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A new Lower Cretaceous bird from China and tooth reduction in early avian evolution

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A new avian genus and species, *Zhongjianornis yangi* gen. et sp. nov., is reported from the Lower Cretaceous lacustrine deposits of the Jiufotang Formation in Liaoning, northeast China. The new taxon is characterized by possessing the following combination of features: upper and lower jaws toothless, snout pointed, humerus with large and robust deltopectoral crest, second phalanx of the major manual digit longer than the first phalanx, unguals of the alular and major digits of similar length and significantly shorter than the corresponding penultimate phalanges, tibiotarsus slender and more than twice the length of the tarsometatarsus, and metatarsal IV longer than the other metatarsals. Phylogenetic analysis indicates that *Zhongjianornis* is phylogenetically basal to *Confuciusornis* and the dominant Mesozoic avian groups, Enantiornithes and Ornithurae, and therefore provides significant new information regarding the diversification of birds in the Early Cretaceous. It also represents the most basal bird that completely lacks teeth, suggesting that tooth loss was more common than expected in early avian evolution and that the avian beak appeared independently in several avian lineages, most probably as a response to selective pressure for weight reduction. Finally, the presence of a significantly enlarged humeral deltopectoral crest suggests that *Zhongjianornis* shares with other basal birds such as *Jeholornis*, *Sapeornis* and *Confuciusornis* a distinctive mode of adaptation for flight contrasting with that seen in more advanced birds, which instead possess an elongated sternum and a prominent keel.

Keywords: Lower Cretaceous; bird evolution; beak; China

1. INTRODUCTION

Over 30 genera of Early Cretaceous birds have been reported in the last two decades from the Lower Cretaceous of northeastern China (Chiappe 2007, Gao *et al.* 2008, Zhou *et al.* 2008, O'Connor *et al.* 2009), documenting a burst of avian diversification that followed the appearance of the earliest bird *Archaeopteryx*. These early birds occur in association with hundreds of exceptionally preserved feathered dinosaurs, early mammals, pterosaurs, amphibians, flowered plants and insects, which constitute the famous Jehol Biota (Benton *et al.* 2008; Zhang *et al.* 2008).

Recently, a relatively large bird was recovered from the Jiufotang Formation in Jianchang, western Liaoning. The new material is represented by a nearly complete and articulated skeleton. The new bird displays a combination of features that are unknown in any previously reported taxon; in particular, it represents the most basal avian that had completely lost teeth. The robust boomerang-shaped furcula and the large deltopectoral crest of the humerus are strongly reminiscent of *Confuciusornis*. The new discovery adds to our understanding of avian biodiversity in the Early Cretaceous.

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One contribution to a Special Issue 'Recent advances in Chinese palaeontology'.

2. SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758.

Zhongjianornis yangi gen. et sp. nov.
(See figures 1–5).

(a) Holotype: A nearly complete articulated skeleton with some poorly preserved feather imprints (Institute of Vertebrate Paleontology and Paleoanthropology collection, IVPP V15900).

(b) Etytomology: The genus and species names both honour the late Professor Zhongjian Yang (Chung-Chien Young), father of Chinese vertebrate paleontology and founder of the Institute of Vertebrate Paleontology and Paleoanthropology.

(c) Locality and horizon: Jianchang, Liaoning, northeastern China; Early Cretaceous Jiufotang Formation (He *et al.* 2004).

(d) Diagnosis: A pigeon-sized bird (table 1), distinguished from other early birds by possessing the following combination of features: toothless, snout pointed, humerus with a large and robust deltopectoral crest that is as wide as the humeral shaft and more than one-third the total length of the humerus, wing unguals small and slightly curved, metatarsal IV longer than II and III.

3. DESCRIPTION

The holotype of *Zhongjianornis yangi* gen. et sp. nov. is a nearly complete articulated skeleton of an adult individual (figures 1 and 2). The skull is characterized by a pointed snout and toothless upper and lower jaws. The maxillary and nasal processes of the premaxilla form an

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Figure 1. Holotype of *Zhongjianornis yangi* gen. et sp. nov. (IVPP V15900). Scale bar, 5 cm.

