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GIANT CARNOSAURS OF THE FAMILY TYRANNOSAURIDAE

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{132} EDITOR'S NOTE

The manuscript of 'Evgeni Aleksandrovich Maleev, who suddenly passed away in 1966, has remained unfinished. As can be seen from the Introduction, which the author had time to write, he intended to clarify not only, as is usual, the morphology and systematics, but also questions of functional analyses, ecology of carnosaurs, their geologic age and geographic distribution, as well as their significance in the Mesozoic terrestrial vertebrate faunas. But, unfortunately, this was not able to come to pass.

The most complete was the chapter that contained a detailed morphological description of *Tarbosaurus*, which is illustrated with the excellent work of artists P. V. Sivkov and K. P. Meshkov. Undoubtedly this section of E. A. Maleev's work represents a great deal of interesting material for paleontologists in itself, as throughout the world there are only a few monographs published on the gigantic carnosaurian dinosaurs; all of them were published several decades ago, and naturally in several areas they are out of date with respect to the current level of knowledge. In addition, among these monographs there is not a single one that concerns itself with Asian carnosaurs, other than individual articles. For this reason the work of E. A. Maleev is especially valuable, being the first detailed morphological description of Asian carnosaurs, exemplified by *Tarbosaurus*.

In addition to the introduction and the chapter on morphology, the author also wrote a historical sketch on the study of carnosaurs, in which he examines a considerable number of publications on Jurassic and Cretaceous carnosaurs (primarily of North America, where most of the major discoveries are known) over the last hundred years. The sketch remained unfinished, but even in this incomplete state it offers useful information. The chapter dedicated to carnosaur systematics, although not quite completed, had already been published as a separate article (Maleev, 1968), and there is no point in duplicating it here. The remaining chapters listed by the author were still in outline form and contained only notes from various sources.

Some tables of measurements were prepared by the author as blank forms but not filled in with data. The completion of this task was accomplished by S. M. Kurzanov. Preparation of the manuscript for publication was done by A.K. Rozhdestvenskiy.

The work of E. A. Maleev is particularly topical at this time, given the paleontological expeditions currently underway in Mongolia.

INTRODUCTION

In the collection of dinosaurs from Central Asia in the Paleontological Institute of the Academy of Science of the USSR, there is a great deal of gigantic carnosaur material. They are one of the most interesting and highly organized animals among all reptiles. {133} This group first appeared during the Triassic and existed until the end of the Mesozoic. Within the boundaries of the USSR only fragmentary carnosaur remains are known from Kazakhstan, Tadjhikistan, Zabaykal'ye, and the Far East. Thus the materials from the Mongolian National Republic, consisting of several nearly complete skeletons, a series of skulls, and numerous skeletal parts, not only open up the possibilities for research on the structures of these animals, but also reveal a series of biological laws in the evolution of Mesozoic vertebrates.

In order to achieve this goal, the following problems will be addressed: 1) the adaptation of carnosaurs to bipedal locomotion; 2) zonal distribution (biotypes of carnivorous dinosaurs); 3) carnivorous dinosaurs as a biological type; 4) the formation of faunal complexes, the paths of distribution, and the causes of extinction of carnosaurs; 5) geological distribution and comparison of the dinosaur faunas of Asia and North America. Besides these major questions, great attention will be paid to the analysis of particular adaptive structures in the dinosaur skeleton, which are currently insufficiently studied and have not received correct functional explanations.

It can undoubtedly be said that carnosaur evolution is one of the most interesting problems in evolutionary paleozoology. Inasmuch as carnosaur remains are almost unknown in the USSR, the situation arose that they were studied by foreign scientists. They have accumulated a considerable number of facts and observations, but the existing concepts in several cases are challenged by the biological peculiarities and evolution of certain groups.

The wide geographic distribution of carnivorous dinosaurs is of great geological significance. Complex organisms, which rather precisely reflect their living conditions in their structure, become not only records of stratigraphic sequences, but are also reliable indicators of past physico-geographic environments, which are extremely important for paleogeographic constructions and correlations of continental deposits, frequently across distant regions of Europe, Asia and North America.

This work was based on material of gigantic carnosaurs from the family Tyrannosauridae, representing the collections of the Mongolian Paleontological Expedition of the Academy of Sciences of the USSR in 1946-1949 from the Nemegt Basin (Efremov, 1954a, 1955): 1) *Tyrannosaurus bataar* Maleev, 1955 – nearly complete skull with lower jaw and a series of cervical vertebrae (No. 551-1); 2) *Tarbosaurus efremovi* Maleev, 1955 – three nearly complete skeletons (Nos. 551-2, 551-4, 552-1), the first among them with a skull; 3) *Gorgosaurus lancinator* Maleev, 1955 – a complete skull with lower jaw, a series of dorsal and caudal vertebrae, limb bones (No. 553-1); 4) *Gorgosaurus novojilovi* Maleev, 1955 – a nearly complete skeleton with skull (No. 552-2); 5) numerous pieces of skulls and postcranial skeletons, belonging to no fewer than six individuals of *Tarbosaurus efremovi*[1].

Preparation of the Mongolian material was executed with great competence by preparators M. F. Luk'yanova and M. P. Zhukova of the Paleontological Institute of the Academy of Sciences of the USSR.

The structure of the skulls and postcranial skeletons of *Gorgosaurus*, *Tarbosaurus* and *Tyrannosaurus* have a great deal in common in spite of their different sizes. For this reason, the description for all three genera is given based on the most completely preserved skeleton of *Tarbosaurus efremovi*, which makes it possible {134} to avoid unnecessary repetition in the description of the osteological materials and considerably reduces the volume of the article. The

[1]According to A. K. Rozhdenstvenskiy (1965), all the enumerated species are synonymous with one, which should be named *Tarbosaurus bataar* (Maleev). This point of view is also shared by other recent authors (Kielan-Jaworowska, 1967, 1969; Kielan-Jaworowska and Dovchin, 1968; Osmoska and Roniewicz, 1970; and D. Russell, 1970). – *Editor's note.*

excellent line drawings were produced by artists K. P. Meshkov, P. V. Sivkov and N. A. Yan'shinov. The photographs were developed by photographers N. P. Finogenov and A. V. Skinder in the photolab of the Paleontological Institute. The author is very grateful to all the individuals mentioned above.

Chapter I

BRIEF HISTORICAL OUTLINE OF RESEARCH ON CARNIVOROUS DINOSAURS

The initial research on carnivorous and other dinosaurs in North America, where the greatest number of discoveries is known, dates back to the second half of the last century, which corresponded to the explosive development of vertebrate paleontology in the West. During this period, such well-known American paleontologists as J. Leidy, O. C. March and E. D. Cope were studying carnosaurs.

The first article on the carnivorous dinosaurs of North America was published by Leidy in 1856. A tooth from the Cretaceous of Montana was described *Deinodon horridus*.

In 1866, Cope described *Laelaps aquilunguis* from several teeth and fragments of postcranial skeleton from the Cretaceous of New Jersey.

Soon after, Leidy (1868) again described several huge serrated teeth from the Upper Cretaceous of Montana, which he classified as belonging to the new genus *Aublysodon*.

In Leidy's work from 1870, we find the description of the posterior half of a skeleton and caudal vertebrae of a dinosaur, which the author named *Poecilopleuron valens*[2].

Three years later, Leidy (1873) provided an illustration, and redescribed this material with minor changes as a the type species *A. valens* of the new genus *Antrodemus*, transformed from *Poecilopleuron valens*.

In 1876, Cope (1876b) described a new species, *Laelaps incrassatus*, based on a tooth from the Cretaceous of Montana, and stated that it was very closely related to *Aublysodon lateralis*, *Laelaps explanatus* and *L. falculus*, described previously (Cope, 1876a).

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[2] This genus was established in Europe by R. Owen (1842), but is now regarded as a synonym of *Megalosaurus* (Buckland. 1842). – *Editor's note*.

At the same time, Cope (1876b) described three more species of *Laelaps* from Montana: *L. hazenianus*, *L. cristatus* and *L. laevifrons*. In addition, Cope (1892) described two skulls from the uppermost beds of the Laramie (Edmonton) Formation in Alberta, which are identical to *Laelaps incrassatus* in their morphology.

In 1877, O. C. Marsh (1877a) reported that the genus name *Laelaps* was preoccupied by Köch and suggested changing it to *Dryptosaurus*, based on the species *Dryptosaurus (= Laelaps*) *aquilunguis* from the Upper Cretaceous of New Jersey.

In the same year, Marsh (1877b) published a description of a series of dorsal and caudal vertebrae of a carnivorous dinosaur from the Upper Jurassic of Colorado. The vertebrae closely resemble those of *Antrodemus valens* Leidy in shape and size. Marsh, however, created the new genus *Allosaurus*, with *A. fragilis* as the type species; he proposed to eliminate the genus name *Antrodemus*.

In 1884, Marsh published a diagnostic description of the order Theropoda, including *Ceratosaurus nasicornis* from the Jurassic of Colorado, with a description and illustration of the skull and postcranial skeleton. On the basis of the peculiar structure of the skull, he established the new family Ceratosauridae. At the same time, Marsh described a new species based on the fragments of a lower jaw and several teeth from the Upper Jurassic of Colorado – *Labrosaurus ferox*. He stated that the representatives of this genus have more triangular teeth than other theropods.

{135} R. Lydekker (1888) reexamined Marsh’s material of *Ceratosaurus nasicornis* and came to the conclusion that *C. nasicornis* resembled *Megalosaurus* in the structure of its postcranial skeleton, and on that basis removed the genus *Ceratosaurus* to the family Megalosauridae.

Simultaneously with Lydekker’s article, Marsh (1888) published a note on a new species of the genus *Allosaurus* – *A. medius*, based on fragments of teeth from the Lower Cretaceous of Maryland.

Later, in 1890, Marsh gave a description on the new species of the genus *Deinodon* – *D. grandis*, based on some metatarsal bones from the Upper Cretaceous of Montana. In the same year, while preparing his manual on vertebrate paleontology – "Handbuch der Paläontologie" – K. Zittel (1890) reexamined Leidy's (1873) description of the genus *Antrodemus* and transferred it to the family Megalosauridae.

Similarly, Cope (1892) noted that the species *Ceratosaurus nasicornis* described by Marsh (1884) is very similar to members of the family Megalosauridae in its postcranial skeleton, and that it would be more appropriate to assign the specimens described by Marsh to the genus *Megalosaurus*.

In 1896, O.C. Marsh described some isolated limb bones of a large carnivorous dinosaur from the Cretaceous of Wyoming and assigned them to a new species of the genus *Ornithomimus* – *O. grandis*. Later, O. P. Hay (1902) revised dinosaur systematics and transferred all species of *Labrosaurus* to the genus *Antrodemus*.

In 1903, two articles from H. F. Osborn (1903a, b) appeared. In the first, he described the skull and postcranial skeleton of a small carnivorous dinosaur, *Ornitholestes hermanni*, from the Jurassic of Wyoming. In the second article, he described and illustrated the skull of *Creosaurus* from the same deposits in Wyoming. The skull shows several primitive structures, with three antorbital fenestrae; an elongated facial region; a shortened temporal portion; and parietal bones highly extended posteriorly.

In 1905, Osborn described a large carnivorous dinosaur from hind limb bones from the Upper Cretaceous of Montana as a representative of a new genus *Tyrannosaurus*. He reported that the size of this carnosaur is greater any previously described carnivorous dinosaur. In the same article, he gave a brief diagnosis of *Dynamosaurus*, which has small, plate-like dermal ossifications as in other carnivorous dinosaurs. This group of carnosaurs was described earlier as belonging to the single genus *Dryptosaurus*. Further, he mentioned the need to reexamine the nomenclature of carnivorous dinosaurs.

In 1906, Osborn once again returned to his examination of *Tyrannosaurus rex*, using additional, more complete materials from the Laramie formation of Montana, on the basis of which he gave a diagnosis of the species and a short ecological characterization. In the same article, he reexamined Marsh's data on *Ornithomimus grandis*, which Osborn he transferred to *Tyrannosaurus rex* based on its greater size and similarity. The fact that these remains belong to the same genus is also supported by their identical geological age.

In 1909, Hay made the first attempt at a detailed anatomical analysis of the skull and brain cavities of *Triceratops*, *Iguanodon* and *Megalosaurus*, and described the structure of the brain from molds made from the brain cavities of these dinosaurs.

In A.S. Woodward's article (1910), we find the description of the skull of *Megalosaurus bradleyi*. The author pointed out the peculiar structure of the teeth and the elongation of the facial portion of the skull.

R. S. Lull (1911) described a new species of the genus *Dryptosaurus* – *D. potens*, from a single vertebra from the Lower Cretaceous of Maryland.

Subsequently, in 1912 H. F. Osborn returned to his study of the material on gigantic carnosaurs of North America for the third time. He gave a detailed description and illustration of the skull of *Tyrannosaurus rex* and made comparisons with the skull of *Allosaurus*. He described the brain cavity and a brain cast of *Tyrannosaurus rex* for the first time. Five years later, Osborn published (1917) his paper on {136} the morphological analysis of the skeletal structures of *Ornitholestes*, *Struthiomimus* and *Tyrannosaurus*. In this paper, there is a brief discussion of the presumed mode of life of *Tyrannosaurus* and small carnivorous dinosaurs. The author noted that *Tyrannosaurus* had the best predatory mechanism among terrestrial vertebrates. It combined destructive force and speed for hunting. In conclusion, he provided skeletal reconstructions of *Ornitholestes*, *Struthiomimus* and *Tyrannosaurus*.

Almost simultaneously, L. M. Lambe's monograph (1917) was published, with a description of *Gorgosaurus libratus* from the Upper Cretaceous of Alberta (Canada). This was the first description of a complete skeleton of a carnosaur from Canada, where until 1913 there had only been descriptions of isolated bones from carnivorous dinosaurs. The monograph provided excellent illustrations of the skull and many parts of the postcranial skeleton. In the conclusion, the author proposed several ideas concerning the habits of carnivorous dinosaurs.

As the material on the different dinosaur groups accumulated, it became possible to conduct more in-depth research, as well as make comparisons of individual organs and entire organ systems between fossil and contemporary forms, even if only distantly related. Such an attempt was originally made by Gregory and Camp (1918), who reconstructed of the pelvic musculature of the carnivorous dinosaur *Ornitholestes hermanni* based on study of the musculature of the alligator and ostrich. These works have had a great impact on subsequent studies of the musculature of many dinosaurs.

In 1919, C. A. Matley (1919) published an interesting article about the dinosaurs of India. The author gave a list of forms found there: Sauropoda – *Titanosaurus indicus*; Carnosauria – Allosauridae; Coelurosauria – Compsognathidae, Coeluridae, Ornithomimidae. In the conclusion he compared the Indian forms with the dinosaurs from Madagascar, and he concluded that they are quite similar.

In the following year a large monograph by C.W. Gilmore (1920) was published, containing descriptions of all carnivorous dinosaurs deposited in the National Museum of the USA. He described *Antrodemus* and *Ceratosaurus* in particular detail. The author reviewed the systematics and gave a survey of the carnivorous dinosaurs found in the Jurassic and Cretaceous deposits of North America. Following Gilmore's work, W. D. Matthew and B. Brown (1922) published an article on the systematics of carnivorous dinosaurs of North America. At the end of their paper, they gave a description of a skull of a new carnivorous dinosaur – *Dromaeosaurus albertensis* from the Cretaceous of Alberta (Canada). In 1923 the same authors reported a new discovery of *Gorgosaurus libratus* Lambe and a new species – *G. sternbergi* from the Cretaceous of Alberta. In the conclusion of the paper, they made taphonomic observations concerning the burial of carnivorous dinosaurs.

