doi:10.1038/nature12168

A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds

Pascal Godefroit[1], Andrea Cau[2], Hu Dong-Yu[3,4], François Escuillié[5], Wu Wenhao[6] & Gareth Dyke[7]

The recent discovery of small paravian theropod dinosaurs with well-preserved feathers in the Middle–Late Jurassic Tiaojishan Formation of Liaoning Province (northeastern China)[1–4] has challenged the pivotal position of *Archaeopteryx*[3,4], regarded from its discovery to be the most basal bird. Removing *Archaeopteryx* from the base of Avialae to nest within Deinonychosauria implies that typical bird flight, powered by the forelimbs only, either evolved at least twice, or was subsequently lost or modified in some deinonychosaurians[3,5]. Here we describe the complete skeleton of a new paravian from the Tiaojishan Formation of Liaoning Province, China. Including this new taxon in a comprehensive phylogenetic analysis for basal Paraves does the following: (1) it recovers it as the basal-most avialan; (2) it confirms the avialan status of *Archaeopteryx*; (3) it places Troodontidae as the sister-group to Avialae; (4) it supports a single origin of powered flight within Paraves; and (5) it implies that the early diversification of Paraves and Avialae took place in the Middle–Late Jurassic period.

Theropoda Marsh, 1881
Maniraptora Gauthier, 1986
Paraves Sereno, 1997
Avialae Gauthier, 1986
Aurornis xui gen. et sp. nov.

Etymology. *Aurora*, Latin for daybreak, dawn; *Ornis*, Greek for bird; *xui*, in honour of Xu Xing, for his exceptional and continuing contribution to our understanding of the evolution and biology of feathered dinosaurs.

Holotype. Yizhou Fossil and Geology Park (YFGP)-T5198, a complete articulated skeleton with associated integumentary structures.

Locality and horizon. Yaolugou, Jianchang, western Liaoning Province, China; Middle–Late Jurassic Tiaojishan Formation (see Supplementary Information).

Diagnosis. Manual phalanx I-1 distinctly more robust than the radius; robust postacetabular process of ilium not markedly deflected ventrally and with a horizontal dorsal margin; distal end of ischium dorsoventrally expanded and formed by a hook-like ventral process delimiting a prominent distal obturator notch and by a longer dorsal distal process; metatarsal I gracile and elongate (about 30% of metatarsal III length) (see Supplementary Information for differential diagnosis).

Description. The holotype and only currently known specimen of *A. xui* (YFGP-T5198) is 51 cm in length (Fig. 1 and Supplementary Fig. 4) and was probably an adult individual; its frontals are fused, neurocentral sutures of all visible vertebrae are closed, and the astragalus–calcaneum complex is completely fused to the tibia. As in *Anchiornis* and *Eosinopteryx*, the skull is slightly shorter than the femur. The snout of *Aurornis* is about half the basal length of the skull, proportionally longer than in *Eosinopteryx* and *Mei*[6] (Supplementary Table 2), and lower in lateral view than in *Xiaotingia*[3] (Fig. 2a, b). In contrast to *Anchiornis* and *Mei*, the nares of *Aurornis* do not extend beyond the rostral border of the antorbital fenestra[2]. The maxillary process of the premaxilla is long, slender and contacts the nasal, excluding the maxilla from the external naris; in *Archaeopteryx* and *Anchiornis*, the maxillary process of the premaxilla is short and the maxilla participates in the ventral margin of the external naris[3]. The maxillary fenestra is large, separated from the antorbital fenestra by a narrow interfenestral bar, as in *Anchiornis*[2]. The premaxillary fenestra is larger than in *Anchiornis* and has a ventral margin located below that of the maxillary fenestra. The jugal is more gracile than in *Anchiornis*. In contrast to *Mei* and advanced avialans[6], the postorbital process of the jugal is high and involved in the formation of a complete postorbital bar in *Aurornis*. The quadratojugal process is a small posteroventrally directed knob. The triradiate postorbital of *Aurornis* is larger than in *Archaeopteryx*[7], but its frontal process seems proportionally shorter than in *Anchiornis*[2]. The robust lacrimal of *Aurornis* is T-shaped in lateral view, with a

