## Supporting Online Material for

Tyrannosaurid Skeletal Design First Evolved at Small Body Size
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## 1. Material preserved

The holotype and only known specimen of Raptorex kriegsteini (LH PV18) preserves the following bones:

## 1a. Skull

Cranium—Rt. premaxilla, It. maxilla, It. lacrimal, It. and rt. nasal, rt. prefrontal, rt. and It. frontal, portion of the It. parietal, It. postorbital, It. distal quadrate, partial It. palatine, It. side of the basisphenoid, parasphenoid, It. epipterygoid.

Lower jaw—Rt. and partial It. dentary, It. and partial rt. surangular, It. and partial rt. angular, It. and fragment of the rt. prearticular, partial rt. splenial, It. articular.

Dentition—Rt. premaxillary teeth $1,3,4$; It. premaxillary tooth 1 ; It. maxillary teeth 112; rt. dentary teeth $3,5,7-11$; It. dentary teeth $6-11$; 10 isolated maxillary or dentary teeth.


Fig. S1. Partially fused nasals of Raptorex kriegsteini (LH PV18) in dorsal view.
Scale in centimeters.


Fig. S2. Left maxilla of Raptorex kriegsteini (LH PV18) in lateral view. Scale in centimeters.


Fig. S3. Left lacrimal of Raptorex kriegsteini (LH PV18) in lateral view. Scale in centimeters.


Fig. S4. Left jugal of Raptorex kriegsteini (LH PV18) in lateral view. Scale in centimeters.

1b. Postcranial skeleton
Axial skeleton-C1-10, D1-13, S1-5, CA1-11; 3 partial cervical ribs, 18 partial or complete dorsal ribs; 1 pair of fused anterior medial gastral elements, proximal portion of 5 medial gastral elements.

Pectoral girdle—Lt. coracoid, It. scapula.
Forelimb—Rt. and It. humerus, It. radius, It. ulna, It. manual digit I, It. manual phalanges II-1 and II-2.

Pelvic girdle—Nearly complete rt. and It. ilium, proximal rt. and It. ischium, proximal and distal ends of the rt. pubis, It. pubis lacking the foot.

Hind limb—Rt. and It. femur, It. and proximal end of rt. tibia, proximal and distalmost end of It. fibula, It. astragalus, It. metatarsals 2 and 4, distal end of rt. metatarsal 3, five nonungual pedal phalanges, three pedal unguals.


Fig. S5. Right scapulocroacoid of Raptorex kriegsteini (LH PV18) in lateral view.
Scale in centimeters.


Fig. S6. Left astragalus and distal tibia of Raptorex kriegsteini (LH PV18) in anterior view. Scale in centimeters

## 2. Measurements

## 2a. Skull size

The skull in Raptorex measures about 30 cm in length, which is unusually long relative to the postcranial skeleton as in tyrannosaurids. Skull and trunk length are the relative measures used in the present study to estimate relative skull size. Skull length is measured from the tip of the premaxilla to the posterior margin of the quadrate
condyle. Trunk length is measured on a skeletal drawing from the anterior extremity of the pectoral girdle to the posterior extremity of the pelvic girdle. Measured in this or other ways, skull length relative to trunk length is negatively allometric in most dinosaurs (S1) except in tyrannosaurids (S2).

Skull length as a percentage of trunk length is less than $30 \%$ in mid-to-large sized theropods except in the long-snouted spinosaurids, Raptorex and tyrannosaurids: Ornitholestes hermanii (24\%), Gualong wucaii (30\%), Raptorex kriegsteini (40\%), Albertosaurus libratus (42\%), Tyrannosaurus rex (40\%). Percentages were calculated from skeletal drawings in from one source to reduce variation (S3), except for Raptorex (Fig. 1A) and Guanlong (S4).

Skull length in Raptorex is also approximately equal to the summed length of the cervical series (Table S1) and approximately $62 \%$ of the dorsal series. Comparable measurements are available or can be estimated for the Early Cretaceous tyrannosauroid Xiongguanlong (S5), which has a skull approximately 50 cm in length or 1.6 times that of Raptorex. Roughly similar proportions are present relative to the length of the cervical or dorsal vertebrae, suggesting that the skull of Xiongguanlong is also enlarged relative to its trunk length as in Raptorex and tyrannosaurids. This feature was not used in the phylogenetic analysis but does suggest that relative skull enlargement may eventually characterize some basal tyrannosauroids besides Raptorex.

## 2b. Skull and bone measurements

Measurements are given in Table S1 for the skull and postcranial skeleton of the holotype of Raptorex kriegsteini.

