

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 | pneumativity

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

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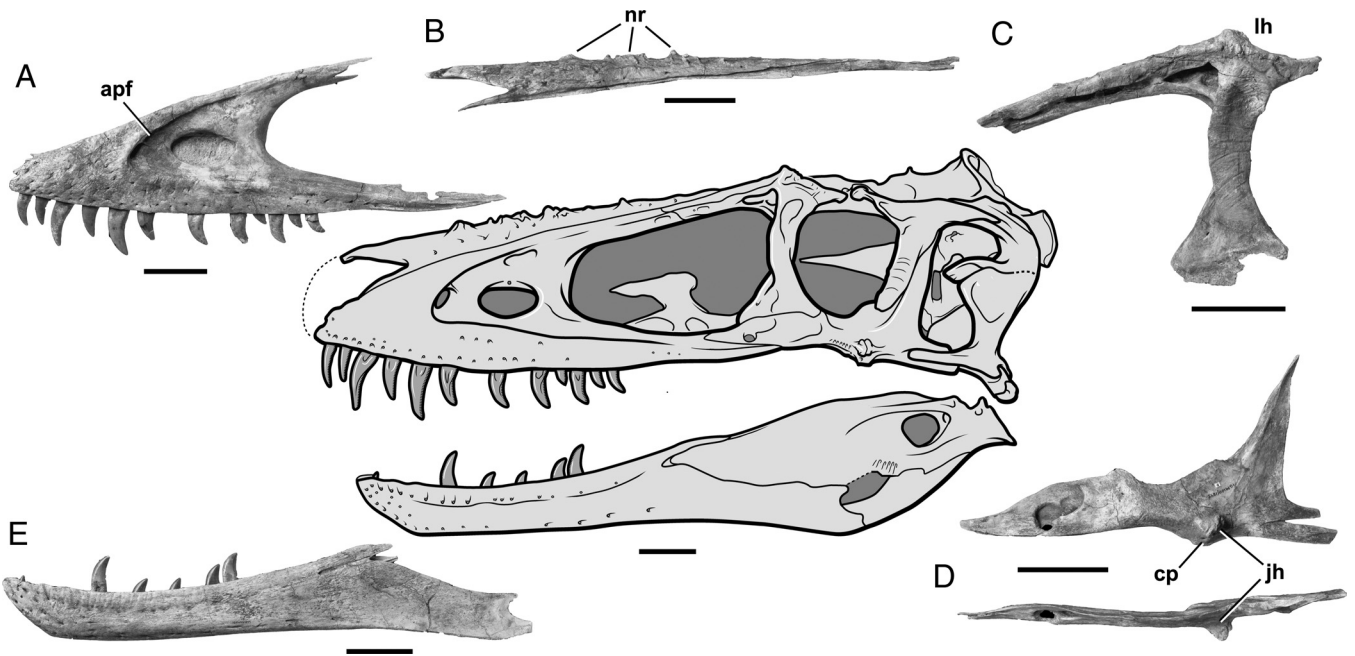


Fig. 1. Skull reconstruction of *A. altai*, based on the holotype (IGM 100/1844) and photos of individual bones of the holotype. (A) Left maxilla in lateral view. (B) Left nasal in lateral view. (C) Left lacrimal in lateral view. (D) Left jugal in lateral and dorsal views. (E) Left dentary in lateral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

