



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia

Citation for published version:

Brusatte, SL, Carr, TD, Erickson, GM, Bever, GS & Norell, MA 2009, 'A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia', *Proceedings of the National Academy of Sciences (PNAS)*, vol. 106, no. 41, pp. 17261-17266. <https://doi.org/10.1073/pnas.0906911106>

Digital Object Identifier (DOI):

[10.1073/pnas.0906911106](https://doi.org/10.1073/pnas.0906911106)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Proceedings of the National Academy of Sciences (PNAS)

Publisher Rights Statement:

Gold Open Access. Published by the National Academy of Sciences - PNAS (2009)

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia

Stephen L. Brusatte^{a,b,1}, Thomas D. Carr^c, Gregory M. Erickson^{a,d}, Gabe S. Bever^a, and Mark A. Norell^a

^aDepartment of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024; ^bDepartment of Earth and Environmental Sciences, Columbia University, New York, NY; ^cDepartment of Biology, Carthage College, 2001 Alford Park Drive, Kenosha, WI 53140; and ^dDepartment of Biological Science, 319 King Building, Florida State University, Tallahassee, FL 32306-4295

Edited by Paul E. Olsen, Lamont–Doherty Earth Observatory of Columbia University, Palisades, NY, and approved September 8, 2009 (received for review June 19, 2009)

Tyrannosaurid theropods are characterized by a generalized body plan, and all well-known taxa possess deep and robust skulls that are optimized for exerting powerful bite forces. The fragmentary Late Cretaceous *Alioramus* appears to deviate from this trend, but its holotype and only known specimen is incomplete and poorly described. A remarkable new tyrannosaurid specimen from the Maastrichtian (Late Cretaceous) of Mongolia, including a nearly complete and well-preserved skull and an extensive postcranium, represents a new species of *Alioramus*, *Alioramus altai*. This specimen conclusively demonstrates that *Alioramus* is a small, gracile, long-snouted carnivore that deviates from other tyrannosaurids in its body plan and presumably its ecological habits. As such, it increases the range of morphological diversity in one of the most familiar extinct clades. Phylogenetic analysis places *Alioramus* deep within the megapredatory Tyrannosauridae, and within the tyrannosaurine subclade that also includes *Tarbosaurus* and *Tyrannosaurus*. Both pneumatization and ornamentation are extreme compared with other tyrannosaurids, and the skull contains eight discrete horns. The new specimen is histologically aged at nine years old but is smaller than other tyrannosaurids of similar age. Despite its divergent cranial form, *Alioramus* is characterized by a similar sequence of ontogenetic changes as the megapredatory *Tyrannosaurus* and *Albertosaurus*, indicating that ontogenetic change is conservative in tyrannosaurids.

Dinosauria | heterochrony | Tyrannosauridae | Theropoda | pneumaticity

The colossal predator *Tyrannosaurus* is undoubtedly the most recognizable dinosaur. *Tyrannosaurus* and several close relatives are grouped together within Tyrannosauridae, a derived clade of large-bodied theropods that were the apex predators in most terminal Cretaceous ecosystems in North America and Asia (1–3). Tyrannosaurids are characterized by a general body plan: All well-known species possess deep skulls, peg-like teeth, and robust lower jaws as adults, features thought to relate to powerful bite forces and an unusual “puncture-pull” feeding style in which the teeth penetrate through bone (4–6). As such, these animals can be referred to as “megapredators.”

One enigmatic tyrannosaurid, *Alioramus remotus* from the Late Cretaceous of Mongolia, appears to deviate from this trend (7). The fragmentary holotype and only known specimen seems to represent a long-snouted and gracile predator with an extreme degree of cranial ornamentation, but further details of its anatomy, biology, and phylogenetic relationships have proven controversial. Some phylogenetic analyses place *A. remotus* deep within the radiation of Asian tyrannosaurids (8), whereas other studies find it as a basal taxon outside of Tyrannosauridae (1, 2; phylogenetic definitions following ref. 9). Furthermore, some authors have suggested that the holotype of *A. remotus* is a juvenile and possibly an immature *Tarbosaurus* (3). These debates are difficult to resolve with the fragmentary holotype material.