Table S1. Skeletal measurements (cm) of the of the Early Cretaceous tyrannosauroid Raptorex kriegsteini n. gen. n. sp. (LH PV18). Parentheses indicate estimate.
Measurements are from the right side for paired bones except as indicated.
Abbreviations: C, cervical vertebra; CA, caudal vertebra; $D$, dorsal vertebra; $S$, sacral vertebra.
Bone MeasurementCranium
Cranium length (premaxilla to quadrate condyle) ..... (30.0)
Occiput height (quadrate condyle to parietal occipital flange) ..... (10.0)
Antorbital fossa maximum height ..... (7.6) ..... (7.0)
Minimum interorbital width ..... 5.7
Quadrate height(6.8)
Endocast, olfactory bulb maximum width ..... 1.2
Endocast, cerebral hemisphere maximum width ..... 2.0
Axial skeleton
C1 intercentrum length ..... 0.8
C2 centrum length (without odontoid) ..... 2.7
C3 centrum length ..... 2.8
C4 centrum length ..... 2.9
C5 centrum length ..... 3.4
C6 centrum length ..... 3.6
C7 centrum length ..... 3.6
C8 centrum length ..... 3.4
C9 centrum length ..... 3.5
C10 centrum length ..... 3.2
D1 centrum length ..... 2.8
D2 centrum length ..... 3.0
D3 centrum length ..... 3.1
D4 centrum length ..... 3.2
D5 centrum length ..... 3.2
D6 centrum length ..... 3.3
D7 centrum length ..... 3.4
D8 centrum length ..... 3.6
D9 centrum length ..... 3.6
D10 centrum length ..... 3.8
D11 centrum length ..... 4.1
D12 centrum length ..... 4.4
D13 centrum length ..... 4.5
S1 centrum length ..... 4.7
S2 centrum length ..... 4.7
S3 centrum length ..... 4.8
S4 centrum length ..... 4.9
S5 centrum length ..... 4.6
CA1 centrum length ..... 4.0
CA2 centrum length ..... 4.0
CA3 centrum length ..... 4.1
CA4 centrum length ..... 4.1
CA5 centrum length ..... 4.2
CA6 centrum length ..... 4.2
CA7 centrum length ..... 4.2
CA8 centrum length ..... 4.3
CA9 centrum length ..... 4.3
CA10 centrum length ..... 4.3
CA11 centrum length ..... 4.2
Pectoral girdle
Scapula length ..... $15.1^{\text {L }}$
Scapular blade, minimum neck width ..... $1.1^{\text {L }}$
Scapular blade, distal width ..... $1.9^{\text {L }}$
Coracoid length ..... $4.2^{\mathrm{L}}$
Coracoid height ..... $5.7^{\text {L }}$
Forelimb
Humerus length ..... 9.9
Humeral head to apex of deltopectoral crest ..... (2.2)
Radius length ..... $5.2^{\text {L }}$
Ulna length ..... $5.7^{\text {L }}$
Manual digit II length ..... (5.5)
Metacarpal 1 length ..... $1.5^{\llcorner }$
Manual phalanx I-1 length ..... $2.6^{\text {L }}$
Manual ungual I-2 length ..... (1.8)
Manual phalanx II-1 length ..... $1.3^{\mathrm{L}}$
Manual phalanx II-2 length ..... (2.2) ${ }^{\text {L }}$
Pelvic girdle
Iliac blade length ..... $33.5^{\text {L }}$
Iliac blade height above acetabulum ..... $8.2^{\mathrm{L}}$
llium, width of pubic peduncle(5.5)
Ischium length(22.5)
Ischium, pubic peduncle length ..... $2.8^{\text {L }}$
Ischium, iliac peduncle ..... $2.5^{\llcorner }$
Ischium, mid shaft vertical height ..... $1.6^{\mathrm{L}}$
Pubis length(28.9)
Pubis shaft proximal to blade, transverse width ..... 4.5
Pubic foot length(13.3)
Hind limb
Femur length ..... 33.8
Tibia length ..... 39.7
proximal end, anteroposterior length ..... 6.8
mid shaft, transverse width ..... 4.6
mid shaft, anteroposterior width ..... 6.9

| distal end, transverse width | $2.6^{L}$ |
| :--- | :--- |
| Fibula proximal end, anteroposterior width |  |
| distal end, anteroposterior width | $5.2^{\mathrm{L}}$ |
| Astragalus, articular surface, transverse width | $3.3^{\mathrm{L}}$ |
| Astragalus, ascending process height | $5.0^{\mathrm{L}}$ |
| Metatarsal 2 length | $5.8^{\mathrm{L}}$ |
| Metatarsal 2 proximal end, transverse width | $24.5^{\mathrm{L}}$ |
| Metatarsal 4 length | $2.9^{\mathrm{L}}$ |
| Metatarsal 4proximal end, maximum transverse width | $26.6^{\mathrm{L}}$ |
| Pedal phalanx III-1 length | $3.2^{\mathrm{L}}$ |
| Pedal ungual I-2 length | $(6.2)^{\mathrm{L}}$ |
| Pedal phalanx II-1 length | $1.7^{\mathrm{L}}$ |
| Pedal phalanx II-2 length | 5.5 |
| Pedal phalanx III-1 length | $3.5^{\mathrm{L}}$ |
| Pedal phalanx III-2 length | $3.6^{\mathrm{L}}$ |
| Pedal ungual IV-5 length | 3.7 |
| Pedal ungual IV-5 length | 2.7 |

[^0]
## 3. Maturity and age assessment

The holotypic skeleton appears to be nearing maturity based on several gross skeletal features. In the skull, the internasal suture is obliterated in the zone of fusion, and the interfrontal, frontoparietal, and several sutures in the braincase appear partially coossified (Fig. S1). In the axial column, all of the neural arches are attached in natural articulation with their centra. The only neurocentral sutures that remain open are in the posterior dorsal and anterior caudal vertebrae. Neurocentral sutures have closed and are coossified in cervical, anterior and mid dorsal, and sacral vertebrae (Fig. 2B, C).

