A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin

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Recent fossil discoveries have substantially reduced the morphological gap between non-avian and avian dinosaurs, yet avians including *Archaeopteryx* differ from non-avian theropods in their limb proportions. In particular, avians have proportionally longer and more robust forelimbs that are capable of supporting a large aerodynamic surface. Here we report on a new maniraptoran dinosaur, *Anchiornis huxleyi* gen. et sp. nov., based on a specimen collected from lacustrine deposits of uncertain age in western Liaoning, China. With an estimated mass of 110 grams, *Anchiornis* is the smallest known non-avian theropod dinosaur. It exhibits some wrist features indicative of high mobility, presaging the wing-folding mechanisms seen in more derived birds and suggesting rapid evolution of the carpus. Otherwise, *Anchiornis* is intermediate in general morphology between non-avian and avian dinosaurs, particularly with regard to relative forelimb length and thickness, and represents a transitional step toward the avian condition. In contrast with some recent comprehensive phylogenetic analyses, our phylogenetic analysis incorporates subtle morphological variations and recovers a conventional result supporting the monophyly of Avialae.

Early Cretaceous, maniraptoran theropod, coelurosaurian phylogeny, wrist evolution, avian origin

1 Systematic paleontology

1.1 Taxonomy

Maniraptora Gauthier. 1986
   Avialae Gauthier. 1986
      Anchiornis huxleyi gen. et sp. nov.

1.2 Etymology

Anchiornis is from the Greek '*Anchi*' (meaning 'nearby') and '*ornis*' (meaning bird), referring to the animal's being very closely related to birds; the specific epithet honors T. H. Huxley, who pioneered research into avian origins.

1.3 Holotype

Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V14378, an articulated skeleton missing only the skull, the anterior and middle cervical vertebrae, and the posterior caudal vertebrae, with faint feather impressions preserved on the slab and counter slab (Figure 1).

1.4 Locality and horizon

Yaolugou locality, Jianchang County, western Liaoning, China; lacustrine deposits of uncertain Jurassic-Cretaceous age.

1.5 Diagnosis
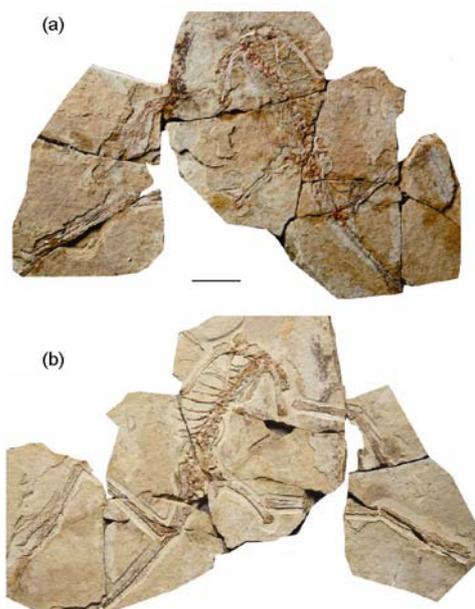
A small maniraptoran dinosaur with the ventral surface

Figure 1 Photograph of *Anchiornis huxleyi* holotype slab (a) and counter slab (b) (IVPP V14378). Scale bar = 3 cm.
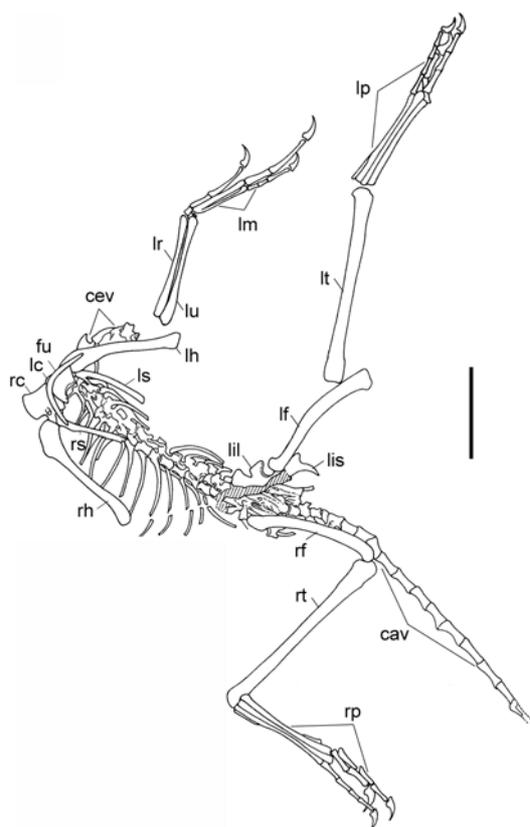

