

LETTERS

A gigantic bird-like dinosaur from the Late Cretaceous of China

Xing Xu¹, Qingwei Tan², Jianmin Wang³, Xijin Zhao¹ & Lin Tan²

An evolutionary trend of decreasing size is present along the line to birds in coelurosaurian theropod evolution^{1,2}, but size increases are seen in many coelurosaurian subgroups, in which large forms are less bird-like^{2,3}. Here we report on a new non-avian dinosaur, *Gigantoraptor erlianensis*, gen. et sp. nov., from the Late Cretaceous Iren Dabasu Formation of Nei Mongol, China. Although it has a body mass of about 1,400 kg, a phylogenetic analysis positions this new taxon within the Oviraptorosauria, a group of small, feathered theropods rarely exceeding 40 kg in body mass^{2,4–7}. A histological analysis suggests that *Gigantoraptor* gained this size by a growth rate considerably faster than large North American tyrannosaurs such as *Albertosaurus* and *Gorgosaurus*⁸. *Gigantoraptor* possesses several salient features previously unknown in any other dinosaur and its hind limb bone scaling and proportions are significantly different from those of other coelurosaurs^{9,10}, thus increasing the morphological diversity among dinosaurs. Most significantly, the gigantic *Gigantoraptor* shows many bird-like features absent in its smaller oviraptorosaurian relatives, unlike the evolutionary trend seen in many other coelurosaurian subgroups^{2,3}.

Theropoda Marsh, 1881

Oviraptorosauria Barsbold, 1976

Gigantoraptor erlianensis gen. et sp. nov.

Etymology. The generic name refers to the animal being a gigantic raptor dinosaur; the specific name is derived from the Erlian basin where the holotype was collected.

Holotype. LH V0011, an incomplete skeleton preserving a nearly complete mandible, several partial presacral vertebrae, most caudal vertebrae, nearly complete right scapula, much of the forelimbs, partial ilium, and nearly complete pubes and hind limbs.

Type locality and horizon. Saihangaoobi, Sunitezuoqi, Nei Mongol Autonomous Region. Iren Dabasu Formation, Senonian, Late Cretaceous¹¹.

Diagnosis. An oviraptorosaur distinguishable from other species in the following features: a short mandible less than 45% of femoral length, a fossa on the lateral surface of the dentary close to the anterior end and a second fossa bounded dorsally by a lateral flange anterodorsal to the external mandibular fenestra, a long posteroventral process of the dentary extending to the level of the glenoid, a small, posteriorly tapered retroarticular process much deeper than wide, a tail composed of opisthocoeleous anterior caudal vertebrae, amphicoeleous middle ones and procoeleous posterior ones, pleurocoels present on most caudal vertebrae, a pair of vertically arranged pneumatic openings present on the lateral surface of anterior caudal centra, a large pneumatic opening present on the ventral surface of anterior and middle caudal centra, anterior caudal vertebrae with tall neural spines (about three times as tall as wide) and robust and rod-like transverse processes located posteriorly, posteroventral margin of anterior caudal centra

extending considerably ventrally, well-developed laminal system on the anterior caudal vertebrae (prespinal, postspinal, spinopostzygapophyseal, anterior centrodiapophyseal, posterior centrodiapophyseal, and prezygodiapophyseal laminae present on anterior caudal vertebrae), middle caudal vertebrae with vertical prezygapophyseal articular facets located proximal to the distal extremity of the process, a prominent convexity ventral to the acromion process on the lateral surface of the scapula, a laterally bowed humerus with a prominent, spherical humeral head and a strongly medially curved deltopectoral crest, a centrally constricted thick ridge running along the posterior margin of the proximal half of the humerus, a straight ulna with a sub-circular, concave proximal articular surface, a radius with a sub-spherical distal end, metacarpal I with a slightly convex medial margin of the proximal end and a medial condyle three times as high as and extending much more distally than the lateral one on the distal end, a metacarpal II with a prominent dorsolateral process on the proximal end and a longitudinal groove on the ventral margin of the proximal third of the shaft, manual unguals with a triangular set of lateral grooves, a laterally compressed pubis, a femur with a straight shaft, a constricted neck between the posteromedially oriented, spherical femoral head and the anteroposteriorly wide trochanteric crest which is much more robust and higher anteriorly than posteriorly, a distinct narrow groove medial to the trochanteric crest extending down the posterior margin of the femoral shaft, and a patellar groove present on the anterior surface of the distal end, a small calcaneum obscured from anterior view by the wide astragalar main body, a proximal projection on the lateral margin of distal tarsal IV, metatarsal III with ginglymoid distal end, and pedal unguals with two lateral grooves and a constricted proximal articular surface (Fig. 1b–g, i–t).