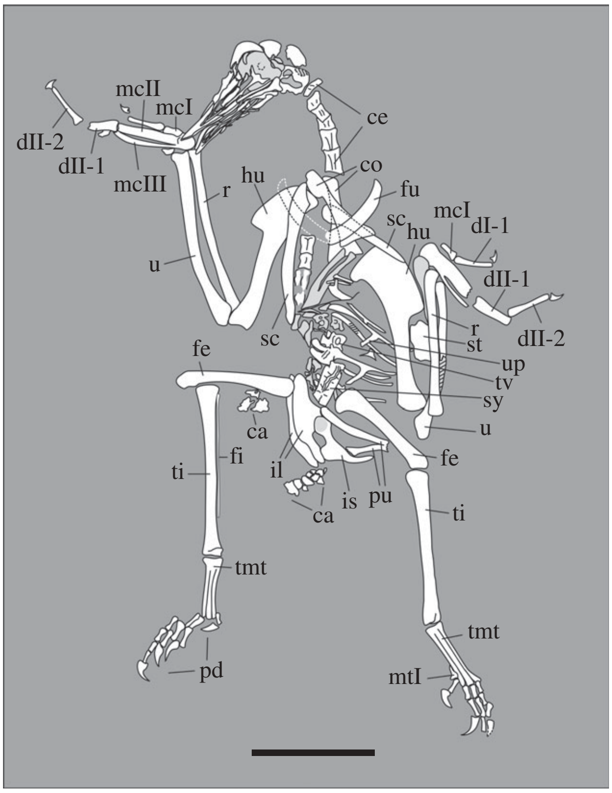

Figure 2. Line drawing of the holotype of *Zhongjianornis yangi* gen. et sp. nov. (IVPP V15900). Abbreviations: ca, caudal vertebra; ce, cervical vertebra; co, coracoid; dI-1, first phalanx of alular digit; dII-1, first phalanx of major digit; dII-2, second phalanx of major digit; fe, femur; fi, fibula; fu, furcula; hu, humerus; il, ilium; is, ischium; mcI, alular metacarpal, mcII, major metacarpal; mcIII, minor metacarpal; mtI, metatarsal I; pd, pedal digits; pu, pubis; r, radius; sc, scapula; st, sternum; sy, synsacrum; ti, tibia; tmt, tarsometatarsus; tv, thoracic vertebra; u, ulna; up, uncinate process of rib. Scale bar, 5 cm.

angle of less than 30°. The two nasal bones are long and strap-like and seem to be slightly constricted in the middle part and to flare towards the posterior end. The frontal is large and domed. The posterior end of the maxillary process of the left premaxilla contacts the maxilla, which is massively built and shorter than the premaxilla. The maxilla articulates posteriorly with the long, rod-shaped jugal.

A single occipital condyle is evident. Two flanges extend laterally from the posterior end of the basipterygoid process. A broad bone lying near the basipterygoid process is tentatively identified as a pterygoid, and a pair of slender bones between the nasal and maxilla is tentatively identified as the palatines.

The right mandible is well exposed in medial view. The dentary is strongly forked, with a long, straight ventral process and a short dorsal process that is slightly curved and nearly half the total length of the mandible. The angular appears massive, while the surangular is more slender. A triangular bone that tapers both anteriorly and posteriorly is recognized as the splenial, and a pair of slender rod-like bones is identified as hyoid elements (figure 3).

The cervical vertebrae are ventrally exposed. The posterior cervicals seem to be more elongated than the anterior ones. Because of crushing, it is difficult to determine the type of central articulation. The thoracic vertebrae are incompletely preserved, and their number is difficult to determine. One of the thoracics, located near the synsacrum, can be seen to have an opisthocoelous centrum. The lateral surface of each thoracic centrum appears to be excavated.

The thoracic ribs appear to be slender. At least three of them display tightly associated uncinate process, which are expanded proximally but taper distally (figure 4*a*). No gastralia have been recognized, but it is unclear whether they are genuinely absent or simply not preserved.

The synsacrum is completely fused and exposed in the ventral view (figure 5*a*). However, its posterior end is obscured by the pelvis, and the transverse process of the last sacral is partly exposed through the acetabular opening. The number of sacral vertebrae is estimated to be no greater than eight.

The caudal series is incompletely preserved, although five caudal vertebrae are preserved in articulation posterior to the pelvis. A short rod-like chevron is associated with the most cranial of these vertebrae. The caudals are short and small, with short, flat transverse processes and apparently procoelous intercentral articulations. Near the right femur are a few more isolated caudals. One of them appears to be larger than the others and might possibly represent the pygostyle. Based on the morphology of the preserved caudals, it is probable that *Zhongjianornis* has only a short caudal series, although the presence of a pygostyle is questionable (figure 5*a*).

