Tyrannosaur Paleobiology: New Research on Ancient Exemplar Organisms

Stephen L. Brusatte,[1,2]* Mark A. Norell,[1] Thomas D. Carr,[3] Gregory M. Erickson,[1,4] John R. Hutchinson,[5] Amy M. Balanoff,[1,2]† Gabe S. Bever,[6]† Jonah N. Choiniere,[1,7]† Peter J. Makovicky,[8]† Xing Xu[9]†

Tyrannosaurs, the group of dinosaurian carnivores that includes *Tyrannosaurus rex* and its closest relatives, are icons of prehistory. They are also the most intensively studied extinct dinosaurs, and thanks to large sample sizes and an influx of new discoveries, have become ancient exemplar organisms used to study many themes in vertebrate paleontology. A phylogeny that includes recently described species shows that tyrannosaurs originated by the Middle Jurassic but remained mostly small and ecologically marginal until the latest Cretaceous. Anatomical, biomechanical, and histological studies of *T. rex* and other derived tyrannosaurs show that large tyrannosaurs could not run rapidly, were capable of crushing bite forces, had accelerated growth rates and keen senses, and underwent pronounced changes during ontogeny. The biology and evolutionary history of tyrannosaurs provide a foundation for comparison with other dinosaurs and living organisms.

Tyrannosaurs, the group of carnivores that includes *Tyrannosaurus rex* and its closest relatives, are archetypal dinosaurs (*1*) (Fig. 1 and table S1). They are pop culture icons, but also valuable research subjects, and have become an exemplar group used to study many themes in vertebrate paleontology. Research on tyrannosaurs is undergoing a renaissance, as new discoveries and technological approaches are helping to elucidate the biology and evolution of these animals in unprecedented detail.

Tyrannosaurus rex was initially described 105 years ago (*2*), and for most of the 20th century tyrannosaurs were known almost solely from fossils of *T. rex* and four closely related species of large, multi-ton Late Cretaceous predators (*3*). Within the last decade, however, the diversity of tyrannosaurs has more than doubled, and during the past year alone, six new species were described, some of which are 100 million years older and 1/100 the size of *T. rex* (*4*, *5*) (Fig. 1). These discoveries have fostered an increased understand-

ing of tyrannosaur anatomy (*6*, *7*), growth dynamics (*8*, *9*), population structure (*10*), feeding (*11*), locomotion (*12*), biogeography (*13*), and soft tissue morphology (*14–16*). This breadth of information, and of research activity, on a restricted group of organisms is unparalleled in contemporary dinosaur paleontology.

Here we assess the current state of tyrannosaur research, with a focus on the phylogenetic relationships and large-scale evolutionary patterns exhibited by the group, the biology of tyrannosaurs as living organisms, and information revealed from the newest discoveries.

Phylogenetic Relationships and Evolution of Tyrannosaurs

Tyrannosaurs, which formally comprise the clade Tyrannosauroidea, are a relatively derived group of theropod dinosaurs, more closely related to birds than to other large theropods such as allosauroids and spinosaurids (*1*, *17*). Approximately 20 tyrannosauroid genera are currently known, 5 of which were described during the past year. To assess their interrelationships, we conducted a phylogenetic analysis, which includes all
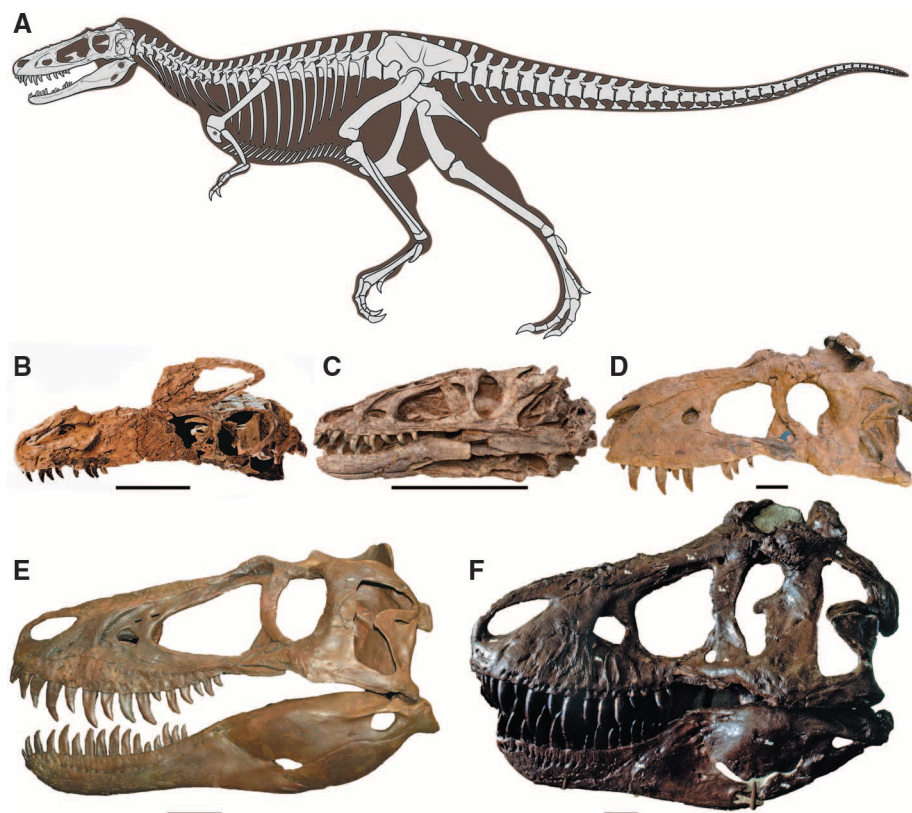
[1]Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA. [2]Department of Earth and Environmental Sciences, Columbia University, New York, NY 10964, USA. [3]Department of Biology, Carthage College, Kenosha, WI 53140, USA. [4]Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA. [5]Department of Veterinary Basic Sciences, The Royal Veterinary College, Hatfield, Herts AL9 7TA, UK. [6]Department of Geology and Geophysics, Yale University, New Haven, CT 06520, USA. [7]Department of Biological Sciences, The George Washington University, Washington, DC 20052, USA. [8]Department of Geology, The Field Museum of Natural History, Chicago, IL 60605, USA. [9]Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, People's Republic of China.

*To whom correspondence should be addressed. E-mail: sbrusatte@amnh.org
†These authors contributed equally to this work.

Fig. 1. The anatomy of tyrannosaurs, showing the variety of skeletal and cranial morphology in the group. (**A**) A skeletal reconstruction of *Alioramus*, a gracile and long-snouted tyrannosaurid, which exhibits many features of the generalized tyrannosaurid body plan (large skull, small arms, long hindlimbs, long tail). (**B** to **D**) Skulls of the basal tyrannosauroids *Guanlong* (B), *Dilong* (C), and *Bistahieversor* (D). (**E** and **F**) Skulls of juvenile (E) and adult (F) *Tyrannosaurus* scaled to the same length, illustrating the transition from a longer to a deeper skull during ontogeny. All scale bars equal 10 cm. Credits: F. Ippolito, American Museum of Natural History (AMNH) (A); I. Block, National Geographic Stock (B); M. Ellison, AMNH (C); D. Baccadutre, New Mexico Museum of Natural History and Science (D); S. Williams, Burpee Museum of Natural History (E); AMNH Photo Archives (#2752, *Tyrannosaurus* skull as mounted in the old hall) (F).

well-known genera scored for 307 morphological characters (*18*). The data set is based on personal observation of specimens and includes 123 novel characters (40% of total) based on recently discovered tyrannosaur taxa (*4, 19–21*).

Tyrannosaurs are a long-lived group that originated by the Middle Jurassic, ~165 million years ago (*5*) (Fig. 2). The oldest and most basal tyrannosaurs comprise a speciose subclade, Proceratosauridae, which includes mostly small-bodied animals no larger than a human, many of which possessed elaborate cranial crests (*22*). Progressively more derived tyrannosaurs form a pectinate series on the line toward Tyrannosauridae, the subclade of multi-ton, deep-skulled behemoths from the terminal Cretaceous (Campanian-Maastrichtian), including *Tyrannosaurus, Tarbosaurus, Albertosaurus*, and close relatives (*1*). Taxa phylogenetically intermediate between proceratosaurids and tyrannosaurids include a range of genera from the Late Jurassic–early Late Cretaceous of Asia, North America, and Europe, most of which have been recently discovered (*4, 14, 20, 21, 23, 24*). These taxa run the gamut from small to medium size (~1.4 to 9.0 m in length), and few were likely apex predators in their ecosystems (*21*).

Until recently, the prevailing notion was that tyrannosaur body size gradually, and progressively, increased over time, in concert with the piecemeal accumulation of signature tyrannosaur skeletal features (*14, 21*). However, new discoveries have led to a reassessment. The Early Cretaceous proceratosaurid *Sinotyrannus* may have approached 10 m in body length, demonstrating that tyrannosaurs could attain a large size early in their history (*25*). More striking, the close tyrannosaurid outgroup *Raptorex* is only 2 to 3 m in length, suggesting that there was great size variability among close tyrannosaurid relatives and perhaps that the immediate ancestors of tyrannosaurids were small animals (*4*). Truly enormous size, however, is restricted to the latest Cretaceous tyrannosaurids, some of which grew to lengths of 13 m and masses of 5 to 8 tons (*8*). Therefore, for the first 80 million years of their history tyrannosaurs were mostly small- to mid-sized animals that lived in the shadow of other giant predators (e.g., allosauroids, megalosauroids), and only during the final 20 million years of the Mesozoic did they develop into some of the largest terrestrial carnivores to ever live (*26*). The dominance of tyrannosaurs as megapredators was purely a latest Cretaceous phenomenon.

Tyrannosaur Anatomy

The spate of new discoveries has prompted a renewed focus on tyrannosaur anatomy, including external, internal, and soft-tissue morphology (Fig. 3). All tyrannosaurs are bipedal predators and possess several unique features, including a small premaxilla with D-shaped "incisor"-like teeth, fused nasals, extreme pneumaticity in the skull roof and lower jaws, a pronounced muscle attachment ridge on the ilium, and an elevated femoral head (*6, 27, 28*).
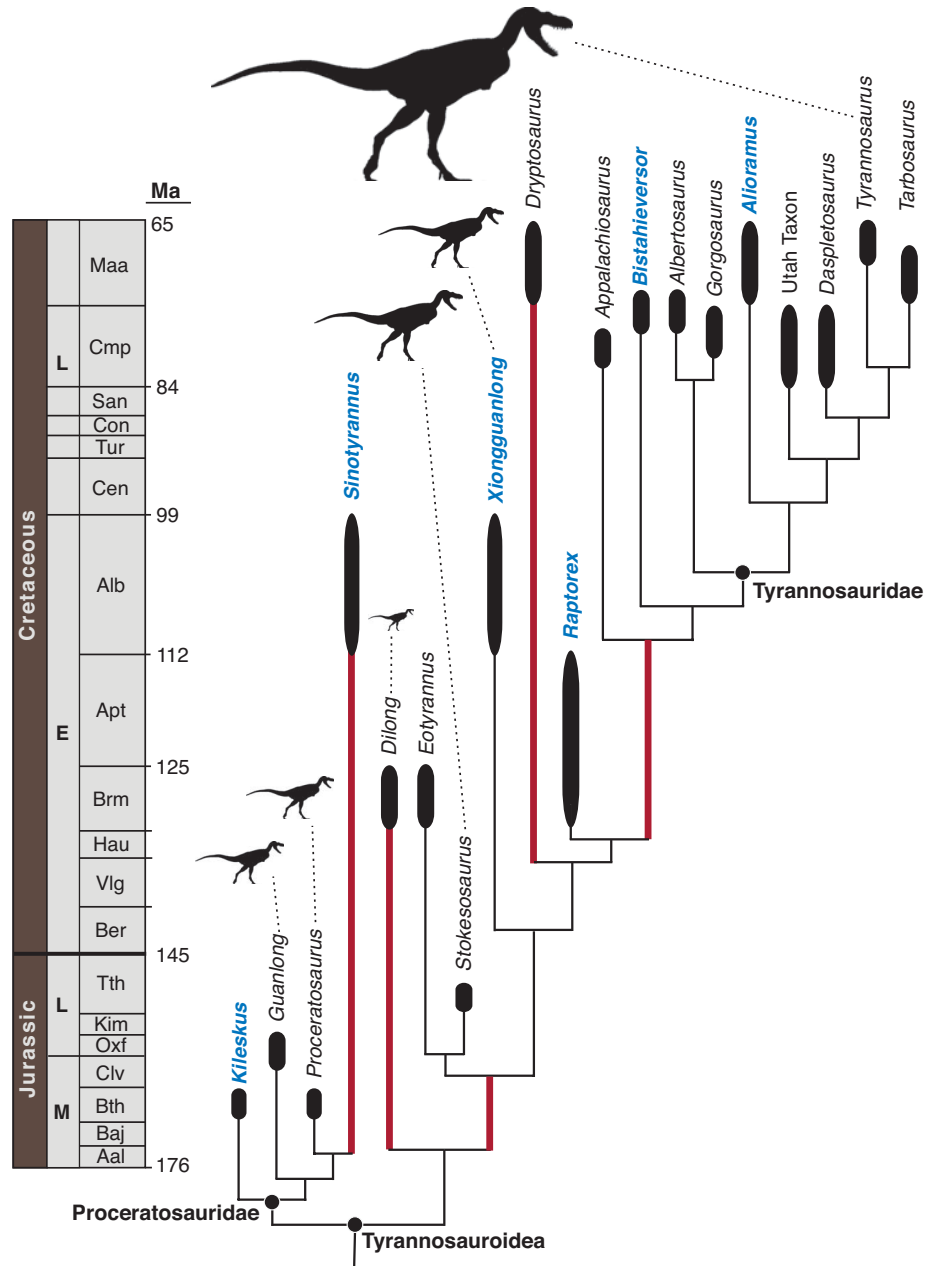

Fig. 2. Phylogenetic relationships of tyrannosauroid theropods, assessed by a cladistic analysis (*18*). Single most parsimonious tree, showing the relationships of 19 tyrannosaurs, scaled to the geologic time scale (in millions of years ago, Ma). Taxa in blue are those that have been described during the past year. Silhouettes indicate relative body size (based on femur length as a proxy). Thick red bars indicate major ghost lineages. Thick black bars represent the finest age resolution for each taxon, not actual duration.

A number of derived specializations characterize the giant tyrannosaurids: a large and deep skull with powerful jaw muscles, robust teeth, reinforced sutures between skull bones, and tiny forelimbs (*6, 29*), features often considered adaptations for a hypercarnivore to function at large size (*4*). Basal tyrannosauroids, in contrast, have smaller skulls and longer arms and generally resemble sleek, bird-like theropods more than their enormous tyrannosaurid cousins (*14, 22*). New discoveries have shown, however, that the hallmark tyrannosaurid body plan (large and deep skull, robust teeth, etc.) does not uniquely

or uniformly characterize the tyrannosaurid clade. Most of these features are now known to be present in *Raptorex*, the man-sized tyrannosaurid outgroup that lived 40 million years before tyrannosaurids originated (*4*). Furthermore, the gracile and long-snouted *Alioramus*, a tyrannosaurid that is about half the size of close relatives such as *Tarbosaurus* and *Tyrannosaurus*, lacks a deep and muscular skull and thick teeth (*19*). Thus, characteristic tyrannosaurid features did not evolve as a consequence of large body size, but likely originated in small animals, and not even all derived, Late Cretaceous tyranno-

saurids are united by a characteristic morphotype (*4, 19*).

Much is also known about the internal anatomy of the tyrannosaur skull, thanks to the discovery of exceptionally preserved fossils and the application of digital techniques such as computerized tomography (CT) scanning (*7, 30, 31*). Tyrannosaurs possessed the required neuroanatomy to lead the active, predatory life-style expected of derived theropods (*7, 30*). Their encephalization quotient—an estimate of relative brain size—varies between 2.0 and 2.4, larger than in basal theropods but lower than that of birds and their closest relatives (*19*). Large olfactory lobes indicate a strong sense of smell (*7, 31*). Elongate cochlear and semicircular canals apparently support elevated sensitivity to low-frequency sound and highly coordinated head and eye movements (*7*).

