

Tyrannosaurids (Dinosauria) of Asia and North America

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ABSTRACT

The theropod family Tyrannosauridae (Dinosauria) is composed of four genera and seven species. All taxa are known from nearly complete skeletons and/or skulls, thus making it one of the best documented large theropod families. The stratigraphic and palaeobiogeographic distribution of the Tyrannosauridae extends from the lower Campanian to upper Maastrichtian of North America, and to the Campanian-Maastrichtian of Asia.

INTRODUCTION

Tyrannosaurid theropods are known only from the Upper Cretaceous of Asia and North America. Their earliest record is a fragmentary skeleton (genus unknown) from the lower Campanian Eagle Ford Sandstone of Montana (U. S. A.) (Gilmore, 1920). By the upper Campanian, however, tyrannosaurids occur throughout the western Interior and Gulf Coast of North America. They are known to have survived until the latest Maastrichtian in the Western Interior. In Asia, tyrannosaurids are known only from the Nemegt Formation estimated to be Campanian-Maastrichtian in age (Fox, 1978). Their apparent absence from upper Maastrichtian deposits in Asia is probably not due to extinction, but due to the lack of upper Maastrichtian deposits.

The earliest tyrannosaurids described were the result of explorations by the geological surveys of Canada and the United States. The first specimen consisted of several isolated and scattered teeth collected from the Judith River Formation of Montana. These were the first theropod teeth found in North America and were named *Deinodon horridus* by Leidy (1857). Years later, two skulls and associated postcrania were found in the Horseshoe Canyon Formation near Drumheller, Alberta (Canada). These skulls were briefly described by Cope (1892), who named them *Laelaps incrassatus*. Lambe (1904) later redescribed the skulls in greater detail, but referred them to the genus *Dryptosaurus* as *Dryptosaurus incrassatus* (Cope). In 1905, Osborn designated the two skulls as the type (=holotype) and cotype (=paratype) of a new genus and species he called *Albertosaurus sarcophagus*.

A few years earlier, in 1902, the American Museum of Natural History expedition, led by Barnum Brown, began collecting in the Upper Cretaceous of Montana and

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Wyoming (U. S. A.). Among the material recovered were two partial skeletons, which Osborn named in 1905 as *Tyrannosaurus rex* and *Dynamosaurus imperiosus*. But the following year, Osborn (1906) synonymized *Dynamosaurus* with *Tyrannosaurus*. In subsequent papers much of the skeleton and skull of *Tyrannosaurus* were described in detail (Osborn 1912, 1913, 1917).

Barnum Brown later began collecting, with great success, in the Judith River (=Belly River, =Oldman) Formation of Alberta. This prompted the Canadian Geological Survey to hire the Sternberg family to collect on their behalf. Among the numerous specimens they found was a nearly complete tyrannosaurid skeleton, that Lambe (1914b) named *Gorgosaurus libratus*. This specimen revealed the didactyl nature of the manus in tyrannosaurids for the first time (Lambe, 1914a, 1917). The tyrannosaurid specimens collected by Brown were described and illustrated by Matthew and Brown (1923). These included skeletons of *Gorgosaurus libratus* and one of a new species, *G. sternbergii*.

The success of both the American Museum of Natural History and the Canadian Geological Survey led the University of Toronto to also begin collecting in Alberta. In the Horseshoe Canyon Formation, a headless and tailless tyrannosaur was found. This specimen was named *Albertosaurus arctunguis* by Parks (1928).

The success of the American Museum of Natural History in obtaining dinosaurs from the Hell Creek Formation of Montana led the Cleveland Museum of Natural History to make a small collection in the area 1942. Among the specimens found was a skull of a small tyrannosaurid. The specimen was not described until after World War II when it was named *Gorgosaurus lancensis* by Gilmore (1946). Also in 1946, Soviet palaeontologists began the first of several expeditions to the Mongolian People's Republic. Several skulls and skeletons of tyrannosaurids were recovered, and subsequently described as *Tyrannosaurus bataar*, *Tarbosaurus efremovi*, *Gorgosaurus lacinator* and *G. novojilovi* by Maleev (1955a, 1955b). A monograph on these animals was begun by Maleev, but never completed. A large portion was eventually published posthumously (Maleev, 1974). A review of Maleev's work led Rozhdestvensky (1965) to conclude that the Mongolian tyrannosaurids were different growth stages of a single species, and so referred all the specimens to *Tarbosaurus bataar*.

Polish palaeontologists began collecting in Mongolia during the 1960's and early 1970's. Several skeletons found were referred to *Tarbosaurus* (Kielan-Jaworowska and Dovchin, 1968; Kielan-Jaworowska and Barsbold, 1972). None of these specimens, which include both juveniles and very large adults, have been described yet.

In recent years, several additional specimens of tyrannosaurids have been found in North America. This includes two *Tyrannosaurus rex* from the Hell Creek Formation of Montana, one collected by the Museum of the Rockies (Bozeman, Montana), and the other collected by the Natural History Museum of Los Angeles County (California). Two other specimens were collected from the Hell Creek Formation of South Dakota (U. S. A.) by the South Dakota School of Mines. A *Tyrannosaurus rex* has been collected from the Scollard Formation of Alberta and a second specimen from the Willow Creek Formation by the Tyrrell Museum of Palaeontology (Drumheller, Alberta). The Tyrrell Museum has also collected six new *Albertosaurus* specimens from the Judith River and Horseshoe Canyon formations of Alberta. Another *Albertosaurus* specimen has been collected from the marine Mooreville Chalk of Alabama

by Auburn University (Auburn, Alabama, U. S. A.). The importance of all these specimens is that all are at least partial skeletons, and several also include skulls or skull elements. The specimen from Alabama demonstrates the presence of that genus east of the Western Interior Seaway.

The first review of the tyrannosaurids was by Matthew and Brown (1922). Their revision synonymized *Gorgosaurus* and *Albertosaurus* with *Deinodon*. *Deinodon*, with *Dryptosaurus* and *Tyrannosaurus*, made the family Deinodontidae, which they noted was the oldest name given to a family of theropods.

