A longirostrine tyrannosauroid from the Early Cretaceous of China

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The fossil record of tyrannosauroid theropods is marked by a substantial temporal and morphological gap between small-bodied, Barremian taxa, and extremely large-bodied taxa from the latest Cretaceous. Here we describe a new tyrannosauroid, *Xiongguanlong baimoensis* n. gen. et sp., from the Aptian–Albian Xinminpu Group of western China that represents a phylogenetic, morphological, and temporal link between these disjunct portions of tyrannosauroid evolutionary history. *Xiongguanlong* is recovered in our phylogenetic analysis as the sister taxon to Tyrannosauridae plus *Appalachiosaurus*, and marks the appearance of several tyrannosaurid hallmark features, including a sharp parietal sagittal crest, a boxy basicranium, a quadratojugal with a flaring dorsal process and a flexed caudal edge, premaxillary teeth bearing a median lingual ridge, and an expanded axial neural spine surmounted by distinct processes at its corners. *Xiongguanlong* is characterized by a narrow and elongate muzzle resembling that of *Alioramus*. The slender, unornamented nasals of *Xiongguanlong* are inconsistent with recent hypotheses of correlated progression in tyrannosauroid feeding mechanics, and suggest more complex patterns of character evolution in the integration of feeding adaptations in tyrannosaurids. Body mass estimates for the full-grown holotype specimen of *Xiongguanlong* fall between those of Late Cretaceous tyrannosaurids and Barremian tyrannosauroids, suggesting that the trend of increasing body size observed in North American Late Cretaceous Tyrannosauridae may extend through the Cretaceous history of Tyrannosauroidea though further phylogenetic work is required to corroborate this.

Keywords: China; Cretaceous; Dinosauria; Tyrannosauroidea; Xinminpu Group;
Xiongguanlong baimoensis

1. INTRODUCTION

Until the last decade, the fossil record of Tyrannosauroidea consisted primarily of derived, large-bodied taxa from the Late Cretaceous of Mongolia and western North America. More recently, basal tyrannosauroids have been described from Barremian-age sediments in England (Hutt *et al.* 2001) and China (Xu *et al.* 2004). Fragmentary remains from the Late Jurassic of Utah, Portugal (Rauhut 2003*a*) and England (Benson 2008) have been interpreted as belonging to tyrannosauroids, but are largely restricted to pelvic elements, while *Guanlong* from the Middle Jurassic of Xinjiang, China, was posited as the earliest and basalmost tyrannosauroid (Xu *et al.* 2004). Except for very fragmentary remains such as *Alectrosaurus* from the Cenomanian of Mongolia (Gilmore 1933; Perle 1977), there is a remarkable gap in the tyrannosauroid fossil record between the Barremian and Campanian. The Albian *Siamotyrannus*, originally described as a basal tyrannosauroid (Buffetaut *et al.* 1996) was found to be a basal neotetanuran in detailed phylogenetic analyses (Rauhut 2003*b*; Holtz *et al.* 2004).

Here we describe a new tyrannosauroid from probable Aptian–Albian sediments of western China that sheds light on this missing middle chapter of tyrannosauroid evolutionary history. The new taxon is intermediate in size between earlier Barremian tyrannosauroids and more derived taxa from the Campanian and provides crucial insights into the evolution of tyrannosaurid characters.

