

Giant theropod dinosaurs from Asia and North America: Skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared

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Hurum, J.H. and Sabath, K. 2003. Giant theropod dinosaurs from Asia and North America: Skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontologica Polonica* 48 (2): 161–190.

The skull of a newly prepared *Tarbosaurus bataar* is described bone by bone and compared with a disarticulated skull of *Tyrannosaurus rex*. Both *Tarbosaurus bataar* and *Tyrannosaurus rex* skulls are deep in lateral view. In dorsal view, the skull of *T. rex* is extremely broad posteriorly but narrows towards the snout; in *Ta. bataar* the skull is narrower (especially in its ventral part: the premaxilla, maxilla, jugal, and the quadrate complex), and the expansion of the posterior half of the skull is less abrupt. The slender snout of *Ta. bataar* is reminiscent of more primitive North American tyrannosaurids. The most obvious difference between *T. rex* and *Ta. bataar* is the doming of the nasal in *Ta. bataar* which is high between the lacrimals and is less attached to the other bones of the skull, than in most tyrannosaurids. This is because of a shift in the handling of the crushing bite in *Ta. bataar*. We propose a paleogeographically based division of the Tyrannosaurinae into the Asiatic forms (*Tarbosaurus* and possibly *Alioramus*) and North American forms (*Daspletosaurus* and *Tyrannosaurus*). The division is supported by differences in anatomy of the two groups: in Asiatic forms the nasal is excluded from the major series of bones participating in deflecting the impact in the upper jaw and the dentary-angular interlocking makes a more rigid lower jaw.

Key words: Dinosauria, Theropoda, Tyrannosauridae, *Tarbosaurus*, *Tyrannosaurus*, skull, anatomy, Mongolia.

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Introduction

The Asiatic members of the tyrannosaurid family have received less attention than those from North America (for a review of Tyrannosauridae see Holtz 2001), even though tyrannosaurid remains are among the most common dinosaur fossils found in the uppermost Cretaceous Nemegt Formation of the Mongolian part of the Gobi Desert. The Mongolian expeditions of the Soviet Academy of Sciences (1946–1949) discovered several tyrannosaurid skeletons in the Nemegt Basin, southern Mongolia (Efremov 1949, 1954). Preliminary descriptions (Maleev 1955a, b, c, 1965, 1974) and later revisions (Rozhdestvenskiy 1965; Barsbold 1983) left doubts as to the number of tyrannosaurid taxa present in the Gobi material, whether or not they belonged to the same as those from North America. Since the 1960s the amount of Asian tyrannosaurid material available for study has grown substantially, but little has been made known. Among the few exceptions is a description of *Alioramus remotus* Kurzanov, 1976 a peculiar, long-snouted tyrannosaurid from Nogoon Tsav. Molnar et al. (1990) reported that at least five skulls and postcrania belonging to about 30 individuals of *Tarbosaurus* are known. This estimate is conservative, and may be tripled (the list of catalogued specimens with skull material attributable to *Tarbosaurus* is provided herein, but it

does not include probable specimens in the Chinese collections nor uncatalogued material in the Mongolian and Japanese collections).

The main object of this study is to discuss the taxonomic status of *Tarbosaurus* based on the cranial morphology of *Tarbosaurus bataar* and to compare it with *Tyrannosaurus rex*. The paper is based mainly on the material collected in the Gobi Desert by the Polish-Mongolian Palaeontological Expeditions (1963–1971), and housed in the Institute of Palaeobiology of the Polish Academy of Sciences in Warsaw. Comparative material from the Geological Institute in Ulaanbaatar, housed in the National Museum in Ulaanbaatar (especially specimens GIN 100/65, 100/70, 107/1 and 107/2) and the types of Mongolian tyrannosaurids housed in the Palaeontological Museum in Moscow have also been studied.

Both the geographical and stratigraphical distributions of the Tyrannosauridae are restricted. Unequivocal remains of tyrannosaurids are known only from the uppermost Cretaceous of North America and Central Asia (Molnar et al. 1990). The large Gondwanan theropods attributed to Tyrannosauridae (South American *Genyodectes serus* Woodward, 1901, Indian *Indosuchus raptorius* Huene and Matley, 1933) are known from very fragmentary remains and probably belong to the Abelisauridae (Molnar, 1990). *Prodeinodon mongoliensis* Osborn, 1924 cannot be placed

within the Tyrannosauridae with certainty because of the poor type material, and other Lower Cretaceous Sino-Mongolian material attributed to this genus by Bohlin (1953) and by Hou et al. (1975; *Prodeinodon kwangshiensis*) is also doubtful. For a discussion on the systematic position of *Siamotyrannus isanensis* Buffetaut, Suteethorn, and Tong, 1996, and *Shanshanosaurus houyanshanensis* Dong, 1977, see Holtz (2001) and Currie and Dong (2001). The finding of an Early Cretaceous alleged tyrannosaurid from England, *Eotyrannus lengi* Hutt, Naish, Martill, Barker, and Newberry, 2001, may further change the basal relationship, of tyrannosaurids, but unfortunately the skull material is very fragmentary and only the nasal will be discussed in this paper.