Description and comparison. The *Gigantoraptor* holotype is estimated to be 8 m in total length and 3.5 m high at the hip (Fig. 1a) and to be about 1,400 kg in body mass (see Supplementary Information). The mandible is intermediate in morphology between basal oviraptorosaurs and highly specialized oviraptorids^{12–15}: the mandible is comparable to that of *Oviraptor philoceratops* in relative depth, the mandibular symphysis is U-shaped with an extended shelf, the large external mandibular fenestra is relatively shallow and is located more anteriorly than in basal oviraptorosaurs but less so than in oviraptorids, the dentary is edentulous, dorsoventrally deep, and posteriorly bifurcated, the coronoid region is high but lacks a dorso-medially extended surangular process, the surangular lacks a anterior projection to divide the external mandibular fenestra and is not as enlarged as in oviraptorids, and the glenoid articulation is convex in lateral view and expanded transversely (Fig. 1b, c). As in Caenagnathidae^{13,15}, the mandibular symphysis is completely fused without any trace of suture (Fig. 1c).

Postcranially, *Gigantoraptor* also displays numerous derived similarities seen in the Oviraptorosauria or its more exclusive

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groups^{12,13,16}: a deep groove present on the ventral surface of the caudal vertebral centra, short middle and posterior caudal vertebrae with dorsoventrally compressed centra, ventrally located transverse processes present on the posterior caudal vertebrae, caudal neural arches positioned on the anterior half of the respective centra, a radius as long as the ulna, and a pubis with a concave anterior margin. Like other oviraptorosaurs^{12,13}, the caudal vertebrae are pneumatic, but in a previously unknown manner: the anterior caudal vertebrae bear a pair of vertically arranged pneumatic foramina on the central lateral surface (Fig. 1d) and a large pneumatic opening on the central ventral surface (Fig. 1g). Interestingly, despite a lack of pneumatic opening, the posterior caudal centra have spongy internal structures (Fig. 1h), superficially similar to those of the sauropod group Titanosauria, a feature probably related to weight saving¹⁷.

However, *Gigantoraptor* exhibits many features that are not seen in other oviraptorosaurians but do occur in more derived

maniraptorans^{2,3,18,19}. The anterior caudal centra are wider transversely than deep dorsoventrally. The scapular blade is shallower distally without an expanded distal end. The forelimbs are proportionally long, with a humerus+radius+metacarpal II to femur+tibiotarsus+metatarsal III ratio of 0.60. The radius bears a sub-spherical distal end. Metacarpal I is less than one-third the length of metacarpal II and the latter is much more robust than the former (Fig. 1n). The pubis is laterally compressed and straplike for most of its length, though a long pubic symphysis is present. The femur is avian-like in having a spherical femoral head with a distinct neck, a high and prominent trochanteric crest much thicker and higher anteriorly than posteriorly (Fig. 1q), a shallow popliteal fossa distally bounded by a low shelf, and lacks a fourth trochanter. The tibia has a lateral margin subequal in depth to the medial margin on the distal end. The astragalar main body extends laterally to hide the small calcaneum from anterior view (Fig. 1s). A distinct proximal projection is present on