Another review of the tyrannosaurids was made by Russell in 1970. Although he concentrated on Canadian species, some comments were made about those from the United States and Mongolia as well. Russell concluded that Leidy's *Deinodon horridus* was not a valid taxon, a conclusion previously reached by Gilmore (1920, 1946). Accordingly, Russell used Tyrannosauridae in place of Deinodontidae; this is in agreement with the International Code of Zoological Nomenclature (third edition), art. 23 (e). Russell synonymized *Gorgosaurus* with *Albertosaurus*, and demonstrated that *Gorgosaurus sternbergi* was a juvenile *Albertosaurus libratus*. A new taxon, *Daspletosaurus torosus*, was named for a nearly complete skeleton from the Judith River Formation of Alberta.

More recently, Barsbold (1983) made a comparative review all of the theropods from Mongolia, including *Tarbosaurus*. He accepts Rozhdestvensky's (1968) assertion that there is only a single species of *Tarbosaurus*, but refers to this species as *T. e-fremovi* for reasons not given. Considering that *Tarbosaurus bataar* has priority, Barsbold's useage is in error.

Functional studies of tyrannosaurids include the bipedal stance of *Tyrannosaurus* by Newman (1970), and cranial kinesis with a reconstruction of cranial musculature by Molnar (1973).

Currently, detailed studies of tyrannosaurids are in preparation by P. Currie, G. Paul, and myself. Although these studies are far from complete, a preliminary review of the existing species of the Tyrannosauridae can be presented.

Terminology and Abbreviations

A summary of cranial terminology is presented in Fig. 1. A new term, pro-maxillary fenestra, replaces anterior-most antorbital fenestra of some authors.

AMNH - American Museum of Natural History; CM - Carnegie Museum of Natural History; CMNH - Cleveland Museum of Natural History; GI SPS - Geological Institute, Section of Palaeontology and Stratigraphy, Mongolian People's Republic Academy of Sciences; LACM - Natural History Museum of Los Angeles County; MOR - Museum of the Rockies; NMC - National Museums of Canada; PIN - Palaeontological Institute, USSR Academy of Sciences.

Systematic Paleontology
Class ARCHOSAURIA
Order THEROPODA
Family TYRANNOSAURIDAE Osborn 1906

Diagnosis: (General) Head large relative to body size; neck, trunk and forelimbs are short. (Cranial) Nasals very rugose, often fused along the midline, and constricted between the lacrymals; frontals excluded from the orbits by the lacrymals; jugal pierced by large foramen; premaxillary teeth D-shaped in cross-section, with carinae along the posteromedial and posterolateral margins; vomer with diamond-shaped process between the maxillae; ectopterygoid with large ventral opening; surangular foramen large. (Postcranial) Cervical centra slightly opisthocoelous, anteroposteriorly compressed, and broad; scapula long and slender; humerus with weakly- to moderately-well developed deltopectoral crest; manus reduced to two functional digits (II and III), with digit IV reduced to a splint; pubis with well developed anterior foot; distal end of the ischium not expanded; ascending ramus of astragalus broad and tall.

Discussion: Among the various specimens which have at one time or the other been referred to the tyrannosaurids, there are several that form a natural, cohesive group. These define the family Tyrannosauridae to the exclusion of all others (a detailed examination of all taxa which have been referred to the Tyrannosauridae is in preparation). The result is that the family is now known only from the Campanian and Maastrichtian of Asia and North America.

The family Tyrannosauridae is considerably more derived from any other theropod. This is especially evident in the reduction of many bones; the cervicals are anteroposteriorly compressed discs, the scapula is a slender bone, the forelimbs reduced in size relative to body size, and the manus has only two functional digits. Other bones, however, are more developed, e. g., the much larger size of the skull relative to the body, and the anterior foot of the pubis is very well-developed compared to *Allosaurus*. The presence of a jugal fenestra and the large size of the surangular fenestra are also derived conditions over that seen in the Allosauridae and Megalosauridae.

The Abelisauridae is convergent with the Tyrannosauridae in several features, including the relative large size of the skull to body size and reduced forelimbs (Bonaparte, 1985). However, the elongated quadrate, peculiar peg-like descending process of the squamosal, and enormous antorbital and lateral temporal fenestra are derived conditions for the Abelisauridae.

Tyrannosaurus Osborn, 1905

= *Dynamosaurus* Osborn 1905

= *Tarbosaurus* Maleev 1955a

= *Gorgosaurus* (in part)

Diagnosis: (Cranial) Viewed dorsally, muzzle well-differentiated from cranium so that stereoscopic vision well-developed; descending process of postorbital extends into orbit; premaxillary contacts nasal below external nares and medial to maxilla (not

visible in lateral profile); lacrymal horn not developed, but is rugose, as is the dorsal part of the postorbital; pro-maxillary fenestra not visible when the skull is viewed in lateral profile; prefrontal forms a wedge between lacrymal and fused frontals; ectopterygoids are swollen and have a very large sinus opening. (Postcranial) Ilium with a well developed notch along the front margin of the preacetabular blade; postacetabular blade of ilium slender; wrist composed of a single element; pubic shaft has a pronounced curve.

Tyrannosaurus rex Osborn, 1905

Figs. 2A, 3, 5A

= *Dynamosaurus imperosus* Osborn 1905

Holotype: CM 9380 (formerly AMNH 973) partial skull and skeleton from the Hell Creek Formation, Montana, U. S. A.

Diagnosis: Angular terminates posterior to the surangular fenestra. Surangular fenestra much larger than in *Tyrannosaurus bataar*. Maxilla terminates below the lacrymal.

Stratigraphic and Paleobiogeographic Distribution: Scollard and Willow Creek formations of Alberta; Frenchman Formation of Saskatchewan; Hell Creek Formation of Montana, North Dakota, and South Dakota; Lance Formation of Wyoming; and Laramie Formation of Colorado.