The first tyrannosaurid fossils recorded from Central Asia consisted of postcranial material from Inner Mongolia, collected in 1920 by the Central Asiatic Expeditions of the American Museum of Natural History. It was described as *Alectrosaurus olseni* by Gilmore (1933). Mader and Bradley (1989) revised the original diagnosis. The remains were assigned in part to tyrannosaurids (the lectotype consists of a pes and two manual unguals, but the attribution of the latter to tyrannosaurids is questionable), and in part to ?therizinosauroids (forelimb elements). The material included also caudal vertebrae of a small unidentifiable theropod. Other early Asiatic finds of fragmentary tyrannosaurid remains include those named *Albertosaurus periculosus* by Riabinin (1930) from Belye Kruchi on the Chinese bank of the Amur (Heilongjiang) River, and those from the Red Beds of the Sichuan Basin, near Jung Hsien (cf. *Tyrannosaurus rex*; Louderback 1935). Young (1958) described *Chingkankousaurus fragilis* based on a large theropod scapula from Wangshi Series, Shandong; although originally described as megalosaurid, it belonged to a tyrannosaurid, because of its slenderness (Molnar et al. 1990). Later more Chinese tyrannosaurids were found in the Redbeds of Yunnan ("*Tyrannosaurus lanpingensis*" tooth, Ye 1975), in the Subashi Formation of the Turpan Basin, Xinjiang (*Tarbosaurus* sp., Dong 1977; *Tyrannosaurus turpanensis*, Zhai, Zheng, and Tong, 1978), as well as in the Quiba Formation of the Tantou Basin, Henan Province and attributed to *Tyrannosaurus luanchuanensis* (Dong 1979; Tong and Wang 1980). A summary of tyrannosaurid distribution from the Chinese Upper Cretaceous has been included in a stratigraphic review of Chinese dinosaurs by Dong (1980, and expanded 1992). Poorly preserved tyrannosaurid remains are known also from Kazakhstan (Nessov 1995). Currie (2000) made a brief review of tyrannosaurids from Mongolia and China.

This present study deals mainly with the Mongolian tyrannosaurids, those assigned by Rozhdestvensky (1965) to the species *Tarbosaurus bataar*, i.e., excluding the primitive *Alioramus* Kurzanov, 1976 and poorly known *Alectrosaurus* Gilmore, 1933. The large Mongolian tyrannosaurids were first described in the 1950s following the discovery by the Soviet Palaeontological Expeditions in late 1940s. Maleev originally distinguished four Gobi tyrannosaurid species. He

first described *Tyrannosaurus bataar* (1955a), followed by *Tarbosaurus efremovi*, *Gorgosaurus lancinator*, and *G. novojilovi* (1955b). In a later review of the Theropoda, Maleev (1964) mentioned *Tarbosaurus efremovi*, an Asiatic *Tyrannosaurus* (meaning obviously *Tyrannosaurus bataar*) and the two species of *Gorgosaurus* he synonymized with *Deinodon* Leidy, 1856, and named them *Deinodon lancinator* and *D. novojilovi*. All the Mongolian tyrannosaurids were later synonymized under the name *Tarbosaurus bataar* by Rozhdestvensky (1965). In Maleev's posthumous work on Mongolian tyrannosaurids (1974), written in 1966 and edited by Rozhdestvensky and Kurzanov, the original multi-species classification is retained in the introduction, but only *Tarbosaurus efremovi* is used throughout the text. The genus *Gorgosaurus* with the North American tyrannosaurids *G. libratus* Lambe, 1916/7 and *G. lancensis* Gilmore, 1946, was regarded as a synonym of *Albertosaurus* by Russell (1970), but see Holtz (2001) and Currie (2003). Russell (1970) also considered *Deinodon* a nomen vanum. Barsbold (1983) agreed with Rozhdestvensky (1965) as to the conspecific nature of all tyrannosaurid taxa erected by Maleev (1955a,b), but accepted *Tarbosaurus efremovi* (used originally by Maleev 1955b, and then in Maleev 1974) rather than *Tarbosaurus bataar*. The priority principle would, however, favour the combination of Rozhdestvensky (1965), consisting of the earliest specific name *bataar* (misspelled Mongolian word "baatar" meaning "hero") applied to this taxon by Maleev (1955a) and the generic name *Tarbosaurus* (meaning "horrible lizard"; Maleev 1955b). The specific name *efremovi* should be regarded as a junior synonym.