Several tyrannosaurid specimens have been reported to preserve integumentary structures and other soft tissues, which rarely fossilize in dinosaurs. Although impressions of scaly skin have been described for large tyrannosaurids (*32*), simple filamentous integument, interpreted as homologous to feathers, is clearly preserved in a specimen of the basal tyrannosauroid *Dilong* (*14*). These branched filaments appear to have extensively covered the body, as they are observed near the skull and tail. A recent study suggests that much larger tyrannosauroids were covered with elongate, broader integumentary structures (*33*), which were likely used for display (*34*). Several easily degraded soft tissues, such as cells, blood vessels, and collagen, have been reported from a specimen of *Tyrannosaurus* (*15, 35*). Some of these findings have been met with skepticism (*36*), and they remain to be validated by other research groups. However, if correct, they promise to give radical new insight into the process of fossilization and may allow for molecular phylogenetic analysis of these extinct taxa (*37*).

Tyrannosaur Growth

Arguably we know more about tyrannosaur biology than that of any other dinosaurs (Figs. 3 and 4). Much of this knowledge has been gained over the past 20 years, through the collection of skeletons of both adults and juveniles, bones of their prey with bite marks, coprolites (fossil feces), stomach contents, and pathological specimens (*38*).

Much attention has focused on how tyrannosaurs grew, especially on how giants such as *T. rex* achieved such massive size and how their skeletons changed during the transition from embryo to multi-ton adult. Comparative growth curves for

several species, which plot body mass (calculated from femur size) against age in years (calculated from counting growth lines in histological section) (*8*) (Fig. 4B), show that large tyrannosaurids reached somatic maturity around 20 years old, though most rarely lived for more than 25 years. *T. rex* evidently attained its large size via acceleration of growth rates relative to closely related species, not by extending its life span. Its maximum growth rate may have exceeded 767 kg per year, equivalent to adding a remarkable 2 kg per day (*8*).

Tyrannosaur skeletons changed substantially as individuals matured. Although less is known about the growth of small, basal tyrannosaurs, tyrannosaurids and their closest large-bodied relatives are united by a conservative pattern of growth in which the skulls of juveniles were entirely reshaped during ontogeny (*9, 20, 39*). This sequence has been reconstructed by cladistic analysis, based on the principle that ontogeny, like phylogeny, involves a hierarchically nested series of character changes (*19, 39*). During the growth of an individual species, the skull and jaws deepened, pneumatic bones inflated, ornamented structures enlarged and coarsened, sutural surfaces deepened and became more rugose, and the teeth became larger and thicker (*9, 40*) (Fig. 1). Changes have also been documented in the postcranial skeleton. Most notably, the forearm shortened and the long shin and foot of juveniles became shorter and stockier in adults (*40*). The differ-

ences between juvenile and adult tyrannosaurids are so great that different growth stages have often been mistaken for different species (*3, 9*).

Tyrannosaur Behavior

A variety of studies have used biomechanical modeling, which incorporates mathematics, physics, and computer programming (*41*), to infer tyrannosaur behavior. Tyrannosaurs, especially the large, derived forms, have often been used as exemplars to demonstrate the utility of such computer models.

Most studies have suggested that although large tyrannosaurids might have been able to run at slow to moderate speeds at best (top speeds between 5 and 11 ms^{-1}), they could not run nearly as fast as large athletic animals today, such as
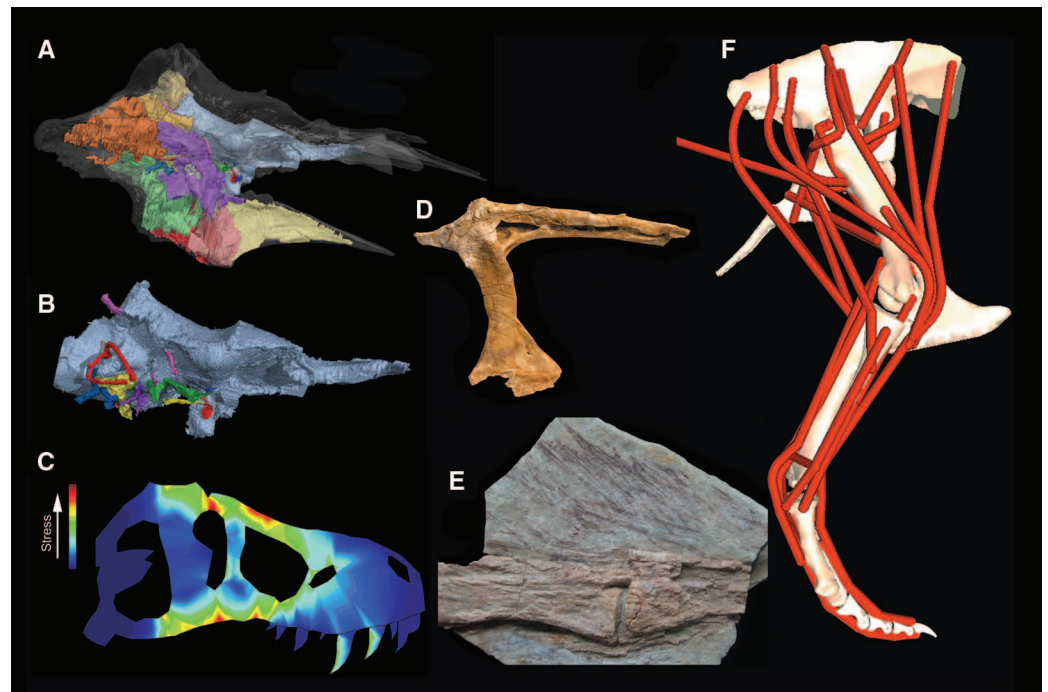

Fig. 3. Tyrannosaur soft tissues, feeding, and locomotion. (**A**) CT imagery of internal pneumatic sinuses of the braincase of *Alioramus altai* (*19*). (**B**) Endocast of brain, cranial nerves, and semicircular canals of *A. altai* (*19*). (**C**) Finite element analysis of a skull of *T. rex* (*11, 47*), showing high stresses (red colors) in the nasal and cheek regions (courtesy of E. Rayfield). (**D**) Lacrimal of *A. altai* (reversed), showing pneumatic spaces that housed air sacs (credit: M. Ellison). (**E**) Feathery integument along the tail of *Dilong paradoxus*. (**F**) Three-dimensional biomechanical model based on muscle reconstruction of the right hindlimb of *T. rex* (*16*), used to assess running mechanics.

racehorses (~20 ms^{-1}) (*12, 41, 42*). Consensus also is building that even though large tyrannosaurids were not restricted to a pillar-like columnar limb posture to maximize mechanical advantage, they were still far from having very crouched, more birdlike postures (*12, 41, 42*). Aspects of tyrannosaurid anatomy, such as the long legs and large pelvic limb muscles, which intuitively seem to indicate fast running capacity, were inherited from small, presumably fast-running ancestors. Modeling studies have incorporated these features and shown that they did not make large tyrannosaurids extremely fast. However, it is worth noting that these studies rely on estimates of muscle size and attachment points, a somewhat conjectural

exercise, albeit constrained by the anatomy of extant relatives (12, 16), that plagues all such functional analyses.

Both trace fossils (bite marks, coprolites) and quantitative techniques have helped to reveal what tyrannosaurs ate and how they fed. Tyrannosaurid bite marks have been found on the bones of a wide diversity of species, including various other tyrannosaurs, demonstrating that they were ecological generalists (43). Bite mark patterns show that tyrannosaurids characteristically bit deeply into carcasses, often through bones, and then pulled back, creating long cuts [puncture-pull sensu (44)]. Some *T. rex* bite marks (44) and coprolites with bone chunks (45) indicate that bone was fractured, ingested, and used for sustenance, a mammal-like attribute not seen in extant reptiles. The bite forces needed to crunch through bone would have been enormous. Biomechanical experiments have replicated the size and depth of fossilized bite marks and suggest that *T. rex* generated bite forces of at least 13,400 N. Maximal bite forces were probably greater (46).

Such large bite forces would have exerted tremendous stress on the skull. Tyrannosaurid skull shape and its relation to bite-induced stress have been extensively studied by finite element analysis. The results indicate that large tyrannosaurids had skulls optimized to endure strong bites, as various sutures absorbed stress and the fused nasals strengthened the snout (11, 47, 48). Similar biomechanical techniques have also been used to examine the role of the tyrannosaur neck in feeding, showing that it was important for generating pulling forces on food items and in inertial feeding (49), and the function of the unusual "pinched metatarsus" of the foot in turning, indicating that it was structured to resist shearing and twisting forces (50).

Little is known about the ecological community structure for most extinct animals, but large sample sizes permit some understanding of tyrannosaur ecology. Late Cretaceous tyrannosaurids were the first dinosaurs for which population dynamics—the balance between deaths and births that create a population's age structure—could be assessed (10) (Fig. 4C). Like large birds and mammals, but unlike living reptiles, tyrannosaurids probably experienced extremely high neonate mortality, followed by few deaths after 2 years of age (presumably a release from predation), and then increased mortality at mid-life (probably from the rigors of reproduction), so that few individuals had a long reproductive life span. Furthermore, a number of fossil sites have preserved multiple individuals, suggesting that tyrannosaurs were at least occasionally gregarious (51). Bite marks indicate that individuals of the same species bit each other in the face during encounters (52), and many older individuals with gout, bacterial legions, and bone fractures have been reported, showing that disease and injury were common (53).

Multiple lines of evidence indicate that tyrannosaur ecological habits changed during ontogeny.

In Late Cretaceous tyrannosaurids, the difference in form between the lightly built, fleet juveniles and the larger, bulkier adults suggests that foraging behavior and targeted prey size changed as tyrannosaurs grew. The deep and muscular adult skull, with reinforced sutures and robust teeth, is well suited for sustaining high bite forces, whereas juveniles had none of these features (9, 39). Furthermore, the longer and more gracile hind limbs of juveniles indicate that they were relatively faster than adults (40), which has been corroborated by biomechanical analysis (12). These differences could have promoted major size-related shifts in ecology and behavior. It is plausible that adults preferentially attacked larger, but less mobile, prey than their younger counterparts. Such an ontogenetic shift is not seen in many familiar predators today (e.g., lions), but is present in extant crocodylians (54). As most basal tyrannosauroids are similar in skull and body proportions to juvenile Late Cretaceous tyrannosaurids, it is likely that they behaved and fed in a similar manner. However, detailed biomechanical analyses have yet to be carried out for most non-tyrannosaurid tyrannosauroids.

Whether *T. rex* and other large tyrannosaurs were scavengers or predators has generated much speculation and dispute. Bite marks from mass death assemblages of herbivorous dinosaurs show that tyrannosaurs scavenged on occasion (38). However, multiple reports of healed tyrannosaur bite marks on prey bones (55, 56) and tyrannosaur stomach contents containing remains of young dinosaurs (57) indicate that tyrannosaurs were capable of active predation. Like most carnivores, tyrannosaurs probably both scavenged and hunted.

One of the largest voids in our understanding of dinosaur biology is the sex of individual specimens. It has been suggested that female tyrannosaurs required a larger pelvic outlet for the passage of eggs, reflected by a greater span between the ischial bones and a smaller or more posteriorly located first tail chevron, but these indices find little neontological support in living archosaurs (58, 59). More recently, medullary bone, a calcium phosphate deposit for the use of shelling in eggs, was reported in one *T. rex* specimen (60). This provides a surefire identification of sex in dino-
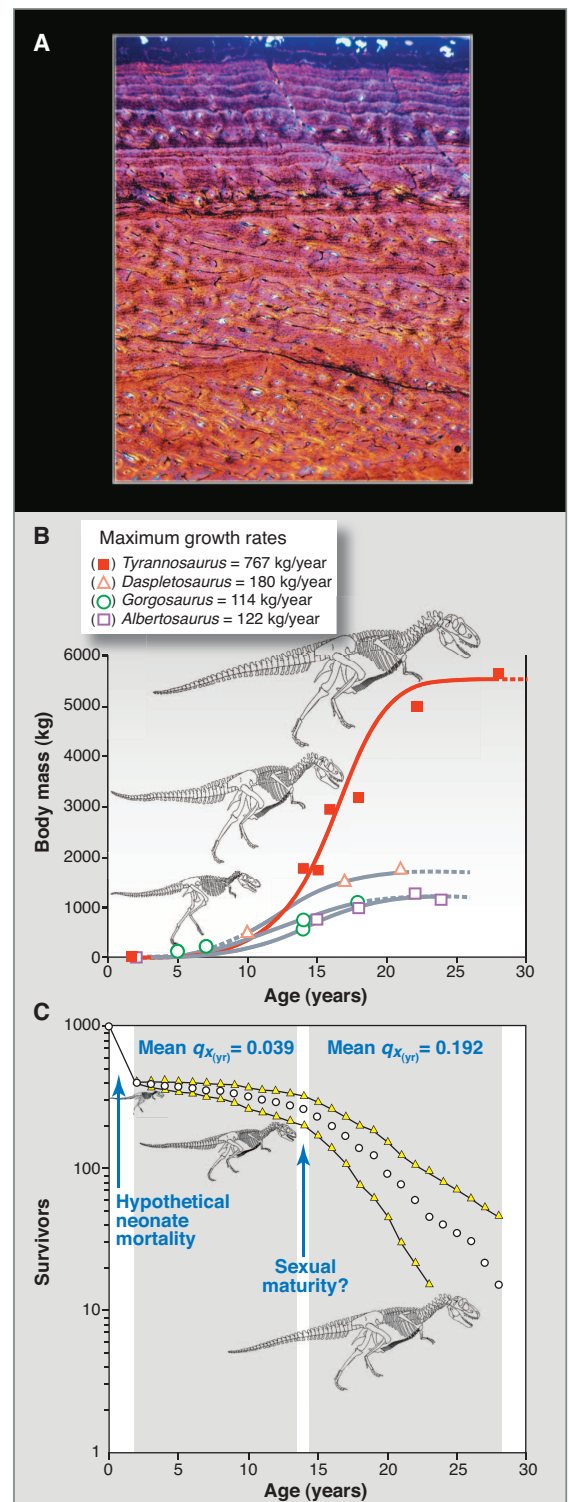
Fig. 4. Tyrannosaur growth and ecology. (**A**) Histological section of a *T. rex* dorsal rib, showing growth lines whose counts are used to reveal age and longevity. (**B**) Growth curves for North American tyrannosaurids derived from growth line counts and body size estimations for individuals showing how size changes with age. No sampled tyrannosaurid adults were more than 30 years old, and accelerated rather than prolonged development was the key to the great size of *T. rex* (8). (**C**) Survivorship curve for *Albertosaurus sarcophagus*. This tyrannosaur exhibited high neonate mortality, then few deaths after age two, and then increased mortality at mid-life (8).

saurs, and holds much promise for future studies of dinosaur sex and ecology.

Tyrannosaur Biogeography

Until recently, all tyrannosaur fossils were limited to Asia and North America, but the discovery and recognition of basal tyrannosauroids over the last decade reveals a more cosmopolitan distribution during their early evolution (*5, 22–24, 61*). Members of the Middle–Late Jurassic proceratosaurid radiation are known from Europe and Asia (*5*), whereas the Late Jurassic genus *Stokesosaurus* is known from both Europe and North America (*24*). However, all well-known tyrannosaurs more derived than *Eotyrannus* and *Stokesosaurus* exhibit a purely Asian or North American distribution. Faunal interchange between these continents is characteristic of most Campanian-Maastrichtian dinosaur clades and reflects an increasing Laurasian-Gondwanan provincialism during the final stages of the Age of Dinosaurs (*62*). Tyrannosaurs, because of their rich fossil record and well-studied phylogenetic relationships, are one of the primary sources of evidence for this long-established biogeographic hypothesis.

Emerging evidence, however, indicates that tyrannosaurs were likely present on the southern continents during their early evolutionary history. An isolated pubis from the Early Cretaceous of Australia was recently identified as belonging to a derived tyrannosaur (*13*). As contemporary Early-mid Cretaceous dinosaurs mostly belong to globally distributed clades (*26*), the absence of Gondwanan tyrannosaurs during this time had been a puzzling anomaly. Even with this discovery, if it is from a tyrannosaur, tyrannosaurs are absent in the well-sampled mid-Late Cretaceous units of South America, Africa, and Madagascar (*63*). It is possible that tyrannosaurs were rare on the southern continents during the Early-mid Cretaceous, and it is likely that Gondwanan forms did not persist into the latest Cretaceous, at least as common and ecologically dominant carnivores.