In the same year, three articles by A. S. Romer (1923a, b, c) were published, containing reconstructions of the pelvic musculature of dinosaurs. In the first article, the author made a comparison of the pelvis of dinosaurs with that of birds. He wrote that for these groups the ilium is typically elongated anteriorly, but that this character is not present in primitive Paleozoic reptiles. Morphologically and functionally, this part of the pelvis has significant differences in the two groups, which obviously indicates that they had independent histories. In the second article, Romer some observations on the homology of the pelvic musculature of crocodiles, birds and reptiles, and in the third – he gave a reconstruction of the pelvic musculature of the dinosaur order Saurischia – reptile-like pelvis – with reference to the musculature of crocodiles.

In 1928, W. A. Parks (1928) described *Albertosaurus arctunguis* from an incomplete skeleton from the Cretaceous of Alberta. The author made a detailed comparison with other previously described carnosaurs. In L. S. Russell’s article (1930), we find a brief survey of the Cretaceous dinosaurs from Canada and the USA. The author provided detailed faunal lists from various localities, {137} the geological distribution of well-known forms, and a correlation of Cretaceous deposits of Canada and USA.

In the same year, O. Abel (1930) published his work on the reconstructed appearance and habits of *Tyrannosaurus rex.* The author noted the weak development of the forelimbs and the fact that the animal's locomotion was achieved exclusively on the hind legs.

In 1933, the article of C. W. Gilmore appeared on the Cretaceous dinosaurs of Inner Mongolia. The author indicated that Granger and Berkey (1922) and later Matthew (in Berkey and Morris, 1927) incorrectly assigned the Iren Dabasu Formation to the Lower Cretaceous. After a critical study of all the known species, Gilmore came to the conclusion that this fauna is very similar to the Late Cretaceous fauna of North America, and apparently developed simultaneously. Only the Ceratopsidae is missing in the Iren Dabasu faunal complex. In the same article, the author described a large carnivorous dinosaur – *Alectrosaurus olseni* from the bones of the fore- and hind limbs. The unusually gigantic size of the humerus and the large unguals did not resemble those known earlier from Cretaceous deinodonts[3].

In 1935, C. L. Camp (1935) described the fragmentary remains of carnivorous dinosaurs from deposits thought to be Cretaceous in Xinjiang province (China). In the author's opinion, these remains (several limb bone and pelvic fragments as well as teeth) indicate the presence of huge carnivorous dinosaurs in Central Asia, possibly related to *Tyrannosaurus*. Further, the author compared the Chinese finds with known carnosaurs, studied the histologic structure of the bones, and on the basis of such studies determined the geologic age of the Xinjiang dinosaurs as Jurassic.

In 1946, Gilmore described from a complete skull a new species of the genus *Gorgosaurus – G. lancensis* from the Cretaceous of Montana. In the same article he reviewed the systematics of Cretaceous carnosaurs, and designated a series of type species for many genera, giving a greater taxonomic significance to the shape and number of teeth.

Five years later, E. H Colbert (1951) published an article on the evolution of dinosaurs. The author recognized four lines of adaptive radiation, as well as one of the characteristic peculiarities in the evolution of carnosaurs -- the disproportionate enlargement of the skull.

[3] The family Deinodontidae Cope, 1886 is now regarded as synonymous with Tyrannosauridae Osborn, 1906 – *Editor's note*.

The first discovery of carnivorous dinosaurs in Tien Shan was published in a 1957 article by Young and Sun (1957), along with a description of the new species *Szechuanosaurus campi* from the Cretaceous of the Turpan Basin.

W. Langston (1959), in a survey paper on the fossil vertebrates from Alberta, recorded the great variety of fossil remains of carnosaurs in the Cretaceous deposits of North America. For the Cretaceous of Canada, he recognized the presence of *Gorgosaurus*, *Albertosaurus*, and *Tyrannosaurus*.

Until the 1960's, reports on the carnosaurs of Central Asia were confined to the brief articles of Gilmore (1933), Camp (1935) and a few others.

The extensive investigation of the dinosaurs of Asia were initiated by Soviet paleontologists after the works of the Mongolian Paleontological Expedition by the Academy of Sciences of the USSR (1946-1949). This expedition discovered a wealth of localities of dinosaur and Tertiary mammal faunas. The Mongolian locations, such as Nemegt, Bayn-Shire, Altan-Teeli and others, are as rich as those of Europe, Africa and North America in terms of the completeness of their paleontological material.

I. A. Efremov holds a special place among the investigators of the fauna of Central Asia (Efremov 1949, 1950, 1953, 1954a,b, 1955, 1963). He wrote a series of survey papers on various problems associated with the study of dinosaurs. These papers shed new light on the historical development of dinosaurs, their habitat zones, formation of faunal complexes, burial conditions, and geographical and geological distributions. {138} A series of articles describing the dinosaurs of Central Asia was published by E. A. Maleev (1952a, b, c, 1953a, b, c, 1956, 1964a, b, 1965). In them he provided a monographic description of the armored dinosaurs and preliminary descriptions of several genera and species of gigantic carnosaurs. A. K. Rozhdestvenskiy (1952a, b, 1955, 1957, 1964) published papers on ornithopods.

Review of the literature over the last hundred years[4] indicates that most of them characteristically lack, or are deficient in, the functional and ecological aspects of the studied material. Some publications present brief descriptions of isolated small collections, and many genera and species are identified by poorly recognizable, fragmentary fossils. Characterizing

[4] In addition to this survey of literature, among it European, there is also the article of E.A. Maleev (1968), published posthumously. – *Editor's note*.

this period of development in vertebrate paleontology, L. S. Davitashvilii (1940, 1948) correctly remarked that each scientist tried to identify as many species as possible. This lead to an excessive number of taxa and complicated the systematics considerably.

Chapter II

SYSTEMATIC DESCRIPTION

SUBORDER THEROPODA

INFRAORDER CARNOSAURIA

FAMILY TYRANNOSAURIDAE OSBORN, 1906 (= DEINODONTIDAE COPE, 1866)

Diagnosis. Carnivorous dinosaurs of gigantic size and massive proportions. Skull large with long, high jaws. Three antorbital fenestrae. Orbits rounded or bean-shaped. No mobility between frontal and parietal. Quadrate highly elongated ventrally and firmly united with the quadratojugal. Teeth large, saber-shaped, slightly recurved, and serrated on the edges. Premaxillary teeth smaller than those following. Neck short, wide; cervical vertebrae short, opisthocoelous. Abdominal [ventral] ribs well developed. Forelimbs are highly reduced. Manus bears two digits (I and II). Metacarpal Mc_1 very short and wide; Mc_2 longer, Mc_3 rudimentary. Manual phalanges very short; ungual phalanges highly curved and compressed. Pelvic bones firmly connected; ilium high, elongated; ischium moderately flattened distally but not widened; pubis long, with a large distal symphysis. Hind limbs long, massive. Femur approximately as long as the large tibia. Astragalus massive with an ascending process. Metatarsals uniformly elongate. Middle metatarsal Mt_3 sharply narrowed proximally and tightly compressed between the two adjacent bones. Pedal phalanges massive, robust; unguals moderately curved but not compressed.

Family composition. The following genera are assigned to the family Tyrannosauridae: *Aublysodon* (= *Gorgosaurus*), *Tarbosaurus*, *Tyrannosaurus*, and probably *Prodeinodon*, *Alectrosaurus*, and also *Genyodectes*.

Geographical distribution. Asia and North America.

Geological age. Late Cretaceous.

{139} **Genus *Tarbosaurus* Maleev, 1955**

Tarbosaurus: Maleev, 1955 – *Doklady Academy of Science USSR* 104, No. 5, p. 780.

Genus type – *Tarbosaurus efremovi* Maleev, 1955[5].

Diagnosis. Size up to 10-12 meters in length. Skull lower but longer than that of *Tyrannosaurus*. Lacrimal bony projections poorly developed or absent. Teeth laterally compressed, elongate-oval in cross-section, with anteroposterior diameter greater than transverse diameter; each tooth is differentiated by the more or less labial position of the serrated edges and the size of the crown. Premaxilla bearing four teeth, maxilla 12-13, dentary 15; crown of largest tooth reaches 112 mm in height. First maxillary tooth considerably larger than premaxillary teeth. Length ratio of humerus to scapula and of ulna to humerus is 1:3. Femur massive, long, with a well-developed head. Length ratio of femur to humerus is 4:1. Tibia massive, robust. Length ratio of femur to tibia is 1:1. Tail consists of no fewer than 35-45 caudal vertebrae.

Comparison. In terms of absolute size, *Tarbosaurus* is smaller than *Tyrannosaurus*; the skull of the former is less massive and more elongate, and the teeth are more laterally compressed. The Mongolian form differs from *Aublysodon* (= *Gorgosaurus*) by its larger skull, the absence of lacrimal bony projections, bean-shaped orbits, and greater forelimb reduction. All these features suggest that this is an independent genus in the family Tyrannosauridae (= Deinodontidae).

Composition of species. The genus *Tarbosaurus* contains presently only one species – *T. efremovi* Maleev, 1955[5].

Geographical distribution. Central Asia.

Location. Mongolia National Republic, Nemegt, 350 km west-southwest of the Aimak [provincial] center of Dalan-Dzadagad.

Geological age. Late Cretaceous.

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[5] If one accepts the synonyms of A. K. Rozhdestvenskiy (1965), then the holotype would be skull No. 551-1, depicted and described by E. A. Maleev (1955a) as *Tyrannosaurus bataar* (in this case Figs. 48-51, Plate I, Fig. 1); all the remaining specimens (in this case Figs. 1-47, 52-66, Plate II, Figs. 1-2) would become paratypes. – *Editor's note*.

Tarbosaurus efremovi Maleev, 1955[5]

Tarbosaurus efremovi: Maleev, 1955. – *Doklady Academy of Sciences USSR* 104, No. 5, p. 780.

S p e c i e s t y p e . Skull and postcranial skeleton. No. 551-2, collection of PIN AN SSSR [Paleontological Institute, Academy of Sciences, USSR].

D i a g n o s i s . See diagnosis for the genus *Tarbosaurus*.

DESCRIPTION

Skull and lower jaw (Figs. 1-20, Plate II, Fig. 1)

E x t e r n a l m o r p h o l o g y

The skull is massive, high, and triangular in outline. The lateral sides of the skull are directed toward each other in such a manner that the bottom is wider than the top. In lateral view, the skull appears quite light but strong, with several openings on each side. The posterior part is high dorsoventrally and moderately widened in the orbital region. The facial part is considerably elongated and slightly narrowed toward the rounded end of the snout.

{140} The orbit is large, with a bean-shaped outline. The upper margin of the orbit is formed by the lacrimal, prefrontal and postorbital, its anterior margin by the lacrimal, ventrally it is bordered by the jugal, and posteriorly by the postorbital. The first antorbital fenestra (ant_1) is the largest opening in the skull. Its upper margin is formed by the lacrimal and maxilla, its anterior margin by the maxilla, ventrally by the maxilla and jugal, posteriorly by the lacrimal. The second antorbital fenestra (ant_2) is pentagonal in shape, much smaller, and lies completely in the posterior part of the maxilla. The third antorbital fenestra (ant_3) is very small and oval-shaped. Anteriorly it is delimited by the premaxilla, posteriorly by the maxilla.

The external nares are located near the edge of the face, and are elongate-oval in outline. Anteriorly they are delimited by the premaxillae, posteriorly by the nasals. The maxilla does not participate in the formation of the nares.

The jugal foramen (f. j.) is located in the anterior part of the jugal, directly below its articulation with the lacrimal, and is oval shaped.

The lateral temporal fenestra (l. f.) has an irregular shape, and is elongated dorsally. Dorsally it is delimited by the postorbital and squamosal, anteriorly by the descending process of the postorbital and the ascending process of the jugal, ventrally by the jugal and quadratojugal, and posteriorly by the quadratojugal and squamosal.

The upper temporal fenestra is large and elongated anteroposteriorly. Anteriorly it is delimited by the parietal, postfrontal and postorbital, laterally by the postorbital and squamosal, posteriorly by the squamosal, and internally by the parietal and squamosal.

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Dermal bones of the dorsal and lateral sides of the skull

Premaxillae (Figs. 1, 2) – short right-triangular bones with long, thin processes that proceed from the dorsal edge of the premaxillae and extend dorsally and posteriorly to meet the nasal processes and form the outline of the external nares. Each premaxilla bears four teeth. The premaxillary teeth are smaller in size than the maxillary teeth. The body of the bone is slightly curved along the long axis up to the articulation with the opposite premaxilla. The contact surface bears shallow pits and protuberances that firmly connect the two premaxillae. Internally, directly below the naris, there is a deep, elongated furrow to accommodate the thin anterior process of the maxilla. The external surface of the bone is slightly concave in dorsal view, but in the middle it is convex, roughened, and bears numerous foramina and traces of blood vessels that nourished the bone and teeth.

Nasals – (Figs. 1, 3) – long, massive, fused along the center into a single element. The separation of the bones is visible anteriorly for a short distance in the shape of a longitudinal narrow slit. In the anterior part the nasals are widened and thickened, but posteriorly they are narrower and more dorsoventrally compressed. The dorsal surface is convex and roughened for two-thirds of its length, while the posterior third is flat and smooth. Along the whole length of the bone, small and {142} shallow openings for blood vessels are present. The ventral surface is smooth, deeply concave transversely.

Anteriorly, each nasal is divided by deep groove into two processes: the massive, V-shaped upper process, which meets with the rising process of the premaxilla above the external naris; and a weaker descending process along the upper surface of the anterior edge of the maxilla, where by meetings with the premaxilla it excludes the maxilla from participation in bordering the external naris. The nasals articulate with the frontals by a narrow, triangular suture. Laterally the nasal bones are articulated with the maxilla, lacrimal and prefrontal by well-defined sutures.

M a x i l l a e (Figs. 1, 4) – the largest bones in the skull, triangular in outline, with a bluntly sharpened anterior end, bear 12-13 teeth. The height of the maxilla gradually increases posteriorly. Dorsally and posteriorly it extends into a large, narrowing process that meets the nasal. and lacrimal. Together with the premaxilla, the maxilla limits a very small, oval-shaped third antorbital fenestra (ant3) anteriorly. At the base of the palatal process, the bone is slightly concave and perforated by the second antorbital fenestra (ant2). The posterior end of the maxilla is deeply notched, bordering the first antorbital fenestra (ant1) anteriorly and ventrally. The ventral process of the maxilla is long, V-shaped, and elongated posteriorly, with its narrowing end reaching the center of the orbit vertically and meeting the anterior end of the jugal by an oblique suture. The ventral edge of the maxilla is convex in profile, rising slightly toward the anterior end of the face. Below the alveolar edge of the maxillae protrude interdental or alveolar plates, with a rough lingual surfaces.