2. SYSTEMATIC PALAEONTOLOGY

Theropoda Marsh 1881
Tetanurae Gauthier 1986
Coelurosauria von Huene 1914
Tyrannosauroidea Walker 1964
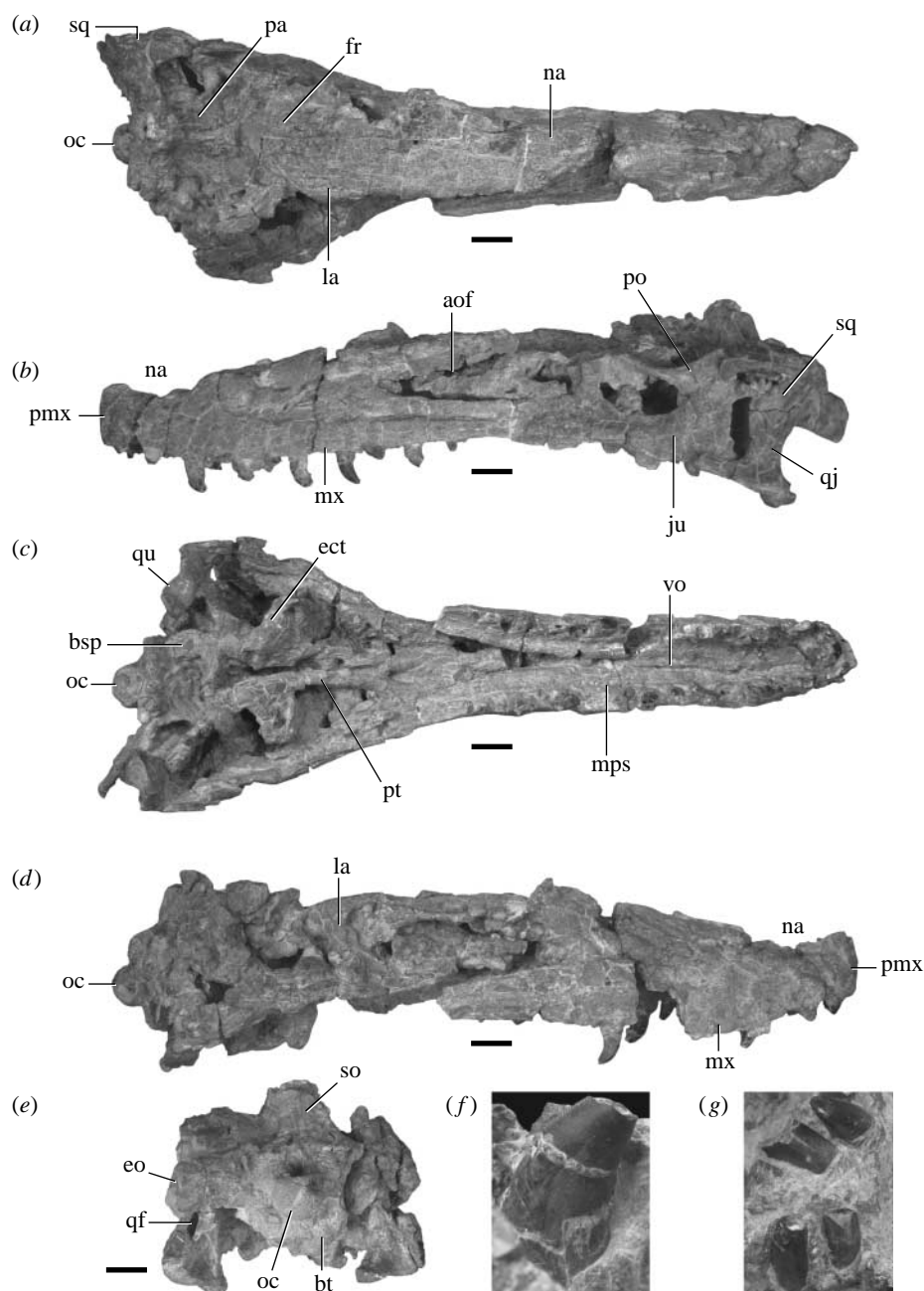*Xiongguanlong baimoensis* n. gen. et sp.

Figure 1. Skull of the holotype specimen of *X. baimoensis* FRDC-GS JB16-2-1 in (*a*) dorsal, (*b*) left lateral, (*c*) ventral, (*d*) right lateral, and (*e*) occipital views. Close-up views of (*f*) the sixth right maxillary tooth crown and (*g*) the first and second teeth of the left (upper two teeth) and right premaxillae. Abbreviations: aof, antorbital fenestra; bsp, basisphenoid; bt, basal tuber; ect, ectopterygoid; eo, exoccipital; fr, frontal; ju, jugal; la, lacrimal; mps, maxillary palatal shelf; mx, maxilla; na, nasal; nar, naris; oc, occipital condyle; pa, parietal; po, postorbital; pmx, premaxilla; pt, pterygoid; qj, quadratojugal; qf, quadrate foramen; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Scale bar equals 3 cm.

(a) Etymology: *Xiongguanlong*—from the Mandarin *Xiong Guan* for Grand Pass, a historic name for the nearby city of Jiayuguan, and *long* for dragon; and *baimoensis* from Mandarin for White Ghost in reference to a prominent topographic feature in the field area dubbed the White Ghost Castle.

(b) Material: FRDC-GS JB16-2-1 (see the electronic supplementary material 1 for institutional abbreviations), a complete skull without lower jaws (figure 1), complete presacral vertebral series (figure 2*a–f*), partial right ilium (see the electronic supplementary material, figure 6*a*), and right femur (figure 2*g–j*).

(c) Locality and horizon: White Ghost Castle field area, Yujingzi Basin, Gansu, China. The specimen derives