We report the discovery of a peculiar new tyrannosaurid from the Late Cretaceous of Mongolia that is known from a remarkably complete and well-preserved skeleton, including a disartic-

ulated skull that allows for meticulous observation of tyrannosaurid cranial anatomy. This new tyrannosaur is small-bodied and possesses a bizarre long-snouted and gracile skull with eight discrete horns, an unusual cranial form for a Late Cretaceous tyrannosaurid. It is extremely similar to, and shares many unique characters with, the holotype of *A. remotus*, but it is also distinguishable by numerous characters and thus is referred to as a new species of *Alioramus*. The new specimen helps clarify the body form and systematic affinities of this long-enigmatic genus, which is now strongly placed as a derived tyrannosaurid closely related to *Tyrannosaurus*. Thus, *Alioramus* is a small, sleek, longirostrine tyrannosaurid, which lived alongside the megapredatory *Tarbosaurus*.

Systematic Paleontology. Theropoda Marsh, 1881; Tetanurae Gauthier, 1986; Coelurosauria Huene, 1914; Tyrannosauroida Osborn, 1905; Tyrannosauridae Osborn, 1905; Tyrannosaurinae Osborn, 1905; *Alioramus* Kurzanov, 1976; *Alioramus altai*, sp. nov.

Holotype. Institute of Geology, Mongolia (IGM), Ulaan Baatar 100/1844 is a substantially complete skeleton found associated and belonging to a single individual that includes a nearly complete and disarticulated skull and is missing the forelimbs, regions of the hindlimbs, the pubes, and much of the dorsal and caudal vertebral series (Figs. 1–3 and Tables S1–S3).

Etymology. *Altai* is in reference to the Altai mountain range, a prominent topographic feature of southern Mongolia.

Horizon and Locality. The specimen was collected in 2001 at Tsagaan Khushuu (originally called Tsagaan Uul) (10). These beds are part of the Maastrichtian Nemegt Formation, which crops out extensively at a number of localities in the area. The type locality for *A. remotus*, Nogon-Tsav, is often referred to as a Nemegt equivalent, but detailed correlations have yet to be undertaken, and faunal differences suggest that Tsagaan Khushuu and Nogon-Tsav may be different in age (10).

Diagnosis. *A. altai* is a tyrannosaurid theropod possessing the following autapomorphies: an accessory pneumatic fenestra posterodorsal to promaxillary fenestra of maxilla; enlarged and elongated maxillary fenestra (length:depth ratio of 1.9); a laterally projecting horn on the jugal; a thick ridge on the dorsal surface of the ectopterygoid; a palatine pneumatic recess ex-

Author contributions: S.L.B., T.D.C., G.M.E., G.S.B., and M.A.N. designed research; S.L.B., T.D.C., G.M.E., and G.S.B. performed research; T.D.C. and G.M.E. contributed new reagents/analytic tools; S.L.B., T.D.C., G.M.E., G.S.B., and M.A.N. analyzed data; and S.L.B., T.D.C., G.M.E., G.S.B., and M.A.N. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: sbrusatte@amnh.org.

This article contains supporting information online at www.pnas.org/cgi/content/full/0906911106/DCSupplemental.