Tyrannosaurus bataar Maleev 1955a

Figs. 2B, 4, 5B

= *Tarbosaurus efremovi* Maleev 1955b

= *Gorgosaurus lancinator* Maleev 1955b

= *Tarbosaurus bataar* (Maleev) 1955b

Holotype: PIN 551-1 partial skull from the Nemegt Formation, Mongolian People's Republic.

Diagnosis: Angular terminates anterior to the surangular fenestra; surangular fenestra proportionally smaller than in *Tyrannosaurus rex*; surangular fenestra proportionally smaller than in *T. rex*.

Stratigraphic and Paleobiogeographic Distribution: Nemegt Formation and Upper White Beds of Khermeen Tsav, Mongolian People's Republic; possibly the Subashi Formation, Xinjiang, People's Republic of China.

Discussion: Maleev (1955a, b; 1974) recognized three genera and four species of tyrannosaurids from Mongolia: *Tyrannosaurus bataar*, *Tarbosaurus efremovi*, *Gorgosaurus lancinator* and *Gorgosaurus novojilovi*. Rozhdestvensky (1965), however, argued that most of the differences cited by Maleev were ontogenetic, and that only a single species was represented. Rozhdestvensky also argued that this single species

was intermediate between *Albertosaurus* and *Tyrannosaurus* and, thus, represented a distinct genus for which the name *Tarbosaurus* was available. Accordingly, Rozhdestvensky referred all Mongolian tyrannosaurid to *Tarbosaurus bataar*.

Re-examination of Maleev's figures (Maleev, 1955a, 1955b; 1974), as well as photographs of these specimens and of those collected by the Polish palaeontological expeditions to Mongolia, reveal that Rozhdestvensky erred in a number of points in his analysis. The quadratojugal process of the jugal in *T. bataar* reaches the posterior rim of the lateral temporal fenestra as it does in *T. rex*. The tetragonal-shaped ascending process of the jugal in *T. rex*, this observation is based on AMNH 5027 (Osborn, 1912). A new skull of *T. rex*, LACM 23844, has a tapering ascending process as in PIN 551-3, thus showing the shape of this bone is variable. Development of the ascending process into the orbit is variable as indicated by the holotype *T. bataar*, PIN 551-1, which shows a slight development of the jugal within the orbit. This makes it intermediate in shape between AMNH 5027 and PIN 551-3.

Another taxonomical difference Rozhdestvensky stated was the smaller size of the Mongolian tyrannosaurid. However, the holotype skull, PIN 551-1, has premaxillary to occipital condyle length of 1220 mm (Maleev, 1955a, 1974). This compares to 1210 mm for AMNH 5027, *T. rex* (Osborn, 1912).

Thus, contrary to Rozhdestvensky's (1965) claims, *T. bataar* is not intermediate between *Albertosaurus* and *Tyrannosaurus*, but is generically indistinguishable from *Tyrannosaurus*. It is remarkable that of the five skulls of *T. rex* known all are adults (however see below). This is not the case with *T. bataar*. Figure 4 shows a growth series of skulls from the smallest with a premaxillary-occipital condyle length of 825 mm to the largest with a premaxillary-occipital condyle length of 1220 mm. The general ontogenetic trend is a deepening of the skull, shortening of the muzzle, and an increase in the rugosity of the region dorsal to the orbit. As may be seen, the smaller skulls resemble that of *Albertosaurus* (compare Figs. 4C, D with Fig. 2E), especially because of the longer muzzle. Thus, it is understandable that Maleev referred these skulls to *Gorgosaurus* (= *Albertosaurus*). However, the well-developed stereoscopic vision (due to the differentiation of the muzzle from the cranium) separates these skulls from *Albertosaurus*. Variation in the skulls is apparent in the posterior portion of the lateral temporal fenestra where the squamosal may butt against the quadratojugal (Fig. 4B and D) or there may be an overlap (Fig. 4C). A similar pattern is seen in *T. rex* as well (Carpenter, in press).

There has been some confusion about the astragalus in *Tyrannosaurus*. Welles and Long (1974) figured an element associated with AMNH 5827 that they ascribed as a *Tyrannosaurus* astragalus. This element, however, is unlike any theropod astragalus known, and is certainly very different from the astragalus associated with MOR 009, *Tyrannosaurus rex*. This astragalus resembles that of *Albertosaurus* as would be expected. Comparison of the original drawings by Christman of the element figured by Welles and Long show that it is, in fact, a medial and dorsal view of the right quadrate of AMNH 5027 (Fig. 3).

At this time the specific differences between the postcrania of *T. rex* and *T. bataar* have not been established. This is due to the considerable amount of variation among the *T. rex* specimens (Carpenter, in press). Some of the differences may be individual, but most appear to be sexual. Until the range of this variation can be determined, it is not certain what postcranial characters separate *T. rex* from *T. bataar*.

With regard to the maxilla from the Tornillo Formation of Texas ascribed by Lawson (1976) to *T. rex*, it does not belong to *Tyrannosaurus* (Carpenter, in press), but another short-faced theropod.

A description of the postcrania of *Tyrannosaurus* is in preparation.

Maleevosaurus n. g.

Etymology: For the late Eugene Alexandrovich Maleev who first studied the tyrannosaurids of the Mongolian People's Republic.

Maleevosaurus novoilovi (Maleev) 1955b

Figs. 2C, 5C

= *Gorgosaurus novoilovi* Maleev 1955b

Holotype: PIN 552-2 partial skull and skeleton.

Diagnosis: (Cranial) Maxillary fenestra small; pro-maxillary fenestra not visible laterally; antorbital fenestra proportionally very large, and much longer than high; lacrymal horn moderately developed, not rugose; postorbital not very rugose; lower ramus of maxilla low and slender; jugal slender resulting in a very large orbit; dentary slender. (Postcranial) Cervical neural spines tall, not as reduced as in other tyrannosaurids. Acromion process of scapula virtually non-existent. Ischium has a very pronounced spur-like obturator process, and distally, the shaft curves downward. Metatarsal IV does not overlap metatarsal III at midshaft, nor does metatarsal III have much of an overlap of metatarsal II at midshaft.

