

A basal tyrannosauroid dinosaur from the Late Jurassic of China

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The tyrannosauroid fossil record is mainly restricted to Cretaceous sediments of Laurasia, although some very fragmentary Jurassic specimens have been referred to this group^{1,2}. Here we report a new basal tyrannosauroid, *Guanlong wucaii* gen. et sp. nov., from the lower Upper Jurassic of the Junggar Basin^{3,4}, northwestern China. *G. wucaii* is the oldest known tyrannosauroid and shows several unexpectedly primitive pelvic features^{5,6}. Nevertheless, the limbs of *G. wucaii* share several features with derived coelurosaurs^{7–9}, and it possesses features shared by other coelurosaurian clades¹⁰. This unusual combination of character states provides an insight into the poorly known early radiation of the Coelurosauria. Notably, the presumed predatory *Guanlong* has a large, fragile and highly pneumatic cranial crest that is among the most elaborate known in any non-avian dinosaur and could be comparable to some classical exaggerated ornamental traits among vertebrates.

Theropoda Marsh, 1881

Coelurosauria von Huene, 1914

Tyrannosauroida Osborn, 1905

Guanlong wucaii gen. et sp. nov.

Etymology. The generic name is derived from the Chinese *Guan* (crown) and *long* (dragon); the specific name is from the Chinese *wucui* (five colours), which refers to the rich colours of rocks that produced the specimens.

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V14531 is a partly articulated skeleton preserving most of the elements.

Referred material. IVPP V14532 is much smaller than the holotype and is a fully articulated, nearly complete skeleton.

Locality and horizon. Wucaiwan area, Junggar Basin, Xinjiang; Oxfordian upper part of the Shishugou Formation^{3,4}.

Diagnosis. Medium-sized tyrannosauroid with the following autapomorphies: a deep and narrow groove along the anterior margin of the premaxilla; a distinct opening on the maxilla close to the premaxilla–maxilla contact; a complex, highly pneumatic nasal crest; a low, rugose ridge along the midline of the frontals; a dorsally flattened parietal with two parallel sagittal crests; a transverse ridge within the supratemporal fossa; a centropostzygapophyseal lamina on cervicodorsal vertebrae with its dorsal end expanding laterally; deep, longitudinal sulci on both ventral and dorsal surfaces of the distal caudal vertebrae (independently evolved in troodontids⁸); ventral part of scapular blade with sub-equilateral triangular cross-section and thick posterior margin; metacarpal II with prominent medioventral and laterodorsal processes proximally; manual phalanx II-2 with prominent medioventral process proximally; femoral greater trochanter much narrower anteroposteriorly than the lesser trochanter; distinct fossa on posterodistal surfaces of astragalus and

calcaneum; and pedal phalanx II-1 with prominent paired ventral processes proximally (Figs 1 and 2a, b; see also Supplementary Figs 1 and 2).

Both specimens (holotype and referred specimen) were collected from a tabular bed of finely laminated to massive, tan-coloured, tuffaceous mudstone, with characteristics indicating a paludal (wetlands) setting. Their preservational features indicate that IVPP V14532 died *in situ*, was possibly trampled at a later date by IVPP V14531, and was buried before subaerial disarticulation, and that IVPP V14531 was subaerially exposed for a significant time after death (see Supplementary Information for further analysis).

Description. The total body length of the *Guanlong* holotype is about 3 m. As in *Dilong*^{11,12}, a horizontal ridge is present along the ventral margin on the external surface of the jugal, the descending process of the squamosal is extremely long, and the posterior serrations are larger than the anterior ones on lateral teeth (also independently evolved in dromaeosaurids¹³). As in *Dilong*^{11,12} and alvarezsaurids, a row of foramina is located within a sharply defined groove on the external surface of the dentary. In troodontids, a similar groove is present, but is much wider and more ventrally positioned¹⁴. The most striking feature of *Guanlong* is a complex nasal crest consisting of a highly pneumatic median crest that is about 1.5 mm thick for most of its length, and four supporting lateral laminae. The mandible of *Guanlong* displays a relatively large external mandibular fenestra, an extremely weak surangular ridge and appears to lack a surangular foramen.

The cervical vertebrae are amphicoelous, with the anterior ones bearing axially long neural spines. The dorsal and sacral centra lack pneumatic openings.

The relative lengths of the forelimb and its components are similar to those of derived coelurosaurs^{8,9}, but are much longer than those of other tyrannosauroids^{1,15}. The length of the forelimb is only slightly less than 60% of the hindlimb length. The length of the humerus is more than 60% of the femoral length. The ulna and manus (which has a phalangeal formula of 2-3-4; Fig. 2d) are about 80% and 140% of the humeral length, respectively. Also similar to some derived coelurosaurs is the posteriorly bowed ulna and distally flattened radius with a slightly hooked and round distal margin^{7–9}. A tiny splint of bone attached to the proximal part of metacarpal III might represent a reduced metacarpal IV (Fig. 2d; see also Supplementary Fig. 2f), a feature also reported in *Ornitholestes*¹⁶ among the Coelurosauria. A distal carpal possesses a transverse trochlea proximally and a semilunate shape in ventral view (Fig. 2d; see also Supplementary Fig. 2f, g), representing the first known ‘semilunate’ carpal in an adult tyrannosauroid specimen¹. Interestingly, its position (mainly contacting metacarpal I) is similar to the condition in *Allosaurus*¹⁷ and oviraptorosaurs, whereas in therizinosauroids¹⁸, troodontids,

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dromaeosaurids and basal birds⁹ it primarily articulates with metacarpal II. The latter condition is also consistent with some embryonic evidence from extant birds¹⁹. This suggests that a semilunate shape may have evolved on different carpals in different theropod groups, and thus caution should be used in identifying a semilunate carpal in phylogenetic analyses owing to uncertainties regarding homology.

The ilia are moderately inclined towards the midline but do not contact. The dorsal part of the pubis narrows to a thin sheet of bone posteriorly, which might be pierced by an obturator foramen (Fig. 2e). A relatively large foramen pierces the extremely thin sheet of bone on the anterodorsal part of the ischium, which is continuous with the thin sheet of bone down the shaft. Pedal digit I is attached to the posterior margin of metatarsal II (Fig. 2f), indicating a partially reversed hallux (see additional description in Supplementary Information).

