doi:10.1038/nature10288

An *Archaeopteryx*-like theropod from China and the origin of Avialae

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***Archaeopteryx* is widely accepted as being the most basal bird, and accordingly it is regarded as central to understanding avialan origins; however, recent discoveries of derived maniraptorans have weakened the avialan status of *Archaeopteryx*. Here we report a new *Archaeopteryx*-like theropod from China. This find further demonstrates that many features formerly regarded as being diagnostic of Avialae, including long and robust forelimbs, actually characterize the more inclusive group Paraves (composed of the avialans and the deinonychosaurs). Notably, adding the new taxon into a comprehensive phylogenetic analysis shifts *Archaeopteryx* to the Deinonychosauria. Despite only tentative statistical support, this result challenges the centrality of *Archaeopteryx* in the transition to birds. If this new phylogenetic hypothesis can be confirmed by further investigation, current assumptions regarding the avialan ancestral condition will need to be re-evaluated.**

The origin of the Avialae (defined as the most-inclusive clade containing *Passer domesticus* but not *Dromaeosaurus albertensis* or *Troodon formosus*; see Supplementary Information) represents one of the most heavily researched topics in evolutionary biology[1,2]. Being widely accepted as the most basal bird, *Archaeopteryx* has remained central to our understanding of avialan origins[1,3]. However, several recently reported basal avialans differ considerably from *Archaeopteryx* and instead share some salient similarities with oviraptorosaurs and, to a lesser degree, therizinosauroids[4]; conversely, *Archaeopteryx* and some *Archaeopteryx*-like theropods[5], including the one reported here (Figs 1 and 2), possess some deinonychosaurian synapomorphies[6] (Fig. 3). These observations necessitate a re-evaluation of widely accepted hypotheses of paravian phylogeny; such an exercise will have significant implications for our understanding of avialan origins and related issues such as the origin of flight.

Theropoda Marsh, 1881
Coelurosauria Huene, 1924
Archaeopterygidae Huxley, 1871
Xiaotingia zhengi gen. et sp. nov.

Etymology. The name is in honour of Zheng Xiaoting for his efforts in establishing the Shandong Tianyu Museum of Nature as a repository for vertebrate fossils from China.

Holotype. STM (Shandong Tianyu Museum of Nature) 27-2, an articulated skeleton, missing parts of the pelvis and hindlimbs and most of the caudal vertebrae, with some associated integumentary structures (Fig. 1; see Supplementary Information for the provenance and authenticity of the holotype specimen).

Locality and horizon. Linglongta, Jianchang, western Liaoning, China; Late Jurassic Tiaojishan Formation[7].

Diagnosis. A small paravian with the following unique features: the maxillary posterior ramus has a depth at mid-length exceeding that of the dentary; the surangular has little lateral exposure and forms a wide, flat dorsal surface over the posterior part of the mandible; an extremely large surangular foramen extends over more than 6% of the total mandibular length; the posterior end of the mandible is blunt and dorsoventrally expanded; the anteriormost caudal centra are less than half as long as the posterior dorsal centra; metacarpal IV is more robust than metacarpals II and III; and manual phalanx III-2 is longer than metacarpal III (we identify the three manual digits of *Xiaotingia* and other maniraptorans as II-III-IV, rather than as I-II-III as in many other studies[8]).

Morphological description and comparison

The holotype specimen of *Xiaotingia zhengi* has completely closed neurocentral sutures on all exposed vertebrae and has a completely fused synsacrum, indicative of a late ontogenetic stage (probably adult). The body mass is estimated to be 0.82 kg based on an empirical bivariate equation[9], similar to values calculated for other basal paravians[10].

As in many maniraptorans including *Archaeopteryx*[11], the antorbital fenestra is considerably shorter anteroposteriorly than it is high dorsoventrally. Similar to troodontids[11] and possibly *Archaeopteryx* (Fig. 3b), the descending process of the lacrimal is inset relative to the anterior and posterior processes (Fig. 2a). As in *Archaeopteryx*, *Anchiornis*, troodontids and some basal dromaeosaurids[11], the jugal has a posterodorsally oriented, mediolaterally thick postorbital process and a small quadratojugal process that fails to extend as far posteriorly as the postorbital process (Fig. 2a). The posteriorly strongly curved quadrate bears a small pterygoid ramus, similar to the condition in *Archaeopteryx*, *Anchiornis* and some basal deinonychosaurs[11]. The pterygoid ramus is larger in basal avialans such as scansoriopterygids, *Sapeornis* and *Jeholornis*, and in oviraptorosaurs[12]. As in *Archaeopteryx* (Fig. 3c), *Anchiornis*, troodontids[13] and some basal dromaeosaurids[14], the dentary bears a groove that widens posteriorly and contains a row of foramina (Fig. 2a). The retroarticular process is minimal, and the posterior end of the mandible is blunt as in confuciusornithids[15].