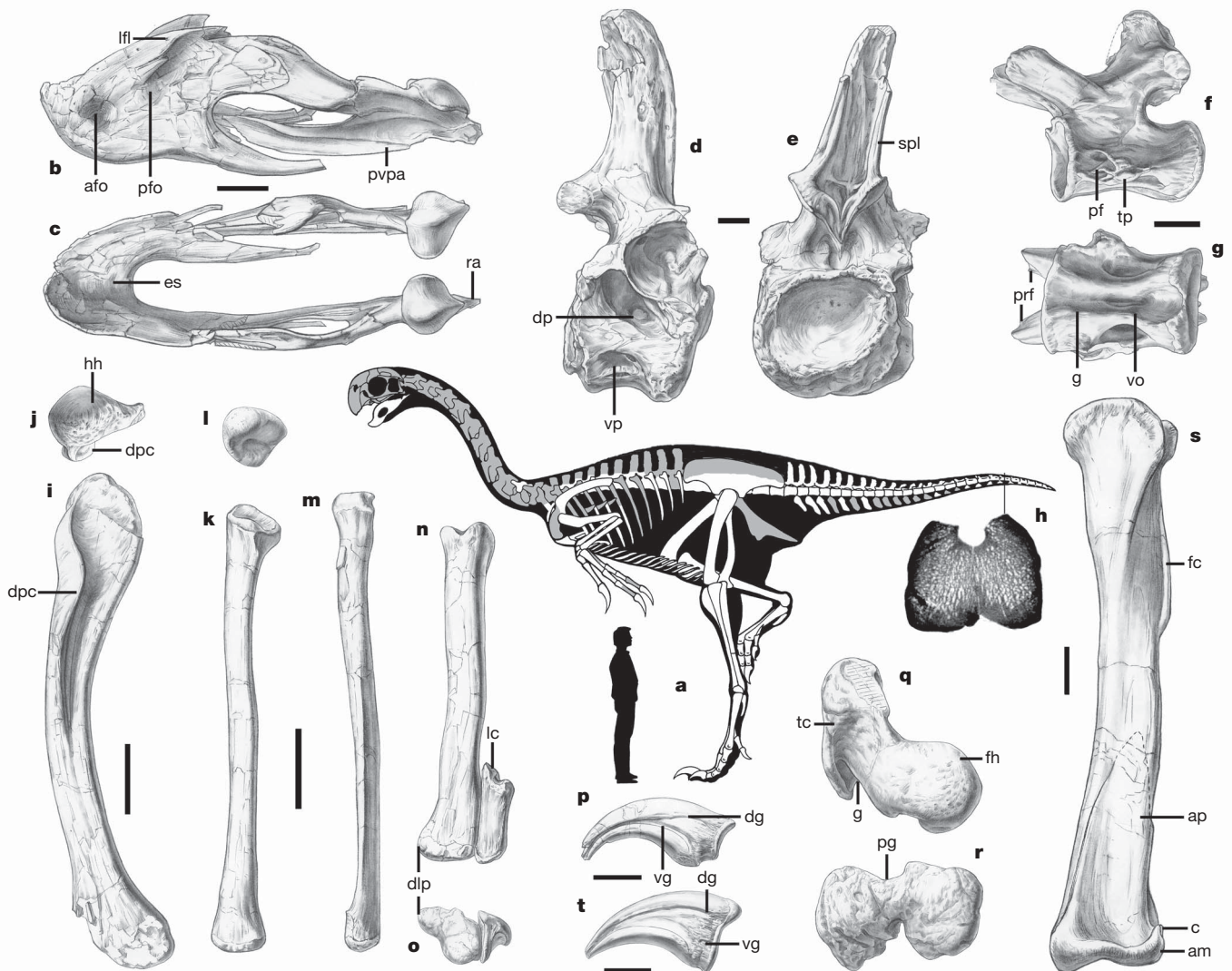


Figure 1 | Skeletal anatomy of *Gigantoraptor* holotype (LH V0011).

a, Skeletal reconstruction showing preserved elements, with a 175-cm-tall man for a scale. Bones are: mandible in lateral (**b**) and dorsal (**c**) views; anterior caudal vertebra in lateral (**d**) and posterior (**e**) views; middle caudal vertebra in lateral (**f**) and ventral (**g**) views; computed tomographic scan of a posterior caudal vertebral centrum showing the spongy internal structure (**h**); left humerus in anterior (**i**) and proximal (**j**) views; left ulna in anterior (**k**) and proximal (**l**) views; left radius in anterior view (**m**); left metacarpals I and II in anterior (**n**) and proximal (**o**) views; manual ungual in lateral view (**p**); right femur in proximal view (**q**) and left femur in distal view (**r**); left tibiotarsus in anterior view (**s**); pedal ungual in lateral view (**t**). Scale bars in

b, **c**, and **p**, 5 cm, in **d–f**, **g**, **n**, and **t**, 3 cm, and in **i**, **k**, **m**, and **s**, 10 cm. Abbreviations: afo, anterior fossa; am, astragalar main body; ap, ascending process; c, calcaneum; dg, dorsal groove; dlp, dorsolateral process; dp, dorsal pneumatic foramen; dpc, deltopectoral crest; es, extended shelf; fc, fibular crest; fh, femoral head; g, groove; hh, humeral head; lc, lateral condyle; lfi, lateral flange; pf, pneumatic foramen; pfo, posterior fossa; pg, patellar groove; prf, prezygopophysial articular facet; pvpa, articular facet for posteroventral process of dentary; ra, retroarticular process; spl, spinopostzygopophysial lamina; tc, trochanteric crest; tp, transverse process; vg, ventral groove; vo, ventral opening; vp, ventral pneumatic foramen.

the lateral margin of tarsal IV and metatarsal III is ginglymoid distally.