A histological analysis was conducted to determine the longevity and developmental stages for the specimens. The results suggest that IVPP V14531 reached full adult size in 7 years and was a relatively old, late stationary stage individual at the time of death in its twelfth year of life (Fig. 2g). IVPP V14532 appears to have died during its sixth year of life. This animal was still actively growing and was in the exponential stage of development, as indicated by the same degree of

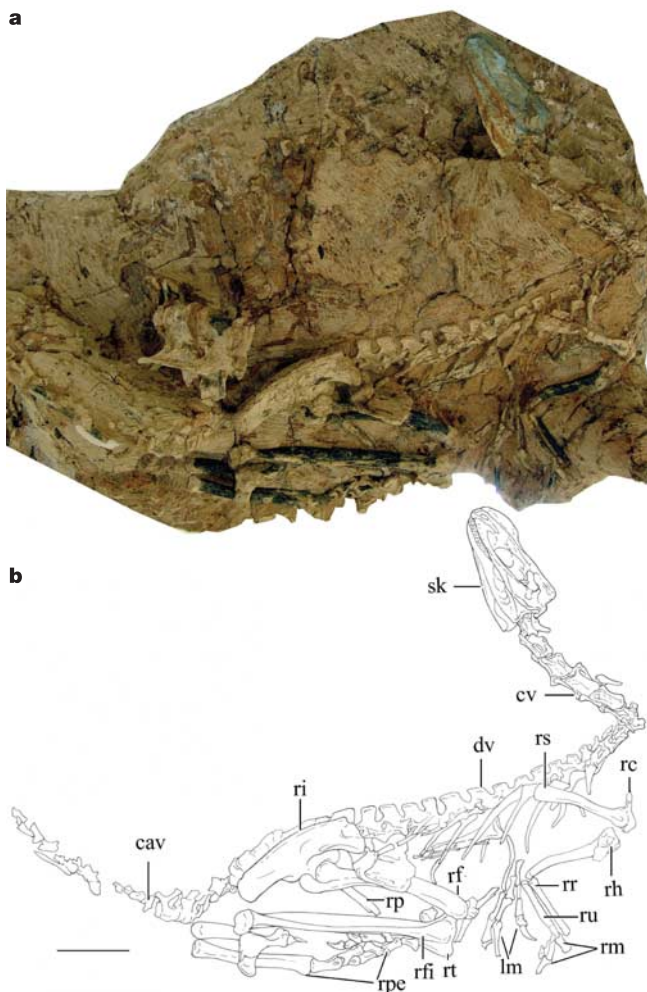


Figure 1 | *Guanlong wucaii* (IVPP V14532). **a**, Photograph, **b**, Line drawing of IVPP V14532. cav, caudal vertebrae; cv, cervical vertebrae; dv, dorsal vertebrae; lm, left manus; rc, right coracoid; rf, right femur; rfi, right fibula; rh, right humerus; ri, right ilium; rm, right manus; rp, right pubis; rpe, right pes; rr, right radius; rs, right scapula; rt, right tibia; ru, right ulna; sk, skull. Scale bar, 8 cm.

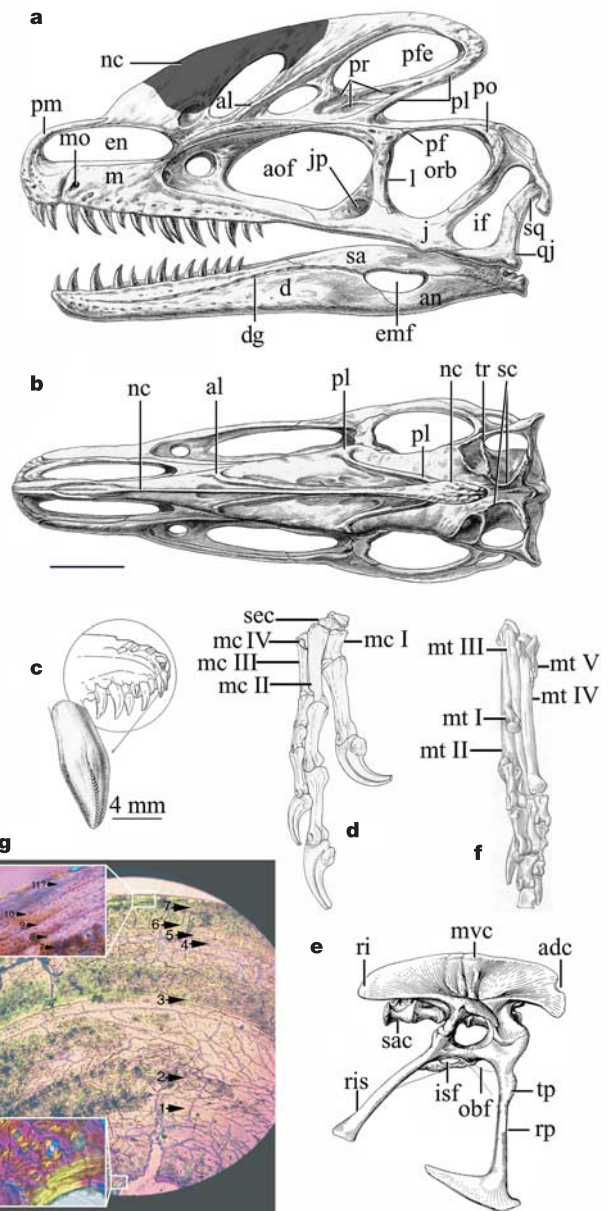


Figure 2 | *Guanlong wucaii* (IVPP V14531). **a**, **b**, Cranial reconstruction in left lateral (**a**; shaded area indicates the unpreserved portion) and dorsal (**b**) views. **c**, Close up of a premaxillary tooth. **d**, Ventral view of left manus. **e**, Pelvis in right lateral view. **f**, Ventral view of left pes. **g**, Histological section from the fibular shaft of *Guanlong wucaii* (IVPP V14531), shown in polarized microscopy (original magnification $\times 6.5$). Numbers and arrows denote growth lines used to age the specimen (see Supplementary Information for a detailed explanation). adc, anterodorsal concavity; al, anterior lamina; an, angular; aof, antorbital fenestra; d, dentary; dg, dentary groove; emf, external mandibular fenestra; en, external naris; if, infratemporal fenestra; isf, foramen on ischium; j, jugal; jp, pneumatic jugal foramen; l, lacrimal; m, maxilla; mc I–IV, metacarpals I–IV; mt I–V, metatarsals I–V; mvc, median vertical crest; nc, nasal crest; obf, obturator foramen; orb, orbit; pf, prefrontal; pfe, pneumatic fenestra; pl, posterior lamina; pm, premaxilla; po, postorbital; pr, pneumatic recess; qj, quadratojugal; ri, right ilium; rs, right ischium; rp, right pubis; sa, surangular; sac, sacrum; sc, sagittal crest; sec, semilunate carpal; sq, squamosal; tp, tubercle on pubis; tr, transverse ridge. Scale bar: 5 cm (**a**, **b**), 7 cm (**d**), 12 cm (**e**) and 8 cm (**f**).