The dentary tooth count (probably fewer than 10) is smaller than in other deinonychosaurs but greater than in basal avialans and oviraptorosaurs[4]. The teeth in the symphyseal region appear to be closely packed as in *Anchiornis*, troodontids and some basal dromaeosaurids[11,13]. The tooth crowns are short apicobasally and thick labiolingually, basally bulbous with a constriction below the bulbous

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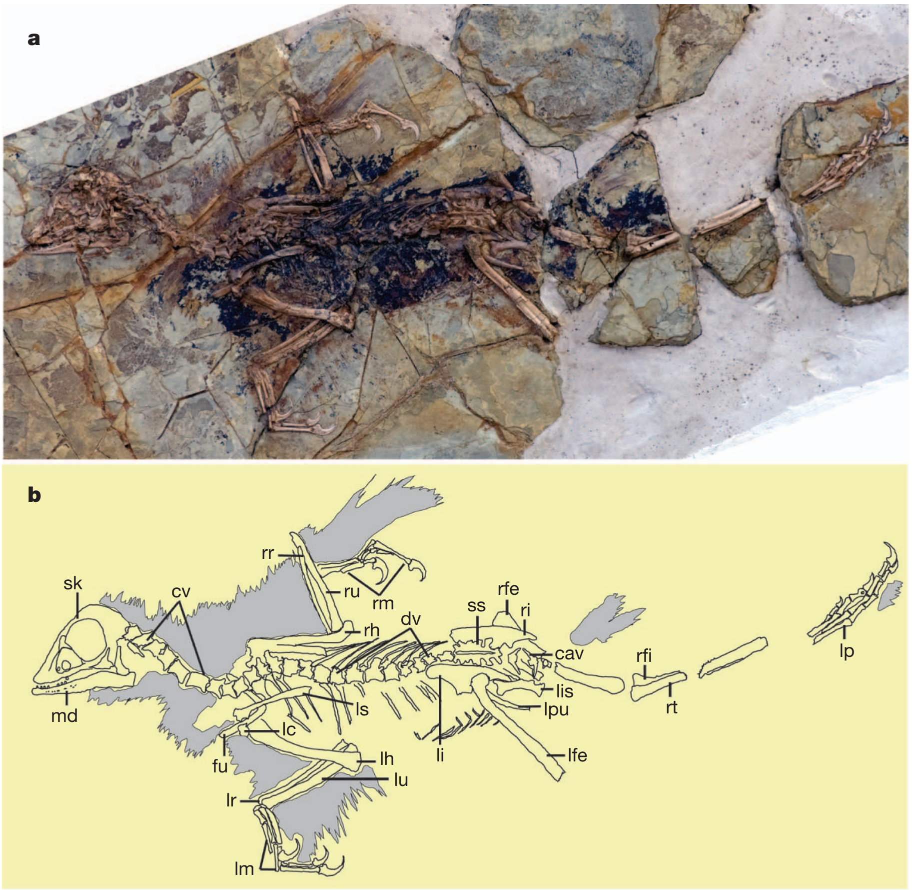

Figure 1 | *Xiaotingia zhengi* holotype (STM 27-2). a, **b**, Photograph (**a**) and line drawing (**b**). Integumentary structures in **b** are coloured grey. cav, caudal vertebra; cv, cervical vertebra; dv, dorsal vertebra; fu, furcula; lc, left coracoid; lfe, left femur; lh, left humerus; li, left ilium; lis, left ischium; lm, left manus; lp, left pes; lpu, left pubis; lr, left radius; ls, left scapula; lu, left ulna; md, mandible; rfe, right femur; rfi, right fibula; rh, right humerus; ri, right ilium; rm, right manus; rr, right radius; rt, right tibiotarsus; ru, right ulna; sk, skull; ss, synsacrum.

swelling, and nearly symmetrical in labial view. They are similar in their general morphology to those of some basal avialans[16,17].

The posterior cervical vertebrae have strongly divergent postzygapophyses, so that each vertebra is more than twice as wide as it is long. Pneumatic foramina are seen in the middle and posterior dorsal vertebrae (Fig. 2b), in contrast to the condition in most basal deinonychosaurs[11]. Five sacral vertebrae form a short synsacrum (less than 60% as long as the ilium), as in other archaeopterygids and basal deinonychosaurs. The zygapophyses of the sacral vertebrae are fused to form a platform lateral to the fused neural spines, a feature also known in dromaeosaurids and basal troodontids[18]. The anteriormost caudal centra are less than half as long as the posterior dorsal centra and have long, slender and distally tapering transverse processes (Fig. 2c), as in troodontids[5,13].