from a grey mudstone near the bottom of the Early Cretaceous sedimentary series exposed in the basin. Other faunal elements from these strata include turtles, therizinosauroids (Li *et al.* 2007, 2008), ornithomimosaurs (Makovicky *et al.* in press), sauropods and ornithopods, whereas overlying red-bed facies yield a fauna dominated by a small neoceratopsian cf. *Auroraceratops* (You *et al.* 2005). Clear faunal similarities exist with the Xinminpu Group (Tang *et al.* 2001; Li *et al.* 2008) in the nearby Mazongshan and Suanjingzi basins, but some litho-logical and faunal differences at the species level indicate that these localities may not be completely correlative. These faunal similarities along with
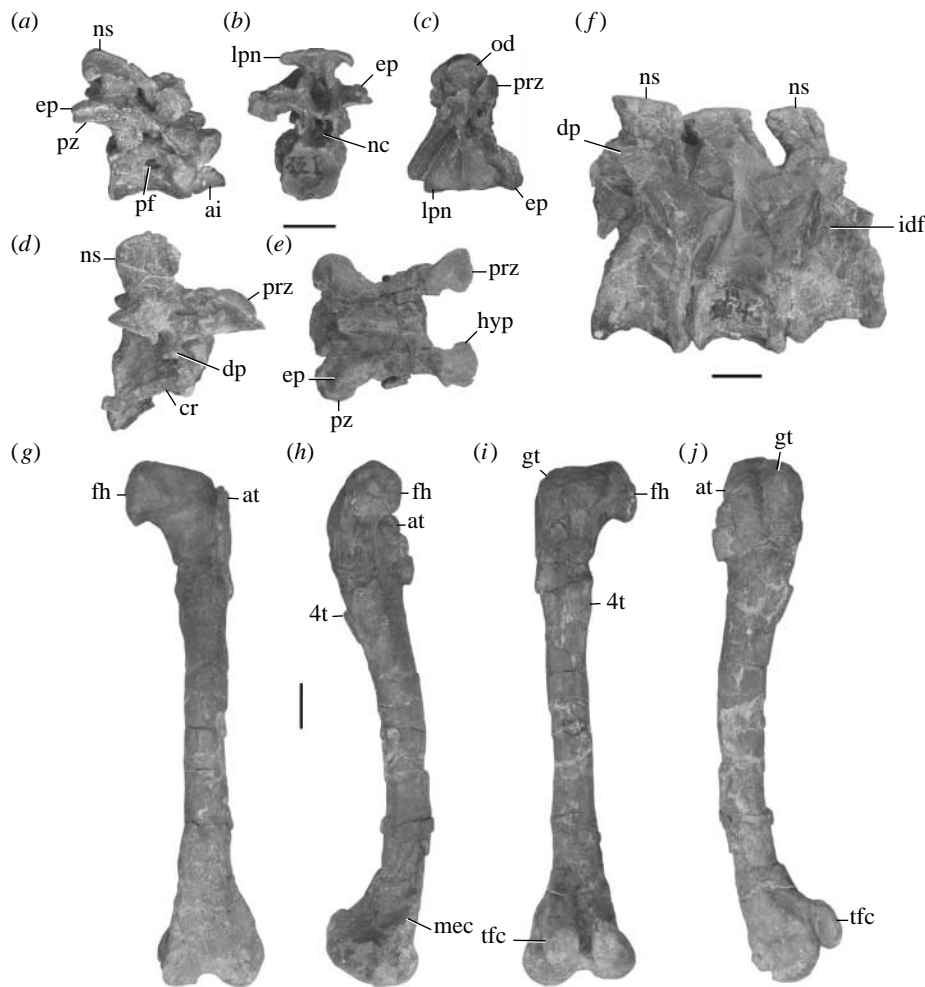
Figure 2. Select postcranial elements of the holotype specimen of *X. baimoensis* FRDC-GS JB16-2-1. Axis in (*a*) right lateral, (*b*) caudal, (*c*) dorsal views, (*d*) cervical 5 in right lateral view, (*e*) cervical 6 in dorsal view, and (*f*) dorsals 3–5 in right lateral view. (*g–j*) left femur in rostral (*g*), medial (*h*), caudal (*i*), and lateral (*j*) views. Abbreviations: ai, axis intercentrum; at, anterior (lesser) trochanter; dp, diapophysis; ep, epipophysis; fh, femoral head; gt, greater trochanter; hyp, hypantrum; idf, infradiapophyseal fossa; lpn, lateral process on neural spine; nc, neural canal; ns, neural spine; od, odontoid; pf pneumatic foramen; pz, prezygapophysis; pz, postzygapophysis; tfc, tibiofibular crest. Vertebral scale bars equal 3 cm, femoral scale bars equals 5 cm.

preliminary palynological examination indicate an Aptian–Albian age for the rocks that yielded the holotype of *Xiongguanlong*.

(d) Diagnosis: Midsized tyrannosauroid (see electronic supplementary material 2 for measurements) with a uniquely elongate preorbital region reaching over two thirds of skull length. It can be distinguished from Late Cretaceous tyrannosaurids in lacking synapomorphies such as a rugose texture on the fused nasals, a distinct cornual process on the lacrimal, a pneumatic quadrate, and two pairs of cervical pleurocoels (figure 3). It is more derived than Barremian tyrannosauroids in the possession of a basicranium that is wider than long, absence of pneumatic foramina along the lateral edge of the nasal, premaxillary teeth with a median lingual ridge, and lateral processes at the corners of the axial neural spine (figure 3). *Xiongguanlong* differs from *Dilong*, *Eotyrannus*, *Gorgosaurus* and adult specimens of *Tyrannosaurus* in lacking serrations along the carinae of the premaxillary dentition. Our taxonomic usage of the terms tyrannosauroid and tyrannosaurid follows Sereno *et al.* (2005).

