

LETTERS

A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus

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The early evolution of the major groups of derived non-avian theropods is still not well understood, mainly because of their poor fossil record in the Jurassic. A well-known result of this problem is the 'temporal paradox' argument that is sometimes made against the theropod hypothesis of avian origins¹. Here we report on an exceptionally well-preserved small theropod specimen collected from the earliest Late Jurassic Tiaojishan Formation of western Liaoning, China². The specimen is referable to the Troodontidae, which are among the theropods most closely related to birds. This new find refutes the 'temporal paradox'¹ and provides significant information on the temporal framework of theropod divergence. Furthermore, the extensive feathering of this specimen, particularly the attachment of long pennaceous feathers to the pes, sheds new light on the early evolution of feathers and demonstrates the complex distribution of skeletal and integumentary features close to the dinosaur–bird transition.

Anchiornis huxleyi has been recently described, based on an incomplete specimen, as a basal avialan filling the morphological gap between non-avian and avian dinosaurs³. A nearly complete, extensively feathered specimen (LPM-B00169, housed in Liaoning Paleontological Museum) referable to *Anchiornis huxleyi* (Supplementary Information) has now been recovered from the Tiaojishan Formation at the Daxishan locality, Jianchang County. The Tiaojishan Formation has traditionally been regarded as Middle Jurassic but was recently dated to between 161 and 151 Myr (ref. 2) (Fig. 1; Supplementary Information). It is therefore older than the *Archaeopteryx*-bearing strata near Solnhofen, Germany, which date to less than 150 Myr (ref. 4).

The new specimen exhibits a sub-triangular skull in lateral view and a large surangular foramen, as in other paravians and deinonychosaurs, respectively^{5–7} (Figs 2 and 3a). It has a large maxillary fenestra separated from the antorbital fenestra by a narrow interfenestral bar, a dorsoventrally flattened internarial bar, a distinct, posteriorly widening groove on the labial surface of the dentary housing the neurovascular foramina, and closely packed premaxillary and dentary teeth in the symphyseal region, derived features shared with other troodontids^{5,7–9}. Furthermore, *Anchiornis* resembles *Mei* in having a large external naris extending posteriorly well beyond the anterior border of the antorbital fossa², a longitudinal groove along the dorsomedial margin of the slender sub-orbital ramus of the jugal, a maxillary tooth row that approaches the preorbital bar posteriorly⁵ and unserrated teeth (also seen in the troodontid *Byronosaurus*⁸). A large paraquadrate foramen is present, in contrast to other troodontids but in agreement with dromaeosaurs⁶.

Postcranially, *Anchiornis* also possesses a few troodontid features, including relatively long and slender transverse processes on the dorsal vertebrae and anterior-most caudal vertebrae⁸. As in *Archaeopteryx*⁴, the middle and posterior caudal vertebrae each bear a distinct groove

on the lateral surface near the junction of the neural arch and centrum (Fig. 3b), and the coracoid bears a laterally located coracoid tubercle (Fig. 3c). The ischium is strongly curved posteriorly, with an obturator