The boomerang-shaped furcula is more robust than those of most other non-avialan theropods, has an interclavicular angle of about 75°, and bears a small acromial process (Fig. 2b) as in *Anchiornis* and *Archaeopteryx* (Fig. 3d). The scapula has a strongly laterally everted acromial process overhanging a groove along the lateral surface and also bears a distinct short groove along the ventral edge immediately distal to the glenoid fossa, a feature also known in some previously described basal deinonychosaurs including *Anchiornis*. The coracoid has a relatively narrow proximal end and bears a fossa on the posterior surface (Fig. 2b), as in dromaeosaurids[11].

The relatively long humerus is as robust as the femur. Metacarpal IV is the most robust metacarpal, and extends distally beyond metacarpal III (Fig. 2d), a feature known in enantiornithines. As in some basal oviraptorosaurs[19], the phalangeal portion of the manus is much longer than the metacarpus. The penultimate manual phalanges are significantly longer than the more proximal ones, a feature indicative of arboreal habits[20]. Phalanx IV-1 is significantly longer than IV-2 and has a nearly immobile contact with the latter, as indicated by the absence of a pulley-like joint and the presence of a prominent proximoventral heel (Fig. 2d), as in *Archaeopteryx*[16] (Fig. 3e) and most dromaeosaurids[11]. The collateral ligament pits appear to be poorly developed.

The pre-acetabular process of the ilium is long (about 1.6 times as long as the postacetabular process) and anteriorly convex, as in other basal paravians[11]. The postacetabular process is rod-like and has a flat, thickened ventral surface as in *Archaeopteryx* and some basal troodontids[11]. The ischium has a groove along its anterior margin as in dromaeosaurids[11].

The second pedal digit is similar to those of *Archaeopteryx*[16] (Fig. 3h), *Anchiornis*[5] and other deinonychosaurs in having a prominent dorsal expansion and a dorsally located lateral collateral ligament fossa at the distal ends of both phalanx II-1 and phalanx II-2 (Fig. 2e), indicating that the second digit was highly extensible. Also as in troodontids and dromaeosaurids, phalanx II-2 has a medially positioned ridge on the ventral surface near the proximal end. Unlike in troodontids and dromaeosaurids[21,22], phalanx II-2 is not reduced in length and lacks a prominent proximoventral heel, and the ungual of digit II is only slightly longer than that of digit III and lacks a large flexor tubercle.

Faint feather impressions can be seen around the whole skeleton, including the skull, vertebral column, forelimbs and hindlimbs (Fig. 1). Some faint integumentary impressions are even preserved near the pedal phalanges, a feature also known in *Anchiornis*[6]. Unfortunately, the feathers are too poorly preserved for details of their