3. DESCRIPTION

(a) *Skull*

Although complete, the skull was preserved in a mineralized nodule leading to poor separation between bone and matrix obscuring many cranial sutures. Furthermore, some features are obscured by postdepositional deformation. The skull is relatively long and low, with an extended preorbital region that is just over twice as long as the postorbital region (figure 1*b,d*). The postorbital region is laterally expanded as in Late Cretaceous tyrannosaurids, and is almost twice as wide as the rostrum (figure 1*a–d*).

The body of each premaxilla is short, roughly as tall as it is long, and holds four teeth. The maxilla is long and low, and lacks the ventral expansion along the anterior section of tooth row seen in more derived tyrannosaurids such as *Daspletosaurus* and *Tyrannosaurus* (figure 1*b,d*). The antorbital fossa is clearly defined on the lateral surface of the maxilla, and extends far rostral to the ascending process of the maxilla as it is in Late Cretaceous tyrannosaurids. Dorsoventral crushing of the skull obscures the floor of the antorbital fossa, but the maxillary fenestra, if present, was small and far removed from the

ventral edge of the antorbital fossa as in basal tyrannosauroids (Carr *et al.* 2005). The antorbital fenestra is short and covers less than half of the antorbital fossa. It is dorsoventrally deep as is seen in other tyrannosaurids where it exposes the palatines in lateral view. The maxillary palatal shelves (figure 1*c*) extend far caudally, creating an extensive bony palate along most of the rostrum as in tyrannosaurids and *Dilong* (IVPP V11579).

The nasals are fused rostrally as in other tyrannosauroids, although the poor state of preservation makes it difficult to discern the rostrocaudal extent of this fusion. Their lateral edges are more parallel than the hour-glass shaped nasals of adult tyrannosaurids (figure 1*a*). The lateral edge of each nasal is not pneumatic in contrast to *Eotyrannus* and *Dilong* (Xu *et al.* 2004), and unlike these taxa, the lateral edges of the nasals are not developed into low crests. Although the nasals are thick, they display neither the dorsal rugosities (figure 1*a*) observed in all Late Cretaceous tyrannosauroids (Carr *et al.* 2005) nor the pronounced vaulting observed in large tyrannosaurids (Snively *et al.* 2006). Although nasal rugosities become more pronounced with age in Late Cretaceous tyrannosauroids, some development of dorsal rugosities is observed in even the youngest specimens of *Gorgosaurus* (Carr 1999) and juvenile *Tyrannosaurus* (BMR P.2002.4.1) indicating that this difference is taxonomic in nature.

The rostral process of the Γ- shaped lacrimal bears a dorsolateral ridge defining the border of the antorbital fossa (figure 1*d*), but lacks the dorsal cornual process and inflated lacrimal pneumatic recess seen in Late Cretaceous tyrannosauroid taxa (Carr *et al.* 2005), although it has a convex dorsal edge above the ventral process as in *Eotyrannus* (MIWG 1997.550). The prefrontal is triangular in dorsal view and excluded from the orbital rim by contact between the lacrimal and postorbital as in tyrannosaurids, but unlike *Dilong* (IVPP V11579), where the prefrontal is exposed. Its posterior process is longer and more tapered than in either *Albertosaurus* and *Tyrannosaurus*.

A small jugal pneumatic recess perforates the dorsal rim of the jugal on the right side of the holotype. It is minute in contrast to that of even juvenile Late Cretaceous tyrannosaurids, in which this recess expands throughout ontogeny (Carr 1999). The postorbital process is wide and has a vertical caudal border forming the rostral margin of the infratemporal fenestra as in tyrannosaurids. In the basal taxon *Dilong*, the postorbital process is wider than reconstructed by Xu *et al.* (2004), but is posteriorly inclined rather than vertical as in more derived forms.

The postorbital ventral process overlaps the jugal to form a broad postorbital bar (figure 1*d*) as in tyrannosaurids, but due to poor preservation the exact course of the suture between these elements is difficult to trace. A large concave extension of the supratemporal fossa extends on to the dorsal surface of the deep orbital process (figure 1*a*). The intertemporal bar of the postorbital is long and extends across the infratemporal fenestra slotting deep into the squamosal. The ventral process of the squamosal is broad and set at an acute angle to the intertemporal process. Together with the broad dorsal process of the quadratojugal, it forms a wide convex wedge protruding into the infratemporal fenestra as in tyrannosaurids (figure 1*b*), but unlike *Dilong*. In dorsal view the squamosal forms a massive, rounded posterolateral corner

to the supratemporal fenestra. The postquadratic process of the squamosal is wide and curves sharply ventrally.

The quadratojugal has a slender rostral process and a flaring dorsal process (figure 1*b*). The caudal rim of the dorsal process is flexed transversely as in other tyrannosaurids, forming a thin lamina along the lateral border of the enlarged quadrate foramen (figure 1*e*; see the electronic supplementary material, figure 6*a*) as in *Tyrannosaurus* (FMNH PR 2081; BMR P.2002.4.1) and *Gorgosaurus* (Carr 1999).