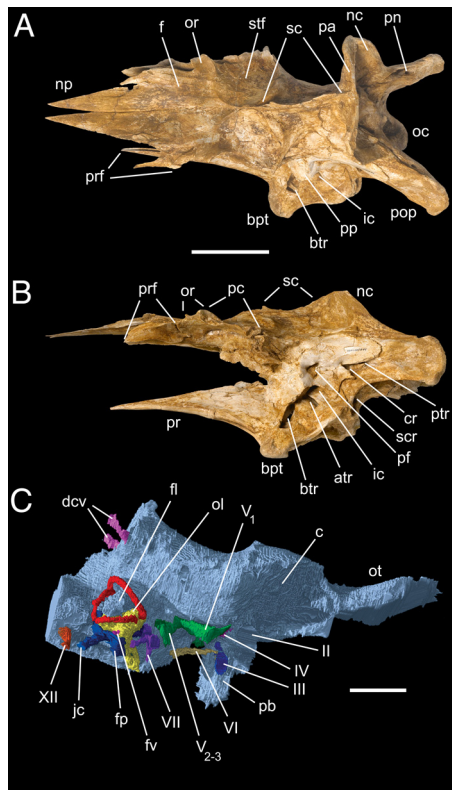


Fig. 2. Brainscase of *A. altai* (IGM 100/1844). (A and B) Photographs in dorsal (A) and left lateral (B) views. (C) A digital endocast reconstructed from computed tomography. atr, anterior tympanic recess; btp, basiptyergoid process; btr, basiptyergoid recess; c, cerebrum; cr, columellar recess; dcv, caudal middle cerebral vein; f, frontal; fl, flocculus; fp, fenestra pseudorotunda; fv, fenestra vestibuli; ic, internal carotid recess; jc, jugular canal (nerves X and XI); nc, nuchal crest of parietal; np, nasal process of frontal; oc, occipital condyle; ol, osseous labyrinth; or, orbital rim of frontal; ot, olfactory tract; pa, parietal; pb, pituitary body; pc, postorbital contact; pf, prootic fenestra (nerves V and VII, prootic recess); pn, pneumatic foramen; pop, paroccipital process; pp, preotic pendant; pr, parasphenoid rostrum; prf, prefrontal; ptr, posterior tympanic recess; sc, sagittal crest; scr, subcondylar recess; stf, supratemporal fossa. Roman numerals denote cranial nerves. (Scale bars: A and B, 5 cm; C, 2 cm.)

process of the postorbital is a rugose ridge that overhangs the posterodorsal corner of the orbit, not a swollen horn as is commonly seen in other tyrannosaurids (3, 16, 17). The ventral process of the postorbital does not project into the orbit as it does in large tyrannosaurids (18), and its lateral surface is scoured by several deep, arcuate sulci like those common in juvenile tyrannosaurids (15). The squamosal, quadrate, palatine, and ectopterygoid house large pneumatic recesses. The triradiate pre-

frontal makes a narrow contribution to the skull roof, and the parietal is expanded into pronounced nuchal and sagittal crests.

The brainscase is exceptionally well preserved, and sutures between most bones are visible (Fig. 2). The supraoccipital makes a narrow contribution to the foramen magnum and is not bifurcated dorsally as in large tyrannosaurids (15, 17). The heavily pneumatized paroccipital processes have a ventral flange at their distal end and are penetrated by anterior and posterior pneumatic foramina. Pneumatic foramina enter into the subcondylar recess to penetrate each basal tuber. The basisphenoid is extensively pneumatized and houses five separate recesses, including a large basiptyergoid recess that opens laterally as a rectangular fenestra. This prootic also houses an internal recess, which opens laterally into a large fossa, bounded entirely by the prootic, which also houses external foramina for both the trigeminal and facial nerves. The antotic crest of the laterosphenoid, which separates the lateral wall of the brainscase from the orbital space, is bifurcated. A foramen for the ophthalmic branch of the trigeminal nerve opens through the laterosphenoid as in *Tyrannosaurus* (13).

A digital cast of the endocranial cavity, cranial nerve roots, and inner ears reveals a series of plesiomorphic and derived features. For example, based on a horizontal, lateral, semicircular canal, *A. altai* held its head in a slightly downturned position while “alert” (19). The angle of this alert position is slightly greater than the nearly horizontal orientation of non-coelurosaurian theropods (e.g., *Majungasaurus*; see ref. 20) but less than the strongly downturned orientation of maniraptorans (including birds; see ref. 19). The telencephalon is not greatly expanded beyond that of basal theropods, but the geniculate and gasserian ganglions of the facial and trigeminal nerves, respectively, both lie in the derived intracranial position. The volume of the endocranial cavity is $\approx 81 \text{ cm}^3$ (compared with the 343-cm^3 endocranial volume of *Tyrannosaurus*; see ref. 21). The encephalization quotient, a unitless estimate of relative brain size based on body mass (methods following ref. 20), of *A. altai* is 2.4, which is slightly larger than that of *Tyrannosaurus* (2.0).

