

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, therizinosaurs⁴; conversely, *Archaeopteryx* and some *Archaeopteryx*-like theropods⁵, including the one reported here (Figs 1 and 2), possess some deinonychosaurian synapomorphies⁶ (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 Formation⁷.

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 studies⁸).

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 equation⁹, similar to values calculated for other basal paravians¹⁰.

As in many maniraptorans including *Archaeopteryx*¹¹, the antorbital fenestra is considerably shorter anteroposteriorly than it is high dorsoventrally. Similar to troodontids¹¹ 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 dromaeosaurids¹¹, 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 deinonychosaurs¹¹. The pterygoid ramus is larger in basal avialans such as scansoriopterygids, *Sapeornis* and *Jeholornis*, and in oviraptorosaurs¹². As in *Archaeopteryx* (Fig. 3c), *Anchiornis*, troodontids¹³ and some basal dromaeosaurids¹⁴, 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 confuciusornithids¹⁵.

The dentary tooth count (probably fewer than 10) is smaller than in other deinonychosaurs but greater than in basal avialans and oviraptorosaurs⁴. 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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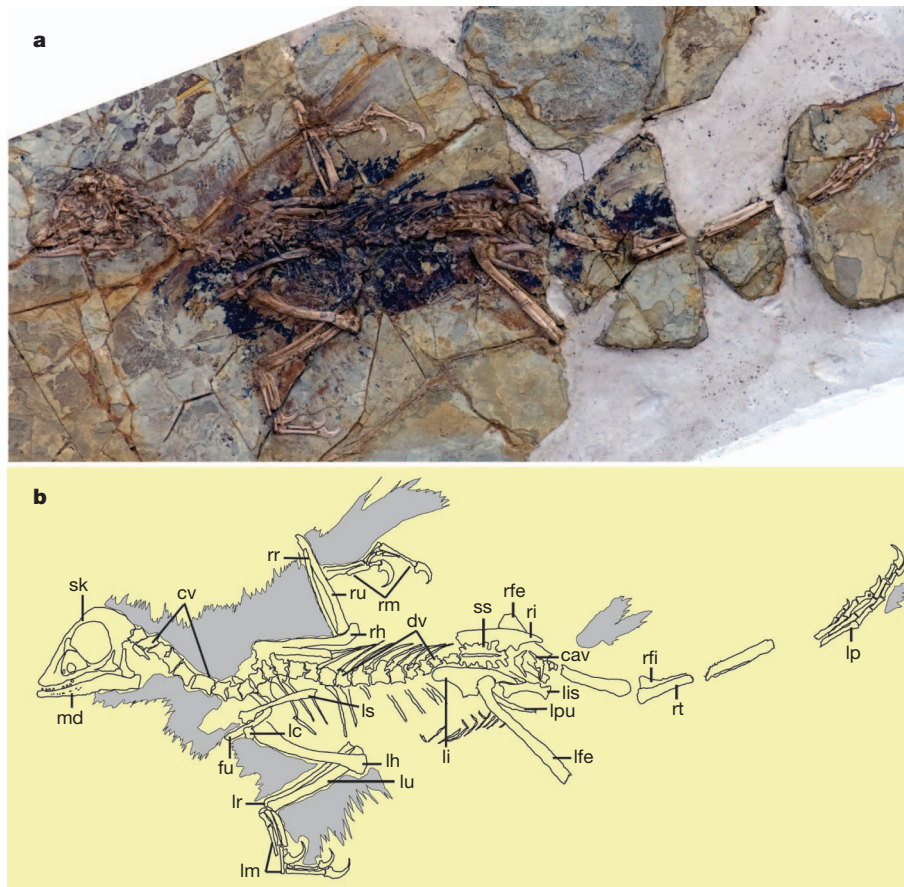


Figure 1 | *Xiaotingia zhengi* holotype (STM 27-2). **a**, **b**, Photograph (**a**) and line drawing (**b**). Integumentary structures in **b** are coloured grey. cav, caudal vertebra; cv, cervical vertebra; dv, dorsal vertebra; fu, furcula; lc, left coracoid; lfe, left femur; lh, left humerus; li, 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 deinonychosaurs¹¹. 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 troodontids¹⁸. 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-avian 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 dromaeosaurids¹¹.

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 oviraptorosaurs¹⁹, 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 habits²⁰. 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 dromaeosaurids¹¹. 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 paravians¹¹. The postacetabular process is rod-like and has a flat, thickened ventral surface as in *Archaeopteryx* and some basal troodontids¹¹. The ischium has a groove along its anterior margin as in dromaeosaurids¹¹.

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

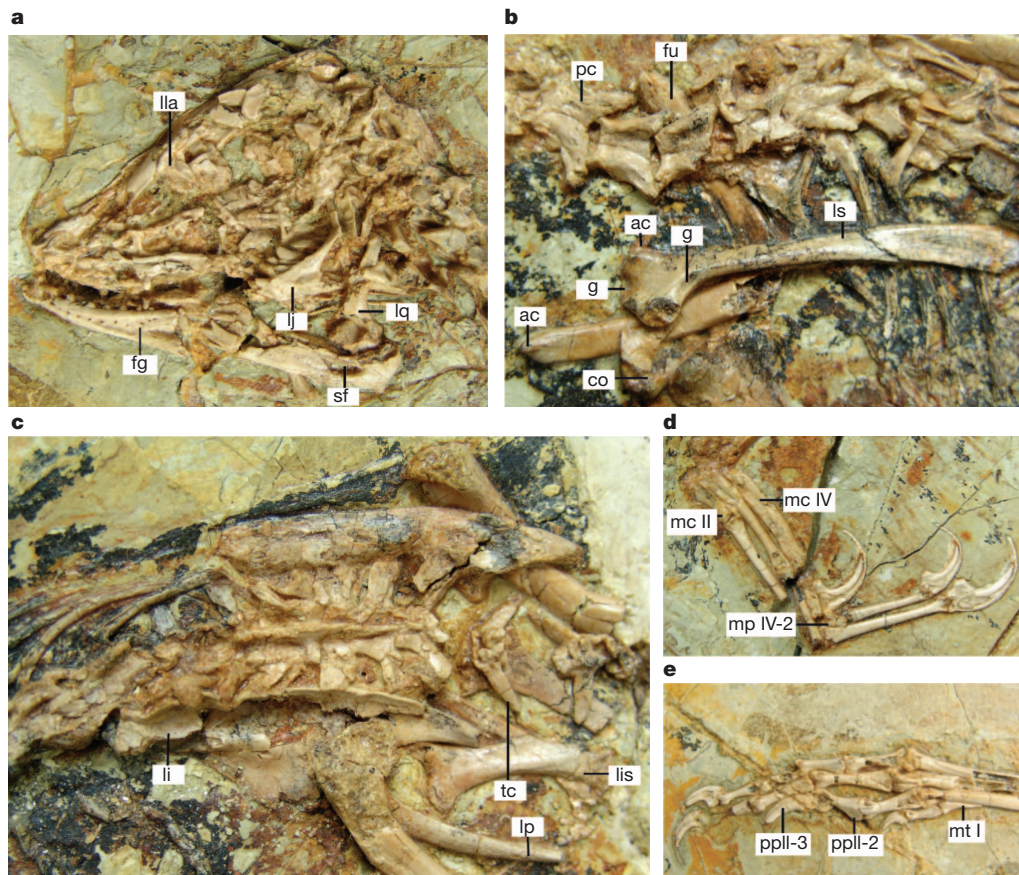


Figure 2 | Selected skeletal elements of STM 27-2. **a**, Skull and mandible. **b**, Middle presacral vertebrae, furcula and left scapulocoracoid. **c**, Pelvis and anterior caudal vertebrae. **d**, Left manus. **e**, Left pes. ac, acromial process; co, coracoid; fg, groove with foramina; fu, furcula; 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 deinonychosaurians 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 deinonychosaurians^{16,28}, and a close relationship between *Archaeopteryx* and dromaeosaurids has been proposed²², 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 phylogeny²⁹. *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 groups³⁰, 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

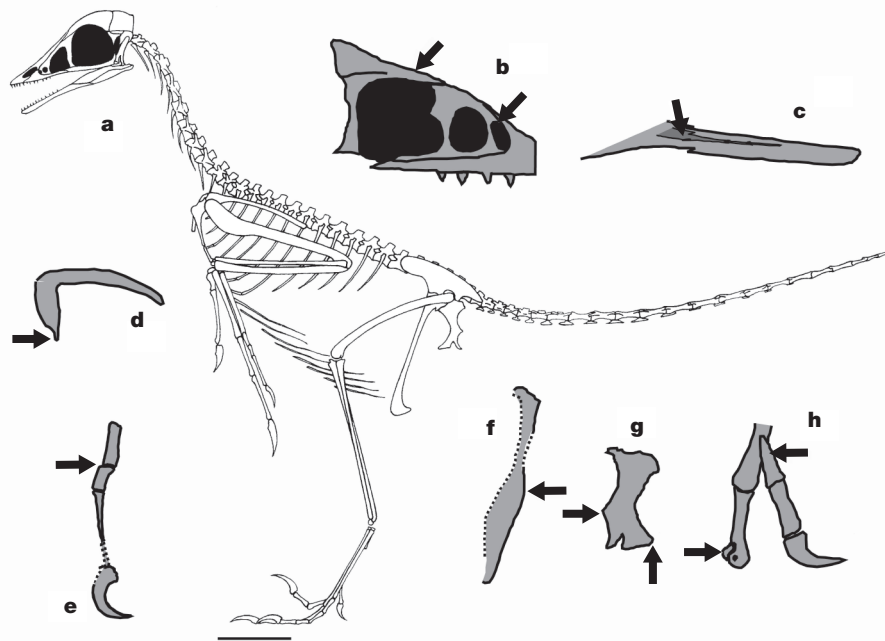


Figure 3 | Selected skeletal elements of *Archaeopteryx*. **a**, Skeletal reconstruction (modified from Fig. 6.53 in ref. 16). **b**, Preorbital region of the Thermopolis specimen in lateral view. Arrows point to the long anterior process of the lacrimal and the large promaxillary fenestra. **c**, Anterior 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

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 region¹⁶ (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 deinonychosaurs¹¹. 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

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**).

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 avialans¹⁵.

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 foramina³⁵. *Archaeopteryx* has five sacral vertebrae as in *Anchiornis*, *Xiaotingia*, basal troodontids and basal dromaeosaurids^{11,33}. By contrast, basal avialans have a greater number of sacral vertebrae³⁵.

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

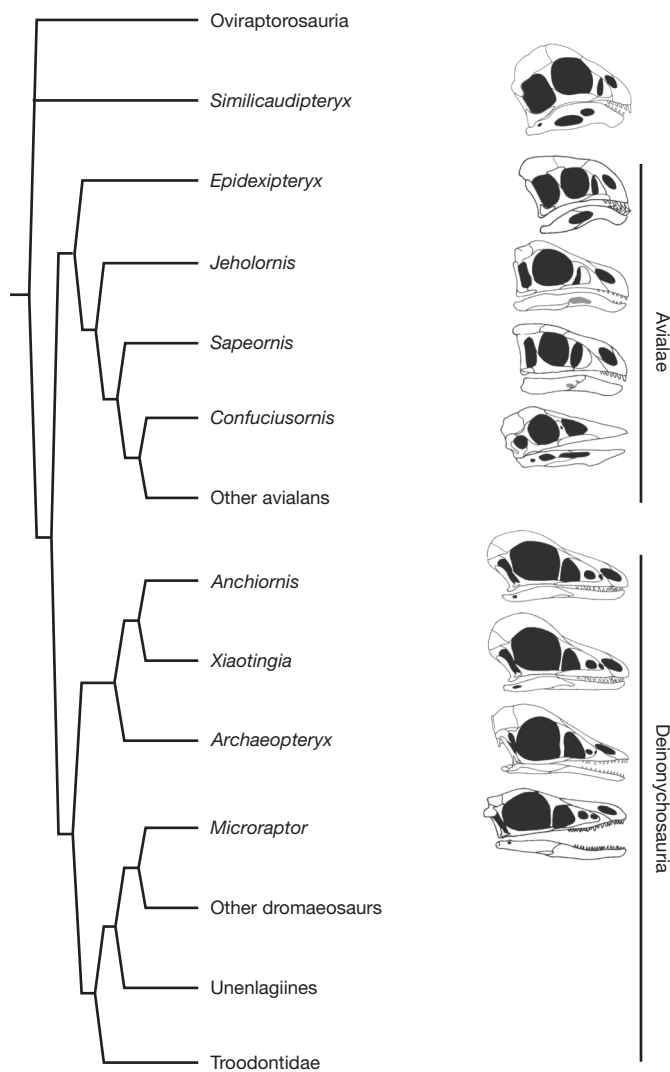


Figure 4 | A simplified cladogram showing the systematic position of *Xiaotingia* among the Coelurosauria (see Supplementary Information). Morphological features in grey areas need confirmation by better preserved specimens. Taxa recovered as basal avialans by our analysis are more similar in general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

subglenoid fossa. An ossified sternum and uncinat processes are absent as in *Anchiornis*, *Xiaotingia* and troodontids. The humerus has a proximodistally long internal tuberosity, as in *Anchiornis*, *Xiaotingia* and other deinonychosaurians¹¹. 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 deinonychosaurians.

As in *Anchiornis*, *Xiaotingia* and deinonychosaurians^{14,36,37}, but unlike in basal avialans¹⁷, the pre-acetabular process of the ilium is relatively deep. The supraacetabular crest is distinct as in *Xiaotingia*, *Anchiornis* and basal deinonychosaurians. 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 troodontids¹¹. The very short and wide ischium has a distally located obturator process (Fig. 3g), as in *Anchiornis* and basal deinonychosaurians^{11,33,37}. In most maniraptorans including oviraptorosaurs, the ischium is short, but not to the degree seen in *Archaeopteryx* and deinonychosaurians, 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

deinonychosaurians 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 condition²⁸ in that the proximal end of the third metatarsal is laterally compressed as in *Anchiornis* and basal deinonychosaurians. In basal avialans, metatarsal III is not laterally compressed^{4,17}.