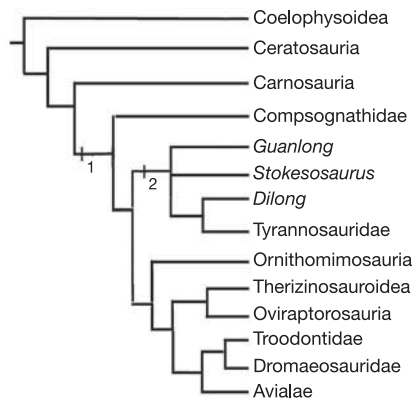


Figure 3 | A simplified cladogram representing an Adams consensus of 6,336 most parsimonious trees showing the phylogenetic position of *Guanlong wucaii* (see Supplementary Information for a detailed analysis). Reduced consensus analysis demonstrates that *Guanlong* is outside of the Tyrannosauridae–*Dilong* clade on all trees, but the position of *Stokesosaurus* is unstable (see Supplementary Information). 1, Coelurosauria; 2, Tyrannosauroidae. Bootstrap value (90%) is high for the Tyrannosauroidae including *Guanlong wucaii*.

vascularization throughout the cortices, broad spacing between growth lines near the periosteal surface, the presence of only a thin, single lamellae of endosteal bone, and just several haversian canals^{20,21} (see Supplementary Information for a more detailed explanation).

Compared to IVPP V14531, IVPP V14532 has a proportionally shorter snout, a shorter pre-antorbital ramus of the maxilla with a less distinct step, a larger orbit, a dorsoventrally taller quadrate, apicobasally shorter teeth, a longer manus relative to the humerus, a longer pubis with a less-developed anterior expansion of the pubic boot, a longer distal segment of the hindlimb, and a slightly posteriorly curved pubic shaft compared to a straight one in IVPP V14531. These features are closer to the conditions present in derived coelurosaurs than are those of IVPP V14531. A few other features, however, are closer to the conditions present in more derived tyrannosauroids than are those of IVPP V14531, such as a shorter humerus relative to the femur, a less bowed ulna, a more prominent anteroventral process of the ilium, and a deeper and less curved post-acetabular process of the ilium.

Guanlong possesses numerous tyrannosauroid apomorphies: large foramina on the lateral surface of the premaxilla; tall premaxillary body; fused nasals; a large frontal contribution to the supratemporal fossa; a pneumatic jugal foramen in the posterior rim of the antorbital fossa; a deep basisphenoidal sinus with large foramina; a subcondylar recess on the basisphenoid; the supraoccipital excluded from the foramen magnum; the short retroarticular process; the relatively small, U-shaped premaxillary teeth that are arranged in a row more transversely than anteroposteriorly oriented; and labiolingually thick maxillary and dentary teeth^{1,15,22,23} (Fig. 2a–c; see also Supplementary Fig. 1). Striking tyrannosauroid pelvic features^{1,2,6} include an ilium subequal to femoral length, a distinctive dorsal concavity on the pre-acetabular process, a supracetabular crest that is straight in dorsal view, a prominent median vertical crest on the lateral surface of the ilium, a concave anterior margin of the pubic peduncle, a pubic tubercle close to the dorsal part of the pubic shaft, an extremely large pubic boot (55% of pubic length), and a thin sheet of bone extending from the obturator process down the ischial shaft (Fig. 2e; see also Supplementary Fig. 2k).

However, *Guanlong* lacks several synapomorphies shared by other tyrannosauroids, such as a reduced external mandibular fenestra, a prominent surangular ridge and a robust manual digit II. Additionally, several features are intermediate between the typical coelurosaurian and tyrannosauroid conditions, such as the relative size of the

premaxillary teeth and the squamosal–quadratojugal flange and the moderately medially inclined ilium. These data suggest a basal-most position for *Guanlong* among the Tyrannosauroidae, as supported by a numerical cladistic analysis (Fig. 3). However, its larger size relative to *Dilong* is inconsistent with the evolutionary trend of increasing size within more derived tyrannosauroids as suggested by previous studies^{11,20}. Furthermore, numerous autapomorphies set *Guanlong* apart from other tyrannosauroids. Thus, *Guanlong* represents a specialized lineage in the early evolution of tyrannosauroids.

The discovery of *Guanlong* also provides an insight into the poorly known early evolution of coelurosaurs. *Guanlong* demonstrates the primitive trait of a pelvic fenestra, also seen in the basal coelurosaur *Mirischia asymmetrica*²⁴ but more typical of basal tetanurans⁵. However, *Guanlong* is similar to derived coelurosaurs in having a large external naris extending posteriorly beyond the anterior margin of the antorbital fossa and a proportionally long forelimb with a bowed ulna and elongate manus⁹. This unusual combination of primitive tetanuran and derived coelurosaurian features suggests a complex pattern of character evolution at the base of the Coelurosauria. Interestingly, *Guanlong* also displays some features that are similar to the proposed synapomorphies of a Therizinosauroidae–Ornithomimosauria–Alvarezsauridae clade¹⁰, such as a long maxillary pre-antorbital ramus, a proportionally long dentary, a weak surangular ridge and paired flexor processes on the proximal end of manual phalanx II-1 and III-1. It is possible that these features might diagnose a more inclusive group, the Coelurosauria, but were lost in more derived members. Consequently this character distribution shows that the basal conditions for some coelurosaurian clades are highly modified in derived members of each group and underscores the need for more taxonomic sampling at the base of each coelurosaurian group.

The hypertrophied cranial crest of *Guanlong* provides a surprising case for the presence of an exaggerated ornament among non-avian predatory dinosaurs, comparable to well-known exaggerated ornamental traits in other vertebrate groups such as the large antlers of *Megaloceros* (Irish elks) and the long tail of peacocks²⁵. Cranial horns, bosses and crests are present in many non-avian theropods and are best exemplified by *Dilophosaurus*, *Monolophosaurus* and oviraptorids, among others²⁶. The function of these often pneumatic structures in theropods has been considered to be ornamentation involved in display or species recognition²⁷. The cranial crest of *Guanlong*, however, is larger and more elaborate than any yet reported for a non-avian theropod dinosaur²⁶. It seems paradoxical that this predatory taxon possessed a seemingly delicate, highly pneumatized cranial crest. In this regard, *Guanlong*'s cranial crest is similar to the sexually selected ornaments widely present in extant and extinct vertebrates, which have been suggested to exact a viability cost for the bearer²⁵. *Guanlong*'s cranial ornament may be a sexually selected trait, which has also been a suggested explanation for similar structures in some other non-avian dinosaur groups²⁸.