The shallow dentary is unexpanded anteriorly, meets its counterpart at a flat and weak symphysis, and contains 20 alveoli, two more than in any other tyrannosaurid (11). The surangular foramen is enormous and is bordered posteriorly by a deep pocket that leads into an internal recess. The retroarticular process is short, the external mandibular fenestra is small, and the anterior mylohyoid foramen of the splenial is autapomorphically ovoid and oriented horizontally. Modifications for jaw-strengthening in large tyrannosaurids, such as fusion of postdentary bones and interlocking ridges and grooves between the angular and prearticular, are absent (22).

A complete series of 11 highly pneumatic cervical vertebrae is preserved (Fig. 3). Cervical pneumaticity is extreme compared with other tyrannosaurids and includes two unusual features: an

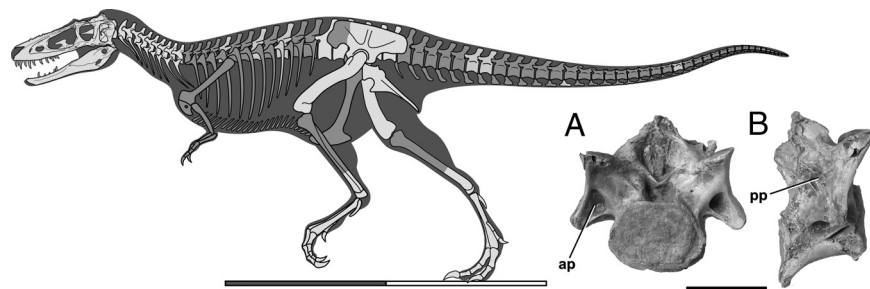


Fig. 3. Skeletal reconstruction of *A. altai*, based on the holotype (IGM 100/1844) and photos of individual bones of the holotype. (A) Midcervical vertebra in anterior view. (B) Midcervical vertebra in right lateral view. ap, anterior pneumatic pocket on transverse process; pp, pneumatic pocket on the web of bone above the transverse process. (Scale bar for the reconstruction, 2 m; scale bar for the vertebrae photos, 5 cm.)