The left scapula is well preserved and articulates with the coracoid at an acute angle, while the left scapula and coracoid are more or less covered by the furcula and right coracoid (figure 4*b*). The elongate scapula is nearly as long as the humerus, with a curved and distally tapering shaft. The coracoid is also elongated and is a

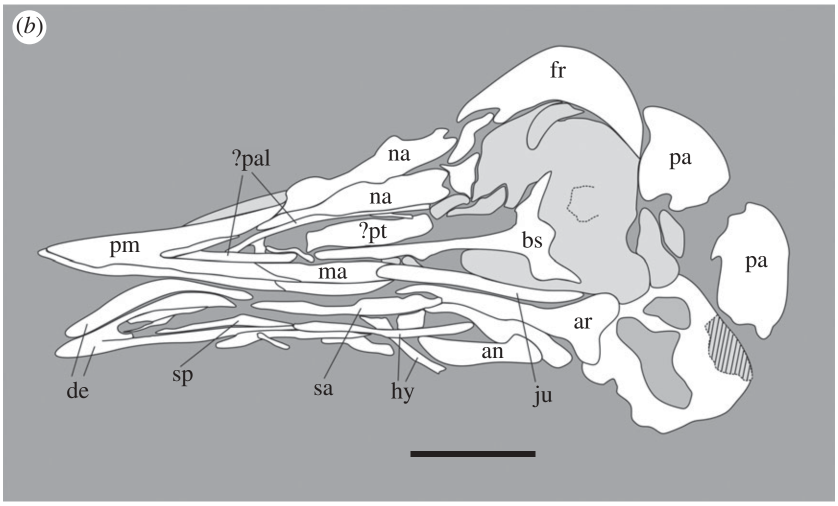

Figure 3. (*a*) Skull of the holotype of *Zhongjianornis yangi* gen. et sp. nov. (IVPP V15900). (*b*) Line drawing of the holotype skull of *Zhongjianornis yangi* gen. et sp. nov. (IVPP V15900). Abbreviations: an, angular; ar, articular; bs, basisphenoid; de, dentary; fr, frontal; ju, jugal; ma, maxilla; na, nasal; pa, parietal; ?pal, ?palatine; pm, premaxila; ?pt, ?pterygoid; sa, surangular; sp, splenial bone. Scale bar, 1 cm.

strut-like bone bearing a blunt acromion process. In contrast to ornithurine birds and at least one enantiornithine, *Protopteryx* (Zhang & Zhou 2000), the coracoid appears to lack a distinct procoracoid process. The sternal margin of the coracoid appears concave, with a maximum width less than half the length of the coracoid. The proximal part of the bone seems to bear a narrow supracoracoidal foramen.

The furcula is incompletely preserved and appears to lack a hypocleidum. Based on the available material, it can be reconstructed as having a robust boomerang-like shape, resembling the furculae of *Archaeopteryx* (Elzanowski 2002; Mayr *et al.* 2005), confuciusornithids (Hou *et al.* 1995; Chiappe *et al.* 1999) and other very basal birds. The furcula lacks grooves on its dorsal surface.

A thin bone between the right humerus and radius can be identified as an incompletely preserved sternum (one of the paired sternal plates), lying in proximity to the distal ends of some thoracic ribs. Although the outline of the whole sternum cannot be precisely reconstructed, this bone seems to be relatively short and more or less rounded, in contrast to elongated sterna of ornithurines. The sternum of *Zhongjianornis* also seems to lack a distinctly developed keel.

The forelimbs are exposed in dorsal view, and preserved in nearly complete articulation. The length ratio of the humerus + ulna + major metacarpal to the femur + tibiotarsus + metatarsal III is about 1.2, which is most similar to that of *Jeholornis* among known Mesozoic avians (Zhou & Zhang 2002). The humerus is robust, with a large deltopectoral crest that extends more than one-third the total length of the humerus. The deltopectoral crest is nearly as wide as the humeral shaft, with a rounded anterioproximal margin and a straight distal margin. The deltopectoral crest lacks a fenestra, in contrast to *Sapeornis* (Zhou & Zhang 2003) and confuciusornithids. The humeri of *Zhongjianornis* are straight and less twisted than in many more advanced birds. Proximally, the bicipital crest is prominent. The head of the humerus is not well exposed in either the right or the left forelimb, but seems not to be dorsally prominent. Distally, the humerus is slightly flared.

The ulna and radius are slightly longer than the humerus. The ulna is bow-shaped and is wider and more strongly curved than the radius. Distally the ulna seems to possess a semilunar external condyle. The right ulnare is preserved in association with the ulna and shows a distinctive metacarpal incision.