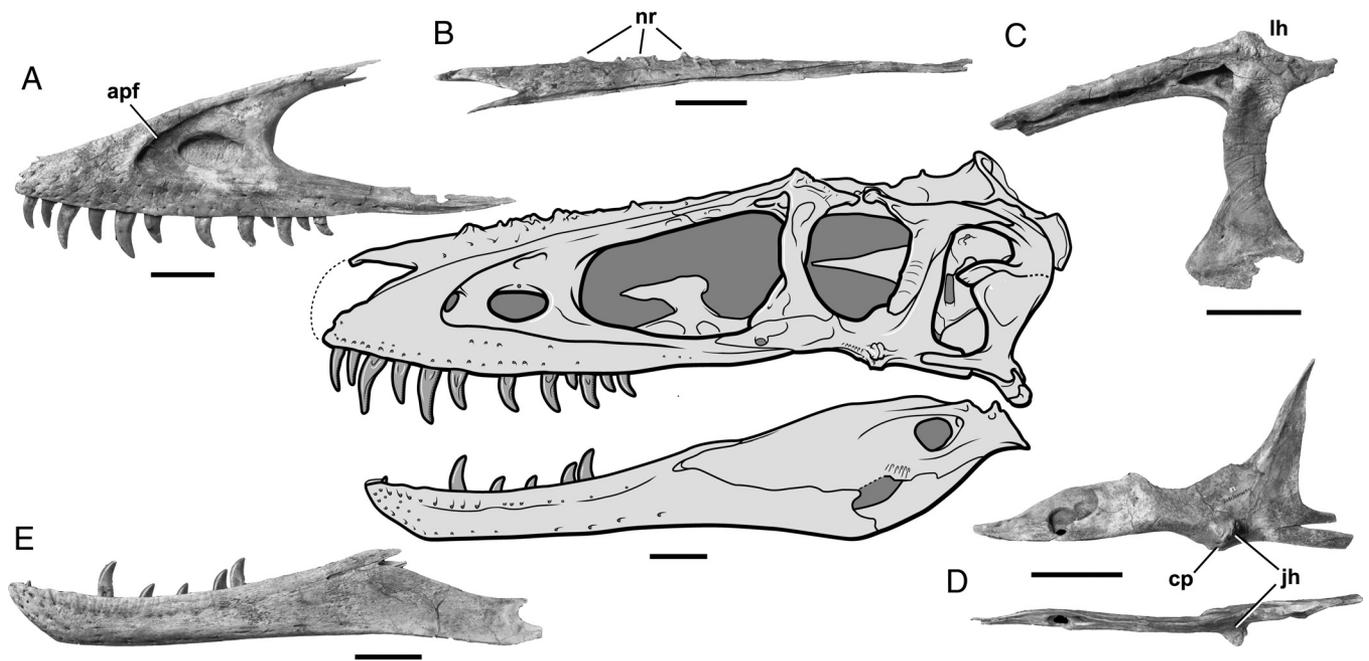


Fig. 1. Skull reconstruction of *A. altai*, based on the holotype (IGM 100/1844) and photos of individual bones of the holotype. (A) Left maxilla in lateral view. (B) Left nasal in lateral view. (C) Left lacrimal in lateral view. (D) Left jugal in lateral and dorsal views. (E) Left dentary in lateral view. apf, accessory promaxillary fenestra; cp, cornual process of jugal; jh, jugal horn; lh, lacrimal hornlet; nr, nasal rugosities. (Scale bars, 5 cm.)

tending posteriorly beyond the posterior margin of the vomer-opterygoid process; 20 dentary alveoli; an anteroposteriorly elongate anterior mylohyoid foramen of the splenial; a thin epiphysis on the atlantal neuropophysis that terminates at a sharp point; a pneumatic pocket on the anterior surface of the cervical transverse processes; an external pneumatic foramina on the dorsal ribs; and an anterodorsally inclined midline ridge on the lateral surface of the ilium. Many of these features are present on elements not preserved in the holotype of *A. remotus* (see *SI Text*).

A. altai is distinguished from the holotype of *A. remotus*, which is at approximately the same ontogenetic stage judging by the slight 3% difference in reconstructed skull length between the two specimens, by: s.c. flange on maxilla (the lateral surface of the maxilla extends dorsally to form a narrow slot between itself and the antorbital fossa below the ventral margin of the antorbital fenestra, which is absent in *A. remotus*); three less-developed rugosities on the nasal (as opposed to six more-prominent rugosities in *A. remotus*); an anterior process of quadratojugal terminates posterior to the anterior margin of the lateral temporal fenestra; a squamosal anterior process that extends anterior to the anterior margin of the lateral temporal fenestra; and an epipterygoid not bifurcated ventrally. *A. altai* also possesses three differences with *A. remotus* that are size-related in other tyrannosaurids but may be significant given the similar size of the holotypes: 17 maxillary and 20 dentary alveoli (16 and 18, respectively, in *A. remotus*); a single dorsoventral groove between the basal tubera (groove bifurcated by ridge in *A. remotus*); and a tapering anterior process of the parietals overlapping frontals on the midline (larger, rectangular process in *A. remotus*).

