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Largest bird from the Early Cretaceous and its implications for the earliest avian ecological diversification

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Abstract With only one known exception, early Cretaceous birds were smaller than their closest theropod dinosaur relatives. Here we report on a new bird from the Early Cretaceous feathered-dinosaur-bearing continental deposits of Liaoning, northeast China, which is not only larger than *Archaeopteryx* but is nearly twice as large as the basal dromaeosaur *Microraptor*. The new taxon, *Sapeornis chaoyangensis* gen. et sp. nov., has a more basal phylogenetic position than all other birds except for *Archaeopteryx*. Its exceptionally long forelimbs, well-developed deltoid crest of the humerus, proximally fused metacarpals, relatively short hindlimbs and short pygostyle indicate powerful soaring capability and further suggest that by the Early Cretaceous ecological diversification of early birds was greater than previously assumed. Electronic supplementary material to this paper can be obtained by using the Springer LINK server located at <http://dx.doi.org/10.1007/s00114-001-0276-9>.

Systematic paleontology

Class Aves

Order and family indet.

Genus *Sapeornis* gen. nov.

Sapeornis chaoyangensis sp. nov.

Type specimen

Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China collection number V 12698 (Fig. 1B, also see cover).

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Etymology

SAPE is the abbreviation for the Society of Avian Paleontology and Evolution. The fifth SAPE conference was held in China in June 2000, shortly before the holotype was collected. The species name is derived from the type locality 'Chaoyang'.

Type locality

Shangheshou, Chaoyang City, Liaoning Province, China.