In the pectoral girdle, the scapula and coracoid are preserved in articulation, but the suture is not obliterated (Fig. S5). In the pelvic girdle, the ilioischial articulation is partially fused; the cone-shaped articular process on the ischial peduncle of the ilium is lodged within, and partially fused with, a conical articular socket on the iliac peduncle of the ischium. The astragalus, in addition, is attached and possibly partially coossified with the distal end of the tibia (Fig. S6). These features collectively suggest that the holotypic skeleton is a subadult or young adult that is nearing its mature body size.

To independently assess the maturity and age of the holotypic skeleton, histological thin-sections were made from the mid shaft region of the right femur (Histology Lab, Montana State University). Most of the cross-section consists of fibro-
lamellar tissue with predominantly circumferentially arranged osteons (Fig. S7). The medullary cavity within the shaft is relatively large. There are two LAGs (lines of arrested growth) within the inner half of the cortex. Both are traceable around the entire cross-section. The large size of the medullary cavity and the close spacing of the two LAGs suggests that at least one and probably two inner LAGs have been lost to growth and remodeling of the medullary cavity. Near or at the periphery of the cortex is located a circumferentially-oriented band of lamellar bone. This band extends around about half of the femoral section, the remaining lost to post-mortem erosion. This band likely represents a growth ring and appears to be associated with a LAG on its inner side. It does not represent an EFS (external fundamental system) of an fully mature adult, as fibrolamellar bone is present external to it in some places.

LAGs 1 and 2 are closely spaced in comparison to the growth between LAG 2 and the peripheral growth band (LAG 3). In consideration of models for growth rate among tyrannosaurids and other dinosaurs (S6), the wider spacing between LAG 2 and 3 may correspond to the more rapid, exponential phase of growth, and the band of lamellar bone associated with LAG 3 may be evidence of slower growth after the final preserved interval of arrested growth. In this interpretation, the thickness of the zone of fibrolamellar bone between LAGs 2 and 3 is evidence of the exponential growth of a "subadult" (S6). It was likely in its sixth year at time of death (2 resorbed initial LAGs, 3 more in cortical bone) and could be classed as either a "subadult" or "young adult", the latter if it were in transition to a stationary growth phase (S6). Basal tyrannosaurids, by contrast, are considerably larger as adults and experience exponential growth in skeletal bone later in development (years 10-15) (S6).

Both skeletal and histological data, thus, suggest that the holotypic skeleton of Raptorex kriegsteini is a "subadult" or "young adult" nearing adult skeletal proportions. Graphical (Fig. 2A) and physical reconstruction of the skeleton yield a body length estimate of 2.5 m . Adding approximately $20 \%$ for final growth yield an adult body length estimate of 3.0 m .


Fig. S7. Histologic thin sections from the mid shaft of the right femur of Raptorex kriegsteini (LH PV18). A, section in circular polarized light. B, cortical section in transmitted light showing three well defined LAGs.

## 4. Body mass estimation

Body mass has been estimated from scale models (S7), femoral circumference (S8), femoral length (S9), and graphical reconstruction (S10, S11). These estimates, in addition, vary depending on the particular adult specimens or reconstructions on which they were based.

Body mass for Raptorex kriegsteini is estimated by comparison to theropods with comparable adult body length (3 m), femoral length, femoral mid shaft diameters, or femoral circumference (length = 338 mm ; anteroposterior diameter 24.7 mm ; anteroposterior diameter $=28.2 \mathrm{~mm}$; circumference $=87 \mathrm{~mm}$ ). The bipedal dinosaurs closest in size are Parksosaurus (S8), Velociraptor and Deinonychus (S10), and Oviraptor (S9). These were given masses of 50, 44, 105, and 58 kg , respectively, for an average of 64.3 or about 65 kg .

The range of body mass estimates for Tyrannosaurus rex varies from 4.50 to approximately 7.50 metric tonnes (S7-11). Some authors (S6) have used the midpoint, which is about 6.0 metric tonnes.

## 5. Horizon, associated fauna and comparisons

## 5a. Horizon and fauna

The skeleton was buried in a massive, poorly sorted, tuffaceous, sandstone that is light green in color with brown mottling. Abundant mica and fibrous gypsum are present. The absence of laminated, fine-grained sediment or conchostracans suggests that the deposit is fluvial in origin and likely pertains to the Lujiatun Beds of the Yixian Formation, dated to the late Early Cretaceous (Barremian-Aptian, ca. 125 Ma ) (S12).

The bones and teeth are preserved in three-dimensions and show only minor crushing. They are light-colored with darkened articular surfaces. These preservational features also suggest the skeleton was found in the Lujiatun Beds of the Yixian Formation, rather than in overlying, laminated lacustrine deposits (S12).