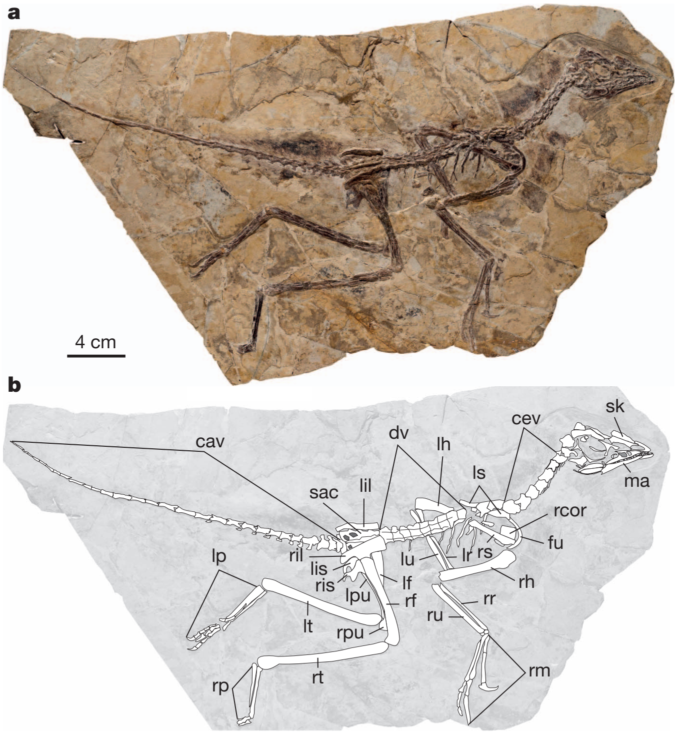

Figure 1 | ***Aurornis xui* YFGP-T5198.** **a**, Photograph. **b**, Line drawing. Abbreviations: cav, caudal vertebrae, cev, cervical vertebrae; dv, dorsal vertebrae; fu, furcula; ga, gastralia; lf, left femur; lh, left humerus; lil, left ilium; lis, left ischium; lp, left pes; lpu, left pubis; lr, left radius; ls, left scapula; lt, left tibia; lu, left ulna; ma, mandible; rcor, right coracoid; rf, right femur; rh, right humerus; ril, right ilium; ris, right ischium; rm, right manus; rp, right pes; rpu, right pubis; rr, right radius, rs, right scapula; rt, right tibia; ru, right ulna; sac, sacrum; sk, skull.

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[1] Operational Direction 'Earth and History of Life', Royal Belgian Institute of Natural Sciences, rue Vautier 29, 1000 Bruxelles, Belgium. [2] Museo Geologico 'Giovanni Capellini', Via Zamboni 63, I- 40127 Bologna, Italy. [3] Paleontological Institute, Shenyang Normal University, 253 North Huanghe Street, Shenyang 110034, China. [4] Key Laboratory of Vegetation Ecology, Ministry of Education, Northeast Normal University, 5268 Renmin Street, Changchun 130024, China. [5] Eldonia, 9 Avenue des Portes Occitanes, 3800 Gannat, France. [6] Research Center of Paleontology and Stratigraphy, Jilin University, 938 Ximinzhu Street, Changchun, 130021, China. [7] Ocean and Earth Science, National Oceanography Centre, University of Southampton, European Way, Southampton SO14 3ZH, UK.