{143} A massive palatal process protrudes in a horizontal direction on the interior side of the bone almost along its whole length. The anterior end of this process is prominently pointed, elongated anteriorly, and bears a deep longitudinal groove and ridge for articulation with the opposite maxilla. The posterior end of the palatine process of the maxilla bears a row of pits and tubercles, marking the location of its connection with the palatine and vomer. The ventral surface of the palatal process is smooth and has a row of transverse indentations only near the alveolar edge, perforated by foramina for blood vessels and nerves.

Above the palatal process, the surface of the maxilla is highly marked by numerous depressions and cavities, separated from each other by bony protuberances, externally resembling the olfactory region of the mammalian skull. In life these cavities may have served as a chambers for a Jacobson’s organ.

J u g a l s (Figs. 1, 5) – thin, triradiate, elongated anteroposteriorly. The anterior end of the jugal is widened dorsoventrally and connected by a deep suture with the posterior process of the maxilla. On the dorsal edge of this section of the bone, there is a notch for articulation with the lower branch of the lacrimal. Below the articulation with the lacrimal, the jugal is perforated by a large, oval jugal foramen. The upper process of the jugal is strongly pointed at the end and articulates with the descending process of the postorbital, forming a wide band that separates the orbit from the lateral temporal fenestra. The posterior process has a deep notch for receiving the finger-like process of the quadratojugal.

The external surface of the jugal is slightly convex, smooth, and is rough and bears a series of foramina on its ventral edge; the internal surface is concave longitudinally and smooth. The jugal limits the orbit and a small part of the first antorbital fenestra ventrally.

L a c r i m a l s (Figs. 1, 6) – V-shaped, forming the posterodorsal edge of the first antorbital fenestra (ant_1) and the anterior edge of the orbit. The upper process of the lacrimal narrows slightly anteriorly and articulates by broad suture with the upper process of the maxilla and nasal, and posteriorly with the prefrontal and postorbital. The lower process is widened ventrally and articulates with the jugal. The external surface of the upper branch of the lacrimal is very rough and bears a large, semilunate foramen, directed posteriorly.

{144} P r e f r o n t a l s – small, has a triangular outline[6], occupies a narrow area in the skull roof between the frontal, lacrimal, nasal and postorbital. It was impossible to examine the detailed morphological characteristics of the prefrontal due to the absence of individual bones.

F r o n t a l s (Fig. 12) are relatively short and wide, occupy a central region of the roof of the brain cavity, and are firmly connected by a deep suture to each other and to the surrounding elements. Anteriorly the frontals are connected to the prefrontals and nasals, laterally with the lacrimals and postorbitals, and posteriorly with the parietals. The median suture between the frontals is easily visible along the anterior one-third of its length; posteriorly the bones are tightly fused and the suture is invisible. On the posterior one-fourth of the bone an external elevation is formed. The lacrimal and postorbital exclude the frontal from participation in the formation of the dorsal margin of the orbit. Above the orbit, the surface of the frontal is concave anteroposteriorly, forming a large part of the anterior border of the upper temporal fenestra. The external surface of the frontal is smooth.

P o s t o r b i t a l s (Figs. 1, 7) – of massive, triradiate construction. The upper process of the postorbital is short, wide, and directed internally. The second, narrower process is directed posteriorly and ventrally, entering into the notch on the external side of the squamosal and forming the upper temporal arch. The third, being the widest and longest process, is

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[6] It is possibile that these may be the posterior processes of the nasals, separated from the basal part by an accidental fissure. – *Editor's note.*

directed ventrally along the upper process of the jugal, and together they form a wide band that separates the orbit from the lateral temporal fenestra. The upper part of the bone is considerably rough.

P a r i e t a l s (Fig. 12) form two crests upon fusing together –sagittal and supraoccipital, the latter rising above the skull roof. The crest is slightly thickened and elongated outward at a right angle from the median {145} axis of the parietals. The surface of the parietal is deeply concave in front of the occipital crest. The median part of the bone is strongly compressed, forming the inner border of the upper temporal fenestra. Posteriorly, the parietals continue to the top of the paroccipital processes, where they enter into the notches of the squamosal and connect with the prootic.

S q u a m o s a l s (Fig. 1) – massive and have a complex outline. The external surface is convex, the internal is concave and cup-shaped. The anterior process is elongated, slightly convex dorsally, and covered externally by the posterior process of the postorbital, which enters into the deep longitudinal notch on the external surface of the squamosal, thus forming the upper temporal arch. The inner process is broad and passes in front of the occipital crest towards the posterior side of the upper temporal fenestra. The lower process is elongated anteriorly and ventrally to contact the upper edge of the quadratojugal. Ventrally there is a deep notch for the articulation with the quadrate.

Q u a d r a t o j u g a l s (Figs. 1, 8) – relatively small with irregular outlines. The external surface is slightly convex transversely in the middle and flattened at the ends; the internal surface is concave anteroposteriorly and bears large, nest-like recesses with sutural edges at the top and bottom. It articulates with the quadrate by a vertical suture along the posterior edge at the top and bottom. The central part of the bone is free and forms the external boundary of the cranio-quadrate passage. The proximal end is moderately widened and externally bears a large, sloping, triangular depression. The upper edge contacts the descending process of the squamosal. The lower process is elongated anteriorly and passes between two spur-like processes of the jugal, forming part of the lower edge of the lateral temporal fenestra.

D e r m a l b o n e s o f t h e v e n t r a l s i d e o f t h e s k u l l a n d t h e p a l a t o q u a d r a t e r e g i o n

P a l a t i n e s – flat, thin, triangular in outline, directed anteriorly with sharp ends. They limit the choanae laterally and posteriorly. The lateral edge is thickened and articulates with the palatal process of the maxilla and jugal by a squamous suture, and medially and posteriorly with pterygoid. The central part of the palatine is perforated by a large, oval foramen. The dorsal side is slightly concave near the lateral edge, the remaining part is flat and bears small rough spots, and the ventral side is smooth with several foramina for vessels.

P t e r y g o i d s (Fig. 9) – long with a complex outline. A thin, narrow process extends forward from the anterior end and turns inward slightly, and is adjacent to the medial edge of the palatine, excluding the contact of the palatines along the midline. The base of the pterygoid is widened and connects to the posterior edge of the palatine by a squamous suture. The thin, wide vertical process is directed posteroexternally, forming a mobile articulation with the basipterygoid process of the basisphenoid, and connecting posteriorly with the plate-like quadrate [pterygoid process]. The small horizontal process is elongated laterally and contacts with the medial branch of the transversum, or ectopterygoid. The opposing pterygoids do not meet along the midline, and the distance between them gradually widens posteriorly.

T r a n s v e r s a , or ectopterygoids (Fig. 10) – massive, short and subtriangular in outline. The lateral branch is bent into a hook and is adjacent to the internal wall of the jugal. A wider medial branch is directed slightly posteroventrally, where it contacts the ventral process of the pterygoid. The dorsal surface is slightly {146} concave and smooth, and the ventral surface is slightly convex and perforated by a large, oval foramen that leads into a huge cavity.

Q u a d r a t e s (Fig. 11) – short and high. The anterior process is directed inward to connect with the ascending process of the pterygoid. Dorsally, the quadrate meets the squamosal, ventrally the lower jaw. The lower end is strongly widened transversely and bears two articular surfaces, or condyles, divided by a wide diagonal furrow that correspond to the articular surfaces of the articular. Externally, the quadrate connects with the quadratojugal. The lateral surface of the quadrate is smooth, slightly concave medially, and bears two large depressions that are divided by a nearly horizontal ridge.

{147} B r a i n c a s e a n d o c c i p i t a l r e g i o n o f t h e s k u l l

The sagittal section of the skull (Fig. 12) shows a large braincase that is elongated anteroposteriorly. The anterior part is narrow, the middle is wide, and the posterior part is high, sharply descending toward the foramen magnum. Inside the cranium, the borders of the different bones and the exit foramina of the cranial nerves are clearly visible. The massive roof of the braincase is formed by the supraoccipital, parietal and frontal. The solid base consists of the laterosphenoid, basisphenoid, and basioccipital.

The solid fusion of many bones in the occipital region of the skull complicates the detailed study of some of the elements. The occipital region is large and wide. The thick occipital crest, formed by the parietals, protrudes sharply from the upper part of the occiput. Its ventral edge continues towards the sides as a pointed process, which rests against the edge of the paroccipitals.

The b a s i o c c i p i t a l (Figs. 12, 13) consists of a massive occipital condyle (condylus occipitalis) and a wide ventral process. The smooth articular surface continues to the lateral and ventral sides of the condyle. The occipital condyle is convexly rounded, protruding sharply posteriorly and sloping slightly ventrally relative to the horizontal axis of the skull. The middle part of the basioccipital borders the round foramen magnum ventrally. The ventral process is elongated ventrally below the occipital condyle, and is connected laterally with the ventral process of the exoccipitals and anteriorly with the basisphenoid. Ventrally the process is slightly concave transversely in the center.

E x o c c i p i t a l s (Figs. 12, 13) are located above and to the side of the basioccipital, and have the appearance of two wing-like plates, fusing laterally with the paroccipital processes. The articulation of the exoccipitals on the midline above the foramen magnum cannot be precisely defined on the existing specimens. Continuing ventromedially, they contact the basioccipital and form the upper part of the lateral surface of the occipital condyle. Dorsally, the exoccipitals articulate in the center with the supraoccipital, parietal and squamosal.

The exit foramina for cranial nerves IX-XI and XII are located on the inner surface of the exoccipital.

S u p r a o c c i p i t a l (Figs. 12, 13) – a relatively small bone, connected to the parietals above and the exoccipitals laterally. The dorsal surface of the supraoccipital has a small notch and a rough surface. This surface continues up to the lateral fossa, where the ligamentum nuchae is attached. The ventral extension of the supraoccipital cannot be determined because the sutures are highly fused, but apparently the supraoccipital is excluded from participation in the upper border of the foramen magnum. A small ridge passes along the middle of the posterior surface, gradually decreasing ventrally.

P a r o c c i p i t a l s , or opisthotics – high and elongated externally, posteriorly and ventrally. Dorsally they contact the parietal and squamosal, medially the exoccipital, ventrally the basisphenoid.

The b a s i s p h e n o i d (Fig. 12) has a subtriangular shape below. The basisphenoid consists of two lateral plates, widened anteroposteriorly, and is adjacent to the basioccipital processes. Posteriorly they connect with the ventral expansion of the paroccipital processes by a suture.

{149} L o w e r J a w

The lower jaw consists of the dentary, splenial, angular, surangular, dental lamina, prearticular, articular, and coronoid. The mandibular rami are relatively high, long, and transversally compressed. The upper edge noticeably descends anteriorly and rises posteriorly in the region of the dentary-surangular articulation. The lower edge is slightly concave for a distance and rises gradually from the anterior end of the angular. There is no complete fusion at the symphysis, and it apparently was held together with the help of cartilage or a ligament.

The d e n t a r y (Figs. 1, 14, 16) is long, high in the posterior part, and transversely compressed. The anterior end is slightly pointed and extends dorsally. The ventral edge is wide and rounded. The posterior end is deeply notched, and articulates dorsally with the surangular and ventrally with the angular so that these bones overlap. The height of the dentary gradually increases posteriorly, reaching a maximum at the articulation with the surangular. Alveoli for 15 teeth are located along the dorsal edge, and the dentition occupies 95% of the total length of the dentary. There are thin alveolar partitions between the alveoli, which are widened lingually and {150} form wrinkled interdental plates, corresponding to similar ones in the upper jaw. A longitudinal furrow for the dental artery passes along the base of these plates. On the lingual side, the dentary is covered by the splenial and the dental lamina. Below the dental lamina, a deep longitudinal groove passes medially along the dentary. The external surface of the dentary is rough, slightly convex transversely, and bears numerous foramina. A row of large foramina passes longitudinally below the tooth row, with one foramen per tooth. These foramina undoubtedly served for the passage of nerves and blood vessels to nourish the teeth.

D e n t a l l a m i n a [Supradentary] (Fig. 16) – thin, saber-shaped, overlaps the interdental plates lingually, and extends for the entire length of the tooth row. The anterior end is pointed, the posterior is curved into the shape of a handle. The external surface is slightly convex anteroposteriorly and bears small fossae that correspond to the interdental plates.

The a n g u l a r (Figs. 1, 17) has a wing-like shape; at top it is partially covered by the surangular, and it extends posterodorsally. A finger-like process protrudes from the anterior edge, inserting between the dentary and the splenial on the lingual side. The posterior end is widened and articulates with surangular by a squamous suture. Below this articulation, the angular limits a small, elongated foramen ventrally. The external surface of the angular is convex, smooth, and the lingual is slightly concave.

S u r a n g u l a r [Supraangular] (Fig. 18) – the second largest element of the mandible, and forming its posterior part. In size it is only slightly smaller than the dentary. It is high in the middle, narrowing slightly toward the ends. Its thin anterior end is thin and articulates with the dentary by a squamous suture; the posterior end is greatly thickened and firmly connected with the articular and prearticular, forming the labial part of the mandibular joint for articulation with the quadrate. Here a short, bent process protrudes inward from the posterior end, giving the surangular its maximal thickness. The suture between the surangular and articular is crookedly curved posteriorly and lingually. The sutural border with the prearticular is clearly visible for a considerable distance ventrally and anteriorly from the articular. The dorsal edge is thick, curving lingually and slightly ventrally. On the anterior end and on the lingual side, the surface for articulation with the edge of the dentary is quite rough. Posteriorly from this articulation, the dorsal edge is perforated by a small foramen, which opens obliquely posterolingually. The mandibular joint is located at the posterior end of the upper edge and is separated from it by a curved, pointed process. The labial surface is convex and slightly rough; the lingual surface is concave and almost smooth. At one-fourth the distance from the posterior end, the bone is deeply concave and perforated by a large, round mandibular foramen. Below this foramen there is a very rough area, elongated anteriorly for articulation with the lingual surface of the angular.

A r t i c u l a r (Fig. 18) – massive and compact, forming the basal part of the mandibular joint. The articular surface is strongly elongated transversely and divided into an anterior, convex part and a posterior, concave section. Externally, the articular is overlapped by the surangular, ventrally and lingually by the prearticular.

P r e a r t i c u l a r (Fig. 18) – narrow, curved, located in front of the articular. Ventrally it articulates with the angular and forms the ventral border of the jaw. At the middle of its length it is strongly curved dorsally, and wedges between the dorsal edge of the splenial and the suture with the surangular with its pointed anterior end. The posterior end is very thick and firmly joins with the articular. The line of contact with the articular is visible only from the medial side.

S p l e n i a l (Fig. 19) – thin, triangular, adjacent to the lingual side of the posterior part of the dentary. The dorsal edge {152} is thin and curved; the ventral is straight, slightly thickened, and rough. The anterior part is perforated by a large, oval foramen.

T e e t h

The upper jaw bears four pre-maxillary and 13 maxillary teeth, and the lower jaw bears 15 teeth.

The premaxillary teeth (Fig. 2) are considerably smaller in size than the subsequent maxillary teeth. The anterior surface of each tooth is strongly convex, and the lateral sides are somewhat compressed and slightly flattened. The anteroposterior diameter is greater than the transverse diameter. The anterior convexity is equal to the posterior concavity. The enamel is thin, forming serrated ridges on all the teeth, which are located on both the labial and lingual surfaces.