The quadrate is relatively massive with a strongly expanded condylar region (figure 1*e*, see the electronic supplementary material, figure 6*a*). The lateral condyle is wider than the medial one, and they are separated by an oblique and wide sulcus. No pneumatic foramina are observed either on the caudal surface of the shaft as in a variety of maniraptorans (Maryanska & Osmólska 1997), or at the juncture of the shaft and quadrate wing as in tyrannosaurids (Molnar 1991; Carr 1999).

The skull table is flat, and the interfrontal suture appears to be open. Sutural contacts between the frontals and neighbouring elements are difficult to discern because of poor preservation, but it appears that the frontals were largely excluded from the orbital margin as in tyrannosaurids. As in tyrannosaurids, the fused parietals are short and bear a short, concave sagittal crest unlike the flat, albeit narrow and caudally tapering, parietal midline of *Guanlong* and *Dilong*.

The braincase of FRDC-GS JB16-2-1 is exposed in ventral and occipital views (figure 1*c,e*, see the electronic supplementary material, figure 6*a*). An oblique suture along each side of the robust and hemispherical occipital condyle marks the contact between the basioccipital and exoccipital contributions. The basioccipital is relatively shallow below the condyle and terminates in two widely separated basal tubera. These are connected by a ventrally concave lamina of bone that forms the back wall of the basisphenoid recess. Low ridges that have been interpreted as insertions for *M. longissimus capitis profundus* (Snively & Russell 2007) extend obliquely from the base of the condyle to the basal tubera. Such ridges are more prominent in larger bodied Late Cretaceous tyrannosauroids (Bakker *et al.* 1988). Although sutures are hard to make out, the exoccipital probably contributes to the lateral edge of the tuber. In tyrannosauroid outgroups, as well as the tyrannosaurids *Gorgosaurus* (Bakker *et al.* 1988) and *Albertosaurus* (RTMP 81.10.1), this exoccipital flange tapers to a point and does not contribute to the basal tuber. Subcondylar recesses as reported in some tyrannosaurids, *Itemirus* and ornithomimids (Witmer 1997) are absent. The openings for cranial nerves X–XII are tucked under the stalk of the occipital condyle, but not inset into a deep depression as in *Daspletosaurus* (FMNH PR 308).

The basicranium is wider than long as in tyrannosaurids (figure 1*c*, see the electronic supplementary material, figure 6*a*), but unlike *Dilong* in which the braincase is about as long as it is wide across the basisphenoid recess. A large, deep recess occupies the ventral face of the basisphenoid. It is bordered rostrally and caudally by thin laminae spanning between the basipterygoid processes and the basal tubera, respectively. The lateral walls of the recess are thicker and bear a ventral depression for muscular insertion (Bakker *et al.* 1988). These muscle scars are smooth as in juvenile *Gorgosaurus*, unlike the

rugose scars of ontogenetically older individuals (Carr 1999). Two irregular foramina pierce the rostral wall of the basisphenoid recess near the roots of the basipterygoid processes (see the electronic supplementary material, figure 6a). Such foramina are present in Late Cretaceous North American tyrannosaurids, but differ in size and exact location among taxa (Bakker *et al.* 1988). In *Dilong*, a single large opening excavates the anterior part of the basisphenoid recess (IVPP 14242).

Xiongguanlong displays an extensive secondary palate (figure 1c). A deep blade-like vomer lacking the diamond shaped rostral expansion observed in adult *Tyrannosaurus* (Osborn 1912; Carr 1999) is exposed between the maxillary palatal shelves on the palatal midline. The caudally positioned interchoanal processes of the palatines indicate a caudal position for the choanae. Each pterygoid displays a wide palatal flange and an interpterygoid vacuity separates the left and right flanges in ventral view. Each palatal flange is broadly overlapped by the ectopterygoid, which is blocky and bears an inflated jugal process (Carr 1999) and an enlarged ventral pneumatic opening as in tyrannosaurids (Currie *et al.* 2003).

Although most of the upper teeth of FRDC-GS JB16-2-1 were preserved in their alveoli, they are poorly preserved and only a few retain well-preserved carinae (figure 1f). The premaxillary teeth are characteristic of tyrannosaurids in having a D-shaped cross section with a raised ridge along the lingual midline (figure 1g). They lack serrations as in juvenile, but not adult, specimens of *Tyrannosaurus* (BMR P.2004.1) and some isolated, diminutive teeth from the Mussentuchit member of the Cedar Mountain Formation (Cifelli *et al.* 1999). The maxillary teeth are labiolingually narrow as in basal tyrannosauroids and juvenile tyrannosaurids (Currie *et al.* 2003), and bear serrations along both carinae (figure 1f). There are 15 tooth positions in the better preserved left maxilla. As in other tyrannosauroids, the tallest crowns occur in the second to sixth sockets. Serrations are small and block-shaped as in Campanian tyrannosaurids (Abler 1992), and are smaller along the mesial carina of each tooth.