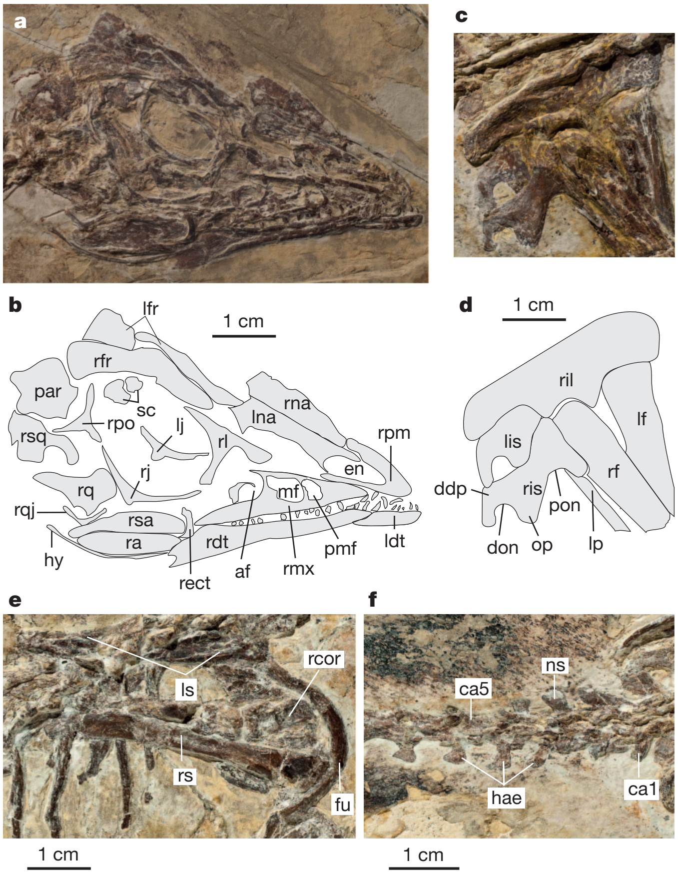

Figure 2 | Selected skeletal elements of *Aurornis xui* YFGP-T5198. **a**, Photograph of skull and mandible in right lateral view. **b**, Line drawing of skull and mandible in right lateral view. **c**, Photograph of pelvis in right lateral view. **d**, Line drawing of pelvis in right lateral view. **e**, Photograph of the scapular girdle. **f**, Photograph of proximal portion of the tail in right lateral view. Abbreviations: af, antorbital fenestra; ca, caudal; ddp, dorsodistal process; don, distal obturator notch; en, external naris; fu, furcula; hae, haemapophyses; hy, hyoid; ldt, left dentary; lf, left femur; lfr, left frontal; lis, left ischium; lj, left jugal; lna, left nasal; lp, left pubis; ls, left scapula; mf, maxillary fenestra; ns, neural spine; op, obturator process; par, parietal; pmf, promaxillary fenestra; pon, proximal obturator notch; ra, right angular; rcor, right coracoid; rdt, right dentary; rect, right ectopterygoid; rf, right femur; rfr, right frontal; ril, right ilium; ris, right ischium; rj, right jugal; rl, right lacrimal; rmx, right maxilla; rna, right nasal; rpm, right premaxilla; rpo, right postorbital; rq, right quadrate; rqj, right quadratojugal; rs, right scapula; rsa, right surangular; rsq, right squamosal; sc, scleral plates.

posterior process that is longer than its anterior process, perpendicular to the descending process and which participates in about half the length of the dorsal margin of the orbit, contrasting with the proportionally shorter posterior process in *Anchiornis*[2], *Archaeopteryx*[3,7] and troodontids[6,8–10], and with the vestigial anterior process in *Eosinopteryx*[4]. The frontal of *Aurornis* is about 45% of total skull length, contrasting with a proportionally shorter element in *Anchiornis*[2]. Unlike in *Anchiornis*[2] and dromaeosaurids[8,11], a paraquadrate notch is not developed on the quadrate. The anterior half of the dentary is more slender than that of *Anchiornis* and has subparallel dorsal and ventral margins. The presence of a posteriorly widening groove on the labial surface of the dentary is a derived feature of *Aurornis* that is also shared with *Anchiornis*[2], *Xiaotingia*[3], *Eosinopteryx*[4], *Archaeopteryx*[3,12] and troodontids[6,9]. The maxillary teeth are tiny, triangular in labial view and unserrated as in *Anchiornis*[2], *Mei*[6] and *Byronosaurus*[13], contrasting with the blunt teeth of *Xiaotingia*[3]. As in *Anchiornis*, the middle and posterior maxillary teeth of *Aurornis* are more sparsely distributed than the anterior ones[2].