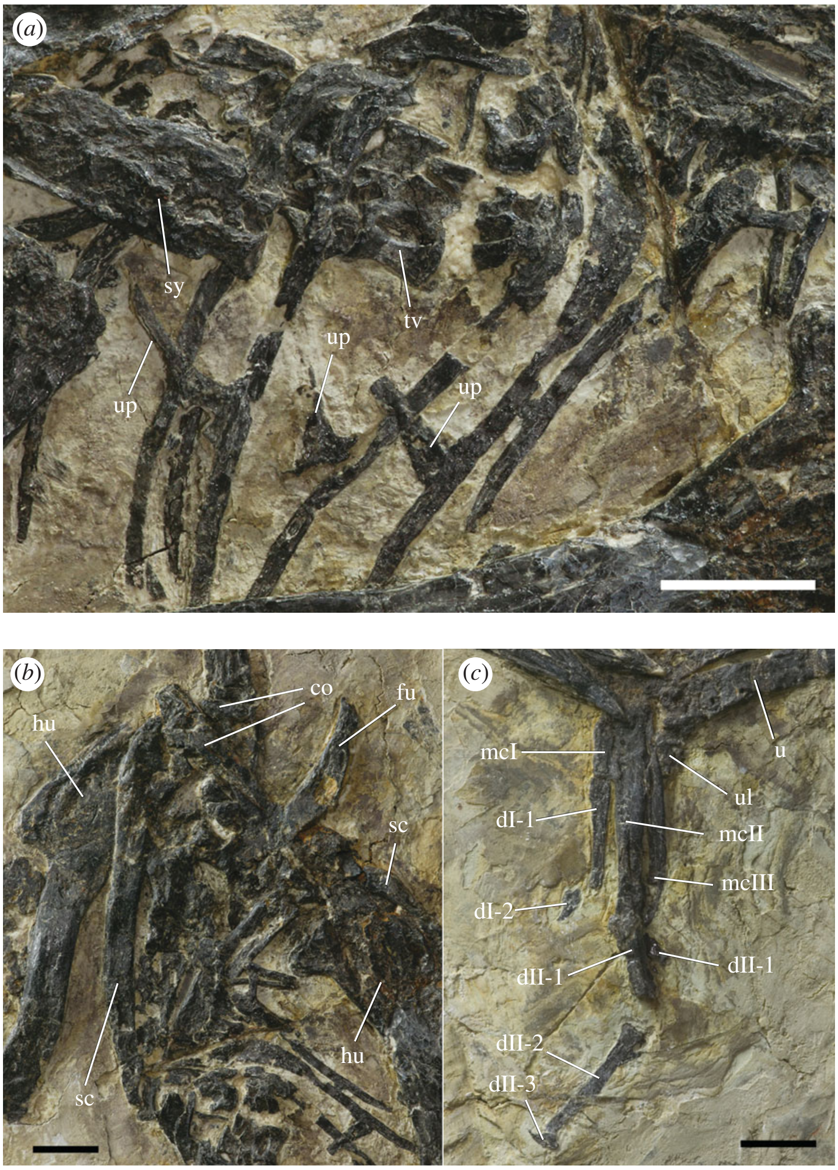

Figure 4. Close-up photos of *Zhongjianornis yangi* gen. et sp. nov. (IVPP V15900), showing (*a*) the thoracic ribs and uncinate processes, (*b*) the pectoral girdle, and (*c*) the hand. Abbreviations: dI-2, second phalanx of the alular digit; dII-3, third phalanx of the major digit; dIII-1, first phalanx of the minor digit; ul, ulnare; see figure 2 for other abbreviations. Scale bar, 1 cm.

The carpometacarpus is only fused at the proximal end, where a prominent carpal trochlea is present. The alular metacarpal is not fused with the major metacarpal and is a slender bone lacking an extensor process. The minor metacarpal is only about half as wide as the major metacarpal. It is only slightly curved near its distal end and does not fuse distally with the major metacarpal although the two bones are closely appressed. The major and minor metacarpals extend distally to about the same level, in contrast to enantiornithines, in which the minor metacarpal extends further distally.

The phalangeal formula of the manus is unclear. The alular digit is slender and does not extend to the distal end of the major metacarpal, and the first phalanx is much longer than the second (the ungual). The major digit comprises three phalanges. The first phalanx is the most robust of all the manual phalanges, whereas the second phalanx is shorter and more slender than the first phalanx and the third phalanx (the ungual) is shorter still. The minor digit is not preserved on the right wing, and only the first phalanx seems to be preserved on the left. Thus, the phalangeal count of the minor digit is unclear. The unguals of the alular and major digits are only slightly curved and are about equal in length, both of them being significantly shorter than the non-ungual phalanges of the manus (figure 4*c*).

The right pelvis is exposed in the lateral view (figure 5*a*). Both ilia are preserved, with the right ilium overlapping much of the left. The ilium is mainly dorsoventrally extended, and its pre-acetabular portion is greater than its slightly tapering post-acetabular portion. The ischium is robust and curved posterodorsally, with a prominent ascending process that contacts the posterior end of the ilium. The posteriorly directed right pubis is preserved in articulation with the ilium. The rod-shaped shaft of the pubis is nearly straight along much of its proximal portion. The distal tip of the pubis is missing, but part of the pubic symphysis is preserved, although its length cannot be reconstructed. The proximal ischium and pubis are preserved in articulation with the ilium, forming a rounded acetabular foramen. No anti-trochanter is evident.