As described above, *Archaeopteryx* is more similar to *Anchiornis*, *Xiaotingia* and basal deinonychosaurians 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 deinonychosaurians 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 deinonychosaurians, 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 deinonychosaurians, thus documented morphological support for the avialan affinities of *Archaeopteryx* is fairly weak. The alternative hypothesis that *Archaeopteryx*, *Anchiornis* and *Xiaotingia* are all deinonychosaurians is better supported by the available morphological data, and these taxa share with some basal deinonychosaurians 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 deinonychosaurians, 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 therizinosaurids⁴ 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 Therizinosauridae, 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 Avialae⁴², and a recent study suggests that the Oviraptorosauria and Scansoriopterygidae are sister taxa, forming a clade at the base of the Avialae³⁸. 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.

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1. Phylogenetic Nomenclature

We used the following definitions of several higher-level theropod taxa in this paper: Coelurosauria, the most inclusive clade containing *Passer domesticus* Linnaeus 1758 but not *Allosaurus fragilis* Marsh 1877, *Sinraptor dongi* Currie and Zhao 1993, and *Carcharodontosaurus saharicus* Depéret and Savornin 1927; Paraves, the most inclusive clade containing *Passer domesticus* Linnaeus 1758 but not *Oviraptor philoceratops* Osborn 1924; Avialae, the most-inclusive clade containing *Passer domesticus* Linnaeus 1758 but not *Dromaeosaurus albertensis* Matthew and Brown 1922 or *Troodon formosus* Leidy 1956; Deinonychosauria, the most-inclusive clade containing *Dromaeosaurus albertensis* Matthew and Brown 1922 but not *Passer domesticus* Linnaeus 1758; Archaeopterygidae, the most inclusive clade including *Archaeopteryx lithographica* Meyer 1861 but not *Dromaeosaurus albertensis* Matthew and Brown 1922 or *Passer domesticus* Linnaeus 1758.

The phylogenetic definition of the Avialae deserves special comment here. The Avialae was first proposed by Gauthier in 1986¹ and he explicitly stated “the name Avialae is applied to Ornithurae plus all extinct maniraptorans that are closer to Ornithurae than they are to Deinonychosauria” (p. 36 in reference 1). However, Gauthier also explicitly included *Archaeopteryx* within the Avialae, making the definition of the clade partially node-based. This led to the adoption of a fully node-based Avialae by a few later studies², though most studies nevertheless followed a stem-based definition³. In 2001, Gauthier and de Queiroz proposed an apomorphy-based definition for the Avialae⁴, but but this has received only limited acceptance mainly because apomorphy-based definitions in general are widely considered to be ambiguous. The node-based Avialae is redundant with the node-based definition of the Aves, which is now widely used in the scientific literature to refer to a group including the common ancestor of *Archaeopteryx* and modern birds and all of its descendants⁵. Gauthier restricted the term “Aves” to the crown clade of birds¹, which is consistent with the original definition of the Aves¹ and would also avoid the problem of redundancy. However, the crown-group definition of Aves has not been accepted in many other studies^{3,5}, because this usage ignores numerous fossil birds including *Archaeopteryx* and would lead to instability as *Archaeopteryx* and many other Mesozoic birds would have to be summarily removed from their traditional position within the Aves³. Given that a stem-based definition for the Avialae is consistent with the original definition¹, and is not redundant with the node-based Aves even if the latter is understood in its broad traditional sense, we adopt a stem-based definition for the Avialae in the present paper.

Many maniraptoran taxa have been controversial in their systematic positions (being basal avialans or non-avialan theropods)⁶⁻⁹, but the avialan status of scansoriopterygids, *Jeholornis*, *Sapeornis*, and *Confuciusornis* has been supported by most phylogenetic analyses¹⁰⁻¹³. In the phylogenetic context proposed by the present paper and also for the convenience of the presentation, we include scansoriopterygids but not archaeopterygids in Avialae, though we admit the systematic positions of scansoriopterygids and archaeopterygids need further investigation.

2. Provenance and authenticity of the *Xiaotingia zhengi* holotype

The holotype and only known specimen of *Xiaotingia zhengi* was acquired by the Shandong Tianyu Museum of Nature from a fossil dealer, according to whom the specimen was collected in the Linglongta area, Jianchang, western Liaoning, China. However, he could not provide accurate information as to the quarry in which the specimen was collected. The Linglongta area mainly exposes the early Late Jurassic Tiaojishan Formation¹⁴, though it also has limited outcrops of the Early Cretaceous Yixian Formation¹⁵. Like other Liaoning specimens preserving soft tissue, the holotype specimen is preserved in a shale slab. The fossil-bearing beds of the Tiaojishan Formation of the Daxishan locality, Linglongta area, western Liaoning have been investigated more extensively than those of other localities, and they are mainly greenish or yellowish mudstone and fine sandstone with tuff, and off-white tuffaceous shale¹⁴. The *Xiaotingia zhengi* holotype is preserved in a shale slab that possesses sedimentary features typically associated with Liaoning feathered dinosaur specimens. It is mainly off-white in colour and also bears patches of filemot colour. This complex colour pattern results from the fact that the slab surface exposes different layers of the shale. The yellowish layer is in fact underneath the fossil-bearing layer, which is off-white in colour. Although the slab preserving the *Xiaotingia zhengi* holotype is most similar to the fossil-bearing beds of the Tiaojishan Formation, it is difficult to distinguish between Tiaojishan and Yixian shale slabs on the basis of macro-sedimentary features. Discoveries of additional specimens with definite locality information, or micro-sedimentary analysis of the slab preserving the *Xiaotingia zhengi* holotype, will help to resolve this issue. It should be emphasized here that the major results of the present study will not be affected by the geological age of the holotype specimen, though such information may be important to other studies relating to this taxon and its relatives.

The holotype specimen is composed of one major block that has multiple breakages and four small separate blocks that are not connected to the major block. All five blocks are lithologically identical and comprise multiple thin layers of shale, the uppermost layer being off-white and the layer immediately below being yellowish in colour. This unique pattern suggests that the blocks are probably from the same depositional layer. The bones in the major block are articulated in a natural way and we did not find any evidence of forgery. Furthermore, the colour, texture, and relative sizes of the bones preserved on all five blocks strongly support the interpretation that the bones belong to the same individual. The blocks show detailed features (such as the colour pattern of the slabs, and the colour and texture of the bone) that are rarely seen in specimens from Liaoning, and the probability that the specimen is a composite is accordingly low. Finally, the morphological information from the different blocks is not discordant based on our current understanding of theropod anatomy. Based on our close examination of the blocks, and our previously accumulated rich experience with Liaoning specimens, we can guarantee the authenticity of the specimen.

3. Selected measurements of the *Xiaotingia zhengi* holotype

Mandible length	62
Basal skull length	61*
Pre-orbital length	30
Antorbital fossa length	16
Cervical series length	80
Dorsal series length	118
Furcula transverse width	42
Interclavicular angle	75 degrees
Left scapula length	55
Left humerus length	71
Left ulna length	65
Left radius length	63
Left mc II length	10
Left mc III length	24
Left mc IV length	24
Manual phalanx II-1 length	21
Manual phalanx II-2 length	14
Manual phalanx III-1 length	15
Manual phalanx III-2 length	25
Manual phalanx III-3 length	14
Manual phalanx IV-1 length	8
Manual phalanx IV-2 length	4
Manual phalanx IV-3 length	15
Manual phalanx IV-4 length	11
Ilium length	52
Preacetabular process length	32
Left ischium length	28*
Left femur length	84*
Left metatarsal I length	9
Left pedal phalanx I-1 length	6
Left pedal phalanx I-2 length	6
Left pedal phalanx II-1 length	12
Left pedal phalanx II-2 length	9
Left pedal phalanx II-3 length	13
Left pedal phalanx III-1 length	17
Left pedal phalanx III-2 length	13

Measurements are in mm except where noted; * refers to estimated value

4. *Xiaotingia zhengi* compared to other paravian dinosaurs

Xiaotingia zhengi independently evolved some salient features seen in other maniraptoran taxa, which highlights the extensive homoplasy that exists among maniraptorans. For example, *Xiaotingia* shares with the Troodontidae the following derived features: descending process of lacrimal inset relative to anterior and posterior processes¹⁶, dentary sub-triangular and bears posteriorly widening groove¹⁷, dentary teeth in symphyseal region closely packed (also seen in some basal dromaeosaurids¹⁶⁻¹⁸), and anteriormost caudal vertebrae with long, slender and distally tapering transverse processes^{17, 19}. It shares with basal avialans²⁰ an anteroposteriorly short antorbital fossa. It shares with the dromaeosaurids a large quadrate foramen (also present in *Anchiornis*)^{12, 21}, fusion of the zygapophyses of the sacral vertebrae to form a platform lateral to the fused neural spines, and a groove along the anterior margin of the ischium. The posterior end of the mandible is blunt in *Xiaotingia*, a resemblance to confuciusornithids²². Metacarpal IV is the most robust metacarpal and extends further distally than metacarpal III, a feature reminiscent of scansoriopterygids and some enantiornithines

5. Additional illustrations of selected basal paravians including *Archaeopteryx*



Figure S1. Photographs of *X. zhengi* holotype. **a**, close-up of skull; **b**, close-up of shoulder girdle. Abbreviations: ap, acromial process; fu, furcula; la, left angular; lc, left coracoid; ld, left dentary; lj, left jugal; ll, left lacrimal; lq, left quadrate; ls, left scapula; mf, maxillary fenestra; pmf, promaxillary fenestra; sf, surangular foramen.

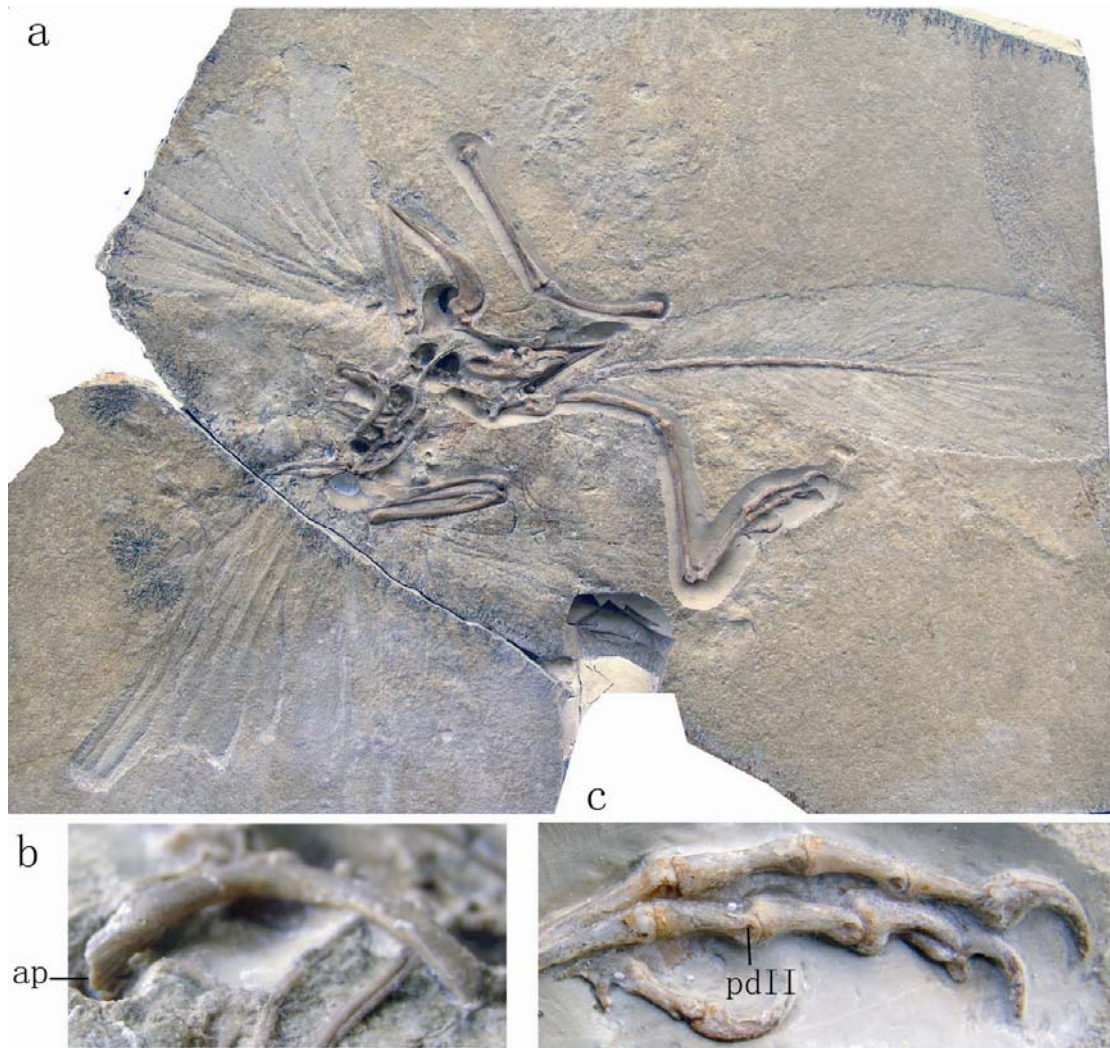


Figure S2. Photographs of London *Archaeopteryx*. **a**, whole specimen; **b**, close-up of furcula; **c**, close-up of pedal digit II. Abbreviations: ap, acromial process; pdII, pedal digit II.