The maxillary teeth (Figs. 1, 4, 20) are large, saber-shaped, and different from one another in size and shape; they are located in sequential order from suboval in cross-section to laterally compressed, in which the serrated edges are located on the anterior and posterior edges of the crown. The teeth change shape towards external or labial surface, which changes its direction and shortens, while the lingual surface expands to the point where both the labial and the lingual surfaces become equal. This change is observed from the first to the fourth tooth in the row; the fourth tooth is intermediate, and the fifth resembles the following teeth in the row.

All the teeth are narrower towards the apex, becoming bluntly pointed and slightly curved posteriorly. This curvature is more pronounced in the distal half of the crown. The anterior serrated edge ends midway between the crown and base, whereas the posterior serrations continue to the base. The edges are serrated along their entire length, with two serrations per millimeter. The serrations are transversely compressed, very regularly positioned, with hardly any noticeable change in size between the apex and the base of the tooth. The first through fifth teeth are the largest in the row. A change in size occurs posteriorly, with teeth 12-13 being the smallest. Several teeth were broken during life and slightly worn down in the middle of the lateral surface of the crown. Most of the maxillary teeth are identical in general morphology to those from the lower jaw.

Mandibular teeth (Figs. 1, 14-16). 15 teeth are located on each side of the jaw. The mandibular teeth are somewhat smaller in size than those of the upper jaw, but are equal in shape. {153} The lingual surface is more convex than the labial. The crowns are slightly concave on the lingual surface near the base of the tooth. The first and third teeth of this row are suboval in cross-section. The anterior surface is strongly convex, and the serrated edge is located somewhat obliquely on the labial and lingual surfaces. The third mandibular tooth is intermediate in shape, whereas the fourth is similar to subsequent teeth. Teeth 4-15 are more laterally compressed, lenticular in cross-section, and have serrated edges that are located directly on the anterior and posterior edges of the crown. The size of the teeth in this row decreases posteriorly starting with the 12th tooth, with teeth 14 and 15 being the smallest.

Succession of teeth (Fig. 20). The teeth of carnosaurs were replaced throughout their life. Each new tooth appeared on the lingual side of the root of the old tooth. At this point, the lingual surface of the root was slightly indented and the apex of the new tooth was initially observed. As the new tooth grew, the root of the functional tooth was partially resorbed and the latter was gradually pushed out. The growing tooth gradually moved toward the center of the alveolus, directly below the old tooth. The cut-in tooth was sharp and double edges, i.e. both the anterior and the posterior sides were serrated. During the last stage, the apex of the tooth became recurved slightly posteriorly, and the tooth became similar in shape to a saber.

Table 1

Skull dimensions of *Tarbosaurus efremovi*, PIN No. 551-3
(in mm)

Length of skull from premaxilla to mandibular condyle	– 1130
Length of skull from premaxilla to occipital condyle	– 1085
Maximum length of maxilla	– 670

Maximum height of maxilla	– 290
Length of dental row of maxilla	– 510
Length of lower jaw	– 1090
Maximum length of dentary	– 780
Maximum height of dentary	– 270
Length of dental row of dentary	– 470
Maximum length of surangular	– 520
Maximum height of surangular	– 210

{154} The posterior edge remained sharp, and the anterior became dull, giving the tooth its necessary strength.

An X-ray shows that behind the growing but not yet functioning tooth, there is the germ of another tooth, which could quickly form and become functional. In this manner we find an interrupted succession of teeth among carnivorous dinosaurs. An analogous succession of teeth can be observed in some modern reptiles, for example in *Gavialis gangeticus* of India.

Postcranial skeleton (Figs. 21-50, Table I, Fig. 2)

The most complete postcranial skeletons are those of specimen No. 552-1 from Tsagan-Ula in the Nemegt Basin (only the last caudal vertebrae are missing), and specimen No. 551-2 from Nemegt itself. From other Nemegt Basin collections there are series of cervical, dorsal and caudal vertebrae, as well as pelvic and limb bones.

Vertebral Column

The vertebral column is compact with highly shortened cervical and trunk sectors. The vertebral formula can be expressed in the following way: C – 9; CD – 2; D – 11; L – 1; S – 5; CO – 40-45.

Cervical vertebrae (Figs. 21-22) are high and massive. In the articulated spine they form a compact cervico-dorsal curvature that is convex dorsally.

The atlas (Fig. 21) is extremely compressed anteroposteriorly and, as in all saurischian dinosaurs, consists of four elements: hypocenter [centrum], two neurapophyses [neural arches], and a serrated (odontoid) process which firmly fuses with the centrum of the axis. The hypocenter is nearly rectangular. The anterior surface is cup-shaped for articulation with the occipital condyle of the skull. The middle of the upper surface is deeply concave and slightly sloping on the posterior side to accommodate the odontoid process. The upper edge is recessed and articulated with the proximal end of the neurapophysis. The posterior surface is smooth and nearly vertical. The ventral surface is transversely convex, slightly roughened, and bears small fossae and facets for articulation with the cervical ribs on both sides. The proximal end of the neurapophysis is widened and bears two articular facets. The posterior facet faces posteroventrally and articulates with the protruding apex of the hypocenter [centrum]. The anterior facet faces slightly anteroventrally and participates in the formation of the cup-like recess (part of the articulation) for the occipital condyle. The upper part of the neurapophysis produces two processes: the first is short and curved, directed inward, and forming the circular foramen of the cerebrospinal canal with the process of the opposite side, but apparently did not close along the midline, so that the articulation between them was accomplished by a ligament or cartilage. The second, or upper, process is extended dorsally and slightly laterally, and leans somewhat posteriorly. Wide postzygapophyseal facets for articulation with the axis are found on the medial side of these processes.

A x i s [Epistropheus] (Fig. 22). The centrum of this vertebra is massive and high. The articular surfaces are transversely widened. The dorsal edge of the anterior surface, with which the odontoid process articulated, is straight, and the lower edge is broadly rounded. The ventral surface is concave anteroposteriorly and convex transversely. The lateral sides are slightly compressed and perforated by a small foramen, which opens {155} behind the anterior end of the axis. The neural arch is high, crowned by a strong neural spine, which rises and extends slightly posteriorly. The dorsal edge of the neural spine has a deep notch and is trident-shaped.

The prezygapophyses are more weakly developed than the postzygapophyses. They consist of small projections extending anterolaterally from the neural arch. The articular facets are elongate-oval. Large, triangular fossae are located behind the facets to accommodate the atlantal postzygapophyses. The postzygapophyses are massive and project far posterolaterally, with articular facets directed ventrolaterally. A large, triangular depression is located medially between the facets, extending inside the neural arch and above the neural canal. The neural canal is narrow and rounded, and the vertical diameter is greater than the other diameters. The diapophyses are weakly developed, and descend below the suture line that connects the neural arch with the centrum.

3 r d – 9 t h c e r v i c a l v e r t e b r a e (Fig. 22). Behind the axis there are seven vertebrae, which are quite similar in shape. The centrum is opisthocoelous. The anterior articular surface is convex and slopes slightly ventrally; the posterior is recessed in a cup-like shape, lower than the anterior, and sharply bent back along the lower edge, which has an almost spoon-like shape. The slope of the articular surfaces gradually diminishes anteriorly, and in the last set of vertebrae in this series the surfaces become parallel. The lateral sides are slightly depressed behind the transverse processes. At this point there are small oval fossae that lead to the spinal cavity, which undoubtedly indicate pneumaticity. The neural arch is wide and high. The neural spines are high and spade-shaped, with slightly widened ends. They gradually

decrease in anteroposterior diameter, widen transversely and shorten in height. The anterior and posterior surfaces of the processes are slightly recessed and rough. {156} There is a conical depression with smooth sides at the base of the spine anteriorly, and a blunt tongue-shaped projection is developed on the posterior side, which is elongated posteriorly. These structure served as accessory articulations, in addition to the zygapophyses. They gradually decrease in size posteriorly. The neural canal is low and triangular in outline. The transverse processes are short, closely appressed to the sides of the vertebrae, and along most of its length are fused with the base of the neural arch and the upper part of the centrum. The tubercular articular facets are directed ventrally. Posteriorly, the neural spines become gradually elongated, thickened, and more horizontal. The capitular facets are large, and protrude sharply laterally in the lower part of the vertebrae, near the anterior end of the centrum.

The prezygapophyses and postzygapophyses are huge, widely-spaced processes. The articular surfaces of the prezygapophyses are slightly convex, oval in outline, and directed dorsomedially; the postzygapophyses are directed ventrolaterally. The size of the pre- and postzygapophyses gradually increases in posteriorly.

{157} D o r s a l v e r t e b r a e (Figs. 23, 24A, B) are sharply differentiated from the cervicals in terms of centrum configuration, the shape of articular surfaces of the transverse processes and neural spines, and the position and shape of capitular and tubercular facets. In the articulated spinal column they form the steepest dorso-sacro curvature along the whole length of the spine up to the pelvic bones.

The first dorsal vertebrae (Fig. 23) are amphicoelous or procoelous, the anterior articular surface is strongly concave, and the posterior is flattened and slightly concave dorsoventrally. The height of the centrum surpasses its length, and the largest diameter is vertical. The lateral surface is strongly concave and perforated by oval foramina. The ventral surface is concave anteroposteriorly and bears a sharply expressed keel. The capitular facets are large, oval-elliptical in shape, located in the lower part of the centrum in anterior vertebrae and then gradually shift position to reach the base of the neural arch in the middle vertebrae of the column. The neural arch is high and relatively narrow. The neural canal is small, oval in outline, and its vertical diameter is the largest. The transverse processes are long, gradually narrow toward the top, elongate laterally and dorsally, and slope slightly posteriorly. Ventrally, the processes are reinforced by vertical plates, which pass from the anterior and posterior end of the neural arch. Above the base of the processes, these plates coalesce to form a single supporting flank. As a consequence, deep depressions are formed lateral to the neural arch, and the transverse process takes on a triangular shape. The tubercular facets are located on the top of the transverse processes, protruding dorsoventrally and articulating by laterally- and slightly ventrally-directed surfaces.

The neural spines are wide, gradually narrowing toward the apex, tilt slightly posteriorly, and the transverse diameter is the greatest. The anterior surface is weakly convex and nearly smooth, and the posterior surface is concave and bears a very rough area to facilitate the attachment of ligaments and muscles. The prezygapophyses are the most strongly developed, extending anterodorsally beyond the limits of the anterior end of the centrum. The articular facets are slightly convex, oval-elongated in shape, directed dorsomedially, and the maximal diameter is transverse. The postzygapophyses project very little beyond the end of the centrum. The articular facets are smooth, and directed ventrolaterally.

In successive dorsal vertebrae some changes can be observed in comparison with the previous vertebrae described above. There is a gradual increase in the height and length of the centrum, although length increases less markedly than height. The degree of concavity at the lateral and ventral sides also increases. Because of the strong ventral concavity, the vertebrae become shorter in the ventral part than at the base of the neural arch. The transverse processes change in shape and the angle of slope. They gradually become narrower and take on a horizontal position. This is particularly noticeable on the vertebrae after the 9th. The neural spines increase in height, become narrow transversely, and elongate anteroposteriorly, almost touching one another. The anterior and posterior sides of the neural spines become more curved/concave and undulating. The capitular facets in all the vertebrae behind the 5th are located at the base of the neural arch and protrude strongly laterally.

In the last few presacral (lumbar) vertebra, the transverse process is shortened and stands at almost a right angle to the neural arch. The capitular facet decreases, the tubercular shifts its position forward on the transverse process. The articular surface is directed anteroventrally.

All of the vertebrae in this series have developed accessory articulations (zygantrum and zygosphene), but they are more weakly expressed than in the cervical vertebrae.

S a c r a l v e r t e b r a e (Fig. 25). The sacrum consists of five vertebrae, which are firmly fused together and are partially covered {159} by the ilia. The first vertebra is located opposite the contact point of the ilium and pubis. The second and third vertebrae are visible through the acetabulum; the fourth is located opposite the junction of the ilium and ischium; the fifth is clearly visible at the end of the postacetabular part of the ilium. The centra of the sacral vertebrae are very similar to those of the last dorsal/presacral, but they are even more compressed laterally and ventrally. The transverse processes are very short, wide, and slightly curved upward. The ventral processes are fused with the thick sacral ribs, and their distal ends firmly fuse with the medial surface of the ilia, creating an immobile connection between the pelvis and spinal column. The neural spines are high, highly elongated anteroposteriorly, and their apices are coarsely roughened and articulated together in the longitudinal vertical plate.

C a u d a l v e r t e b r a e (Figs. 26, 27A, B, 28A, B). The last vertebrae are missing in the series, but we can suppose that the complete tail consisted of 40-45 vertebrae. The first caudal vertebrae are massive, high, and the height of the centrum exceeds its length. The centra are strongly compressed laterally and widened at the ends. The ventral side is concave anteroposteriorly and bears a small groove in the middle. The articular surfaces are amphicoelous; the anterior surfaces are more concave than the posterior, but in the middle of the tail these surfaces become identical. On both ends, there are sloping surfaces for articulation with the chevrons below the articular surface. The transverse processes are wide, short, and extend horizontally from the base of the neural arch, almost at a right angle. In the first two vertebrae they are slightly curved posteriorly and come close to the medial surface of the postacetabular part of the ilium. The neural arch is low and massive. The neural canal is small and circular. The neural spines are high, relatively thin transversely, highly elongated anteroposteriorly, and tilt slightly backwards; the height of the spine is almost equal to the height of the centrum. At the base the spines are strongly recessed anteriorly and posteriorly; in the upper half they are thick and very rough up to the apex of the spine. The prezygapophyses are more developed than the postzygapophyses, widely expanded, and the articular facets face dorsomedially. The postzygapophyses are located at the base of the neural spines, and are considerably higher than the prezygapophyses. Their articular facets are approach slightly, and are directed ventrally and slightly laterally.

More posteriorly, the caudal vertebrae (Fig. 27A, B) gradually decrease in height and increase in length, taking on an elongated cylindrical shape. The neural spines become smaller and shorter, decreasing to the level of the postzygapophyses and becoming even more elongated anteroposteriorly, becoming almost as long as the centrum. The transverse processes are gradually reduced and {160} disappear altogether in the posterior caudal vertebrae. The prezygapophyses are greatly increased in size, reaching almost the length of the centrum. They become less tilted, more laterally compressed, and have a greater vertical diameter. The articular facets are flat and directed medially.

C h e v r o n s (Fig. 29A, B) are located between the caudal vertebrae, starting with the second and continuing up to the 35-37th. In the first vertebrae they are long and V-shaped. The proximal end is divided into two branches, which bear well-developed articular facets for connecting with the centrum. The haemal canal is small and elongated dorsoventrally. The distal end is highly laterally compressed and slightly bent posteriorly.

T a b l e 2

Dimensions of the cervical, dorsal and sacral vertebrae of *Tarbosaurus efremovi*, PIN No. 551-2 (in mm)

Measurements	Vertebrae		
	cervical	dorsal	sacral
	III-VIII	(middle)	I-V
Maximum length of the hypocenter	80	100	170
Maximum height of the hypocenter	110	155	–

A change in chevron morphology occurs in subsequent vertebrae, consisting mainly of the following: chevron length decreases, the distal end becomes highly elongated anteroposteriorly to form a distinctive keel, and the posterior elongation is greater than the anterior at this point. But the anterior and posterior elongations become equal from about the 14-15th vertebrae. The haemal canal is reduced to an inconspicuous foramen. The articular facets approach one another, forming a saddle-like surface. A peculiar relationship between the length of the chevron and the extent of the anteroposterior elongation of the distal end can be observed: the shorter the chevron, the larger the distal end and, conversely, the longer the chevron, the weaker the anteroposterior elongation of the distal end.