Seven postaxial cervical vertebrae are present in *Aurornis*. Shared with *Archaeopteryx*[7], the cervical ribs of *Aurornis* are distinctly longer than their corresponding vertebrae, contrasting with the shorter ribs of *Eosinopteryx*[4] and *Troodon*[9]. The trunk of *Aurornis* is about 30% the length of the hindlimb, similarly proportioned to *Mei*[6], but distinctly shorter (42%) than *Anchiornis*[2]. The neural spines of the middle and posterior dorsals of YFGP-T5198 are particularly shortened. The synsacrum is composed of five vertebrae and the tail of about 30, making the tail in this animal proportionally longer (approximately four times the length of the femur) than in *Mei* (3.17)[6], *Archaeopteryx* (3.27)[7] and *Eosinopteryx* (2.71)[4]. The anteriormost caudals are short. A neural spine is developed on only the anterior third or fourth caudals. The chevrons resemble those of *Archaeopteryx*[7]; between the anteriormost centra, these are vertically oriented rectangular plates but become proportionally lower and develop elongated posterior extensions posteriorly from the seventh to the twelfth caudals (Fig. 2f). *Anchiornis* has hook-like proximal chevrons[1], whereas *Eosinopteryx* is characterized by small rod-like elements that extend below the nine proximal caudals[4].

The scapula of *Aurornis* is slender and perfectly straight (Fig. 2e). The furcula appears more robust than in both *Anchiornis* and *Eosinopteryx*, more resembling the condition in *Archaeopteryx*[7] and *Confuciusornis*[14]. The arm is long, about 80% of leg length, approaching the condition of *Archaeopteryx* (87–104%)[7]. As in *Xiaotingia*[3], the humerus of *Aurornis* is slightly shorter (88%) than the femur, whereas this element is only half the length of the femur in *Mei*[6] and distinctly longer in *Archaeopteryx* (1.12–1.24)[7]. As in *Anchiornis* and *Eosinopteryx*[4], the radius and ulna of *Aurornis* are straight and closely contact each other; in *Xiaotingia*[3], *Archaeopteryx*[7], *Mei*[6], dromaeosaurids[11,15], and *Sinornithoides*[16], the ulna is distinctly bowed distally and is much thicker than the radius. In YFGP-T5198 the manus is slightly longer than the femur (manus/femur lengths =1.09) as in *Eosinopteryx* (1.17)[4], contrasting with the shorter manus in *Mei* (0.82)[6] and the more elongate hands of *Anchiornis* (1.56) (ref. 2) and *Archaeopteryx* (1.4–1.56)[7]. Metacarpal I is about one-third the length of metacarpal II in *Aurornis* (Supplementary Fig. 5a, b); metacarpal III is shorter and more slender than metacarpal II, as in non-scansoriopterygid paravians. The long manual phalanx I-1 (minimum width 3 mm) is more robust than the radius (minimum width 1.5 mm). The dorsal margin of the postacetabular process of the ilium remains subhorizontal along its entire length (Fig. 2c, d), although it is usually oblique ventrally in other known basal paravians[3]. The ischium of *Aurornis* is shortened, less than 30% the length of the femur. A triangular obturator process is present at the mid-point of the ischium; this is proximodistally longer than high, as in *Anchiornis*[1] and *Eosinopteryx*[4], contrasting with the shorter and distally placed obturator process in *Rahonavis*[17]. There is no trace of a proximodorsal process on the ischium, as in Scansiopterygidae[18] and unlike in Unenlagiinae[19], *Rahonavis* and other basal avialans[17]. The distal end of the ischium is dorsoventrally expanded, formed by a long, robust dorsodistal process, and by a shorter and stout hook-like ventrodistal process that distally delimits a distal obturator notch larger than in *Archaeopteryx*[7]. The femur is slightly bowed anteriorly in lateral view and has a prominently developed lesser trochanter. The tibia (137% of femoral length) and pes (111% of the femoral length) are proportionally shorter in *Aurornis* than in *Anchiornis* (respectively 161% and 156%)[2]. Metatarsal I is slender and more elongate than in other known paravians, being about 30% of metatarsus length (Supplementary Fig. 5c, d). Metatarsal III is transversely compressed, suggesting a sub-arctometatarsalian condition. Pedal digit I lies on the medioplantar side of metatarsal II, as in *Archaeopteryx*[7,20], but contrasts with pedal digit I of *Anchiornis* that lies medial to metatarsal II[1]. The phalanges of pedal toes II, III and IV gradually decrease in length proximodistally, as in *Archaeopteryx* and terrestrial cursorial birds[21,22]. Unlike *Anchiornis*[1], the second pedal ungual of YFGP-T5198 is not substantially larger than the others. Traces of plumulaceous feathers, comprising a bundle of filaments joined together proximally and remaining almost parallel as they extend distally, are preserved along the proximal third of the tail, in YFGP-T5198 above the neck and around the chest (Fig. 1). Pennaceous feathers are not preserved.