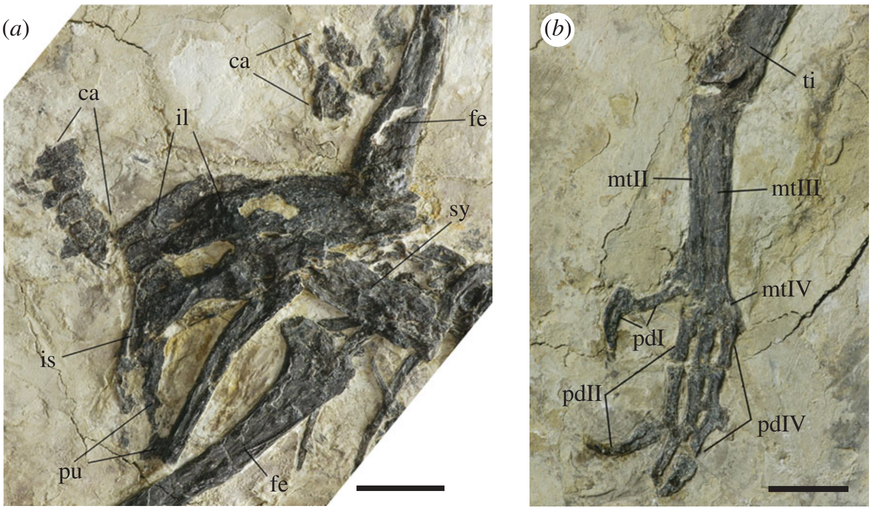

Figure 5. Close-up photos of *Zhongjianornis yangi* gen. et sp. nov. (IVPP V15900), showing (*a*) the pelvis and (*b*) the right foot. Abbreviations: mtII, metatarsal II; mtIII, metatarsal III; mtIV, metatarsal IV; pdI, pedal I; pdII, pedal II; pdIV, pedal IV; see figure 2 for other abbreviations. Scale bar, 1 cm.

The hind-limb elements are preserved in almost complete articulation. The femur is robust and nearly straight. It lacks a distinct neck but has a prominent ball-shaped head, which lacks a capital fossa. The femur is about two-thirds the length of the tibiotarsus and is much longer than the tarsometatarsus.

The tibiotarsus is long and slender, with the proximal and distal ends more or less crushed. Proximally, the tibiotarsus does not appear to form a cnemial crest. Distally, the tibiotarsus is well fused, but both the internal and external condyles are somewhat crushed and their shapes cannot be readily determined. The needle-shaped fibula is not fused with the tibiotarsus and extends along about three-quarters of the length of the latter bone. The right tibiotarsus appears shorter than the left, but we suspect that this is an artificial condition resulting from faulty reconstruction of the specimen by the local farmer before the specimen was obtained by us. Part of the middle segment was probably missing, as can be judged from a crack at the middle tibiotarsus.

The tarsometatarsus is relatively short, measuring only about 0.39 times the length of the tibiotarsus, which distinguishes it from any other known early birds (table 2). The right tarsometatarsus is completely preserved, but the left one is missing its distal end. The tarsometatarsus appears to be well fused at its proximal end. Based on the admittedly imperfect distal portion of the right tarsometatarsus, metatarsal IV appears to be longer than II and III (figure 5*b*), in contrast to most other early birds. However, we are less certain about the relative widths of the three major metatarsals. Metatarsal I is short, with an expanded distal end and a pointed proximal end. It appears to articulate with a facet on metatarsal II. Metatarsal V is absent. The pedal digits are nearly completely preserved, although they are greatly compressed. Digit I is moderately long, with the ungual exceeding the first phalanx in length. Digit II has a short first phalanx and a relatively long second phalanx, which, however, is shorter than the ungual. Digit III is slightly wider than the other digits. The non-ungual phalanges of digit IV are subequal in length and relatively short compared with those of the other digits. All of the pedal unguals are long and curved.

4. COMPARISON AND DISCUSSION

The new specimen represents a bird that is relatively large compared with other known birds from the Lower Cretaceous (table 1). It can be most readily distinguished from other taxa by the following features: skull with a pointed snout and toothless jaws, and robust humerus with a distinctively enlarged deltopectoral crest. Among Early Cretaceous birds of comparable or greater size, both *Jeholornis* and *Sapeornis* have a greater forelimb to hind-limb length ratio (Zhou & Zhang 2003). *Jeholornis* also has a unique skull adapted for seed-eating, with robust jaws bearing reduced teeth (Zhou & Zhang 2002). The skull of *Sapeornis* is adapted for herbivory, but still retains large teeth on the premaxilla, and the humerus of this taxon differs from that of *Zhongjianornis* in displaying a distinct fenestra on the deltopectoral crest. Furthermore, the femur and metatarsal III of *Zhongjianornis* are both significantly shorter in comparison to the tibiotarsus than those in *Sapeornis*.