Table 3

Dimensions of cervical and dorsal vertebrae of *Tyrannosaurus bataar*, PIN No. 551-1 (in mm)

Measurements	Vertebrae			
	cervical		dorsal	
	III	IV	III	IV
Maximum length of the hypocenter	65	75	80	105
Maximum height of the hypocenter	130	140	155	160
Maximum height with the neural arch	270	295	410	415
Transverse diameter of the hypocenter	150	175	145	160

Ribs

{161} Cervical ribs. The first cervical ribs are short, compact, and triangular in outline. The rib head is short, slightly bent down, compressed laterally, and blunt at the end. Behind the head there is a slight widening, which forms a wide neck that bears a tubercle. This widening gives the rib its maximal width. The capitular and the tubercular articular surfaces are equal in size, flat, and nearly circular in outline. More posteriorly, the ribs gradually increase in size, become more massive, and longer; they are wide at the proximal end, quickly narrowing downward and becoming very thin distally. The capitular part of the rib is more elongated anteriorly than in the first rib. All the ribs have the usual double attachment: the head to the centrum of the vertebra, and the tubercle to the transverse process.

D o r s a l (p e c t o r a l) r i b s (Fig. 30 A, B) are long and thin; they gradually increase in size from the first to the fifth and sixth, and {162} and then quickly decrease to the 11th. The proximal part of the rib is widened and strongly curved, and the distal end is narrow and much less curved. The tubercle is separated from the head by a long, laterally compressed neck. The height of the neck increases from the head to the tubercle. In the first ribs, the neck is concave dorsoventrally, and in the more posterior ones it is nearly straight. The proximal end of the neck is slightly bent forward and upward to articulate with the capitular facet of the vertebra. The articular facet of the head is convex, oval-elongate in shape, and the vertical diameter is the largest. The tubercle expands posterodorsally and extends posteriorly almost to the horizontal, with the anteroposterior diameter being the greatest. The articular facet is slightly convex anteroposteriorly and directed laterally and slightly backwards.

The widened part of the rib below the tubercle is strongly curved anteriorly and is L-shaped in cross-section. The dorsal side is nearly flat, the anterior side is slightly concave due to the broad and elongate tubercle, and the posteroventral side is deeply concave. At the lower end, the widened part the rib becomes nearly rectangular; the dorsal and ventral sides are almost equal, and the posterior side is wider than the anterior. More distally, the rib becomes semicircular in cross-section and narrowly oval near the end.

A b d o m i n a l r i b s (Fig. 31) include a two-sided first (central) rib and one-sided side lateral. The lateral ribs are connected in pairs with each other, like interlaced fingers of two hands, forming a strong abdominal armor, similar in its construction to the armor of the tuatara *Sphenodon punctatus*. The armor extended from the posterior edge of the sternum to the distal end of the pubis. The maximum width of the armor was apparently located somewhat anterior to its mid-length, and the anterior end was wider than the posterior. Each rib consists of two parts: the widened, relatively flattened base which bears the head, and a short, weak rod-shaped second part. The head is oval, rough, and bent slightly posteroventrally. At mid-length the rib is rectangular {163} in cross-section; the distal end is narrow and bears a longitudinal groove to accommodate of the rod-shaped part, which connects the abdominal rib with the corresponding dorsal (pectoral) rib.

The articulation of the abdominal ribs with each other at the midline of the armor was formed by interlacing between pairs. On each rib there are two rough surfaces for articulation: one on the upper side of the anterior edge, the other on the lower side near the posterior edge. These structures are irregularly oval, separated by small gaps into two to three parts of unequal size. The presence of such surfaces apparently indicates mobility between ribs. The ribs increase in length from the first to the seventh and then gradually shorten posteriorly.

S t e r n u m . Only small fragments are preserved, which do not provide a full idea of its shape and dimensions.

Shoulder girdle

S c a p u l a (Fig. 32) – long and narrow, widened at both ends, consists of an elongated blade and a short anterior part. The posterior region is strongly curved inward, so that the blade lies on the dorsal surface of the first four dorsal ribs, following their curvature. The blade is almost straight laterally, slightly curved anteriorly, and convex transversely on top. Its anterior part has an oval cross-section, which narrows anteriorly, and is slightly flattened on the inner side. The anterior part of the scapula is widened and highly elongated along the entire contact with the coracoid. The ventral edge of this part is thickened and forms a large part of the glenoid fossa. The contact with the coracoid is marked by a well-defined suture. The lateral and medial surfaces of the scapula are nearly smooth. There is an inconspicuous roughness, present as a longitudinal band along entire posterior part of the blade on the outside.

The glenoid fossa (Fig. 32) is slightly concave and extends parallel to the longitudinal axis of the scapula. The external edge is slightly rounded and protruding.

C o r a c o i d (Fig. 32) – a relatively large, thin bone, subrectangular in shape. The lower anterior and lower posterior angles are rounded. The proximal end is firmly connected to the scapula, forming the lower half of the glenoid fossa. The anterior edge of the coracoid is thin and suggests the presence of a very large cartilaginous part, which connected to the sternum. The posterior edge below the glenoid fossa is thick, curved in an arch, and ovally rounded. The coracoid foramen (foramen coracoideum) is small, rounded, and located a small distance from the glenoid fossa. The external surface of the coracoid is slightly convex, whereas the inner surface is concave anteroposteriorly.

Table 4

Dimensions of the bones of the shoulder region of *Tarbosaurus efremovi*, PIN No. 552-1 (in mm)

S c a p u l a	
Length up to posterior edge of the glenoid cavity	750
Width of the proximal end	215
Thickness of the proximal end	42
Width of the distal end	95
Thickness of the distal end	9
C o r a c o i d	
Width of the proximal end	215
Thickness of the proximal end	42
Width of the distal end	190

Thickness of the distal end	10
G l e n o i d	
Total length (from the upper scapular edge to the lower coracoid)	60
Width in the horizontal direction	45
Depth	17

{164} F o r e l i m b s

The structure of the forelimbs is very interesting, representing one of the most striking characteristics of carnivorous dinosaurs. These limbs are so short that some scientists doubted at first that they belonged to the giant carnosaurs until complete skeletons were discovered. The marked reduction of the forelimbs is also characteristic for the representatives of the genus *Tarbosaurus*.

H u m e r u s (Figs. 33A, B). It is very short, semi-cylindrical, and hollow, slightly curved outwards and slightly tilted anteromedially at the distal end. Its length reaches only one-fourth that of the femur (Figs. 40A, B). Its proximal end is wide and bears a well-developed head of nearly elliptical shape; the maximal diameter is transverse. The articular surface is convex, more elongated posteriorly than anteriorly. Below the head, there is a rough tubercular area on the posterior surface which apparently served as an attachment site for M. latissimus dorsi, M. scapulohumeralis and M. subscapulocoracoideus – muscles that straightened and elevated the humerus. The roughness is considerably less on the medial or anterior surface of the humerus, where apparently M. coracobrachialis, M. supracoracoideus and M. pectoralis were attached. A delta-shaped or radial crest rises a little above the middle of the bone on the anterior edge, curving slightly medially. The dorsal surface of the crest is very rough, and apparently served as the attachment site for M. deltoideus and M. humeroradialis. Below the crest the shaft is compressed, the cross-section is elliptical, and the anteroposterior diameter is the greatest. The distal cross-section becomes semicircular and farther down again takes on an elliptical shape; the largest diameter is transverse. The distal end is less wide transversely; the external surface is convex, the inner slightly concave transversely. A small radial condyle protrudes from the preaxial edge, and a larger, more convex ulnar condyle extends from the postaxial edge. The surface of the bone is flattened between the condyles and is slightly concave. The articular surface of the condyles is turned slightly inward and only insignificantly passes on the external surface. On the distal end of the humerus it is not possible to discern distinct {165} areas for muscle attachments, as this entire surface is nearly smooth. An rough area with inconspicuous relief is present in condylar area, where the extensors of the antebrachium were apparently attached.

The shape of the glenoid fossa of the scapulocoracoid and the outline of the humeral head indicate that, in the articulated forelimb, the humerus was directed with its medial surface anteromedially, and with the lateral surface directed posterolaterally.

The longitudinal axis of the humerus formed a wide angle with the long axis of the scapula, and in general was inclined toward the sagittal plane of the body. Because the articular surface of the condyles – radial and ulnar – are directed slightly inward, consequently the general orientation of the forelimbs was also turned inward.

R a d i u s (Fig. 34). It is short with widened ends, the proximal larger than the distal. Its length is considerably less than half the length of the humerus. The anterior surface is slightly concave and somewhat slanted towards the ulna. The ulnar surface is flat transversely and rough at the point of contact with the ulna. The proximal part of the bone has an oval cross-section, the middle is subangular-subrounded, and the distal part nearly rounded. The proximal articular surface is concave, oval-elongated in shape, and the transverse diameter is the largest. The distal articular surface is flat, rounded, and has a small depression for the radiale. Above the joint, the anterior surface is slightly indented and rough, the roughness serving for attachment of ligaments and musculature.

U l n a (Fig. 34). It is short, thick, widened and proximally thickened. It is slightly longer than the radius, but considerably shorter than the humerus. The ratio of humeral to ulnar length is 2.25:1. The external surface of the bone is convex and slightly rough in the proximal part . The middle part is compressed and slightly twisted along the axis. The proximal end has a subtriangular outline, is directed laterally toward the radius, and bears a shallow incisura radialis which weakly grasps the upper end of the radius. The olecranon process is weakly developed and protrudes slightly above the articular surface. {166} The articular surface for the humerus is transversely narrow and curved anteroposteriorly. The articular surface for connection with the intermedium and ulnare is flat and narrow anteroposteriorly.

C a r p u s (Fig. 35). Of all the carpus bones only the intermedium is well preserved; the others are fragmentary and can only be judged by their position relative to the adjacent bones of the manus.

M e t a c a r p u s (Fig. 36) It consists of three metacarpal bones (Mc). Mc1 is a short, massive bone, slightly tilted inward and closely adjacent to Mc2 in the proximal part. The proximal end is triangular, and the largest diameter is transverse. The articular surface for the intermedium and radiale is flat and slightly curved ventrally. The distal end is narrower than the proximal. The articular surface for the first phalanx of the finger is saddle-shaped, with a deep furrow that divides it into two unequal facets. The external facet is considerably larger than the internal. The articular surface of the facet is widened upward, with equal elevations anteriorly and posteriorly. Ligament fossae are located on the lateral sides of the distal end, with the external outlined much better than the internal. The dorsal surface is flattened transversely and smooth, whereas the palmar surface is slightly concave and rough for ligament attachment. Mc2 is twice as long as Mc1. The proximal end is rectangular, widened transversely, and tilted inward. There is a wide notch for contact with Mc1 on the lateral side. The articular surface for the ulnare and intermedium is rough and concave anteroposteriorly. The distal articular surface is composed of two equal facets divided by a wide groove. The ligament fossae are deeper than on Mc1. The dorsal surface is flattened and tilted slightly externally. Markedly deep grooves are present in the proximal part for the attachment of ligaments, and there is a deep triangular fossa in the distal part. The palmar surface is flattened and slightly rough. Mc3 is a short, thin bone, slightly curved inward and pointed at the distal end.

P h a l a n g e s (Figs. 36, 37A, B, C.). Phalangeal formula: I-2, II-3; the phalanges of the third digit are fully reduced.

First-order phalanges. The basal phalanx of digit I is long, laterally compressed along the axis, and widened on the ends. The proximal {167} surface for articulation with the metacarpus is deeply concave dorsoventrally and divided by a small keel into two unequal facets. The external facet is considerably larger than the inner. The proximal end is more strongly widened than the distal. The surface for the ungual phalanx extends more ventrally than dorsally, is divided by a notch in the middle, and is saddle-shaped. The ligament fossae are deep and oval. The dorsal surface is transversely convex and evenly rounded on both sides; the palmar surface is flat and slightly rough. A wide fossa for muscle attachment is observed on the distal part of this surface.

The first phalanx of digit II is short and wide. It is considerably smaller than the second phalanx of this digit. The proximal end is thickened and widened ventrally. The articular surface is deeply concave dorsoventrally and is divided by a low keel into two equal facets. The ligament fossae are considerably less well-developed and lower in relief than in the basal phalanx of digit I. The distal articular surface is saddle-shaped, the facets are more developed ventrally than dorsally, the surface is convex transversely, and tilted more towards the outside than the inside. A deep, triangular fossa for ligament attachment is observed at the distal end. The palmar surface is flat and slightly concave dorsoventrally.

Second-order phalanges. The second phalanx of digit II is longer than the preceding one. The proximal end is strongly widened anteroposteriorly and bears a smooth, deeply concave articular surface. The ligament fossae are well-developed and pronounced on the distal end. The dorsal surface is transversely convex and sharply rounded laterally. The palmar surface is concave in the proximal part, and flat and rough in the distal part. {168}

T a b l e 5

Dimensions of bones of the front limbs of *Tarbosaurus efremovi*, PIN No. 552-1 (in mm)

Measurements	humerus	radius	ulna	Mc_1	Mc_2	phalanges		
						I ph_1	II ph_1	III ph_2
full length	255	110	115	38	60	65	35	55
transverse diameter of proximal end	70	19	45	20	35	20	25	15
transverse diameter of the distal end	55	23	29	15	25	15	22	17
maximal diameter in the middle of the bone	47	19	22	16	19	14	17	13

Ungual phalanges (Fig. 37A, B, C) are of medium size, strongly laterally compressed, steeply curved and pointed at the end. Along the lateral sides, deep longitudinal grooves are developed anteroposteriorly, which at the proximal end curve downward and pass on the ventral surface. The articular surface is oval-elongate and deeply curved dorsoventrally. On the palmar surface a rough tubercle for the attachment of M. flexor profundus stands out clearly.

P e l v i c g i r d l e

The pelvis is the largest element in the skeleton. The ilia, pubes, and ischia are well-developed and firmly articulated with each other by means of sutures, forming a powerful midline structure to support the entire body.

I l i u m (Fig. 38). The ilium is high, long, strongly arched transversely, and elongated more posteriorly than anteriorly from the acetabulum. The bone is thin along its entire length with the exception of the acetabular region, where it is massive and thick. The preacetabular part is higher than the postacetabular. The greatest height is reached in the anterior part due to the ventral development of the lower end into a nearly hook-like shape. The postacetabular part is more massive, with its ventral edge thickened and is curved obliquely dorsomedially. The dorsal edge has an irregular outline – wavy and slightly rounded beyond the middle of the bone. The bone as a whole is tilted medially, and the opposing dorsal margins approach one another above the sacral neural spines (Fig. 30).

The pubic peduncle is massive, wide, sharply expanded ventrally, and forms a wide, rough articular surface. The posterior edge of the peduncle is concave and limits the acetabulum anteriorly. The ischial peduncle is somewhat weaker than the pubic peduncle, forming a narrower contact surface with the ischium. The anterior surface of the peduncle is slightly concave dorsoventrally and limits the acetabulum posteriorly.