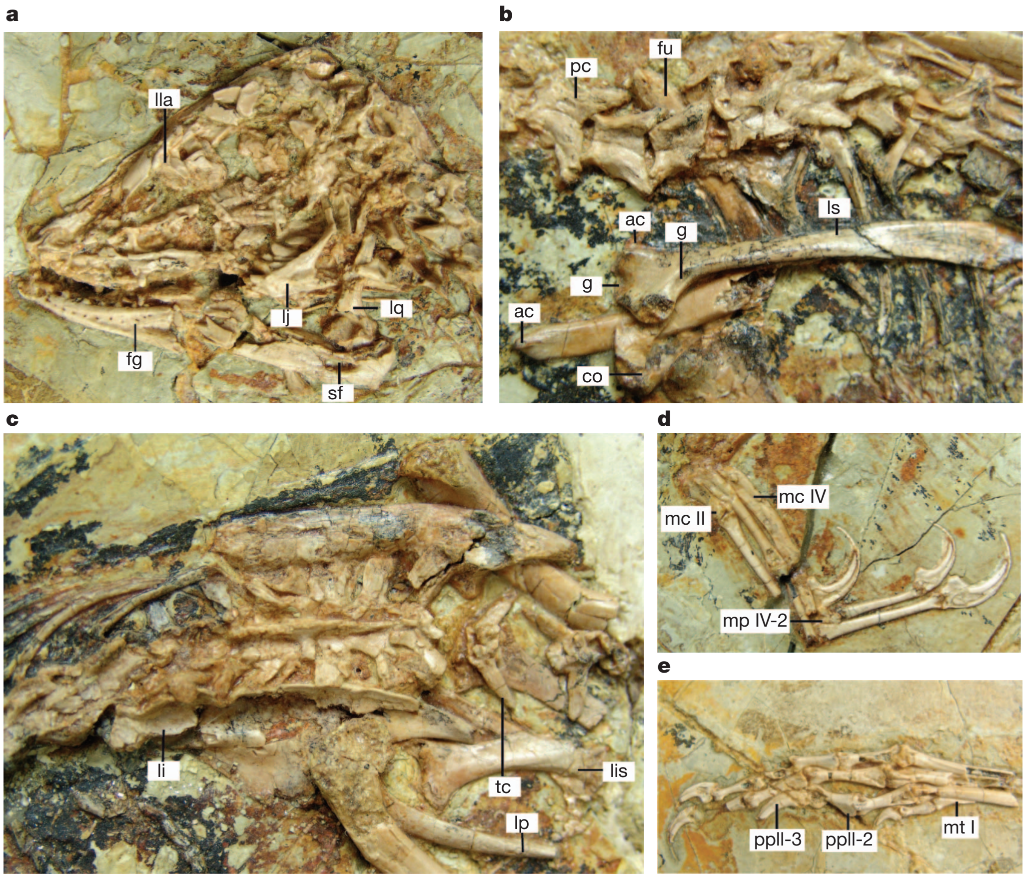

Figure 2 | Selected skeletal elements of STM 27-2. **a**, Skull and mandible. **b**, Middle presacral vertebrae, furcula and left scapulocoracoid. **c**, Pelvis and anterior caudal vertebrae. **d**, Left manus. **e**, Left pes. ac, acromial process; co, coracoid; fg, groove with foramina; fu, furcula; g, groove; li, left ilium; lis, left ischium; lj, left jugal; lla, left lacrimal; lp, left pubis; lq, left quadrate; ls, left scapula; mc II, metacarpal II; mc IV, metacarpal IV; mp IV-2, manual phalanx IV-2; mt I, metatarsal I; pc, posterior cervical; ppII-2, pedal phalanx II-2; ppII-3, pedal phalanx II-3; sf, surangular foramen; tc, caudal transverse process.

structure to be apparent. The feathers near the femur are quite long, measuring more than 55 mm. The presence of such long femoral feathers is consistent with the tetrapterygian condition seen in several other basal paravian taxa[6,23].

Implications for paravian phylogeny

We have added *Xiaotingia* into a comprehensive phylogenetic analysis, which places *Xiaotingia* and *Anchiornis* within the Archaeopterygidae (Fig. 4 and Supplementary Information). Salient synapomorphies of the Archaeopterygidae include: manual phalanx III-1 more than twice as long as IV-1 (character state 292.1 in Supplementary Information); manual phalanx IV-3 markedly longer than IV-1 and IV-2 combined (character state 302.2 in Supplementary Information); furcula lateral end with L-shaped cross-section (character state 369.1 in Supplementary Information); and ventral notch between distal portion of obturator process and ischial shaft (character state 307.0 in Supplementary Information).

The most important result of our analysis is the removal of the Archaeopterygidae from the Avialae and its placement at the base of the Deinonychosauria, which challenges the long-held opinion that *Archaeopteryx* represents a pivotal taxon for understanding the transition to birds by virtue of having a phylogenetic position near the very base of the Avialae[10,21,24–27]. Derived features shared by *Archaeopteryx* and other deinonychosaurs include a large promaxillary fenestra (character state 363.1 in Supplementary Information), a T-shaped lacrimal with a long anterior process (character state 372.1 in Supplementary Information), a groove that widens posteriorly on the dentary (character state 72.1 in Supplementary Information), a manual phalanx IV-2 that is significantly shortened relative to IV-1 (character state 294.1 in Supplementary Information), a short ischium that bears a distally located obturator process as well as a posterodistal process (character states 171.2 and 334.1 in Supplementary Information), and a highly extensible pedal digit II (character state 323.1 in Supplementary Information), among others. Previous studies noted the striking similarities between *Archaeopteryx* and other deinonychosaurs[16,28], and a close relationship between *Archaeopteryx* and dromaeosaurids has been proposed[22], but to our knowledge we are the first to present a numerical phylogenetic analysis supporting deinonychosaurian affinities for the Archaeopterygidae.

It should be noted that our phylogenetic hypothesis is only weakly supported by the available data. Bremer support and bootstrap values for the recovered coelurosaurian subclades are, in general, low, and a bootstrap value less than 50% and a Bremer support value of 2 are obtained for a monophyletic Deinonychosauria including the Archaeopterygidae (see Supplementary Information). This low support is partly caused by various homoplasies, many of which are functionally significant, that are widely distributed across coelurosaurian phylogeny[29]. *Xiaotingia* possesses salient anatomical features also seen in different paravian taxa, further highlighting the phenomenon of widespread homoplasy. This phenomenon is also seen in some other major transitions, including the origins of major mammalian groups[30], and creates difficulties in recovering robust phylogenies.