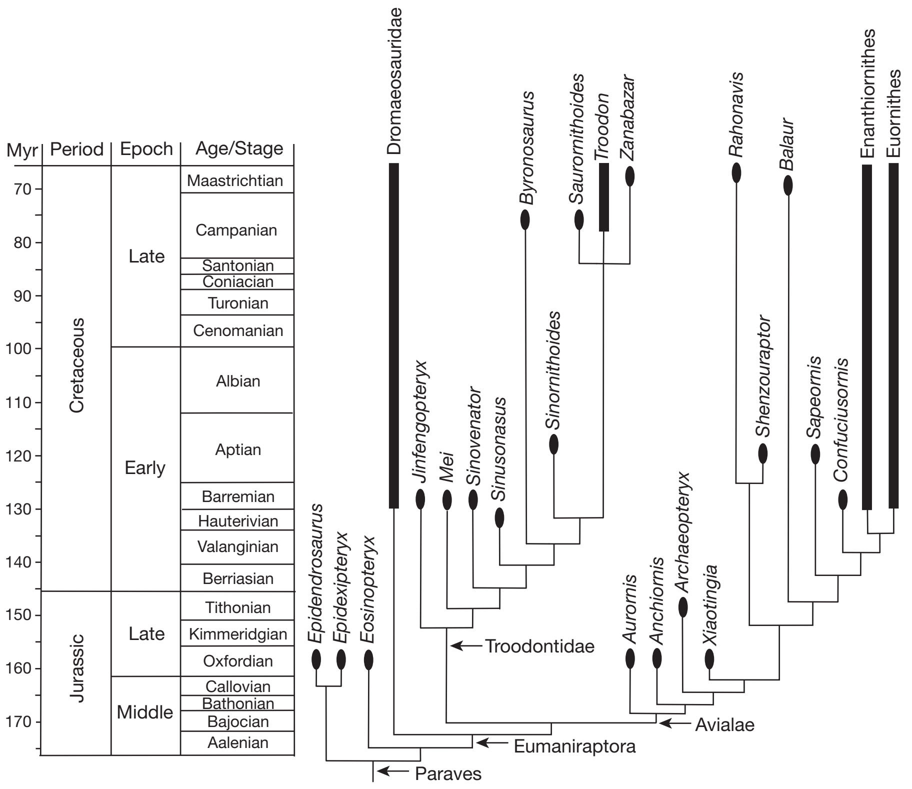

Figure 3 | Phylogenetic relationships of *Aurornis xui* among coelurosaurian theropods. Time-calibrated strict consensus tree of the 216 most-parsimonious trees resulting from our phylogenetic analysis (tree length = 4429; consistency index excluding uninformative characters = 0.27; retention index = 0.58; Supplementary Information). In this hypothesis *Aurornis* is an avialan more basal than *Archaeopteryx*, and Troodontidae is the sister-group of Avialae.