Paul (1988) agreed with Rozhdestvensky (1965) that all of Maleev's forms were conspecific and assigned them to *Tyrannosaurus* (*Tyrannosaurus*) *bataar*, thus rejecting their separate generic status. Paul also doubted the correctness of Maleev's reconstruction of the fragmentary skull of "*Gorgosaurus novojilovi*" (PIN 552-2), shown with very elongated antorbital fenestra and snout, despite the fact that the proportions of bones of this region are very similar to those in *Ta. bataar*. Moreover, the postcranial elements are in the opinion of Paul (1988) indistinguishable from those of *Ta. bataar*. Carpenter (1991), on the contrary, choose PIN 552-2 as the holotype of the new tyrannosaurid genus, *Maleevosaurus* Carpenter, 1991. *Maleevosaurus* was defined on characters that are individually and ontogenetically variable and Carr (1999) in his study of ontogenetic changes in North American tyrannosaurines has shown that the holotype is a juvenile. Olshevsky and Ford (1995) recognised *Maleevosaurus novojilovi* and *Tarbosaurus efremovi*, and assigned the species *bataar* to a new genus *Jenghizkhan* Olshevsky and Ford, 1995 in the clade Tarbosaurini. Carr (1999) followed Rozhdestvensky (1965) and assigned *bataar* to the genus *Tyrannosaurus*. A cladistic analysis led Holtz (2001), to regard all the Nemegt tyrannosaurs as representing a growth series of a single species, possibly congeneric with *Tyrannosaurus rex*. Currie (2000) stated that all the Nemegt tyrannosaurids belong to *Tarbosaurus bataar*.

Material

The material of *Ta. bataar* described below comes from the collection of the Institute of Palaeobiology of the Polish Academy of Sciences (ZPAL). It was collected by members of the Polish-Mongolian Palaeontological Expeditions (1963–1971) at several localities in the Gobi Desert, mostly in the outcrops of the Nemegt Formation in the Nemegt Basin. Other relevant material from the area is stored in the Palaeontological Museum of the Palaeontological Institute of the Russian Academy of Sciences in Moscow (PIN), as well as is in the collections of the Palaeontological Centre of the Mongolian Academy of Sciences (GIN), Ulaanbaatar, Mongolia.

The Warsaw collection consists of the following, previously undescribed, specimens of *Tarbosaurus bataar* including cranial elements (dates of collection are also given; for the history of discoveries and details of location of more complete specimens, see Kielan Jaworowska and Dovchin 1968 and Kielan-Jaworowska and Barsbold 1972):

ZPAL MgD-I/3 fairly complete medium size skeleton: skull, cervical and dorsal vertebrae (21 + 6), 10 proximal caudals, complete ilium, pubis and ischium, ribs and gastralia, complete scapulae, coracoids, left forelimb + fragmentary right, complete hind limbs, Tsagaan Khushuu 1964.

ZPAL MgD-I/4 partially excavated large skeleton: left hind limb, ilium, 13 vertebrae (sacrals and proximal caudals); rest of the skeleton left in situ till 1970, Nemegt, Western Sayr 1965.

ZPAL MgD-I/5 incomplete large skeleton: fragmentary skull (left maxilla and left quadrate, left mandible + fragmentary right), fragments of 11 left-side ribs, fragmentary pubis, ischia, fragmentary ilia, left hind limb plus right metatarsal, numerous debris, Altan Uul (Altan Ula III) 1965.

ZPAL MgD-I/26 fragmentary left maxilla with poorly preserved teeth, Nemegt 1965.

ZPAL MgD-I/29 incomplete large skeleton: partial skull with mandible and well-preserved dentition, 6 cervicals, 5 sacrals and 22 caudals, 11 right ribs, ilium, incomplete pubis and proximal ischium, left humerus, distal part of radius and ulna, digit I?, fairly complete right hind limb plus fragmentary left, numerous bone debris, Nemegt 1964.

ZPAL MgD-I/31 proximal right mandible, Tsagaan Khushuu 1964.

ZPAL MgD-I/34 right lateral fragment of skull, Altan Uul (Altan Ula IV) 1964.

ZPAL MgD-I/38 fragmentary large skeleton: incomplete skull without mandible, 12 rib fragments, distal right femur, distal right tibia, right metatarsals III–IV, proximal phalanx of the IV digit, Altan Uul (Altan Ula I) 1964.

ZPAL MgD-I/44 fragmentary right skull bones (maxilla, nasal and lacrimal) plus mandible, Altan Uul (Altan Ula IV).

ZPAL MgD-I/45 fragmentary skull (left maxilla and mandible), Altan Ula IV 1964.

ZPAL MgD-I/46 fragmentary right mandible, 7 skull fragments and 2 broken left ribs, Altan Uul (Altan Ula IV) 1965.

ZPAL MgD-I/52 left mandibular tooth, Nemegt 1965.

ZPAL MgD-I/67 right jugal, Altan Uul (Altan Ula IV) 1964.

ZPAL MgD-I/93 ?cranium endocast, Altan Uul (Altan Ula West) 1965.

ZPAL MgD-I/109 large skull in matrix, Nemegt, NW Sayr 1970.

ZPAL MgD-I/178 fragmentary skull, vertebrae, femur, Nemegt 1970.

The material housed in the State Museum in Ulaanbaatar, Mongolia, includes the following specimens:

GIN 100/60 skull and postcranial skeleton, Bügiin Tsav (Boogiyn Tsav) 1966.