The fauna found in sediment adjacent to the skeletal bones include pelycepods (5-7 cm width) and disarticulated vertebrae pertaining to the teleost Lycoptera ( 4 mm diameter) (Fig. S8). Pelycepods (S13) and Lycoptera are common faunal components
of the Jehol Biota (S14). These faunal components and the articulation of the skeletal remains differentiate the Jehol Group from other dinosaur-bearing formations in the region with tyrannosauroid remains, such as the Iren Dabasu Formation (S15, S16).


Fig. S8. Fauna associated with the holotypic skeleton of Raptorex kriegsteini (LH PV18). A, pelycepod. B, teleost vertebra cf. Lycoptera. Scale in centimeters.

The Jehol Biota contains many dinosaurs (S14). Theropods known from the Lujiatun Beds include the oviraptorosaurian Incisivosaurus gauthieri, troodontid Sinovenator changii, the dromaeosaurids Mei long and Graciloraptor lujiatunensis, and the tyrannosauroid Dilong paradoxus. It is possible that Dilong and Raptorex were contemporaries.

## 5b. Raptorex versus Xiongguanlong

While it is easy to distinguish the skulls of Guanlong (S12) and Dilong (S13) from that of Raptorex given the diagnostic cranial crests on the former two genera, differences are less obvious between Raptorex and the recently described basal tyrannosaurid Xiongguanlong (S5). Like Raptorex, Dilong comes from the Lujiatun beds (between 128-139 Ma; Hauterivian-Baremian) of the Jehol Group (S14) in Liaoning

Province and an adjacent portion of southeastern Inner Mongolia. Xiongguanlong is probably younger in age from mid Cretaceous (ca. 112 Ma ; ?Aptian-Albian) rocks in northern Gansu Province some 1800 km to the west (S5).

Xiongguanlong is a larger species with a skull length of approximately 50 cm versus about 30 cm in Raptorex. Xiongguanlong has a relatively small maxillary fenestra and a deeper recessed margin (antorbital fossa) ventral to the antorbital fenestra. In dorsal view of the cranium of Xiongguanlong, the nasals are flat rather than vaulted and appear proportionately broader relative to the width across the base of the snout (just anterior to the orbits). The supratemporal fossa also does not appear to be developed as extensively on the frontals as in Raptorex.

Clear differences also are present in the postcrania attributed to Xiongguanlong. The ilium clearly does not have a straight dorsal margin as in Raptorex, and the distal end of the femur has a narrower posterior intercondylar groove (S5).

## 6. Phylogenetic analysis

## 6a. Parsimony analysis

The ingroups sample all of the best known tyrannosauroid species. The outgroups include Ornitholestes hermanni and three suprageneric taxa (Maniraptora, Ornithomimosauria, and Compsognathidae) scored on the basis of basal or well known exemplar species (Table S2). Maniraptora and Ornithomimosauria were positioned in a polytomy as nearest outgroups, and Ornitholestes and Compsognathidae were held as more remote outgroups. Alternatively, all were left as an outgroup polytomy with no difference in results.

Five characters $(6,39,40,61,83)$ involving relative measurements have three states. These multistate characters were ordered, although leaving them unordered did not affect the configuration of the shortest trees. The branch and bound algorithm in PAUP 4.0b10 yielded 28 minimum-length trees of 123 steps $(\mathrm{Cl}=0.862 ; \mathrm{RI}=0.954)$. Guanlong is situated tenuously on the basis of a single synapomorphy as the outgroup to remaining tyrannosauroids (Fig. 4B). One additional step collapses this node, leaving all basal tyrannosauroids with the exception of Raptorex in an unresolved polytomy outside Tyrannosauroidea. It requires 5 steps beyond minimum length for the least well
known of basal tyrannosauroids to break down the sister group relationship between Raptorex and Tyrannosauridae, which is based on approximately 45 ambiguous and unambiguous synapomorphies under delayed transformation.

Table S2. Taxa, references and specimens used for outgroups and ingroups in the phylogenetic analysis.

| Taxa | No. | Terminal Taxon | Exemplars for Supraspecific Terminal Taxa |
| :---: | :---: | :---: | :---: |
| $\begin{aligned} & \text { n } \\ & \frac{0}{3} \\ & \text { ob } \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | 1 | MANIRAPTORA | Sinornithosaurus millennei Velociraptor mongoliensis Citipati osmolskae Caudipteryx zoui |
|  | 2 | ORNITHOMIMOSAURIA | Shenzhousaurus orientalis Sinornithomimus dongi |
|  | 3 | Ornitholestes hermanni |  |
|  | 4 | COMPSOGNATHIDAE | Compsognathus longipes Huaxiagnathus orientalis Sinosauropteryx prima |
|  | 1 | Guanlong wucaii |  |
|  | 2 | Dilong paradoxus |  |
|  | 3 | Eotyrannus lengi |  |
|  | 4 | Stokesosaurus langhami |  |
|  | 5 | Xiongguanlong baimoensis |  |
|  | 6 | Raptorex kriegsteini |  |
|  | 7 | Gorgosaurus libratus |  |
|  | 8 | Albertosaurus sarcophagus |  |
|  | 9 | Daspletosaurus torosus |  |
|  | 10 | Tarbosaurus bataar |  |
|  | 11 | Tyrannosaurus rex |  |

## 6b. Character list and matrix

A total of 101 characters were scored in 11 tyrannosauroids and a series of outgroups. Eighteen characters (in red) are new to tyrannosauroid analysis (2, 16, 22, $32,51,54,63-66,69,71,76,78,81,88,89,101$ ); 83 characters are from previous studies of tyrannosauroid interrelationships (S18-20) or more inclusive analyses within Theropoda (S21-24) as annotated in the character list. All characters are informative for Tyrannosauroidea or tyrannosauroid subgroups.