(b) *Postcranium*

The entire presacral vertebral column is preserved (see the electronic supplementary material, figure 6b–f), although many elements are in poor condition. The atlas intercentrum is semicircular in rostral view, with a concave rostral and a convex caudal face. The neurapophyses are unfused unlike in older specimens of *Tyrannosaurus* (FMNH PR 2081). The neural arch and centrum of the axis (figure 2a; see the electronic supplementary material, figure 6b) are firmly co-ossified as in all other vertebrae, yet the position of the neurocentral suture remains discernible throughout the cervical series. The axial intercentrum and odontoid process are both attached, but incompletely co-ossified with the axial centrum (figure 2b,c). A single, large pneumatic foramen marks the lateral surface of the axial centrum, and a prominent parapophysis occupies the rostroventral corner of the centrum. Paired pneumatic foramina invade the axial corpus in more derived tyrannosaurids including *Albertosaurus* (P. J. Makovicky 1995, unpublished thesis) and *Tyrannosaurus* (Brochu 2002). The neural spine flares laterally at its distal end forming a triangular spine table in

dorsal and caudal view as in Late Cretaceous tyrannosaurids (figure 2b,c), although the degree of expansion is less developed in *Xiongguanlong*.

The postaxial cervical centra of *Xiongguanlong* are not rostrocaudally abbreviated as in Late Cretaceous tyrannosaurid taxa and remain visible beyond the arch in dorsal view (figure 2d,e; see the electronic supplementary material, figure 6b). In *Tyrannosaurus*, the cervical and dorsal centra are entirely hidden below the expanded neural arches in dorsal view (Brochu 2002). The articular facets are flat, as in all tyrannosauroids. Cervicals 3–6 have highly angled rostral and caudal intercentral articulations with the caudal surface projected much further ventrally than the rostral surface (figure 2d). A single pair of small pneumatic foramina is present on each cervical unlike the double pairs of openings observed in, for example, *Albertosaurus*, *Daspletosaurus* and *Tyrannosaurus* (P. J. Makovicky 1995, unpublished thesis; Brochu 2002). As in *Dilong*, but in contrast to tyrannosaurids, the cervical neural spines are not mediolaterally expanded. Prominent epipophyses are present in the anterior cervicals, but are progressively reduced in more caudal elements. Cervicals 5–8 bear small deflections of the medial edge of the prezygapophyses forming small hypantra (figure 2e, see the electronic supplementary material, figure 6c). Such structures are also observed in *Tyrannosaurus rex* (Brochu 2002) and occur independently in *Megaraptor* and carcharodontosaurids (Smith *et al.* 2008).

The anterior dorsal centra are mediolaterally constricted in contrast to tyrannosaurids (see the electronic supplementary material, figure 6d). The first dorsal bears a small tuber on the ventral midline where an enlarged hypapophysis is observed in maniraptorans. Neural spine height increases progressively in the direction of the sacrum, but unfortunately most of the posterior dorsals bear damaged arches (see the electronic supplementary material, figure 6e,f).

A large part of the right and the dorsal margin of the left ilium of FRDC-GS JB16-2-1 were recovered (see the electronic supplementary material, figure 6a). The dorsal iliac borders are highly convex and pressed against each other indicating that contact above the sacrum was present as in Late Cretaceous tyrannosaurids (and ornithomosaurs), but in contrast to the parallel straight-edged ilia of *Guanlong* (Xu *et al.* 2004). The base of the cuppedicus fossa is preserved and the fossa is deepest just ventral to the base of the preacetabular process. A low intramuscular ridge rises dorsally above the damaged acetabulum of the right ilium as in other tyrannosauroids (Rauhut 2003a,b).