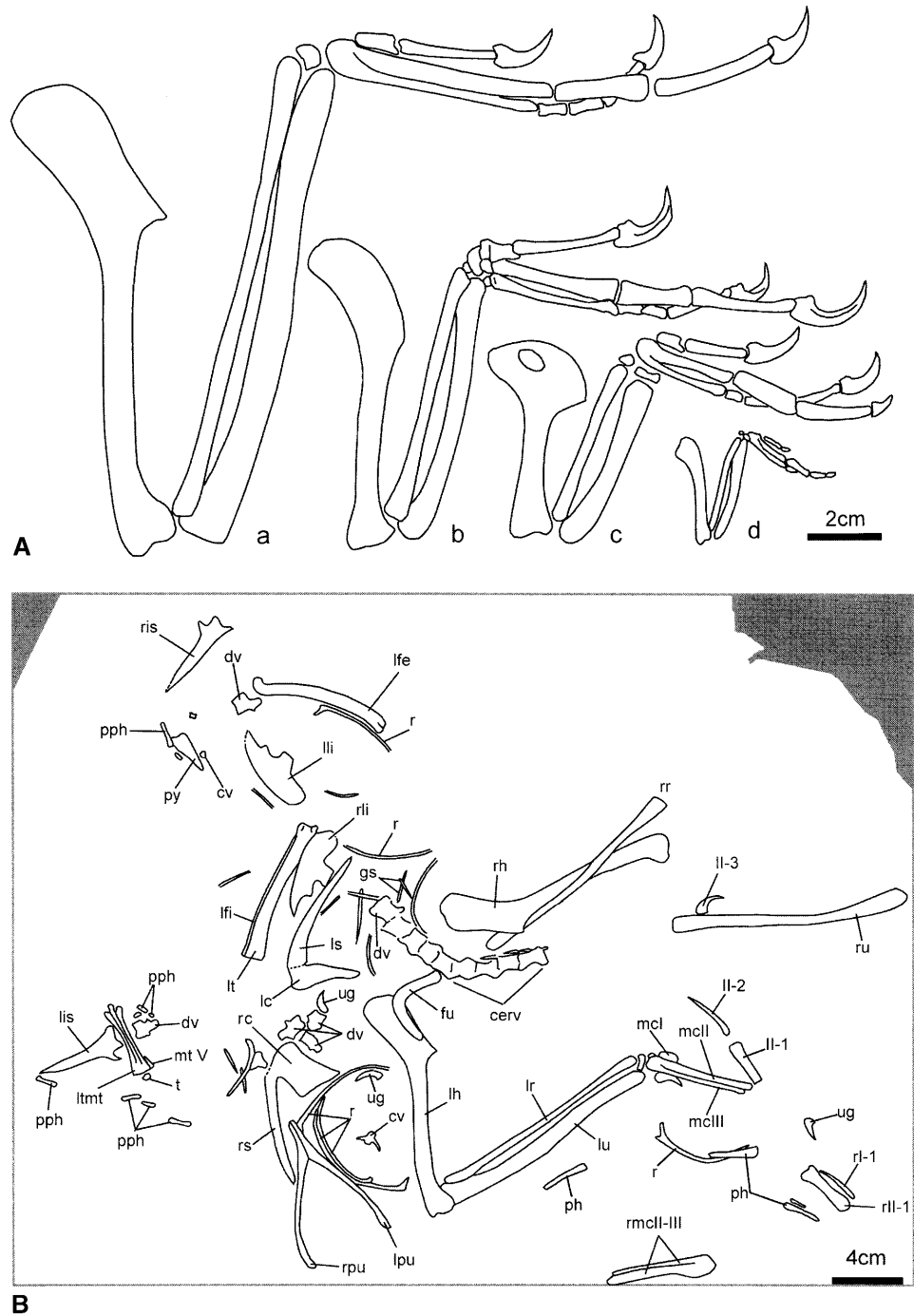
Horizon

Jiufotang Formation, Early Cretaceous.

Diagnosis

Sapeornis possesses more derived features than *Archaeopteryx*, such as a fused pygostyle. It is different from *Confuciusornis* in having, among many features, a well-developed fibula and a significantly different proximal end of the humerus. It differs from all the other avian taxa described from the early Cretaceous of China in retaining many primitive traits including the fifth metatarsal, the long first manual digit and short coracoid. It is also distinguishable from other early Cretaceous birds by possessing a large body size and extremely elongated forelimbs [ratio of forelimb (humerus + ulna + carpo-metacarpus) to hindlimb (femur + tibiotarsus + tarso-metatarsus) is 1.55], the deltoid crest of the humerus measures about one-third of the length of the humerus, the dorso-distal portion of the deltoid crest tapers into an acute process, the tibiotarsus is shorter than the pubis, and the femur nearly as long as the tibiotarsus.

Fig. 1 A Comparison of the left wing of (a) *Sapeornis chaoyangensis* with that of (b) *Archaeopteryx lithographica* (the Solnhofen specimen), (c) *Confuciusornis sanctus* (IVPP V 11619) and (d) *Cathayornis yandica* (IVPP V 9769); B line drawing of the holotype of *Sapeornis chaoyangensis* gen. et sp. nov. (IVPP V 12698). Abbreviations: *cerv* cervical vertebra, *cv* caudal vertebra, *dv* dorsal vertebra, *gs* gastralia, *lc* left coracoid, *lfe* left femur, *lfi* left fibula, *lh* left humerus, *lis* left ischium, *lli* left ilium, *lpu* left pubis, *lr* left radius, *ls* left scapula, *lt* left tibiotarsus, *ltmt* left tarsometatarsus, *lu* left ulna, *mc I-III* metacarpals I-III, *mtV* metatarsal V, *ph* phalanx, *pph* pedal phalanx, *py* pygostyle, *r* rib, *rc* right coracoid, *rh* right humerus, *ris* right ischium, *rli* right ilium, *rmc II-III* right metacarpals II-III, *rpu* right pubis, *rr* right radius, *rs* right scapula, *ru* right ulna, *rI-1* first phalanx of manual digit I of right side, *rII-1* first phalanx of manual digit II of right side, *t* tarsal, *ug* ungual, *fu* furcula, *II-1-3* first, second and third phalanges of manual digit II



Remarks

The specimen was collected by the Liaoning field crew of the Institute of Vertebrate Paleontology and Paleoanthropology in the summer of 2000. Associated with this fossil are several other birds, including *Confuciusornis* (Hou et al. 1995, 1996; Chiappe et al. 1999) and *Longipteryx* (Zhang and Zhou 2001), as well as pterosaurs, “feathered” dromaeosaurs and abundant fishes. The new locality was first discovered in the spring of 2000, and now it is arguably the most important Early Cretaceous

fossil locality except for Sihetun in western Liaoning Province, northeast China.

Description

The holotype consists of a nearly complete postcranial skeleton, which includes the vertebral column, pectoral girdle, the furcula, partially articulated forelimbs, the pelvic girdle, and the left hindlimb (Fig. 1B). The skeletal elements are mostly disarticulated, except for the left forelimb.