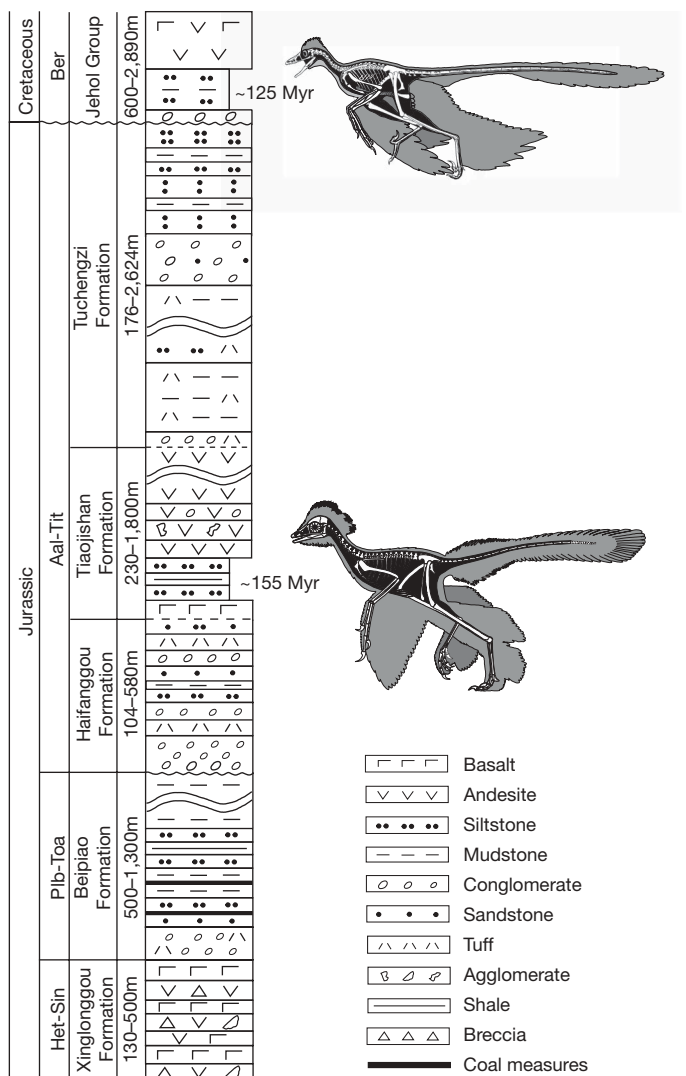


Figure 1 | Stratigraphic column of Jurassic and Lowest Cretaceous strata in western Liaoning, showing horizons from which feathered dinosaurs have been described. Two major horizons have produced such specimens: the Tiaojishan Formation has yielded *Anchiornis huxleyi* LPM-B00169 and dates to about 155 Myr, whereas the Jehol Group has yielded *Microraptor* and other feathered dinosaurs and dates to about 125 Myr.

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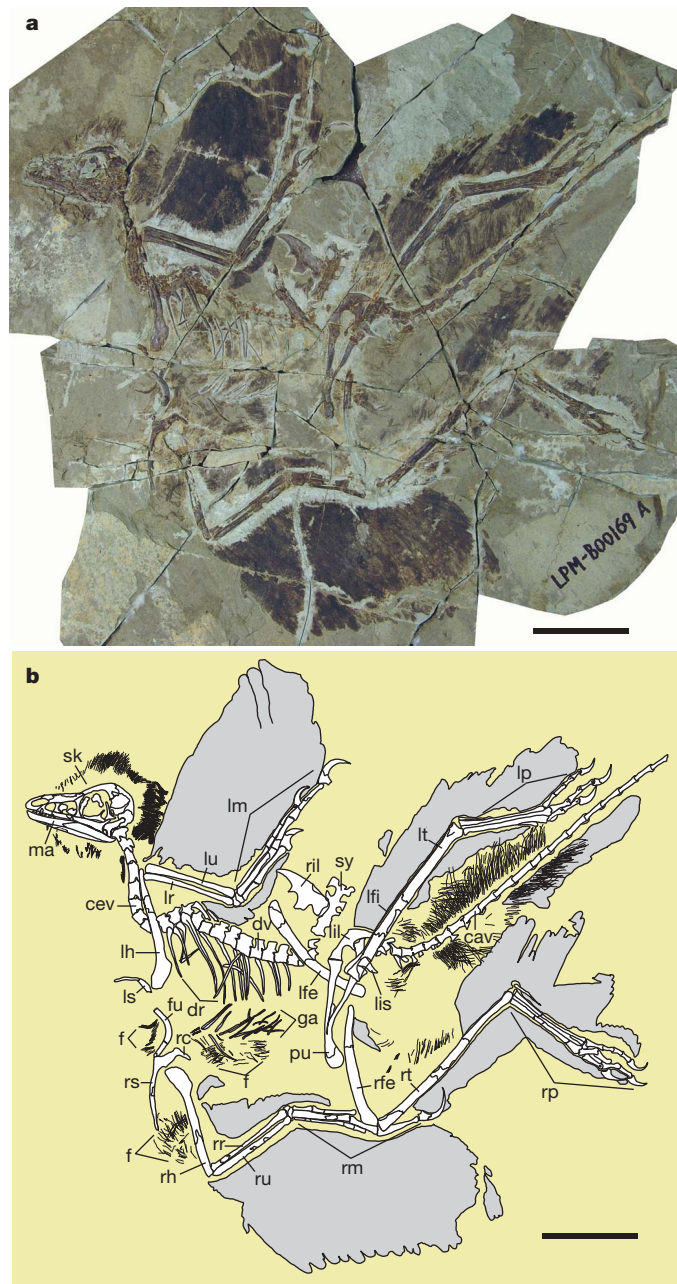