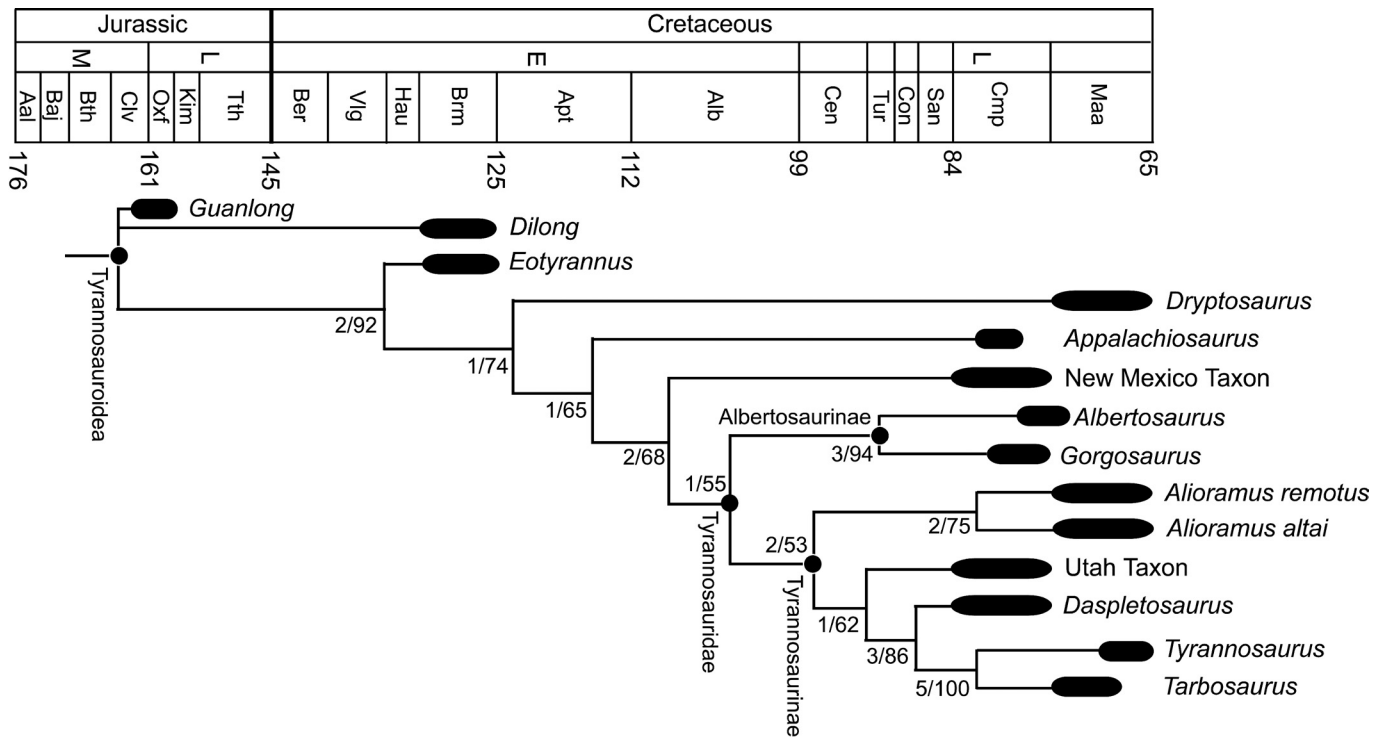


Fig. 4. The strict consensus of four most-parsimonious trees recovered by the phylogenetic analysis (626 steps; consistency index = 0.60; retention index = 0.65) scaled against the Jurassic and Cretaceous time scale. The analysis places *Alioramus* as a derived tyrannosaurid and the most basal member 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-

ever, unlike this study, we do not place *Alioramus* and *Tarbosaurus* within an endemic Asian tyrannosaurine clade, but recover *Alioramus* as the most basal member of a speciose clade of Asian and North American taxa.

Discussion and Conclusions

The discovery of *A. altai* helps clarify the anatomy and systematics of one of the most intriguing, yet poorly understood, large theropod dinosaur genera. The nearly complete and remarkably preserved skull and substantially complete postcranium of *A. altai* clearly demonstrate that *Alioramus* was a small, gracile, heavily ornamented, longirostrine carnivore. The skull is lightly built, and the upper jaw is more than five times longer than it is deep above the antorbital fenestra, an extraordinary ratio otherwise only seen in spinosaurids (26), the small basal tyrannosauroid *Xiongguanlong* (27), and a few coelurosaurids (28) among theropods. Four sets of cranial horns—one on each lacrimal and postorbital and two on each jugal—are present, as well as a series of discrete rugosities on the nasal. This degree of ornamentation exceeds that seen in large-bodied tyrannosaurids such as *Tyrannosaurus* (13) and *Tarbosaurus* (17). The holotype of *A. altai* has a reconstructed mass of 369 kilograms based on equations given by ref. 29. A *Tyrannosaurus* individual of comparable age would have a mass of ≈ 750 kg (24), approximately twice that of *A. altai*. Thus, in total, the new material unmistakably shows that *Alioramus* possessed a distinct body plan relative to other tyrannosaurids, increasing the range of morphological disparity in one of the most familiar extinct clades.

The new material also suggests that tyrannosaurids were more ecologically variable than previously thought. The feeding habits of large-bodied tyrannosaurids have been studied in intense detail, and bite marks, coprolites, gross morphology, and finite element analysis all indicate that *Tyrannosaurus* and kin had skulls well suited to take down large prey and bite through bone (4, 5, 30). *A. altai* lacks many of the cranial adaptations that are integral to using “puncture-pull” feeding in this manner, such as a deep skull, robust bones, fused or interlocking sutures (5), peg-like teeth (4), a rigid lower jaw (22), a strongly interlocking dentary symphysis (31), and a rugose lacrimal–postorbital bar above the orbit (32). This suggests that *Alioramus* exploited a different feeding style, likely focusing on smaller prey, than other Late Cretaceous tyrannosaurids, including the contemporary *Tarbosaurus*, whose remains have also been collected at the Tsaagan Khuushu locality. In fact, it is possible that ecological niche differentiation allowed *Alioramus* and *Tarbosaurus* to coexist, as was originally suggested by Kurzanov (7).