The authors cited below were first to use the character in the context of a cladistic analysis of Tyrannosauroidea; no authors are cited for newly introduced
characters. Many of these characters are discussed in a recent comparative analysis of tyrannosaurid phylogenetics (S25). Character format and structure follow recent recommendations (S26).

## Snout

1. Premaxilla, ventral ramus (lateral view), shape: subquadrate or longer anteroposteriorly (0); deeper dorsoventrally than anteroposteriorly (1). (modified from Holtz 2001)
2. Narial fossa on nasal internarial process, location: limited to ventral margin (0); covers entire process (meets opposite in dorsal midline) (1).
3. Nasal-nasal suture, central portion, form: open (1); fused (1). (modified from Holtz 2001)
4. Nasal posterolateral lacrimal process: present (0); absent (1). (Currie et al. 2003)
5. Nasal anterior ramus, form of dorsal surface: flat (0); arched (1). (modified from Currie et al. 2003)
6. Nasal posterior portion, width: posteriorly expanding (0); subparallel (1); posteriorly tapering (2). (Holtz 2001)
7. Nasal mid section, rugosities and accessory vascular foramina: absent (0); present (1). (modified from Holtz 2001)
8. Nasal border of antorbital fossa: present (0); absent (1). (modified from Holtz 2001).
9. Nasal posterior suture, length of medial and lateral processes: subequal (0); lateral longer than medial (1). (Holtz 2001)
10.Antorbital fenestra proportions, length versus depth: longer than deep (0); subequal or deeper than long (1). (Holtz 2001)
10. Maxillary fenestra, size: less than $50 \%$ (0), or approximately $66 \%$ (1), horizontal diameter of eyeball-bearing portion of orbit. (Holtz 2001).
11. Maxillary fenestra, location: posterior to (0), or partially overlapped laterally by (1), the anterior margin of antorbital fossa. (Holtz 2001)
12. Maxilla, margin of antorbital fossa ventral to maxillary and antorbital fenestrae: present (0); absent (1). (modified from Currie et al. 2003)
13. Maxilla, form of alveolar margin (lateral view): slightly (0), or strongly convex (chord from first to last maxillary tooth runs across the body of the maxilla above the principal row of labial foramina) (1). (modified from Holtz 2001).
14. Maxillary-nasal suture, surface of tongue and groove articulation: smooth (0); interlocking transverse ridges (1). (modified from Currie et al. 20030
15. Lacrimal body, pneumatic space, extent: partial hollowing (0); complete hollowing (1).
16. Lacrimal anterior ramus, anterior portion, form: flat (0); swollen (1). (modified from Holtz 2001)
17. Lacrimal cornual process: absent (0); present (1). (modified from Holtz 2001)
18. Lacrimal cornual process, position: dorsal (0), or anterior (1), to ventral ramus. (Holtz 2001; modified by Carr et al. 2003)
19. Lacrimal-frontal contact (prefrontal removed from orbital margin): absent (0); present (1). (modified from Holtz et al. 2004)
20. Lacrimal-postorbital contact: absent (0); present (frontal excluded from orbital margin) (1). (modified from Gauthier 1986)