Figure 2 Line drawing of *Anchiornis huxleyi* holotype (IVPP V 14378). Abbreviations: cav, caudal vertebrae; cev, cervical vertebrae; fu, furcula; lc, left coracoid; lf, left femur; lh, left humerus; lil, left ilium; lis, left ischium; lm, left manus; lp, left pes; lr, left radius; ls, left scapula; lt, left tibiotarsus; lu, left ulna; rc, right coracoid; rh, right humerus; rf, right femur; rp, right pes; rs, right scapula; rt, right tibiotarsus. Scale bar = 3 cm.

of the coracoid sculptured by numerous small pits and an extremely short ischium (less than one-fourth of the femoral length).

1.6 Description and comparison

The holotype specimen of *Anchiornis* (Figures 1 and 2) is probably a sub-adult or young adult individual, as suggested by the complete fusion of all post-cervical vertebral neurocentral sutures. This ontogenetic interpretation is supported by a suite of histological features (Figure 3). The transverse section of the femur shows a very thin compacta (~0.33 mm) surrounding an exceptionally large central medullary cavity (~2.55 mm in diameter). This attests to the occurrence of substantial periosteal expansion. The primary cortex is composed of woven, fibro-lamellar bone with longitudinal vascularization. The inner third of the compacta is moderately well vascularized, whereas the more peripheral cortex shows diminished vascular canal density and smaller lumen diameter. Such patterning is consistent with a decrease in growth rate leading up to the demise of the individual[1]. The inner-most cortex shows a pronounced resorption line stemming from extensive osteoclastic erosion and substantial infilling of the endosteal medullary cavity with lamellar bone. Intermittent secondary Haversian canals are also present in this region. These attributes are also consistent with the interpretation that the individual survived at least into a sub-adult ontogenetic stage[2]. Lines of arrested growth are absent. Hence, no EFS patterning (external fundamental system = closely packed peripheral growth lines) indicative of late
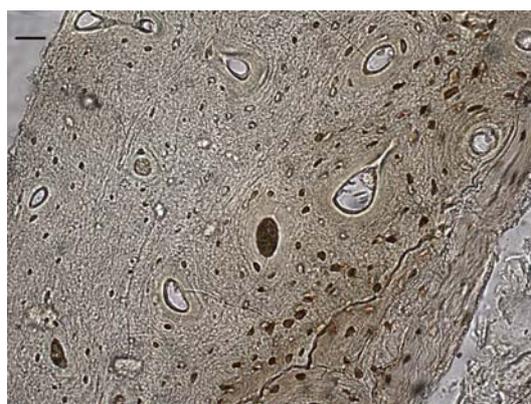
Figure 3 Histological section from the femoral shaft of *Anchiornis huxleyi* holotype (IVPP V14378), shown in normal light microscopy. The periosteal surface is in the upper left quadrant. Note: decreased primary vascular canal density and lumen diameter from lower right to upper left and lamellar and Haversian bone lining the medullary cavity (lower right). Scale bar = 20 μm.

ontogenetic status is evident. Collectively, these histological features are consistent with IVPP V14378's having perished as a sub-adult or early in adulthood.

The *Anchiornis* holotype is estimated to be about 34 cm in total body length (Table 1) and about 110 grams in body mass, smaller than adult specimens of all known non-avian dinosaurs and even some basal birds including *Archaeopteryx*[3,4]. This reinforces the deduction that small size evolved early in the history of birds[3–5].

Table 1 Select measurements of *Anchiornis huxleyi* holotype

Element	Unit (mm)
Cervical vertebral length (?cervical 8)	5.0
Anterior dorsal vertebral length (?dorsal 2)	4.3
Middle dorsal vertebral length (?dorsal 7)	4.8
Posterior dorsal vertebral length (?dorsal 11)	5.1
Anterior caudal vertebral length (caudal 1)	2.8
Middle caudal vertebral length (caudal 10)	7.4
Left scapula length	26.8
Humerus length	41.5*
Left ulna length	37.1
Left manus length	59.7
Right ilium length	26.2#
Femur length	43.2*
Tibiotarsus length	67.8*
Left pes length	67.2

* indicates the averaged length of the left and right elements and # the estimated complete length of a partial element.