The confuciusornithids are a group of birds from northeast China that are similar in size to *Zhongjianornis*, and they also resemble this taxon in having completely toothless jaws (Zhang *et al.* 2008). However, *Zhongjianornis* can be easily distinguished from confuciusornithids by its pointed snout and by the small size of the ungual of the alular manual digit (Hou *et al.* 1995; Chiappe *et al.* 1999). Furthermore, *Zhongjianornis* has a greater forelimb to hind-limb ratio than is seen in confuciusornithids (table 2).

Finally, the basal ornithurines *Hongshanornis* (Zhou & Zhang 2005) and *Archaeorhynchus* (Zhou & Zhang 2006) are two additional Chinese early birds that completely lack teeth. However, both are smaller than *Zhongjianornis*. *Hongshanornis* has far more slender limb bones, lacks an extremely large deltopectoral crest and displays a much smaller forelimb to hind-limb ratio. *Archaeorhynchus*, by contrast, is readily distinguishable from *Zhongjianornis* by its greater forelimb to hind-limb ratio. More advanced ornithurines such as *Yixianornis* and *Yanornis* (Zhou & Zhang 2001; Clarke *et al.* 2006) are toothed. All known enantiornithines from the Early Cretaceous of China have retained at least some teeth in the skull

Table 1. Measurements of *Zhongjianornis yangi* gen. et sp. nov. (IVPP V15900).

elements	measurements (mm)
skull length	61
synsacrum length	28[a]
synsacrum, maximum width	8
scapula length (right)	59
coracoid length (right)	36
coracoid, distal maximum width (left)	16
humerus length (left)	71
humerus, midshaft width (left)	6
ulna length (right)	74
ulna, midshaft width (right)	5
radius length (right)	73[a]
radius, midshaft width (right)	3.5
carpometacarpus length (right)	34
major metacarpal (right)	31
major metacarpal, midshaft width (right)	3.5
minor metacarpal, midshaft width (right)	2
alular metacarpal length (right)	8
major digit phalanx-l length (left)	18
major digit phalanx-2 length (left)	19.5
major digit phalanx-3 length (ungual, right)	5[b]
alular digit phalanx-1 length (right)	15
alular digit phalanx-2 length (ungual, right)	5.5[b]
ilium length (left)	39
ischium length (right)	25[b]
pubis length (right)	32[b]
femur length (left)	46.5
femur length (right)	48
tibiotarsus length (left)	65[a]
tibiotarsus length (right)	71
fibula length (right)	53
tarsometatarsus length (left)	29[a]
tarsometatarsus length (right)	27[b]
metatarsal I length (left)	6
metatarsal II length (left)	26
metatarsal III length (left)	28[a]
metatarsal IV length (left)	29[a]
pedal digit I-l length (left)	5
pedal digit I-2 length (ungual, left)	8[b]
pedal digit II-l length (left)	6.5
pedal digit II-2 length (left)	8
pedal digit II-3 length (ungual, left)	11
pedal digit III-l length (left)	6.5
pedal digit III-2 length (left)	7[a]
pedal digit III-3 length (left)	7[a]
pedal digit III-4 length (ungual, left)	12
pedal digit IV-1 length (right)	7
pedal digit IV-2 length (right)	5
pedal digit IV-3 length (right)	4[a]
pedal digit IV-4 length (right)	6.5
pedal digit IV-5 length (ungual, right)	9.5[b]

[a]Estimated value.
[b]Preserved length.

(Zhang & Zhou 2000; Zhou *et al.* 2005) and are often much smaller than *Zhongjianornis*. This is true even of the largest enantiornithine, *Pengornis* (Zhou *et al.* 2008), which also has greater forelimb to hind-limb and femur to tibiotarsus ratios than *Zhongjianornis* (table 2).

Phylogenetic analysis indicates that *Zhongjianornis* represents one of the most basal known birds. This taxon is more derived than *Archaeopteryx*, *Sapeornis* and

Table 2. Measurements (mm) and proportions of selected limb elements of *Zhongjianornis yangi* (IVPP V15900) and some other early birds from China. l. and r. indicate left and right sides, respectively. Abbreviations are as in figures 2 and 5.