Table 1 Measurements (mm) of major skeletal elements of *Sapeornis chaoyangensis* gen. et sp. nov. (IVPP V 12698) in comparison to other primitive birds and theropods

	<i>Sapeornis chaoyangensis</i> (IVPP V12698)	<i>Archaeopteryx lithographica</i> (Solnhofen specimen)	<i>Confuciusornis sanctus</i> (IVPP V11619)	<i>Microraptor zhaonianus</i> (IVPP V12330)	<i>Sinornithosaurus millenii</i> (IVPP V12811)
Humerus	128 (l)	83	52 (r)	–	134 (r)
Ulna	133 (l)	72 ^a	47 (r)	35 (r)	110 (r)
Metacarpal II	62 (l)	34 (+)	27 (r)	–	63 (r)
Pubis	85 (l)	59	47 (r)	–	116 (l)
Femur	81 (l)	70 ^a	47 (l)	53 (l)	148 ^a (l)
Tibiotarsus/tibia	82 (l)	90	54 (l)	68 (l)	–
Metatarsal III	45 (l)	48	25 (l)	34 (l)	93

^a Estimation, (+) preserved length; (l) and (r) indicate left and right sides, respectively

The vertebral column is composed of incompletely preserved cervical, dorsal, and caudal vertebrae and a pygostyle. The cervicals are heterocoelous and elongate; the length is significantly larger than the width. Short and slender cervical ribs are preserved. The thoracic vertebrae lack pleurocoels or lateral excavations. The centra of the thoracic vertebrae are markedly longer than wide. The sacral vertebrae are not preserved. There are several free caudal vertebrae and a pygostyle. The pygostyle consists of at least four caudals.

The sternum is not preserved. The furcula is cranio-caudally compressed and U-shaped. It is robust and lacks a hypocleidium. Its cranial surface lacks grooves or excavations.

The pectoral girdle is completely preserved. The scapula and the coracoid are tightly joined, although it cannot be discerned whether they are fused. The angle between the scapula and the coracoid is less than 90°. The scapula has a short and blunt acromium. The shaft is straight; it tapers toward the distal end. The coracoid is short and broad; its height approximately equals its medio-lateral dimension. The glenoid facet of the coracoid lies ventral to the acrocoracoid process.

The forelimbs are extremely elongated (Fig. 1A; Table 1). The humerus is most distinctive in possessing an elongated deltoid crest, which is about one-third the total length of the humerus. The deltoid crest is straight along the dorsal margin, but its dorso-distal portion tapers into an acute angle. In proximal view, the head is small and strap-like without a midline convexity. Proximally, the humerus lacks a capital incisure and the ventral tubercle is absent. Distally, the humerus lacks the brachial fossa; the ventral condyle is small and rounded; the dorsal condyle is relatively large but does not project far proximally; the dorsal and ventral epicondyles are not well developed.

The ulna is slightly longer than the humerus on the left side, but these elements have approximately the same length on the right side. The olecranon is short. Distally, the dorsal condyle is not developed as a semilunate ridge as in more advanced birds. The proximal end of the radius is slightly curved in dorso-ventral view. It is expanded distally, but it is not markedly spoon-shaped.

The manus is nearly completely preserved, and is slightly longer than the ulna. The radiale has a well-developed metacarpal incision. The ulnare is not visible. The distal carpals and the proximal end of metacarpals II and III are fused into a carpometacarpus, with a well developed carpal trochlea. Metacarpal I is not fused with the carpometacarpus; it is about one-quarter the length of the carpometacarpus. The intermetacarpal space is narrow. Metacarpal II is slightly longer than III. Metacarpal II is more than twice the width of III. Metacarpal III is medio-laterally compressed; proximally it is dorso-ventrally much wider than the mid-shaft and is dorso-ventrally flattened.

The second manual digit is markedly longer than the carpometacarpus; the first phalanx is robust and slightly shorter than the second; the second phalanx is comparatively slender; the third (ungual) phalanx is sharply curved and approximately half the length of the second phalanx. The first phalanx of the first digit is long and slender, but is less than half the length of the carpometacarpus.