Histological analysis. We have conducted a histological analysis to determine the longevity, developmental stage, and growth strategy for the *Gigantoraptor* holotype (see Supplementary Information). A mid-diaphyseal petrographic thin section was made from the fibula. Although the medullary cavity is very small, the secondary osteons obliterate partial growth record in the inner cortex. A retrocalculation was thus made to assess the missing ages^{20,21}. We calculated the number of the missing annual intervals by using the average width of the innermost three growth zones to divide the distance in question, which resulted in four years missing. The presence of seven sets of lines of arrested growth (LAGs) and the calculated four missing zones suggest that the *Gigantoraptor* holotype probably died during its eleventh year of life (Fig. 2).

The animal is inferred to be adult, as indicated by the extensive development of the secondary osteons, a moderate decrease in spacing between LAGs close to the periphery of the bone, and the presence of the outer circumferential layer comprising of a poorly vascularized layer of lamellar bone which indicates a slow rate of bone accretion²⁰. Interestingly, the fourth to seventh sets of LAGs, which are within the outer circumferential layer, are not tightly packed as in a typical outer circumferential layer. We thus infer that the animal reached its young adult size within seven years and was still at relatively early young adult stage at the time of death and estimate that a full-sized *Gigantoraptor* is considerably heavier than 1,400 kg. This suggests that *Gigantoraptor* has an accelerated growth rate faster than most other theropods, including large North American tyrannosaurs such as *Albertosaurus* and *Gorgosaurus*⁸, a growth strategy seen in most gigantic dinosaurs^{21,22}.

Discussion. As an oviraptorosaurian, *Gigantoraptor* is remarkable in its gigantic size (see Supplementary Information), about 300 times as heavy as basal oviraptorosaurians *Caudiperyx* and *Protarchaeopteryx*^{6,23,24}, species known to bear pennaceous arm feathers and other types of feathers as well. A size disparity so dramatic might cause a change of integumentary coverings, such that large-sized forms lose filamentous integuments for insulation, as is the case in some mammals²⁵ and is inferred for the tyrannosaurs²⁶. But *Gigantoraptor* might have at least retained arm feathers or their homologues from its ancestors, if not other types of feathers, given that the primary function of arm feathers is not to insulate the individual and their development is probably not related to size (see Supplementary Information).

Phylogenetic analysis posits *Gigantoraptor* at the base of the Oviraptoridae (see Supplementary Information), a hypothesis supported mainly by its mandibular morphology, intermediate between basal oviraptorosaurian and derived oviraptorid conditions^{13,16,27}.



Figure 2 | Photograph of transverse thin section of the fibular mid-shaft of *Gigantoraptor* holotype (LH V0011) under a polarized scope. The section shows seven sets of single, paired, or grouped LAGs. Paired or grouped LAGs are seen in some non-avian and avian dinosaurs, some mammals and some ectothermic vertebrates²⁰.

Table 1 | Relative proportions of selected limb elements in oviraptorosaurs and some large theropods

Taxa	Femur circumference/femur length	Tibiotarsus length/femur length	Metatarsus length/femur length
<i>Gigantoraptor</i> (femur length: 110 cm)	0.32	1.07	0.53
Oviraptorids (femur length: 15–30 cm)	0.34	1.23	0.55
Tyrannosauroids (femur length: 100–120 cm)	0.39	0.90	0.54
Carnosaurs and ceratosaurs (femur length: 100–120 cm)	0.40	0.86	0.39

Data were collected from original specimens or published literature^{9,10,30}.

This intermediate systematic position is consistent with its geological age-Senonian, which is earlier than any other oviraptorids are known^{13,16,27}.