Stratigraphic and Palaeobiogeographic Distribution: Nemegt Formation, Mongolian People's Republic.

Discussion: That *Maleevosaurus* is a tyrannosaurid is indicated by the slightly opisthocoelous cervical centra, didactyl manus, anteroposteriorly compressed, broad cervicals, well developed anterior foot of the pubis, and broad and tall ascending process of the astragalus. Originally, the holotype of *Maleevosaurus* was one of four species of tyrannosaurid named by Maleev from Mongolia. He had named it *Gorgosaurus novoilovi* (Maleev, 1955b), but because of its small size (femur length 560 mm), Rozhdestvensky (1965) considered it a juvenile *Tarbosaurus* (= *Tyrannosaurus*) *bataar*. Gradzinski and others (1977) and Osmolska (1980) noted that the third metatarsal was considerably more slender than in *T. bataar*, and doubted that this was a juvenile character. They referred to the specimen as '*Gorgosaurus*' *novoilovi*.

In order to determine if '*Gorgosaurus*' *novoilovi* is a juvenile *T. bataar*, comparisons were made to the similarities and differences between an adult and juvenile *Albertosaurus libratus*. These were AMNH 5458, with a femur length of 1025 mm, and AMNH 5664, with a femur length of 700 mm. Comparisons were also made to a growth series of skulls of *T. bataar* (Fig. 4).

In the juvenile *Albertosaurus*, the lacrymal horn is already well developed and

the jugal proportionally large. In *T. bataar*, there is also no change in development of the lacrymal horn and in size of the jugal. Therefore, the moderately developed lacrymal horn and the slenderness of the jugal in '*G. novojilovi*' are not considered juvenile features. Furthermore, no change occurs in the relative size of the antorbital fenestra in *T. bataar* from juvenile to adult, indicating that the large size of the antorbital fenestra in '*G. novojilovi*' is also not a juvenile feature. However, contrary to Gradzinski and others (1977) and Osmolska (1980), it is possible that the slenderness of the third metatarsal is a juvenile character, as this metatarsal is considerably more slender in the juvenile *Albertosaurus* than in the adult. It is possible, however, that this is not the case in the *Tyrannosaurus* specimens available to Gradzinski and others and Osmolska, but their observations have not yet been published.

It is clear from the above analysis, that except for possibly the slenderness of the third metatarsal, '*G. novojilovi*' is not a juvenile *T. bataar*. Furthermore, '*G. novojilovi*' cannot be referred to the genus *Albertosaurus* (= *Gorgosaurus*), nor to any other known genus of tyrannosaurid because of the large size of the antorbital fenestra, slenderness of the jugal, the very well developed obturator process, and sharply downward curved ischium. For this reason, it is best to assign '*Gorgosaurus novojilovi*' to a new genus, *Maleevosaurus*.

Although it is possible that the holotype of *Maleevosaurus novojilovi* is a juvenile, based on its small size, the neural arches are fused to their centra, and the calcaneum to the astragalus. This suggests that *Maleevosaurus* is a small tyrannosaurid.

Albertosaurus Osborn 1905

- = *Laelaps* (in part)
- = *Dryptosaurus* (in part)
- = *Deinodon* (in part)
- = *Gorgosaurus* Lambe 1914

Diagnosis: (Cranial) Premaxillary contacts nasal below external nares; lacrymal horn often better developed than in *Tyrannosaurus*, and the postorbital considerably smoother; posterior part of the dentary not as deep as in *Tyrannosaurus*. (Postcranial) Wrist composed of five elements. Postacetabular blade of ilium deep, and pubic shaft straight.

Albertosaurus sarcophagus Osborn 1905

Figs. 2D, 5D

- = *Laelaps incrassatus* Cope 1892
- = *Dryptosaurus incrassatus* (Cope) 1892
- = *Albertosaurus arctunguis* Parks 1928

Holotype: NMC 5600 nearly complete skull from the Horseshoe Canyon Formation, Alberta, Canada.

Diagnosis: (Cranial) premaxilla anteroposteriorly very short and broad so that lit-

tle of it is visible in lateral view; pro-maxillary fenestra set well in advance of maxillary fenestra, and visible in lateral view; maxillary fenestra taller than long, and separated from antorbital fenestra by a thin bar of the maxillary; lacrymal horn moderately developed; surangular foramen small for tyrannosaurid. (Postcranial) Body appears to be shorter than in *A. libratus*; distal end of scapular blade strongly inflected forward; tibia more gracile than in *A. libratus*.

Stratigraphic and Palaeobiogeographic Distribution: Horseshoe Canyon Formation, Alberta, Canada.

Albertosaurus libratus (Lambe) 1914

Figs. 2E, 5E

= *Gorgosaurus libratus* Lambe 1914

Holotype: NMC 2120 nearly complete skeleton from the Judith River Formation, Alberta, Canada.

Diagnosis: (Cranial) pro-maxillary fenestra close to the maxillary fenestra; maxillary fenestra oval in shape and separated from the antorbital fenestra by a wide bar of maxillary; lacrymal horn very well developed; surangular very large. (Postcranial) distal end of scapula gradually broadens; acromion process of the scapula very deep; tibia more robust than in *A. sarcophagus*.

Stratigraphic and Palaeobiogeographic Distribution: Judith River Formation of Alberta, Canada, and Montana, U. S. A. . Also possibly the Horseshoe Canyon Formation of Alberta, the Two Medicine Formation of Montana, Fruitland Formation of New Mexico, and the Morreville Chalk of Alabama, U. S. A.

? *Albertosaurus lancensis* (Gilmore) 1946

Fig. 2F

= *Gorgosaurus lancensis* Gilmore 1946

Holotype: CMNH 7541 skull and lower jaws from the Hell Creek Formation of Montana, U. S. A.