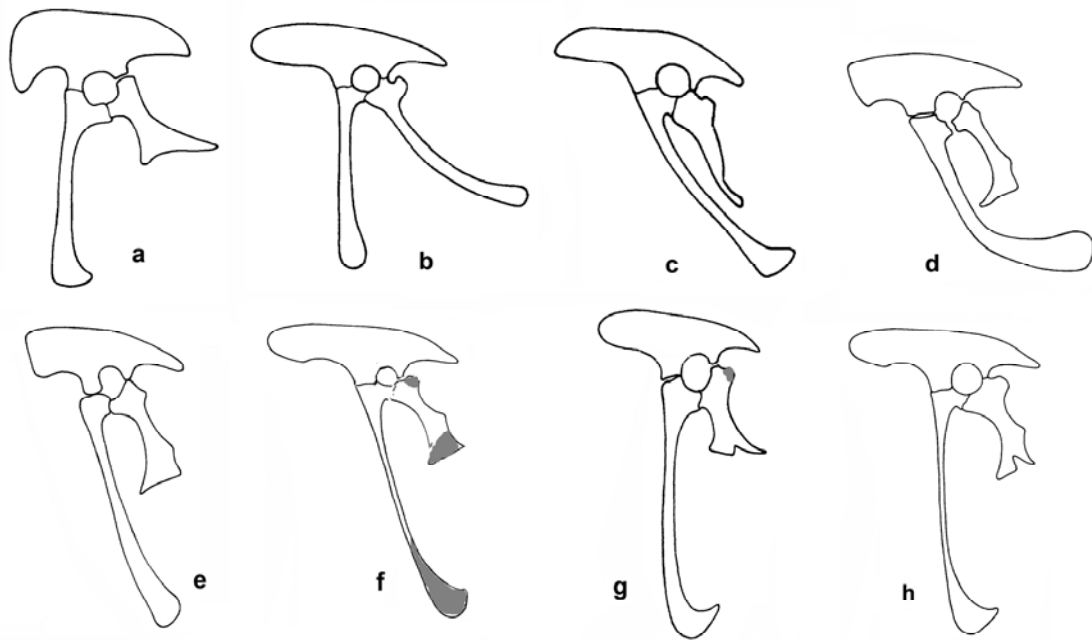


Figure S3. Pelvic morphology in various coelurosaurs. **a**, the oviraptorosaurian *Similicaudipteryx*; **b**, the scansoriopterygid *Epidexipteryx*; **c**, the basal avialan *Jeholornis*; **d**, the basal dromaeosaurid *Microraptor*; **e**, the basal troodontid *Sinovenator*; **f**, *Xiaotingia*; **g**, *Anchiornis*; **h**, *Archaeopteryx*. Morphological features shown in grey need confirmation based on better preserved specimens.

6. Preliminary morphometric analysis of theropod forelimb length and thickness

We evaluated the relative length and robustness of the forelimbs of major theropod groups by comparing the length and diameter of the humerus to the corresponding measurements for the femur in selected theropod taxa that represent the major theropod clades (Table S1). The plotted graph (Figure S4) indicates that the humerus is proportionally longer and more robust in basal avialans, archaeopterygids, and basal dromaeosaurids than in non-paravian theropods, troodontids, and derived dromaeosaurids. The last two groups are interpreted as having secondarily shortened forelimbs.

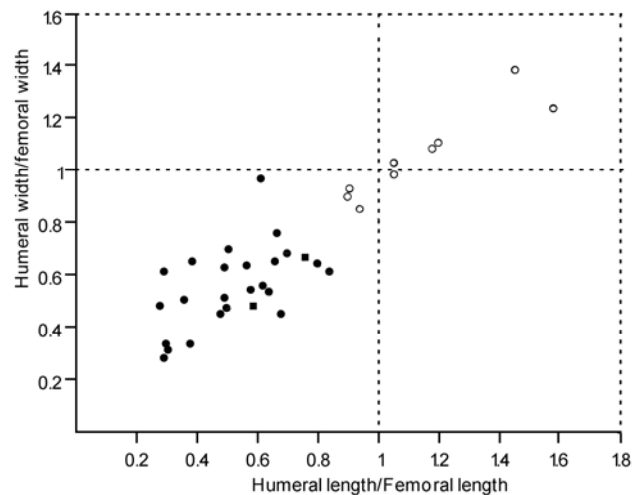


Figure S4. The relative length and diameter of the humerus in several theropod taxa. We use the ratios of humeral length to femoral length, and humeral diameter to femoral diameter, as indicators of forelimb length and robustness. Relative to the femur, the humerus is significantly longer and thicker in basal paravians than in non-paravian theropods, derived dromaeosaurids and troodontids (the relatively short and slender forelimbs in the last two groups are secondarily evolved according to the current phylogenetic analysis). Symbols: open circles, basal paravians, including basal avialans, archaeopterygids and some dromaeosaurids; solid circles, non-paravian theropods; solid squares, troodontids and derived dromaeosaurids.

Table S1. Ratios of humeral length and diameter to femoral length and diameter for selected theropod taxa

	Taxa	Humerus/Femur length ratio	Humerus/Femur diameter ratio
1	<i>Coelophysis</i>	0.57	0.63
2	<i>Limusaurus</i>	0.38	0.33
3	<i>Allosaurus</i>	0.36	0.50
4	<i>Guanlong</i>	0.62	0.55
5	<i>Tyrannosaurus</i>	0.29	0.28
6	<i>Compsognathus</i>	0.49	0.51
7	<i>Sinornithomimus</i>	0.66	0.65
8	<i>Haplocheirus</i>	0.49	0.62
9	<i>Khaan</i>	0.68	0.45
10	<i>Similicaudipteryx</i>	0.58	0.54
11	<i>Epidexipteryx</i>	1.05	0.98
12	<i>Sinornithoides</i>	0.59	0.48
13	<i>Microraptor</i>	0.90	0.89
14	<i>Sinornithosaurus</i>	0.91	0.92
15	<i>Buitreraptor</i>	0.94	0.85
16	<i>Archaeopteryx</i>	1.18	1.08
17	<i>Jeholornis</i>	1.45	1.38
18	<i>Sapeornis</i>	1.58	1.23
19	<i>Baryonyx</i>	0.39	0.65
20	<i>Beipiaosaurus</i>	0.70	0.68
21	<i>Anchiornis</i>	1.05	1.02
22	<i>Xiaotingia</i>	0.86	1.01

*Diameter measured at the mid-length of the femur.

7. Phylogenetic analysis

We built a dataset based on a recently published analysis of coelurosaurian phylogeny²⁰ (see below for complete character list and scorings). The data matrix was analyzed using the TNT software package²³ twice: once with *Xiaotingia* excluded and once with *Xiaotingia* included. The analyses were run using a traditional search strategy, with default settings apart from the following: 30000 maximum trees in memory and 1000 replications.

The former analysis resulted in 270 equally parsimonious trees, each having a length of 1375 steps. These trees each have a CI of 0.32 and an RI of 0.74. Figure S5 shows the strict consensus of the 270 trees. This analysis places *Archaeopteryx* at the base of the Avialae and generates the same topology seen in most published studies of coelurosaurian phylogeny^{1, 13, 24-28}. The latter analysis resulted in 540 equally parsimonious trees, each having a length of 1404 steps. These trees each have a CI of 0.32 and an RI of 0.73. Figure S6 shows the strict consensus of the 540 trees. This analysis generated several novel results including the existence of a monophyletic Archaeopterygidae comprising of *Archaeopteryx*, *Wellnhoferia*, *Archiornis*, and *Xiaotingia* and the deinonychosaurian affinities of the Archaeopterygidae; otherwise, the coelurosaurian phylogeny recovered was nearly the same as in most previous studies^{1, 13, 24-28}.

For the second analysis, we also saved the suboptimal trees with a length of 1405 steps and the strict consensus tree of 540 trees with a length of 1404 and 18371 trees with a length of 1405 is shown in Figure S7, which still places the Archaeopterygidae within the Deinonychosauria.

We ran Bremer support and bootstrap analyses on the data matrix, using TNT with all default settings except that 1000 replications were used. Bremer support values for the recovered clades are indicated on Figure S8, and only clades with bootstrap values greater than 50% are shown in Figure S9. It is notable that only a few clades meet this criterion in the present analysis.

In order to test previous suggestions that oviraptorosaurs might be basal avialans, we ran two additional analyses. The first of these analyses was constrained to produce a monophyletic group comprising all oviraptorosaurian and non-archaeopterygid avialan species, whereas the second was constrained to produce a monophyletic group comprising all oviraptorosaurian and avialan including archaeopterygid species. The first analysis resulted in 1096 most parsimonious trees, each having a length of 1410 steps. Figure S10 shows the strict consensus of the 1096 trees. The second analysis resulted in 216 most parsimonious trees, each having a length of 1413 steps. Figure S11 shows the strict consensus of the 216 trees. These analyses indicate that the hypotheses that recover an Oviraptorosauria-Avialae clade are considerably less parsimonious than the hypothesis shown in Figure 6. However, one reason that the Oviraptorosauria-Avialae hypotheses are worse supported by our dataset might be the large amount of missing data from the palates and braincases of the basal oviraptorosaurs and basal avialans, regions that represent important sources for oviraptorosaurian synapomorphies.

Unambiguous synapomorphies for selected coelurosaurian clades:

Deinonychosauria: 29.1, 72.1, 75.1, 82.0, 111.1, 134.1, 171.2, 183.1, 189.0, 199.1, 233.1, 238.0, 255.0, 294.1, 297.1, 302.1, 323.1, 334.1, 335.2, 359.0, 364.0, 365.0, 366.1, 367.0, 368.0, 371.0, and 372.1

Archaeopterygidae: 136.3, 162.0, 172.2, 235.1, 254.1, 270.3, 292.1, 302.2, 307.0, and 369.1

Avialae: 53.0, 102.0, 104.0, 110.1, 116.2, 122.1, 126.0, 128.1, 130.0, 159.0, 167.0, 175.0, 195.1, 196.1, 197.1, 200.0, 217.1, 274.2, 300.0, 317.1, 318.1, 326.1, 356.1, and 370.1

Paraves: 1.1, 10.1, 13.0, 14.0, 15.1, 20.1, 21.1, 28.1, 39.0, 61.1, 65.0, 66.0, 69.0, 79.0, 91.0, 95.0, 96.1, 97.1, 106.0, 109.1, 119.1, 125.0, 127.1, 129.1, 137.1, 138.1, 139.1, 154.0, 155.1, 156.1, 160.1, 166.0, 176.1, 179.1, 180.1, 184.1, 202.1, 221.1, 232.0, 237.1, 262.1, 267.1, 277.2, 292.0, 304.2, 306.1, 319.1, 320.2, 336.1, 354.0, and 362.1

Paraves-Oviraptorosauria-Therizinosauroidea clade: 13.1, 14.1, 28.0, 29.0, 39.1, 41.2, 54.0, 66.2, 79.1, 91.2, 106.1, 116.1, 117.1, 119.0, 121.1, 125.1, 126.1, 127.0, 130.1, 131.1, 136.1, 144.1, 157.2, 166.2, 167.2, 200.1, 238.1, 255.1, 276.1, 284.1, 300.1, 329.1, 351.1, 354.1, 359.1, 363.1, 364.1, 365.1, 367.1, 368.1, and 371.1.

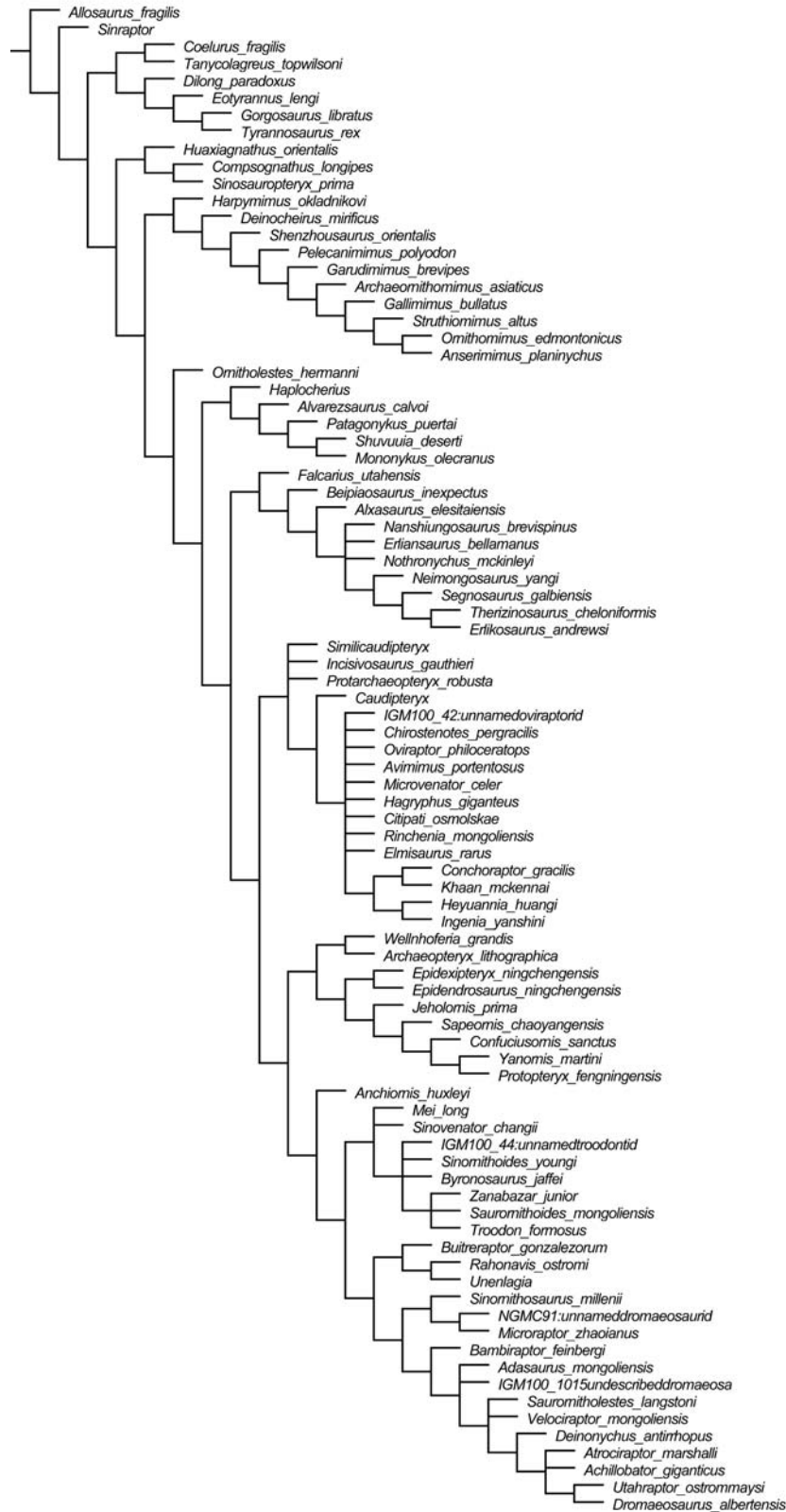


Figure S5. The strict consensus of 270 most parsimonious trees (Tree length = 1375; CI = 0.32; RI = 0.74) resulting from analysis of a matrix that excluded *Xiaotingia*.