Anchiornis shows central pneumatization and incipient development of heterocoely in the posterior cervical vertebrae. The anteriormost caudal vertebrae are significantly shortened, with centra less than 65% as long as those of the posterior dorsal vertebrae. This feature is seen in basal birds, troodontids, and dromaeosaurids. The anteriormost caudals also have posteriorly oriented, rod-like transverse processes (Figure 4(a)) as in basal troodontids[6]. The reduced zygapophyses of the middle caudals are like those seen in basal birds[7]. The anteriorly bifurcated middle chevrons are short, being about half as long as the corresponding centra.

As in most troodontid[6,8] and *Archaeopteryx* specimens[9], an ossified sternum is not preserved. The furcula closely resembles that of *Archaeopteryx* except for the slightly larger interclavicular angle. It is relatively large in size, each ramus measuring about one third of the femoral length. The scapula is slender and short (about 55% of humeral length), as in basal dromaeosaurids and basal avians[10]. One unusual feature of the specimen is that the ventral surface of the sub-

rectangular coracoid is sculpted by numerous small pits.

The humerus has a proportionally short deltopectoral crest (about one-fourth of the humeral length) as in some dromaeosaurids and troodontids. The ulna shows little posterior curvature and is only slightly thicker than the radius. It bears a bowl-shaped, round ventral cotyla on its proximal end and a weak semilunate ridge distally. As in many basal birds[11], the radiale is proportionally large (Figure 4(b)). The convexity at the proximal end of the carpometacarpus is most plausibly identified as a 'semilunate' carpal adhering to the proximal ends of metacarpals II and III, which are probably fused. This closely resembles the condition in most basal birds (Figure 4(b)). A less likely alternative is that the element currently identified as the ulnare, which also has a partially convex proximal surface might be the 'semilunate' carpal. In either case, the 'semilunate' carpal would be laterally positioned, having little contact with metacarpal I. Manual phalanx II-1 is much thicker than all of the other manual phalanges and nearly as thick as the ulna. As in avians, digit III is considerably shorter than digit II.

The small ilium has a slightly concave anterior margin, a pointed anteroventral process, a distinct supra-acetabular crest, an anteroventrally oriented pubic peduncle, a prominent, relatively ventrally located supratrochanteric process, an acetabulum with a peripheral medial wall, and a postacetabular process that extends ventrally to the level of the ischial peduncle (Figure 4(c)).

The hind limb is elongate, with a femur+tibiotarsus+ MT III/trunk length ratio of 2. The distal half of the femur is much thicker than the proximal half (Figure 4(d)), a feature also seen in the basal bird *Sapeornis,* the putative basal bird *Rahonavis*[12], and the basal dromaeosaurid *Buitreraptor*[10]. The length of the tibiotarsus is about 150% of the length of the femur, so that the tibiotarsus is substantially longer in proportional terms than that of any other known non-avian theropod[13]. Such limb proportions also differ from those of basal avialans that have fairly short lower legs relative to the upper legs, but is seen in derived birds that have much longer lower legs relative to the upper ones[13]. The metatarsals are not fused proximally. As preserved, pedal digit I lies medial to metatarsal II, suggesting a non-reversed hallux. Metatarsal III is transversely compressed, suggesting a sub-arctometatarsalian condition as in some dromaeosaurids and troodontids[6]. As in deinonychosaurs
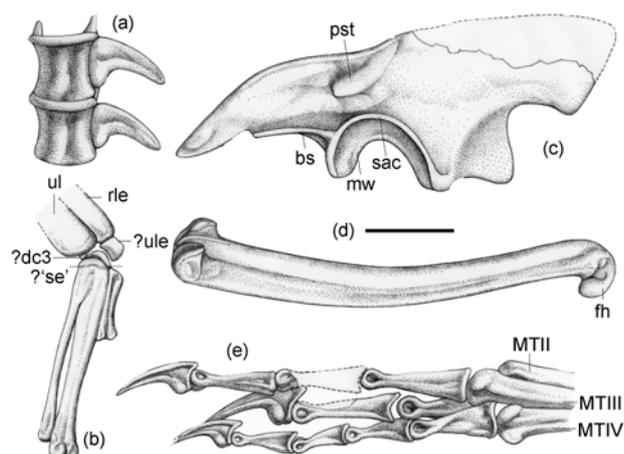
Figure 4 IVPP V 14378 selected elements. (a) Anteriormost caudal vertebrae in ventral view; (b) left carpal region; (c) right ilium in lateral view; (d) left femur in posteromedial view; (e) left pes in dorsolateral view. Abbreviations: bs, brevis fossa; ?dc3, ?distal carpal 3; fh, femoral head; MTII-IV, metatarsals II-IV; mw, medial wall; pst, supra-trochanteric process; ra, radius; rle, radiale; sac, super-acetabular crest; ?'se', ?'semilunate carpal; ul, ulna; ?ule, ?ulnare. Scale bar = 3 mm for (a)－(d) and 1 mm for (e).