Figure 2 | *Anchiornis huxleyi* LPM-B00169. **a**, Photograph and **b**, line drawing of LPM-B00169 A (slab). Abbreviations: cav, caudal vertebra; cev, cervical vertebra; dr, dorsal rib; dv, dorsal vertebra; f, feather; fu, furcula; ga, gastralia; lfe, left femur; lfi, left fibula; lh, left humerus; lil, left ilium; lis, left ischium; lm, left manus; lp, left pes; lr, left radius; ls, left scapula; lt, left tibiotarsus; lu, left ulna; ma, mandible; pu, pubis; rc, right coracoid; rfe, right femur; rh, right humerus; ril, right ilium; rm, right manus; rp, right pes; rr, right radius; rs, right scapula; rt, right tibiotarsus; ru, right ulna; sk, skull; sy, synsacrum. Scale bar, 5 cm.

process located close to the midpoint of the ischial shaft as in the dromaeosaurid *Buitreraptor*¹⁰. As in *Mei* and some dromaeosaurids¹¹, the distal articulation of metatarsal II is about as wide as that of metatarsal III.

There are about ten large pennaceous feathers attached to the forearm, 11 to the manus (Fig. 3d, e), 12–13 to the crus (Fig. 3f) and 10–11 to the metatarsus (Fig. 3g). The primary and secondary remiges are similar in size and morphology (Fig. 3j–l). The longest remiges, located near the distal end of the forearm and the proximal end of the manus, are about 150% of the humeral length. Because the longest wing feathers are close to the wrist, the broadest part of the

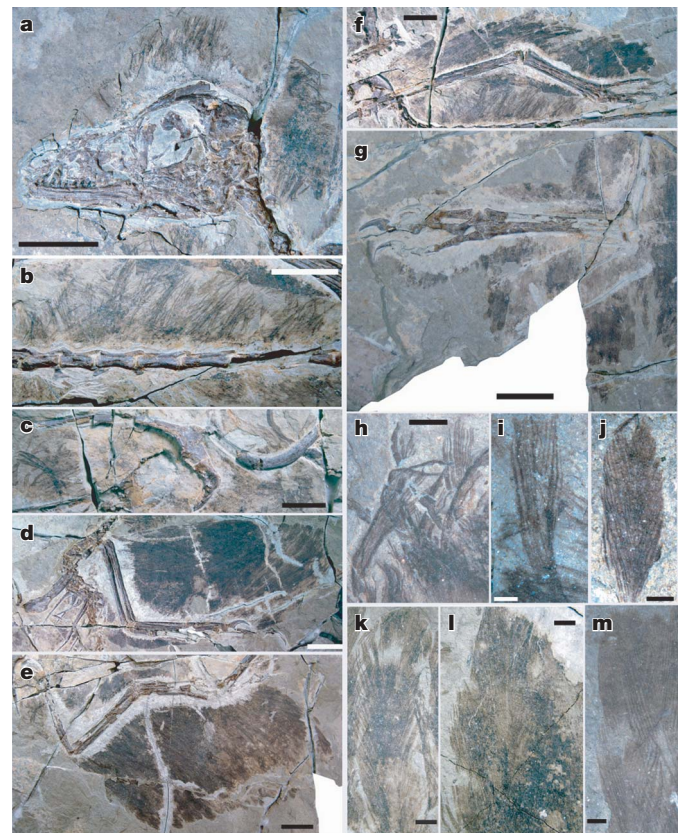


Figure 3 | Selected skeletal elements and associated feathers of LPM-B00169. **a**, Skull and mandible. **b**, Middle caudal vertebrae. **c**, Furcula and right scapulocoracoid. **d**, Left forelimb. **e**, Right forelimb. **f**, Left hindlimb. **g**, Right pes. **h**, Feathers near skull. **i**, Feathers near pectoral region. **j**, Distalmost primary remiges. **k**, Middle primary remiges. **l**, Secondary primary remiges. **m**, Pennaceous feathers attached to metatarsus. Arrows indicate the boundary of the soft tissue. Scale bars: **a**, **b**, **d–g**, 2 cm; **c**, 1 cm; **h**, **k**, **l**, 2 mm in; **i**, **j**, **m**, 1 mm.