Most tyrannosaurs are known from mesic (moderate moisture) or seasonally mesic paleo-environments, and their fossils are notably absent from xeric (dry) facies, even those that interfinger with tyrannosaur-bearing mesic sediments within the same sedimentary rock basins in Asia (*64*). This likely indicates that tyrannosaurs preferred wetter habitats, although it may still reflect a sampling bias. Wherever they were present during the Late Cretaceous in North America and Asia, tyrannosaurs were the sole apex predators in their environments. Multiple large tyrannosaurids co-occurred during some intervals in North America and Asia (*19, 27*), but the Maastrichtian of western North America was solely dominated by *T. rex* (*39*). In contrast, most nontyrannosaurid tyrannosauroids are found alongside larger non-

tyrannosaur predators, demonstrating that tyrannosaurs did not exclusively dominate the apex predator niche, regardless of where they lived, until the final 20 million years of the Cretaceous.

Conclusion

Tyrannosaurus rex and its close relatives are the most intensely studied dinosaurs. Derived tyrannosaurs such as *Albertosaurus*, *Tarbosaurus*, and *Tyrannosaurus* are known from more fossils than are most other dinosaurs, and these specimens span the spectrum from juvenile to adult. Many modern analytical approaches have been pioneered with the use of *Tyrannosaurus* and close kin, and the results of these studies are allowing for quantitative comparisons between the biology of extinct dinosaurs and living species.

References and Notes

1. We use the vernacular "tyrannosaur" to refer to members of the clade Tyrannosauroidea, defined as the most inclusive clade containing *Tyrannosaurus rex* but not *Ornithomimus edmontonicus*, *Troodon formosus*, or *Velociraptor mongoliensis*. The more derived Tyrannosauridae is defined as the least inclusive clade containing *T. rex*, *Gorgosaurus libratus*, and *Albertosaurus sarcophagus* (*4*).
2. H. F. Osborn, *Bull. Am. Mus. Nat. Hist.* **21**, 259 (1905).
3. D. A. Russell, *Nat. Mus. Nat. Sci. Pub. Palaeontol* **1**, 1 (1970).
4. P. C. Sereno *et al.*, *Science* **326**, 418 (2009).
5. O. W. M. Rauhut, A. C. Milner, S. Moore-Fay, *Zool. J. Linn. Soc.* **158**, 155 (2010).
6. C. A. Brochu, *Soc. Vert. Paleontol. Mem.* **7**, 1 (2003).
7. L. M. Witmer, R. C. Ridgely, *Anat. Rec.* **292**, 1266 (2009).
8. G. M. Erickson *et al.*, *Nature* **430**, 772 (2004).
9. T. D. Carr, *J. Vertebr. Paleontol.* **19**, 497 (1999).
10. G. M. Erickson, P. J. Currie, B. D. Inouye, A. A. Winn, *Science* **313**, 213 (2006).
11. E. J. Rayfield, *Proc. Biol. Sci.* **271**, 1451 (2004).
12. J. R. Hutchinson, M. Garcia, *Nature* **415**, 1018 (2002).
13. R. B. J. Benson, P. M. Barrett, T. H. Rich, P. Vickers-Rich, *Science* **327**, 1613 (2010).
14. X. Xu *et al.*, *Nature* **431**, 680 (2004).
15. M. H. Schweitzer, J. L. Wittmeyer, J. R. Horner, J. K. Toporski, *Science* **307**, 1952 (2005).
16. M. T. Carrano, J. R. Hutchinson, *J. Morphol.* **253**, 207 (2002).
17. T. R. Holtz, in *The Dinosauria*, D. B. Weishampel, P. Dodson, H. Osmólska, Eds. (Univ. of California Press, Berkeley, ed. 2, 2004), pp. 111–136.
18. Supporting material is available on *Science* Online.
19. S. L. Brusatte, T. D. Carr, G. M. Erickson, G. S. Bever, M. A. Norell, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 17261 (2009).
20. T. D. Carr, T. E. Williamson, *J. Vertebr. Paleontol.* **30**, 1 (2010).
21. D. Li, M. A. Norell, K. Q. Gao, N. D. Smith, P. J. Makovicky, *Proc. Biol. Sci.* **277**, 183 (2010).
22. X. Xu *et al.*, *Nature* **439**, 715 (2006).
23. S. Hutt, D. W. Naish, D. M. Martill, M. J. Barker, P. Newberry, *Cretac. Res.* **22**, 227 (2001).
24. R. B. J. Benson, *J. Vertebr. Paleontol.* **28**, 732 (2008).
25. Q. Ji, S.-A. Ji, L.-J. Zhang, *Geol. Bull. China* **28**, 1369 (2009).
26. S. L. Brusatte *et al.*, *Naturwissenschaften* **96**, 1051 (2009).
27. P. J. Currie, *Acta Palaeontol. Pol.* **48**, 191 (2003).
28. J. H. Hurum, K. Sabath, *Acta Palaeontol. Pol.* **48**, 161 (2003).
29. R. E. Molnar, *Palaeont. A* **217**, 137 (1991).
30. C. A. Brochu, *J. Vertebr. Paleontol.* **20**, 1 (2000).
31. D. K. Zelenitsky, F. Therrien, Y. Kobayashi, *Proc. Biol. Sci.* **276**, 667 (2009).
32. P. J. Currie, D. Badamgarav, E. B. Koppelhus, *Ichnos* **10**, 1 (2003).
33. X. Xu, X. T. Zheng, H. L. You, *Nature* **464**, 1338 (2010).
34. X. Xu, X. T. Zheng, H. L. You, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 832 (2009).
35. M. H. Schweitzer *et al.*, *Science* **316**, 277 (2007).
36. T. G. Kaye, G. Gaugler, Z. Sawlowicz, A. Stepanova, *PLoS ONE* **3**, e2808 (2008).
37. C. L. Organ *et al.*, *Science* **320**, 499 (2008).
38. G. M. Erickson, *Sci. Am.* **9**, 32 (1999).
39. T. D. Carr, T. E. Williamson, *Zool. J. Linn. Soc.* **142**, 479 (2004).
40. P. J. Currie, *Can. J. Earth Sci.* **40**, 651 (2003).
41. S. M. Gatesy, M. Bäker, J. R. Hutchinson, *J. Vertebr. Paleontol.* **29**, 535 (2009).
42. W. I. Sellers, P. L. Manning, *Proc. Biol. Sci.* **274**, 2711 (2007).
43. A. R. Jacobsen, *Hist. Biol.* **13**, 17 (1998).
44. G. M. Erickson, K. H. Olson, *J. Vertebr. Paleontol.* **16**, 175 (1996).
45. K. Chin, T. T. Tokaryk, G. M. Erickson, L. C. Calk, *Nature* **393**, 680 (1998).
46. G. M. Erickson *et al.*, *Nature* **382**, 706 (1996).
47. E. J. Rayfield, *Zool. J. Linn. Soc.* **144**, 309 (2005).
48. E. Snively, D. M. Henderson, D. S. Phillips, *Acta Palaeontol. Pol.* **51**, 435 (2006).
49. E. Snively, A. P. Russell, *Paleobiology* **33**, 610 (2007).
50. E. Snively, A. P. Russell, *J. Morphol.* **255**, 215 (2003).
51. P. J. Currie, *Gaia* **15**, 271 (2000).
52. D. H. Tanke, P. J. Currie, *Gaia* **15**, 168 (2000).
53. D. H. Tanke, B. M. Rothschild, *New Mex. Mus. Nat. Hist. Sci. Bull* **20**, 1 (2001).
54. P. Dodson, *J. Zool.* **175**, 315 (1975).
55. K. Carpenter, *Gaia* **15**, 135 (2000).
56. J. Happ, in *Tyrannosaurus rex: The Tyrant King*, P. Larson, K. Carpenter, Eds. (Indiana Univ. Press, Bloomington, 2008), pp. 354–368.
57. D. J. Varricchio, *J. Paleontol.* **75**, 401 (2001).
58. G. M. Erickson, A. K. Lappin, P. Larson, *Zool* **108**, 277 (2005).
59. A. Prieto-Marquez, P. M. Gignac, S. Joshi, *J. Vertebr. Paleontol.* **27**, 603 (2007).
60. M. H. Schweitzer, J. L. Wittmeyer, J. R. Horner, *Science* **308**, 1456 (2005).
61. A. O. Averianov, S. A. Krasnolutskii, S. V. Ivantsov, *Proc. Zool. Inst. RAS* **314**, 42 (2010).
62. P. Upchurch, C. A. Hunn, D. B. Norman, *Proc. Biol. Sci.* **269**, 613 (2002).
63. D. B. Weishampel *et al.*, in *The Dinosauria*, D. B. Weishampel, P. Dodson, H. Osmólska, Eds. (Univ. of California Press, Berkeley, ed. 2, 2004), pp. 517–606.
64. P. J. Makovicky *et al.*, *Proc. Biol. Sci.* **277**, 191 (2010).

Supporting Online Material
www.sciencemag.org/cgi/content/full/329/5998/1481/DC1
Materials and Methods
SOM Text
Fig. S1
Table S1
References

10.1126/science.1193304

Supporting Online Material for

Tyrannosaur Paleobiology: New Research on Ancient Exemplar Organisms

Stephen L. Brusatte,* Mark A. Norell, Thomas D. Carr, Gregory M. Erickson, John R. Hutchinson, Amy M. Balanoff, Gabe S. Bever, Jonah N. Choiniere, Peter J. Makovicky, Xing Xu

*To whom correspondence should be addressed. E-mail: sbrusatte@amnh.org

This PDF file includes:

Materials and Methods
SOM Text
Fig. S1
Table S1
References

1) Materials and Methods

Details of the phylogenetic analysis

The new phylogenetic analysis presented in this paper was conducted by two of us (Brusatte, Carr), and utilizes a dataset of 307 discrete morphological characters scored for 19 ingroup tyrannosauroids (Table S1) and four outgroup taxa (*Allosaurus*, Dromaeosauridae, Ornithomimosauria, Compsognathidae). The dataset includes 123 new characters (40%) that have been revealed by personal observation of specimens and descriptive work on new tyrannosauroid taxa. All tyrannosauroid taxa except for *Kileskus*, *Sinotyrannus*, and *Xiongguanlong* were scored from first-hand observations by either Brusatte or Carr, but *Xiongguanlong* was scored from high quality images provided by Makovicky.

Only unequivocal tyrannosauroids, or taxa that have been recovered as tyrannosauroids in multiple higher-level phylogenetic analyses, are included. Potential basal tyrannosauroids such as *Coelurus* and *Tanycolagreus*, which have been placed in this position in one recent phylogenetic analysis (*S1*), are not included, pending corroboration of a tyrannosauroid placement in other higher-level studies of coelurosaur phylogeny. Additionally, taxa based on especially fragmentary material, such as *Aviatyrannis* and *Bagaraatan* (which is also often found as a non-tyrannosauroid in higher-level studies), are not included. The use of supraspecific outgroup taxa is not ideal but is considered a better alternative than scoring a single or multiple exemplars for each outgroup, as most individual taxa are fragmentary and the use of multiple exemplars for each would lead to a profusion of outgroup taxa that would contribute little to the analysis. The three supraspecific outgroups are based primarily on *Velociraptor* (Dromaeosauridae), *Sinornithomimus*, *Garudimimus*, *Harpymimus*, and *Pelecanimimus* (Ornithomimosauria), and *Compsognathus*, *Sinosauropteryx*, *Huaxiagnathus*, and *Juravenator* (Compsognathidae).

The dataset was subjected to a parsimony analysis in TNT v 1.1 (*S2*). As a first step, we analyzed the matrix under the "New Technology search" option, using sectorial search, ratchet, tree drift, and tree fuse options with default parameters. The minimum length tree was found in 10 replicates, which tried to sample as many tree islands as possible. The generated trees were then analyzed under traditional TBR branch swapping, to more fully explore each tree island, which resulted in a single most parsimonious tree of length 555 (consistency index = 0.65; retention index = 0.84). To further check our results, we also subjected the dataset to a heuristic search in PAUP*, which resulted in the same single most parsimonious tree. Bremer supports were calculated using TNT by saving topologies up to 10 steps longer than minimum length.

The single most parsimonious tree (Fig. S1) indicates that tyrannosauroid phylogeny is well-resolved and most ingroup clades have high Bremer support values. Some basal clades collapse one step out from the most parsimonious tree, including Proceratosauridae (and all ingroup clades) and the *Eotyrannus + Stokesosaurus* clade. However, this is likely a figment of missing data: all proceratosaurids except *Guanlong* are known only from extremely limited material, most of which is cranial. *Eotyrannus* is a fragmentary taxon, and *Stokesosaurus* is especially fragmentary and is known from no cranial elements. It is noteworthy that more derived clades, which include taxa for which

multiple well-preserved specimens is the norm, are supported by high Bremer values. Therefore, we conclude that our knowledge of tyrannosauroid phylogeny, especially that of more derived taxa, is robust.

Character list

The full set of 307 characters is listed here. Previous usage of characters is indicated by citations in parentheses. Citations previous to 2009 are generally not included, as a recent comparative phylogenetic study (*S3*) explicitly listed and discussed all tyrannosauroid characters used by studies up to that point. All characters used by Carr and Williamson (2010) (*S4*) were also utilized by Brusatte et al. (2009) (*S5*). Other references pertinent to the citations below include *S6-S9*.

General Skull Features

1) Skull, occipital region, orientation: posteriorly (0); posteroventrally (1). (Carr and Williamson 2010: 3)

2) Skull, general shape: long and low, length: height ratio greater than 3.2 (0); deep, length: height ratio less than 3.2 (1). (Carr and Williamson 2010: 4) Note: Length is premaxilla-quadrate condyle length; height is maximum height of the upper jaw, not counting any cranial crests.

3) Skull, anteroposterior length: less (0) or greater than (1) 40% trunk length. New character, inspired by Sereno et al. 2009. Trunk length is the anterior extremity of the pectoral girdle to the posterior extremity of the pelvic girdle, as defined by Sereno et al. 2009 (supp info).

4) External naris, less (0) or greater than (1) 20% of skull length. (Carr and Williamson 2010: 54). Note: *Sinotyrannus* can be scored for the derived state, even though the entire skull is not known. In *Sinotyrannus* the external naris long axis is as long as the first seven teeth of the maxillary tooth row. In *Proceratosaurus* and *Guanlong* it is as long as the first 8-9 teeth, whereas in all other tyrannosauroids it is as long as the first 4-5 teeth.

5) Lateral temporal fenestra, orientation of long axis relative to long axis of orbit: posterodorsal (0); approximately parallel (1). New character.

Premaxilla

6) Premaxilla, nasal processes of opposing premaxillae, orientation: divergent from each other, with small process of nasals fitting in between them (0); closely appressed to each other (1). (Carr and Williamson 2010: 6)

7) Premaxilla, deep foramen or fossa on the lateral surface of the base of the nasal process, within the anteroventral corner of the narial fossa: absent (0); present (1). (Carr and Williamson 2010: 7)

8) Premaxilla, main body, dorsoventral depth: less than or equal to (0); between 1-1.9 times (1); greater than 2 times (2) anteroposterior length. ORDERED. Modified from Carr and Williamson (2009: 8) and Sereno et al. (2009: 1). Note: Previous studies utilized a binary character, but here we have added a second derived state to encapsulate variation within Tyrannosauroidea. In the most parsimonious tree derived from this analysis the first derived state optimizes as a tyrannosauroid synapomorphy and the second a character of *Tyrannosaurus* and *Tarbosaurus*.

9) Premaxilla, maxillary process orientation: mostly laterally (and resultantly widely visible in lateral view) (0); dorsolaterally (facing almost equally dorsally and laterally) (1); dorsally (and resultantly mostly hidden in lateral view) (2). ORDERED (Carr and Williamson 2010: 10). Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea and distinguish the slightly reduced processes of *Raptorex* and albertosaurines from the basically entirely dorsally facing processes of tyrannosaurines.

10) Premaxilla, orientation of tooth row: strongly parasagitally (anteroposteriorly) (0); first two teeth oriented mediolaterally and third and fourth teeth oriented parasagitally (1); entire tooth row oriented mediolaterally and all teeth visible in anterior view (2). ORDERED (Carr and Williamson 2010: 12). Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea. The first derived state is present in all tyrannosauroids and the second is seen in *Xiongguanlong*, *Raptorex*, and more derived tyrannosauroids.

11) Premaxilla, form of narial fossa ventral to external naris: shallowly excavated (0); deeply excavated, anterior margin invaginated as a deep groove (1). New character.