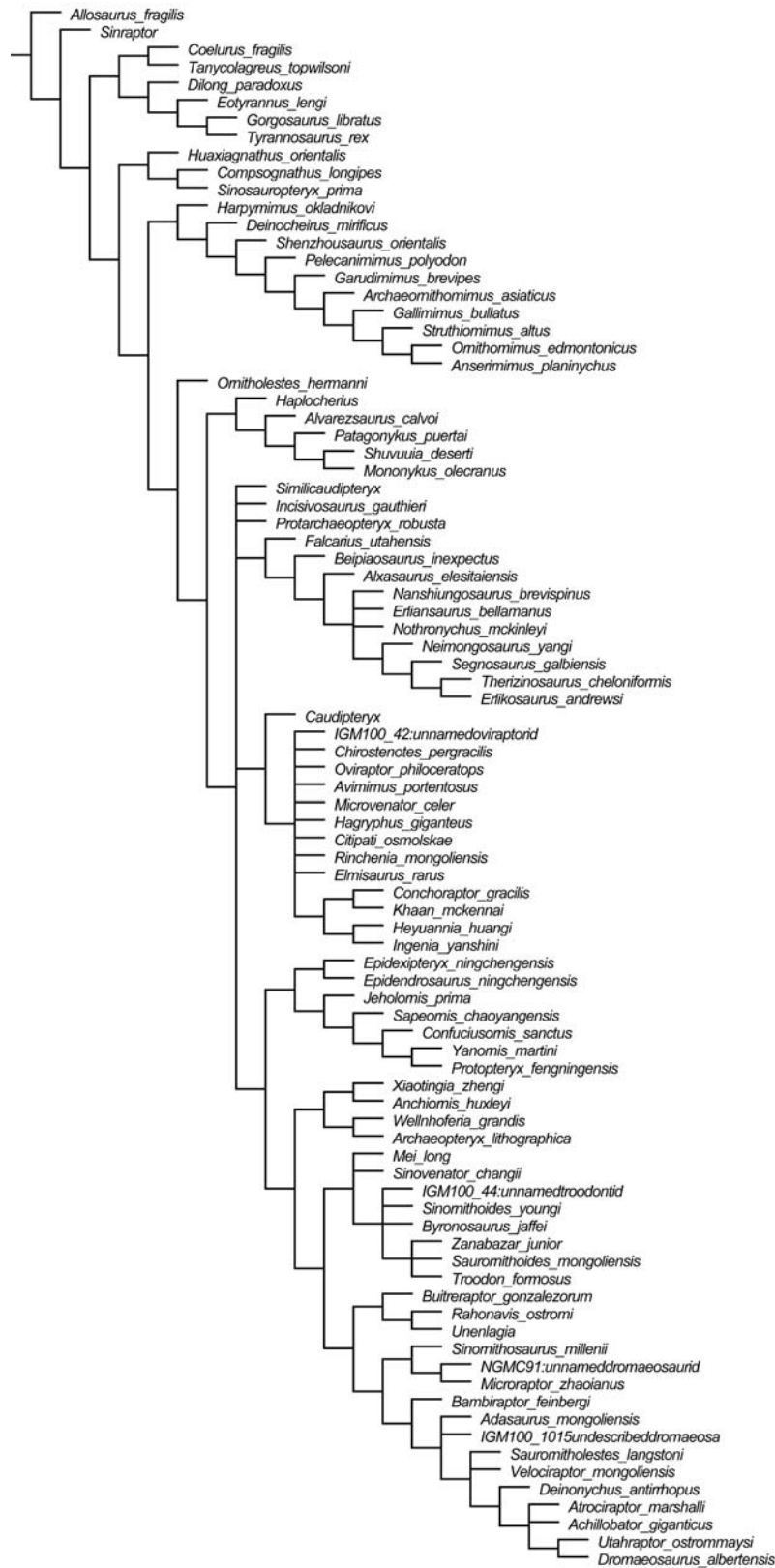


Figure S6. The strict consensus of 540 most parsimonious trees (Tree length = 1404; CI = 0.32; RI = 0.73) with *Xiaotingia zhengi* added into the analysis.

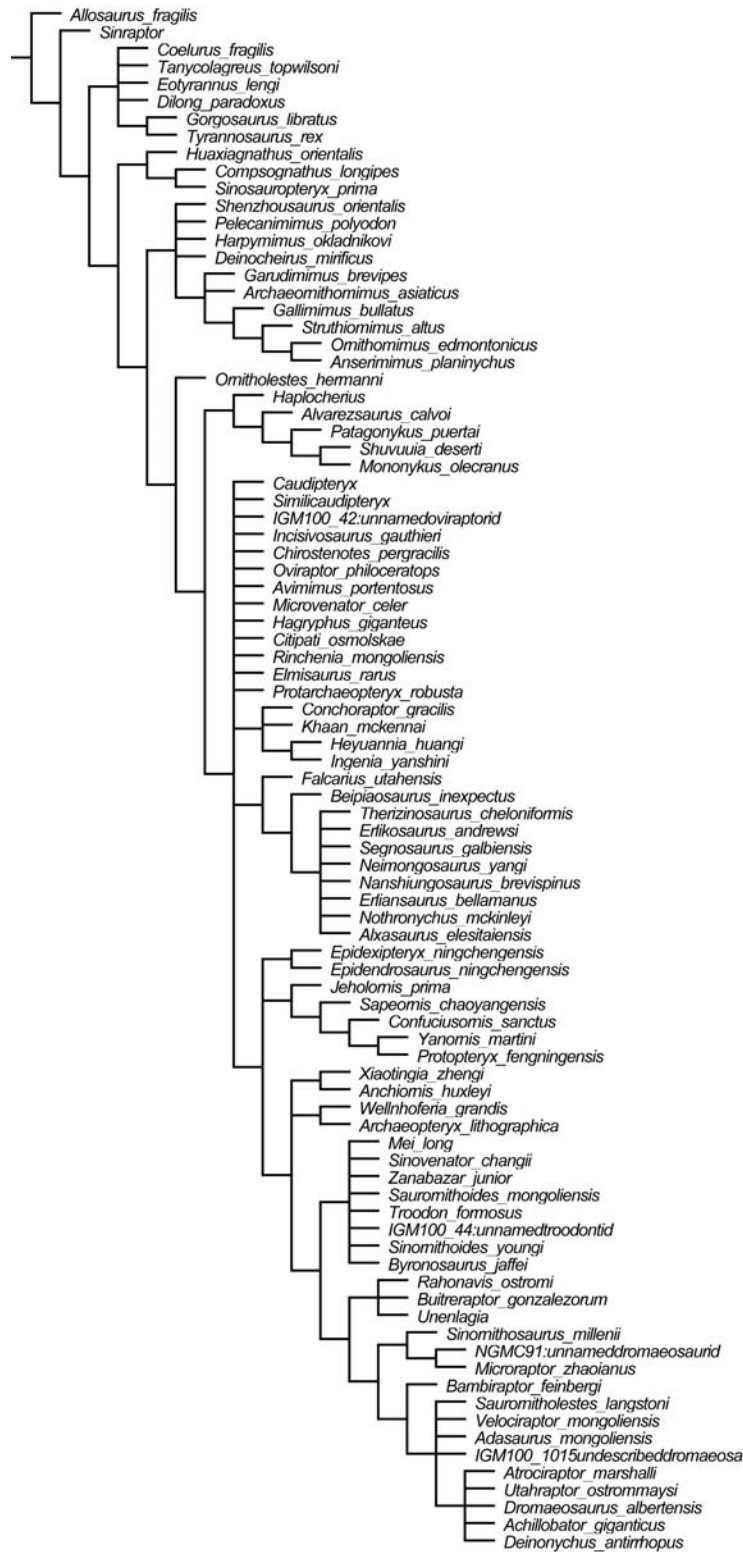


Figure S7. The strict consensus tree of 540 trees with a length of 1404 and 18371 trees with a length of 1405 steps.

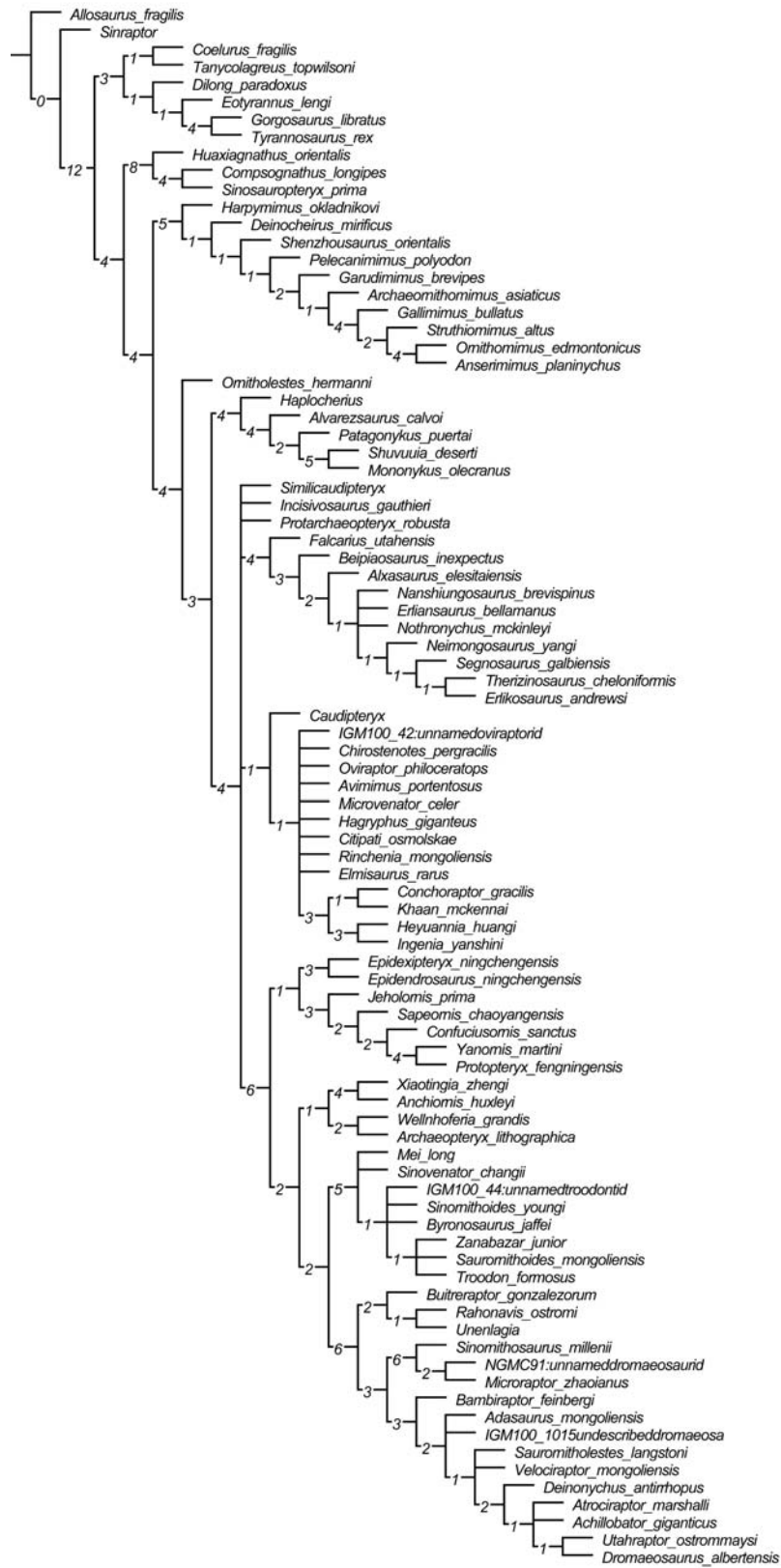


Figure S8. Bremer support values for the clades recovered by our analysis of coelurosaurian phylogeny.