The pelvis consists of three pairs of unfused and disarticulated bones. The preacetabular portion of the ilium is longer than the postacetabular portion and is mainly dorsoventrally oriented; the postacetabular portion tapers distally. The pubic peduncle is robust and much wider than the ischiatic peduncle. The antitrochanter is not well developed. The ischium is straight with a well developed and pointed dorsal process. The pubes are united distally. The pubic symphysis is about one-third the length of the pubis. The distal end of the pubis is not expanded.

The most distinctive feature of the hindlimb is that the femur is nearly as long as the tibiotarsus. The hindlimb is short compared with the significantly elongated forelimb. The posterior trochanter on the proximal end of the femur is present. Distally, the femur has a laterally projecting fibular trochlea, and is fused with the calcaneum and the astragalus into a tibiotarsus. The tibiotarsus lacks a well-developed cnemial crest. Distally, the medial condyle is as wide as the lateral condyle. The intercondylar groove is mediolaterally broad and about one-third the width of the anterior surface. The fibula is slender and long; it reaches the distal end of the tibiotarsus.

Together with two distal tarsals, the proximal end of the major metatarsals is fused into a tarsometatarsus. One free tarsal is retained proximal to the tarsometatarsus; this is large and sub-oval in shape. This feature distinguishes *Sapeornis* from all other early Cretaceous birds except for *Iberomesornis*. A fifth metatarsal is present; it is short and slender. Metatarsals II, III and IV are not fused at the distal end. Metatarsal III is straight and slightly longer than II and IV. Metatarsals II and IV are approximately of the same length and slightly projected medially and laterally. The trochleae of the three major metatarsals are of about same width. Metatarsal III is not pinched at the proximal end. Metatarsal II bears no tubercle on the dorsal surface. Metatarsal I and most of the pedal phalanges are missing.

Discussion

Although several avian taxa have been recovered from the Early Cretaceous in recent years, none of these is larger than *Archaeopteryx*, which remains the only known bird from the Late Jurassic. Compared with the largest individual of *Archaeopteryx*, i.e. the Solnhofen specimen (Wellnhofer 1988), the hindlimb of *Sapeornis* is about the same length (Table 1). The length of the forelimb of the Solnhofen specimen is, however, only about 60% of that of *Sapeornis* (Fig. 1A). Furthermore, both the scapula and the pubis of *Sapeornis* are markedly longer than those of the Solnhofen specimen of *Archaeopteryx*.

Sapeornis is not only larger than *Archaeopteryx* and all Early Cretaceous birds but also considerably larger than the smallest adult theropod *Microraptor* (Xu et al. 2000), and also larger than the dromaeosaur *Sinornithosaurus* (Xu et al. 1999) in several bone dimensions (Table 1).

Concerning its phylogenetic position, *Sapeornis* is found to be the most primitive bird except for *Archaeopteryx* (Fig. 2; see Electronic Supplementary Material). It shares several primitive features with *Archaeopteryx* and dromaeosaurs, such as a short and nonstrut-like coracoid, well developed manual digit I, a fibula reaching the distal end of the tarsal joint, the presence of a free tarsal, and the presence of a fifth metatarsal. On the other hand, *Sapeornis* exhibits more derived characters than *Archaeopteryx*, such as the presence of heterocoelous cervicals, the presence of a pygostyle, a fused carpometacarpus, pubic symphysis about one third the length of the pubis, and the fact that the ulna is longer than the humerus.

Sapeornis exhibits several more primitive features than *Confuciusornis* and other Early Cretaceous birds from China such as *Sinornis*, *Cathayornis* and *Yanornis*: the well-developed fibula, the presence of the free tarsal, and a relatively shorter coracoid. On the other hand, it also shares several more derived characters with *Confuciusornis* and other Early Cretaceous birds than with *Archaeopteryx*, such as the presence of a pygostyle,