## 22. Lacrimal-frontal articulation, form: squamous (0); conical process set in frontal pit

 (1).
## Posterior Skull Roof

23. Jugal, ventral margin below postorbital process, inflection: absent (0); present (1). (modified from Currie et al. 2003)
24. Jugal dorsal (postorbital) process, lateral surface adjacent to laterotemporal fossa, form: convex (0); concave (1). (modified from Currie et al. 2003)
25. Jugal-postorbital, ventral extremity of suture, form: scarf joint (0); notch (1). (modified from Currie et al. 2003)
26. Jugal orbital margin, form: level with lacrimal-jugal suture, weakly concave (0); Ushaped (1). (modified from Currie et al. 2003)
27. Postorbital, orbital margin, form: transversely narrow (0); cupped (1). (modified from Holtz et al. 2004)
28. Postorbital, posterior tip of posterior process, position: reaches (0), or terminates short of (1), the posterodorsal corner of the laterotemporal fenestra. (Carr et al. 2005)
29. Postorbital, form of dorsal surface: smooth (0); rugose (1). (Holtz 2001; modified by Currie et al. 2003)
30. Postorbital, suborbital flange: absent or rudimentary (0); well developed flange (1). (modified from Gauthier 1986)
31. Squamosal-quadratojugal suture, position: level with (0), or elevated dorsal to (1), the postorbital-jugal suture. (modified from Holtz 2001).
32. Squamosal anterior process, flange dorsal to postorbital posterior process: absent (0); present (1).
33. Squamosal, pneumatic opening from supratemporal fossa: absent (0); present (1). (modified from Currie et al. 2003)
34. Quadratojugal, tip of anterior ramus, shape: tapered (0); rounded (1). (modified from Currie et al. 2003)
35. Quadratojugal, distal flaring of dorsal process: absent or moderate (0); extensive (1). (Currie et al. 2003)
36. Quadratojugal, tip of anterior ramus, location: ventral (0), or anterior (1), to the laterotemporal fenestra. (Holtz et al. 2004)
37. Frontal-postorbital suture: undifferentiated (0); subdivided into vertical and horizontal (posterior) parts (1). (Currie et al. 2003)
38. Frontal shape: triangular (0); posterior end expanded (1); rectangular base, small anterior triangle (2). (Holtz 2001)
39. Frontal supratemporal fossa, medial extension: posterolateral corner (0); meet in midline at frontoparietal suture (1); meet at sagittal crest (2). (modified from Holtz 2001)
40. Parietal supratemporal fossa, medial extension: median skull table 20-30\% of fossa width: (0); median skull table 10\% of fossa width (1); sagittal crest (2). (modified from Currie et al. 2003)
41.Parietal nuchal crest, height: less (0), or more (1), than $50 \%$ width. (modified from Holtz 2001)

## Palate

42. Quadrate condyle, position relative to occipital condyle: approximately aligned (0); completely posterior (1). (modified from Holtz et al. 2004)
43. Palatine, jugal process: absent (triradiate) (0); present (tetraradiate) (1). (modified from Holtz 2001)
44. Ectopterygoid sinus, form: hollows bone (0); hollows and inflates bone (1). (modified from Holtz 2001)
45. Vomer anterior end, form: lanceolate (0); diamond-shaped (1). (Currie et al. 2003)

## Braincase

46. Occiput, orientation facing: posteriorly (0); posteroventrally (1). (Holtz 2001)
47. Supraoccipital, pronounced median ridge: absent (0); present (1). (Currie et al. 2003)
48. Basal tubera size: subequal to (0), or significantly smaller than (1), basipterygoid processes. (Holtz 2001).
49. Basal tubera and basipterygoid processes, position: anteroposteriorly (0), or transversely (1), broader. (Currie et al. 2003)
50. Basisphenoid fossa, orientation of central axis: vertical (0); posteroventral (1). (Harris 1998)

## Lower Jaw

51. External mandibular fenestra, vertical depth relative to posterior mandible: approximately $30 \%$ (0); less than 20\% (1).
52. Surangular, posterior foramen, size: foramen (0); fenestra (approximately 30\% depth of posterior surangular) (1). (modified from Gauthier 1986)
53. Surangular shelf, form; low crest (0); prominent shelf (1). (modified from Holtz et al. 2004)
54. Jaw articulation, position relative to level of alveolar margin of dentary: level or ventral (0); dorsal (1).
55. Retroarticular process, shape: longer than broad (0); broader than long (1). (Holtz et al. 2004)

## Dentition

56. Premaxillary crowns 1 and 2, position of anterior carina: offset mesial to distal carina (0); rotated posteriorly (D-shaped cross-section) (1). (modified from Holtz 2001)
57. Premaxillary crown 3, position of carinae: anterior carina offset mesial to distal carina (0); anterior carina rotated posteriorly (D-shaped cross-section) (1). (modified from Holtz 2001)
58. Premaxillary crown 4 , position of carinae: anterior carina offset mesial to distal carina (0); anterior carina rotated posteriorly (D-shaped cross-section) (1). (modified from Holtz 2001)
59. Premaxillary crown 4, size relative to largest maxillary crown: subequal (0); approximately $50 \%$ of height (1). (modified from Holtz, 2001)
60. Premaxillary crowns, median eminence on lingual surface: absent (0); present (1). (Holtz 2001)
61. Maxilla, tooth count: 18 or more (0); 14-17 (1); 13 or fewer (2). (Holtz 2001; modified by Holtz et al. 2004 and here)
62. Largest maxillary and dentary crowns, transverse width of base: less (ziphodont) (0), or more (incrassate) (1), than $60 \%$ of anteroposterior length. (modified from Holtz 2001)

## Axial Column

63. Rib for dorsal 12, form: comma-shaped (0); L-shaped (1).
64. Gastral segment 1 , opposing medial elements, median articulation: overlapping (0); obliterating fusion with subtriangular anterior process (1).
65. Gastral segment 1 and 2, contact: absent (0); present (1).

## Pectoral Girdle and Forelimb

66. Glenoid, location relative to posteroventral margin of blade: offset posteroventrally (approximately by the width of the neck of the blade) (0); offset only slightly posteroventrally (less than $50 \%$ the width of the neck of the blade) (1).
67.Scapular acromion, height relative to neck of scapular blade: 100-150\% (0); 200300\% (1). (modified from Holtz 2001)
67. Scapular acromion, angle between posterior margin of acromion and anterodorsal margin of blade: $40-60^{\circ}(0)$; $70-90^{\circ}$ (1). (modified from Holtz et al. 2004)
68. Scapular blade, width of neck: greater (0), or less than (1), $10 \%$ of blade length.