Figure 5 Phylogenetic position of *Anchiornis*. (a) Strict consensus topology of paravians recovered from analysis of a dataset in ref. [3] with 10 taxa added, showing the systematic position of *Anchiornis*; (b) strict consensus topology of paravians recovered from analysis of a dataset in ref. [3] with 10 taxa and 48 new characters added, showing the systematic position of *Anchiornis*. Note that characters related to the wrist region contribute 18% (fast character optimization; characters 258, 259, 260, 261, 264, 265, and 266) or 10% (unambiguous synapomorphies; characters 258 and 259) of the characters used to diagnose the Avialae, compared to none for the clades Paraves and Aves. Contact the corresponding author for detailed information of the phylogenetic analysis.
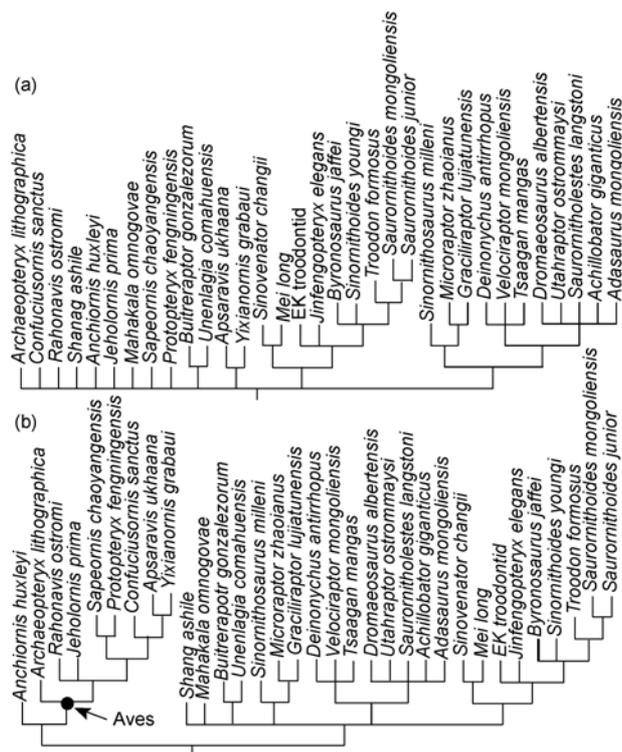
and *Rahonavis*[14], the second pedal ungual is substantially larger than the other unguals (Figure 4(e)).

Preserved soft tissues include horny sheaths around the pedal unguals, and patches of feathers. Specifically, extremely faint carbonized feather impressions are preserved dorsal to the presacral vertebral column and average about 20 mm in length, but their detailed structure is not clear.

2 Discussion

Phylogenetic analysis using a recently published dataset[10], with *Anchiornis* and 9 other newly described paravian taxa added in, produces poor resolution within the Paraves (Figure 5(a)). We added 48 new characters to the dataset, many of which reflect subtle modifications related to flight. Analysis of this expanded dataset recovers a monophyletic Avialae with *Anchiornis* as the basalmost avialan (Figure 5(b)). It is noteworthy that some deinonychosaurian features, such as a specialized pedal digit II, now characterize the more inclusive Paraves.

The discovery of *Anchiornis* has further reduced the morphological gap between non-avian and avian dinosaurs[10,14,15]. The latter differ from the former in a number of flight related features[16] including a proportionally long and robust forelimb that contributes to a large aerodynamic surface facilitating aerial locomotion[17].

As the closest relative of the Aves, *Anchiornis* has a forelimb about 80% as long as the hindlimb, a humerus as long and thick as the femur, and a manus about 130% as long as the femur. These ratios approximate the condition in basal birds, suggesting that *Anchiornis* might have developed a functional forelimb airfoil. Furthermore, *Anchiornis* has a more avian-like wrist than do other non-avian theropods. Wrist characters account for a significantly higher percentage of synapomorphies diagnosing the Avialae than either the Paraves or Aves, suggesting rapid evolution of the carpal region at the base of Avialae (Figure 4(b)).

