

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

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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 tyrannosaurid 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

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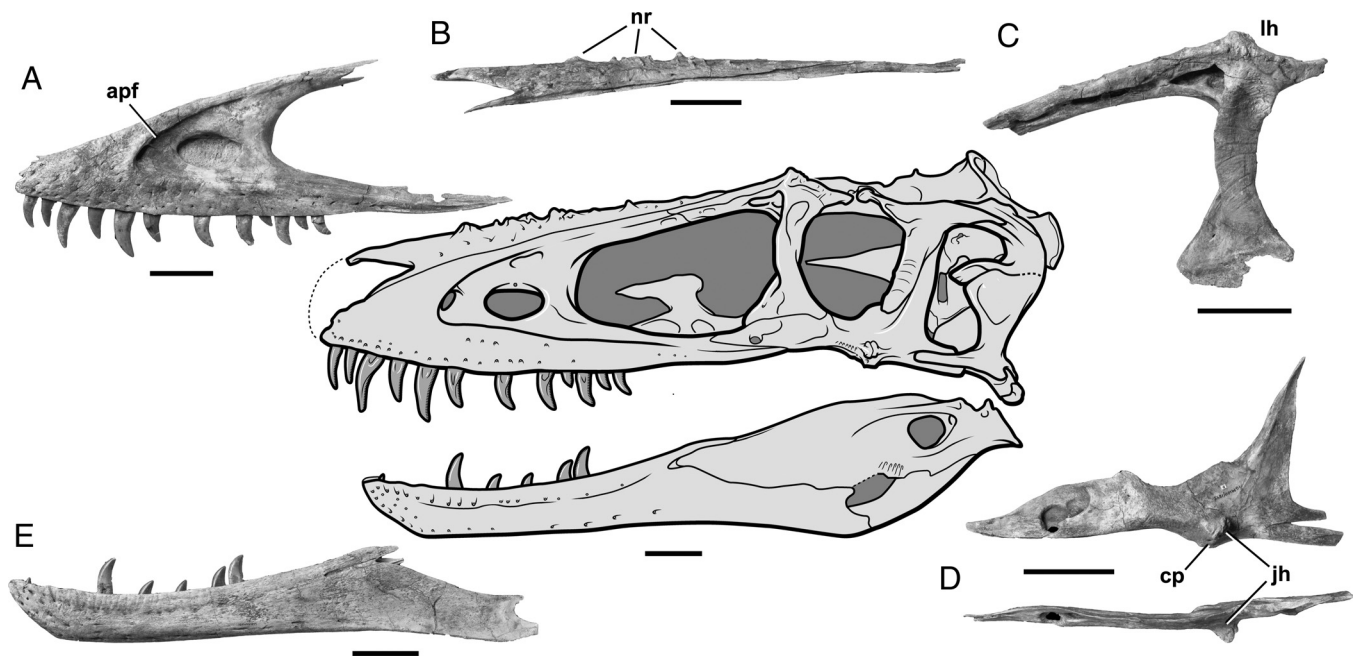
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**Fig. 1.** Skull reconstruction of *A. altai*, based on the holotype (IGM 100/1844) and photos of individual bones of the holotype. (A) Left maxilla in lateral view. (B) Left nasal in lateral view. (C) Left lacrimal in lateral view. (D) Left jugal 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.)

surface of the ectopterygoid; a palatine pneumatic recess extending posteriorly beyond the posterior margin of the vomer-apterygoid 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).

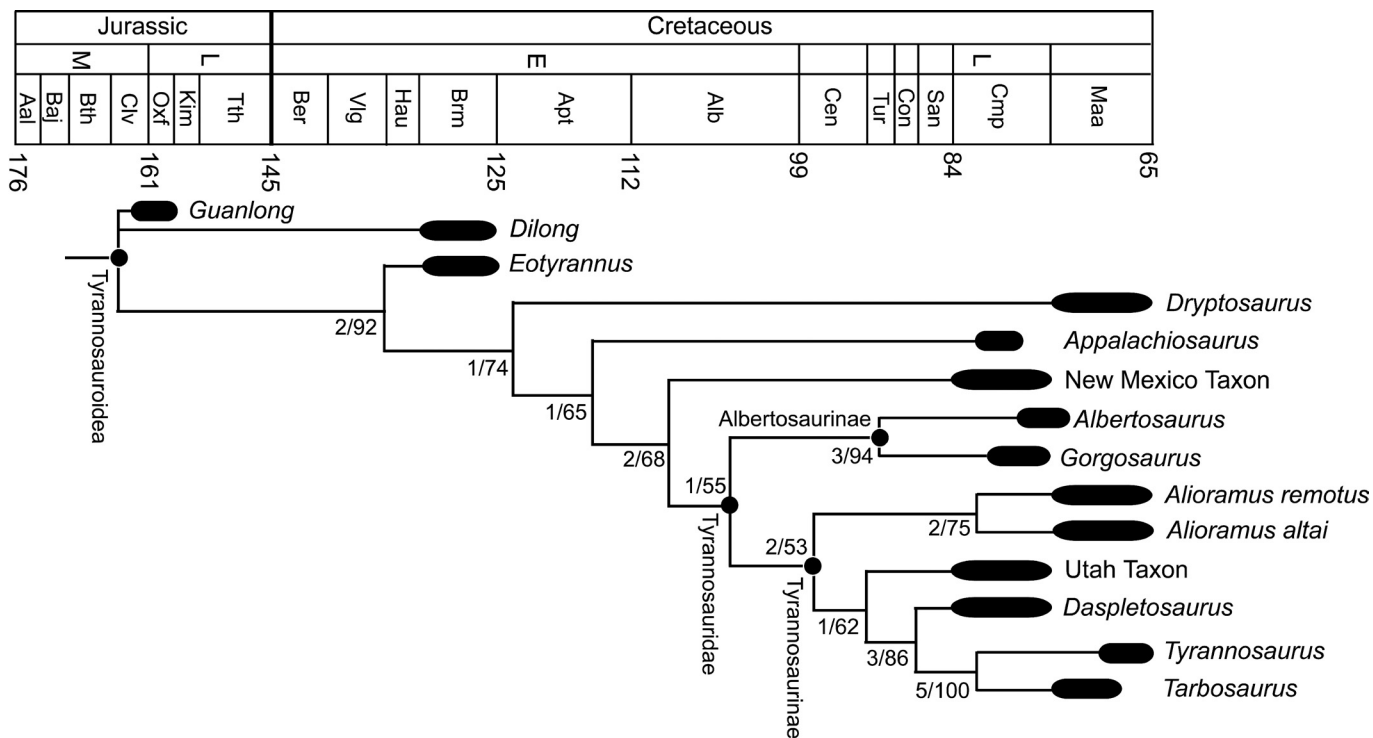
**Description and Comparisons.** Until the discovery of *A. altai*, the anatomy of *Alioramus* was poorly understood because of a number of factors, including the fragmentary nature of the holotype, the fact that it has never been completely described, and difficulties in gaining access to the specimen.

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







**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-



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