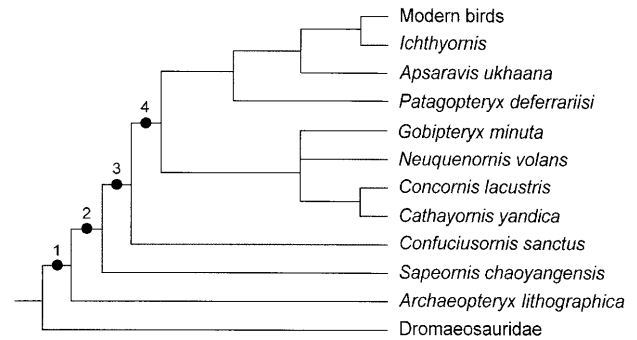


Fig. 2 Cladogram showing phylogenetic relationships between *Sapeornis chaoyangensis* and other major groups of birds; the cladogram is condensed from the four most parsimonious trees (tree length = 322, consistence index = 0.75, retention index = 0.83) based on 201 characters (see Electronic Supplementary Material, from Norell and Clarke 2001) using Paup 4.0b8. Characters are unordered. See Electronic Supplementary Material for the data matrix (revised from Norell and Clarke 2001). Synapomorphies supporting node 2 (*Sapeornis* and its sister group) include: distal caudals fused into a pygostyle, distal condyles of humerus developed on anterior surface, semilunate carpal and metacarpals II and III fused, distal end of pubes straight and subequal in proportions with rest of pubis, and calcaneum and astragalus completely fused with each other and tibia; synapomorphies supporting node 3 (*Confuciusornis* and its sister group) include: coracoid 'strut-like', with the height more than twice the mediolateral dimension, anterior surface of metacarpal I broadly convex, bicipital scar of ulna as a prominent tubercle, and distal tarsals completely fused with major metatarsals

proximally fused metacarpals II and III, a long dorsal process of the ischium and a fused tibiotarsus. However, *Sapeornis* also possesses several characters which are more derived than in *Confuciusornis*, such as the ulna longer than the humerus and the scapular shaft tapering distally, further indicating the mosaic distribution of characters in the early evolution of birds.

Sapeornis differs from all known Early Cretaceous birds outside China in the retention of the following plesiomorphic features: the long first manual digit, well-developed fibula and a relatively shorter coracoid. A free tarsal is present in *Sapeornis* and *Iberomesornis* (Sanz and Bonaparte 1992) but not in the other known Early Cretaceous birds (Sanz et al. 1995).

The forelimbs of *Sapeornis* are extremely long compared with the hindlimbs. The ratio of the forelimb to the hindlimb is 1.55. The same ratio is 0.91 in the Solnhofen specimen of *Archaeopteryx* and 1.0 in *Confuciusornis* (IVPP V 11619). The ratio of the ulna to the femur is 1.64 in *Sapeornis*, while the same ratio is 1.03 in *Archaeopteryx* (the Solnhofen specimen) and 1.0 in *Confuciusornis* (IVPP V 11619).

The significantly elongated forelimbs and relatively short hindlimbs of *Sapeornis* are comparable to the limb proportions of the recently described enantiornithine *Longipteryx* (Zhang and Zhou 2001) from the same locality. The ratio of the forelimb to the hindlimb is 1.55 in *Sapeornis* and 1.36 in *Longipteryx*, while the same ratio is significantly lower in other Mesozoic birds. Aerial and open-country birds such as shorebirds usually have long

wings while those living in dense vegetation often have short wings (King and King 1979; Welty 1982; Gill 1990). Based on this evidence, we propose that like *Longipteryx*, *Sapeornis* probably took advantage of its long wings to soar. The presence of elongate and heterocoelous cervical vertebrae indicates a flexible neck.

Nearly all Early Cretaceous enantiornithine birds, such as *Cathayornis*, *Sinornis* and *Protopteryx*, were perching forms (Zhou and Hou 1998; Zhang and Zhou 2000). Among them, *Longipteryx* is most unique and probably represents the only known enantiornithine adapted for living near the water. Early Cretaceous ornithurine birds such as *Yanornis* and *Yixianornis* (Zhou and Zhang 2001) were slightly larger than their contemporaneous enantiornithines; their elongated toes and the relative shortness of the distal phalanges suggest a near-shore environment. *Yanornis* also possesses an elongated snout and densely packed teeth, which might be an adaptation for a piscivorous diet. Another Early Cretaceous Chinese ornithurine, *Gansus*, is known from a left foot, and the elongated pedal toes indicate water or near-shore habit (Zhou and Zhang 2001).

In summary, with the appearance of perching (Zhou and Hou 1998), wading (Zhou and Zhang 2001) and soaring forms, early birds were probably occupying many ecological niches by the time of the Early Cretaceous, and the ecological diversification of Early Cretaceous birds was greater than previously assumed.

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