	Zhongjianornis yangi (IVPP V15900)	*Jeholornis prima* (IVPP V13274)	*Sapeornis chaoyangensis* (IVPP V12698)	*Confuciusornis sanctus* (IVPP V11619)	*Pengornis houi* (IVPP V15336)	*Longipteryx chaoyangensis* (IVPP V12325)	*Archaeorhynchus spathula* (IVPP V14287)	*Hongshanornis longicresta* (IVPP V14533)	*Yixianornis grabaui* (IVPP V12631)
humerus	71 (l.)	110 (r.)	127 (l.)	52 (r.)	64 (l.)	45 (r.)	53 (l.)	26 (l.)	49 (r.)
ulna	74 (r.)	109 (r.)	133 (l.)	47 (r.)	71 (l.)	47 (r.)	56 (l.)	24 (l.)	50 (r.)
major metacarpal	31 (r.)	47 (r.)	57 (l.)	27 (r.)	27 (r)	19 (r.)	25 (l.)	13 (l.)	21 (r.)
femur	48 (r.)	75 (r.)	80 (l.)	47 (l.)	48 (r.)	31 (r.)	37 (l.)	22 (l.)	42 (r.)
tibiotarsus	71 (r.)	88 (r.)	84 (l.)	54 (l.)	50 (r.)	32 (r.)	42 (l.)	38 (l.)	54 (r.)
metatarsal III	28 (l.)	47 (r.)	44 (l.)	25 (l.)	26 (l.)	21 (r.)	20 (l.)	22 (l.)	26 (r.)
femur/tibiotarsus	0.68	0.85	0.95	0.87	0.96	0.97	0.88	0.58	0.78
mtIII/ti	0.39	0.53	0.52	0.46	0.52	0.66	0.48	0.58	0.48
hu + u + mcII/ fe + ti + mtIII	1.20	1.26	1.52	1.0	1.35	1.32	1.35	0.79	0.98

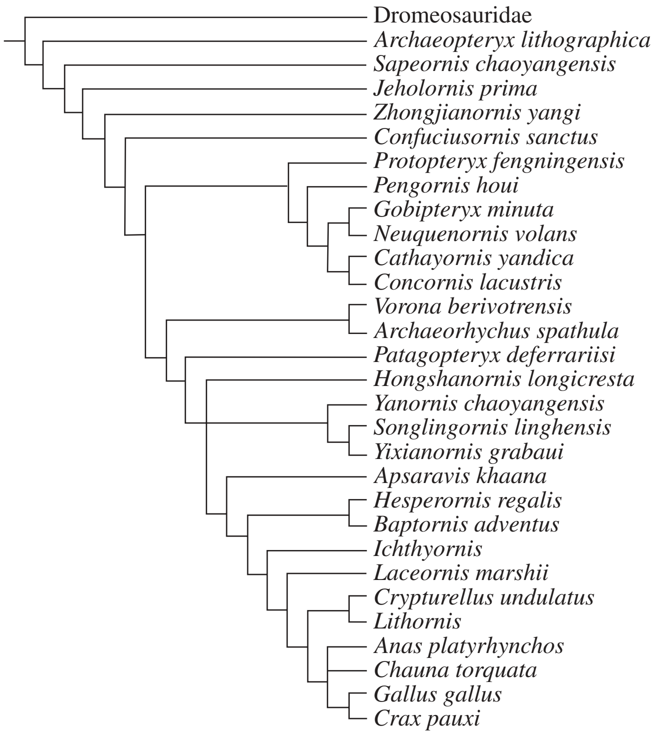

Figure 6. Phylogeny of *Zhongjianornis yangi* gen. et sp. nov. Phylogenetic analysis was conducted using NONA 2.0 and WinClada. All characters were unordered. A total of 205 morphological characters were used, following Zhou *et al.* (2008). The data matrix from Zhou *et al.* (2008) was used in a revised form. Tree length = 487; CI = 0.55; RI = 0.77. The cladogram is based on the strict consensus of four most parsimonious trees.

Jeholornis, but is more basal than other known taxa including *Confuciusornis* and the two dominant Mesozoic avian groups, the enantiornithines and ornithurines (figure 6). The new discovery adds to the known diversity of Lower Cretaceous avian assemblages. Furthermore, it is notable that the most basal currently known avian taxa are all relatively large in comparison with the more derived enantiornithines, confirming that the evolution of improved powered flight was coupled with a size decrease on the lineage leading to enantiornithines. The new cladogram is generally consistent with a recent analysis by Zhou *et al.* (2008), except that *Sapeornis* occupies a more basal position than *Jeholornis* in the current analysis. This result is surprising, as it contrasts with all previous analyses. The new topology readily explains the presence of a primitive non-strut-like coracoid in *Sapeornis*, but would also suggest that the long skeletal tail in *Jeholornis* could have evolved secondarily.