12) Premaxilla, extent of narial fossa: limited to region immediately ventral to external naris (0); extensive, covers most of main body of premaxilla (1). New character.

13) Premaxilla, shape of anterior margin: smoothly curved (0); discrete inflection point between nearly vertical posterior region and more horizontal dorsal region (1). New character. This is not equivalent to the straight anterior margin of the premaxilla, as derived tyrannosaurids have a straight anterior margin that more gradually curves as it continues dorsally, such that there is no discrete inflection point.

14) Premaxilla, position of palatal process: immediately above interdental plates (0); separated from interdental plates by deep lingual surface of premaxilla (1). New character.

Maxilla

15) Maxilla, promaxillary fenestra, exposure: visible in lateral view (0); obscured in lateral view by the lateral lamina of the ascending ramus (fenestra faces completely anteriorly) (1). (Carr and Williamson 2010: 14)

16) Maxilla, promaxillary fenestra, position: anterior margin of antorbital fossa (0); extreme anteroventral corner of antorbital fossa (1). New character.

17) Maxilla, maxillary fenestra, location: posterior to (0) or partially overlapped laterally by (1) the anterior margin of the antorbital fossa (lateral lamina of maxilla). (Carr and Williamson 2010: 15, 16; Sereno et al. 2009: 12).

18) Maxilla, maxillary fenestra, location: dorsal to (0) or abuts (1) ventral margin of antorbital fossa. (Sereno et al. 2009: 13).

19) Maxilla, maxillary fenestra, anteroposterior length compared to the distance between the anterior margins of the antorbital fossa and fenestra: less than half (0); greater than half (1); greater than half and also greater than half of the length of the eyeball-bearing portion of the orbit (2). ORDERED (Carr and Williamson 2010: 17; Sereno et al. 2009: 11). Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea.

20) Maxilla, maxillary fenestra, position within maxillary antrum: does not (0) or does (1) abut dorsal border of the antrum in medial view. New character.

21) Maxilla, antorbital fossa, extent: reaches (0) or does not reach (1) the nasal suture. (Carr and Williamson 2010: 20)

22) Maxilla, interfenestral strut, anteroposterior length: greater than (0) or less than (1) 50% long axis of maxillary fenestra. (Carr and Williamson 2010: 22) Note: this character has been modified from previous usage to make it quantitative.

23) Maxilla, main body, dorsoventral depth at midpoint of antorbital fenestra: less than (0) 16%; between 16-22% (1); or greater than (2) 22% depth of skull. ORDERED. (Carr and Williamson 2010: 23). Note: this character has been modified from previous usage to make it quantitative.

24) Maxilla, antorbital fossa, trend of dorsoventral depth across main body: uniform (0); diminishes (1). (Carr and Williamson 2010: 25)

25) Maxilla, subcutaneous flange bordering the antorbital fossa laterally on the posterior end of the main body, resulting in the fossa forming a channel between the flange and the main body: absent (0); present (1). (Carr and Williamson 2010: 26)

26) Maxilla, dorsolateral process, coverage by antorbital fossa: process absent (0); process covered by subcutaneous surface only (1); ventral half of process covered by antorbital fossa (2); antorbital fossa completely excluded (3). ORDERED. (Carr and Williamson 2010: 28)

27) Maxilla, narrow region of smooth surface texture between anterior margin of antorbital fossa and the subcutaneous surface: absent (0); present (1). (Carr and Williamson 2010: 29)

28) Maxilla, ventral margin of the anterior region of the bone, profile: straight (0); convex (1). (Carr and Williamson 2010: 30; Sereno et al. 2009: 14)

29) Maxilla, joint surface for palatine, depth: shallow, does not obscure the tooth root bulges from view (0); deep, obscures tooth root bulges from view (1). (Carr and Williamson 2010: 31)

30) Maxilla, anterior ramus (demarcated by concave step in anterior margin of maxilla): absent (0); present (1). New character.

31) Maxilla, form of contact with nasal in subadult to adult specimens: smooth (0); weakly scalloped (1); deeply scalloped with interlocking transverse ridges on both elements (2). (Sereno et al. 2009: 15). ORDERED Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea. The first derived state is present in *Raptorex* and albertosaurines, and the second in some tyrannosaurines.

32) Maxilla, form of external subcutaneous surface texturing: random foramina and shallow grooves and ridges (0); deep, prominent, dorsoventrally trending grooves and ridges (1). New character.

33) Maxilla, swollen rim separating antorbital fossa and subcutaneous surface: present (0); absent (1). New character.

34) Maxilla, size of ascending ramus, anteroposterior chord directly above maxillary fenestra compared to dorsoventral depth of maxilla below anterior edge of antorbital fenestra: greater than 1.75 times (ascending ramus large) (0); less than 1.60 times (ascending ramus small) (1). New character.

35) Maxilla, posterior region of the main body (portion including the final 3-5 teeth and anterior to the jugal process), shape: maintains a relatively constant dorsoventral depth (0); tapers in depth posteriorly (1). New character.

36) Maxilla, primary row of neurovascular foramina, form: continues as a row posteriorly (0); transitions into a sharp groove, paralleling the antorbital fossa rim, posteriorly (1). New character.

37) Maxilla, antorbital fossa, extent on main body: covers more (0) or less (1) than half of the depth of the main body beneath the anterior margin of the antorbital fenestra. New character.

Nasal

38) Nasals, shape of dorsal surface: flat or slightly convex (0); convex (vaulted) anteriorly, above and immediately posterior to the external naris (1); vaulted across most of their length (2). ORDERED (Carr and Williamson 2010: 37; Sereno et al. 2009: 5). Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea. Crested taxa are scored as inapplicable ("?").

39) Nasals, midline crest on dorsal surface: absent (0); present (1). (Carr and Williamson 2010: 50)

40) Nasal, external texture of mid section of bone: smooth to slightly rugose (0); pronounced rugosities and accessory vascular foramina present (1). (Carr and Williamson 2010: 48; Sereno et al. 2009: 7)

41) Nasal, shape in dorsal view: expands in width posteriorly (0); relatively constant width across the length of the bone, due to subparallel lateral sides (1); tapers in width posteriorly (2). UNORDERED (Sereno et al. 2009: 6)

42) Nasal, frontal process, mediolateral width: unconstricted (0); constricted, less than ½ width of widest point of nasal (1). (Carr and Williamson 2010: 41)

43) Nasal, internal pneumatic recess: present (0); absent (1). (Carr and Williamson 2010: 39)

44) Nasal, posterolateral process that overlaps the lateral surface of the lacrimal: absent (0); present (1). (Carr and Williamson 2010: 40; Sereno et al. 2009: 4)

45) Nasal, extent of narial fossa on premaxillary process: limited to ventral margin of process (0); covers entire process, and thus meets opposite fossa on dorsal midline (1). (Sereno et al. 2009: 2)

46) Nasal, medial processes of frontal articulation, shape: processes absent (0); lanceolate (1); tapered (2). UNORDERED (Carr and Williamson 2010: 44)

47) Nasal, thin, low, and laterally projecting crest at the corner where lateral and dorsal surfaces meet: absent (0); present (1). New character. Note: The derived state describes the Y-shaped crest of *Dilong*, originally described as an autapomorphy, which is also present (albeit in as a much smaller and less pronounced structure) in *Eotyrannus*.

Lacrimal

48) Lacrimal, shape in lateral view: inverted L (0); 7 shaped (1). (Carr and Williamson 2010: 55).

49) Lacrimal, cornual process on dorsal surface: absent (0); present as a broad, shallow, dorsally convex, laterally overhanging swelling across most of the length of the anterior ramus (1); present as a discrete conical projection (2); small, conical, smooth projection that rises 2-3 millimeters from skull roof (3). UNORDERED (Carr and Williamson 2010: 56; Sereno et al. 2009: 18) Note: Relative to previous studies, a new character state is added here to take into account the tiny cornual process of *Guanlong* and *Dilong*. Therefore, a cornual process itself is a tyrannosauroid synapomorphy.

50) Lacrimal, cornual process, form: smoothly rounded (0); discrete apex present (1). (Carr and Williamson 2010: 57) Note: *Tyrannosaurus* and *Tarbosaurus* are scored as inapplicable ("?"), since they do not possess a discrete cornual process.

51) Lacrimal, cornual process, position of apex: dorsal to ventral ramus (0); anterior to ventral ramus (1). (Carr and Williamson 2010: 59; Sereno et al. 2009: 19)

52) Lacrimal, extent of pneumaticity: limited, partially hollows bone in the region where the anterior and ventral rami meet (0); extensive, completely hollows bone (1). (Sereno et al. 2009: 16)

53) Lacrimal, anterior ramus: not inflated (0); inflated by pneumatic recess (1). (Carr and Williamson 2010: 64; Sereno et al. 2009: 17).

54) Lacrimal, size of primary external opening for lacrimal recess: small, anterior end located approximately at the same level as the anterior end of the ventral ramus (0); large, anterior end located far anterior to the ventral ramus (1). (Carr and Williamson 2010: 60)

55) Lacrimal, interaction of primary external opening for lacrimal recess and antorbital fossa: separate (0); blend (1). (Carr and Williamson 2010: 63)

56) Lacrimal, accessory external openings for lacrimal recess on the anterior ramus: absent (0); present and proximally located (1); present and distally located (2). UNORDERED (Carr and Williamson 2010: 67)

57) Lacrimal, pneumatic recess opening internally onto medial surface of bone: absent (0); present (1). (Carr and Williamson 2010: 68)

58) Lacrimal, dorsal prong of anterior ramus for articulation with maxilla ("anterodorsal process"): absent or small (0); present and elongate (1). (Carr and Williamson 2010: 65) Note: We have combined two characters used by Carr and Williamson, referring to the presence and then the size of the anterodorsal process, into a single character, because the subtle process can easily be mistaken for absent if it is broken or poorly preserved.

59) Lacrimal, ventral ramus, extent of medial lamina: greater (0) or less than (1) half of the dorsoventral depth of the ramus. (Carr and Williamson 2010: 72)

60) Lacrimal, orbitonasal ridge on medial surface, position: anterior (0) or adjacent to or contacting (1) posterior margin of ventral ramus. (Carr and Williamson 2010: 69).

61) Lacrimal, articulation with frontal, form: squamous (0); conical lacrimal process set into deep pit in frontal (1). (Sereno et al. 2009: 22)

62) Lacrimal, posterior process for articulation with frontal, inflated by pneumatic recess: no (0); yes (1). New character.

63) Lacrimal, extent of antorbital fossa on ventral ramus: covers greater (0) or less than (1) 60% of anteroposterior length along the contact with the jugal. New character.

64) Lacrimal, maxillary process of anterior ramus, visibility in lateral view: both dorsal and ventral margins visible (0); dorsal margin concealed by subcutaneous surface above antorbital fossa and only ventral margin visible (1). (Carr and Williamson 2010: 66)

Jugal

65) Jugal, maxillary ramus, depth: shallow, not expanded relative to suborbital portion of bone (0); deep, expanded relative to suborbital portion of bone (1). (Carr and Williamson 2010: 73)

66) Jugal, antorbital fossa, extent on maxillary ramus: edge of fossa undercut and continues posterodorsal to jugal recess (0); fossa edge does not extend past the jugal recess (1). (Carr and Williamson 2010:75)

67) Jugal, pneumatic recess, location relative to ventral ramus of lacrimal: ventral (0); anterior (1). (Carr and Williamson 2010:76)

68) Jugal, pneumatic recess, orientation of long axis: approximately horizontal (0); inclined at approximately 45 degrees relative to the ventral skull margin (1). (Carr and Williamson 2010:78)

69) Jugal, secondary fossa for pneumatic recess, position relative to recess: ventral (0); dorsal (1). (Carr and Williamson 2010:80)

70) Jugal, suture with lacrimal, angle of the posterior half of the contact: low (0); steep (1). (Carr and Williamson 2010:81)

71) Jugal, fossa on lateral surface of postorbital ramus, depth inset into bone: shallow (0); deep (1). (Carr and Williamson 2010:82; Sereno et al. 2009:24)

72) Jugal, articulation with postorbital, form of ventral extremity of suture: tapering scarf joint (0); interlocking notch for postorbital (1). (Carr and Williamson 2010:83; Sereno et al. 2009:26)

73) Jugal, articulation with postorbital, extent of scarf joint on lateral surface of postorbital ramus: limited, occupies less than 50% of anteroposterior length of the process (0); extensive, occupies approximately 50-75% of the anteroposterior length of the process (1). New character.

74) Jugal, articulation with postorbital, braced by a pronounced ridge on the lateral surface of the postorbital ramus, which borders the postorbital posteriorly: no (0); yes (1). New character.

75) Jugal, postorbital ramus, orientation relative to ventral margin of jugal: approximately perpendicular (0); posterodorsal (obtuse angle between the long axis of the process and the ventral margin) (1). New character.

76) Jugal, cornual process: absent (0); present (1); present and distinctive (mediolaterally wide and heavily rugose (2). ORDERED (Carr and Williamson 2010:84, 85)

77) Jugal, dorsal prong of quadratojugal ramus, slope in lateral view: horizontal (0); posterodorsal (1). (Carr and Williamson 2010:91)

78) Jugal, ventral prong of quadratojugal ramus, slope of joint surface in lateral view: approximately anteroposteriorly oriented, angled less than 45 degrees from horizontal (0); angled anterodorsally at greater than 45 degrees from horizontal (1). (Carr and Williamson 2010:90)

79) Jugal, shape of orbital margin, weakly concave, approximately level with lacrimal-jugal suture (0); U-shaped, extends ventral to lacrimal-jugal suture (1). (Sereno et al. 2009: 26)

80) Jugal, raised rim on the lateral surface, paralleling the ventral margin of the bone and anteriorly confluent with the antorbital fossa rim of the maxilla: absent (0); present (1). New character.

Postorbital

81) Postorbital, cornual process: absent (0); limited to rugose rim at posterodorsal corner of orbit (1); present as a rugose, convex boss (2). ORDERED (Sereno et al. 2009:29)

82) Postorbital, cornual process, position: separated from dorsal margin of postorbital by a smooth, convex region (0); approaches or extends past dorsal margin of bone (1). (Carr and Williamson 2010:94).

83) Postorbital, cornual process, position: located at orbital margin (0); located posterodorsal to orbital margin (1). (Carr and Williamson 2010:95)

84) Postorbital, squamosal ramus, form of posterodorsal margin: uninterrupted convex arc (0); emarginated by squamosal (discrete concave notch within the margin) (1). (Carr and Williamson 2010:99)

85) Postorbital, squamosal ramus, extent: reaches or extends posterior to (0) or terminates anterior to (1) posterior margin of lateral temporal fenestra. (Carr and Williamson 2010:100; Sereno et al. 2009:28)

86) Postorbital, suborbital process that extends into the orbit: absent, ventral ramus tapers (0); present and large in adults, small and unpronounced (ventral ramus tongue-shaped) in sub-adults (1); present and large in sub-adults and adults (2). ORDERED (Carr and Williamson 2010:101; Sereno et al. 2009:30) Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea. The first derived state describes the somewhat expanded postorbital ventral ramii of albertosaurines, *Alioramus*, and *Daspletosaurus* (these are tongue-shaped as juveniles and then, at least in albertosaurines, develop the discrete flange as adults. State 1 is assumed to be present in *Alioramus* because it has the characteristic juvenile shape of albertosaurines and *Daspletosaurus*), although it is possible that future discoveries will reveal that *Alioramus* did not possess a suborbital flange in adults (and thus would need to be scored as state 0).

87) Postorbital, suborbital process, position: at ventral end of ventral process (0); flange-like, separated from ventral tip of ventral process by a notch (1). (Carr and Williamson 2010:102)

88) Postorbital, anterior ramus, form: short and stout, long axis is approximately half the length of the ventral ramus and the thickness at the base is approximately the same as the thickness of the midpoint of the ventral ramus (0); long and slender, long axis is greater than 60% of the length of the ventral ramus and the thickness at the base is approximately half that of the midpoint of the ventral ramus (1). (Li et al. 2010:252).

89) Postorbital, ventral ramus, anteroposterior width at midpoint: approximately the same width as (0) or substantially wider than (1) ventral ramus of the lacrimal. (Li et al. 2010: 268).