wing is relatively proximal, in contrast to the basal dromaeosaurid *Microraptor* and basal avians such as *Archaeopteryx*¹². The distal primary remiges resemble those of *Microraptor* and basal avians^{4,12,13} in having curved rachides, but the remiges are relatively small, with thin rachides, symmetrical vanes, and blunt ends. In *Microraptor* and basal avians¹², the primary remiges are not only significantly longer than the secondary ones but also possess prominent rachides, asymmetrical vanes and somewhat pointed tips. Large pennaceous feathers also cover nearly the whole length of the lower leg of *Anchiornis* (Fig. 3m). The crural feathers are longer than the metatarsal feathers, which are nearly perpendicular to the long axis of the metatarsus. Much shorter feathers also attach to the pedal phalanges, apart from the unguals. These feathers appear to be pennaceous, a condition previously unknown in any fossil taxon.

Two types of plumulaceous feather can be distinguished, corresponding to types previously identified in the dromaeosaurid *Sinornithosaurus*¹⁴. Feathers of the first type are each composed of a bundle of filaments that are joined together proximally and remain nearly parallel as they pass distally (Fig. 3h). Feathers of the second type each consist of a series of filaments branching laterally from a slender central rachial filament (Fig. 3i).

Anchiornis huxleyi is posited as a basal troodontid by our phylogenetic analysis (Fig. 4) but also possesses several salient features of the Avialae and Dromaeosauridae, further blurring distinctions among the three major paravian groups (Supplementary Information). In particular, the forelimbs of *Anchiornis* are proportionally much longer than those of other troodontids, but similar in length to those of basal avialans and dromaeosaurids. *Anchiornis huxleyi* even exceeds *Microraptor* in the length of the forelimbs³, a feature often

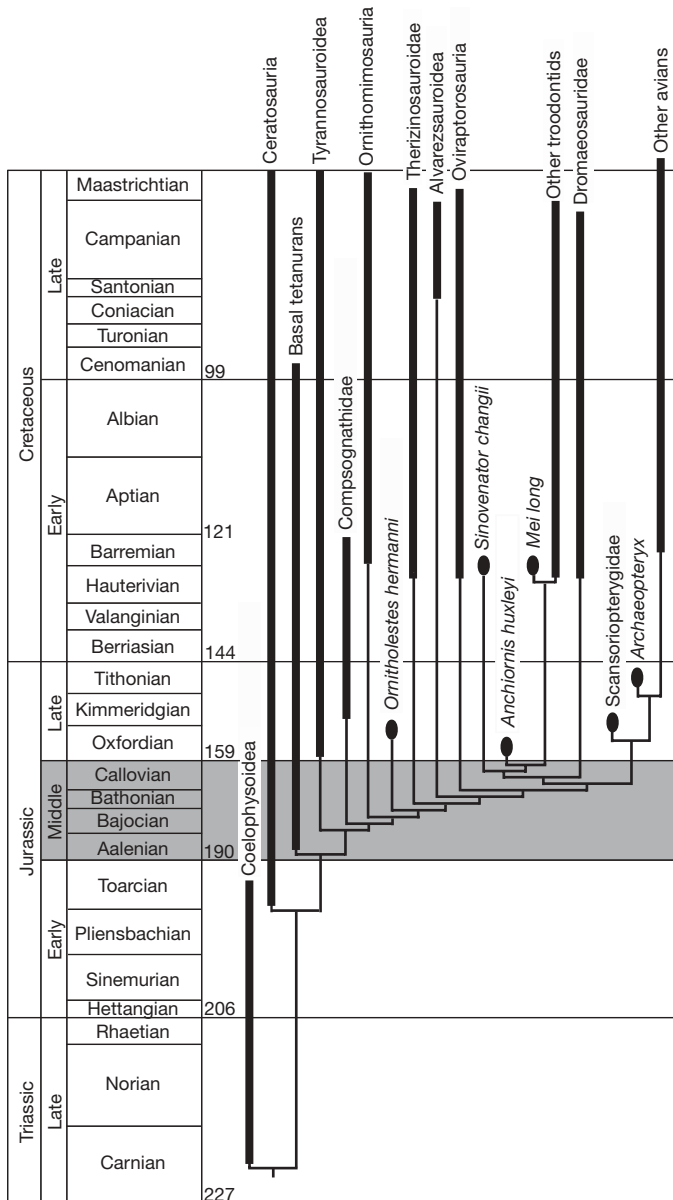


Figure 4 | Temporally calibrated phylogeny of the Theropoda. (See Supplementary Information for details.) The known temporal durations (solid bars) of the major theropod groups, based on well-corroborated fossil occurrences, indicate that the major tetanuran theropod groups diverged rapidly in the Middle Jurassic to earliest Late Jurassic.