Diagnosis: (Cranial) skull long and low; maxillary fenestra small and separated from antorbital fenestra by a wide bar of the maxillary; antorbital fenestra longer than tall; nasals do not form, a wedge between the frontals as in *A. libratus* and *A. sarcophagus*, in dorsal view, muzzle well differentiated from cranium so that there was stereoscopic vision. (Postcranial) fourth trochanter more proximal than in *A. libratus*; proximal articular face of tibia almost triangular, rather than quadrangular as in most tyrannosaurids (except for *Maleevosaurus*) proximal expansion of fibula is symmetrical relative to long axis of the shaft.

Stratigraphic and Palaeobiogeographic Distribution: Hell Creek Formation of Montana, U. S. A.

Discussion: I agree with Russell (1970) that *A. arctunguis* is a junior synonym of *A. sarcophagus* despite the supposed differences between the tarsus of *A. sarcophagus* and *A. arctunguis* as noted by Welles and Long (1974). I do not consider these differences significant because Parks (1928) stated that part of the astragulus of *A. arctunguis* was damaged, and that both the astragulus and calcaneum were displaced. New skeletons of *A. sarcophagus* presently under study by Phil Currie are expected to verify these observations.

Russell (1970) synonymized *Gorgosaurus* with *Albertosaurus* claiming that the holotype and paratype skulls closely resemble those referable to *Gorgosaurus libratus*. However, both the holotype and paratype skulls of *A. sarcophagus* are incomplete and crushed making such comparisons suspect. AMNH 5222, on the other hand, is a partial, disarticulated skull. Nevertheless, it shares with the holotype and paratype skulls a number of features, such as the short, broad premaxillaries, a pro-maxillary fenestra that is visible in lateral profile and widely separated from the maxillary fenestra, and in having a narrow bar of the maxillary separating the maxillary fenestra from the antorbital fenestra.

AMNH 5222 has been rearticulated and gives us an undistorted view of the skull of *A. sarcophagus*. This shows that the skull is short and deep, as in *Tyrannosaurus*, rather than long and low as in *A. libratus* (compare Fig. 2D with Figs. 2E). *A. sarcophagus* differs from *A. libratus* in a number of other points as well. These include a pro-maxillary fenestra clearly visible in lateral profile, a broad bar of the maxillary separating the pro-maxillary from the maxillary fenestra, and a narrow bar of the maxillary separating the maxillary fenestra from the antorbital fenestra. There is also some indication that the postorbital extended into the orbit in *A. sarcophagus* in a manner similar to that seen in adult *Tyrannosaurus*. Postcranially, *A. sarcophagus* differs from *A. libratus* in having more gracile limbs, and in having a short, *Tyrannosaurus*-like trunk (compare Figs. 5D and E).

The differences between *A. sarcophagus* and *A. libratus* seem extreme enough to suggest that two distinct genera are present. However, pending a complete review of *A. sarcophagus* by P. Currie based on several new skeletons, Russell's synonymy of *Gorgosaurus* with *Albertosaurus* is tentatively accepted.

Albertosaurus libratus is the best known tyrannosaurid in North America, being represented by nine skulls and partial skeletons. Among this wealth of material includes juveniles permitting Russell (1970) to document ontogenetic changes. Not surprisingly, many of these changes paralleled those seen in *Tyrannosaurus bataar* (Rozhdestvensky, 1965).

A. lancensis is a problematical species despite it being represented by a complete skull. In profile, the skull most closely resembles that of *A. libratus*, especially in the development of the muzzle (compare Figs. 2E and F). Thus, it is understandable why Gilmore assigned it to *Gorgosaurus*. However, when the skull is viewed dorsally, the muzzle is well differentiated from the cranium, a feature only known in *Tyrannosaurus*. In addition, as shown with *T. bataar*, juvenile *Tyrannosaurus* skulls are *Albertosaurus*-like in profile. Therefore, is *A. lancensis* a juvenile *T. rex*? Gilmore (1946) stated that many sutures are coalescent, indicating an adult individual. This condition is exaggerated, as the only completely coalescent bones are the parietals; both the frontals and nasals are separate anteriorly. The coalescence of cranial bones is known

to be variable in dinosaurs (Brown and Schlaikjer, 1940), making its usability to 'age' individuals suspect.

Besides the *Albertosaurus*-like profile, two other features of the ?*A. lancensis* skull that seem to differ from *T. rex* are the oval-shaped orbit and the shape of the antorbital fenestra. The shape of the orbit changes ontogenetically in *T. bataar* as may be seen in Figure 4. In the smallest skull the orbits are almost oval in shape, whereas in the larger skulls the orbit becomes progressively taller and is subdivided by the orbital process of the postorbital. Considering that the skull of *A. lancensis* is smaller than the smallest *T. bataar* skull, and by extending backwards ontogenetically the changes that occur in *T. bataar* skulls, the oval shape of the orbit in *A. lancensis* might be a juvenile character.

The shape of the antorbital fenestra in *A. lancensis*, however, seems to exceed that expected ontogenetically based on *T. bataar*. As may be seen in Figure 4, the anterior edge of the fenestra remains rounded throughout life in *T. bataar*. In *T. rex* this area is variable, being rounded, as in *T. bataar*, to squared (Carpenter, in press). In ? *A. lancensis*, this region is more acute (Fig. 2F). But because the *A. lancensis* skull is considerably smaller than the smallest known *T. bataar* skull, it is possible that area undergoes early ontogenetic change (this hypothesis is partially inferred from the early ontogenetic changes in the hadrosaur *Maiasaura*; Horner in preparation).

A single fragmentary skeleton of *A. lancensis* is known, and identification is tentative (Molnar, 1980). Molnar does describe a partial lacrymal, which, if it belongs to ?*A. lancensis* would indicate the absence of a horn. In the holotype skull this region is either damaged or restored, but enough of the horizontal ramus exists on the left side to indicate that at a small horn was present. Because Molnar did not figure the element, it is not possible to verify his identification. Molnar's identification of the material to *A. lancensis* is due to its small size and more gracile appearance. However, as discussed above, a juvenile *A. libratus* (AMNH 5664) is more gracile than the adult (AMNH 5458) and the small size might also indicate a young animal. One feature Molnar (1980) noted about the fragmentary skeleton that might differentiate it from *T. rex* is the bisymmetrical proximal expansion of the fibula. However, this is more apparent than real and is based upon the orientation of the specimen. At this time there is nothing about the fragmentary skeleton to prevent its being a juvenile *T. rex*.

