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LETTERS

A basal tyrannosauroid dinosaur from the Late Jurassic of China

Xing Xu[1,2], James M. Clark[3], Catherine A. Forster[4], Mark A. Norell[2], Gregory M. Erickson[5], David A. Eberth[6], Chengkai Jia[1] & Qi Zhao[1]

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 clades[10]. 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
Tyrannosauroidea 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 *wucai* (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 troodontids[8]); 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 dromaeosaurids[13]). 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 positioned[14]. 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 specimen[1]. Interestingly, its position (mainly contacting metacarpal I) is similar to the condition in *Allosaurus*[17] and oviraptorosaurs, whereas in therizinosauroids[18], troodontids,

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[1]Institute of Vertebrate Paleontology and Paleoanthropology, Beijing 100044, China. [2]American Museum of Natural History, New York, New York 10024, USA. [3]Department of Biological Sciences, George Washington University, Washington DC 20052, USA. [4]Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794, USA. [5]Department of Biological Science, Florida State University, Tallahassee, Florida 32306, USA. [6]Royal Tyrrell Museum, Drumheller, Alberta T0J 0Y0, Canada.

dromaeosaurids and basal birds[9] it primarily articulates with metacarpal II. The latter condition is also consistent with some embryonic evidence from extant birds[19]. 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

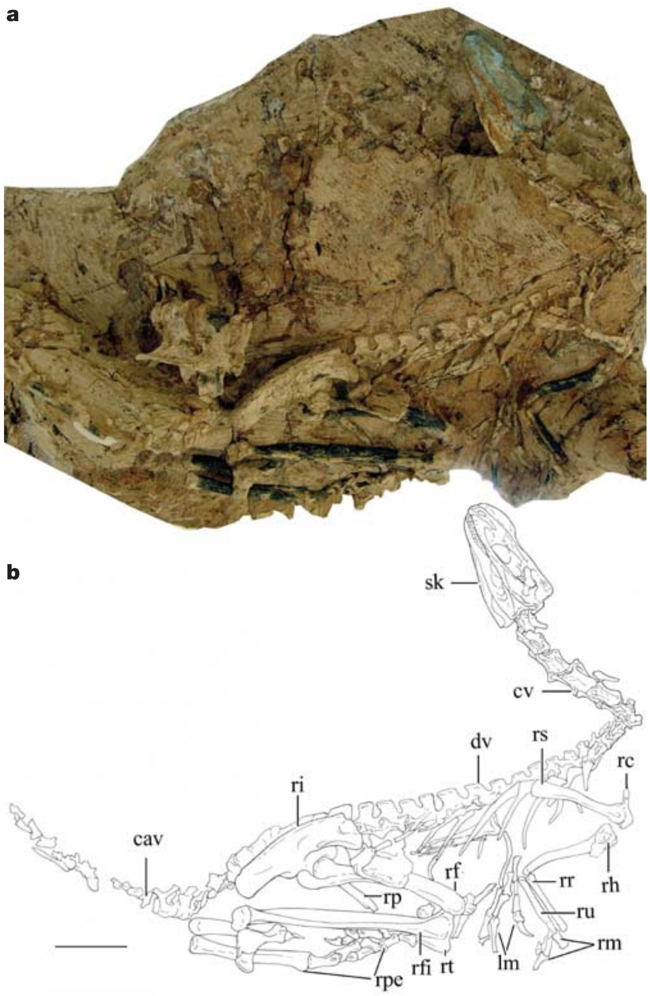

Figure 1 | ***Guanlong wucaii* (IVPP V14532).** **a**, Photograph, **b**, Line drawing of IVPP V14532. cav, caudal vertebrae; cv, cervical vertebrae; dv, dorsal vertebrae; lm, left manus; rc, right coracoid; rf, right femur; rfi, right fibula; rh, right humerus; ri, right ilium; rm, right manus; rp,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