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- Holtz, T. R. in *The Dinosauria* 2nd edn (eds Weishampel, D. B., Dodson, P. & Osmolska, H.) 111–136 (Univ. California Press, Berkeley, 2004).
- Rauhut, O. W. M. A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. *Palaeontology* **46**, 903–910 (2003).
- Eberth, D. A. et al. Sequence stratigraphy, paleoclimate patterns and vertebrate fossil preservation in Jurassic–Cretaceous strata of the Junggar Basin, Xinjiang Autonomous Region, People's Republic of China. *Can. J. Earth Sci.* **38**, 1627–1644 (2001).
- Chen, P. J. in *The Continental Jurassic* (ed. Morales, M.) 395–412 (Museum of Northern Arizona, Flagstaff, 1996).
- Holtz, T. R., Molnar, R. E. & Currie, P. J. in *The Dinosauria* 2nd edn (eds Weishampel, D. B., Dodson, P. & Osmolska, H.) 71–110 (Univ. California Press, Berkeley, 2004).
- Rauhut, O. W. M. *The Interrelationships and Evolution of Basal Theropod Dinosaurs. Special Papers in Palaeontology* 69 (Palaeontological Association, London, 2003).
- Gauthier, J. in *The Origin of Birds and the Evolution of Flight* (ed. Padian, K.) 1–55 (California Academy of Sciences, San Francisco, 1986).

8. Norell, M. A., Clark, J. M. & Makovicky, P. J. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. & Gall, L. F.) 49–67 (Yale Univ. Press, New Haven, 2001).
9. Xu, X. *Deinonychosaurian Fossils from the Jehol Group of Western Liaoning and the Coelurosaurian Evolution*. Thesis, Chinese Academy of Sciences (2002).
10. Sereno, P. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. A. & Gall, L. F.) 69–98 (Yale Univ. Press, New Haven, 2001).
11. Xu, X. *et al.* Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* **431**, 680–684 (2004).
12. Hutt, S., Naish, D., Martill, D. M., Barker, M. J. & Newbery, P. A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Res.* **22**, 227–242 (2001).
13. Currie, P. J. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *J. Vert. Paleontol.* **15**, 576–591 (1995).
14. Makovicky, P. J. & Norell, M. A. in *The Dinosauria* 2nd edn (eds Weishampel, D. B., Dodson, P. & Osmolska, H.) 184–195 (Univ. California Press, Berkeley, 2004).
15. Brochu, C. A. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *J. Vert. Paleontol. Mem.* **7**, 1–138 (2003).
16. Osborn, H. F. Skull adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. *Bull. Am. Mus. Nat. Hist.* **35**, 733–771 (1916).
17. Chure, D. J. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. A. & Gall, L. F.) 283–300 (Yale Univ. Press, New Haven, 2001).
18. Xu, X., Tang, Z.-L. & Wang, X.-L. A therizinosauroid dinosaur with integumentary structures from China. *Nature* **399**, 350–354 (1999).
19. Hinchliffe, J. R. in *The Beginnings of Birds* (eds Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 141–148 (Freunde des Jura-Museum, Eichstatt, 1985).
20. Erickson, G. M. *et al.* Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature* **430**, 772–775 (2004).
21. Reid, R. E. H. in *The Complete Dinosaur* (eds Farlow, J. O. & Brett-Surman, M. K.) 403–413 (Indiana Univ. Press, Bloomington, 1997).
22. Currie, P. J. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontol. Pol.* **48**, 191–226 (2003).
23. Hurum, J. H. & Sabath, K. Giant theropod dinosaurs from Asia and North America: skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontol. Pol.* **48**, 161–190 (2003).
24. Naish, D., Martill, D. & Frey, E. Ecology, systematics and biogeographical relationships of dinosaurs, including a new theropod, from the Santana Formation (?Albian, Early Cretaceous) of Brazil. *Hist. Biol.* **16**, 57–70 (2004).
25. Andersson, M. *Sexual Selection* (Princeton Univ., Princeton, 1994).
26. Horner, J. R. Dinosaur reproduction and parenting. *Ann. Rev. Earth Planet. Sci.* **28**, 19–45 (2000).
27. Vickaryous, M. K. & Byan, M. J. in *Encyclopedia of Dinosaurs* (eds Currie, P. J. & Padian, K.) 488–493 (Academic Press, San Diego, 1997).
28. Sampson, S. D., Ryan, M. J. & Tanke, D. H. Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): taxonomic and behavioral implications. *Zool. J. Linn. Soc.* **121**, 293–337 (1997).

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

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1. Additional geological, morphological, and histological information
2. Phylogenetic analysis

1. Additional geological, morphological, and histological information.

Geology and preservational history. Both specimens were collected from the middle of an approximately 2.0 meter thick tabular bed of finely laminated to massive, tan-coloured, tuffaceous mudstone. Small, horizontal to sub-vertical carbonaceous root traces and plant fragments are present. Fine laminations and horizontally-oriented roots indicate a paludal (wetlands) setting in which sediment accumulated over many years.

Both specimens lie on their left sides in superposition, with IVPP V14531 overlying IVPP V14532 (Fig. 1) but separated from it by 20-25 cm of sediment. The hind limbs are tightly folded against the body in both animals. In IVPP V14531 the proximal caudals are disarticulated, but the mid-caudals form an articulated series that extends vertically downward below IVPP V14532. In IVPP V14532 the skull and first six cervicals are sharply dislocated from the posterior cervicals. There are no bone surface modifications in either specimen other than a black and tan colour mottling, which is likely the result of diagenesis. The superposition of IVPP V14531 above IVPP V14532, and IVPP V14532's better preservation indicate that IVPP V14532 died in-situ and was buried before subaerial disarticulation. Sharp dislocation of the cervical series in IVPP V14532 indicates that the neck sustained a highly focused impact, most likely due to trampling possibly caused by IVPP V14531. More thorough disarticulation in IVPP V14531 suggests that parts of its body were subaerially exposed for a significant time after death. The near vertical and downward orientation of the mid-caudal vertebrae in IVPP V14531 indicates that the host sediment had semi-fluid properties during emplacement and burial of the specimens.