Gigantoraptor possesses a large number of autapomorphies (see ‘Diagnosis’ section), indicating that it represents a highly specialized lineage in oviraptorosaurian evolution. In particular the presence of many features unknown in any other dinosaur, such as the highly specialized caudal vertebrae and the bizarre humerus, suggests that morphological diversity among the dinosaurs is higher than previously known. This is further indicated by *Gigantoraptor*’s unusual limb allometry. Among theropods, the tibiotarsus and metatarsus show negative allometry relative to the femur when size increases^{9,28} and limb circumference scales to limb length¹⁰, though other factors, including phylogeny, contribute to the relative proportions and robustness of the limb elements as well⁹. A comparison of the femur circumference-to-length ratio, tibiotarsus-to-femur length ratio and metatarsus-to-femur length ratio values in *Gigantoraptor* and oviraptorids indicates that *Gigantoraptor* has values similar to those in its much smaller relatives (Table 1) and significantly different from theoretically predicted ones^{9,10,28}. This is inconsistent with a general pattern that large-sized members of non-avian theropod sub-groups have proportionally stouter limbs and shorter lower legs than their small-sized relatives⁹. Compared with other similar-sized theropods including tyrannosauroids, *Gigantoraptor* has much more slender limbs and longer lower legs as indicated by the femur circumference-to-length ratio, tibiotarsus-to-femur length ratio and metatarsus-to-femur length ratio values (Table 1), suggesting that it might be the most cursorial theropod of comparable size.

Gigantoraptor is an exception to some general patterns seen during the gigantism of non-avian theropods. Contrary to the evolutionary trend of size decrease in coelurosaurian evolution¹², which plays a key part in the origin of birds^{2,3,29}, most non-avian coelurosaurian subgroups display a trend of size increase and their large-sized members tend to reverse to more primitive conditions in many bird-like characters^{2,3}. The discovery of *Gigantoraptor* complicates this pattern, however. Although much larger than its close relatives, *Gigantoraptor* has proportionally the longest forelimb among oviraptorosaurs^{6,12,13}, a manus resembling basal eumaniraptorans, bird-like hind limbs, and many other advanced features. These features are close to the conditions in birds but absent in other smaller oviraptorosaurs¹³, indicating an unusual pattern for the Oviraptorosauria among the non-avian coelurosaurian subgroups.

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

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1. Estimation of longevity, body mass and growth rate
2. Size comparison of *Gigantoraptor* and other dinosaurs
3. Feather development in *Gigantoraptor*.
4. Bird-like features in *Gigantoraptor*.
5. Cladistic analysis

1. Estimation of longevity, body mass and growth rate

Histological methods are now widely used to estimate the longevity of extinct vertebrate¹. The most common method is aging the animal by counting the LAGs, which are observable directly on the cross section of analyzed bones. In some cases, LAGs formed in relatively early ontogenetic stage were resorbed and a retro-calculation is needed to estimate the missing ages. There are several different ways to assess the missing LAGs², which result slightly different numbers of missing ages. We observed 7 sets of LAGs on the cross section of the fibula of *Gigantoraptor* holotype. In regard to the estimation of the missing ages, we used a traditional method which averages the innermost three growth zones (Erickson, personal communication) to divide the distance in question on the cross section of the analyzed element and resultant missing ages are 4 years. This suggests that *Gigantoraptor* holotype died at the 11th year of life and had a averaged growth rate of 128-140 kg per year.

We estimate that *Gigantoraptor* holotype is about 1400000g based on the equation³: $W=0.16*C_f^{2.73}$ (minimum femoral circumference of *Gigantoraptor* is 349 mm).

2. Size comparison between *Gigantoraptor* and other dinosaurs.

In general coelurosaurs are small or medium sized dinosaurs, yet there are several gigantic species, including the possible ornithomimosaur *Deinocheirus mirificus*, the therizinosaur *Therizinosaurus cheloniformis*, and several species of the Tyrannosauoidea. These species are comparable to or even larger than *Gigantoraptor* in size, but are much less bird-like in general built than is *Gigantoraptor*. Within the Iren Dabasu Fauna⁴, the largest known theropod is the tyrannosauroid *Alectrosaurus*, which has a tibia of about 60% of the length of *Gigantoraptor*'s tibiatarsus; the largest known ornithischian is the hadrosaurid *Gilmoreosaurus mongoliensis*, the tibia length of which is less than 70% of that of *Gigantoraptor*; the only known sauropod *Sonidosaurus* is small in size in sauropod standard, but is slightly larger than *Gigantoraptor*. *Gigantoraptor* is clearly the largest known theropod from the fauna and comparable to or even larger than the largest members of other dinosaurian groups in the Iren Dabasu Fauna.

