A basal tyrannosauroid dinosaur from the Late Jurassic of China.

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

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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 remodelling [1]. 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 species [3]. It has a particularly long and shallow snout, a relatively small orbit and a moderately constricted infratemporal fenestra. As in other tyrannosauroids [4-7], 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 coracoid [4]. But unlike other tyrannosauroids[4], 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 tetanurans[10]. 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 dromaeosaurids [12], 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 others[13]. 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 recognition[14]. 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 bearer[15]. *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 groups[16]. 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 vetrolateral 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**.
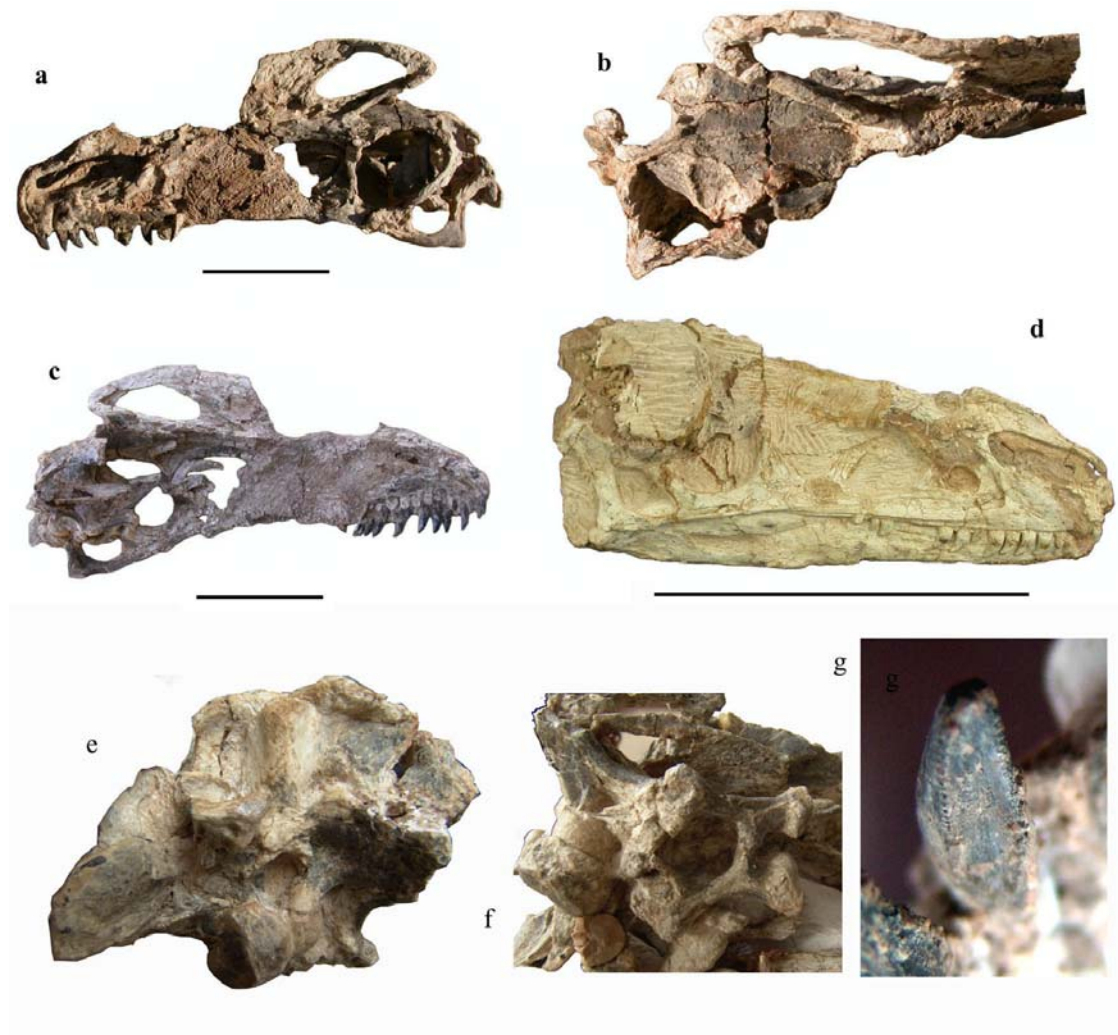
Fig. 2. Photographs of selected postcranial elements of *Guanlong wucaii* holotype. A cervicodorsal in anterior (a) and posterior (b) views; Distal caudal vertebrae in dorsal (c) and ventral (d) views; e, humerus, ulna, radius, and manual digit II length comparison; f, Left metacarpals I-III in ventral 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 Rauhut[9]. We deleted *Deltadromeus* from our analysis as new information indicates that it is a ceratosaurian rather than a coelurosaurian[17]. 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?102211011010011000000-01011?001?10011?1?0?0?03?0200111?1???0000000111????0??01??11?0?0110112000?1010101000111?100010010000103111112101021200 00?1011011101?10100?0110000000001012110111 1222??10112111100220