Histological analysis. A histological analysis was conducted to determine the longevity and developmental stages for the specimens. Mid-diaphyseal petrographic thin sections were made from the fibulae, an element that has been shown to be efficacious for ageing living reptiles and theropod dinosaurs owing to its general lack of remodelling¹. IVPP V14531 shows 10 definitive growth lines and what appears to be an 11th very near the periosteal surface (Fig. 2g in main paper). Hence the animal likely perished during the 12th year of life. What appears to be a growth line below ring number three is a circumferential crack that opened up parallel to one of the layers of bone lamellae that compose the growth mark during polishing. The upper inset box shows four to five tightly packed growth lines on the periphery of the element (a structure known as an external fundamental system, or EFS) separated by avascular growth zones (Fig. 2g in main paper), suggesting that the animal reached full-adult size in seven years and was a “stationary stage” individual at the time of death. The presence of moderate Haversian remodeling, shown in the lower inset (circles in upper left domain) and a thick endosteal border resulting from at least three cycles of deposition (yellow and purple fibrous bone layers in lower right domain nearest the medullar cavity) and substantial decreases in vascularization towards the periphery of the element support this developmental stage assessment. IVPP V14532 appears to have been into its sixth year of life at death, and appears to have been actively growing, perhaps in the exponential stage of development as indicated by the same degree of vascularization throughout the cortices, the broad spacing between growth lines towards the periosteal surface, the presence of only a thin, single lamellae of endosteal bone, and just several Haversian canals^{1,2}.

Additional morphological description. The *Guanlong* holotype is larger than the basal tyrannosauroid *Dilong* but considerably smaller than most tyrannosauroid species³. It has a particularly long and shallow snout, a relatively small orbit and a moderately constricted infratemporal fenestra. As in other tyrannosauroids⁴⁻⁷, large foramina are distributed along the lateral surface of the premaxilla, the main body of the premaxilla is taller dorsoventrally than it is long rostrocaudally, the nasals are fused for most of their length except at the anterior end, the supratemporal fossa occupies a large portion of the frontal, the jugal is pneumatized by a foramen in the caudal rim of the antorbital fossa, a deep basisphenoid sphenoidal sinus with large foramina is present, the basisphenoid has a well-developed subcondylar recess, the supraoccipital is excluded from the foramen magnum, the retroarticular process is short, the premaxillary teeth are U-shaped, have well-developed vertical ridge on the distal surface, are smaller than the maxillary teeth, and are arranged in a row more transversely than rostrocaudally oriented, and the maxillary and denary teeth are relatively thick labiolingually. *Guanlong* differs from other tyrannosauroids in many cranial features, some of which are very unusual. Posteriorly on the skull roof, two parallel, low but sharp sagittal crests are developed to form the medial border of the supratemporal fossae, respectively. Most theropods have either one or no sagittal crest. Also unique is a distinct transverse ridge along the parietofrontal suture dividing the supertemporal fossa into an anterior and a posterior part. The most striking feature of *Guanlong* is a complex ornament formed by the fused nasals. It consists of a median crest and four supporting lateral laminae. The crest covers most of the skull roof, is extremely thin for most length (about 1.5 mm in transverse thickness), and posteriorly widens (about 13 mm in transverse thickness) to roof a large pneumatic fenestra. Two additional smaller fenestrae are located more anteriorly and ventrally. Four pneumatic fossae are also present on the lateral surface of the crest. Two pairs of lateral laminae are obliquely developed on the lateral surface of the median crest, the posterior pair of which are prominent and extend anteroventrally close to the posterodorsal corner of the antorbital fenestra. In the lower jaw of the referred specimen, *Guanlong* displays a relatively large external mandibular fenestra and an extremely weak surangular ridge, and appears to lack a surangular foramen.

Postcranially, the cervical vertebrae are amphicoelous, but the posterior ones have extremely weakly convex anterior central articular surface. The neural spines are elongated axially on the anterior cervical vertebrae but much narrower on the posterior cervical vertebrae. Those on the posteriormost ones are laterally flared distally such that they are wider transversely than axially. The dorsal and sacral centra lack pneumatic openings, though moderately deep fossae are present laterally. Distal caudal vertebrae bear deep longitudinal sulcus both on the ventral surface of the centrum and the dorsal margin of the neural arch, a feature also seen in troodontids. Their prezygapophyses reaches close to the anterior end of the preceding vertebra and postzygapophyses are level with the junction with the succeeding vertebra.

The scapula-coracoid is similar to other tyrannosauroids in having a large and abruptly dorsally deflected acromion process and a dorsoventrally long and rostrocaudally narrow coracoid⁴. But unlike other tyrannosauroids⁴, the scapula is only slightly longer than the humerus.

The tyrannosauroid features^{4,8,9} of the pelvis include a relatively long ilium (subequal to femoral length), a dorsal concavity on the preacetabular process, straight supraacetabular crest in dorsal view, a prominent median vertical crest on the lateral surface of the ilium, a concave cranial margin of the pubic peduncle, a pubic tubercle close to the proximal end of the pubic shaft, an extremely large pubic boot (about 55% of pubic length), and a thin sheet of bone extending from the obturator process down the ischial shaft. Unlike other tyrannosauroids, however, the ilia are moderately inclined toward the midline but do not contact, a foramen pierces the thin sheet of bone ventral to the pubic process of the ischium, and an obturator foramen might pierce the extremely thin sheet of bone ventral to the ischial process of the pubis continuing onto the thin pubic apron. The last two features are closer to conditions in more basal tetanurans¹⁰. Among the Coelurosauria, only the compsognathid *Mirischia asymmetrica*¹¹ has pelvic fenestrae.

The hindlimb is proportionally long, with a hindlimb (femur+tibiotarsus+metatarsal III)-to-dorsal-series length ratio of about 1.8. The tibiotarsus/femur and metatarsal III/tibia length ratios are about 1.15 and 0.60, respectively. The alariform lesser trochanter of the femur is lower than the greater trochanter, the posterior trochanter and fourth trochanter are prominent, and as in some oviraptorosaurs and dromaeosaurids¹², an accessory trochanter is present distal to the lesser trochanter. The middle three metatarsals contribute sub-equally to the proximal articular surface of the metatarsus, though the more dorsally positioned metatarsal III is moderately compressed along the ventral margin. Pedal digit I is attached to the posteromedial margin of metatarsal II, indicating the presence of a partially reversed hallux. The pedal digits are both highly extensible and flexible as indicated by the well-developed distal hemicondyles and deep extensor pits distally.

Possible function of the cranial crest. Cranial horns, bosses, and crests are present in many non-avian theropods and are best exemplified by *Dilophosaurus*, *Monolophosaurus*, and oviraptorids, among others¹³. The known *Monolophosaurus* specimen was also collected from Shishugou Formation (from the lower part of the formation).