The avian wrist is highly modified for both wing folding and flying[18]. One of the key developments in the evolution of the avian wrist was the appearance of the 'semilunate' carpal, a historically important structure linking non-avian and avian dinosaurs[19]. However, the

homologies of the 'semilunate' carpal are debated[20–22]. The 'semilunate' morphology first came to characterize distal carpal 1 early in theropod evolution[22] with the appearance of a convex trochlea that would have facilitated abduction and adduction of the manus. However, the range of this motion would have been limited, as indicated by the large radius of curvature. In many non-avian maniraptorans, the 'semilunate' carpal is enlarged (covering the proximal ends of metacarpals I and II, and probably III as well[23]) and has a strongly convex trochlear proximal surface, indicating extensive mobility of the manus in the radio-ulnar plane. In particular, the convexity of the trochlea would have facilitated considerable abduction (ulnar deflection) of the manus, corresponding in part to the wing-folding movements of the avian wrist. Although the enlarged 'semilunate' carpal has been suggested to represent fused distal carpals 1 and 2[20], no convincing ontogenetic data supports this assertion and the possibility that the 'semilunate' carpal is actually an enlarged distal carpal 1 or 2 cannot be excluded. The fusion of the 'semilunate' carpal to metacarpals II and III, but not to metacarpal I in many basal birds[11] and probably in *Anchiornis* is consistent with embryological data from extant birds showing that distal carpal 1 does not contribute to the 'semilunate' carpal[24]. In these avialans, the range of abduction permitted by the trochlea would have been large, and may have been slightly increased by the fact that metacarpal III articulated with the 'semilunate' carpal rather than projecting beyond it laterally. Furthermore, the proximal surface of the protruding first metacarpal would have contacted the distal face of the radiale in adducted positions of the carpus, and could therefore have acted as a bracing surface helping to prevent hyper-adduction of the wrist. The proximal surface of the carpometacarpus in *Anchiornis* and basal birds is topographically similar to its counterpart in extant birds (a distinct flat or concave proximal surface medial to the trochlear surface), contributing to a highly specialized joint whose mobility could have facilitated wing folding and flight[18] (Figure 6).

An accurate phylogeny is the basis for understanding avian origins, but coelurosaurian systematics is plagued by large amounts of missing data and prevalent homoplasies, which weaken phylogenetic signals. One effective way to improve phylogenetic accuracy is the addi-
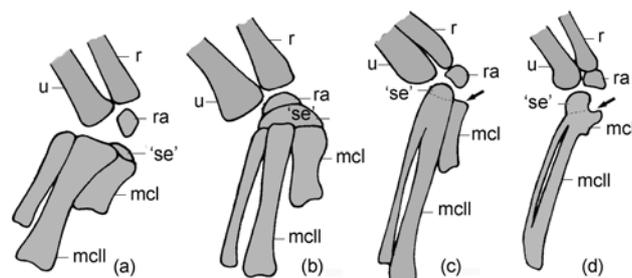
Figure 6 Schematic representation of theropod wrist evolution. (a) wrist region based on *Allosaurus* (DINO 11541); (b) wrist region based on *Deinonychus* (YPM 5206); (c) wrist region based on *Anchiornis* (IVPP V 14378); (d) wrist region based on extant bird *Gallicrex* (IVPP 1151). Among the carpals, only the radiale and 'semilunate' carpal are illustrated, whereas the others are omitted. The trochlear curvature of the 'semilunate' carpal is obliquely aligned in *Allosaurus*, but lies parallel to the radio-ulnar plane in the other taxa shown. Subsequently in the ropod evolution, the 'semilunate' carpal (as defined based on morphology) shifted its position laterally, providing a degree of abductor mobility and adductor stability that may have facilitated the evolution of the wing folding mechanism and flight capability. Arrow points to the proximal surface of metacarpal I in *Anchiornis* and extant birds, which is medial to the trochlear proximal surface of the manus. Abbreviations: mc I-II, metacarpals I-II; r, radius; ra, radiale; 'se', 'semilunate' carpal; u, ulna.

tion of more characters[25] and we have achieved a higher resolution by incorporating a large number of new characters into our analysis. Significantly, and in contrast to some recent comprehensive phylogenetic analyses[4,10,15], our analysis places *Rahonavis* and *Confuciusornis* within the Avialae[14] rather than the Dromaeosauridae[4,10,15]. This results in a relatively simple pattern of morphological evolution along the line to birds. Many of the newly added characters are derived from subtle morphological variations among coelurosaurians. Defining character states on the basis of subtle and continuous morphological variations is admittedly a relatively subjective procedure, but these variations clearly contain strong phylogenetic signals. However, a more objective methodology for employing this potentially rich source of data in phylogenetic analyses is needed[26], given that there is an increasing demand for new characters based on morphological subtleties in fine scale analyses with dense taxonomic sampling.

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