The acetabulum is large, deep, and generally rounded. The dorsal surface of the acetabulum, formed by the ilium, is concave anteriorly, flattened posteriorly, and tilted outward. The acetabulum is directed slightly posteroexternally.

The external surface of the ilium is very rough and bears numerous grooves, tubercles and fossae for muscle attachment. Rough regions are clearly visible on the ventral surface, indicating the contact between the ilium and the transverse processes of the sacral vertebrae (Fig. 39).

{169} P u b i s (Fig. 38). It is massive and long. The proximal end is widened anteroposteriorly and connects dorsally with the pubic peduncle of the ilium by a straight suture, and posteriorly with the anterior edge of the ischium to form the lower border of the acetabulum. Farther ventrally, the bone is strongly curved laterally, deeply concave anteriorly and correspondingly convex posteriorly, and gradually narrows but then quickly widens distally to acquire a foot-shape at the end. This end is thickened transversely at the anterior end and pointed in a V-shape posteriorly. It is more elongated posteriorly than anteriorly from the longitudinal axis of the bone. The general length of the distal widening is twice the maximum width (anteroposterior diameter) of the proximal part. In its upper half, the bone is oval in cross-section and the anteroposterior diameter is the greatest, whereas in the lower half the shaft thickens and becomes rounded anteriorly, the largest diameter changing from anteroposterior to transverse. In the articulated pelvis, the pubic bones bound a narrow, V-shaped pseudo-cavity laterally (Fig. 39). Ventrally they articulate medially via their tubercular surfaces, the roughness of which diminishes distally on the medial surface and the pubic foot, and the two pubes come very close to each other, forming a huge hammer-like symphyseal "foot" (Fig. 39), which is nearly triangular at the bottom. The widened base of the symphysis is directed anteriorly at a low angle to the horizontal axis of the ilia, but the general direction is parallel to the longitudinal axis. Its external surface is slightly concave dorsoventrally and nearly smooth, whereas the ventral surface {170} is very rough and bears numerous fossae and tubercles, indicating the possibility of a thick cartilaginous "cushion" underneath. Complete fusion of the pubes at the symphysis is not observed, and it apparently occurred via a very strong ligament.

The i s c h i u m (Fig. 38) is not as thick as the pubis. The proximal end is wide, flat, and forms two well-developed processes. The anterior process articulates with the posterior process of the pubis by a straight suture forms part of the lower edge of the acetabulum, while the posterior process contacts peduncle of the ilium. This contact surface is deeply concave and very rough. On its posterior edge, below the articulation with the ilium, there is a very clearly defined rough area for muscle attachment. The bone is inclined posteroventrally, and gradually narrows and becomes thin in the lower half, terminating in a narrow, round ends. The distal end bears some roughness, the medial surface of the distal half is flat, and the lateral is convexly rounded. The ends of the ischia approach each other very closely and seem to be almost fused, but there was no actual fusion, and articulation was apparently achieved via a strong, elastic ligament.

Table 6

Dimensions of the pelvic bones of *Tarbosaurus efremovi*, PIN No. 551-2
(in mm)

Ilium	
Maximum length	1080
Length of the preacetabular part from the middle of the dorsal edge of acetabulum	530
Length of the postacetabular part from the middle of the dorsal edge of acetabulum	580
Height from the upper edge of the acetabulum (with restoration	350
Height from the lower edge of the ischial foot	460
Height from the lower edge of the pubic foot	480
External diameter of the acetabulum	220
Ischium	
Maximum length from the middle of the suture with the ilium to the distal end	750
Length of the chord, which limits the acetabulum	90
Vertical length of the contact with the pubis	110
Maximum width of the proximal end	230
Maximum thickness near the distal end	35
Pubis	
Maximum length from the middle of the contact with the ilium to the anterior edge of the distal symphysis	860
Length of the chord, which limits the acetabulum	120
Maximum width in the middle of the bone	75
Maximum thickness (transverse diameter) in the middle of the bone	70
Maximum length of the distal symphysis	590

Hind limbs

The hind limbs are massive, long, and very similar in structure to those of giant running birds. The femur, tibia, and fibula are of almost the same length, but the tarsus is especially elongated. The total length of the hind limbs is four times that of the forelimbs.

{171} Femur (Fig. 40A, 41). This is the longest and thickest limb bone, slightly curved laterally in the anteroposterior direction. The middle part of the shaft is angularly round in cross-section. The head is large, cylindrical, and sits at almost a right angle to the longitudinal axis, with a small deviation anterodorsally. In the pelvic-femoral articulation, the head enters deeply inside the acetabulum (Fig. 39). The articular surface of the head is well rounded and not separated from the greater trochanter by a neck. The greater trochanter is located on the same line as the head, the upper surface of which extends onto the trochanter. The lesser trochanter is very well-developed, located on the anterior edge of the lateral surface, and its free upper end rises up to the level of the greater trochanter, where it is separated sharply by a narrow groove that passes mediolaterally. The external surface of the lesser trochanter is convex, very rough, and rounded posteriorly toward the widely convex posterior surface of the bone; the inner surface is concave and extends smoothly to the anterior surface of the proximal end.

{172} A triangular rough area clearly stands out on the medial surface of the femur, at the level of the upper third – the inner or fourth trochanter.

The anterior surface of the femur is free of any irregularities or crests, but in its distal sector there is a wide, triangular fossa with a sharply expressed longitudinal intercondylar groove (fossa intercondyloidea), for attachment of the tibial extensor muscles. Its distal end is wider transversely than anteroposteriorly, and the condylar part is well developed.

The condyles are expanded ventrally and markedly posteriorly from the longitudinal axis of the bone. The fibular condyle is wider and more ventrally elongated than the inner tibial condyle. On the lateral surface of the former, there is a wide groove for the tendons of the tibial flexor muscles. Above the condyles, the surface is very rough for attachment of the knee ligaments.

T i b i a (Fig. 42). It is a little shorter than the femur; it is slightly twisted along the long axis and weakly curved anterolaterally. The proximal end is wide anteroposteriorly, and the distal end is widened transversely. The shaft is flattened anteroposteriorly and oval in transverse cross-section. The proximal articular surface is very rough, subtriangular in outline, with its apex directed anteriorly, and the posterior part has two tubercles divided by a wide groove. The surface of the tubercles is smooth and projects considerably onto the posterior part of the bone. A huge tibial process – processus tibialis – projects from the medial side, with the apex directed vertically and anteroexternally. The lateral surface is deeply concave transversely and very rough along the contact with the proximal end of the fibula. The medial surface is convex and very rough. The cnemial process – processus cnemialis – is strongly developed and projects as a vertical crest from the external edge of the bone. The anterior surface of the process is flattened, the posterior is curved and very rough. The external edge is curved anteriorly and contacts the fibula. Below the cnemial process, the external surface of the bone is flattened with sharp edges.

On the distal end of the tibia, two well-defined callosities protrude for contact with the astragalus and calcaneum. The external callosity is more convex and more elongated ventrally than the inner one. The anterior side is concave transversely and closely contacts the ascending process of the astragalus; the posterior side is flat and smooth.

F i b u l a (Fig. 43). It is long, narrow, and nearly straight; its is little shorter than the tibia. The proximal end is slightly thickened and widened anteroposteriorly. The upper half of the bone is crescentic in transverse cross-section; it is concave on the medial side and convex on the lateral; at mid-length the cross-section is semicircular – the medial side is flat and the anteroposterior diameter is the largest. The distal end is curved laterally, convex ventrally, semi-oval in cross-section, and narrows posteriorly. The fibula is closely appressed to the tibia along most of its length, having rough contacts with the external tubercle of the proximal end, the cnemial process, the ascending process of the astragalus, and the upper surface of the calcaneum, which extends forward from the edge of the tibia.

T a r s u s . The tarsus consists of five bones: the astragalus and calcaneum, which form the proximal row, and three flat, angular bones in the distal row.

A s t r a g a l u s (Fig. 42). The astragalus is largest bone in comparison with the other tarsals. It has a massive, wide base and a long, thin ascending process that is closely appressed to the anterior surface of the tibia. The base of the astragalus, is convex anteroventrally and slightly laterally compressed. This compression is more noticeable {173} near the fibula than on the medial side, as a result of which the medial convexity is broader and less steep than the lateral. The dorsal surface corresponds to the distal end of the tibia, being deeply concave anteroposteriorly and transversely. The surface opposite the calcaneum is more concave than the free medial surface, which is slightly tilted and flattened. The ascending process is triangular in outline, wide at its base, and narrows rapidly towards the apex, becoming very thin at the top. Its lateral edge is rough and flattened for close contact with the medial edge of the fibula. The anterior surface of the ascending process is slightly bent posteriorly from the base of the astragalus and bears a considerable notch in the middle. Apparently complete fusion between the astragalus and tibia did not occur.

C a l c a n e u m (Fig. 42). The calcaneum is small and laterally compressed. The anteroposterior diameter is greater than the vertical. The dorsal articular surface is slightly widened and deeply concave anteroposteriorly for contact with the distal end of the fibula. Posteriorly, the calcaneum meets the tibia with a surface that continues posteroventrally, with its greatest curvature medially. The medial surface is convex and contacts the astragalus. The ventral and anterior surfaces are convex and their curvature matches that of the astragalus. The lateral surface is smooth, slightly medially concave, and separated from the rounded surface of the anterior end by an elevated edge.

D i s t a l t a r s a l s (Fig. 44A). These are flat, disc-shaped bones, almost all of the same size and located at the same level – on the posterior edge of the dorsal surface of metatarsals II, III, and IV. The posterolateral edge of the tarsals is thick; the anteromedial is thinner.

M e t a t a r s u s (Fig. 43-45). The metatarsus consists of five bones – metatarsals I-V. Metatarsals II, III, and IV are long, massive, and have wide ends; they functioned fully as elements of support. They are closely pressed together along their entire length, except for a short distance where Mt II and Mt IV are curve outward from Mt III, leaving its distal end free.

In general, the metatarsal region is similar in construction to that of birds and saltatory mammals (jerboas, kangaroo).

Metatarsal I is strongly reduced to a short, phalanx-like bone, which is attached to the medial edge of the posterior surface of Mt II, below mid-length (Fig. 44B). Its general orientation {174} is directly posteriorly, at 40-45^{o} to the longitudinal axis of Mt II. In this posterior position Mt I is turned outward from the medial edge of Mt II. The dorsal surface is directed medially, the plantar laterally. The external surface is turned slightly anteriorly, while the inner is directed posteriorly. The plantar surface is wide, smooth, dorsally narrow, and rough. The distal articular surface is trochlear-shaped, divided by a small groove that becomes a wide depression on the plantar surface. The articular surface extends more onto the posterior side and is insignificantly elongated dorsally. Above the articular surface, the anterior and posterior sides are compressed and bear large ligament fossae; the anterior fossa is deeper than the posterior. The upper half of the bone is tilted and turned anteriorly for contact with Mt II. The surface of the contact is flat and rough.

Metatarsal II is a little shorter than Mt III and Mt IV, but is broader and more massive. The proximal end is widened more anteroposteriorly than transversely. Laterally the bone shows some bending – it is concave anteriorly, and the distal condyle is directed slightly posteromedially; in posterior view it is straighter and a low crest projects posteriorly {175} at mid-length. The external surface is wide, flat, and slightly concave on the side facing Mt III; the anterior surface is convex and distally it is slightly tilted externally; the inner surface is wide and deep in the region contacting Mt III; the posterior surface is somewhat rounded and rough. The proximal articular surface has a triangular outline, is flat, and very rough. Below the proximal widening, the becomes rounded in cross-section, but distally it is more oval. The distal articular surface for the first phalanx of the digit II is more expanded than on Mt V, bent slightly inward, and convex in both direction, but more anteroposteriorly. The surface extends more anterodorsally than posterodorsally. Posteriorly, it is divided by a deep groove into two lateral convexities. Deep, rough-surfaced ligament fossae are developed above the articular surface, on the inner and outer sides. The inner fossa facing Mt III is larger than the outer fossa. The surface for contact with Mt I is slightly depressed and rough. The anterior and posterior proximal regions of the bone are very rough. The bone is hollow throughout its length.

Metatarsal III is considerably longer than Mt II and Mt IV; it is elongated more ventrally and anteriorly at its distal end. The bone has a spool-shaped outline dorsally, is highly laterally compressed, and reaches its maximum dimension in the distal half of its length. Proximally it is displaced posteriorly, being compressed between Mt II and Mt IV, and visible only from the posterior (Fig. 44A); ventrally the bone widens considerably and becomes visible in both directions. Here the bone is flattened laterally and closely contacts Mt II and Mt IV by a clearly defined suture; these latter practically cover it posteriorly. The contact surface opposite Mt II is more tilted than that opposite Mt IV. At the point where Mt II and Mt IV deviate outwards, Mt III abruptly widens posteriorly but still retains a smaller diameter than on the anterior surface. The distal end is wider than that of Mt II and the Mt IV; the anteroposterior diameter of the side facing Mt II is greater than that facing Mt IV.

The articular surface for the first phalanx of digit III is slightly flattened transversely and extends more anterodorsally than posterodorsally. There is no clear division of the posterior part of the surface into lateral convexities as is the case with Mt II and Mt IV (Fig. 44C). The ligament fossae are deeper than in Mt II and Mt IV. The fossa located laterally, and the one facing Mt II is larger than the external fossa. Anteriorly, a groove is present above the articular surface, extended across the bone and deepened in its middle part.

Metatarsal IV is slightly longer than Mt II. The proximal end is wider anteroposteriorly than transversely; the anterior surface is convex, slightly laterally compressed, and rounded externally; the external surface is flat and meets the posterior at a sharp angle. The inner side is curved at the top and partially encircles the proximal part of Mt III; farther down, the surface becomes flattened and contacts Mt III for the most part. Below this contact, the bone bends sharply outward – the anterointernal edge extends anteriorly in an undulating manner, and it is noticeably extended into an anterior position at the distal end. Thus from this point of divergence, the anterior surface becomes equally convex {176} from the anterointernal to the posteroexternal edge. Below, the internal surface is longitudinally concave and bears a deep ligament fossa. At the top, the bone is triangular in cross-section, it is square at mid-length, and again resumes a triangular shape with a rounded external side. The posterior surface is curved below the proximal widening; in the middle it is flat and widened inward, reaching the contact with Mt II and fully covering the posterior side of Mt III at this point. On the distal end, there is a deep groove and the bone is slightly compressed. A blunt crest passes curvilinearly upward from the external edge of the articular surface to the inner edge of the middle of the opposite side. The articular surface for the first phalanx of digit IV is less transversely widened than on Mt III and Mt II; it is equally convex anteroposteriorly and transversely, and posteriorly it is divided by a deep groove into two lateral convexities.

Metatarsal V (Fig. 45) is strongly reduced, short, and curved. Its length is considerably less than half that of Mt III. The upper half is widened transversely and slightly convex; the distal half is strongly laterally compressed and passes curvilinearly inward. The curvature of the bone is most conspicuous at mid-length. The anterior surface in the proximal part is tilted gently outwards, tubercular, and closely contacts the rough area on the posterior surface of Mt IV. The internal surface is rounded and nearly smooth; the posterior surface is slightly convex and rough along the edges. The distal end has furrows directed lengthwise.