Daspletosaurus Russell 1970

Daspletosaurus torosus Russell 1970

Figs. 2G, 5F

Holotype: NMC 8506, skeleton lacking hind legs from the Judith River Formation of Alberta.

Diagnosis: (Cranial) Premaxilla does not contact nasals under external nares; lacrymal horn well developed; postorbital rugose, although less than *Tyrannosaurus*; pro-maxillary fenestra very small; surangular foramen very large. (Postcranial) Postacetabular blade of ilium very long; ischium straight; scapula broadens gradually posteriorly; acromion process of scapula forms a continuous arc with the coracoid.

Stratigraphic and Palaeobiogeographic Distribution: Judith River and Horseshoe Canyon formations of Alberta, Canada; Judith River Formation of Montana.

Discussion: As Russell (1970) has pointed out, adult *Daspletosaurus* the same length as an adult *Albertosaurus* is heavier and more powerfully built. This gives it the appearance of *Tyrannosaurus*, but this resemblance is superficial. Numerous differences between the two animals, such as the lack of the postorbital extending into the orbit and no contact between the nasal and premaxilla below the external nares, indicate that *Daspletosaurus* is distinct from *Tyrannosaurus* (see also Russell, 1970).

As yet, *Daspletosaurus* is too poorly represented with skulls and skeletons to determine the full range of variation, including individual, sexual and ontogenetic. The largest individual (CM 9401) is represented by a nearly complete right lacrymal larger than that of the holotype of *T. rex* (CM 9380). This suggests a skull with a premaxillary-occipital condyle length of over 1200 mm. A detailed osteology of *Daspletosaurus* is in preparation.

DISCUSSION

Numerous theropods have, at one time or the other, been referred to the Tyrannosauridae. A review of those theropods is currently in preparation. Nevertheless, it is clear that *Tyrannosaurus*, *Maleevosaurus*, *Albertosaurus* (including *Gorgosaurus*) and *Daspletosaurus* form a very cohesive group to the exclusion of all other theropods. It might be argued that these four genera constitute a single genus, *Tyrannosaurus*, with several subgenera, but I do not see the advantage of this. To do so would be to accept a considerable amount of specific variation within the genus *Tyrannosaurus*. I prefer, instead, to redefine the family Tyrannosauridae so as to exclude other theropods. Under this system, the Tyrannosauridae is restricted to North America and Asia, although related families are also known from Argentina, India, and possibly Madagascar. These might be combined into the superfamily Tyrannosauroidea. Pending a completion of the analysis of these other theropods, no attempt is made to determine the cladistic relationship of the Tyrannosauridae.

Sexual dimorphism is known in other dinosaurs and would be expected in tyrannosaurids. It is present and is best seen in *Tyrannosaurus rex* where both a robust and a gracile form are known. This is similar to what Raath (1977) reported for *Syntarsus*. The robust form of *T. rex* is best exemplified by CMNH 9380, while AMNH 5027 and LACM 23844 typify the gracile form (the skulls of all three are about the same size). In the skull, CMNH 9380 has a more robust maxillary, slightly more pronounced lacrymal horn, larger teeth, and a more massive mandible (especially the dentary). Postcranially, the differences are less noticeable, although the pelvis and vertebrae of CMNH 9380 are a little more robust than in AMNH 5027. The condition of the postcrania in LACM 23844 is unknown to me. I suspect that analysis of *T. bataar* and *Albertosaurus libratus* will also reveal robust and gracile forms. A more detailed discussion of sexual dimorphism and individual variation is presented in Carpenter (in press).

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This study began while mounting a cast of *Tyrannosaurus rex* at The Academy of Natural Sciences of Philadelphia. The cast is of the splendid skeleton presently on display at the American Museum of Natural History. The fine workmanship of the cast is the responsibility of Martin Cassidy and his crew, and to them I owe a special thanks, especially for their record time in making the molds and the cast. Once the cast was delivered to the Academy, my crew was remarkably patient with me; I thank them all; W. Altimari, C. Barut, C. Forster, P. Leiggi, and W. Pinder.

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LEGENDS FOR FIGURES

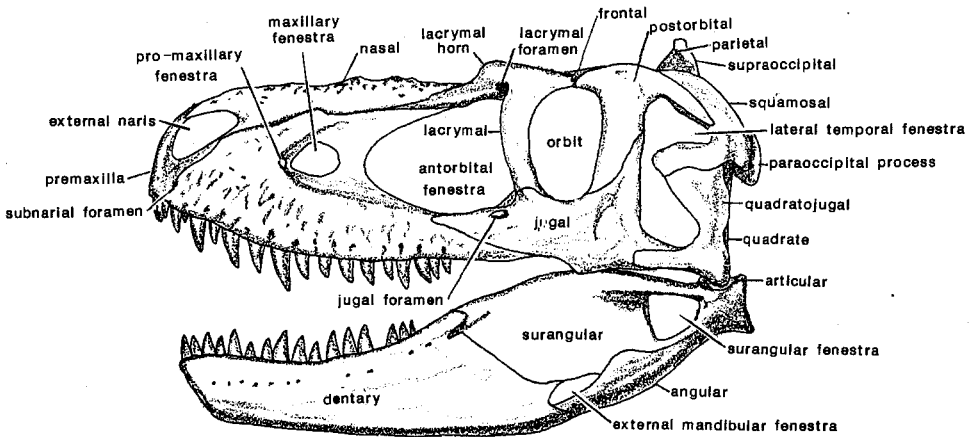


Figure 1. The skull of *Albertosaurus libratus* with cranial terminology used in this paper.