Morphology and systematics of *Archaeopteryx*

Although *Archaeopteryx* has been known for about 150 years, debate continues regarding various aspects—including even some skeletal morphological features—of this extremely important taxon[16,31] (Fig. 3a). Recent findings, particularly the discovery of the tenth

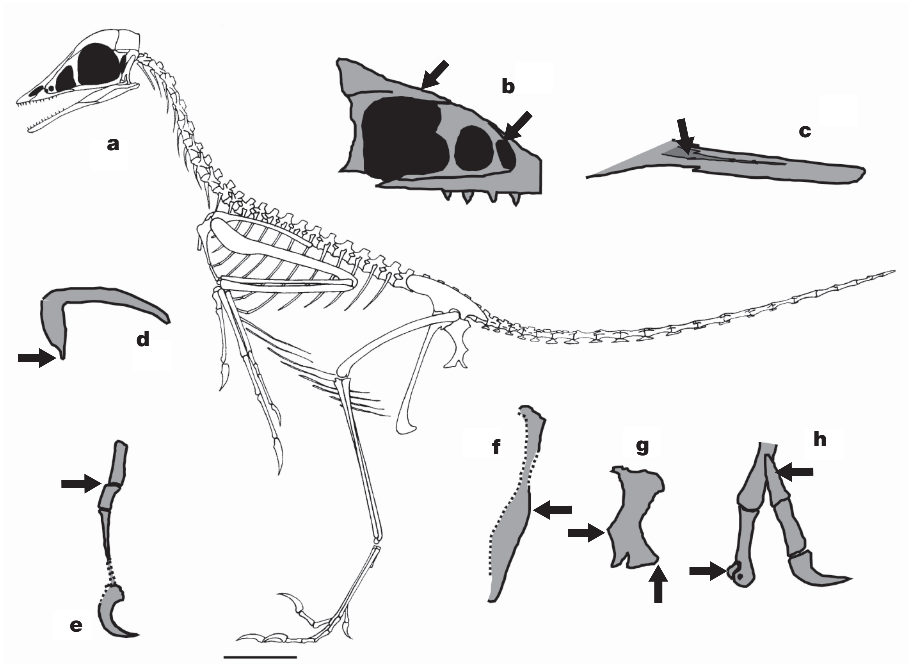

Figure 3 | Selected skeletal elements of *Archaeopteryx*. **a**, Skeletal reconstruction (modified from Fig. 6.53 in ref. 16). **b**, Preorbital region of the Thermopolis specimen in lateral view. Arrows point to the long anterior process of the lacrimal and the large promaxillary fenestra. **c**, Anterior half of the mandible of the Eichstätt specimen in lateral view. Arrow points to a posteriorly widening groove. **d**, The furcula of the London specimen in oblique view. Arrow points to an L-shaped cross-section of the lateral end of the furcula. **e**, Manual digit IV of the Berlin specimen in dorsal view. Arrow points to the rigid connection between the long phalanx IV-1 and the short IV-2. **f**, Right pubis of the Solnhofen specimen in posterior view. Arrow points to a lateral expansion at the pubic mid-shaft. **g**, Right ischium of the Thermopolis specimen in lateral view. Arrows point to the distally located obturator process and a triangular posterodistal process. **h**, Right pedal digits I and II of the Thermopolis specimen in oblique view. Arrow points to the medially positioned pedal digit I and the prominent dorsal expansion at the distal end of phalanx II-1. Most of the illustrated features here are only seen in archaeopterygids and other Deinonychosauria. Scale bar: 3 cm (**a**).

specimen, have greatly improved our knowledge of the morphology of *Archaeopteryx*[16,28,31]. In addition to the similarities between *Archaeopteryx*, *Xiaotingia* and some other deinonychosaurs described above, we provide further information to highlight the similarities between *Archaeopteryx*, *Anchiornis*, *Xiaotingia* and other deinonychosaurs on the one hand, and the differences between *Archaeopteryx* and other widely accepted basal avialans on the other.

The skull of *Archaeopteryx* is, in general, similar to those of *Anchiornis*, *Xiaotingia* and other deinonychosaurs in having a subtriangular lateral profile produced by a shallow snout and expanded postorbital region[16] (Fig. 4). In most basal avialans, including *Epidexipteryx*, *Sapeornis* and *Jeholornis*[4,32], the skull is relatively tall and short with a deep, short snout, more reminiscent of the oviraptorosaurian condition (Fig. 4). As in *Anchiornis*, *Xiaotingia* and other basal deinonychosaurs[6,11,16], the orbit is proportionally large and the infratemporal fenestra is extremely narrow anteroposteriorly and strongly inclined posteriorly. For comparison, oviraptorosaurs and basal avialans have a proportionally smaller orbit and a larger infratemporal fenestra that is much wider anteroposteriorly and less posteriorly inclined[4,15,32]. The external naris is ventrally located as in *Anchiornis*, *Xiaotingia* and other basal deinonychosaurs, in contrast to the high naris of oviraptorosaurs and basal avialans such as *Epidexipteryx* and *Jeholornis*[4,32].