GIN 100/61 fragmentary skull and postcranial skeleton, Bügiin Tsav 1964.

GIN 100/62 fragmentary skull and postcranial skeleton, Bügiin Tsav 1966.

GIN 100/65 right half of the skull, Nemegt 1965.

GIN 100/67 fragmentary skull, braincase, Altan Uul 1970.

GIN 100/69 occiput, Hermin Tsav (Khermiyn Tsav) 1973.

GIN 100/70 fragmentary skull and vertebra (medium size), Bügiin Tsav 1978.

GIN 107/2 complete skeleton, Bügiin Tsav 1984.

GIN 107/3 skull, Bügiin Tsav 1986.

transferred skull of PIN 552-1

The Moscow collection includes the following described specimens (Maleev 1955a, b, 1964, 1974; Rozhdestvenskiy 1965):

PIN 551-1 (holotype of “*Tyrannosaurus bataar*” Maleev, 1955).

PIN 551-2 skeleton (holotype of “*Tarbosaurus efremovi*” Maleev, 1955), Nemegt.

PIN 551-3, 551-4 skeletons (“*Tarbosaurus efremovi*”) from Nemegt.

PIN 551-91 fragment of right maxilla (“*Tarbosaurus efremovi*”).

PIN 552-1 (“*Tarbosaurus efremovi*”) cast (original transferred to the National Museum in Ulaanbaatar; Maleev 1974).

PIN 552-2 partial skull and postcranium (?*Gorgosaurus novojilovi*? holotype), Tsagaan Khushuu (Tsagan-Ula).

PIN 553-1 skull, vertebrae, metacarpals and metatarsals (“*Gorgosaurus lancinator*” holotype), Altan Uul.

PIN 553-2 (*Tarbosaurus efremovi*).

PIN collections also contains several other skeletons, including fragmentary remains of at least six individuals from Nemegt, collected during the Soviet expeditions in the years 1946–1949 (Maleev 1974).

New tyrannosaurid skeletons have been found in 1990s by the Japanese-Mongolian Paleontological Expeditions in Nemegt, Bügiin Tsav, Hermin Tsav and Guriliin Tsav (Ishii et al. 2000), and Nomadic Expeditions (Philip Currie personal communication 2002).

Comparative studies include the North American tyrannosaurid material with the main focus on a bone by bone cast of a specimen of *Tyrannosaurus rex* (BHI-3033, known also under a nickname “Stan”) housed in Black Hills Institute, South Dakota; the cast of the skull of *Tyrannosaurus rex* CM 9380 (formerly AMNH 973), cast in Geological Museum, University of Oslo, Norway.

The North American tyrannosaurids have been extensively described (e.g., Osborn 1912; Lambe 1917; Russell 1970; Bakker et al. 1988; Molnar 1991; Bakker 1992; Carr 1999). Here we attempt to supplement descriptions of the Mongolian counterparts of the North American Tyrannosauridae, revealing previously unnoticed features. The descriptions of *Ta. bataar* osteology will of necessity recapitulate some features mentioned in the works of Maleev (especially 1974), based on the specimens available to him in the 1950s, supplemented with those resulting from examination of the new material from Warsaw and Ulaanbaatar collections. Inclusion of Maleev’s observations into the descriptions rather than simply referring to his papers may benefit readers not fluent in Russian.

The terminology used will adhere mostly to that of Madsen (1976), Molnar et al. (1990), Bakker et al. (1988), and Molnar (1991).

The Mongolian geographic and stratigraphic names are given here in versions proposed in Benton (2000) and intended as a uniform standard for future palaeontology works concerning the area.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BHI, Black Hills Institute of Geological Research, Hill City, South Dakota, USA; CM, Carnegie Museum, Pittsburgh, Pennsylvania, USA; GIN, Palaeontological Centre, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—NAT, North American Tyrannosaurinae.

Methods

The skull of ZPAL MgD-I/4 was selected as the main basis of this study because it was partly eroded and only the left side was preserved. For us, the erosion of the skull was fortunate. We took the skull apart bone by bone to reveal each bone in three dimensions. This specimen is the first *Tarbosaurus* skull that can be studied disarticulated. For more information on the preparation of the skull see <http://www.nhm.uio.no/palmus/tarbosaurus/english/>.

Geological setting and taphonomy

The fossils of the Central Asiatic tyrannosaurids occur in the uppermost Cretaceous sediments of the ?late Campanian–early Maastrichtian Nemegt Formation (see Jerzykiewicz 2000 and Shuvalov 2000 for discussion and references on stratigraphy and lithology) of fluvial and lacustrine origin. For example, out of the 17 specimens found during the 1964 and 1965 Polish-Mongolian expeditions, the four best preserved skeletons, as well as four incomplete skeletons and three fragmentary remains, were found in sands with intraformational gravel intercalations. One incomplete skeleton was found in sandy siltstone with intercalations of intraformational clasts, and five fragmentary specimens came from intraformational conglomerates and pebbly-sandy sediments (Gradziński 1970).