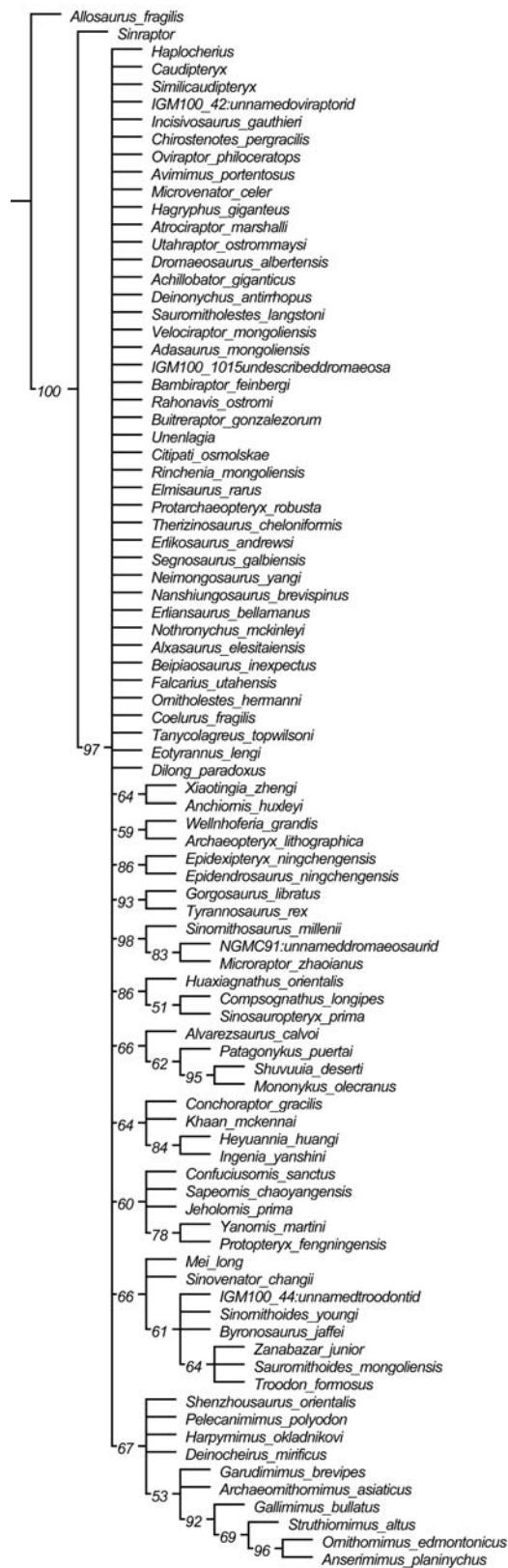


Figure S9. Bootstrap values for the clades recovered by our analysis of coelurosaurian phylogeny (only clades with bootstrap values greater than 50% are shown).

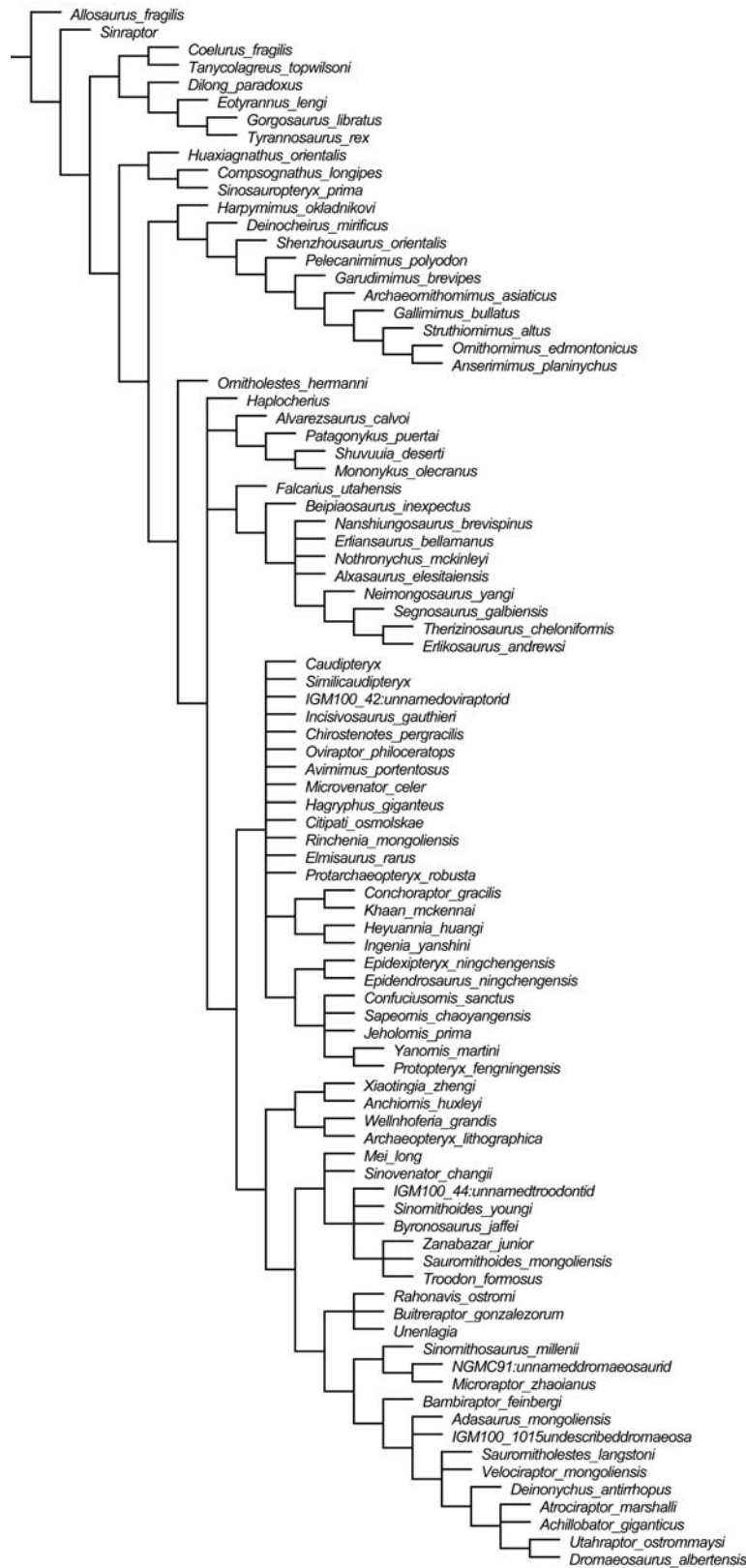


Figure 10 The strict consensus of the 1096 most parsimonious trees with a length of 1410 steps that resulted from an analysis constrained to produce a monophyletic group comprising all oviraptorosaurian and non-archaeopterygid avialan species.

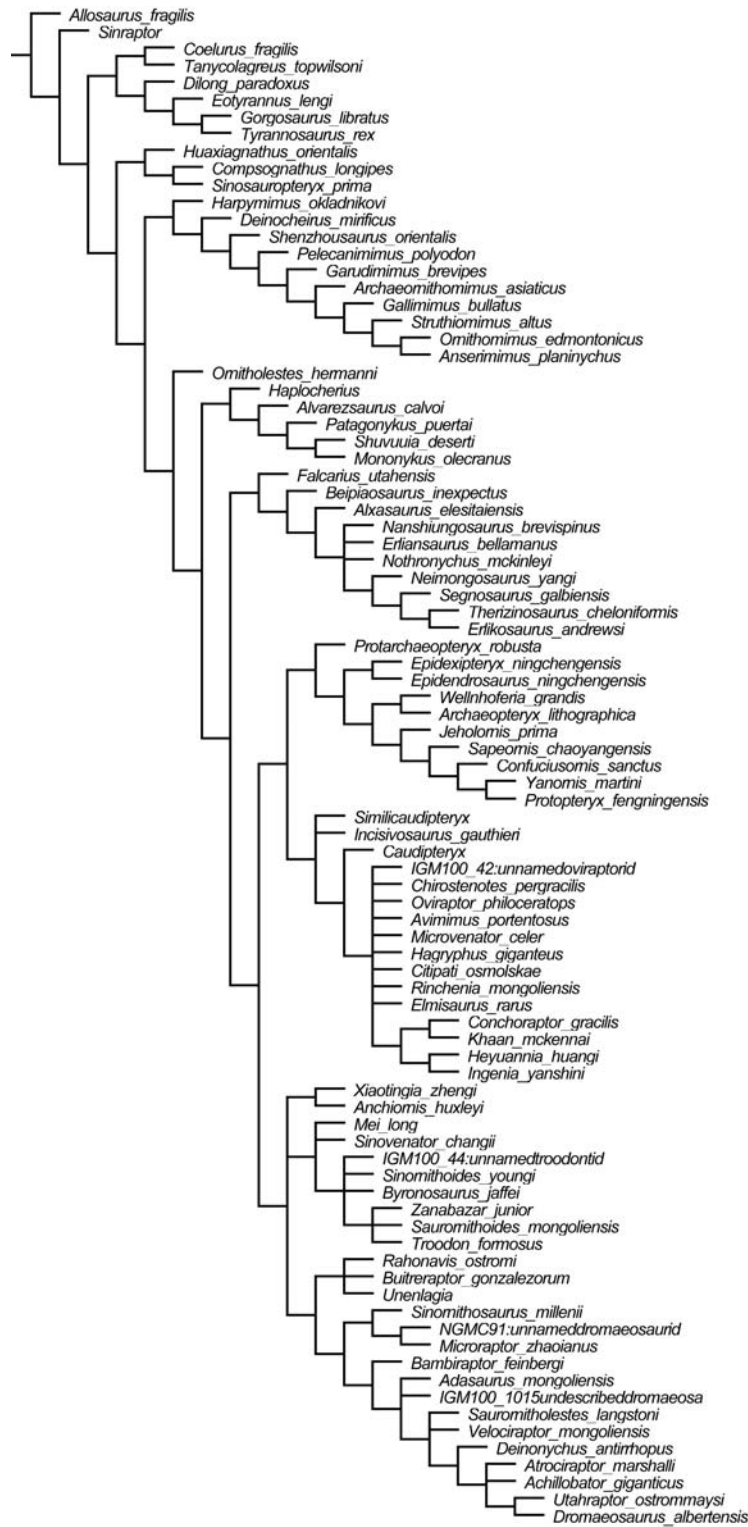


Figure 11. The strict consensus of the 216 most parsimonious trees with a length of 1413 steps that resulted from an analysis constrained to produce a monophyletic group comprising all oviraptorosaurian and avialan including archaeopterygid species.

Character list (Characters 1-363 are from Hu *et al.* (2009), whereas 364-374 are newly added).

1. Vaned feathers on forelimb symmetric (0) or asymmetric (1). The barbs on opposite sides of the rachis differ in length; in extant birds, the barbs on the leading edge of flight feathers are shorter than those on the trailing edge.
2. Orbit round in lateral or dorsolateral view (0) or dorsoventrally elongate (1). It is unclear that the eye occupied the entire orbit of those taxa in which it is keyhole shaped.
3. Anterior process of postorbital projects into orbit (0) or does not project into orbit (1).
4. Postorbital in lateral view with subhorizontal anterior (frontal) process (0) or frontal process diagonal (anterior tip of process higher than base of process) (1). [Formerly: postorbital in lateral view with straight anterior (frontal) process (0) or frontal process curves anterodorsally and dorsal border of temporal bar is dorsally concave (1)]
5. Postorbital bar parallels quadrate, lower temporal fenestra rectangular in shape (0) or jugal and postorbital approach or contact quadratojugal to constrict lower temporal fenestra (1).
6. Otosphenoidal crest vertical on basisphenoid and prootic, and does not border an enlarged pneumatic recess (0) or well developed, crescent shaped, thin crest forms anterior edge of enlarged pneumatic recess (1). This structure forms the anterior, and most distinct, border of the “lateral depression” of the middle ear region (see Currie, 1985; Currie and Zhao, 1992) of troodontids and some extant avians.
7. Crista interfenestralis confluent with lateral surface of prootic and opisthotic (0) or distinctly depressed within middle ear opening (1).
8. Subotic recess (pneumatic fossa ventral to fenestra ovalis) absent (0) or present (1)
9. Basisphenoid recess present between basisphenoid and basioccipital (0) or entirely within basisphenoid (1) or absent (2).
10. Posterior opening of basisphenoid recess single (0) or divided into two small, circular foramina by a thin bar of bone (1).
11. Base of cultriform process not highly pneumatized (0) or base of cultriform process (parasphenoid rostrum) expanded and pneumatic (parasphenoid bulla) (1).
12. Basipterygoid processes ventral or anteroventrally projecting (0) or lateroventrally projecting (1).
13. Basipterygoid processes well developed, extending as a distinct process from the base of the basisphenoid (0) or processes abbreviated or absent (1).
14. Basipterygoid processes solid (0) or processes hollow (1).
15. Basipterygoid recesses on dorsolateral surfaces of basipterygoid processes absent (0) or present (1).
16. Depression for pneumatic recess on prootic absent (0) or present as dorsally open fossa on prootic/opisthotic (1) or present as deep, posterolaterally directed concavity (2). The

dorsal tympanic recess referred to here is the depression anterodorsal to the middle ear on the opisthotic, not the recess dorsal to the crista interfenestralis within the middle ear as seen in *Archaeopteryx lithographica*, *Shuuvuia deserti* and Aves.