The premaxilla of *Archaeopteryx* is shallow in lateral view and much smaller than the maxilla, as in many theropods including deinonychosaurs[11]. In oviraptorosaurs and basal avialans such as *Epidexipteryx*, *Sapeornis* and *Jeholornis*[4,32], the premaxilla is deep, and larger than the maxilla. The anteroposterior length of the antorbital fossa considerably exceeds its dorsoventral height, as in most theropods including *Anchiornis*, *Xiaotingia* and deinonychosaurs[6,13,18]. In oviraptorosaurs and basal avialans[12,32], the opposite is true, and the antorbital fenestra within the fossa is thus much higher than anteroposteriorly long in lateral view. The promaxillary fenestra is large (Fig. 3b) as in *Anchiornis*, *Xiaotingia* and basal deinonychosaurs[6,11,16,33]—the promaxillary fenestra, if present, is very small in other non-avian theropods. Many other theropods, including oviraptorosaurs and basal avialans such as *Epidexipteryx*, *Sapeornis* and *Jeholornis*[4,12], lack a promaxillary fenestra (Fig. 4). The lacrimal has a long anterior process, close in length to the descending process and extending anteriorly to a point close to the anterior border of the antorbital fenestra, a feature also seen in deinonychosaurs[11,13,18]. In most other theropods and particularly in oviraptorosaurs and other basal avialans, the anterior process is proportionally much shorter. The lacrimal also has a posterior process, albeit a small one, as in oviraptorosaurs, *Anchiornis*, *Xiaotingia*, dromaeosaurids and troodontids, and the process is directed almost straight posteriorly as in *Anchiornis*, *Xiaotingia* and deinonychosaurs[13,18]. In oviraptorosaurs, the posterior process points posterodorsally, which seems also to be the case in some basal avialans[15].

The mandible of *Archaeopteryx* is long and slender as in *Anchiornis*, *Xiaotingia* and basal deinonychosaurs[6,11]. For comparison, basal avialans all have oviraptorosaur-like mandibles: the mandible is relatively robust, the external mandibular fenestra is large and anteriorly located, and the dentary has a convex dorsal margin and a concave ventral one (however, the external mandibular fenestra is poorly known in *Jeholornis* and *Sapeornis*)[4,32].

As in *Anchiornis* and basal deinonychosaurs[11,34], the dorsal vertebrae of *Archaeopteryx* bear no distinct pneumatic foramina and instead have shallow, elongate depressions on the lateral surface of the centrum. In oviraptorosaurs and basal avialans such as *Jeholornis* and *Sapeornis*, the dorsal vertebrae bear distinct pneumatic foramina[35]. *Archaeopteryx* has five sacral vertebra as in *Anchiornis*, *Xiaotingia*, basal troodontids and basal dromaeosaurids[11,33]. By contrast, basal avialans have a greater number of sacral vertebrae[35].

The scapula is significantly shorter and more slender than the humerus, a feature also seen in other paravians[11,35]. Similar to the condition in other deinonychosaurs, the coracoid bears a distinct