Monolophosaurus is a basal carnosaur, significantly different from *Guanlong* in numerous features throughout the skeleton (for detailed differences, compare the codings of *Monolophosaurus* in reference 9 and *Guanlong* below). The cranial crest of *Guanlong* is also proportionally much larger and much more elaborate than that of *Monolophosaurus*. Among tyrannosauroids no species except *Guanlong* is known to have a cranial crest, though some tyrannosaurids have bony cranial rugosities. Among archosaurs the cranial crest in *Guanlong* is only comparable to the large crests of some pterosaurs, lambeosaurine hadrosaurids and some neornithine birds such as hornbills in terms of relative size. The function of these often pneumatic structures in theropods, has been considered to be ornamentation involved in display or species recognition¹⁴. The extreme fragility and elaboration of the cranial crest in *Guanlong* is against a function for combating or fighting; there is also no direct evidence for a vocal or thermoregulatory function. The latter function is often associated with the presence of numerous vessels, but *Guanlong*'s crest does not show relevant osteological correlates. It seems paradoxical that this predatory taxon possessed a seemingly delicate, highly pneumatized cranial crest. In this regard, *Guanlong*'s cranial crest is similar to the sexually selected

ornaments widely present in extant and extinct vertebrates, which have been suggested to exact a viability cost for the bearer¹⁵. *Guanlong*'s cranial ornament may be a sexually selected trait, which has also been a suggested explanation for similar structures in some other non-avian dinosaur groups¹⁶. A large sample of specimens is needed to confirm this hypothesis, however.

Additional figures for *Guanlong wucaii*

Fig. 1. Photographs of skull and mandible. a, *Guanlong wucaii* holotype skull in lateral view; b, *Guanlong wucaii* holotype posterior region of skull in dorsal view; c, *Guanlong wucaii* holotype skull in ventrolateral view; d, *Guanlong wucaii* referred specimen skull and mandible in lateral view; e, *Guanlong wucaii* holotype skull in posterior view; f, *Guanlong wucaii* braincase in ventral view; g, a premaxillary tooth in lingual view. Scale bar = 10 cm for a, c, and d.

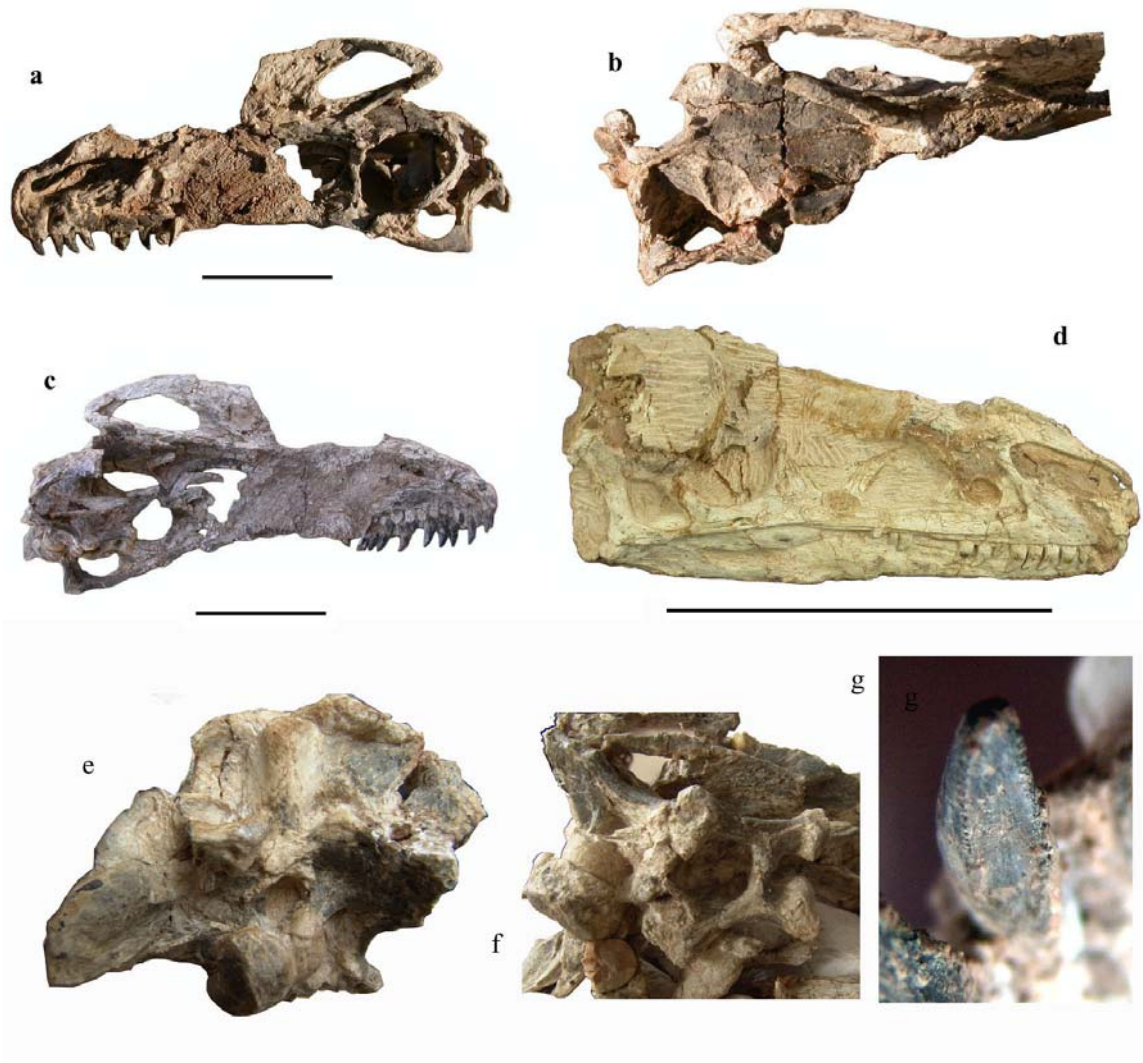


Fig. 2. Photographs of selected postcranial elements of *Guanlong wucaii* holotype. A cervicodorsal in anterior (a) and posterior (b) views; Distal caudal vertebrae in dorsal (c) and ventral (d) views; e, humerus, ulna, radius, and manual digit II length comparison; f, Left metacarpals I-III in ventral view; g, Left metacarpal I and “semilunate” distal carpal in dorsal view; h, Left metacarpals I-III in proximal view; i, Left manual phalanges II-1 and III-1 in proximoventral view; j, Left manual phalanx II-2 in proximal view; k, Left pelvis lateral view; l, Left femur in lateral view; m, Left femur in posterior view; n, Left tibia and fibula in lateral view; o, Left astragalus-calcaneum in posterodistal view; p, Right pes in posterior view; and q, Right pedal phalanx II-1 in ventral view. Scale bar = 2 cm.