17. Accessory tympanic recess dorsal to crista interfenestralis absent (0) small pocket present (1) or extensive with indirect pneumatization (2). According to Witmer (1990), this structure may be an extension from the caudal tympanic recess, although it has been interpreted as the main part of the caudal tympanic recess by some authors (e.g., Walker, 1985).
18. Caudal (posterior) tympanic recess absent (0) present as opening on anterior surface of paroccipital process (1) or extends into opisthotic posterodorsal to fenestra ovalis, confluent with this fenestra (2).
19. Exits of C. N. X-XII flush with surface of exoccipital (0) or cranial nerve exits located together in a bowl-like basisphenoid depression (1).
20. Maxillary process of premaxilla contacts nasal to form posterior border of nares (0) or maxillary process reduced so that maxilla participates broadly in external naris (1) or maxillary process of premaxilla extends posteriorly to separate maxilla from nasal posterior to nares (2).
21. Internarial bar rounded (0) or flat (1).
22. Crenulate margin on buccal edge of premaxilla absent (0) or present (1).
23. Caudal margin of naris farther rostral than (0), or nearly reaching or overlapping (1), the rostral border of the antorbital fossa (Chiappe et al. 1998).
24. Premaxillary symphysis acute, V-shaped (0) or rounded, U-shaped (1).
25. Secondary palate short (0) or long, with extensive palatal shelves on maxilla (1).
26. Palatal shelf of maxilla flat (0) or with midline ventral ‘tooth-like’ projection (1)
27. Pronounced, round accessory antorbital fenestra absent (0) or present (1). A small fenestra, variously termed the accessory antorbital fenestra or maxillary fenestra, penetrates the medial wall of the antorbital fossa anterior to the antorbital fenestra in a variety of coelurosaurs and other theropods.
28. Accessory antorbital fossa situated at rostral border of antorbital fossa (0) or situated posterior to rostral border of fossa (1).
29. Tertiary antorbital fenestra (fenestra promaxillaris) absent (0) or present (1).
30. Antorbital fossa without distinct rim ventrally and anteriorly (0) or with distinct rim composed of a thin wall of bone (1). A rim is most strongly developed in the therizinosauroid *Erlikosaurus andrewsi* (Clark et al., 1994) but is nearly absent in ornithomimosaur.
31. Narial region apneumatic or poorly pneumatized (0) or with extensive pneumatic fossae, especially along posterodorsal rim of fossa (1).
32. Jugal and postorbital contribute equally to postorbital bar (0) or ascending process of

- jugal reduced and descending process of postorbital ventrally elongate (1).
33. Jugal quadratojugal process tall beneath lower temporal fenestra, twice or more as tall dorsoventrally as it is wide transversely (0) or rod-like (1) or concealed by quadratojugal (2).
 34. Jugal pneumatic recess in posteroventral corner of antorbital fossa present (0) or absent (1).
 35. Medial jugal foramen present on medial surface ventral to postorbital bar (0) or absent (1).
 36. Quadratojugal without horizontal process posterior to ascending process (reversed “L” shape) (0) or with process (i.e., inverted ‘T’ or ‘Y’ shape) (1).
 37. Jugal and quadratojugal separate (0) or quadratojugal and jugal fused and not distinguishable from one another (1).
 38. Supraorbital crests on lacrimal in adult individuals absent (0) or dorsal crest above orbit (1) or lateral expansion anterior and dorsal to orbit (2).
 39. Enlarged foramen or foramina opening laterally at the angle of the lacrimal, absent (0) or present (1).
 40. Lacrimal posterodorsal process absent (0) or present (1)
 41. Prefrontal large, dorsal exposure similar to that of lacrimal (0) or greatly reduced in exposure (1) or without exposure (2).
 42. Frontals narrow anteriorly as a wedge between nasals (0) or end abruptly anteriorly, suture with nasal transversely orientated (1) or suture with nasals W-shaped (2).
 43. Anterior emargination of supratemporal fossa on frontal straight or slightly curved (0) or strongly sinusoidal and reaching onto postorbital process (1).
 44. Frontal postorbital process (dorsal view): smooth transition from orbital margin (0) or sharply demarcated from orbital margin (1).
 45. Frontal edge smooth in region of lacrimal suture (0) or edge notched (1).
 46. Dorsal surface of parietals flat, lateral ridge borders supratemporal fenestra (0) or parietals dorsally convex with very low sagittal crest along midline (1) or dorsally convex with well developed sagittal crest (2).
 47. Parietals separate (0) or fused (1).
 48. Descending process of squamosal parallels quadrate shaft (0) or nearly perpendicular to quadrate shaft (1).
 49. Descending process of squamosal contacts quadratojugal (0) or does not contact quadratojugal (1).
 50. Posterolateral shelf on squamosal overhanging quadrate head absent (0) or present (1).
 51. Dorsal process of quadrate single headed (0) or with two distinct heads, a lateral one contacting the squamosal and a medial head contacting the braincase (1).

52. Quadrate vertical (0) or strongly inclined anteroventrally so that distal end lies far forward of proximal end (1).
53. Quadrate solid (0) or hollow, with depression on posterior surface (1).
54. Lateral border of quadrate shaft straight (0) or with lateral tab that touches squamosal and quadratojugal above an enlarged quadrate foramen (1)
55. Foramen magnum subcircular, slightly wider than tall (0) or oval, taller than wide (1).
56. Occipital condyle without constricted neck (0) or subspherical with constricted neck (1).
57. Paroccipital process elongate and slender, with dorsal and ventral edges nearly parallel (0) or process short, deep with convex distal end (1).
58. Paroccipital process straight, projects laterally or posterolaterally (0) or distal end curves ventrally, pendant (1).
59. Paroccipital process with straight dorsal edge (0) or with dorsal edge twisted rostrolaterally at distal end (1).
60. Ectopterygoid with constricted opening into fossa (0) or with open ventral fossa in the main body of the element (1).
61. Dorsal recess on ectopterygoid absent (0) or present (1).
62. Flange of pterygoid well developed (0) or reduced in size or absent (1).
63. Palatine and ectopterygoid separated by pterygoid (0) or contact (1).
64. Palatine tetroradiate, with jugal process (0) or palatine triradiate, jugal process absent (1).
65. Suborbital fenestra similar in length to orbit (0) or about half or less than half orbital length (1) or absent (2).
66. Symphyseal region of dentary broad and straight, paralleling lateral margin (0) or medially recurved slightly (1) or strongly recurved medially (2).
67. Dentary symphyseal region in line with main part of buccal edge (0) or downturned at rostral end (1)
68. Mandible without coronoid prominence (0) or with coronoid prominence (1).
69. Posterior end of dentary without posterodorsal process dorsal to mandibular fenestra (0) or with dorsal process above anterior end of mandibular fenestra (1) or with elongate, strongly arched dorsal process extending over most of fenestra (2).
70. Labial face of dentary flat (0) or with lateral ridge and inset tooth row (1).
71. Dentary subtriangular in lateral view (0) or with subparallel dorsal and ventral edges (1).
72. Nutrient foramina on external surface of dentary superficial (0) or lie within a deep groove that widens posteriorly (1).
73. External mandibular fenestra oval (0) or subdivided by a spinous rostral process of the surangular (1).
74. Internal mandibular fenestra small and slit-like (0) or large and rounded (1).

75. Foramen in lateral surface of surangular rostral to mandibular articulation, absent (0) or present (1).
76. Splenial not widely exposed on lateral surface of mandible (0) or exposed as a broad triangle between dentary and angular on lateral surface of mandible (1).
77. Coronoid ossification large (0) or only a thin splint (1) or absent (2).
78. Articular without elongate, slender medial, posteromedial, or mediodorsal process from retroarticular process (0) or with process (1).
79. Retroarticular process short, stout (0) or elongate and slender (1).
80. Mandibular articulation surface as long as distal end of quadrate (0) or twice or more as long as quadrate surface, allowing anteroposterior movement of mandible (1).
81. Premaxilla toothed (0) or edentulous (1).
82. Second premaxillary tooth approximately equivalent in size to other premaxillary teeth (0) or second tooth markedly larger than third and fourth premaxillary teeth (1) or first premaxillary tooth considerably larger than the posterior ones (2) modified.
83. Maxilla toothed (0) or edentulous (1).
84. Maxillary and dentary teeth serrated (0) or some without serrations anteriorly (except at base in *S. mongoliensis*) (1) or all without serrations (2).
85. Dentary and maxillary teeth large, less than 25 in dentary (0) or large number of small teeth (25 or more in dentary) (1) or small number of dentary teeth (≤ 11) (2) or dentary without teeth (3).
86. Serration denticles large (0) or small (1).
87. Serrations simple, denticles convex (0) or distal and often mesial edges of teeth with large, hooked denticles that point toward the tip of the crown (1).
88. Teeth constricted between root and crown (0) or root and crown confluent (1).
89. Dentary teeth evenly spaced (0) or anterior dentary teeth smaller, more numerous, and more closely appressed than those in middle of tooth row (1).
90. Dentaries lack distinct interdental plates (0) or with interdental plates medially between teeth (1).
91. In cross section, premaxillary tooth crowns sub-oval to sub-circular (0) or asymmetrical (D-shaped in cross section) with flat lingual surface (1) or first premaxillary tooth with flat lingual surface, other premaxillary teeth without flat lingual surfaces (2).
92. Number of cervical vertebrae: 10 (0) or 12 or more (1).
93. Axial epiphyses absent or poorly developed, not extending past posterior rim of postzygopophyses (0) or large and posteriorly directed, extend beyond postzygopophyses (1).
94. Axial neural spine flared transversely (0) or compressed mediolaterally (1).

95. Epipophyses of cervical vertebrae placed distally on postzygapophyses, above postzygapophyseal facets (0) or placed proximally, proximal to postzygapophyseal facets (1).
96. Anterior cervical centra level with or shorter than posterior extent of neural arch (0) or centra extending beyond posterior limit of neural arch (1).
97. Carotid process on posterior cervical vertebrae absent (0) or present (1).
98. Anterior cervical centra subcircular or square in anterior view (0) or distinctly wider than high, kidney shaped (1).
99. Cervical neural spines anteroposteriorly long and dorsoventrally tall (0) or anteroposteriorly short, dorsoventrally low and centred on neural arch, giving arch an 'X' shape in dorsal view (1) or anteroposteriorly short and dorsoventrally tall (2) or anteroposteriorly long and dorsoventrally short (3).
100. Cervical centra with one pair of pneumatic openings (0) or with two pairs of pneumatic openings (1).
101. Cervical and anterior trunk vertebrae amphiplatyan (0) or opisthocoelous (1).
102. Anterior trunk vertebrae without prominent hypapophyses (0) or with large hypapophyses (1).
103. Parapophyses of posterior trunk vertebrae flush with neural arch (0) or distinctly projected on pedicels (1).
104. Hyosphene -hypantrum articulations in trunk vertebrae absent (0) or present (1).
105. Zygapophyses of trunk vertebrae abutting one another above neural canal, opposite hyosphenes meet to form lamina (0), or zygapophyses placed lateral to neural canal and separated by groove for interspinous ligaments, hyosphens separated (1).
106. Middle and posterior dorsal vertebrae not pneumatic (0) or pneumatic (1).
107. Transverse processes of anterior dorsal vertebrae long and thin (0) or short, wide, and only slightly inclined (1).
108. Neural spines of dorsal vertebrae not expanded distally (0) or expanded to form 'spine table' (1).
109. Scars for interspinous ligaments terminate at apex of neural spine in dorsal vertebrae (0) or terminate below apex of neural spine (1).
110. Number of sacral vertebrae: 5 (0) or 6 (1) or 7 or more (2).
111. Sacral vertebrae with unfused zygapophyses (0) or with fused zygapophyses forming a sinuous ridge in dorsal view (1).
112. Ventral surface of posterior sacral centra gently rounded, convex (0) or ventrally flattened, sometimes with shallow sulcus (1) or centrum strongly constricted transversely, ventral surface keeled (2).
113. Pleurocoels absent on sacral vertebrae (0) or present on anterior sacrals only (1) or

- present on all sacrals (2).
114. Last sacral centrum with flat posterior articulation surface (0) or convex articulation surface (1).
 115. Caudal vertebrae with distinct transition point (0) or without transition point (1).
 116. Transition point in caudal series begins distal to the 10th caudal (0) or between 7th and 10th caudal vertebra (1) or proximal to the 7th caudal vertebra (2).
 117. Anterior caudal centra tall, oval in cross section (0) or with box-like centra in caudals I-V (1) or anterior caudal centra laterally compressed with ventral keel (2).
 118. Neural spines of caudal vertebrae simple, undivided (0) or separated into anterior and posterior alae throughout much of caudal sequence (1).
 119. Neural spines on distal caudals form a low ridge (0) or spine absent (1) or midline sulcus in center of neural arch (2).
 120. Prezygapophyses of distal caudal vertebrae between 1/3 and whole centrum length (0) or with extremely long extensions of the prezygapophyses (up to 10 vertebral segments long in some taxa) (1) or strongly reduced as in *Archaeopteryx lithographica* (2).
 121. More than 30 caudal vertebrae (0) or 21–30 caudal vertebrae (1) or < 10 caudal vertebrae, followed by pygostyle (2) or 11–20 vertebrae (3).
 122. Proximal end of chevrons of proximal caudals short anteroposteriorly, shaft proximodistally elongate (0) or proximal end elongate anteroposteriorly, flattened and plate-like (1).
 123. Distal caudal chevrons are simple (0) or anteriorly bifurcate (1) or bifurcate at both ends (2).
 124. Shaft of cervical ribs slender and longer than vertebra to which they articulate (0) or broad and shorter than vertebra (1).
 125. Ossified uncinat processes absent (0) or present (1).
 126. Ossified ventral rib segments absent (0) or present (1).
 127. Lateral gastral segment shorter than medial one in each arch (0) or distal segment longer than proximal segment (1).
 128. Ossified sternal plates separate in adults (0) or fused (1).
 129. Sternum without distinct lateral xiphoid process posterior to costal margin (0) or with lateral xiphoid process (1).
 130. Anterior edge of sternum grooved for reception of coracoids (0) or sternum without grooves (1).
 131. Articular facet of coracoid on sternum (conditions may be determined by the articular facet on coracoid in taxa without ossified sternum): anterolateral or more lateral than anterior (0); almost anterior (1).
 132. Hypocleidium on furcula absent (0) or present (1). The hypocleidium is a process

- extending from the ventral midline of the furcula, and is attached to the sternum by a ligament in extant birds.
133. Acromion margin of scapula continuous with blade (0) or anterior edge laterally everted (1).
 134. Anterior surface of coracoid ventral to glenoid fossa unexpanded (0) or anterior edge of coracoid expanded, forms triangular subglenoid fossa bounded laterally by coracoid tuber (1).
 135. Scapula and coracoid separate (0) or fused into scapulacoracoid (1).
 136. Coracoid in lateral view subcircular, with shallow ventral blade (0) or subquadrangular with extensive ventral blade (1) or shallow ventral blade with elongate posteroventral process (2) or subtriangular (proximal end constricted, distal end wide) (3).
 137. Scapula and coracoid form a continuous arc in posterior and anterior views (0) or coracoid inflected medially, scapulocoracoid 'L' shaped in lateral view (1).
 138. Glenoid fossa without (0) or with extension of glenoid floor onto external surface of scapula (the surface opposite the costal surface) (1).
 139. Scapula longer than humerus (0) or humerus longer than scapula (1).
 140. Deltopectoral crest large and distinct, proximal end of humerus quadrangular in anterior view (0) or deltopectoral crest less pronounced, forming an arc rather than being quadrangular (1) or deltopectoral crest very weakly developed, proximal end of humerus with rounded edges (2) or deltopectoral crest extremely long (3) or proximal end of humerus extremely broad, triangular in anterior view (4).
 141. Anterior surface of deltopectoral crest smooth (0) or with distinct groove or ridge near lateral edge along distal end of crest (1).
 142. Olecranon process weakly developed (0) or distinct and large but not hypertrophied (1) or hypertrophied (2).
 143. Distal articular surface of ulna flat (0) or convex, semilunate surface (1).
 144. Proximal surface of ulna a single continuous articular facet (0) or divided into two distinct fossae separated by a median ridge (1).
 145. Lateral proximal carpal (ulnare?) quadrangular (0) or triangular in proximal view (1).
 146. Two distal carpals in contact with metacarpals, one covering the base of metacarpal I (and perhaps contacting metacarpal II) the other covering the base of metacarpal II (distal carpals 1 and 2 unfused) (0) or a single distal carpal capping metacarpals I and II (distal carpals 1 and 2 fused) (1).
 147. Distal carpals not fused to metacarpals (0) or fused to metacarpals, forming carpometacarpus (1).
 148. Distal carpals 1+2 well developed, covering all of proximal ends of metacarpals I and II (0) or small, cover about half of base of metacarpals I and II (1) or cover bases of all metacarpals (2).