The bones are usually light coloured (whitish to beige, rarely brownish because of an iron content of 2.2–8 percent; Gradziński 1970), thus differing from most fossils of their North American relatives, which are dark, even black, due to secondary permineralization. In the Gobi specimens only crowns of the teeth tend to be that dark. The relatively undisturbed tyrannosaurid skeletons are often preserved lying on one side with dorsally bent tail and neck, with widely open jaws, and limbs close to the body, in so called opisthotonic

position, described also for the North American *Albertosaurus* (= *Gorgosaurus*) *libratus* (Matthew and Brown 1923), see Molnar and Farlow (1991). The resulting asymmetrical erosion of bones may destroy one side of the skull (as in ZPAL MgD-I/4, GIN 100/65). Dorsoventral crushing of the skull, like that in GIN 107/2, is seldom found.

The presence of many articulated specimens suggests little distortion of skeletons after burial by fluvio-lacustrine sediments. They could have been buried by deposits of ephemeral streams, as the opisthotonic, dorsal bending of the vertebral column is typical for desiccated carcasses of large vertebrates; the arrangement of bones and relative completeness of skeletons suggest little *post mortem* transportation of the animal remains (Gradziński 1970).

On the other hand, the frequency of fossils of apparently desiccated bodies of large animals in otherwise relatively humid, fluvial environment attributed to the Nemegt Formation (Gradziński 1970), implies existence of periods of prolonged droughts (see Jerzykiewicz 2000 for environmental model of cyclic sedimentation regimes). Such a taphonomic mode also indicates that the exposed, drying carcasses were rarely disrupted by scavengers, probably because megafauna migrated to more humid refuges. Thus the continental climate extremes that helped to preserve the tyrannosaurid skeletons might have also contributed to their mortality.

Systematic paleontology

Subclass Dinosauria Owen, 1842

Order Saurischia Seeley, 1887

Suborder Theropoda Marsh, 1881

Intraorder Coelurosauria von Huene, 1914

Family Tyrannosauridae Osborn, 1906

Subfamily Tyrannosaurinae Matthew and Brown, 1922

Genus *Tarbosaurus* – monospecific, see diagnosis of the species *Ta. bataar*.

Tarbosaurus bataar (Maleev, 1955a, b)

Holotype: PIN 551-1.

Paratype: PIN 551-2.

Type locality: Nemegt, Mongolia.

Type horizon: Nemegt Formation (?late Campanian/early Maastrichtian).

Description of the skull of *Tarbosaurus bataar*
ZPAL MgD-I/4 with additional remarks on
Tyrannosaurus rex BHI-3033

The skull as a whole (Figs. 1, 2, for measurements see Tables 1–5).—The skull of *Tarbosaurus bataar* in lateral view resembles that of *Tyrannosaurus rex*, both are deep and have powerful jaws. In dorsal view the skull of *T. rex* is extremely broad posteriorly but narrows towards the snout; in *Ta.*