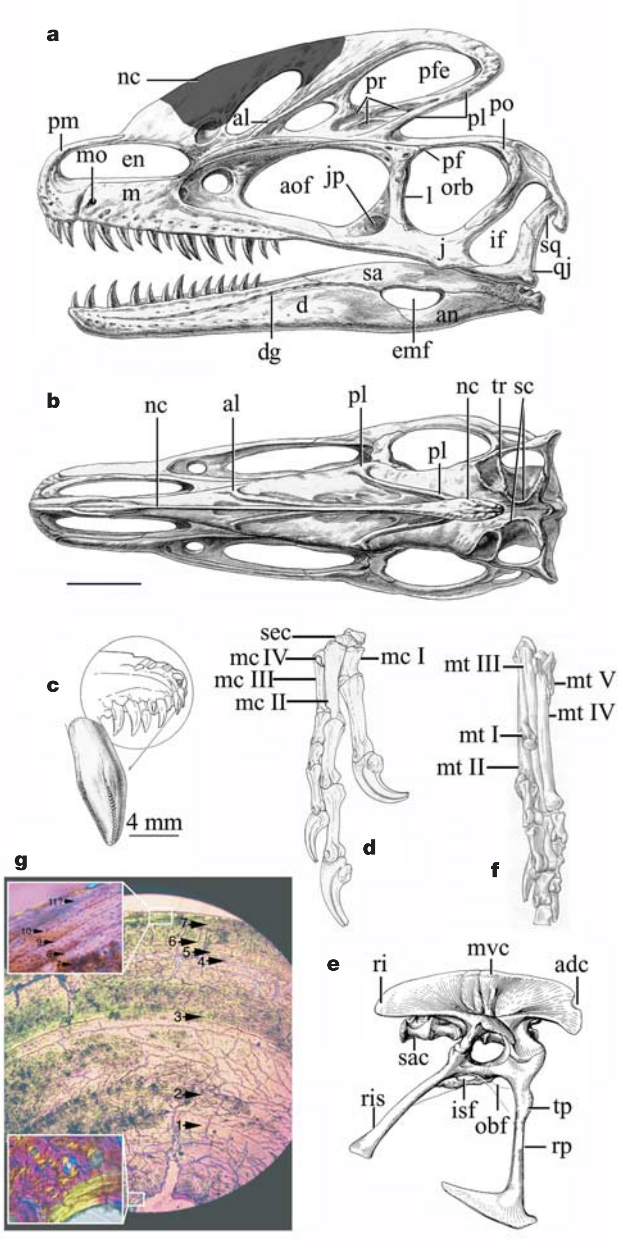

Figure 2 | ***Guanlong wucaii* (IVPP V14531).** **a**, **b**, Cranial reconstruction in left lateral (**a**; shaded area indicates the unpreserved portion) and dorsal (**b**) views. **c**, Close up of a premaxillary tooth. **d**, Ventral view of left manus. **e**, Pelvis in right lateral view. **f**, Ventral view of left pes. **g**, Histological section from the fibular shaft of *Guanlong wucaii* (IVPP V14531), shown in polarized microscopy (original magnification × 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; mo, maxillary opening; 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; ris, 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**).

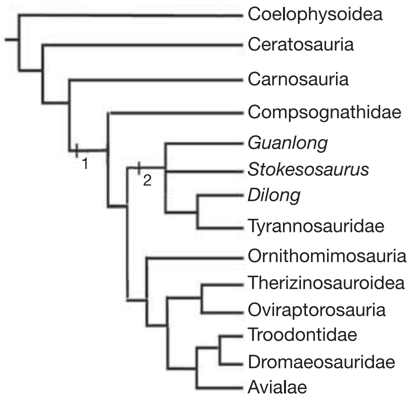

Figure 3 | **A simplified cladogram representing an Adams consensus of 6,336 most parsimonious trees showing the phylogenetic position of *Guanlong wucaii* (see Supplementary Information for a detailed analysis).** Reduced consensus analysis demonstrates that *Guanlong* is outside of the Tyrannosauridae–*Dilong* clade on all trees, but the position of *Stokesosaurus* is unstable (see Supplementary Information). 1, Coelurosauria; 2, Tyrannosauroidea. Bootstrap value (90%) is high for the Tyrannosauroidea 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 Tyrannosauroidea, 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 tetanurans[5]. 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 manus[9]. 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 Therizinosauroidea–Ornithomimosauria–Alvarezsauridae clade[10], 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 peacocks[25]. Cranial horns, bosses and crests are present in many non-avian theropods and are best exemplified by *Dilophosaurus*, *Monolophosaurus* and oviraptorids, among others[26]. The function of these often pneumatic structures in theropods has been considered to be ornamentation involved in display or species recognition[27]. The cranial crest of *Guanlong*, however, is larger and more elaborate than any yet reported for a non-avian theropod dinosaur[26]. 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[25]. *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[28].

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

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