149. Metacarpal I half or less than half the length of metacarpal II, and longer proximodistally than wide transversely (0) or subequal in length to metacarpal II (1) or very short and wider transversely than long proximodistally (2).
150. Third manual digit present, phalanges present (0) or reduced to no more than metacarpal splint (1).
151. Flexor tubercles of manual unguals proximal (0) or displaced distally from articular end (1) or proximodistally elongated with proximal end close to articular facet (2).
152. Unguals on all digits generally similar in size (0) or digit I bearing large ungual and unguals of other digits distinctly smaller (1).
153. Proximodorsal ‘lip’ on first manual ungual – a transverse ridge immediately dorsal to the articulating surface – absent (0) or present (1).
154. Ventral edge of anterior ala of ilium straight or gently curved (0) or ventral edge hooked anteriorly (1) or very strongly hooked (2).
155. Preacetabular part of ilium roughly as long as postacetabular part of ilium (0) or preacetabular portion of ilium markedly longer (more than 2/3 of total ilium length) than postacetabular part (1).
156. Anterior end of ilium gently rounded or straight (0) or anterior end strongly curved (1) or pointed at anterodorsal corner (2).
157. Supraacetabular crest on ilium as a separate process from antitrochanter, forms “hood” over femoral head present (0) reduced, not forming hood (1) or absent (2).
158. Postacetabular ala of ilium in lateral view squared (0) or acuminate (1).
159. Postacetabular blades of ilia in dorsal view parallel (0) or diverge posteriorly (1).
160. Tuber along dorsal edge of ilium, dorsal or slightly posterior to acetabulum absent (0) or present (1).
161. Brevis fossa shelf-like (0) or deeply concave with lateral overhang (1).
162. Antitrochanter posterior to acetabulum absent or poorly developed (0) or prominent (1).
163. Ridge bordering cuppedicus fossa extends far posteriorly and is confluent or almost confluent with acetabular rim (0) or ridge terminates rostral to acetabulum or curves ventrally onto anterior end of pubic peduncle (1).
164. Cuppedicus fossa deep, ventrally concave (0) or fossa shallow or flat, with no lateral overhang (1) or absent (2).
165. Posterior edge of ischium without (0) or with prominent proximodorsal prong (1).
166. Shaft of ischium straight in lateral view (0) or ventrodorsal end curved anteriorly (1) or curved dorsally (posterodorsally concave) (2) (Maryańska et al. 2002).
167. Obturator process of ischium absent (0) or proximal in position (1) or distally displaced (2).
168. Obturator process does not contact pubis (0) or contacts pubis (1).

169. Length of pubic boot $\leq 30\%$ length of pubis (0) or $\geq 40\%$ (1).
170. Semicircular scar on posterior part of the proximal end of the ischium, absent (0) or present (1).
171. Ischium, ischium length as measured by ischial length/pubis length ratio: between 70%-100% (0), or between 50%- 70% (1) or below 50% (2) or above 100% (3).
172. Distal ends of ischia form symphysis (0) or approach one another but do not form symphysis (1) or widely separated (2).
173. Ischial boot (expanded distal end) present (0) or absent (1).
174. Tubercle on anterior edge of ischium absent (0) or present (1).
175. Pubis propubic (0) or pubis vertical (1) or pubis moderately posteriorly oriented (2) or pubis fully posteriorly oriented (opisthopubic) (3).
176. Pubic boot projects anteriorly and posteriorly (0) or with little or no anterior process (1) or no anteroposterior projections (2).
177. Shelf on pubic shaft proximal to symphysis ('pubic apron') extends medially from middle of cylindrical pubic shaft (0) or shelf extends medially from anterior edge of anteroposteriorly flattened shaft (1).
178. Pubic shaft straight (0) or distal end curves anteriorly, anterior surface of shaft concave in lateral view (1) or anterior surface of shaft convex in lateral view (2).
179. Pubic apron about half of pubic shaft length (0) or less than 1/3 of shaft length (1).
180. Femoral head without fovea capitalis (for attachment of capital ligament) (0) or circular fovea present in center of medial surface of head (1).
181. Lesser and greater trochanters unfused (0) or fused (1).
182. Lesser trochanter of femur alariform (0) or cylindrical in cross section (1).
183. Posterior trochanter absent or represented only by rugose area (0) or posterior trochanter distinctly raised from shaft, mound-like (1).
184. Fourth trochanter on femur present (0) or absent (1).
185. Accessory trochanteric crest distal to lesser trochanter absent (0) or present (1).
186. Anterior surface of femur proximal to medial distal condyle without longitudinal crest (0) or crest present extending proximally from medial condyle on anterior surface of shaft (1).
187. Popliteal fossa on distal end of femur open distally (0) or closed off distally by contact between distal condyles (1).
188. Fibula reaches proximal tarsals (0) or short, tapering distally, and not in contact with proximal tarsals (1).
189. Medial surface of proximal end of fibula concave along long axis (0) or flat (1).
190. Deep oval fossa on medial surface of fibula near proximal end absent (0) or present (1).

191. Distal end of tibia and astragalus without distinct condyles (0) or with distinct condyles separated by prominent tendinal groove on anterior surface (1).
192. Medial cnemial crest absent (0) or present on proximal end of tibia (1).
193. Ascending process of the astragalus tall and broad, covering most of anterior surface of distal end of tibia (0) or process short and slender, covering only lateral half of anterior surface of tibia (1) or ascending process tall with medial notch that restricts it to lateral side of anterior face of distal tibia (2).
194. Ascending process of astragalus confluent with condylar portion (0) or separated by transverse groove or fossa across base (1).
195. Astragalus and calcaneum separate from tibia (0) or fused to each other and to the tibia in late ontogeny (1).
196. Distal tarsals separate, not fused to metatarsals (0) or form metatarsal cap with intercondylar prominence that fuses to metatarsal early in postnatal ontogeny (1).
197. Metatarsals not co-ossified (0) or co-ossification of metatarsals begins proximally (1) or distally (2).
198. Distal end of metatarsal II smooth, not ginglymoid (0) or with developed ginglymus (1).
199. Distal end of metatarsal III smooth, not ginglymoid (0) or with developed ginglymus (1).
200. Metatarsal III, proximal end: not pinched (0) or pinched, but visible in anterior view (1) or pinched, and invisible in anterior view (2).
201. Ungual of pedal digit II similar in size to that of III (0) or pedal unguis II about 50% larger than pedal unguis III (1).
202. Metatarsal I articulates at middle of metatarsal II (0) or metatarsal I attaches to distal quarter of metatarsal II (1) or metatarsal I articulates with metatarsal II near its proximal end (2) or metatarsal I absent (3).
203. Metatarsal I attenuates proximally (0) or proximal end of metatarsal I similar to that of metatarsals II–IV (1).
204. Shaft of MT IV round or thicker dorsoventrally than wide in cross section (0) or shaft of MT IV mediolaterally widened and flat in cross section (1).
205. Foot symmetrical (0) or asymmetrical with slender MTII and very robust MT IV (1).
206. Neural spines on posterior dorsal vertebrae in lateral view rectangular or square (0) or anteroposteriorly expanded distally, fanshaped (1).
207. Shaft diameter of phalanx I-1 less (0) or greater (1) than shaft diameter of radius.
208. Angular exposed almost to end of mandible in lateral view, reaches or almost reaches articular (0) or excluded from posterior end angular suture turns ventrally and meets ventral border of mandible rostral to glenoid (1).
209. Laterally inclined flange along dorsal edge of surangular for articulation with lateral process of lateral quadrate condyle absent (0) or present (1).

210. Distal articular ends of metacarpals I + II ginglymoid (0) or rounded, smooth (1).
211. Radius and ulna well separated (0) or with distinct adherence or syndesmosis distally (1).
212. Kink and downward deflection in dentary buccal margin at rostral end of dentary: absent (0) or present (1).
213. Quadrate head covered by squamosal in lateral view (0) or quadrate cotyle of squamosal open laterally exposing quadrate head (1).
214. Brevis fossa poorly developed adjacent to ischial peduncle and without lateral overhang, medial edge of brevis fossa visible in lateral view (0), or fossa well developed along full length of postacetabular blade, lateral overhang extends along full length of fossa, medial edge completely covered in lateral view (1).
215. Vertical ridge on lesser trochanter present (0) or absent (1).
216. Supratemporal fenestra bounded laterally and posteriorly by the squamosal (0) or supratemporal fenestra extended as a fossa on to the dorsal surface of the squamosal (1).
217. Dentary fully toothed (0) or only with teeth rostrally (1) or edentulous (2).
218. Posterior edge of coracoid not or shallowly indented below glenoid (0), or posterior edge of coracoid deeply notched just ventral to glenoid, glenoid lip everted (1).
219. Retroarticular process points caudally (0) or curves gently dorsocaudally (1) (Kobayashi, 2001).
220. Flange on supraglenoid buttress on scapula (see Nicholls and Russell, 1985) absent (0) or present (1).
221. Depression (possibly pneumatic) on ventral surface of postorbital process of laterosphenoid absent (0) or present (1).
222. Basal tubera set far apart, level with or beyond lateral edge of occipital condyle and/or foramen magnum (may connected by a web of bone or separated by a large notch) (0) or tubera small, directly below condyle and foramen magnum, and separated by a narrow notch (1).
223. Basioccipital without pneumatization on occipital surface (0) or with subcondylar recess (1).
224. Ventral surface of dentary straight or nearly straight (0) or descends strongly posteriorly (1).
225. Distal humerus with small or no medial epicondyle (0) or with large medial epicondyle, medial condyle centered on distal end (1).
226. Distal humeral condyles on distal end (0) or on anterior surface (1).
227. Ilium and ischium articulation flat or slightly concavo-convex (0) or ilium with process projecting into socket in ischium (1).
228. Roots of dentary and maxillary teeth mediolaterally compressed (0) or circular in cross-section (1).

229. Preacetabular portion of ilium parasagittal (0) moderately laterally flaring (1) strongly laterally flaring (2).
230. Maxillary and dentary teeth labiolingually flattened and recurved, with crowns in middle of tooth row more than twice as high as the basal mesiolateral width (0) or lanceolate and subsymmetrical (1) or conical (2) or labiolingually flattened and recurved, with crowns in middle of tooth row less than twice as high as the basal mesiolateral width (fore–aft basal length) (3).
- 231.** Dentary teeth do not (0) or do increase in size anteriorly, becoming more conical in shape (1).
232. Length of skull more than 90% femoral length (0) or less than 80% (1).
233. Height of skull (minus mandible) at middle of naris more than half the height of skull at middle of orbit (0) or less than half (1).
234. Dorsal margin of naris below level of dorsal margin of orbit (0) or above (1).
235. Snout does not (0) or does taper to an anterior point (1).
236. Area of antorbital fenestra greater than that of orbit (0) or less than that of orbit (1).
237. Body of premaxilla dorsoventrally deep (0) or dorsoventrally shallow (1).
238. Antorbital fossa anteriorly bounded by maxilla (0) or by premaxilla (1).
239. Maxillary antorbital fossa: small, from 10% to less than 40% of the rostrocaudal length of the antorbital cavity (0), large, greater than 40% of the rostrocaudal length of the antorbital cavity (1).
240. Maxillary fenestra large and round (0), a large, craniocaudally elongate oblong (1), a small, craniocaudally elongate slit, not dorsally displaced (2), or a small, dorsally displaced opening (3).
241. Nasal fusion: absent, nasals separate (0) or present, nasals fused together (1).
242. Nasal surface: smooth (0) or rugose (1).
243. Suborbital process of jugal short and dorsoventrally stout (0) or elongate and dorsoventrally narrow (1).
244. Nasals at least as long as frontals (0) or shorter than frontals (1).
245. Anterior upturning of nasals absent (0) or present (1).
246. Jugo-maxillary bar at ventral end of antorbital fenestra dorsoventrally deep (0) or dorsoventrally narrow (1).
247. Anteroventral corner of premaxilla does not (0) or does form an acute, ventrally orientated point in lateral view (1).
248. Length of preorbital region of cranium > height at anterior edge of preorbital bar (exclusive of midline sagittal ridge, if any) (0) or ≤ height at anterior edge of preorbital bar (1).