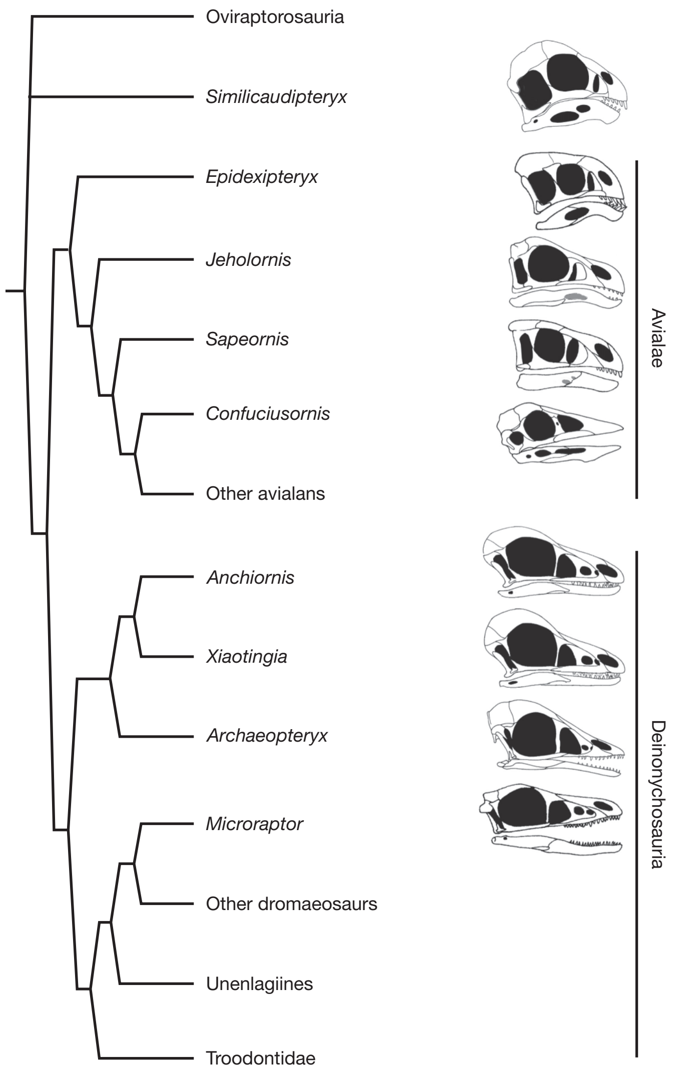

Figure 4 | A simplified cladogram showing the systematic position of *Xiaotingia* among the Coelurosauria (see Supplementary Information). Morphological features in grey areas need confirmation by better preserved specimens. Taxa recovered as basal avialans by our analysis are more similar in general morphology to the oviraptorosaurs than to the archaeopterygids and basal deinonychosaurs.

subglenoid fossa. An ossified sternum and uncinate processes are absent as in *Anchiornis*, *Xiaotingia* and troodontids. The humerus has a proximodistally long internal tuberosity, as in *Anchiornis*, *Xiaotingia* and other deinonychosaurs[11]. The length of manual phalanx IV-3 is considerably greater than the combined lengths of IV-1 and IV-2, a feature also seen in *Anchiornis*, *Xiaotingia* and other deinonychosaurs.

As in *Anchiornis*, *Xiaotingia* and deinonychosaurs[14,36,37], but unlike in basal avialans[17], the pre-acetabular process of the ilium is relatively deep. The supraacetabular crest is distinct as in *Xiaotingia*, *Anchiornis* and basal deinonychosaurs. In oviraptorosaurs and basal avialans the supraacetabular crest is absent. In the Solnhofen specimen, a lateral expansion is present on the mid-shaft of the pubis (Fig. 3f), a feature also seen in basal dromaeosaurids and troodontids[11]. The very short and wide ischium has a distally located obturator process (Fig. 3g), as in *Anchiornis* and basal deinonychosaurs[11,33,37]. In most maniraptorans including oviraptorosaurs, the ischium is short, but not to the degree seen in *Archaeopteryx* and deinonychosaurs, and in all basal avialans the ischium has a different shape: relatively long and slender, posteriorly curved, and without an obturator process. The ischium has a distally located process on the posterior margin (Fig. 3g) as in basal deinonychosaurs and *Xiaotingia*, although the posterior margin of the ischium of *Jeholornis* admittedly seems to bear a large convexity. A trait uniquely shared with *Anchiornis* (condition unknown in *Xiaotingia*) is the constricted base of the distally located obturator process.

The metatarsus of *Archaeopteryx* approaches the arctometatarsalian condition[28] in that the proximal end of the third metatarsal is laterally compressed as in *Anchiornis* and basal deinonychosaurs. In basal avialans, metatarsal III is not laterally compressed[4,17].

As described above, *Archaeopteryx* is more similar to *Anchiornis*, *Xiaotingia* and basal deinonychosaurs than to known basal avialans and oviraptorosaurs in numerous features, some of which are uniquely shared. On the other hand, basal avialans such as scansoriopterygids, *Sapeornis*, *Jeholornis* and the confuciusornithids are more similar to oviraptorosaurs than to *Archaeopteryx*, *Anchiornis*, *Xiaotingia* and basal deinonychosaurs in many features, particularly cranial and vertebral ones. This supports the hypothesis that *Archaeopteryx*, *Anchiornis* and *Xiaotingia* are referable to the Deinonychosauria, a hypothesis consistent with some previous work on *Anchiornis*[6,38].

Although *Archaeopteryx* is placed within the Avialae by nearly all numerical phylogenetic studies[10,11,21,24–26,39,40], some recent studies have demonstrated that some of the suggested synapomorphies purportedly shared by *Archaeopteryx* and basal avialans are questionable. For example, two salient avialan features—the absence of a jugal process on the palatine and the presence of a reversed hallux—are now considered to be absent in *Archaeopteryx*[28,31] (Fig. 3h). Some other suggested synapomorphies are present in recently described basal deinonychosaurs, and are thus likely to represent paravian rather than avialan synapomorphies[23,37]. These features include an antorbital fossa that is dorsally bordered by the nasal and lacrimal, a relatively small number of caudal vertebrae, a relatively large proximodorsal process of the ischium, a relatively long pre-acetabular process of the ilium, and fusion of the proximal part of the metatarsus[11,37,41]. Consequently, there are few derived features shared by *Archaeopteryx* and basal avialans but absent in basal deinonychosaurs, thus documented morphological support for the avialan affinities of *Archaeopteryx* is fairly weak. The alternative hypothesis that *Archaeopteryx*, *Anchiornis* and *Xiaotingia* are all deinonychosaurs is better supported by the available morphological data, and these taxa share with some basal deinonychosaurs some unique features unknown in any other theropod group (Figs 3 and 4; see also Supplementary Information).