70 . Scapular blade, distal expansion relative to neck: subequal (0), approximately $200 \%$ (1). (modified from Holtz 2001)
71. Coracoid, length relative to width of acromion at mid height: 100-150\% (0); approximately $200 \%$ (1).
72. Humerus relative to the femur, length: 50-70\% (0); 25-30\% (1). (modified from Holtz 2001)
73. Humeral head, form: low, poorly differentiated (0); bulbous, occupies the majority of the proximal end (1). (modified from Holtz et al. 2004)
74. Humeral deltopectoral crest apex, location from proximal end: 40-50\% (0); 20-30\% (1). (modified from Holtz et al. 2004)
75. Ulnar shaft axis, form: bowed (0); straight (1). (Gauthier 1986)
76. Ulnar distal articular surface, form: convex (0); flat (1).
77. Ulnar olecranon process, form: rounded, blunt (0); pointed, prominent (1). (modified from Holtz et al. 2004)
78. Metacarpal 1, medial distal condyle: well formed (1); rudimentary (0).
79. Metacarpal 2-metacarpal 1 length ratio: 2-1.8 (0); 1.8-1.6 (1). (modified from Holtz 2001)
80. Manual digit l-phalanx 1, length: longer than (0), subequal to (1), metacarpal 2. (modified from Holtz 2001)
81. Manual phalanx II-1, length: longer than (0), or subequal to (1), the length of metacarpal 1.
82. Manual digit III, form: functional digit (phalanges present) (0); vestigial (no phalanges, rudimentary metacarpal) (1). (Gauthier 1986)

## Pelvic Girdle and Hind Limb

83. Ilium, length relative to femur: 70-85\% (0), $95-105 \%$ (1), 110-115\% (2). (modified from Holtz 2001)
84. Ilium, vertical ridge dorsal to acetabulum: absent or low convexity (0); present (1). (modified from Holtz 2001)
85. Iliac blade, dorsal margin, position relative to sacral neural spines: separated by gap (0); contact along dorsal margin of iliac blade (1). (modified from Holtz 2001)
86. Ilium, anterior margin of preacetabular process, dorsal portion, form: straight or nearly straight (0); concave (depth at least $15 \%$ of the length of the concave margin) (1). (modified from Holtz 2001)
87. Iliac preacetabular process, anteroventral corner, form: subtriangular (0); subquadrate with recurved anterior margin, projecting farther anteriorly than reminder of anterior end (1). (modified from Holtz 2001)
88. Iliac preacetabular (cuppedicus) fossa, transverse width: less than (0), or subequal to (1), pubic peduncle.
89. Iliac pubic peduncle, posteromedial margin, form: concave (0); recurved (1).
90. Iliac acetabular antitrochanter, posterior end of supraacetabular shelf: absent (0); present (1). (modified from Holtz 2001)
91. lliac acetabular crest, maximum lateral projection relative to ischial peduncle: significantly greater (0); subequal (1). (modified from Holtz et al. 2004)
92. Ischium, articular surface for ilium, form: shallow concavity (0); conical pit (1). (modified from Holtz et al. 2004)
93. Ischium, attachment area ventral to iliac peduncle, form: rugose scar or pit (0); pointed, subtriangular flange with scar facing laterally (1). (modified from Holtz 2001)
94. Ischial mid shaft diameter (anteroposterior) relative to pubic mid shaft diameter: 6590\% (0); 30-50\% (1). (modified from Holtz et al. 2004)
95. Ischial foot (distal expansion): present (0); absent (1). (Holtz 2001)
96. Pubic obturator opening, posterior margin: present (foramen) (0); absent (notch) (1). (modified from Holtz et al. 2004)
97. Pubic foot, anterior ramus, length relative to posterior ramus: 20-40\% (0); subequal (1). (modified from Holtz et al. 2004)
98. Femoral anterior trochanter, height relative to greater trochanter: shorter (0); subequal or slightly taller (1). (modified from Holtz 2001)
99. Tibia, length relative to femur (compared to theropods of comparable body size): short (subequal or shorter than femur) (0); long (110\% or more of femur length) (1). (modified from Holtz 2001)
100. Metatarsal 3 shaft, form: subcylindrical, proximal end exposed anteriorly (0); wedge-shaped, proximal end covered anteriorly by metatarsal 2-4 contact (1). (modified from Holtz 1994)
101. Metatarsal 3, ventral nonarticular surface immediately proximal to the distal condyles, form: concave (0); raised subtriangular platform (1).