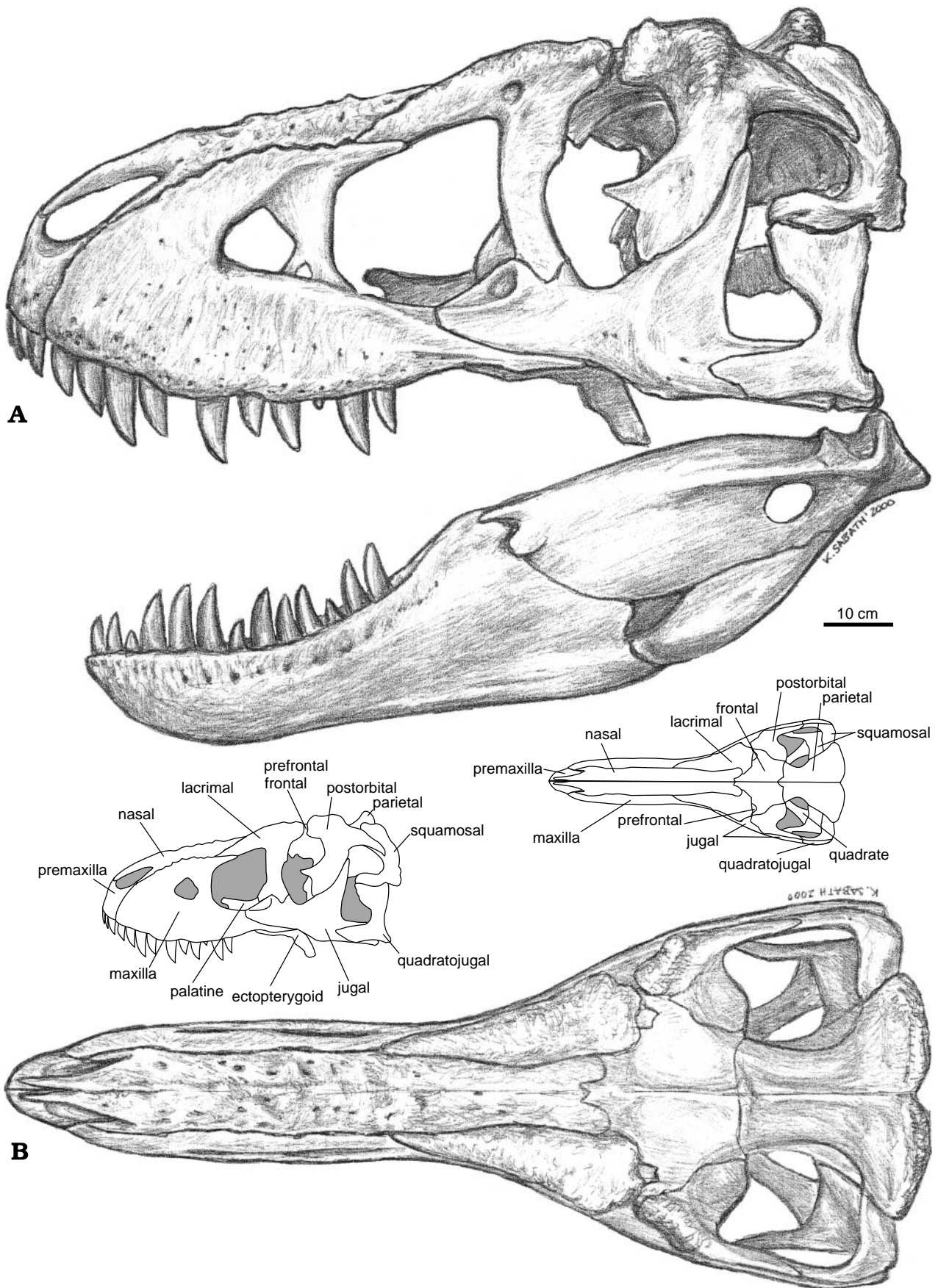


Fig. 1. Skull of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A) and dorsal (B) views.

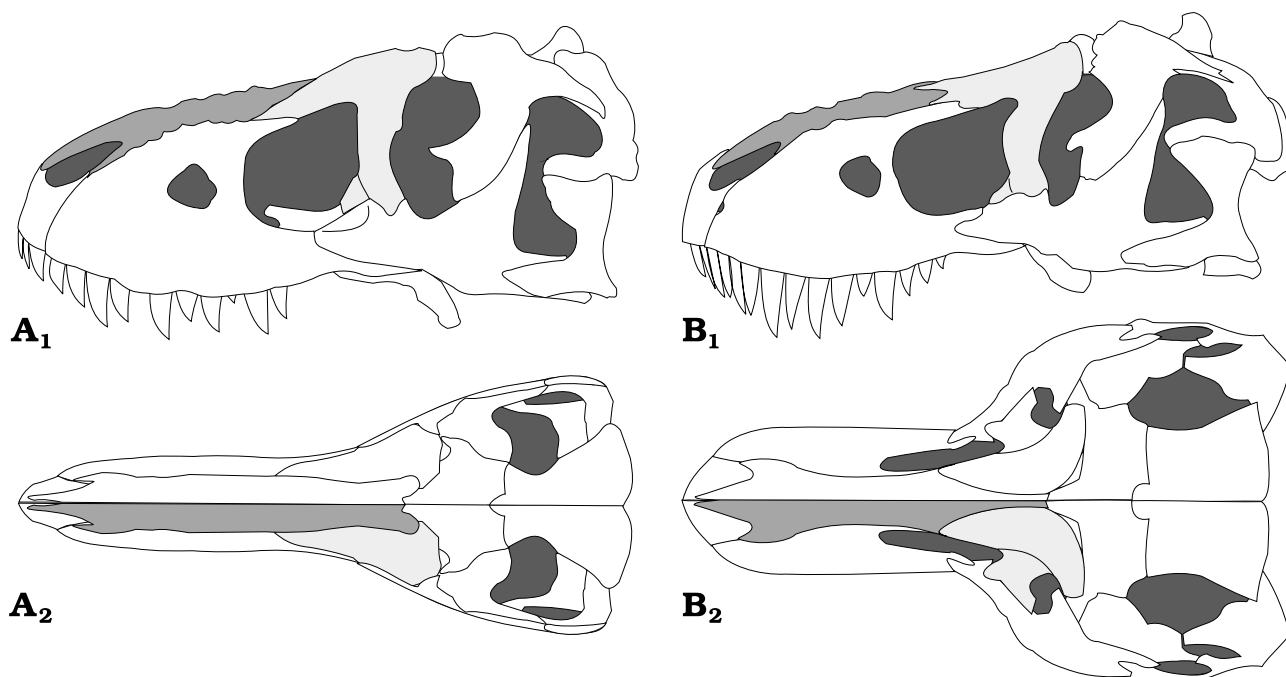


Fig. 2. **A.** Generalized skulls of *Tarbosaurus bataar* in lateral (A_1) and dorsal (A_2) views. **B.** *Tyrannosaurus rex* in lateral (B_1) and dorsal (B_2) views compared (not to scale). Light grey, lacrimal; dark grey, nasal.

bataar the skull is narrower (especially in its ventral part: the premaxilla, maxilla, jugal, and the quadrate complex), and the expansion of the posterior half of the skull is less abrupt. In *T. rex*, the jugal flares out posteriorly so strongly that the ventral part of the lacrimal shaft is visible in dorsal view. The slender snout of *Ta. bataar* is reminiscent of more primitive NATs (see, e.g., Currie 2003). The modifications of the *T. rex* skull shape, compared to all other tyrannosaurids, concentrate in the jaw apparatus, while the braincase is less affected.