Within the Deinonychosauria, *Archaeopteryx* is more similar to *Anchiornis* and *Xiaotingia* than to dromaeosaurids and troodontids in many features, although few of these features are uniquely shared by the three taxa. Of note, however, are some unique features related to the pelvis. For example, the ischium appears to be proportionally even shorter in *Archaeopteryx* and *Anchiornis* than in other deinonychosaurs, and these two taxa also share a basally constricted obturator process (condition unknown for both characters in *Xiaotingia*). On the other hand, *Archaeopteryx*, *Anchiornis* and *Xiaotingia* lack many derived similarities shared by troodontids and dromaeosaurids, such as lateral exposure of the splenial, a muscle scar on the deltopectoral crest, and an enlarged, raptorial ungual on pedal digit II. This suggests that *Archaeopteryx*, *Anchiornis* and *Xiaotingia* are probably most closely related to each other, whereas dromaeosaurids and troodontids form a separate clade within the Deinonychosauria (see additional comparative figures in Supplementary Information).

Implications for avialan origins

The discovery of *Xiaotingia* further demonstrates that many features previously regarded as distinctively avialan actually characterize the more inclusive Paraves. For example, proportionally long and robust forelimbs are optimized in our analysis as a primitive character state for the Paraves (see Supplementary Information). The significant lengthening and thickening of the forelimbs indicates a dramatic shift in forelimb function at the base of the Paraves, which might be related to the appearance of a degree of aerodynamic capability. This hypothesis is consistent with the presence of flight feathers with asymmetrical vanes in both basal avialans and basal deinonychosaurs[6,23].

All taxa recovered as basal avialans by our analysis, such as the scansoriopterygids, *Sapeornis* and *Jeholornis*, resemble oviraptorosaurs and to a lesser degree therizinosaurs[4] but differ from deinonychosaurs including archaeopterygids in having such cranial and dental characteristics as a dorsoventrally high premaxilla that is significantly larger than the maxilla, a dorsally positioned external naris, a dorsoventrally tall antorbital fossa, a jugal with a relatively vertical postorbital process and a long quadratojugal process, a quadrate with a large pterygoid ramus, a relatively long parietal, an anteriorly downturned and strongly dorsally convex mandible, a large external mandibular fenestra, and enlarged anterior teeth. Some of these features are optimized by our analysis as synapomorphies of a clade containing the Oviraptorosauria, the Therizinosauroidea, the Avialae and the Deinonychosauria, but are lost in the last group (see Supplementary Information). Some previous phylogenetic analyses have placed the Oviraptorosauria within the Avialae[42], and a recent study suggests that the Oviraptorosauria and Scansoriopterygidae are sister taxa, forming a clade at the base of the Avialae[38]. However, our analysis indicates that placing the Oviraptorosauria outside the Paraves is much more parsimonious than placing it within the Avialae (see Supplementary Information). In either case, many oviraptorosaur-like features are plesiomorphic for the Avialae. These features contribute to forming a relatively tall and robust cranium, in contrast to the shallower and more gracile cranium seen in the Deinonychosauria. These results invite a re-evaluation of the ancestral condition for birds from the perspective of morphology, behaviour and ecology. Under the phylogenetic framework shown in Fig. 4, a robust skull and a herbivorous diet (which has been suggested to characterize the Maniraptoriformes[43,44]) probably represent ancestral traits that are retained in basal birds, and the Deinonychosauria is exceptional in having a more gracile skull and a carnivorous diet.

Received 16 November 2010; accepted 10 June 2011.

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

Acknowledgements The authors thank X. Zheng for permission to study the holotype specimen of *Xiaotingia zhengi* and for discussions; P. Chen, L. Hou and Z. Zhou for coordinating the project; C. Sullivan for editing and commenting on the manuscript; R. Li for illustrations; T. Yu for preparing the specimen; X. Ding for editing the illustrations; D. Pol for help in using the TNT software package; P. Barrett, O. Rauhut, M. Kölbl-Ebert and M. Röper for facilitating access to the *Archaeopteryx* specimens under their care; and G. Mayr for discussions. This work was supported by grants from the National Natural Science Foundation of China, Chinese Academy of Sciences, and Special Funds for Major State Basic Research Projects of China.

Author Contributions X.X. designed the project, X.X., H.Y., K.D. and F.H. performed the research, and X.X. wrote the manuscript.

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