regarded as an indicator of aerial capability. However, the remiges of *Anchiornis* are not obviously flight-adapted as in *Microraptor* and basal avians¹². Furthermore, the extreme elongation of the lower legs in *Anchiornis huxleyi* suggests strong cursorial capability³, but their long and extensive plumage is not common among cursorial animals: in cursorial birds and mammals, the lower legs tend to show reduction or even complete loss of the feathers or hair, respectively. Similarly, the recently reported Jurassic basal avialan *Epidexipteryx hui* closely resembles basal birds in various skeletal features usually interpreted as being related to aerial capability, but lacks pennaceous feathers that would facilitate aerial locomotion¹⁵. Collectively, these data point to a complex pattern of morphological evolution at the base of the Paraves.

The distribution of large pennaceous feathers, both phylogenetic and anatomical, implies that these structures first evolved on the distal portions of the forelimbs and tail in maniraptoran theropods and only spread proximally at a subsequent stage in theropod evolution¹². Interestingly, such a distal-first pattern seems also to apply to the

evolution of pennaceous feathers on the hindlimbs of paravians. Large pennaceous feathers are now known to occur on the lower leg and particularly the metatarsus of at least one basal member of each of the three major paravian groups, namely the basal troodontid *Anchiornis*, the basal avialan *Pedopenna* and the basal dromaeosaurid *Microraptor*^{13,16}. Furthermore, many basal avians have proportionally large pennaceous feathers on the lower leg^{13,17}, which are reduced in large derived birds. This suggests that large pennaceous feathers first evolved distally on the hindlimbs, as on the forelimbs and tail. This distal-first development led to a four-winged condition at the base of the Paraves. Whereas the large feathers of the forewing developed further in subsequent avian evolution, the large hindwing feathers were reduced and even lost¹². This suggests that extensive feathering of the pes was a critical modification in the transition to birds and that the pedal scales of extant birds might be secondarily derived structures, a possibility also supported by some developmental studies¹⁸.

Extensive feathering of the pes is also seen in some modern birds, and serves an insulating or protective function¹⁹. In most cases the feathers are not organized into a coherent planar surface as in *Microraptor*, *Pedopenna* and *Anchiornis*²⁰, which indicates that the pedal feathers of these fossil taxa may have differed from those of extant birds in having an aerodynamic function. This would imply that a four-winged condition played a role in the origin of avian flight, as suggested by previous studies^{12,17}, although this conclusion is not universally accepted²¹. However, the significant differences noted above between the large pedal feathers of *Anchiornis* and those of *Microraptor* suggest that these feathers might have been less aerodynamically effective in *Anchiornis* than in *Microraptor*.

The poor fossil record of derived non-avian theropods has hindered understanding of early coelurosaurian theropod evolution, and has created an apparent discrepancy between stratigraphy and phylogeny that has sometimes been used to argue against the theropod hypothesis of bird origins¹. Although derived theropods including troodontids have been reported in the Jurassic, all have been based on fragmentary material^{22–25}. *Anchiornis huxleyi* is probably Oxfordian in age, and unquestionably represents the oldest troodontid reported so far⁷. The presence of a troodontid in the earliest Late Jurassic indicates that all groups of derived theropods had originated by this time. A calibrated theropod phylogeny based only on well-corroborated fossil occurrences suggests that all major tetanuran groups, including Aves, might have originated and diversified rapidly in the Middle to earliest Late Jurassic (Fig. 4). This rapid divergence event would have coincided with documented palaeogeographical changes that took place around the same time. Alternatively, a calibrated theropod phylogeny incorporating fragmentary material suggests that tetanurans have a much longer evolutionary history, and that great potential exists for discovering derived theropod fossils, even in the Triassic²⁴.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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