet its diet remains unclear. Recent studies have revealed the presence of seed eating in the basal bird *Jeholornis* (Zhou & Zhang 2002), and of probing feeding in the enantiornithine *Longirostravis* (Hou *et al.* 2004). Lower Cretaceous ornithurines are generally believed to have been fish-eating birds, occupying a near-shore habitat (Martin 1983; Hou & Liu 1984; Zhou & Zhang 2005). For instance, *Yanornis* is believed to have been mainly piscivorous, although there is also evidence for seasonal diet switching (Zhou *et al.* 2004). *Archaeorhynchus* clearly represents a new trophic type that is

different from other ornithurine birds, adding to our understanding of the diversification in diet of early birds in the Lower Cretaceous.

The discovery of a new and basal ornithurine contributes to our understanding of the evolution of many characters in Ornithurinae, and shows that the Lower Cretaceous was a critical time for the appearance of many flight-related features that are seen in extant birds, i.e. in the wing, sternum and the pectoral girdle, providing important information on the evolutionary transitions towards the morphology and flight apparatus in extant birds.

Acknowledgements

We thank X. Wang for help in the field, D. Miao for reading the manuscript, Y. Li for preparing the specimen and M. Yang for the illustration. We thank two anonymous reviewers for their critical and helpful suggestions. Supported by the National Natural Science Foundation of China (40121202, 40472018) and the Chinese Academy of Sciences (kzcx3-sw-142).

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