Squamosal

90) Squamosal, lateral ridge delimiting supratemporal fossa, form: ridge unpronounced or undivided (0); divided (1). (Carr and Williamson 2010:106)

91) Squamosal, supratemporal fossa, surface morphology: flat or concave (0); convex (1). (Carr and Williamson 2010:107)

92) Squamosal, quadratojugal process, orientation of long axis: dorsoventral or slightly oblique (0); anteroposterior (1). (Carr and Williamson 2010:111)

93) Squamosal, quadratojugal process, morphology of anterior tip in those taxa with horizional processes: tapered point (0); squared off (1). (Carr and Williamson 2010:110)

94) Squamosal, quadratojugal process, flange that is covered laterally by the quadratojugal, dorsoventral depth of entire process compared to portion of process that is exposed in lateral view when in articulation with quadratojugal: flange absent (0); thinner (1); substantially thicker (2). ORDERED (Carr and Williamson 2010:112)

95) Squamosal, posterior process, inflated by squamosal recess: no (0); yes (1). (Carr and Williamson 2010:114)

96) Squamosal, posterior process, length of the long axis compared to the long axis of the quadratojugal process: long, approximately 1/3-1/2 (0); short, approximately 1/6 (1). (Carr and Williamson 2010:115).

97) Squamosal, anterior process, flange that extends dorsal to the postorbital posterior process: absent (0); present (1). (Sereno et al. 2009:32)

Quadratojugal

98) Quadratojugal and squamosal, constriction of lateral temporal fenestra: absent, anterior margins of both bones are approximately vertical (0); present, convex kink along the suture between the two bones that projects into the fenestra, constricting it to approximately one half of its maximum anteroposterior length (1); present, dorsal region of quadratojugal moderately expanded anteroposteriorly relative to the remainder of the bone, constricting fenestra to approximately one half of its maximum anteroposterior length (2); present, dorsal region of quadratojugal expanded anteroposteriorly by at least twice the minimum anteroposterior dimension of the bone, forming a flange that meets the ventral ramus of the squamosal to nearly divide the fenestra (3). ORDERED (Carr and Williamson 2010:116; Sereno et al. 2009:35).

99) Quadratojugal, dorsal process, ridge along anterior margin of lateral surface: absent (0); present, subtle and fades in strength dorsally (1); present, robust and extends to the dorsal margin of the bone (2). ORDERED. (Carr and Williamson 2010:117) Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea.

100) Quadratojugal, form of jugal articulation: dorsal prong of posterior process of jugal does not (0) or does (1) approach the base of the quadratojugal (the corner where the anterior and dorsal processes of the quadratojugal meet). (Carr and Williamson 2010:120)

101) Quadratojugal, anterior process for articulation with jugal, form of anterior region: tapered (0); rounded (1); squared off or double pronged (2). UNORDERED (Carr and Williamson 2010:121; Sereno et al. 2009:34)

102) Quadratojugal, anterior process, extent: terminates posterior (0) or level with or anterior (1) to anterior margin of lateral temporal fenestra. (Carr and Williamson 2010:88; Sereno et al. 2009:36)

103) Quadratojugal, curvature of bone: mediolaterally compressed and flat (0); posterior region flexed so that it curves posteriorly, thus delimiting the lateral edge of a deep pocket that borders the quadrate foramen laterally in posterior view (1). (Li et al. 2010: 281)

104) Quadratojugal, posterior process, length and orientation: short, oriented mostly laterally (0); elongate, wraps onto the posterior surface of the quadrate condyles (1). New character.

Quadrate

105) Quadrate foramen, size: small, long axis approximately 10% of the dorsoventral depth of the quadrate shaft (0); large, long axis greater than 20% of the dorsoventral depth of the quadrate shaft (1). (Carr and Williamson 2010:125)

106) Quadrate, pneumaticity: absent (0); present, deep recess on the anterior surface where the pterygoid wing and condyles meet (1). (Carr and Williamosn 2009:126)

107) Quadrate condyles, position relative to occipital condyle when skull is in articulation: approximately aligned (0); completely posterior (1). (Carr and Williamson 2010:127; Sereno et al. 2009:42)

108) Quadrate, quadratojugal articulation, extent on lateral surface of lateral condyle: limited, occupies only part of the surface (0); extensive, covers entire lateral surface and extends dorsally to partially enclose quadrate foramen laterally (1). New character.

109) Quadrate, articular surface for quadratojugal on quadrate lateral condyle, orientation of medial margin as seen in posterior view where quadratojugal wraps around quadrate: vertical or dorsomedial (0); dorsolateral (1). (Carr and Williamson 2010:124)

Prefrontal

110) Prefrontal, contacts nasal: yes (0); no, excluded by frontal-lacrimal contact (1). New character.

111) Prefrontal, exposure in dorsal view: widely exposed, forms much of orbital rim and usually separates or nearly separates frontal and lacrimal (0); reduced, not exposed along the orbital rim and allows for wide contact between frontal and lacrimal (1). (Carr and Williamson 2010:131; Sereno et al. 2009:20)

112) Prefrontal, ventral process, extent: large, extends more than halfway down the ventral ramus of the lacrimal to make an extensive contribution to the preorbital bar (0);

reduced or absent, ventral process is a thin flange that is continuous with the crista cranii of the frontal, and does not extend more than approximately ¼ of the length of the preorbital bar (1). (Carr and Williamson 2010:132)

Frontal

113) Frontal, shape: triangular (0); posterior end expanded into a rectangular shape, with a small anterior triangle (1). (Sereno et al. 2009:38)

114) Frontal, size of single frontal: ratio of anteroposterior length of exposed portion on skull roof to mediolateral width at midpoint: greater than 2.5 (0); less than 2.0 (1). New character.

115) Frontal, supratemporal fossa, anteroposterior length compared to overall length of exposed portion of frontal on skull roof: less than 30% (0); between 30-50% (1); between 50-60% (2); greater than 60% (3). ORDERED (Carr and Williamson 2010:136-137)

116) Frontal, supratemporal fossa, medial extension: fossa restricted to posterolateral corner of frontal (0); meets opposing fossa at the midline (1). (Sereno et al. 2009:39).

117) Frontal, sagittal crest: absent or subtle, only discernable as a slight midline bulge (0); present and pronounced (dorsoventrally tall), single structure (1); present and pronounced (dorsoventrally tall), paired structure (2). UNORDERED (Carr and Williamson 2010:139).

118) Frontal, sagittal crest: anteroposterior length: absent or subtle and short, less than 15% length of the frontal (0); extensive, approximately 25% of the length of the frontal (1). (Carr and Williamson 2010:141)

119) Frontal, postorbital suture: dorsoventrally shallow and undifferentiated (0); dorsoventrally shallow (approximately 6 times longer than deep) and differentiated into a vertical region anteriorly and a horizontal region posteriorly (1); dorsoventrally deep (approximately twice as long as deep) and subtly differentiated into vertical and horizontal regions). (Carr and Williamson 2010:145; Sereno et al. 2009:37). ORDERED Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea.

120) Frontal, contribution to orbital rim: extensive (0); present but limited to a small notch (1); excluded by postorbital-lacrimal contact in large specimens (2); excluded by postorbital-lacrimal articulation and novel "palpebral" ossification (3). ORDERED (Carr and Williamson 2010:104; Sereno et al. 2009:21)

Parietal

121) Parietal-frontal suture, form: transversely smooth (0); tab-like wedge from parietal extends anteriorly to overlie frontal on midline (1). (Carr and Williamson 2010:147)

122) Parietal, sagittal crest: absent (0); present (1). (Carr and Williamson 2010:148)

123) Parietal, sagittal crest, form: comprised of two parallel crests (0); comprised of a single midline crest (1). (Carr and Williamson 2010:150)

124) Parietal, skull table between supratemporal fossae, width: broad, 10-30% of the mediolateral width of the fossa (0); extremely reduced, sagittal crest or crests pinched between opposing fossae (1). (Sereno et al. 2009:40)

125) Parietal, sagittal crest, dorsoventral depth: consistent across length of crest (0); peaked anteriorly at frontal-parietal suture (1). (Carr and Williamson 2010:146)

126) Parietal, nuchal crest, dorsoventral depth: as low as or lower (0) or extends higher (1) than the dorsal surface of the interorbital region. (Carr and Williamson 2010:149; Sereno et al. 2009:41)

127) Parietals, fusion: unfused (0); fused on the midline in sub-adults and adults (1). New character.

Vomer

128) Vomer, shape of anterior end: lanceolate (lateral margins parallel-sided) (0); expanded into a diamond (1). (Carr and Williamson 2010:176; Sereno et al. 2009:45).

Ectopterygoid

129) Ectopterygoid, extent of internal recess: does not (0) or does (1) inflate the body of the bone and the pterygoid process. (Carr and Williamson 2010:178; Sereno et al. 2009:44)

130) Ectopterygoid, jugal process, external pneumatic foramina leading into jugal recess: absent (0); present (1). (Carr and Williamson 2010:180)

131) Ectopterygoid, jugal process, is not (0) or is (1) inflated by the internal recess. (Carr and Williamson 2010:181)

132) Ectopterygoid, external opening of pneumatic recess, shape: thin ovoid slot (0); larger, round or triangular (1). (Carr and Williamson 2010:183)

133) Ectopterygoid, surface posteriorly adjacent to external opening of pneumatic recess, form: flat, recess grades smoothly into the floor of the lateral temporal fenestra (=subtemporal fenestra) (0); lip, recess separated from lateral temporal fenestra (=subtemporal fenestra) (1). (Carr and Williamson 2010:185)

Palatine

134) Palatine, vomeropterygoid process, anteroposterior length of dorsal margin ratio to length of greatest constriction of process neck: greater (0) or less than (1) 2.0. (Carr and Williamson 2010:188) Note: This character has been modified relative to previous usage to make it quantitative.

135) Palatine, vomeropterygoid process, orientation of neck: inclined anterodorsally (0); vertical (1). (Carr and Williamson 2010:189)

136) Palatine, pneumaticity: absent (0); present (1). (Carr and Williamson 2010: 190)

137) Palatine, pneumatic recess, number of external pneumatic openings: one (0); two (1). (Carr and Williamson 2010: 190) Note: What some authors have considered a second external pneumatic opening is actually the posterior region of the internal antorbital fossa. Two pneumatic openings, along with the posterior fossa, are only present in *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus*.

138) Palatine, primary external opening of palatine recess, location of posterior margin: level with or extends posterior to (0) or located far anterior to (1) posterior margin of the vomeropterygoid process neck. (Carr and Williamson 2010:194)

139) Palatine, primary opening of palatine recess, location of anterior margin: level with or posterior to (0) or anterior to (1) anterior margin of the vomeropterygoid process neck. (Carr and Williamson 2010:195)

140) Palatine, jugal process, location of contact surface for lacrimal: posterior ("distal"), separated from opening of palatine recess by wide margin (0); anterior ("proximal"), closely approaches opening of palatine recess (1). (Carr and Williamson 2010:196)

141) Palatine, maxillary process, form of maxillary articulation: flat (0); deeply excavated as a slot, demarcated dorsally by a pronounced lip of bone (1). (Carr and Williamson 2010:197)

142) Palatine, extension of pneumatic recess into jugal process: no (0); yes, process visibly inflated (1). (Carr and Williamson 209:199)

143) Palatine, maxillary articulation, form: maxilla abuts lateral surface of maxillary process and anterior region of jugal process (0); contact reinforced by a "brace" at the anteroventral corner of the jugal process, which sits within internal antorbital fossa (1). New character.

144) Palatine, morphology of maxillary articulation brace: projects ventrally due to a jugal process that extends further ventrally than the maxillary process, such that there is a discrete corner between the two processes in lateral view (0); projects laterally, with no discrete corner between the smoothly confluent jugal and maxillary processes in lateral view (1). New character.

Palatal Openings

145) Internal choana, shape: anteroposteriorly elongate oval (0); nearly circular (1). New character.

146) Suborbital fenestra, shape: anteroposteriorly elongate oval (0); nearly circular (1). New character.

Braincase

147) Braincase, orientation of occipital surface: faces posteriorly (0) or posteroventrally (1). (Sereno et al. 2009:46) Note: This character differs slightly from character 1, which refers to the orientation of the entire posterior surface of the skull and not just the braincase; as a result, some taxa are scored differently for these two characters.

148) Supraoccipital, contribution to dorsal rim of foramen magnum: forms entire rim (0); makes limited contribution to rim via triangular ventral process (1); completely excluded from rim (2). UNORDERED (Carr and Williamson 2010:158) Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea. The first derived state is present in most tyrannosauroids, but the second derived condition is only seen in *Guanlong* and *Dilong*, although often it is erroneously considered a tyrannosauroid synapomorphy. The proper tyrannosauroid synapomorphy, therefore, is a limited supraocciptal contribution to the foramen magnum.

149) Supraoccipital, form of dorsal margin: smoothly convex and undivided (0); divided into two processes ("forked") (1). (Carr and Williamson 2010:172)

150) Exoccipital-opisthotic, paroccipital process, ventral flange at distal end: absent (0); present (1). New character.

151) Exoccipital-opisthotic, paroccipital processes, deep fossa on posterior surface dorsolateral to the foramen magnum: present (0); absent (1). New character.

152) Exoccipital-opisthotic, crista tuberalis (=metotic strut), extent in posterior view: limited, mediolateral width across opposing cristae less than one half the dorsoventral depth of the braincase from the dorsal tip of the supraoccipital to the ventral tip of the basal tubera (0); extensive, width greater than one half the braincase depth (1). New character.

153) Exoccipital-opisthotic, fossa for cranial nerves X-XII: shallow (0); deep (1). New character.

154) Basioccipital, basal tubera, dorsoventral depth: less than (0) or greater than (1) depth of occipital condyle. New character.

155) Basioccipital, basal tubera, concave notch ventrally between opposing tubera, dorsoventral depth: shallow, less than 40% depth of tubera (0); deep, approximately 50% depth of tubera (1). New character.

156) Basioccipital, subcondylar recess, depth of pneumatic fossae on posterior surface of basal tubera: absent or shallow (0); deep (1). (Carr and Williamson 2010:168)

157) Basisphenoid, basipterygoid recess (pneumatic recess above basipterygoid processes on lateral surface of braincase), absent or present as shallow pneumatic fossa (0); present as a large rectangular fenestra (1). (Carr and Williamson 2010:160) Note: The derived state refers solely to the large, window-like pneumatopore and not subtle pneumatic fossae, the latter of which are often difficult to recognize on fossils.

158) Basisphenoid, basisphenoid recess, orientation of central axis: vertical, recess obscured in posterior view (0); posteroventral, recess partially visible in posterior view (1); extremely posteroventral, recess compressed anteroposteriorly and widely visible in posterior view, and basipterygoid processes located beneath the basal tubera (2). ORDERED (Carr and Williamson 2010:163,165; Sereno et al. 2009:50) Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea. The second derived state refers to the highly modified condition of *Tyrannosaurus* and *Tarbosaurus*.

159) Basisphenoid, basisphenoid recess, inflation of the ceiling of the recess: absent (0); present (1). (Carr and Williamson 2010:166)

160) Basisphenoid recess, shape in ventral view: funnel-like, expands in mediolateral width posteriorly (0); ovoid or circular, no posterior expansion (1). New character.

161) Basisphenoid, shape of basicranium (rectangle defined by positions of both basal tubera and both basipterygoid processes): anteroposteriorly longer than mediolaterally wide (0); wider than long (1). (Carr and Williamson 2010:169; Sereno et al. 2009:49; Li et al. 2010: 272)

162) Parasphenoid, shape of rostrum: anteroposteriorly expanded, ventral margin is a smooth concave arch (0); dorsoventrally expanded, ventral margin is nearly vertical posteriorly and then abruptly transitions to horizontal trend anteriorly (1). New character.

163) Prootic, dorsal tympanic recess: present (0); absent (1). New character.

164) Laterosphenoid, antotic crest separating lateral wall of braincase from orbital and temporal spaces: absent or indistinct (0); present and robust and rugose (1). (Carr and Williamson 2010:152, 155).

165) Laterosphenoid, antotic crest, form: single structure (0); bifurcates ventrally (1). New character.

166) Laterosphenoid, fossa on lateral surface that houses head of epipterygoid: absent or shallow (0); present, deep and rugose (1). New character.

167) Ossified sphenethmoid and mesethmoid (when not fossilized, can be inferred by presence of scars on ventral surface of frontal): absent (0); present (1). New character.