The most obvious difference between *T. rex* and *Ta. bataar* is the doming of the nasal in *Ta. bataar* which is high between the lacrimals and is less attached to the other bones of the skull than in most tyrannosaurids. This is because of a shift in the handling of the crushing bite in *Ta. bataar* which will be discussed in more detail below.

Premaxilla (Fig. 3).—The premaxilla is a short, stout bone, resembling a subvertically oriented prism with rounded outer edges, and with elongated mediodorsal (supranarial) and dorsolateral (subnarial) processes that border much of the external naris. The premaxillae fit tightly together, with their medial faces sculpted in small grooves and protuberances. In *T. rex* BHI-3033 there are six ridges situated on the supranarial process, while the rest of the surface possess only small grooves. The anterior margin of the premaxilla is perpendicular to the palatal plane and at a level with the external naris, where it bends strongly posteriorly. This curvature is similar to that in *Albertosaurus*, while in *T. rex*, “*Nanotyrannus*”, *Albertosaurus sarcophagus* (TMP 81.9.1, Bakker et al. 1988), and in e.g., *Allosaurus*, the snout tip gently

curves posteriorly along the premaxilla. The thin, medial, dorsoposteriorly bent nasal processes of the premaxillae separate the external nares and border them anteriorly. The processes become narrower dorsoposteriorly to fit between the processes of the nasals, that join them approximately one third of their length posteriorly. There is a pronounced depression (narial fossa) surrounding the anterior margin of each external naris. The suture between the premaxilla and the maxilla runs obliquely anteroventrally. The surface in contact with the maxilla has three main ridges pointing posterodorsally. In *T. rex* (BHI-3033) the surface is divided by a main ridge and several grooves. The premaxillary tooth row is bordered by a shallow depression on the palatal side. The bone contains four D-shaped, serrated teeth that are smaller than lateral teeth, and the tooth row arcade is more mediolaterally than posteroanteriorly oriented (Holtz 2001). The palatal surface of the premaxilla is almost flat, forming a narrow palatal shelf. On the labial side, along the tooth row, there are three rounded vascular pits, situated between the teeth bases, and about one tooth diameter upwards from the lower margin of the premaxilla. Several smaller pits are visible still higher on the labial side of the bone. The position of the foramina corresponds exactly to the pattern seen in *T. rex* (BHI-3033).

Maleev (1974: 141) stated that on the internal side of the premaxilla, just below the naris, there is a deep, longitudinal groove for the thin anterior process of the maxilla. Obviously he meant the lower (maxillary) process of the nasal and not the maxilla itself. He also described an oval opening between the maxilla and premaxilla (ant3) as the third antorbital