Although representing a juvenile animal (see *Histological and Ontogenetic Analysis*), the holotype of *A. altai* can be distinguished from juveniles of the contemporary *Tarbosaurus* by numerous characters. Namely, *Tarbosaurus* subadults have a deeper maxilla, a deeper tooth-bearing region of the maxilla, fewer teeth anterior to the antorbital fossa, a rounder maxillary fenestra, more closely spaced maxillary and promaxillary

fenestrae, low and indistinct lacrimal horns, low nasal rugosities, a larger postorbital horn, and a considerably lower tooth count in the maxilla and dentary (11, 12).

Description and Comparisons. Until the discovery of *A. altai*, the anatomy of *Alioramus* was poorly understood because of a number of factors, including the fragmentary nature of the holotype, the fact that it has never been completely described, and difficulties in gaining access to the specimen.

The skull of *A. altai* is remarkably long and low compared with those of other tyrannosaurids, and the snout comprises 2/3 of the skull length (Fig. 1). Individual bones of the snout, most notably the maxilla, nasal, jugal, and dentary, are elongate, whereas those of the posterior skull roof, braincase, and circumtemporal series are similar in proportion to other tyrannosaurids. Other than its overall shape, the most conspicuous features of the skull are several ornamental projections. These include, on each side of the skull, a lacrimal horn, a postorbital cornual process, and a ventrally projecting jugal cornual process, as is usual for tyrannosaurids. In addition, *A. altai* possesses an autapomorphic horn that projects laterally from the jugal and a series of three discrete bumps along the midline of the fused nasals, similar to the six rugose mounds of *A. remotus* (7). This degree of cranial ornamentation is greater than in all other tyrannosaurids.

The maxilla is extensively pneumatic, with an enormous antorbital fossa that houses an autapomorphically large maxillary fenestra, a smaller promaxillary fenestra with a unique accessory pneumatic foramen posterodorsally, and an elongate fossa on the lateral surface of the ascending ramus. The ventral margin of the maxilla is nearly straight—not deeply convex as in most tyrannosaurids (3, 13)—and contains 17 alveoli. The fused and vaulted nasals lack the ventrolateral process that projects onto the lacrimal in *Tyrannosaurus* (13, 14). The heavily pneumatic lacrimal is marked by a single, discrete, conical horn positioned above the ventral ramus, as in many juvenile tyrannosaurids (15). The jugal contributes widely to the antorbital fenestra and is extensively pneumatic in this region. The cornual process of the postorbital is a rugose ridge that overhangs the