Lower Jaw

168) Mandibular ramus, dorsoventral depth of dentary at level of dentary-surangular contact on the dorsal margin of the lower jaw: less (0) or greater than (1) 18% of the total anteroposterior length of the lower jaw (1). (Carr and Williamson 2010:200)

169) External mandibular fenestra, dorsoventral depth relative to depth of mandible at midpoint of fenestra: greater (0) or less than (1) 25%. (Carr and Williamson 2010:217; Sereno et al. 2009:51)

170) Lower jaw, articulation, glenoid position relative to level of alveolar margin of dentary: level or ventral (0); dorsal (1). (Sereno et al. 2009:54) Note: This character is not equivalent to character 168 (shallow vs. deep lower jaw) because *Alioramus* has a shallow lower jaw but a dorsally positioned glenoid.

Dentary

171) Dentary, position of the transition point between the ventral and anterior margins of the bone in lateral view: below alveoli 1-3, anterior margin rounded (0); below alveolus 4, anterior margin nearly straight and projects posteroventrally (1). (Carr and Williamson 2010:215).

172) Dentary, ventrally projecting rugose process ("chin") where the anterior and ventral margins of the dentary meet: absent (0); present, visible as a pointed projection in lateral view and convex in medial view, braces dentary symphysis (1). New character.

173) Dentary, symphysis, texture: generally smooth (0); strongly rugose and beveled, with interlocking ridges and convexities for articulation with the opposing symphysis (1). New character.

174) Dentary, articular surface for splenial along ventral region of dentary ramus below the Meckelian fossa, form: dorsoventrally shallow and smooth (0); dorsoventrally deep (nearly as deep as anterior depth of fossa) and rugose (1). New character.

175) Dentary, anterior alveoli, size in comparison to alveoli in middle of tooth row: approximately same size (0); first two alveoli substantially smaller (1); first alveolus substantially smaller (2). UNORDERED. New character.

176) Dentary, primary neurovascular foramina, arrangement: distinct foramina or set into a shallow groove posteriorly (0); set into a deep and sharp groove across the middle and posterior regions of the dentary (1). New character.

177) Dentary, dorsal margin of bone in lateral view, profile: straight (0); strongly concave (1). New character.

178) Dentary, Meckelian groove, form: dorsoventrally deep and shallowly inset into medial surface of bone (0); dorsoventrally shallow and deeply inset into bone, groove appears as a thin, sharp structure (1). New character.

Surangular

179) Surangular, posterior foramen, size: absent or small foramen (0); large fenestra, approximately 30% depth of posterior surangular (1). (Carr and Williamson 2010:204; Sereno et al. 2009:52)

180) Surangular, surangular shelf on lateral surface, form: low ridge (0); prominent ridge that is offset laterally from the bone but dorsoventrally thin (1); prominent shelf that is dorsoventrally deep (2). ORDERED (Carr and Williamson 2010:209; Sereno et al. 2009:53)

181) Surangular, surangular shelf, position and form: placed far dorsal to posterior surangular foramen (0); foramen abuts shelf but shelf projects laterally and does not overhang foramen (1); shelf projects ventrolaterally to overhang foramen (2). ORDERED (Carr and Williamson 2010:208)

182) Surangular, surangular shelf, orientation relative to the long axis of the lower jaw: anterodorsal (0); anteroventral (1); straight anteroposteriorly (2). New character.

183) Surangular, pneumatic fossa posterodorsal to posterior surangular foramen: absent (0); present and shallow (1); present and deeply invaginated (2). ORDERED New character.

184) Surangular, adductor muscle attachment site dorsal to surangular shelf, orientation: faces primarily dorsally (0); faces almost equally dorsally and laterally (1); faces primarily laterally (2). ORDERED New character.

185) Surangular, triangular fossa on the lateral surface of the surangular shelf immediately anteroventral to glenoid: absent (0); present (1). New character.

186) Surangular, fossa on the lateral surface of the bone immediately ventral to, and separated from, the glenoid: absent (0); present (1). New character.

187) Surangular, anteroposterior length of anterior flange (region anterior to anterior margin of external mandibular fenestra) compared to overall length of surangular: less than (0) or greater than (1) 30%. New character.

Angular

188) Angular, ventral margin, form: smoothly convex (0); anterior region "flexed" relative to posterior region, such that there is a discrete step between them (1). New character.

Articular

189) Articular, mediolateral width of jaw muscle attachment site: less than (0) or equal to or greater than (1) width of glenoid for articulation with quadrate. New Character, inspired by Rauhut et al. (2010).

190) Articular, smooth non-articular region between glenoid and attachment site for depressor mandibular muscles: present (0); absent (1). New character, inspired by Rauhut et al. (2010).

Splenial

191) Splenial, anterior mylohyoid foramen, shape and size: small circular or ovoid opening (0); large, anteroposteriorly ovoid shape (1); extremely large, approximately as deep dorsoventrally as the anterior process of the splenial (2). ORDERED (Carr and Williamson 2010:210).

192) Splenial, dorsal region overlapped medially by prearticular: absent (0); present (1). New character.

Prearticular

193) Prearticular, ventral bar, series of ridges on lateral surface to strengthen articulation with angular: absent (0); present (1). New character.

Supradentary and Coronoid

194) Supradentary ossification, shape: elongate, shallow strip (0); deep, crescentic shape (1). New charcter.

195) Supradentary and coronoid ossifications, form of contact at their zone of fusion: smoothly confluent (0); offset by a concave notch (1). New character.

Dentition

196) Premaxillary teeth, position of mesial carina: offset mesial to distal carina on all teeth (teeth ziphodont) (0); rotated distally on premaxillary teeth 1 and 2 (anterior teeth "D-shaped" and posterior teeth ziphodont) (1); rotated distally on all teeth (2). (Carr and Williamson 2010:219; Sereno et al. 2009:56-58). ORDERED Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea, as made explicit by Sereno et al. (2009).

197) Premaxillary tooth crown 4, apicobasal height relative to largest maxillary crown: subequal (0); approximately 50% (1). (Sereno et al. 2009:59)

198) Premaxillary teeth, median vertical ridge on lingual surface: absent (0); present as subtle structure in anterior (mesial) premaxillary teeth (1); present as pronounced structure in all premaxillary teeth (2). ORDERED (Sereno et al. 2009:60)

199) Premaxillary teeth, curvature of distal (posterior) teeth: recurved (0); straight (1). New character.

200) Maxillary teeth, number: 13 or more (0); less than 13 in the largest adult specimens (1). (Carr and Williamson 2010:220; Sereno et al. 2009:61)

201) Maxillary and dentary teeth, form: ziphodont, transverse width of base less than 60% of mesiodistal length (0); incrassate, width greater than 60% of length (1); incrassate, width nearly equal to length (2). ORDERED (Sereno et al. 2009:62)

Cervical Vertebrae

202) Axis and postaxial cervicles, anteroposterior length of centrum compared to dorsoventral height of posterior centrum face: greater (0); less than or equal to (1). Originally used by Holtz (2001). Note: It is possible that this character is related to size and ontogeny (larger and/or older individuals may possess deeper centra), but we retain it here in the absence of explicit data on how vertebral morphology changes throughout ontogeny in a single tyrannosauroid taxon.

203) Axis, pneumatic foramen (pleurocoel), position: near midheight of centrum (0); dorsally located, directly underneath neurocentral suture and directly posterior to diapophysis (1). New character.

204) Axis, pneumatic foramen, extent of surrounding fossa: limited to margins of foramen (0); extensive, occupies most of lateral surface of centrum (1). New character.

205) Axis, ridge on ventral surface of axis: absent (0); present (1). New character.

206) Axis, pneumatic foramina and fossae on each side of the anterior ridge on the neural spine: absent (0); present (1). New character.

207) Axis, neural spine, texture of dorsal region of anterior surface: generally smooth or with subtle texture (0); highly rugose, with series of grooves, ridges, and eminences (1). New character.

208) Axis, dorsal region of neural spine, number of projections on "crown" region: two lateral projections, dorsal surface of spine smoothly concave (0); two lateral projections and one dorsal projection on the midline (1). New character.

209) Axis, supradiapohyseal fossa (fossa posterodorsal to diapophysis): absent or shallow (0); deeply excavated and funnel-like (1). New character.

210) Axis and anterior-middle postaxial cervicals, epipophysis, form: small, pyramidal mound that extends only slightly posterior to postzygapophysis (0); large, rugose flange that extends far posterior to postzygapophysis (1). New character.

211) Cervical vertebrae, neural spines in middle-posterior cervicals, shape: elongate rectangle, much longer anteroposteriorly than wide transversely (0); stout rectangle, base is essentially square shaped due to nearly equal anteroposterior and transverse dimensions (1). New character.

212) Cervical vertebrae, neural spines in middle-posterior cervicals, dorsoventral height: substantially shorter (0); or approximately the same length as or longer (1) than posterior centrum face. Originally used by Holtz (2001).

213) Cervical vertebrae, morphology of posterior centrodiapophyseal laminae in anterior-middle cervicals: absent or present as a weak ridge (0); present as a thick, laterally offset lamina that demarcates a deep infradiapophyseal fossa anteriorly (1). New character.

214) Cervical vertebrae, hypapophysis on anterior region of ventral surface: absent (0); present (1). New character.

215) Cervical vertebrae, position of prezygapophysis in middle cervicals: slightly overhangs centrum laterally (0); strongly overhangs centrum laterally, entire prezygapophyseal facet placed lateral to centrum (1). New character.

216) Cervical vertebrae, orientation of posterior centrodiapophyseal lamina in anterior-middle cervicals: projects posteroventrally, infrapostzygapophyseal fossa located primarily posterior to lamina (0); nearly horizontal, fossa located primarily dorsal to lamina (1). New character.

Dorsal Vertebrae

217) Cervical and dorsal vertebrae, rugose ligament attachment scars in pre- and postspinal fossae: absent or weakly developed (0); present as prominent, rectangular flanges that extend outside of the fossae and are visible in posterior view, but on the

dorsal vertebrae only (1); prominent in dorsals and cervicals (2). ORDERED New character.

218) Dorsal vertebrae, extent of pneumaticity, presence of pneumatic foramina on lateral centrum surface: absent or limited to anterior dorsals (0); present throughout dorsal column (1). (Carr and Williamson 2010:226)

219) Dorsal vertebrae, neural spine, level of posterior termination: at approximately the same level as the posterior centrum face (0); far posterior to the posterior centrum face (1). (Carr and Williamson 2010:227)

220) Dorsal vertebrae, anteroposterior length of middle-posterior dorsal centra compared to dorsoventral height of posterior centrum face: greater (0); less than or equal (1). New character, modified from Carr and Williamson 2010: 228)

221) Dorsal vertebrae, middle-posterior dorsals, position of postzygapophysis relative to prezygapophysis: at same level (0); elevated dorsally (1). New character.

222) Dorsal vertebrae, middle-posterior dorsals, form of anterior and posterior centrodiapophyseal laminae: make contact on ventral surface of transverse process, demarcating a triangular infradiapophyseal fossa (0); do not make contact but roughly parallel each other, infraprezygapophyseal and infradiapophyseal fossa merged into a single fossa (1). New character.

Sacral Vertebrae

223) Sacral vertebrae, pneumatic foramina on lateral surfaces of centra: absent (0); present (1). (Carr and Williamson 2010:229)

224) Sacral vertebrae, fenestrae between fused neural spines: neural spines unfused (0); spines fused but fenestrae absent (1); spines fused and fenestrae present (2). ORDERED New character.

225) Sacral ribs, position of central ribs on sacrum: span two sacrals (0); limited to a single sacral (1). New character.

226) Sacral ribs, position of rib attachment for central ribs on individual sacrals: span centrum and neural arch (0); limited to neural arch only (1). New character.

227) Sacral vertebra five, position of ventral margin of posterior articular face in lateral view: at same level as (0) or positioned ventral to (1) ventral margin of anterior articular face. New character.

228) Sacral vertebrae, form of hyposphene in posteriormost sacral: absent or present as a single midline structure (0); present and comprised of two parallel-sided sheets (1). New character.

Caudal Vertebrae

229) Caudal vertebrae, anterior caudals, position of base of neural spine: anterior to (0) or level with or posterior to (1) posterior surface of centrum. New character.

230) Caudal vertebrae, anterior caudals, shape of transverse processes in dorsal view: rectangular, with parallel anterior and posterior sides, or slightly ovoid with a gradual expansion in width distally (0); distal end expanded into a spatulate bulb (1). New character.

231) Caudal vertebrae, anterior caudals, two laminae linking prezygapophysis and transverse process, between which is a deep, triangular fossa: absent (0); present (1). New character.

Scapula

232) Scapula, angle between posterior margin of glenoid and dorsal margin of blade: greater (0) or approximately (1) 90 degrees. (Carr and Williamson 2010: 234; Sereno et al. 2009: 68).

233) Scapula, acromion, dorsoventral depth: less (0) or greater (1) than 3.0 times minimum dorsoventral depth of blade. (Sereno et al. 2009: 67).

234) Scapula, ratio of anteroposterior length of bone to minimum dorsoventral depth of blade: less (0) or greater (1) than 10.0. (Sereno et al. 2009: 69)

235) Scapula, ratio of dorsoventral depth of distal expansion to minimum dorsoventral depth of blade: less (0) or greater (1) than 2.5. (Sereno et al. 2009: 70)

236) Scapula and coracoid, glenoid, position 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). (Sereno et al. 2009: 66)

Coracoid

237) Coracoid, anteroposterior length at midpoint: approximately 100-150% (0) or 200% or greater (1) than the length of the scapular acromion at midheight. (Sereno et al. 2009: 71)

238) Coracoid, coracoid foramen: present (0); absent or extremely small (1). New character.

Humerus

239) Humerus, length relative to the femur: 50-70% (0); 40-30% (1); 25-30% (2). ORDERED (Carr and Williamson 2010: 235; Sereno et al. 2009: 72). Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea. The first derived state refers to an "intermediate" condition exhibited by *Eotyrannus* and *Dryptosaurus*, relative to the longer humeri of basal tyrannosauroids and the atrophied humeri of tyrannosaurids and *Raptorex*. In cases where the femur is unknown, tibial length or length of the scapular blade can be used as a rough proxy.

240) Humerus, head, form: low, poorly differentiated, crescentic shaped in proximal view, overhangs posterior surface and does not overhang anterior surface (0); enlarged, occupies the majority of the proximal end, bulbous in proximal view, overhangs both posterior and anterior surfaces (1). (Sereno et al. 2009: 73).

241) Humerus, apex of deltopectoral crest, location from proximal end: 40-50% (0); 25-35% (1); less than 25% (2) of the length of the humerus. ORDERED (Sereno et al. 2009: 74) Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea.

242) Humerus, rotation along shaft, orientation of long axis of proximal end relative to that of distal end: approximately 30-45 degree angle (0); approximately parallel, shaft rotation absent (1). (Carr and Williamson 2010: 236)

243) Humerus, additional muscle attachment tubera at the corner of the anterior and lateral surfaces distal to the deltopectoral crest: absent (0); present (1). New character.

244) Humerus, concave notch between external tuberosity and deltopectoral crest: present, two structures clearly separated (0); absent, two structures smoothly confluenet (1). New character.

245) Humerus, form of distal condyles: lateral and medial condyles expanded equally (offset from shaft in anterior or posterior view is equal) (0); medial condyle expanded further medially than the lateral condyle is laterally (1). New character.

Ulna

246) Ulna, shaft axis, form: bowed (0); straight (1). (Sereno et al. 2009: 75) Note: The supposed ulna of *Eotyrannus* is actually a distal tibia, so this taxon cannot be scored for this or the following character.

247) Ulna, distal articular surface, form: convex (0); flat (1). (Sereno et al. 2009: 76)

Carpus and Manus

248) Principal distal carpal, shape: semilunate in lateral view with trochlear proximal surface (0); discoid with flat proximal surface (1). (Carr and Williamson 2010: 238; Li et al. 2010: 276).

249) Manus, number of functional digits: three or more (0); two, metacarpal III is absent or rudimentary, without phalanges (1). (Carr and Williamson 2010: 239; Sereno et al. 2009: 82) Note: We consider *Dryptosaurus* and *Raptorex* to possess the derived state, as the preserved digits I-II of both taxa are extremely similar in morphology to those of tyrannosaurids with only two functional digits. It is possible, however, that a functional digit III may have been present but is only missing due to poor preservation.

250) Metacarpal I, medial distal condyle, form: well formed and large (0); rudimentary (1). (Sereno et al. 2009: 78)

251) Metacarpal I, medial margin, shape in proximal view: concave (0); smooth convexity (1). New character.