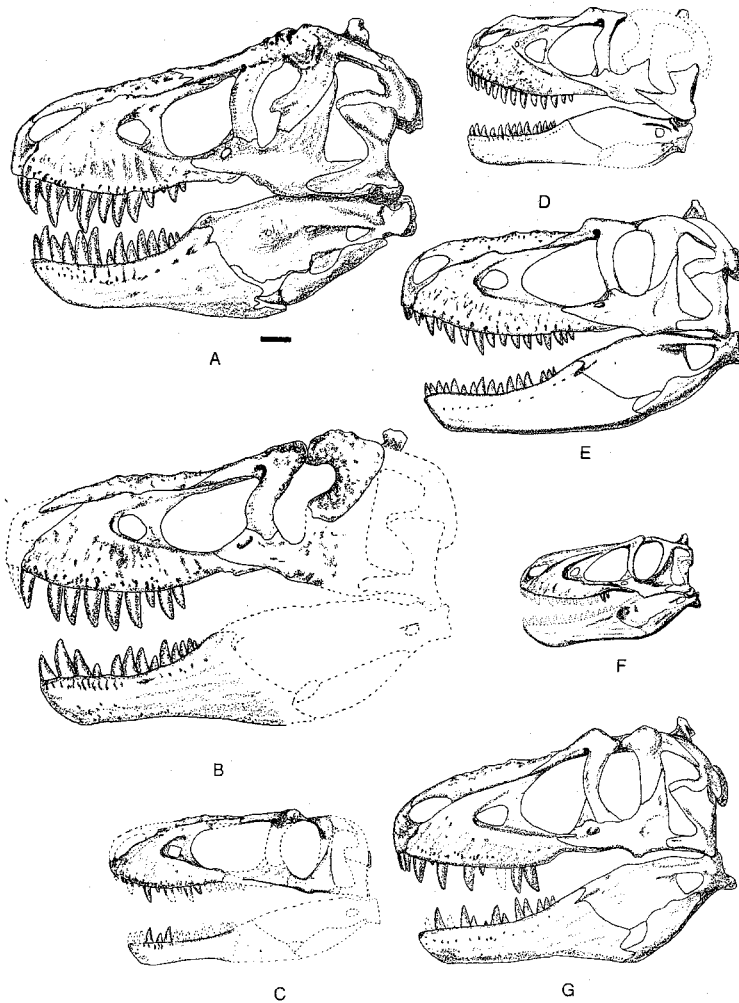


Figure 2. Comparison of tyrannosaurid skulls; A-*Tyrannosaurus rex* AMNH 5027 (modified from Osborn, 1912); B-*Tyrannosaurus bataar* holotype PIN 551-1, with missing areas restored after PIN 551-3 and GI SPS 100/59 (from photographs, Maleev, 1974 and Barsbold, 1983); C-*Maleevosaurus novoilovi* holotype PIN 552-2 (modified from Maleev, 1974); D-*Albertosaurus sarcophagus* AMNH 5222, with lower jaws based on NMC 5600 and NMC 5601 (modified from photographs and Lambe, 1904); E-*Albertosaurus libratus* (modified from Russell, 1970); F-? *Albertosaurus lancensis* holotype CMNH 7541, composite of the left and right side (modified from photographs); G-*Daspletosaurus torosus* (modified from Russell, 1970 and photographs of NMC 8506). All drawn to scale; scale beneath *Tyrannosaurus rex* = 10 cm.

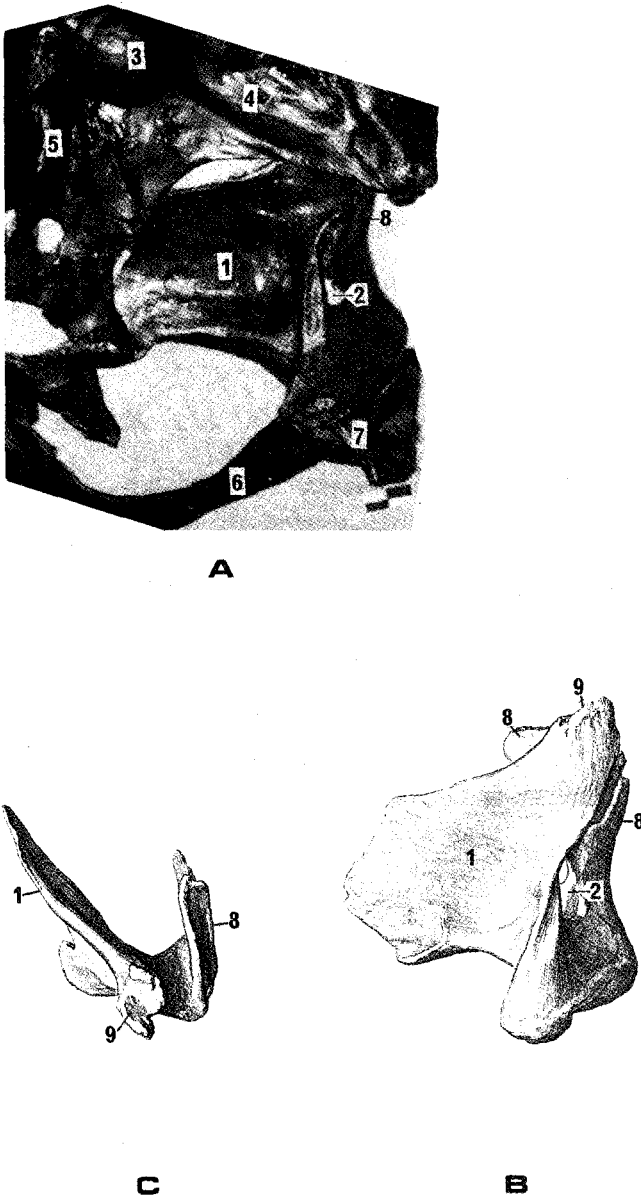


Figure 3. Medial view of the quadrate of *Tyrannosaurus rex* (cast at the ANSP) with B, drawings made by Erwin Christman and identified by Welles and Long (1974) as the astragalus. 1-pterygoid process of the quadrate. 2-quadrate foramen. 3-occipital condyle. 4-paroccipital process. 5-basisphenoid. 6-prearticular. 7-articular. 8-quadratejugal. 9-articulating surface for the squamosal. Scale below the articular in A = 2 cm.