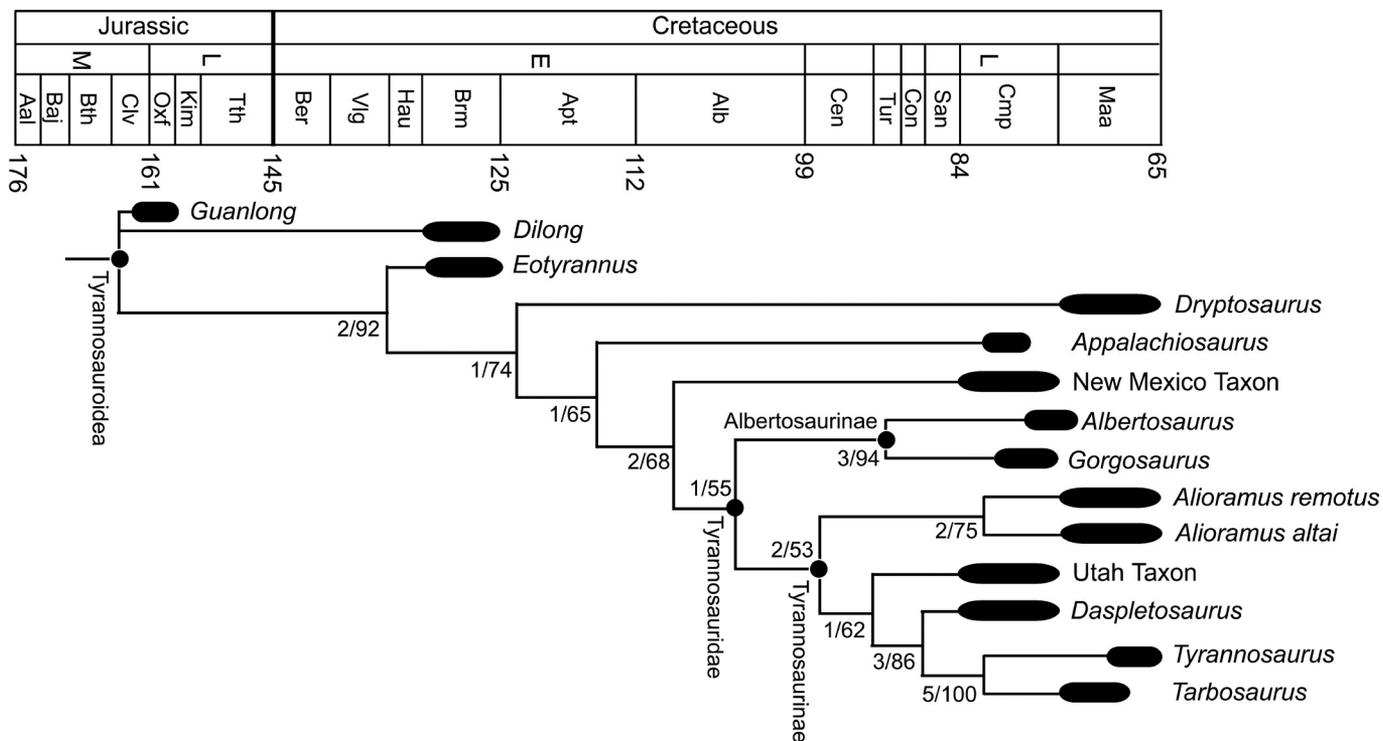


Fig. 4. The strict consensus of four most-parsimonious trees recovered by the phylogenetic analysis (626 steps; consistency index = 0.60; retention index = 0.65) scaled against the Jurassic and Cretaceous time scale. The analysis places *Alioramus* as a derived tyrannosaurid and the most basal member of Tyrannosaurinae, the subclade that also includes *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus*. Numbers next to nodes denote Bremer support/bootstrapped values (1,000 interations). Thick black bars represent the finest stratigraphic age resolution for each taxon, not actual observed ranges.

autapomorphic pocket on the anterior surface of the transverse processes and a deep pneumatic fossa on the dorsal surface of the posterior centrodiapophyseal lamina, otherwise only seen in juvenile *Tarbosaurus* (11). Additionally, the dorsal ribs are pneumatic, a unique feature among tyrannosaurids. The ilium displays an anterodorsally oriented midline ridge, which differs from the more dorsal inclination in most other tyrannosauroids (23). The ischial peduncle of the ilium terminates in a conical peg, which fits into a socket on the ischium. The lateral malleolus of the tibia extends only a short distance distally relative to the medial malleolus, differing from the deeper lateral malleoli of other tyrannosaurids.

Histological and Ontogenetic Analysis. A histological analysis of several hindlimb elements (see *SI Text*) indicates that the holotype of *A. altai* is a young, actively growing juvenile-to-subadult animal that died as a nine year old (see *Figs. S1 and S2*). However, its body size, based on femoral length, conforms more closely to a seven- to eight-year-old *Albertosaurus* or *Gorgosaurus* and a five- to six-year-old *Daspletosaurus* or *Tyrannosaurus* (much larger taxa and the closest relatives of *Alioramus*; see *Systematics*) among tyrannosaurids for which growth curves have been established (24). Thus, the holotype of *A. altai* is relatively smaller than other tyrannosaurids at a similar age, suggesting that it may have attained a smaller adult size.