The elongate and gracile skull of *Alioramus* is similar to that of *Xiongguanlong*, a recently described basal tyrannosauroid from the Aptian–Albian (Early Cretaceous) of China (27). *Xiongguanlong* is more primitive, smaller, and more than 35 million years older than *Alioramus*, and is a non-tyrannosaurid that occupies a basal position on the tyrannosauroid stem. As *Xiongguanlong* and *Alioramus* are phylogenetically distant, their longirostrine skulls optimize as convergence (see *SI Text*). However, as little is known about the cranial anatomy of basal tyrannosauroids, and Early Cretaceous forms in particular, it may be that the elongate skull of *Xiongguanlong* is primitive for Tyrannosauridae or close outgroup nodes. If so, the presence of a long and gracile skull in *Alioramus* could potentially be a reversal to the primitive condition, but this hypothesis requires testing with additional basal tyrannosauroid discoveries, most likely from the Early Cretaceous.

The holotype of *A. altai* is remarkably pneumatic, more so than in any other tyrannosaurid specimen. Tyrannosaurids generally exhibit a greater degree of pneumaticity than other theropods, and all of the normal tyrannosaurid pneumatic recesses are present in *Alioramus* (e.g., jugal, lacrimal, squamosal, palatine, ectopterygoid, supraoccipital, prootic, parocci-

tal). In addition, the lateral wall of the braincase is extensively pneumatized, with a fenestra-like basiptyergoid recess and separate pneumatic openings for the anterior tympanic recess and internal carotid. The maxilla also exhibits a heightened degree of pneumaticity associated with the antorbital fossa, and the cervical vertebrae and ribs display autapomorphic recesses and pneumatic pockets. It is interesting that the greatest degree of pneumaticity in a tyrannosaurid is present in one of the smallest and most gracile tyrannosaurid specimens. This argues against the hypothesis that pneumaticity is correlated with body size and is primarily an adaptation to weight reduction (33). Instead, pneumaticity may be exceptionally variable among individuals (34) or may decrease throughout ontogeny. Indeed, an ontogenetic decrease is seen in *Allosaurus* (35), and juvenile *Tarbosaurus* specimens exhibit vertebral pneumatic features not seen in adults (11).

Because the holotype of *A. altai* represents a young individual, it is possible that its aberrant skull form and cranial ornamentation are ephemeral juvenile features that would not be present in the *Alioramus* adult. However, it is worth noting that the holotype is much smaller and more slender than comparably aged *Tyrannosaurus* (24) and has a longer snout than any known juvenile of *Albertosaurus*, *Tyrannosaurus*, or *Tarbosaurus* (11, 14, 15). Additionally, well-studied growth series of other dinosaur taxa show that ornamentation increases throughout ontogeny (36), suggesting that the adult *Alioramus* would possess even more elaborate horns and rugosities. Thus, the aberrant cranial and skeletal form of *Alioramus* was likely maintained in the adult individual.

With this in mind, it is interesting that *Alioramus* appears to follow a sequence of ontogenetic cranial changes similar to other tyrannosaurids despite its atypical morphology. There is no evidence that the elongate skull of *Alioramus* is the result of paedomorphosis, as this would predict that *Alioramus* maintains juvenile characters of close relatives until later in adulthood. Instead, the nine-year-old holotype of *A. altai* possesses a set of characters predicted for a nine-year-old *Albertosaurus* or *Tyrannosaurus*. Thus, the extreme differences in skull shape between *Alioramus* and close relatives must have been the result of another process, and the sequence of discrete character changes in tyrannosaurids appears to be highly conserved despite vast differences in morphology and growth rate (24) among taxa.

Materials and Methods

To compare the ontogenetic stage of the holotype of *A. altai* with its close relative *Tyrannosaurus*, we included the holotype in an analysis of *Tyrannosaurus* ontogeny presented by Carr and Williamson (15). The data matrix includes 84 characters scored for six ingroup taxa, following the analytical procedures outlined in ref. 15. The matrix was run in PAUP 4.0b under an exhaustive search. To specify the phylogenetic relationships of *A. altai*, we added it to the data matrix of Carr and Williamson (25). The data matrix includes 279 characters scored for 15 ingroup taxa and four outgroups (*SI Appendix*). The matrix was run in PAUP 4.0b under branch-and-bound search with the characters equally weighted and unordered, as described by Carr and Williamson (25).

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