Among previously reported beaked birds from the Mesozoic of China, confuciusornithids represent the most basal forms to display this advanced feature. *Jeholornis* and *Sapeornis* have greatly reduced their teeth, but in neither of these taxa are teeth completely lacking (Zhou *et al.* 2005; Zhou & Zhang 2007). All known Chinese enantiornithines are also toothed, although some of them, including *Longipteryx* (Zhang *et al.* 2001), *Longirostravis* (Hou *et al.* 2004) and *Shanweiniao* (O'Connor *et al.* 2009), have their teeth restricted to the premaxilla and anterior dentary. Among known basal ornithurines, both *Hongshanornis* and *Archaeorhynchus* are completely toothless. An analysis of 31 avian genera from the Lower Cretaceous of China shows that seven of them are edentulous (table 3), and most are either completely toothed (i.e. teeth present in premaxilla, maxilla and dentary) or partially toothed (i.e. teeth absent on either one or two of the same three bones). The avian assemblage from the Lower Cretaceous of China documents a transition from completely toothed birds in the Late Jurassic to completely toothless ones in the Cenozoic.

The new bird also represents the most basal form to completely lose its teeth, although tooth loss undoubtedly occurred independently in several early avian lineages. Among known toothless birds, *Confuciusornis* is the next most advanced. We assume that tooth loss in both cases was probably owing to selective pressure for a reduction in body weight, and it would be especially advantageous to reduce the weight of the head rather than, for instance, the trunk, because the former is further from the centre of gravity. Many ornithurines that retained teeth, such as *Yanornis* and *Yixianornis*, also appear to have been strong flyers, and the selection pressure for weight reduction was probably less severe in these taxa.

The great variations in jaw and rostral morphology that existed among early birds may also suggest that significant trophic differentiation played a key role in the explosive radiation of birds approximately 20 million years after *Archaeopteryx* (Chiappe & Walker 2002; Chiappe 2007; Zhou & Zhang 2007).

Zhongjianornis appears to retain a boomerang-shaped furcula like those of more basal avians and non-avian theropods. Unlike *Archaeopteryx*, *Jeholornis* and *Sapeornis*, it possesses well-developed uncinate processes, as in *Confuciusornis* and more derived taxa.

The humerus has a robust deltopectoral crest, much as in confuciusornithids, but lacks a fenestra of the kind seen in *Sapeornis* and most confuciusornithids. Zhang *et al.* (2008) showed that a remarkably enlarged humeral

Table 3. List of 31 known avian genera from the Lower Cretaceous of China.

	genera
completely toothed (11)	*Protopteryx*, *Eoenantiornis*, *Cathayornis*, *Sinornis*, *Liaoxiornis*, *Jibeinia*, *Vescornis*, *Songlingornis*, *Yanornis*, *Yixianornis*, *Pengornis*
partially toothed (6)	*Jeholornis*, *Sapeornis*, *Boluochia*, *Longirostravis*, *Longipteryx*, *Shanweiniao*
edentulous (7)	*Confuciusornis*, *Changchengornis*, *Jinzhouornis*, *Eoconfuciusornis*, *Hongshanornis*, *Archaeorhynchus*, *Zhongjianornis*
unknown (7)	*Gansus*, *Chaoyangia*, *Eocathayornis*, *Otogornis*, *Liaoningornis*, *Paraprotopteryx*, *Zhongornis*

deltopectoral crest represents an adaptation for increasing flight capability between 131 and 120 Ma for confuciusornithids. It is notable that both *Jeholornis* and *Sapeornis* have a large deltopectoral crest, a condition unknown in enantiornithine and ornithurine birds (Zhou & Zhang 2001; Clarke & Norell 2002; Clarke *et al.* 2006). Besides, none of these most basal birds possesses an elongated sternum or a prominent sternal keel. The presence of a large deltopectoral crest in these basal birds probably compensated to some extent for the lack of an elongate, keeled sternum.

The proportions of the hind-limb and pes, as well as the shapes of the pedal unguals, seem to indicate an arboreal habit for *Zhongjianornis*. For instance, metatarsal III is only about 0.39 times as long as the tibiotarsus, a smaller ratio than in other known Early Cretaceous birds. The ratio of the length of the femur to that of the tibiotarsus is 0.68, also a smaller value than is typical of Early Cretaceous birds. The pedal unguals are all long and curved, and significantly longer than other phalanges. The hand of *Zhongjianornis* still retains some primitive features, such as the presence of a long major digit in which the second phalanx is longer than the first. However, it is also notable that the wing unguals seem to be relatively reduced and less curved than in more basal birds such as *Jeholornis*, *Sapeornis* and *Confuciusornis*, possibly indicating that they have lost their former presumed role in climbing.

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