With longevity and developmental stage estimates derived from histology, it is interesting to determine whether the holotype of *A. altai* corresponds to the same general growth stage (sensu 15) as similarly aged individuals of closely related taxa. We added the holotype of *A. altai* to an ontogenetic analysis presented by Carr and Williamson (14) for *Tyrannosaurus*. Because the two taxa are close relatives (see *Systematics*), and because many observed features on the holotype of *A. altai* correspond with discrete character states observed in *Tyranno-*

saurus ontogeny, this procedure gives a reasonable estimate of the *Tyrannosaurus* growth stage with which the holotype of *A. altai* roughly corresponds. This analysis returned a single most-parsimonious tree (99 steps; consistency index = 0.91; retention index = 0.91) (see *Fig. S3*). The holotype of *A. altai* is placed between LACM 23845 (which has been histologically aged at 14 years old) and LACM 238471 (histologically aged at two years old; see ref. 24) and CMNH 7541 (an extremely small *Tyrannosaurus* individual that is certainly less than nine years old). Thus, the holotype of *A. altai* has a set of features predicted for a *ca.* nine-year-old juvenile *Tyrannosaurus*. A similar sequence of ontogenetic changes is present in *Albertosaurus* (15). This suggests that, despite its divergent cranial form and smaller size, *Alioramus* followed a growth trajectory similar to other tyrannosaurids and that the sequence of character change throughout ontogeny is highly conserved in tyrannosaurids.

Systematics. We added *A. altai* to the phylogenetic analysis of Carr and Williamson (25) (see *SI Appendix*), which produced four most-parsimonious trees (strict consensus in Fig. 4). *A. altai* is recovered as the sister taxon to *A. remotus*, as is necessary to maintain both species in the same genus. This sister relationship is supported by several characters, including the unambiguous presence of a low skull, a shallow horizontal ramus of the maxilla, a subtle and undifferentiated postorbital cornual process, a long posterior process of the squamosal, and 16 or more maxillary alveoli. *Alioramus* is placed not only as a member of Tyrannosauridae but also within the derived clade Tyrannosaurinae, which also includes *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus*. Within Tyrannosaurinae, *Alioramus* falls out as the most basal taxon. Thus, our analysis disagrees with studies that place *Alioramus* as a basal tyrannosauroid outside of Tyrannosauridae (1–2) and is generally concordant with a recent study that recovered *Alioramus* nested within Tyrannosaurinae (8). How-