252) Metacarpals, ratio of the length of metacarpal II:length of metacarpal I: 2-1.8 (0); 1.8-1.6 (1). (Sereno et al. 2009: 79)

253) Metacarpals, metacarpal II, mediolateral width at midpoint: equal to or narrower than (0); or more robust than (1) metacarpal I. (Carr and Williamson 2010: 240)

254) Manual phalanx II-1, length: longer (0); or subequal to (1) the length of metacarpal 1. (Sereno et al. 2009: 81)

255) Manual unguals, flexor tubercle, form: large, robust, rugose, conical structure (0); reduced to a small convexity (1). New character.

256) Manual unguals, degree of recurvature: extensive, flexor margin deeply concave (0); reduced, flexor margin shallowly concave (1). New character.

Ilium

257) Ilium, anteroposterior length compared to length of femur: 70-85% (0); 95-105% (1); 105-115% (2). ORDERED. (Carr and Williamson 2010: 251; Sereno et al. 2009: 83)

258) Ilium, linear ridge dorsal to the acetabulum on the lateral surface of the blade: absent or low convexity (0); present and vertical or anterodorsally oriented (1); present and posterodorsally oriented (2). UNORDERED (Carr and Williamson 2010: 246-248; Sereno et al. 2009: 84)

259) Ilium, preacetabular process, anteroventral corner, form: subtriangular (0); subquadrate with recurved anterior margin, projecting farther anteriorly than remainder of anterior end ("hook" present) (1). (Carr and Williamson 2010: 249; Sereno et al. 2009: 87)

260) Ilium, dorsal margin of blade, position relative to sacral neural spines: separated by a gap (0); lies against neural spines and opposing iliac blades may make contact above neural spines in some individuals (1). (Sereno et al. 2009: 85)

261) Ilium, acetabular antitrochanter at posterior end of supraacetabular shelf: absent or limited in extent (0); present and visible in lateral view as an extensive flange, which is deeply inset from the remainder of the ischial peduncle (1). (Sereno et al. 2009: 90)

262) Ilium, acetabular crest, maximum lateral projection relative to ischial peduncle: significantly greater (0); subequal (1). (Sereno et al. 2009: 91)

263) Ilium, acetabular crest, extent on pubic peduncle: extensive, extends along most or all of the edge of the peduncle (0); limited, discretely offset from acetabular edge of pubic peduncle (1). (Li et al. 2010: 278)

264) Ilium, pubic and ischial peduncles, anteroposterior lengths at dorsal base: pubic peduncle much larger than ischial peduncle (0); both peduncles approximately the same length (1). New character, inspired by Li et al. (2010: 292) but with different scores.

265) Ilium, ventral margin of postacetabular process, shape: straight to slightly convex (0); highly convex, forming a discrete "lobe"-like flange (1). New character.

266) Ilium, dorsal margin, shape: smoothly convex or flat across entire length (0); convex anteriorly and straightens out posteriorly (1). New character.

267) Ilium, postacetabular process, form of posterior margin: tapering, posterior margin convex (0); squared-off, posterior margin vertical (1). New character.

268) Ilium, ratio of anteroposterior length to dorsoventral depth above acetabulum: greater than 3.00, ilium is long and low (0); less than 2.8, ilium is subovoid shape (1). New character.

Pubis

269) Pubis, shaft, anterior margin: straight or convex (bowed anteriorly) (0); concave (bowed posteriorly (1). (Carr and Williamson 2010: 252)

270) Pubis, pubic tubercle: absent (0); present as a convexity on the anterior margin of the pubis (1); present as a rugose flange that is discretely offset from the anterior margin of the pubis and is bordered posteriorly by heavy rugosities on the lateral surface on the obturator region of the pubis (2). ORDERED (Carr and Williamson 2010: 255) Note: Previous studies utilized a binary character, but we have added a second derived state to encompass variation within Tyrannosauroidea.

271) Pubis, pubic tubercle, position: distally positioned, located ventral to the level of the obturator notch (0); proximally positioned, located level with or dorsal to the obturator notch (1). New character.

272) Pubis, pubic boot, anteroposterior length relative to total long axis length of pubis: less than (0) or greater than (1) 60%. New character.

273) Pubis, pubic boot, anterior ramus, length relative to posterior ramus: 10-40% (0); subequal (1). (Carr and Williamson 2010: 256-258; Sereno et al. 2009: 97).

274) Pubis, pubic boot, position of anterior process relative to posterior process: displaced dorsally, resulting in a highly convex ventral margin of the boot (0); placed at the same level, ventral margin of the boot essentially straight (1). (Carr and Williamson 2010: 259)

275) Pubis, orientation of shaft relative to long axis of ilium when pelvis is in articulation: perpendicular, shaft approximately vertical (0); oblique, shaft is propubic (1). New character.

276) Pubis, anteroposterior expansion of proximal obturator plate region relative to the anterior edge of the pubis shaft at its midpoint: less than (0) or greater than (1) twice the anteroposterior thickness of the shaft at its midpoint. New character.

277) Pubis, obturator notch, form: discrete structure, demarcated ventrally by extensive obturator flange (0); essentially absent, no ventral flange (1). New character.

Ischium

278) Ischium, ischial tubercle ventral to iliac peduncle: absent or present as a groove (0); present as a convex bulge on the posterior surface of the ischium (1); present as a rugose, ovoid or triangular flange whose lateral surface is depressed relative to the remainder of the ischium (2). ORDERED (Carr and Williamson 2010: 261; Sereno et al. 2009: 93)

279) Ischium, distal end, expansion relative to midshaft: expanded, "foot" present (0); tapering, "foot" absent (1). (Carr and Williamson 2010: 264; Sereno et al. 2009: 95)

280) Ischium, midshaft diameter (anteroposterior) relative to pubic midshaft diameter: 60-100% or ischium is greater (0); 30-50% (1). (Carr and Williamson 2010: 265; Sereno et al. 2009: 94)

281) Ischium, position of apex of obturator flange, distance between apex and proximal end of ischium: approximately 40% of ischium length ("distal flange") (0); less than 30% of ischum length ("proximal flange") (1). New character.

282) Ischium, position of medial apron: along posterior margin of shaft (0); along anterior margin of shaft (1). New character.

Femur

283) Femur, circular scar on posterior surface of shaft distal to fourth trochanter, position: absent, low, or positioned approximately centrally on the shaft (0); abuts medial edge of shaft (1). (Carr and Williamson 2010: 268)

284) Femur, lesser trochanter, height relative to greater trochanter: shorter, terminates further distally (0); subequal or slightly taller, the two structures extend to approximately the same level proximally (1). (Carr and Williamson 2010: 269; Sereno et al. 2009: 98)

285) Femur, proximal margin in posterior view: approximately straight (0); concave, due to a greater trochanter that is elevated substantially relative to the lateral portion of the proximal surface of the head (1). New character.

286) Femur, fossa on the medial surface of the head, lateral to the trochanteric fossa, form: absent or shallow (0); deep fossa (1); deep, extensive triangular depression that covers most of the medial surface of the femur proximally and is demarcated medially and ventrally by a pronounced, curving, swollen ridge (2). ORDERED New character.

287) Femur, lesser trochanter, accessory trochanter along the anterior margin, form: present as a pronounced flange ventrally, which is distinguishable from the remainder of the lesser trochanter in lateral view (0); reduced to a subtle convexity, barely distinguishable from the remainder of the trochanter (1). New character.

288) Femur, fourth trochanter, position, measurement from proximal margin of head to distal termination of trochanter relative to total length of the femur: 35% or less (0); 40% or greater (1). New character.

289) Femur, lateral condyle, shape in distal view: circular or ovoid (0); ovoid, but with an anterior bulge that is slightly separated from the remainder of the condyle (1). New character.

290) Femur, extensor groove on anterior surface of distal end, form: absent or extremely shallow, anterior surface flat between the condyles in distal view (0); groove present but shallow, expressed as a broad concave anterior margin in distal view but present as an extensive depression on the anterior surface of the femur (1); groove present and deep, expressed as a deep, U-shaped cleft in distal view and present as an extensive depression on the anterior surface of the femur (2). ORDERED New character.

291) Femur, mesiodistal crest, form: single structure (0); bifurcates distally to enclose fossa on the medial surface of the medial condyle (1). New character.

Tibia

292) Tibia, length relative to the femur: 1.05 or greater (0); less than 1.00 (1). (Sereno et al. 2009: 99)

293) Tibia, lateral condyle of proximal end, anterior process: absent (0); present (1). (Carr and Williamson 2010: 270)

294) Tibia, lateral malleolus, lateral extent: limited, mediolateral measure is less than 40% of mediolateral width of adjacent shaft (0); extensive, mediolateral measure greater than 40% of mediolateral width of adjacent shaft (1). (Carr and Williamson 2010: 271)

295) Tibia, lateral malleolus, position relative to medial malleolus: extend to approximately the same level distally (0); lateral malleolus extends significantly further distally than medial malleolus (1). New character.

Fibula

296) Fibula, iliofibularis tubercle, form: single crest (0); large, rugose, and formed by two crests separated by a depressed fossa ("bipartite" condition) (1). (Carr and Williamson 2010: 272)

Astragalus

297) Astragalus, ascending process, mediolateral width of base compared to width of entire bone: half or less (0); greater than half (1). (Carr and Williamson 2010: 273)

298) Astragalus, fossa on anterior surface of ascending process, form: shallow concavity that covers most of the ventral region of the ascending process (0); deep, triangular or ovoid fossa immediately above midpoint of condyles, set within a broad fossa that covers most of the ventral region of the ascending process (1). New character.

Pes

299) Pes, arctometatarsalian condition, form of shaft of metatarsal III: pes not arctometatarsalian, mt III subcylindrical and its proximal end is exposed anteriorly (0); pes arctometatarsalian, mt III wedge-shaped and its proximal end is covered anteriorly by contact between metatarsals II and IV (1). (Carr and Williamson 2010: 276; Sereno et al. 2009: 100)

300) Pes, metatarsal III, form of medial surface in anterior or posterior view: straight or subtly convex (0); with medial convex expansion forming a bulge along the distal part of the shaft (1). (Li et al. 2010: 289)

301) Pes, metatarsal III, ventral nonarticular surface immediately proximal to the distal condyles, form: concave (0); raised subtriangular platform (1). (Sereno et al. 2009: 101)

302) Pes, metatarsals II-IV, distal separation when in articulation: metatarsals closely appressed and distance between II-III and III-IV is approximately equal (0); distal ends of II and IV diverge from III, and distance between III-IV greater than that between II-III (1). New character.

303) Pes, metatarsal II, articular scar for metatarsal III on distal portion of lateral surface of shaft, form: subtle (0); enlarged as a rugose fossa that occupies more than half of the proximodistal length of the shaft and expands in anterposterior width distally (1). New character.

304) Pes, metatarsal II, lateral surface in proximal view, shape: flat or weakly concave (0); strongly concave (1). New character.

305) Pes, metatarsal IV, distal end, ratio between anteroposterior long axis (measured from midpoint of condyles posteriorly to anterior surface of bone) and mediolateral width (measured at midpoint): greater than 1.40, distal surface is elongate anteroposteriorly (0); between 1.40 and 1.20 (1); less than 1.20, distal surface nearly square-shaped with nearly flat anterior surface (2). ORDERED New character.

306) Pes, proximal pedal phalanges, ratio of length to midshaft width: greater than (0) or less than (1) 3.0. New character.

307) Pes, pedal unguals, lip overhanging proximal articular surface dorsally (on extensor surface): present (0); absent or reduced to a subtle tuber (1). New character.

Data matrix

We here present a copy of our TNT matrix. An excel spreadsheet, with characters and taxa separated into columns and rows, is available from the authors by request.

xread
307 23
Allosaurus0100000000000101000000100000010001100000000002102100010000001000
1????0000000001?0??100?00000?000000000000011000001000000000?0?10000000000
????000?0001001000000001000000000000000000002000000000000000000000100000
010000002001000[0,1]0000100000000010000000000001001010000000000100?000101
000100000010201100000000000110

Maniraptora00000?0000000000000?00100?00?000111000000001000000??000000000?0
1?00???0000000000?0??010?01000?000000001001000????0000000000?0?0?0000??001
000?0?0?00000[0,1]000000[0,1]010000000000000000000001[0,1]0000000?000000[
0,1]0000000[0,1]0[0,1]00001?111100[0,1]1000?00000000000010000000000000000000
0000000001100??0110000000010000000000100000000000

Ornithomimos0000001000000?00000?00000?00?00010000000001?00000??00000?00??
00?0000?0000000000?0??010?00?00??00000?01000000?000000000?000?0?0000??000

01000?????0?00000100000000[0,1]00???000000??00000000000000000???000000000?00?000000000000100[1,2]00000000000000001000000[0,1]000[0,1]0101000100100[0,1]0000?0[0,1]0001100110000000000000100100?0000

Compsogs?0000000000000000000?00100?00?0?0000?000000??02000??00000?00??00?0????000000000010??010?10??0??0000?000???????100000000?000?0??0??????00?????????0?????????????????????0?000000000000000??0?0??????0000[0,1]00??????00000??00000?000?0?0??0000010000?0??00100?[0,1]0000000[0,1]0?00000000?00?0010000??0??00???0??00?000?0???00

Kileskus???1??110111100100???0?00?0000?0000?0??0100010?????????????00???000?????0

Guanlong0001000101111001000?10100?00?10000010?1000000?003??00000??0??00?10001000001100010??010?10000?000010000000000?100000011?00100000?00000?????????????020?01000001000000000000????10?0000000010???????1010100???????0000001000001010000?0?000000100000010000000000001000000000001000000000000?001000000010000000?0000

Proceratosaurus00?1001101111?01000?10100?00?1?000010?1???0?0?????????????????0?100010000011000?1?????0??0??0?0???100000000??0??0???????????????0000??000????0??0?0?0??????00?100???????0001???110?000000001000?????111000???0???????????

Dilong0000001101001?01001?10000100?0?000000100000000103??00100?00??000101111000011000 10??000?11000??0001000000010?????000000?00101000?????????????????020?0100?0010?0??????01001??100?010002?00?11?????1011100000001000000010000000???????000000110000001???0??010000100?0?000010??00010??000??001?00000000010000??0100

Eotyrannus???0??11?100?01110????????00?0?01????20110000?1010?0?1??0?00?00???????????????0??????????????????????01?1???0?????????????????????001??????0?00?????????????????????000?100002110100?????????2?2??00??00?0??00???1?0???????????00???011011011??0000???00?2????????????????????????????????????01???0000?00100

Stokesosaurus???0???????00?00?10000100?00100?0????????????????????????120000000001?1000110010010??????1100001????????????

Xiongguanlong00100?1102000????0??1??00?01?0?01?0001001010??0010?00100??0??0??0?????0???01000?0???00?01000??0021?111110010?1????100?1?111??100?100???????????00100100000?10?1???????????????????????????????2?2?000??00000000011000010??????????????????????????????11?101??0011???????????01010012?????????????

Raptorex?1100?111200?00000101100010100101110120110100200110?10101?00?0000000110000001000000??000?01000??0012?011???1?1??11011100001111?????????0?????????0????1??????100?0????00100000101112121??0011??0??212100000?0000000??100110??1?????0??0110000212101111?11???1111011110001001??????1112101??1??1?12?0?1??111?1??????

Dryptosaurus??????????????????????????????0??0??1212?1?1??10100?????1?????11???????????1???????12????0???1012?1?011111?????1??

Appalachiosaurus??1???????????000000?0100?01?010111?12011?1?1?0020?101?10??0?0???00000001010?0010?00??????????????????11?110??01??????????0??1????2?2?0?????????????????????????0?????????????????????????????????????1???????12111?010110???1111111111011?0

Albertosaurus01101011120000000000[0,1]12001[0,1]10010111012012011110021111[0,1]1[0,2]1?01?0010000001000102010020011100100101?1131011111111101101210011111111000[0,1]000110[0,1][0,1]11110000101101110110111111011111111100101112121111100?12?10?2121011???????11??????????????????01111102121011111111?0101121111111111012111101211111012111??1???1???11111111111111201

Gorgosaurus01101011120000000000[0,1]120010100101110120120111200211101[0,2]1001000100000010001020100200111001001010101131011111111011012100111111111000100011011111??00110110101101111110111111110010111212111100112?10?2121011???????11????11101?????1?0??111111021210101111101011211111110110121111012111?010?11?2?11111111111?1201

Alioramus001011??2????0000011110111110?011101201101012012101010211101011100010000102000010000100101110011320111111110011012100111111111?101110010011101000110110111111011011111011100101112122111110??10000????000001000001111101101121011111???????????????????????1?1111101110?????????21?11?10111121??00?11111?11?01

Daspletosaurus0110101122000110112011200211102111101201211012012101101[1,2]11111111111101101020000211001101110111132121111111001?1121012211111111101110011011110011111101111110111111111111110010111222211101112?1002121011000110111110211110????????1111111?212111?11111?111112111111??1??1?11111?12111??1?????2?11???1?111?11???