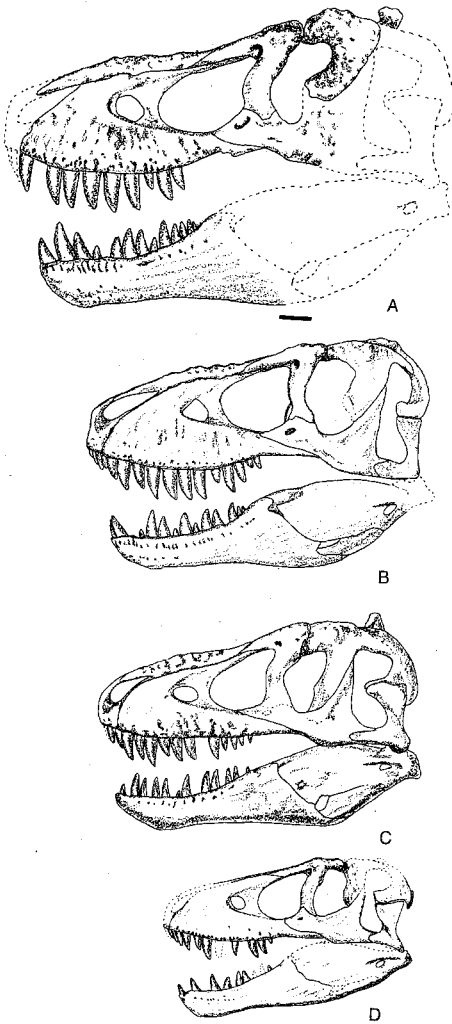


Figure 4. Growth series for skulls of *Tarbosaurus bataar*; A-PIN 551-1 (holotype) with missing areas reconstructed from PIN 551-3 and GI SPS 100/59 (from photographs, Maleev, 1974, and Barsbold 1980); B-PIN 551-3 (holotype of *Tyrannosaurus bataar*) (from photographs and Maleev, 1974; the posterior margins of the squamosal and quadratojugal are apparently incomplete or curved away from the viewer, hence the different shape of these bones compared to the other skulls); C-GI SPS 100/59 (modified from Barsbold, 1980); D-PIN 552-2 (holotype of *Gorgosaurus lancinator*) (modified from Maleev, 1974). All skulls to scale; scale under A = 10cm.

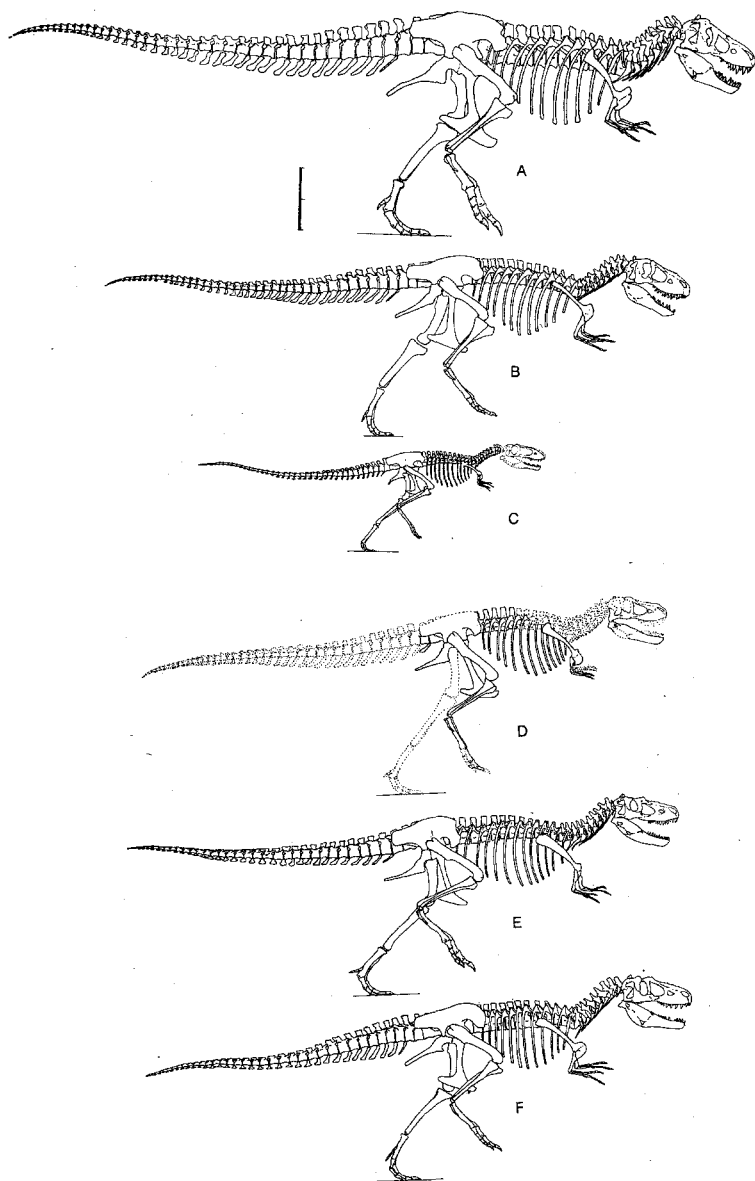


Figure 5. Comparison of tyrannosaurid skeletons; A-*Tyrannosaurus rex* (based on drawings and photographs of AMNH 5027 and CM 9380); B-*Tyrannosaurus bataar* (based on photographs of PIN 552-1, a young adult); C-*Maleevosaurus novojilovi* (modified from Maleev, 1974); D-*Albertosaurus sarcophagus* (skeleton based on photographs and drawings of ROM 807, with the skull based on photographs and drawings of AMNH 5222, NMC 5600 and NMC 5601); E-*Albertosaurus libratus* (skeleton modified from Lambe, 1914, and skull modified from Russell, 1970); F-*Daspletosaurus torosus* (modified from Russell, 1970). All drawn to scale; height of scale beneath *Tyrannosaurus rex* tail = 1 m.