We coded *Aurornis xui* into the largest phylogenetic analysis of basal Paraves so far constructed, including all morphological characters discussed by recent conflicting[2–6,9,10,12,18,19,23] hypotheses (101 taxa versus 992 phylogenetically informative characters, see Supplementary Information). Our result recovers *Aurornis* and *Anchiornis*, both from the Tiaojishan Formation of western Liaoning, as successive basal-most avialans, confirms the Avialan status of *Archaeopteryx* and places Troodontidae as the sister-group for Avialae (Fig. 3). *Epidendrosaurus*, *Epidexipteryx* and *Eosinopteryx*, also from the Middle–Late Jurassic of northeastern China, are here regarded as basal, non-eumaniraptoran paravians. Thus our phylogeny is entirely consistent with the presence of a tetrapterygian condition (= four winged) and elongated rectrices in basal eumaniraptorans. We also postulate a single origin for typical forewing-powered flight, generally inferred to be present only in more derived birds[5,24]; shifting *Archaeopteryx* into deinonychosaurs[3,4] minimally implies two origins (in *Archaeopteryx* and in 'true' birds) or a much more complex situation, with an earlier origin close to the base of Paraves for forewing-driven flight and subsequent modifications to the tetrapterygian condition in various deinonychosaurs[5]. These relationships are also consistent with the recent discovery of potentially four-winged flight surfaces in a range of Mesozoic basal birds[25].

This new comprehensive phylogeny shows that basal avialans (*Aurornis*, *Anchiornis*, *Xiaotingia*) were already diversified in northern China during the Middle–Late Jurassic. These new data, combined with the presence of *Archaeopteryx* in the Tithonian stage of Germany, show that avialans were widespread throughout Eurasia at the end of the Jurassic. In contrast, dromaeosaurids and troodontids are conspicuously absent from Jurassic deposits in Asia, and only a few isolated teeth from the Late Jurassic of Europe have tentatively been identified as belonging to dromaeosaurids[26,27]. Possibly paravian teeth have also been reported from the Middle Jurassic of England[28]. The Jehol Biota of northeastern China testifies to the early diversification of dromaeosaurids (that is, four described genera so far, bearing in mind that many taxa have yet to be formally described), troodontids (also four described genera so far) and the evolutionary explosion of avialans (more than 30 named genera, albeit with nomenclatural problems) at the beginning of the Cretaceous period.

METHODS SUMMARY

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The ZooBank life science identifiers can be resolved and the associated information viewed by appending the life science identifiers to the prefix http://zoobank.org/. The life science identifiers for this publication are urn:lsid:zoobank.org:pub:ACD22438-7DAE-407E-9D79-266D781E1ED2 and urn:lsid:zoobank.org:act:7C240271-6ED2-4633-9597-EF480AC4B811.

Received 8 February; accepted 8 April 2013.

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Supplementary Information is available in the online version of the paper.

Acknowledgements We thank B. Pohl for making fossils available for study, S. Ge for help and comments on the manuscript and T. Hubin for photographs. This study was supported by a grant (BL/36/62) to P.G. from the SPP Politique scientifique (Belgium). D.H. was supported by the Key Laboratory of Evolutionary Systematics of Vertebrates (CAS2011LESV011) and by the National Natural Science Foundation of China (41172026).

Author Contributions P.G., F.E., A.C. and W.W. designed the project. P.G., A.C., G.D. and H.D.-Y. performed the research. P.G., A.C. and G.D. wrote the manuscript.

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