1. Holtz TR, Jr (2001) The phylogeny and taxonomy of the Tyrannosauridae. In *Mesozoic Vertebrate Life*, eds Tanke DH, Carpenter K (Indiana Univ Press, Bloomington, IN), pp. 279–297.
2. Holtz TR, Jr (2004) Tyrannosauroida. In *The Dinosauria*, eds Weishampel DB, Dodson P, Osmolska H (Univ California Press, Berkeley, CA), 2nd Ed, pp 111–136.
3. Currie PJ (2003) Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontol Polonica* 48:191–226.
4. Erickson GM, et al. (1996) Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature* 382:706–708.
5. Rayfield EJ (2004) Cranial mechanics and feeding in *Tyrannosaurus rex*. *Proc R Soc London Ser B* 271:1451–1459.
6. Molnar RE (2000) Mechanical factors in the design of the skull of *Tyrannosaurus rex* (Osborn, 1905). *Gaia* 15:193–218.
7. Kurzanov SM (1976) A new Late Cretaceous carnosaur from Nogon-Tsav Mongolia. *Sovmestnaâ Sovetsko-Mongolskaâ Paleontologiceskaâ Ekspeditciâ, Trudy* 3:93–104 (in Russian).
8. Currie PJ, Hurum JH, Sabath K (2003) Skull structure and evolution in tyrannosaurid dinosaurs. *Acta Palaeontol Polonica* 48:227–234.
9. Sereno PC, McAllister S, Brusatte SL (2005) TaxonSearch: A relational database for suprageneric taxa and phylogenetic definitions. *Phyloinformatics* 8:1–21.
10. Kurochkin EN, Barsbold R (2000) The Russian–Mongolian expedition and research in vertebrate paleontology. In *The Age of Dinosaurs in Russia and Mongolia*, eds Benton MJ, Shishkin MA, Unwin DM, Kurochkin EN (Cambridge Univ Press, Cambridge, UK), pp. 235–255.
11. Currie PJ, Dong Z (2001) New information on *Shanshanosaurus huoyanshanensis*, a juvenile tyrannosaurid (Theropoda, Dinosauria) from the Late Cretaceous of China. *Can J Earth Sci* 38:1729–1737.
12. Maleev EA (1974) Gigantic carnosaur of the family Tyrannosauridae. *Paleontologîi i biostratigrafiâ Mongolii, Sovmestnaâ Sovetsko-Mongolskaâ Paleontologiceskaâ Ekspeditciâ, Trudy* 1, ed Kramarenko NN, pp. 132–191.
13. Brochu CA (2003) Osteology of *Tyrannosaurus rex*: Insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Soc Vertebr Paleontol Mem* 7:1–138.
14. Carr TD, Williamson TE (2004) Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America. *Zool J Linn Soc* 142:479–523.
15. Carr TD (1999) Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *J Vertebr Paleontol* 19:497–520.
16. Russell DA (1970) Tyrannosaurs from the Late Cretaceous of western Canada. *Nat Mus Nat Sci Pub Palaeontol* 1:1–34.
17. Hurum JH, Sabath K (2003) Giant theropod dinosaurs from Asia and North America: Skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontol Polonica* 48:161–190.
18. Chure DJ (2000) On the orbit of theropod dinosaurs. *Gaia* 15:233–240.
19. Witmer LM, Chatterjee S, Franzosa J, Rowe T (2003) Neuroanatomy of flying reptiles and implications for flight, posture, and behavior. *Nature* 425:950–953.
20. Sampson SD, Witmer LM (2007) Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Soc Vertebr Paleontol Mem* 8:32–102.
21. Larsson HCE, Sereno PC, Wilson JA (2000) Forebrain enlargement among nonavian theropod dinosaurs. *J Vertebr Paleontol* 20:615–618.
22. Hurum JH, Currie PJ (2000) The crushing bite of tyrannosaurids. *J Vertebr Paleontol* 20:619–621.
23. Benson RBJ (2008) New information on *Stokesosaurus*, a tyrannosauroid (Dinosauria: Theropoda) from North America and the United Kingdom. *J Vertebr Paleontol* 28:732–750.
24. Erickson GM, et al. (2004) Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature* 430:772–775.
25. Carr TD, Williamson TE, A new tyrannosauroid from New Mexico and the origin of deep snouts in Tyrannosauroida. *J Vertebr Paleontol*, in press.
26. Sues HD, Frey E, Martill DM, Scott DM (2002) *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *J Vertebr Paleontol* 22:535–547.
27. Li D, Norell, MA, Gao K, Smith ND, Makovicky PJ (2009) A longirostrine tyrannosauroid from the Early Cretaceous of China. *Proc R Soc London Ser B*, 10.1098/rspb.2009.0249.
28. Novas FE, Pol D, Canale JI, Porfiri JD, Calvo JO (2009) A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. *Proc R Soc London Ser B* 276:1101–1107.
29. Christiansen P, Farina RA (2004) Mass prediction in theropod dinosaurs. *Hist Biol* 16:85–92.
30. Barrett PM, Rayfield EJ (2006) Ecological and evolutionary implications of dinosaur feeding behaviour. *Trends Ecol Evol* 21:217–224.
31. Therrien F, Henderson DM, Ruff CB (2005) Bite me: Biomechanical models of theropod mandibles and implications for feeding behavior. In *The Carnivorous Dinosaurs*, ed Carpenter K (Indiana Univ Press, Bloomington, IN), pp 179–237.
32. Young MT, Brusatte SL, Ruta M, Andrade MB (2009). The evolution of Metriorhynchoida (Mesoeucrocodylia, Thalattosuchia): An integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. *Zool J Linn Soc*, in press.
33. Bühler P (1992) Light bones in birds. In *Papers in Avian Paleontology Honoring Pierce Brodkorb*, ed Campbell KE (Natural History Museum of Los Angeles County, Los Angeles), pp 385–393.
34. Witmer LM (1997) The evolution of the antorbital cavity of archosaurs: A study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Soc Vertebr Paleontol Mem* 3:1–73.
35. Rauhut OWM, Fechner R (2005) Early development of the facial region in a non-avian theropod dinosaur. *Proc R Soc London Ser B* 272:1179–1183.
36. Horner JR, Goodwin MB (2006) Major cranial changes during *Triceratops* ontogeny. *Proc R Soc London Ser B* 273:2757–2761.