Tarbosaurus111011122200011011210121130110211110120121101201 0??11012111111
10111110111102101021100210111111111321211111110010113121230111111 1111111
01101111111111111011100201111111111111111201112221 2?101112111121211211111
1?11111?102111111??1??1?11111110212111011111?11111211111111111011 21111111112
11111112111211111111111111211

Tyrannosaurus111011122200011011210121012[0,1]0[1,3]01102111101201211 11201 0??110
121011111011[0,1]11011111021010211002101111111113[1,2]121111111001111312123
0111111111111110110111111111111110111002011111111111111112011122222110 11121
1112121121111110111111102111101211111111111111021211101111111111121111111 1
11101211111112111111121112111111111111111211

Bistahieversor?0?0101112000000000?10210101?0101110120110110100201100010 01??
?10000??000000020000211001001000 00??13111111?1?100110121001211111 11?01000?
010011111??????11???1?0101?1101111111100?011121220110011 2?10?2?2?00????111
??????????????????????0111?11??010?1
????0110111111?11001

Utah?????????????????000?????0?01???????????????????2?021?100010?10??????? ??0???
21?1?????0????01???0?13??21?111?1001111210 1211??????????????????????????011
?????020?1?1???11??1100?011??????????11????????10????????1????1??????? ??????
??????1?0211????1????????????????????????????????????010?11?1????????????????

Sinotyrannus???1???10?1?1?0110??10????0??1?00????1?????????????????????????????
??
??????????????????????0????1?????????????????????????0??????????????????????????
??????????????????????????00?10?0??00001??
;
ccode - 0.250;

2) Text

Synapomorphy List from Phylogenetic Analysis

The following synapomorphy list was compiled in TNT using the "list synapomorphies" command.

```
Tyrannosauroidea
      Char. 6: 0 --> 1
      Char. 7: 0 --> 1
      Char. 9: 0 --> 1
      Char. 20: 0 --> 1
      Char. 75: 0 --> 1
      Char. 97: 0 --> 1
      Char. 121: 0 --> 1
      Char. 157: 0 --> 1
```

```
        Char. 174: 0 --> 1
        Char. 195: 0 --> 1
        Char. 197: 0 --> 1
        Char. 215: 0 --> 1
        Char. 237: 0 --> 1
        Char. 244: 0 --> 1
        Char. 257: 0 --> 1
        Char. 269: 0 --> 1
        Char. 285: 0 --> 1
Proceratosauridae
        No unequivocal synapomorphies
Sinotyrannus + Proceratosaurus + Guanlong
        Char. 29: 0 --> 1
All Tyrannosauroidea more derived than Proceratosauridae
        Char. 88: 0 --> 1
        Char. 105: 0 --> 1
        Char. 123: 0 --> 1
        Char. 168: 0 --> 1
        Char. 188: 0 --> 1
        Char. 189: 0 --> 1
        Char. 198: 0 --> 1
        Char. 252: 0 --> 1
All Tyrannosauroidea more derived than Proceratosauridae and Dilong
        Char. 32: 0 --> 1
        Char. 40: 0 --> 1
        Char. 48: 3 --> 1
        Char. 79: 1 --> 0
        Char. 179: 1 --> 2
        Char. 180: 0 --> 1
        Char. 195: 1 --> 2
        Char. 197: 1 --> 2
        Char. 220: 0 --> 1
        Char. 238: 0 --> 1
        Char. 240: 0 --> 1
        Char. 243: 0 --> 1
        Char. 256: 0 --> 1
        Char. 273: 0 --> 1
        Char. 280: 0 --> 1
        Char. 288: 0 --> 1
        Char. 289: 0 --> 1
Stokesosaurus + Eotyrannus
        Char. 257: 1 --> 2
All Tyrannosauroidea more derived than Proceratosauridae, Dilong,
Stokesosaurus, and Eotyrannus
        Char. 9: 1 --> 2
        Char. 27: 0 --> 1
        Char. 42: 0 --> 1
        Char. 104: 0 --> 1
        Char. 213: 0 --> 1
        Char. 215: 1 --> 0
        Char. 259: 0 --> 1
        Char. 261: 0 --> 1
        Char. 266: 0 --> 1
        Char. 289: 1 --> 2
Dryptosaurus + Raptorex + Appalachiosaurus + Bistahieversor +
Tyrannosauridae
        Char. 286: 0 --> 1
```

Raptorex + *Appalachiosaurus* + *Bistahieversor* + Tyrannosauridae
      Char. 238: 1 --> 2
      Char. 239: 0 --> 1
      Char. 240: 1 --> 2
      Char. 293: 0 --> 1
Appalachiosaurus + *Bistahieversor* + Tyrannosauridae
      Char. 48: 1 --> 2
      Char. 167: 0 --> 1
      Char. 170: 0 --> 1
      Char. 171: 0 --> 1
      Char. 279: 0 --> 1
Bistahieversor + Tyrannosauridae
      Char. 22: 1 --> 2
      Char. 138: 0 --> 1
      Char. 140: 0 --> 1
      Char. 142: 0 --> 1
      Char. 190: 1 --> 2
      Char. 302: 0 --> 1
      Char. 306: 0 --> 1
Tyrannosauridae
      Char. 21: 0 --> 1
      Char. 49: 0 --> 1
      Char. 73: 0 --> 1
      Char. 91: 0 --> 1
      Char. 130: 0 --> 1
      Char. 304: 1 --> 2
Albertosaurinae
      Char. 68: 1 --> 0
      Char. 69: 0 --> 1
      Char. 77: 0 --> 1
      Char. 83: 0 --> 1
      Char. 84: 0 --> 1
      Char. 108: 0 --> 1
      Char. 134: 0 --> 1
      Char. 158: 0 --> 1
      Char. 200: 0 --> 1
Tyrannosaurinae
      Char. 8: 1 --> 2
      Char. 28: 0 --> 1
      Char. 57: 0 --> 1
      Char. 64: 0 --> 1
      Char. 90: 0 --> 1
      Char. 92: 0 --> 1
      Char. 98: 1 --> 2
      Char. 128: 0 --> 1
      Char. 131: 0 --> 1
      Char. 132: 0 --> 1
      Char. 163: 0 --> 1
      Char. 228: 0 --> 1
Utah Taxon + *Daspletosaurus* + *Tarbosaurus* + *Tyrannosaurus*
      Char. 53: 1 --> 0
      Char. 100: 1 --> 2
      Char. 112: 0 --> 1
      Char. 117: 0 --> 1
      Char. 118: 1 --> 2
      Char. 209: 0 --> 1
Daspletosaurus + *Tarbosaurus* + *Tyrannosaurus*

```
        Char. 16: 0 --> 1
        Char. 17: 0 --> 1
        Char. 18: 0 --> 2
        Char. 52: 0 --> 1
        Char. 54: 0 --> 1
        Char. 59: 0 --> 1
        Char. 70: 0 --> 1
        Char. 89: 0 --> 1
        Char. 94: 0 --> 1
        Char. 119: 1 --> 2
        Char. 148: 0 --> 1
        Char. 200: 0 --> 1
Tarbosaurus + Tyrannosaurus
        Char. 0: 0 --> 1
        Char. 7: 1 --> 2
        Char. 20: 1 --> 0
        Char. 48: 2 --> 0
        Char. 72: 0 --> 1
        Char. 76: 0 --> 1
        Char. 78: 0 --> 1
        Char. 85: 1 --> 2
        Char. 114: 2 --> 3
        Char. 116: 0 --> 2
        Char. 119: 2 --> 3
        Char. 120: 1 --> 0
        Char. 129: 0 --> 1
        Char. 133: 0 --> 1
        Char. 144: 0 --> 1
        Char. 145: 0 --> 1
        Char. 155: 1 --> 0
        Char. 172: 0 --> 1
        Char. 173: 0 --> 1
        Char. 174: 1 --> 2
        Char. 183: 1 --> 2
        Char. 193: 0 --> 1
        Char. 194: 0 --> 1
        Char. 200: 1 --> 2
        Char. 202: 0 --> 1
        Char. 203: 0 --> 1
        Char. 208: 0 --> 1
```

Specimen numbers for the panels in Figure 1: (**A**) *Alioramus* (Institute of Geology, Ulaan Baatar, Mongolia 100/1844); (**B**) *Guanlong* (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, V14531); (**C**) *Dilong* (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, V14243); (**D**) *Bistahieversor* (New Mexico Museum of Natural History and Science, Albuquerque, P-27469); (**E**) juvenile *Tyrannosaurus* (Burpee Museum of Natural History, Rockford, Illinois, 2002.4.1); (**F**) adult *Tyrannosaurus* (American Museum of Natural History, New York, 5027).
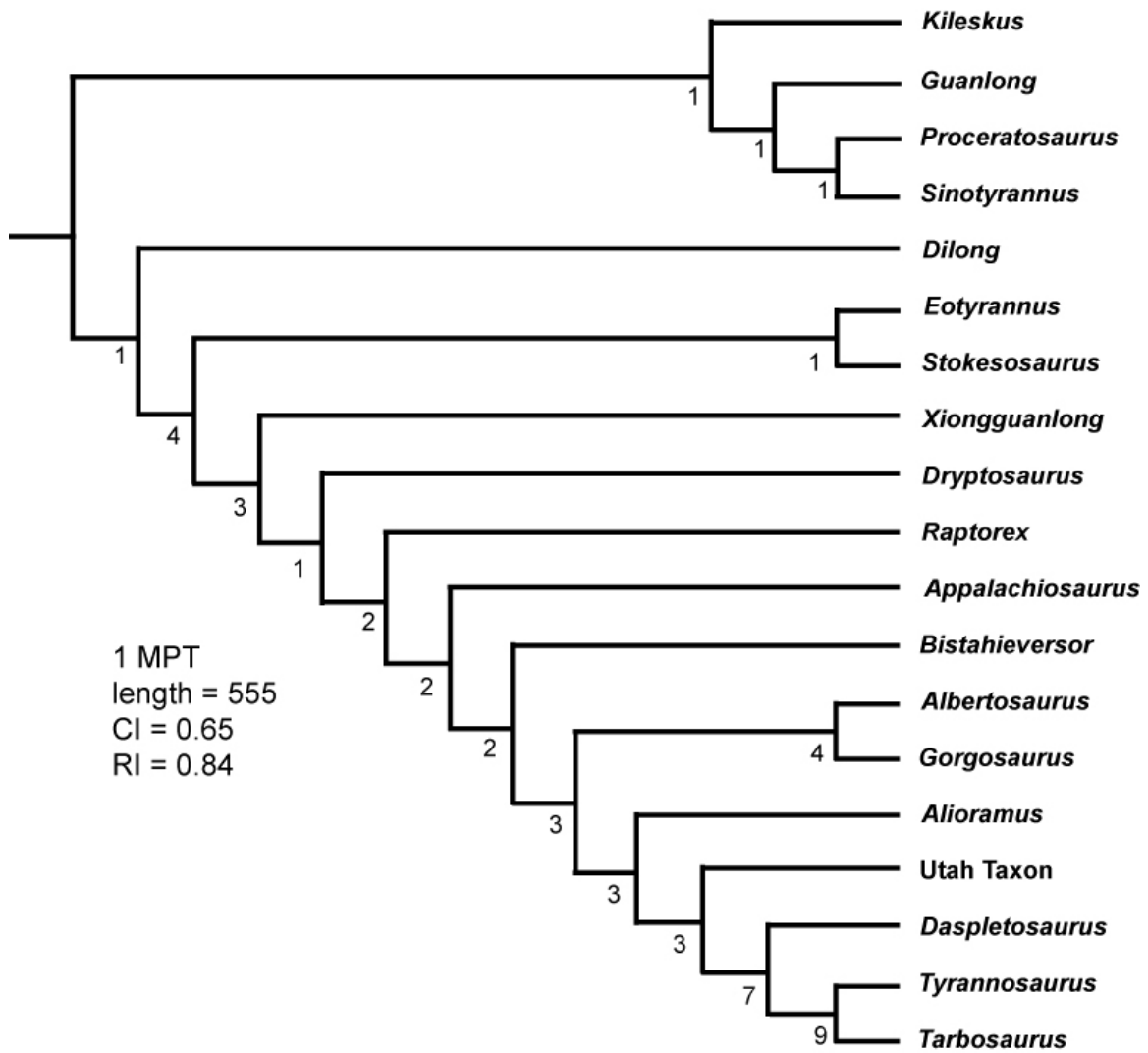
Fig. S1. Single most parsimonious tree recovered by the phylogenetic analysis, showing Bremer support values for each node.

Table S1: Listing of tyrannosauroid genera included in the phylogenetic analysis, as well as additional taxa that belong to the tyrannosauroid clade (denoted by asterisk), with information on their temporal and spatial distribution. E and W denote eastern and western North America, respectively.

Genus	Distribution	Age	Year of Description
Albertosaurus	North America (W)	Campanian	1905
*Alectrosaurus**	Asia	Campanian	1933
Alioramus	Asia	Maastrichtian	1976
Appalachiosaurus	North America (E)	Campanian	2005
*Aviatyrannis**	Europe	Kimmeridgian	2003
Bistahieversor	North America (W)	Campanian	2010
Daspletosaurus	North America (W)	Campanian	1970
Dilong	Asia	Barremian	2004
Dryptosaurus	North America (E)	Maastrichtian	1877
Eotyrannus	Europe	Barremian	2001
Gorgosaurus	North America (W)	Campanian	1914
Guanlong	Asia	Oxfordian	2006
Kileskus	Asia	Bathonian	2010
Proceratosaurus	Europe	Bathonian	1910
Raptorex	Asia	E. Cretaceous	2009
Sinotyrannus	Asia	Albian	2009
Stokesosaurus	North America (W), Europe	L. Jurassic	1974
Tarbosaurus	Asia	L. Cretaceous	1955
Tyrannosaurus	North America (W)	Maastrichtian	1905
Xiongguanlong	Asia	Albian	2010
Utah Taxon	North America (W)	Campanian	---

3) References

S1. P. Senter, A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). *J. Syst. Palaeontol.* **5**, 429-463 (2007).

S2. P. A. Goloboff, J.S. Farris, K.C. Nixon, TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774-786 (2008).

S3. P. C. Sereno, S. L. Brusatte, Comparative assessment of tyrannosauroid interrelationships. *J. Syst. Palaeontol.* **7**, 455-470 (2009).

S4. T. D. Carr, T. E. Williamson, *Bistahieversor sealeyi*, gen. et sp. nov. a new tyrannosauroid from New Mexico and the origin of deep snouts in Tyrannosauroidea. *J. Vert. Paleontol.* **30**, 1-16 (2010).

S5. S. L. Brusatte, T. D. Carr, G. M. Erickson, G. S. Bever, M. A. Norell. A long snouted, multi-horned tyrannosaurid from the Late Cretaceous of Mongolia. *Proc. Nat. Acad. Sci. (USA)* **106**, 17261-17266 (2009).

S6. P. C. Sereno, L. Tan, S. L. Brusatte, H. J. Keiegstein, X. Zhao, K. Cloward, Tyrannosaurid skeleton design first evolved at small body size. *Science* **326**, 418-422 (2009).

S7. O. W. M. Rauhut, A. C. Milner, S. Moore-Fay, Cranial osteology and phylogenetic position of the theropod dinosaur Proceratosaurus bradleyi (Woodward, 1910) from the Middle Jurassic of England. Zool. J. Linn. Soc. **158**, 155–195 (2010).

S8. T. R. Holtz, in *Mesooic Vertebrate Life*. (eds Tanke, D. H., Carpenter, K.) 64-83 (Indiana University Press, Bloomington) (2004).

S9. D. Li, M. A. Norell, K. Gao, N. D. Smith, P. J. Makovicky, A longirostrine tyrannosauroid from the Early Cretaceous of China. *Proc. R. Soc. Lond. B* **277**, 183-190 (2010).