## Rejected Characters in Previous Analyses

The following characters were rejected as either uninformative, problematic for other reasons (e.g., correlated, ambiguous), or size-related (following S25):

Maxilla, promaxillary fenestra, exposure in lateral view: exposed (1); obscured (by ascending ramus of maxilla) (0);. (Currie et al. 2003)
Maxilla, flange enclosing anterior extremity of antorbital fossa/maxillary fenestra: absent (0); rudimentary crest (1); flange (2). (Holtz 2001)

Lacrimal-nasal-maxilla contact form: multiple anterior lacrimal prongs (0); lacrimal process dominant (1); nasal lacrimal process lost (2). (Currie et al. 2003)
Lacrimal, housing for pneumatic openings: single (0), or multiple (1), fossa(e). (Currie et al. 2003)
Lacrimal border of antorbital fossa: present (0); absent (1). (Currie et al. 2003)
Lacrimal, position of accessory recess: proximal (0); distal (1). (Carr et al. 2005)
Lacrimal, size of pneumatic recess: small (0); large (1). (Carr et al. 2005)
Lacrimal cornual process, form: subtriangular, prominent (0); rounded ridge (1). (Currie et al. 2003)
Parietal nuchal crest, thickness and texture: thin, smooth (0); thick, rugose (1). (Holtz 2001)

Postorbital, form of orbital rim: rounded (0); tab-shaped (1); C-shaped. (Currie et al. 2003)

Ectopterygoid with ventral pocket to chambers: present (0); greatly reduced (1).
Jugal antorbital fossa: present (0); absent (1). (modified from Holtz 2001)
Jugal, depth of anterior ramus below pneumatic opening: tapering (0); deep (1). (Currie et al. 2003)
Jugal pneumatopore, axis: inclined at $45^{\circ}$ (0); horizontal (1). (Currie et al. 2003)
Postorbital ventral ramus, orientation of principal axis: subvertical (0); sloping anteroventrally (1). (Holtz et al. 2004)
Palatine, height of the dorsal process: tall (0); short (1). (Carr et al. 2003)
Palatine, length of the dorsal process: short (0); long (1). (Carr et al. 2003)
Palatine lateral foramina, number: 1 (0); 2 or more (1).
Palatine foramen (dorsal aspect of palatine recess), size: small (0); large (1). (Holtz et al. 2004)
Ectopterygoid, length of jugal process: short (0); wide (1). (Carr et al. 2005)
Ectopterygoid, position of pneumatic recess: restricted to posterior aspect (0); extends anteriorly (1). (Carr et al. 2005)
Ectopterygoid, number of pneumatic foramina: 1 (0); 2 (1). (Holtz et al. 2004)
Ectopterygoid, pneumatic foramen rim: flat (0); rounded (1). (Carr et al. 2005)
Ectopterygoid, posterior surface of jugal process: imperforate (0); perforate (1). (Carr et al. 2005)
Supraoccipital, contribution to dorsal margin of foramen magnum: present (0); absent (exoccipitals contact) (1). (Holtz 2001)
Dentary, tooth-bearing ramus, relative relation of dorsal and ventral margins: subparallel (0); posteriorly divergent (1). (Holtz et al. 2004)

Dentary, depth of posterior end: $150 \%$ (0), or greater than $200 \%$ (1), of the depth at the symphysis. (Holtz 2001).

Surangular shelf, orientation: horizontal (0); pendant (1). (Holtz 2001).
Maxillary crown 1, position of carinae: anterior carina offset mesial to distal carina (0);
anterior carina rotated posteriorly, D-shaped crown cross-section (1).
Dentary tooth count: 16 or more (0); 15 or fewer (1). (Holtz 2001)
Mid cervical centrum length: 2 times (0), or less than $50 \%$ (1), the diameter of the anterior face. (Holtz 2001)
Cervical neural spines, greatest height: less (0), or more (1), than the vertical diameter of the centrum. (Holtz 2001)
Humeral deltopectoral crest size: large (0); reduced (1). (Holtz 2001).
Manual unguals, form of distal end: tapers to a point (0); blunt (1). (Holtz 2001)
Manual ungual shape (lateral view): trenchant (0); straight (1). (Holtz et al. 2004)
Femoral scar (caudifemoralis longus), location: posterior (0), or posteromedial (1), side of shaft.
Metatarsal 3, form of shaft (anterior view); straight (0); sigmoid (1). (Holtz et al. 2004)


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## Tyrannosaurus

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## 6c. Notes on character state scores

The premaxillary and anterior maxillary teeth of Guanlong and Dilong were examined under magnification for characters related to their form and ornamentation. Whereas it is clear that the anterior two premaxillary teeth are incisiform with a nearly symmetrical, D-shaped cross-section and posteromedian crest, the posterior two premaxillary teeth are much less modified along these lines. Their crowns are laterally compressed, rather than D-shaped, and there is no discrete ridge between the serrate crown edges. Crown size in both Guanlong and Dilong, in addition, is gradational from
the premaxillary to the maxillary series. This was shown correctly in the cranial reconstruction of Guanlong (S4) but was shown with a stepped size increase and intervening diastema in Dilong (S12). In Dilong, the length of the fourth premaxillary and first maxillary crowns is the same $(6 \mathrm{~mm})$, and the mesiodistal crown width increases gradually from 2 to 3 mm from distal (posterior) premaxillary to mesial (anterior) maxillary teeth.

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[^0]:    ${ }^{L}$ Left side.