P e d a l P h a l a n g e s (Figs. 43, 44). Phalangeal formula: I–1, II–3, III–4, IV–5. The first digit is the most highly reduced in comparison with the remaining three. It is not opposed to the other three, but rather is located almost at a right angle to them, and was not used at a supportive element of the foot (Fig. 44B). The end of its ungual phalanx hardly reached below the end of Mt II, and was located a considerable distance above the ground. Three other digits, DII, DIII and DIV, are long and massive, supplied with strong, sharp claws. The third digit is the longest and extends farther forward than DII and DIV; the fourth digit is slightly longer than the second.

The basal phalanges are massive, and are larger proximally than distally. They are compressed at mid-length and curved dorsoventrally at the bottom. All the phalanges of the third digit are bilaterally symmetrical, while in DII and DIV they are higher on the side directed toward DIII, and gently tilted on the opposite side. In the first-order phalanges, the proximal articular surface is slightly curved dorsoventrally, whereas in the second- and third-order phalanges it is more depressed and slightly convex transversely. A vertical crest is developed in the middle of the surface, which passes

T a b l e 7

Dimensions of hind limb bones of *Tarbosaurus efremovi*, PIN No. 551-2 (in mm)

F e m u r	
Maximum length	– 970
Distance from the medial surface of the head to the lateral surface of the greater trochanter	– 210
Anteroposterior diameter of the trunk at mid-length	– 110
Circumference of the trunk at mid-length	– 390
T i b i a	
Maximum length	– 850
Anteroposterior diameter at mid-length	– 100
Transverse diameter at mid-length	– 100
Length, including astragalus	– 880
Maximum transverse diameter of the proximal end	– 170
Maximum anteroposterior diameter of the proximal end	– 370
Transverse diameter of the distal end	– 200
F i b u l a	
Maximum length	– 780
Anteroposterior diameter of the proximal end	– 190
Anteroposterior diameter of the axis in the middle	– 550
Anteroposterior diameter of the distal end	– 550
A s t r a g a l u s	
Maximum height	–
Width at the bottom	– 170
Distance from the anterior surface of the external convexity to the posterior edge	– 95

Distance from the anterior surface of the inner convexity to the posterior edge	– 130
Distance from the anterior surface of the central depression to the posterior edge	– 50

C a l c a n e u m

Maximum length	– 85
Maximum height	– 90
Maximum width at bottom	– 30

M e t a t a r s a l s

Metatarsal I, maximum length (restoration)	– 90?
Width of the distal articular surface of Mt I	– 35
Length of contact surface for Mt Il	– 60
Metatarsal II, maximum length	– 455
Width of the distal articular surface at the mid-length of Mt II	– 75
Metatarsal III, maximum length	– 540
Width of the distal articular surface at the mid-length of Mt III	– 75
Metatarsal IV, maximum length	– 510
Width of the distal articular surface at the mid-length of Mt IV	– 60
Metatarsal V, maximum length (reconstructed)	– 220?
Anteroposterior diameter near the upper end of the Mt IV	– 35
Transverse width near the dorsal end	– 10

P e d a l P h a l a n g e s

DI length	– 105	Ph_1, width	– 20
Ph_1, length	– 75	Ph_2 (ungual), length	– 55
DII (incomplete)		DIV (incomplete)	
Ph_1, length	– 140	Ph_1, length	– 100
Ph_1, width	– 50	Ph_1, width	– 60
DIII length	– 380	Ph_2, length	–
Ph_1, length	– 135	Ph_2, width	–
Ph_1, width	– 60	Ph_3, length	– 60
Ph_2, length	– 100	Ph_3, width	– 55
Ph_2, width	– 50	Ph_4, length	– 45
Ph_3, length	– 80	Ph_4,width	– 45
Ph_3, width	– 45	Ph_5 (ungual), length	–
Ph_4 (ungual), length	– 95		

{183} more dorsally and posteriorly than ventrally. The distal articular surface is saddle-shaped. In the first-order phalanges, this surface is elongated more posterodorsally than posteroventrally. In contrast, the distal articular surface expands more posteroventrally in other phalanges. All the phalanges have well-developed, deep ligament fossae on the distal end. They are equal on the phalanges of the third digit, but unequal on the phalanges of DII and DIV. The ligament fossae on the side directed toward DIII are larger and deeper than those on the opposite side. The dorsal surface of the phalanges is convex transversely and concave at the distal end. The palmar surface is concave, rough, and at the proximal end bears large tubercles at the edges for muscle attachment.

Table 8

Comparative measurements of skull elements of carnosaurs from the Late Cretaceous of Central Asia (in mm)

Nomenclature	*Gorgosaurus novojilovi* PIN No. 552-2	*Gorgosaurus lancinator* PIN No. 553-1	*Tarbosaurus efremovi* PIN No. 551-3	*Tarbosaurus bataar* PIN No. 551-1
Length of skull from premaxilla to mandibular joint	–	970	1130	–
Length of skull from premaxilla to occipital condyle	700	825	1085	1220
Maximum length of maxilla	270	490	670	–
Maximum height of maxilla	–	240	290	–
Length of dental row of maxilla	200	370	510	–
Length of lower jaw	–	830	1090	–
Maximum length of dentary	380	600	780	–
Maximum height of dentary	–	150	270	–
Length of dental row of dentary	210	370	470	–
Maximum length of surangular	–	400	520	–
Maximum height of surangular	–	160	210	–
Number of teeth:				
in the premaxilla	–	4	4	–
in the maxilla	12	12	13	–
in the lower jaw	15	–	15	–

Table 9

Comparative measurements of skulls of North American and Central Asian carnivorous dinosaurs from the Late Cretaceous (in mm)

Nomenclature	North America[1]					Central Asia			
	Gorgosaurus lancensis No. 7541	*G. sternbergi* No. 5664	*G. libratus* No. 2120	*G. libratus* No. 5336	*Tyrannosaurus rex* AMNH	*Gorgosaurus novojilovi* PIN No. 552-2	*G. lancinator* PIN No. 553-1	*Tarbosaurus efremovi* PIN No. 551-3	*Tyrannosaurus bataar* PIN No. 551-1
Length of skull from premaxilla to mandibular condyle	570	678	–	980	1355	–	970	1130	–
Length of skull from premaxilla to occipital condyle	572	–	–	925	1210	700	825	1085	1220
Height of skull from upper occipital crest to mandibular joint	205	–	393	635	–	–	–	–	190
Width of skull along quadratojugal	–	–	–	380	835	–	–	–	–
Length of dental row of upper jaw	300	340	–	495	–	200	370	510	–
Length of lower jaw	570	690	950	999	1205	–	830	1090	–
Height of snout over the last tooth	171	160	–	260	–	–	240	370	–

[8] Measurements after C. W. Gilmore (1946).

Table 10

Comparative measurements of pelvic bones of North American and Central Asian carnivorous dinosaurs from the Late Cretaceous (in mm)

Nomenclature	North America[1]				Central Asia	
	Albertosaurus[2]	*Gorgosaurus*[2]	*Tyrannosaurus*[2]	*Antrodemus*[2]	*Gorgosaurus novojilovi* PIN No. 552-2	*Tarbosaurus efremovi* PIN No. 551-2
Ilium						
External length	980	984	1515	672-720	625	1080
Length of the preacetabular part from middle of acetabulum	505	457	–	–	350	530
Length of postacetabular part from middle of acetabulum	475	527	–	–	275	580
Height of anterior plate	400	438	–	–	190	–
Height of posterior plate	250	216	–	–	140	–
Horizontal diameter of acetabulum	210 (?)	216	590	180-222	120	350 (?)
Height over the middle of acetabulum	300 (?)	393	530	283-335	175	350 (?)
Height over the foot for pubis	420 (?)	457	770	392	250	480 (?)
Ischium						
Maximum length from the middle of suture with ilium to distal end	660	762	1110	–	–	750
Width across foot	210	–	360	–	125	230
Width of distal end	30	43	–	93-135	–	–
Thickness of distal end	18	18	–	–	–	35 (?)
Pubis						
Maximum length	1030	980	1320	680-740	460	860
Length of distal symphysis	600	563	600	370-465	335	590
Thickness of distal symphysis at mid-length	140	106	260	370-465	335	590
Circumference of shaft above distal symphysis	212	–	–	–	130	–

[1] Measurements after W. A. Parks (1928). [2] Species not indicated.

Table 11

Comparative measurements of vertebral columns of North American and Central Asian carnivorous dinosaurs from the Late Cretaceous (in mm)

Nomenclature	North America[1]			Central Asia	
	Gorgosaurus sternbergi No. 5664	*Gorgosaurus libratus* No. 2120	*Tyrannosaurus*	*Gorgosaurus novojilovi* PIN No. 552-2	*Tarbosaurus efremovi* PIN No. 551-2[2]

Length of 9 cervical vertebrae	600	–	960	450	660
Length of 23 presacral vertebrae	1642	–	3144	880?	2160
Length of sacrum	472	690	975	450	700
Length of 24 caudal vertebrae	2450	–	–	1970?	–

[1] According to W. D. Matthew and B. Brown (1923).
[2] – *Editor's Note.*

Table 12

Comparative measurements of forelimb bones of North American and Central Asian carnivorous dinosaurs from Late Cretaceous (in mm)

Nomenclature	North America[1]				Central Asia	
	Albertosaurus[2]	*Gorgosaurus*[2]	*Tyrannosaurus*[2]	*Antrodemus*[2]	*Gorgosaurus novojilovi* PIN No. 552-2	*Tarbosaurus efremovi* PIN No. 552-1
Humerus						
Maximum length	303	324	180?	310	–	255
Transverse width of distal end	40?	55	–	118	30	70
Width along deltoid crest	58	64	–	100	–	55
Anteroposterior diameter of external condyle	65	–	–	–	30	–
Anteroposterior diameter of inner condyle	33	–	–	–	–	–
	23	–	–	–	–	
Ulna						
Maximum length	163	180	–	263	–	115
Maximum diameter of proximal end	53	55	–	90	–	45
Maximum diameter of distal end	37	34	–	55	–	29
Radius						
Maximum length	136	156	–	222	–	110
Maximum width of proximal end	36	37	–	56	–	19
Maximum width of distal end	–	30	–	40	–	23
Metacarpal I, length	40	48	–	73	35	38
Width near proximal end	23	22	–	35	15	20
Width near distal end	25	26	–	36	15	15
Metacarpal II, length	80	98	–	122-125	45	60
Width near proximal end	42	32	–	56-63	15	35
Width near distal end	28	27	–	46	14	25
Phalanges						
D1						
Ph_1, length	85	98	–	136-138	–	65
Width near proximal end	28	30	–	–	–	20
Width near distal end	28	25	–	–	–	15
Ph2 (ungual), length along upper curvature	115	95	–	118-120	–	–
Ph2 height of articular facet	42	36	–	–	–	–
DII						
Ph_1 length	45	57	–	94	45	35

Width of proximal end	30	32	–	–	17	25
Ph_2 length	70	83	–	102	–	55
Width of proximal end	20	30	–	–	–	15
Width near distal end	18	24	–	–	–	17
Ph_3 length along upper curvature	100	–	–	95	–	–
Height of articular facet	32	-	–	–	–	–

[1] Measurements after W. A. Parks (1928). [2] Species not indicated.

{187} The ungual phalanges (Fig. 46A, B, C) are thick, curved downward, and pointed at the end, being subcircular in cross-section. The dorsal and palmar surfaces are widened and convex. The ungual phalanx of DIII is bilaterally symmetrical. The surface of the ungual phalanges of DII and DIV directed toward DIII is flatter than the opposite surface, which is convex away from DIII. Along the sides of the phalanges, deep longitudinal grooves extend from the top to the proximal end. The groove facing DIII is deeper than the opposite one. Both furrows are equal on the ungual phalanx of the third digit. The proximal articular surface is curved transversely and more strongly elongated dorsally and posteriorly. The palmar surface is slightly flattened and very rough in the proximal part. The ungual phalanx of DIII is considerably larger than that of DII and DIV. During life, the horny cover which covered these phalanges formed solid, sharp claws.

Table 13

Comparative measurements of the shoulder girdle of North American and Central Asian carnivorous dinosaurs from the Late Cretaceous (in mm)

Nomenclature	North America[1]				Central Asia	
	Albertosaurus[2]	*Gorgosaurus*[2]	*Tyrannosaurus*[2]	*Antrodemus*[2]	*Gorgosaurus novojilovi* PIN No. 552-2	*Tarbosaurus efremovi* PIN No. 552-1
Joint length of scapula and coracoid	830	1086	–	795	–	–
Length of scapula	740	876	950	652	330	–
Width distal end of scapula	225	175	–	145	40	95
Minimum width	63	56	–	52	25	–
Thickness of scapula at articulation with coracoid	28?	40	–	–	15	42
Width of proximal end	150	–	–	175	60	215
Coracoid						
Maximum length	148	210	–	120	90	–
Maximum height	245	–	–	–	110	–

[1] Measurements after W. A. Parks (1928). [2] Species not indicated.

Table 14

Number of teeth in the jaws of North American and Central Asian carnivorous dinosaurs from the Late Cretaceous

Nomenclature / Skull elements	North America[1]					Central Asia			
	Gorgosaurus lancinator	*G. sternbergi*	*G. libratus*	*Albertosaurus sarcophagus*	*Tyrannosaurus rex*	*Gorgosaurus novojilovi* PIN No. 552-2	*G. lamcinator* PIN No. 553-1	*Tarbosaurus efremovi* PIN No. 551-2[2]	*Tyrannosaurus bataar* PIN No. 551-1
Maxilla	4	15 (?)	13	12	12	12	12	13	13
Premaxilla	4	(?)	4	–	4	4	4	4	4
Dentary	–	–	14	14-15	13-14	15	–	15	15

[1] Measurements after C. W. Gilmore (1946). [2] Specimen No. 551-3 has 12 teeth in the maxilla – *Editor's note*.