3. Feather development in *Gigantoraptor*.

The evidence supporting the presence of feathers on arms and tail of *Gigantoraptor* is mainly derived from the fact that basal oviraptorosaurs bear pennaceous feathers on their arms and tail⁵. There is no persuasive evidence to expect a loss of arm and tail feathers in the gigantic *Gigantoraptor* as in some large mammals and possibly tyrannosaurs⁶ because arm and tail feathers' primary function is not insulating the individual and their development is probably less affected by large size. Additional indirect evidence for the presence of feathers on *Gigantoraptor* comes from oviraptorosaur's brooding behavior. There is direct fossil evidence supporting the presence of bird-like brooding behavior in oviraptorosaurs⁷. The arm feathers are suggested to be used to brood the nest⁸ in oviraptorosaurs. If *Gigantoraptor* retains this behavior from its ancestry and the Hopp and Orsen's hypothesis holds true, *Gigantoraptor* would be expected to bear feathers on its arms. Nevertheless, the

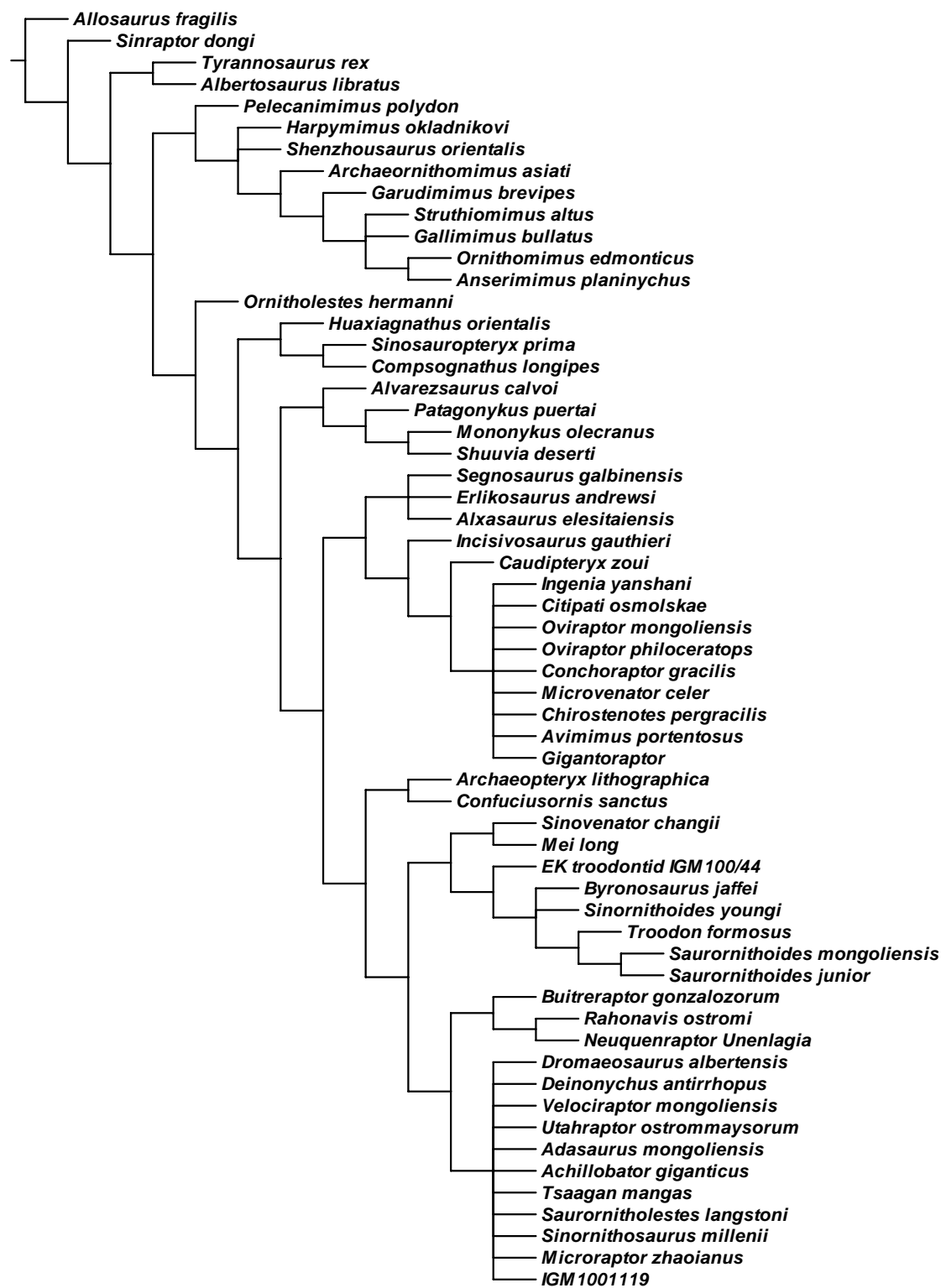


Figure 1. Phylogenetic hypothesis of relationships of *Gigantoraptor* to other coelurosaurs.

We further investigated the systematic position of *Gigantoraptor* by coding *Gigantoraptor* and *Incisivosaurus* into a recently published dataset on oviraptorosaurian phylogeny¹³. The scorings are as follows:

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Incisivosaurus      ?0100010110000000?0110?011001?00?0000?10011????2011