Dilong paradoxus
100011000101011111001022110110110110000002?1011?001?10011?1?0?0?0??02001110111?0000000111????1??01?01??0?011?11?????????101000????000010010011???1111112101021?0000010110??10?????????1100??????110121??????222?????1211??0?220

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 Rauhut [9]. 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 Radcon [18]. 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 list[9] 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,

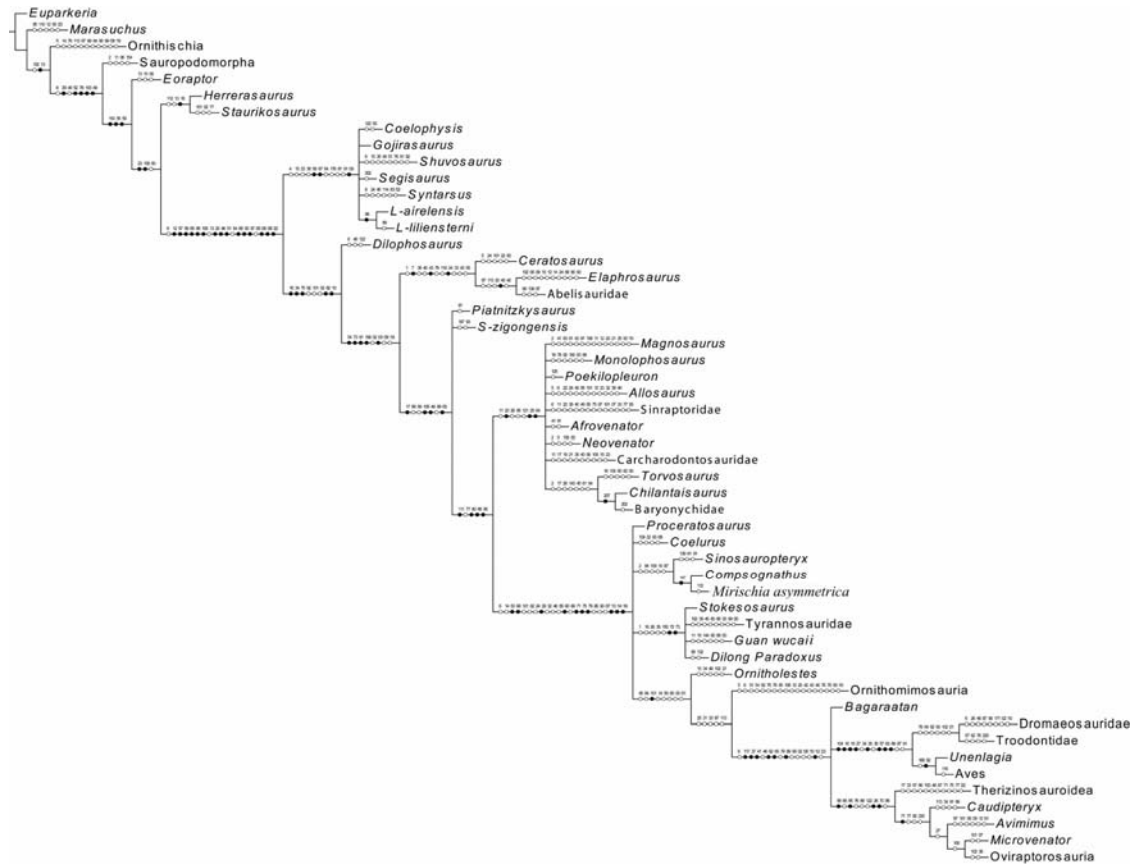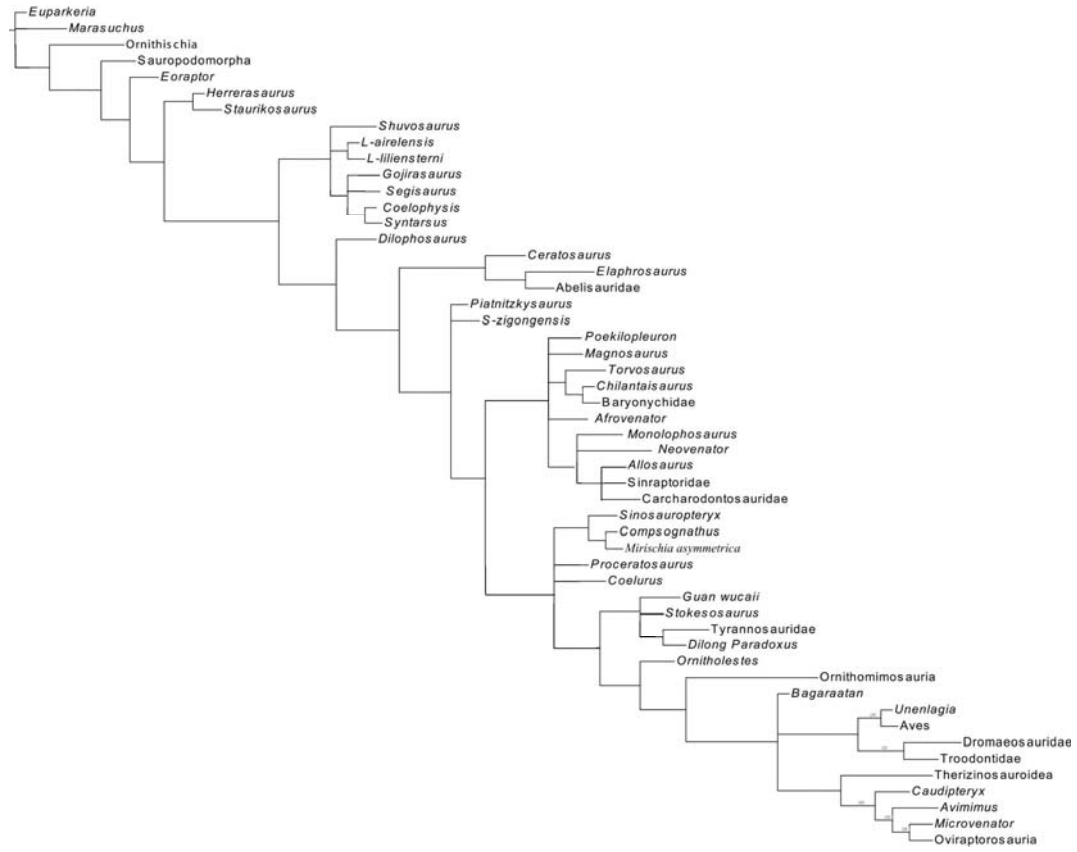Fig. 3. A strict consensus of 6336 equally parsimonious trees.

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

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

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