2. Cladistic analysis

We coded *Guanlong wucaii* and the recently described basal tyrannosauroid *Dilong paradoxus* into a matrix which was published by Rauhut⁹. We deleted *Deltadromeus* from our analysis as new information indicates that it is a ceratosaurian rather than a coelurosaurian¹⁷. Including *Deltadromeus* in the analysis will be done after recoding the information on this taxon which is currently unavailable. The scorings for the two taxa are as follows:

Guanlong wucaii

1000110001210111111?1022110110100110000000-
01011?001?10011?1?0?0?03?0200111?1??0000000111????0?01??11?0?0110112000?1
010101000111?100010010000103111111210102120000?1011011101?10100?011000000
00010121101111222??10112111100220

Dilong paradoxus

1000110001010111110010221101101101100000002?1011?001?10011?1?0?0?0??02001
110111?0000000111????1??01?01??0?011?111?????????101000????000010010011??11
11112101021?0000010110??10?????????1100?????110121?????222?????1211??0?22
0

The data matrix was analyzed cladistically using the NONA (ver 2.0) software package (Goloboff, 1993) and formatting and character exploration was performed in WinClada (Nixon, 2000). 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 Rauhut⁹. Trees were rooted on *Euparkeria*. The analysis resulted in 6336 equally parsimonious trees with a length of 668 steps. These trees have a CI of 0.41 and an RI of 0.74. An Adams consensus was calculated in PAUP* 4.0b10 (Swofford, 2002) and reduced consensus trees were found using the program Radcon¹⁸. Figures 3 and 4 show the strict and Adams consensus trees of these trees, respectively. Both trees posit *Guanlong wucaii* within the Tyrannosauroidea. The basal positions of *Guanlong* and *Stokesosaurus* on the Adams tree are due to the instability of *Stokesosaurus*, which is either with *Dilong*, *Dilong*+Tyrannosauridae, or at the base of the Tyrannosauroidea. This is verified by the reduced consensus analysis, which shows that *Guanlong* outside of *Dilong*+Tyrannosauridae is a stable subtree. The proposed tyrannosauroid interrelationships here are concordant with the tyrannosauroid biostratigraphical record. Bootstrap values are 95% for the Tetanurae, 90% for the Coelurosauria, 90% for Tyrannosauroidea including *Guanlong*, 57% for (*Stokesosaurus*+(*Dilong*+Tyrannosauridae)), and 58% for (*Dilong*+Tyrannosauridae). Unambiguous character support for clades found in the analysis of the data set is presented below. The first number refers to the character on the list⁹ and the second number to derived state.

Unambiguous synapomorphies for the Coelurosauria:

6.1, 14.1, 53.1, 68.1, 101.0, 102.1, 124.1, 129.1, 132.1, 146.2, 155.0, 166.2, 169.1, 171.1, 175.1, 179.1, 185.1, 190.0, 207.2, 213.1, 214.1, and 216.1.

Unambiguous synapomorphies for the Tyrannosauroidea:

1.1, 18.1, 26.1, 35.1, 150.1, 172.1, and 173.1

Software references:

Goloboff, P. A. 1993. NONA (ver 2.0) published by the author, S. M. de Tucuman, Argentina.

Nixon, K. C. 1999. Winclada (BETA) ver. 0.9.9 published by the author, Ithaca, New York, USA.

Both packages available from <http://www.cladistics.org>.

Swofford, D. L. (2002). PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sunderland Massachusetts, Sinauer Associates,

Fig. 3. A strict consensus of 6336 equally parsimonious trees.