A complete left femur is preserved with FRDC-GS JB16-2-1 (figure 2g–j). The femoral head is confluent with the greater trochanter and projects laterally and slightly proximally, as in *Tyrannosaurus* (Brochu 2002). The wing-like anterior or lesser trochanter almost (figure 2g,j) reaches the level of the greater trochanter from which it is separated by a cleft. The fourth trochanter is formed as a robust ridge along the caudomedial face of the shaft and is located a short distance below the base of the lesser trochanter (figure 2h,i). The femoral shaft is bowed, but this is probably exaggerated by taphonomic distortion. The deep popliteal fossa is flanked by a block-shaped tibiofibular crest (figure 2i,j, see the electronic supplementary material, figure 6a). A deep, well-developed extensor groove bordered by a medial entepicondylar crest
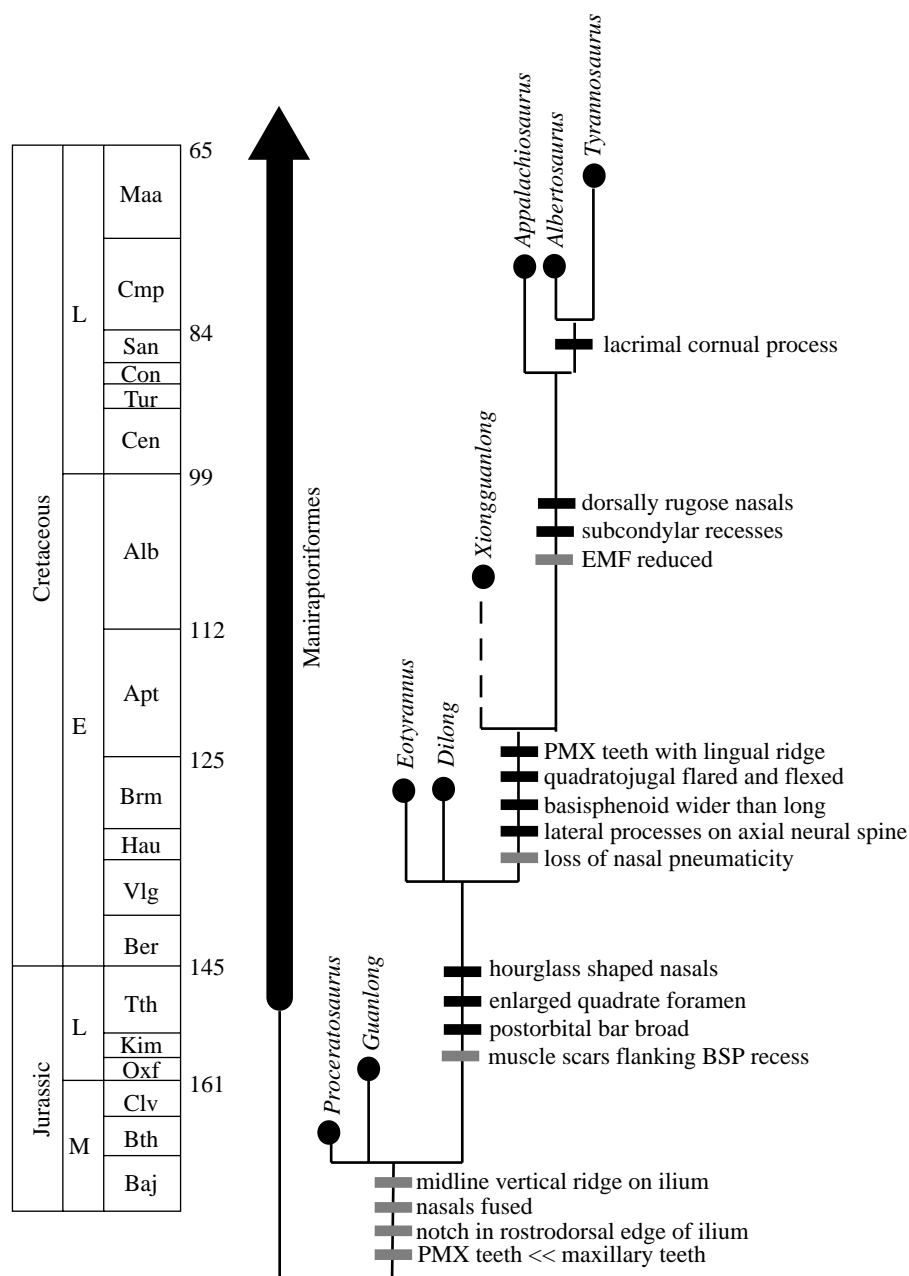
Figure 3. Calibrated cladogram showing relationships of *X. baimoensis* to other tyrannosauroids with optimizations of select tyrannosauroid characters discussed in the text. The branch for *Xiongguanlong* is stippled to indicate uncertainty regarding its age. The topology is derived from analysis of 293 characters in 72 theropod taxa using the program TNT (Goloboff *et al.* 2008; see the electronic supplementary material 3–5). Synapomorphies marked with a black bar represent unambiguous optimizations, whereas those indicated in grey are ambiguous due to either missing data or unresolved relationships at adjacent nodes. Abbreviations: BSP, basisphenoid; EMF, external mandibular fenestra; PMX, premaxillary.

(figure 2*h*) is present as in Late Cretaceous tyrannosaurids (Brochu 2002). A theropod tibia discovered alongside FRDC-GS JB16-2-1 is probably not from the holotype as it is markedly shorter and more slender than the femur, although morphologically consistent with being from a coelurosaur.

4. DISCUSSION
Phylogenetic analysis (see the electronic supplementary material 3–5 for character definitions, matrix and expanded presentation of results) demonstrates that *Xiongguanlong* occupies an intermediate phylogenetic position within the tyrannosauroid radiation as the sister taxon to the Tyrannosauridae plus *Appalachiosaurus* (figure 3), and represents the most complete tyrannosauroid from the entire time span bracketed by the Barremian and Campanian. *Xiongguanlong* marks the earliest phylogenetic and temporal appearance of several tyrannosaurid hallmarks such as a sharp parietal sagittal crest, a quadratojugal with a dramatically flaring dorsal process and a flexed caudal edge, premaxillary teeth bearing a median lingual ridge, and a flaring axial neural spine surmounted by distinct processes at its corners (figure 3). Remarkably, *Xiongguanlong* has dorsally smooth nasals indicating no phylogenetic continuity between the caudally flaring and paired nasal ridges of *Dilong* and *Eotyrannus* on the one hand, and the irregularly sculpted tyrannosaurid nasals on the other. In other traits, however, *Xiongguanlong* retains the plesiomorphic condition relative to its Late Cretaceous relatives. Unlike the conical tooth

crowns of taxa such as *Tyrannosaurus*, *Xiongguanlong* has mediolaterally compressed tooth crowns. The cervical vertebrae display only a single pair of pneumatic foramina, and the dorsal centra are not pneumatic in contrast to *Albertosaurus* and more derived tyrannosaurids.