Table 15

Comparative measurements of hind limb bones of North American and Central Asian carnivorous dinosaurs from the Late Cretaceous

Nomenclature	North America[1]				Central Asia	
	Albertosaurus	*Gorgosaurus*	*Tyrannosaurus*	*Antrodemus*	*Gorgosaurus novojilovi* PIN No. 552-2	*Tarbosaurus efremovi* PIN No. 551-2
Femur					rt.-lt.	rt.-lt.
Maximum length	1020	1040	1300	645-850	560-560	960-970
Anteroposterior diameter at mid-length	118	136	180	72-95 (?)	55-60	-110
Width through condyles	?	–	340	145-182	120-115	220-
Thickness of external condyle	200	–	–	–	95-105	160-
Circumference at mid-length	350	–	–	–	205-195	-390
Tibia						
Maximum length	980	–	1140	690	585-585	890-850
Length with astragalus	1030 (?)	1000	–	–	605-605	880
Anteroposterior diameter at mid-length	73	–	–	–	45-45	100
Transverse diameter at mid-length	115	–	–	–	60-55	100
Transverse diameter of proximal end	215	–	–	210	85-90	170
Transverse diameter of distal end	265	–	–	185	130-110	200
Fibula						
Maximum length	875	883	1025	623	– 525	780
Width of proximal end	195	180	250	145	– 110	165 –
Diameter of shaft at mid-length	42	47	–	–	25	55
Width of distal end	55	50	130	59	30	55
Astragalus						

Vertical length	250	300	270	115-125		200		–
Maximum width	260	208	300	132-155		125		170
Metatarsals								
Metatarsal II, length	540	508	615	270-320		365	470-455	
Transverse diameter (width) of proximal end	85	–	–	60-67		70	140	
Thickness of proximal end	155	–	–	-		95	135	
Width of distal end	80	77	–	72-76		45	75	
Metatarsal III, length	590	594	600	327-353		420	530-540	
Width of distal end	88	92	140	80-80		50		75
Metatarsal IV, length	558	546	600	275-324		395		510
Width of distal end	65	65	–	57-65		40		60
Metatarsal V, length	225	216	–	–		–		220
Anteroposterior diameter of proximal end	45	41	–	–		–		35
Thickness near proximal end	30	27	–	–		–		10
Thickness near distal end	20	26	–	–		–		15
Phalanges								
D III								
Ph_1, length	200	163	–	110-116		90	135	
Width of proximal end	100	82	–	–		50	95	
Width of distal end	90	–	–	–		45	85	
Ph_2, length	140	122	–	90-94		70	100	
Width of proximal end	90	64	–	–		45	85	
Width of distal end	70	–	–	–		40	75	
Ph_3, length	100	93	–	66-74		55	80	
Width of proximal end	73	54	–	–		40	65	
Width of distal end	58	–	–	–		30	55	
Tibia-femur ratio	0.96	0.93	0.90	–		> 1.00	0.93-0.96	
Fibula-femur ratio	0.85	0.85	0.71	–		0.94	0.80	
Metatarsal III-tibia ratio	0.60	0.60	0.60 (?)	–		0.72	0.59-0.64	
Metatarsal II-tibia ratio	0.55	0.52	0.54	–		0.63	0.53-0.54	
Metatarsal-femur ratio	0.53	0.50	0.47	–		0.75	0.55-0.56	
Ph_2 D III-metatarsal III ratio	0.34	0.27	–	–		0.17		0.19

[1] Measurements after W. A. Parks (1928).

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FIGURE CAPTIONS

Fig. 1. *Tarbosaurus efremovi*. PIN No. 551-3. Lateral view of skull and lower jaw (Maleev, 1955b).

ang – angular;
d – dentary;
ju – jugal;
l – lacrimal;
mx – maxilla;
n – nasal;
pmx – praemaxilla;
po – postorbital;
qj – quadratojugal;
sa – surangular;
sq – squamosal;
ant_1 – first antorbital fenestra;
ant_2 – second antorbital fenestra;
ant_3 – third antorbital fenestra;
jf – jugal foramen;
lf – lateral temporal fossa;
nr – nasal opening;
or – orbit.

Fig. 2. *Tarbosaurus efremovi*. PIN No. 551-3. Anterior view of premaxillae.

md – maxillary teeth;

pd – premaxillary teeth;
nu – upper premaxillary process.
Other designations are the same as in Fig. 1.

Fig. 3. *Tarbosaurus efremovi*. PIN No. 551-3. Dorsal view of nasals.
pu – processes of the nasal for articulation with the premaxilla and maxilla.

Fig. 4. *Tarbosaurus efremovi*. PIN No. 551-3. Lingual view of maxilla.
dm – functioning teeth;
dr – replacement tooth;
jo – maxillary cavity;
nmx – palatal process of the maxilla;
nu – process for articulation with nasal and lacrimal;
oc – openings for blood vessels;
pu – edge for articulation with praemaxilla;
tp – alveolar plates.
Remaining designations are the same as in Fig. 1.

Fig. 5. *Tarbosaurus efremovi*. PIN No. 551-2. Lateral view of left jugal.
cu – posterior edge for articulation with quadratojugal; lu – notch for articulation with lacrimal; mu – edge for articulation with maxilla; on – lower margin of orbit; vp – process for articulation with postorbital.

Fig. 6. *Tarbosaurus efremovi*. PIN No. 551-3. Lateral view of right lacrimal.
j – process for articulation with jugal; mj – process for articulation with maxilla and nasal.

Fig. 7. *Tarbosaurus efremovi*. PIN No. 551-2. Lateral view of left postorbital.
fi – process for articulation with frontal; ij – process for articulation with jugal; is – process for articulation with squamosal.

Fig. 8. *Tarbosaurus efremovi*. PIN No. 551-2. Lateral view of left quadratojugal.
sj – process for articulation with jugal; su – edge for articulation with the process of squamosal.

Fig. 9. *Tarbosaurus efremovi*. PIN No. 551-2. Ventral view of left pterygoid.
bu – process for articulation with basisphenoid;
eu – process for articulation with ectopterygoid;
pp – process for articulation with palatine and vomer;
qu – process for articulation with quadrate;
sn – process for articulation with palatine.

Fig. 10. *Tarbosaurus efremovi*. PIN No. 551-2. Ventral view of right ectopterygoid.
ov – oval opening;
pu – process for articulation with pterygoid;
us – process for articulation with jugal.

Fig. 11. *Tarbosaurus efremovi*. PIN No. 551-2. Medial view of left quadrate.
pu – process for articulation with pterygoid;
sd – condyles for articulation with articular;
su – surface for articulation with squamosal.

Fig. 12. *Tarbosaurus efremovi*. Sagittal section of skull through braincase.
boc – basioccipital; bsp – basisphenoid; exoc – exoccipital; fr – frontal; osp – orbitosphenoid (+ laterosphenoid?); pa – parietal; psp – presphenoid; soc – supraoccipital; on – exit foramen for nerves.

Fig. 13. *Tarbosaurus efremovi*. Occipital region of the skull.
coc – condylus occipitalis; fmo – foramen magnum.
Other designations are the same as in Fig. 12.

Fig. 14. *Tarbosaurus efremovi*. PIN No. 551-2. Medial view of left dentary.
sl – symphyseal region.
Other designations are the same as in Figs. 1 and 4.

Fig. 15. *Tarbosaurus efremovi*. PIN No. 551-3.
A – crown of a functional mandibular tooth;
B – cross-section.

Fig. 16. *Tarbosaurus efremovi*. PIN No. 551-3. Medial view of anterior part of the right lower jaw.
sd – dental lamina [supradentary]. Other designations are the same as in Figs. 1 and 14.

Fig. 17. *Tarbosaurus efremovi*. PIN No. 551-2. Medial view of left angular.
Other designations are the same as in Fig. 1

Fig. 18. *Tarbosaurus efremovi*. PIN No. 551-2. Medial view of posterior part of the left lower jaw.
art – articular; prart – prearticular; fos – surangular foramen. Other designations are the same as in Fig. 1.

Fig. 19. *Tarbosaurus efremovi*. PIN No. 551-2. Medial view of right splenial.
au – process for contact with angular; du – side adjacent to dentary; pu – process for contact with prearticular.

Fig. 20. *Tarbosaurus efremovi*. PIN No. 551-1. Medial view of part of the upper jaw.
Other designations are the same as in Figs. 1 and 4.

Fig. 21. *Tarbosaurus efremovi*. PIN No. 551-2. Anterior view of first cervical vertebra (atlas).
ain – hypocenter; np – neuropophysis.

Fig. 22. *Tarbosaurus efremovi*. PIN No. 551-2. Lateral view of axis and subsequent cervical vertebrae.
ax. in – odontoid process; d – transverse process; p – capitular facets; pz – postzygapophysis; s – neural spine of the axis; z – prezygapophysis.

Fig. 23. *Tarbosaurus efremovi*. PIN No. 551-2. Lateral view of anterior dorsal vertebrae.
Other designations are the same as in Fig. 22.

Fig. 24. *Tarbosaurus efremovi*. PIN No. 551-2. Dorsal vertebra.
A – anterior view;
B – posterior view;
nc – neural canal;
zf – zygosphene;
zg – zygantrum.
Other designations are the same as in Fig. 22.

Fig. 25. *Tarbosaurus efremovi*. PIN No. 551-2. Lateral view of sacral vertebrae (S_1–S_5).

Fig. 26. *Tarbosaurus efremovi*. PIN No. 551-2. Lateral view of caudal vertebra from the middle part of the tail.
Other designations are the same as in Fig. 22.

Fig. 27. *Tarbosaurus efremovi*. PIN No. 553-2. Posterior caudal vertebrae in dorsal view (*A*) and lateral view (*B*).
Other designations are the same as in Fig. 22.

Fig. 28. *Tarbosaurus efremovi*. PIN No. 553-2. Posterior caudal vertebra in anterior view (*A*) and posterior view (*B*).
Other designations are the same as in Fig. 22.

Fig. 29. *Tarbosaurus efremovi*. PIN No. 552-1. Lateral view of chevrons of the anterior (*A*) and posterior (*B*) caudal vertebrae.

Fig. 30. *Tarbosaurus efremovi*. PIN No. 551-2. Anterior (*A*) and middle (*B*) dorsal ribs.
c – head;
t – tubercle.

Fig. 31. *Tarbosaurus efremovi*. PIN No. 552-1. Ventral view of abdominal ribs.
cr – anterior (central rib); cb – lateral ribs.

Fig. 32. *Tarbosaurus efremovi*. PIN No. 551-6. Medial view of left scapulocoracoid.
k – coracoid; s – scapula; cf – coracoid foramen; gv – glenoid fossa.

Fig 33. *Tarbosaurus efremovi*. PIN No. 552-1. Left humerus in external view (*A*) and internal view (*B*).
cr – radial condyle;
cu – ulnar condyle;
dg – deltoid crest;
hc – humeral head.

Fig. 34. *Tarbosaurus efremovi*. PIN No. 552-1. Bones of the antebrachium in articulation.
r – radius;
u – ulna.

Fig. 35. *Tarbosaurus efremovi*. PIN No. 552-1. Left carpus – intermedium.

Fig. 36. *Tarbosaurus efremovi*. PIN No. 552-1. Anterior view of left manus in articulation (Maleev, 1964a).

Fig. 37. *Tarbosaurus efremovi*. PIN No. 552-1. Ungual phalanx of manual digit I in lateral view.
A – overall view;
B – articular surface for preceding phalanx;
C – cross-section in middle part.

Fig. 38. *Tarbosaurus efremovi*. PIN No. 551-2. Lateral view of pelvic girdle (Maleev, 1955a).
il – ilium; is– ischium; p – pubis; s – sacral vertebra; vp – acetabulum.

Fig. 39. *Tarbosaurus efremovi*. PIN No. 551-2. Pelvic and hind limb bones in articulation.
f – femur; dp – transverse process and rib of sacral vertebra; s – centrum of sacral vertebra; sp – pubic symphysis.
Other designations are the same as in Fig. 38.

Fig. 40. *Tarbosaurus efremovi*. PIN No. 551-2. Comparison of femur (*A*) with humerus (*B*) (Maleev 1955c).
gt – greater trochanter; h – femoral head; lt – lesser trochanter; tc – tibial condyle; nc – fibular condyle.

Fig. 41. *Tarbosaurus efremov*. PIN No. 551-2. Posterior view of left femur (Maleev, 1955c).
rt – 4th trochanter. Other designations are the same as in Fig. 40.

Fig. 42. *Tarbosaurus efremovi*. PIN No. 551-2. Anterior view of left tibia and tarsus.
as – astragalus; ca – calcaneum; fb – fibula; t – tibia; cp – cnemial crest; vp – ascending process of astragalus; pt – tibial process.

Fig. 43. *Tarbosaurus efremovi*. PIN No. 552-1. Anterior view of left pes (Maleev, 1964a).
Mt_2–Mt_4 – metatarsals; II–IV – digits.

Fig. 44. *Tarbosaurus efremovi*. PIN No. 552-1. Metatarsals in dorsal view (*A*), posterior view (*B*), ventral view (*C*) and disarticulated (*D*).
Mt_1–Mt_4 – metatarsals; td – distal tarsals.

Fig. 45. *Tarbosaurus efremovi*. PIN No. 552-1. Lateral view of 5th metatarsal (Mt_5).

Fig. 46. *Tarbosaurus efremovi*. PIN No. 552-1. Ungual pedal phalanx.
A – lateral view; *B* – articular surface for preceding phalanx; *C* – cross-section at mid-length.

Fig. 47. Skeleton of *Tarbosaurus efremovi*. Reconstruction (Maleev, 1964a).

Fig. 48. *Tyrannosaurus bataar*. PIN No. 551-1. Lateral view of skull and lower jaw (Maleev, 1955a).
Other designations are the same as in Fig. 1.

Fig. 49. *Tyrannosaurus bataar*. PIN No. 551-1. Functional tooth.
A – lateral view; B – cross-section at mid-length of the crown.

Fig. 50. *Tyrannosaurus bataar*. PIN No. 551-1. Anterior view of posterior cervical vertebra (Maleev, 1955a).
Other designations are the same as in Fig. 22.

Fig. 50. *Tyrannosaurus bataar*. PIN No. 551-1. Lateral view of first two dorsal vertebrae.
Other designations are the same as in Fig. 22.

Fig. 52. *Gorgosaurus lancinator.* PIN No. 553-1. Lateral view of skull and lower jaw (Maleev, 1955b).
Other designations are the same as in Fig. 1.

Fig. 53. *Gorgosaurus lancinator.* PIN No. 553-1. Functional tooth of the lower jaw.

Fig. 54. *Gorgosaurus lancinator.* PIN No. 553-1. Lateral view of dorsal vertebrae.

Fig. 55. *Gorgosaurus novojilovi*. PIN No. 552-2. Lateral view of skull and lower jaw (Maleev, 1955b).
Other designations are the same as in Fig. 1.

Fig. 56. *Gorgosaurus novojilovi*. PIN No. 552-2. Functioning tooth of the lower jaw.
A – lateral view; *B* – cross-section at mid-length of the crown.

Fig. 57. *Gorgosaurus novojilovi*. PIN No. 552-2. Lateral view of third cervical vertebra.
Other designations are the same as in Fig. 22.

Fig. 58. *Gorgosaurus novojilovi*. PIN No. 552-2. Lateral view of first dorsal vertebra.
Other designations are the same as in Fig. 22.

Fig. 59. *Gorgosaurus novojilovi*. PIN No. 552-2. Lateral view of left scapulocoracoid.
Other designations are the same as in Fig. 32.

Fig. 60. *Gorgosaurus novojilovi*. PIN No. 552-2. Anterior view of left femur.
Other designations are the same as in Fig. 40.

Fig. 61. *Gorgosaurus novojilovi*. PIN No. 552-2. Bones of the right lower hind limb.
A – dorsal view; *B* – anterior view. Other designations are the same as in Fig. 42.

Fig. 62. *Gorgosaurus novojilovi*. PIN No. 552-2. Anterior view of right pes (Maleev, 1964a).
Other designations are the same as in Fig. 43.

Fig. 63. *Gorgosaurus novojilovi*. PIN No. 552-2. Mounted skeleton.

PLATE CAPTIONS

P l a t e I

Fig.1. Skull of *Tyrannosaurus bataar*, PIN No. 551-1.

Fig. 2. Skeletons of *Tarbosaurus efremovi*. Left – No. 552-1[7]; right – No. 551-2.

P l a t e I I

Fig. 1. Skull of *Tarbosaurus efremovi*.

Fig. 2. Skull of *Gorgosaurus lancinator*, PIN No. 553-1.

[7] see note page 154.