11111100100001110000?2101?002??000110???????010-----
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Gigantoraptor      ?????????????????????????????????????????????????
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?????1??1111111000?0?

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The data matrix was analyzed using the NONA (ver 2.0) software package¹¹ and formatting and character exploration was performed in WinClada¹². The analysis protocol consisted of 1000 Tree Bisection and Regrafting tree searches followed by branch swapping. Settings included collapsing unsupported branches and counting all states in polymorphic codings. Other settings including the character ordering follow ref. 13. The analysis resulted in 13 equally parsimonious trees with a length of 284 steps. These trees have a CI of 0.67 and an RI of 0.69. Figure 2 shows the strict consensus tree of these trees. *Gigantoraptor* is systematically intermediate between basal oviraptorosaurs and other oviraptorids. Basal oviraptorosaurs have proportionally longest lower legs among theropods, but those of the slightly larger Oviraptoridae are proportionally much shorter, suggesting a change in locomotory style. Interestingly, the gigantic *Gigantoraptor* appear to be grouped with basal oviraptorosaurs rather than with other oviraptorids in terms of limb proportions.

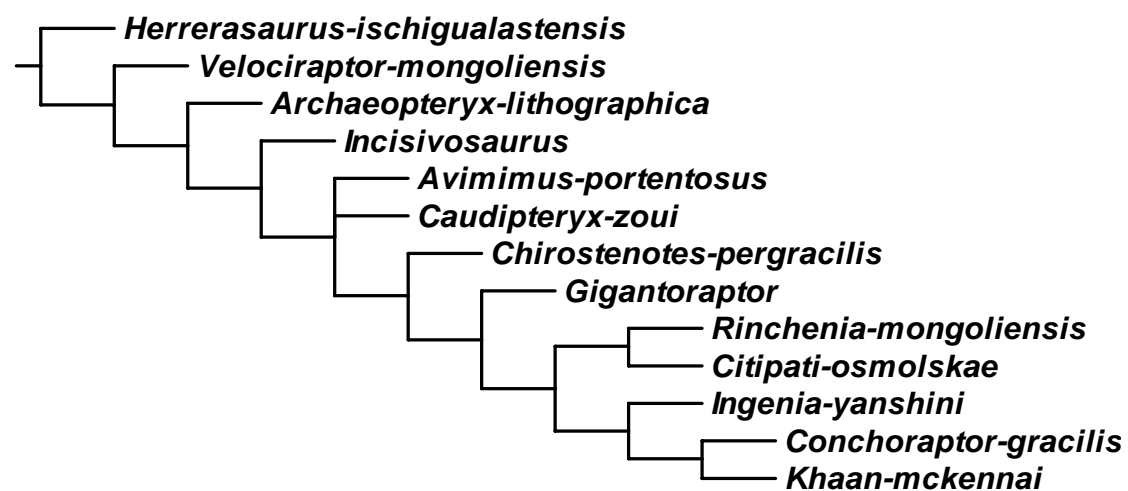


Figure 2. Phylogenetic hypothesis of relationships of *Gigantoraptor* to other oviraptorosaurs.

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