Xiongguanlong is remarkable in having a shallow and narrow snout forming more than two thirds of skull length (figure 1a–d). Only *Alioramus* from the Late Cretaceous of Mongolia (Kurzanov 1976) approaches these proportions among tyrannosauroids. Although juvenile specimens of some other tyrannosaurid species display more elongate preorbital regions than adults (Carr 1999), most tyrannosaurids have short deep snouts mechanically optimized for powerful biting (Rayfield 2004). Such robust proportions are most evident in the largest taxa *Tyrannosaurus* and *Tarbosaurus*, which also possess the most strongly vaulted nasals that probably represent an adaptation to extreme bite forces (Snively *et al.* 2006). The nasals of *Xionguanlong* display little transverse vaulting with little or no dorsal ornamentation, indicating that this animal was not as well adapted to withstand extreme asymmetrical bite forces as its Late Cretaceous relatives, an observation consistent with its longirostrine and shallow snout that would have tempered rostral bite forces with a disproportionately long lever arm to the mandibular glenoid. In light of our recovered phylogeny, the slender, unornamented nasals observed in *Xiongguanlong* suggest a more complex order of transformations in the mechanical integration of adaptations for increased bite forces in tyrannosaur evolution than the stepwise scenario proposed by Snively *et al.* (2006). Although *Dilong* exhibits a relatively greater degree of nasal vaulting in the narial region and *Eotyrannus* displays a proportionately greater thickening of the midnasal region than in *Xiongguanlong*, this is probably accentuated by the extreme elongation of the nasals in the latter taxon. The seemingly greater robustness of the nasals in these Barremian taxa is also compromised by deep, lateral pneumatic pockets that invade the nasals at their narrowest points. Optimization of nasal traits on our tree (figure 3) indicates that loss of nasal pneumatics and narial crests of basal tyrannosauroids precedes the development the thickened and gnarly nasals of tyrannosaurids. The relatively narrow, thin, less ornamented, and less vaulted nasals of juvenile specimens of *Albertosaurus* (Snively *et al.* 2006), *Tyrannosaurus* (Carr 1999) and *Tarbosaurus* (Maleev 1955) parallel the condition in *Xionguanlong* and *Alioramus*, which appears to be plesiomorphic for tyrannosaurids. The development of broader, thicker and more 'warty' nasals and the proportionately wider snouts in adults of *Tyrannosaurus* and *Tarbosaurus* compared with those of more basal taxa is probably the result of heterochronic processes as indicated by Carr (1999) and is tied to shifts in life-history parameters such as maximum size and growth rate (Erikson *et al.* 2004).

Xiongguanlong is smaller than other presumably non-predatory theropods from the Xinminpu Group of the Yujingzi Basin such as the therizinosaur *Suzhousaurus* (Li *et al.* 2007, 2008) and the ornithomimosaur *Beishanlong* (Makovicky *et al.* in press), following a pattern seen in other Cretaceous Central Asian Formations for which presumably beaked theropod taxa rival or exceed the size of tyrannosauroid predators. Near complete closure of neurocentral sutures indicates that the holotype of *Xiongguanlong* is close to being fully grown, with an estimated body mass of 272 kg according to equations developed by Christiansen & Fariña (2004). All known Late Cretaceous tyrannosaurids possess significantly greater adult body masses, whereas *Dilong* is much smaller in size than *Xiongguanlong*. The holotype of *Eotyrannus* is also smaller, although it derives from a subadult specimen and it is possible that it had a similar adult size to *Xiongguanlong*. Our phylogenetic hypothesis suggests that the trend towards increasing body size through time observed in North American Late Cretaceous tyrannosaurids (Erikson *et al.* 2004) may extend through the Cretaceous history of Tyrannosauroidea, though *Dilong* may alternatively represent a case of body size reduction if taxa such as *Guanlong* and *Stokesosaurus* represent the basal tyrannosauroid condition (Xu *et al.* 2006; Benson 2008). Such trends are sensitive to phylogenetic accuracy, and further sampling of taxa and characters is required to accurately reconstruct relationships for the diversity of Jurassic coelurosaurs described in recent years. Our results corroborate inclusion of *Guanlong* within Tyrannosauroidea, however, rather than supporting affinities with the sympatric, crested theropod *Monolophosaurus* as has been recently suggested (Carr 2006).

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