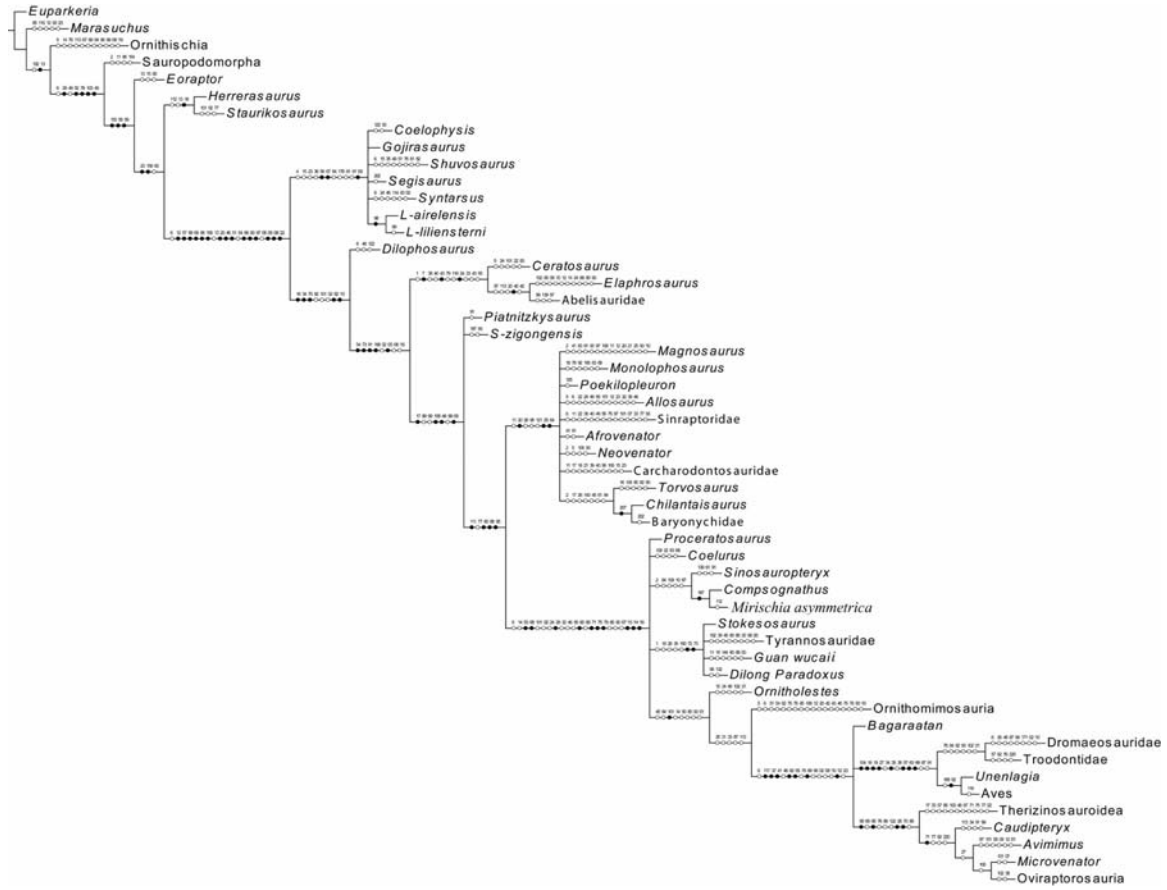
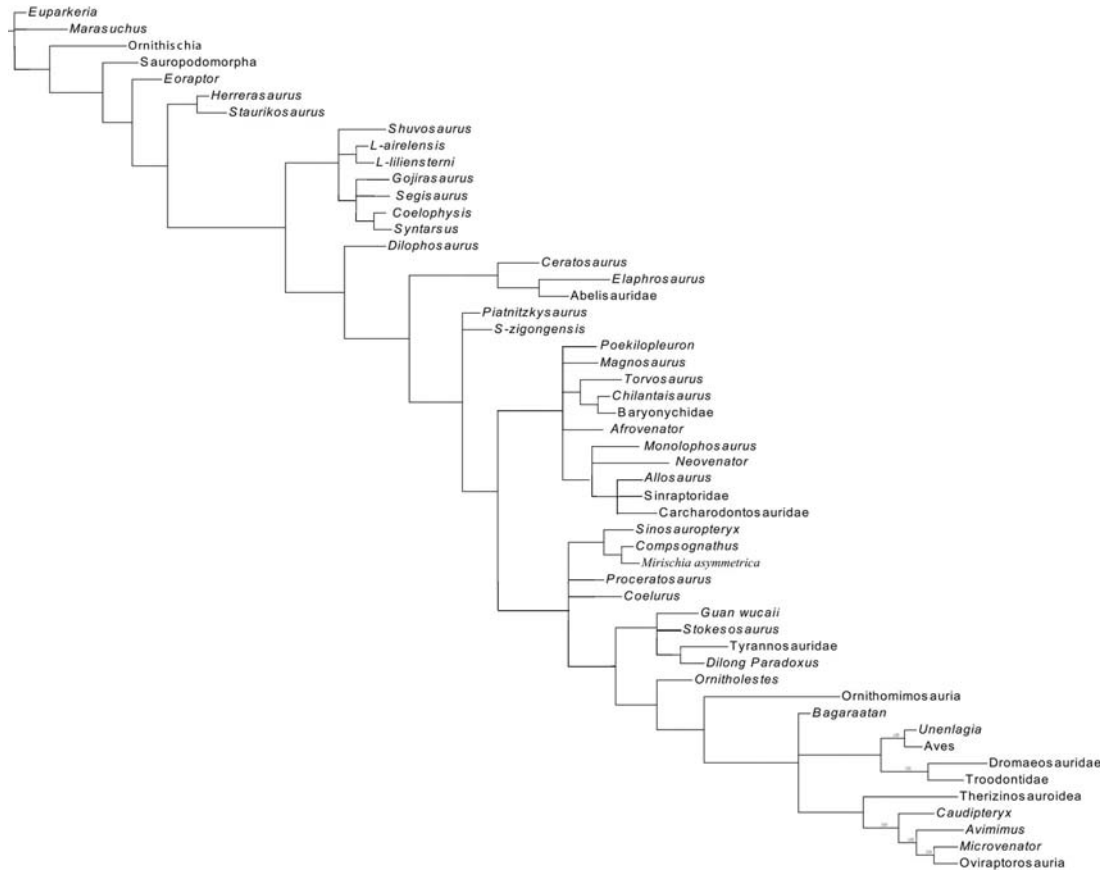


Fig. 4. An Adams consensus of 6336 equally parsimonious trees.



References

1. Erickson, G. M. et al. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature* **430**, 772-775 (2004).
2. Reid, R. E. H. in *The complete dinosaur* (eds. Farlow, J. O. & Brett-Surman, M. K.) 403-413 (Indiana University Press, Bloomington, 1997).
3. Xu, X. et al. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* **431**, 680-684 (2004).
4. Holtz, T. R. in *The Dinosauria (the second edition)* (eds. Weishampel, D. B., Dodson, P. & Osmolska, H.) 111-136 (University of California Press, Berkeley, 2004).
5. Currie, P. J. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontologica Polonica* **48**, 191-226 (2003).
6. Brochu, C. A. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology Memoir* **7**, 1-138 (2003).
7. Hurum, J. H. & Sabath, K. Giant theropod dinosaurs from Asia and North America: skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontologica Polonica* **48**, 161-190 (2003).
8. Rauhut, O. W. M. A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. *Palaeontology* **46**, 903-910 (2003).
9. Rauhut, O. W. M. *The interrelationships and evolution of basal theropod dinosaurs. Special papers in Palaeontology* 69 (Palaeontological Association, London, 2003).
10. Holtz, T. R. J., Molnar, R. E. & Currie, P. J. in *The Dinosauria (the second edition)* (eds. Weishampel, D. B., Dodson, P. & Osmolska, H.) 71-110 (University of California Press, Berkeley, 2004).
11. Naish, D., Martill, D. & Frey, E. Ecology, systematics and biogeographical relationships of dinosaurs, including a new theropod, from the Santana Formation (?Albian, Early Cretaceous) of Brazil. *Historical Biology* **16**, 57-70 (2004).
12. Xu, X., Zhou, Z.-H. & Wang, X.-L. The smallest known non-avian theropod dinosaur. *Nature* **408**, 705-708 (2000).
13. Horner, J. R. Dinosaur reproduction and parenting. *Annual Review of Earth and Planetary Sciences* **28**, 19-45 (2000).
14. Vickaryous, M. K. & Byan, M. J. in *Encyclopedia of dinosaurs* (eds. Currie, P. J. & Padian, K.) 488-493 (Academic Press, San Diego, 1997).
15. Andersson, M. *Sexual selection* (Princeton University, Princeton, 1994).
16. Sampson, S. D., Ryan, M. J. & Tanke, D. H. Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia : Ceratopsidae): taxonomic and behavioral implications. *Zoological Journal of the Linnean Society* **121**, 293-337 (1997).
17. Sereno, P.C., Wilson, J.A. & Conrad, J. 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proceedings: Biological Sciences* **271**, 1325-1330
18. Thorley, J. L. & Page, R. D. M. RadCon: Phylogenetic tree comparison and consensus. *Bioinformatics* **16**, 486-487 (2000).