249. Frontals without supraorbital rim (0) or with supraorbital rim (1).
250. Parietals shorter than frontals (0) or longer (1).
251. Length of ventral border of infratemporal fenestra comparable to that of orbit (0) or much shorter (1).
252. Foramen magnum smaller than or subequal to size of occipital condyle (0) or larger than occipital condyle (1).
253. Dentary not bowed (0) or bowed (concave dorsally) (1).
254. Meckelian groove of dentary deep (0) or shallow (1).
255. Dentary without posteroventral process extending to posterior end of external mandibular fenestra (0) or with such a process (1).
256. Horizontal shelf on the lateral surface of the surangular, rostral and ventral to the mandibular condyle: absent or faint ridge (0), prominent and extending laterally (1).
257. Premaxillary teeth subequal in size to (0) or much smaller than (1) the maxillary teeth.
258. Approximately the same number of denticles per 5 mm on mesial keels of teeth as on distal keels (0) or markedly more denticles per 5 mm on mesial keels (1).
259. Maxillary teeth subperpendicular to ventral margin of maxilla (0) or strongly inclined (1).
260. Dentary tooth implantation: in sockets (0), in paradental groove (1).
261. Dentary dentition continues cranially to tip of dentary (0) or terminates before reaching dentary tip (1).
262. Length of mid-cervical centra approximately the same as dorsal centra (0) or markedly longer than dorsal centra (1).
263. Cervical prezygapophyses unflexed (0) or flexed (1).
264. Dorsal centra $\geq 1.2 \times$ taller than long (0) or height \leq length (1).
265. Posterior dorsal neural spines $\geq 1.5 \times$ taller than long (0) or height $< 1.5 \times$ length (1).
266. Postzygapophyses of middle and posterior dorsal vertebrae do not extend posterior to centrum (0) or do (1).
267. Antermost haemal arches $\geq 1.5 \times$ longer than associated centra (0) or $< 1.5 \times$ as long as centra (1).
268. Angle between furcular arms $> 80^\circ$ (0) or $< 60^\circ$ (1).
269. Acromion process contacts coracoid (0), or reduced and does not contact coracoid (1).
270. Acromion process does not match any of the following descriptions: (0) rectangular with its dorsal edge forming a 90° angle with the dorsal edge of the scapular blade (1) or a quarter-circle in shape (2) or triangular, with apex pointing away from and subparallel to scapular blade (3).
271. Scapulocoracoid dorsal margin: pronounced notch between the acromion process and the

- coracoid (0) or margin smooth (1).
272. Wide distal expansion of scapula absent (0) or present (1).
273. Acrocoracoid process absent (0) or present (1).
274. Humeral length is half femoral length or less (0) or shorter than femur but more than half femoral length (1) or longer than femur (2).
275. Length of humeral shaft between deltopectoral crest and distal condyles $<4.5 \times$ shaft diameter (0) or $>4.5 \times$ shaft diameter (1).
276. Ulna not bowed away from humerus (0), or bowed away from humerus (1).
277. Length of radius $<1/3$ femoral length (0) or between $1/3$ and $2/3$ femoral length (1) or between $2/3$ and $1 \times$ femoral length (2) or $>$ femoral length (3).
278. Radial diameter $>0.5 \times$ ulnar diameter (0) or $\leq 0.5 \times$ (1).
279. Distal carpals 1+2 flattish (0) or semilunate in shape (1).
280. Length of manual digit II (including metacarpal) less than $1.25 \times$ femoral length (0) or $\geq 1.25 \times$ femoral length (1).
281. Distal end of metacarpal I medially (0) or laterally rotated (1).
282. Medial side of metacarpal II: expanded proximally (0), not expanded (1).
283. Metacarpal III $>0.8 \times$ length of metacarpal II (0) or $<0.8 \times$ (1).
284. Manual phalanx I-1 longer than metacarpal II (0) or shorter (1).
285. Length of metacarpal II $<$ length of metacarpal I + phalanx I-1 (0) or \geq (1).
286. Metacarpals II and III are not (0) or are appressed for their entire lengths (1).
287. Proximal end of metacarpal III is not (0) or is mainly palmar to that of metacarpal II (1).
288. Length of manual phalanx II-2 $<1.2 \times$ length of phalanx II-1 (0) or $>1.2 \times$ (1).
289. Medial ligament pits of manual phalanges deep (0) or shallow (1).
290. Posterior flange on manual phalanx II-1 absent (0) or present (1).
291. Combined lengths of manual phalanges II-1 and II-2 $>$ length of metacarpal II + carpus (0) or \leq length of metacarpal II + carpus (1).
292. Length of manual phalanx II-1 $<2 \times$ length of III-1 (0) or $\geq 2 \times$ length of III-1 (1).
293. Length of manual phalanx II-2 $<2 \times$ length of II-1 (0) or $\geq 2 \times$ (1).
294. Length of manual phalanx III-1, sub-equal to III-2 (0) or considerably longer (1) or considerably shorter (2). Modified.
295. Manual phalanx I-1 straight (0) or bowed (palmar surface concave) (1).
296. With proximal articular surface of ungual orientated vertically, dorsal surface of manual ungual I does not (0) or does arch higher than level of dorsal extremity of proximal articular surface (1).

297. With proximal articular surface of ungual orientated vertically, dorsal surface of manual ungual II does not (0) or does arch higher than level of dorsal extremity of proximal articular surface.
298. Manual ungual I strongly curved (0), weakly curved (1), or straight (2).
299. Manual unguals II and III strongly curved (0), weakly curved, (1), or straight (2).
300. Proximodorsal 'lip' on manual unguals II and III absent (0) or present (1).
301. Manual digit III with four phalanges (0) or less than four phalanges (1).
302. Manual phalanx III-3 markedly shorter than combined lengths of phalanges III-1 and III-2 (0), subequal in length to their combined lengths (1), or markedly longer (2).
303. Arching of preacetabular iliac blade above height of postacetabular blade absent or small (0) or extreme (1).
304. Shaft of ischium subequal in thickness to the pubis (0), slenderer than the pubic shaft (1), thicker than the pubic shaft (2).
305. Obturator process does not (0) or does form a strongly acute angle in lateral view (1).
306. Obturator process does not (0) or does reach tip of ischium (1).
307. Ventral notch between the distal portion of the obturator process and the shaft of the ischium: present (0), absent (1).
308. Strong kink of pubis at midshaft absent (0) or present, displacing distal half of pubis caudally (1).
309. In adult, femur longer than tibia (0) or shorter (1)
310. Tip of lesser trochanter below level of femoral head (0) or level with femoral head (1).
311. Proximolateral (fibular) condyle of the tibia, development in proximal view: bulge from the main surface of the tibia (0), conspicuous narrowing between the body of the condyle and the main body of the tibia (1).
312. Metatarsus less than half length of femur (0) or more than half femoral length (1) or longer than femur (2).
313. Metatarsal cross-sectional proportions: subequal or wider mediolaterally than craniocaudally at midshaft (0), deeper craniocaudally than mediolaterally at midshaft (1).
314. Shafts of metatarsals not appressed (0) or appressed (1).
315. Length of metatarsal V $\geq 0.5 \times$ length of metatarsal IV (0) or $< 0.5 \times$ (1).
316. Marked decrease in transverse width of metatarsus distally, absent (0) or present (1).
317. Plantar surface of hallux faces posteriorly (0) or hallux reorientated so that plantar surface faces medially or anteriorly (1).
318. Hallucal ungual reduced in size relative to other pedal unguals (0) or not reduced (1).
319. Hallucal ungual weakly curved (0) or strongly curved (1).

320. Length of pedal phalanx II-2 between $0.6 \times$ and $1 \times$ length of phalanx II-1 (0), $\leq 0.6 \times$, or $(1) \geq 1 \times (2)$.
321. Total length of pedal phalanx II-2 (not counting posteroventral lip, if any) $> 2 \times$ length of distal condylar eminence (0) or $\leq 2 \times (1)$.
322. Pedal phalanx II-2 without posteroventral lip or keel (0) with transversely wide posteroventral lip (1) with transversely narrow posteroventral keel (2).
323. Pedal phalanx II-1 without dorsal extension of distal condyles (0) or with extension (1).
324. Pedal unguals III and IV straight or weakly curved (0), or strongly curved (1).
325. With fingers extended, tip of ungual III extends no further distally than flexor tubercle of ungual II (0) or extends further (1).
326. Manual ungual III smaller than ungual II (0) or approximately the same size (1).
327. Diameter of non-ungual phalanges of manual digit III $> 0.5 \times$ diameter of non-ungual phalanges of digit II (0) or $< 0.5 \times (1)$.
328. Manual phalanx II-1 shorter than I-1 (0) or longer (1).
329. Ischial shaft rodlike (0) or flat, platelike (1).
330. Lateral face of ischial shaft flat (or round in rodlike ischia) (0) or laterally concave (1) or with longitudinal ridge dividing lateral surface into anterior and posterior parts (2).
331. Contact between pubic apron contributions of both pubes meet extensively (0) or contact interrupted by a slit (1) or no contact (2).
332. Dorsal margin of postacetabular iliac blade straight or convex (0) or concave (1).
333. Large, longitudinal flange along caudal or lateral face of metatarsal IV absent (0) or present (1).
334. Distally placed dorsal process along caudal edge of ischial shaft absent (0) or present (1).
335. Length of metatarsus $< 3.5 \times$ transverse midshaft diameter (0) or $3.5\text{--}8 \times$ midshaft diameter (1) or $> 8 \times$ midshaft diameter (2).
336. Lengths of mid-caudal centra subequal to or less than those of proximal caudal centra (0) or \geq twice as long as proximal caudal centra (1).
337. Pubic peduncle of ilium craniocaudally longer (0) or shorter (1) than ischial peduncle of ilium.
338. Phalanges of pedal digit III not blocky (proximal phalanx length $\geq 2 \times$ diameter) (0) or blocky (proximal phalanx length $< 2 \times$ diameter) (1).
339. Width of distal humeral expansion $< 1/3$ humeral length (0) or $\geq 1/3$ humeral length (1).
340. Lateral epicondyle of humerus not expanded laterally (0) or expanded laterally (1).
341. Distal end of metatarsal I reduced in size relative to distal ends of other metatarsals (0) or comparable in size to distal ends of other metatarsals (1).
342. Pedal phalanx II-1 longer (0) or shorter (1) than pedal phalanx IV-1.

343. Dentary ramus elongate (0) or shortened, not much longer than tall (1).
344. Metacarpal II $\geq 1/3$ humeral length (0) or $< 1/3$ humeral length (1).
345. With fingers extended, tip of unguis I does not extend past flexor tubercle of unguis II (0) or extends past flexor tubercle of unguis II but does not extend past tip of unguis II (1) or extends past tip of unguis II (2).
346. Premaxillary teeth serrated (0) or unserrated (1).
347. Sublacrimar process of jugal dorsoventrally expanded (taller than suborbital bar of jugal) (0) or not dorsoventrally expanded (1).
348. Flexor tubercles of manual unguis $\geq 1/3 \times$ height of articular facet (0) or $< 1/3$ (1).
349. Distal chevrons straight or L-shaped in lateral view (0) or upside-down T-shaped (1).
350. Metacarpal III distally not ginglymoid (0) or ginglymoid (1).
351. Breadth of acromion process perpendicular to long axis of scapular blade: deep (0) or shallow (1).
352. Proximal end of metatarsal IV curls around plantar side of proximal end of metatarsal III (0) or does not (1).
353. Midsagittal ridge formed by dorsal displacement of midline of frontals, nasals and premaxillae, absent (0) or present (1).
354. Ectopterygoid lateral to pterygoid (0) or rostral to pterygoid (1).
355. Palatine-ptyerygoid-ectopterygoid bar does not (0) or does (1) arch below ventral cheek margin.
356. Co-ossification of angular and surangular absent (0) or present (1).
357. Cervical ribs unfused to cervical vertebrae (0) or fused to cervical vertebrae (1).
358. Anterior caudal vertebrae without pneumatopores (0) or with pneumatopores (1).
359. External mandibular fenestra not rostrally displaced (sits beneath orbit) (0) or rostrally displaced (sits largely anterior to orbit) (1).
360. Ilium, pubic peduncle: substantially larger than (0) or subequal to (1) ischial peduncle.
361. Ischium, shape: distally narrower (0) or distally wider (1) (excluding obturator process).
362. Humerus, thickness relative to femur: much thinner (0) or subequal (1).
363. Promaxillary fenestra, exposure in lateral view: minimal (0) or significant (1).
364. Antorbital fossa, shape: anteroposterior diameter greater (0) or less (1) than dorsoventral diameter.
365. Antorbital fenestra, size relative to external naris: larger (0) or smaller (1).
366. Jugal, postorbital process, location: considerably anterior to the posterior end of the jugal (0) or nearly at the posterior end so that the quadratojugal process is minimal (1).
367. External mandibular fenestra, size: small (0) or large (1).

368. Dentary, dorsal margin: straight or concave (0) or convex (1) in lateral view.
369. Furcula, cross-section of lateral end: elliptical (0) or L-shaped (1).
370. Ilium, preacetabular process: deep (0) or shallow (1).
371. Dentary, ventral margin: straight or convex (0) or concave (1).
372. Lacrimal, posterodorsal process, orientation: subvertical (0) or posteriorly inclined (1)
373. Anterior caudal vertebrae, transverse processes, distal tapering: absent (0) or present (1).
374. Lacrimal, anterior process, extending anteriorly to interfenestral bar: absent (0) or present (1).

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Oviraptor_philoceratops

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Conchoraptor_gracilis

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Chiostenotes_pergracilis

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