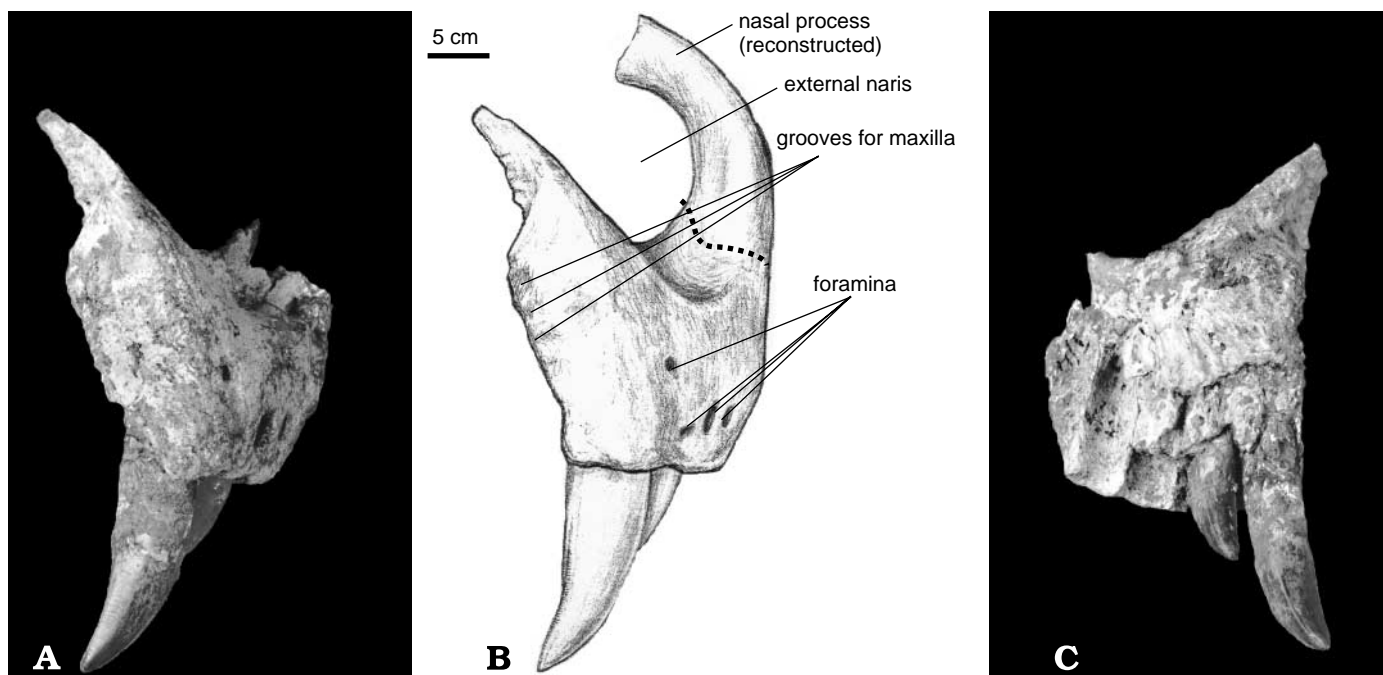


Fig. 3. Right premaxilla of *Tarbosaurus bataar* ZPAL MgD-I/4 mirrored to be comparable to other bones from the left side of the skull in lateral (A, B) and medial (C) views.

fenestra (Maleev 1974: 140). Molnar (1991: 141) described a similar feature in *T. rex* as a dorsoventrally elongate foramen that leads through a short channel with smooth walls and opens into the oral cavity just below the palate. This internal opening is, however, not shown in Molnar's restoration of the skull of *T. rex* (Molnar 1991: fig 9A), Molnar's (1991) and Osborn's (1912) restorations are mislabelled—on the figure they are labelled A and B, respectively, and in the caption: B and A. In *Ta. bataar* the opening is barely visible on the oral side, and the shape of the external fenestra varies, from an oval to a long cleft. In *T. rex* it occupies one third of the maxillary contact surface of the premaxilla (Molnar 1991), while in *Ta. bataar* it tends to be smaller. In a composite reconstruction of *Gorgosaurus libratus* (Carr 1999: fig 5A) the foramen is named foramen subnarialis and is small in lateral view, see also Currie (2003) on subnarial foramen. Madsen (1976) described a homologous structure in *Allosaurus fragilis* and it is widespread in Saurichia (Seren and Novas 1993; Sereno 1999).

The premaxillae are missing from the otherwise well preserved skull of ZPAL MgD-I/3, but are present in ZPAL MgD-I/4, ZPAL MgD-I/175, ZPAL MgD-I/44, GIN 100/60, GIN 100/65, GIN 107/2 and GIN 107/3, as well as in PIN 551-1, PIN 551-2, PIN 552-1.

Maxilla (Fig. 4).—The maxilla is the largest bone of the *Ta. bataar* skull. It is roughly triangular in shape, with the alveolar edge convex and the posterior edge deeply emarginated for the antorbital fenestra. The outer side of the bone is smooth within the antorbital fossa but rugose elsewhere. There are numerous pits along the labial margin, within

about 10 cm above the tooth row. The blunt anterior apex contacts the premaxilla, the dorsal edge forms a suture with the nasal and, at the dorso-posterior end, contacts the lacrimal. The ventral edge contacts the jugal posteriorly. The suture to the nasal bone is very different from what can be observed in *Gorgosaurus libratus* (Witmer 1997: fig. 30) where the suture is a smooth surface. In *Ta. bataar* the suture consists of deep transverse cavities and ridges fitting exactly into the nasal. This is also the case in *T. rex* (BHI-3033: Fig. 11A). The anterior part, which contacts the premaxilla, has a small invagination for the promaxillary fenestra. The massive, posterodorsal process of the maxilla has the anterior end of the lacrimal as a sheath around its posterior end. This posterodorsal process is thin and plate-like in *T. rex*.

There is a large foramen in the middle of the maxilla. This has been called the second antorbital fenestra (ant2) by Maleev (1974) and termed maxillary fenestra by Molnar (1991) and Witmer (1997). This fenestra has an ovate-triangular shape with sharper end facing forward and opens into the lateral surface of maxilla in the anterior part of the antorbital fossa. The maximum height and length of the maxillary fenestra are the same.

On the medial surface just below the maxillary fenestra, the posterior end of a horizontal palatal shelf protrudes medially from the mid-anterior part of maxilla and meets the palatal shelf of the contralateral maxilla along the midline of the skull. The palatal shelf of the maxilla contacts the palatine along its rear end, and the front is overlain by the vomer. Molnar (1991: 142) indirectly suggested that the maxillae are entirely separated by the vomer. This is true only in ventral view of the palate. In *Ta. bataar* the vomer only underlies the

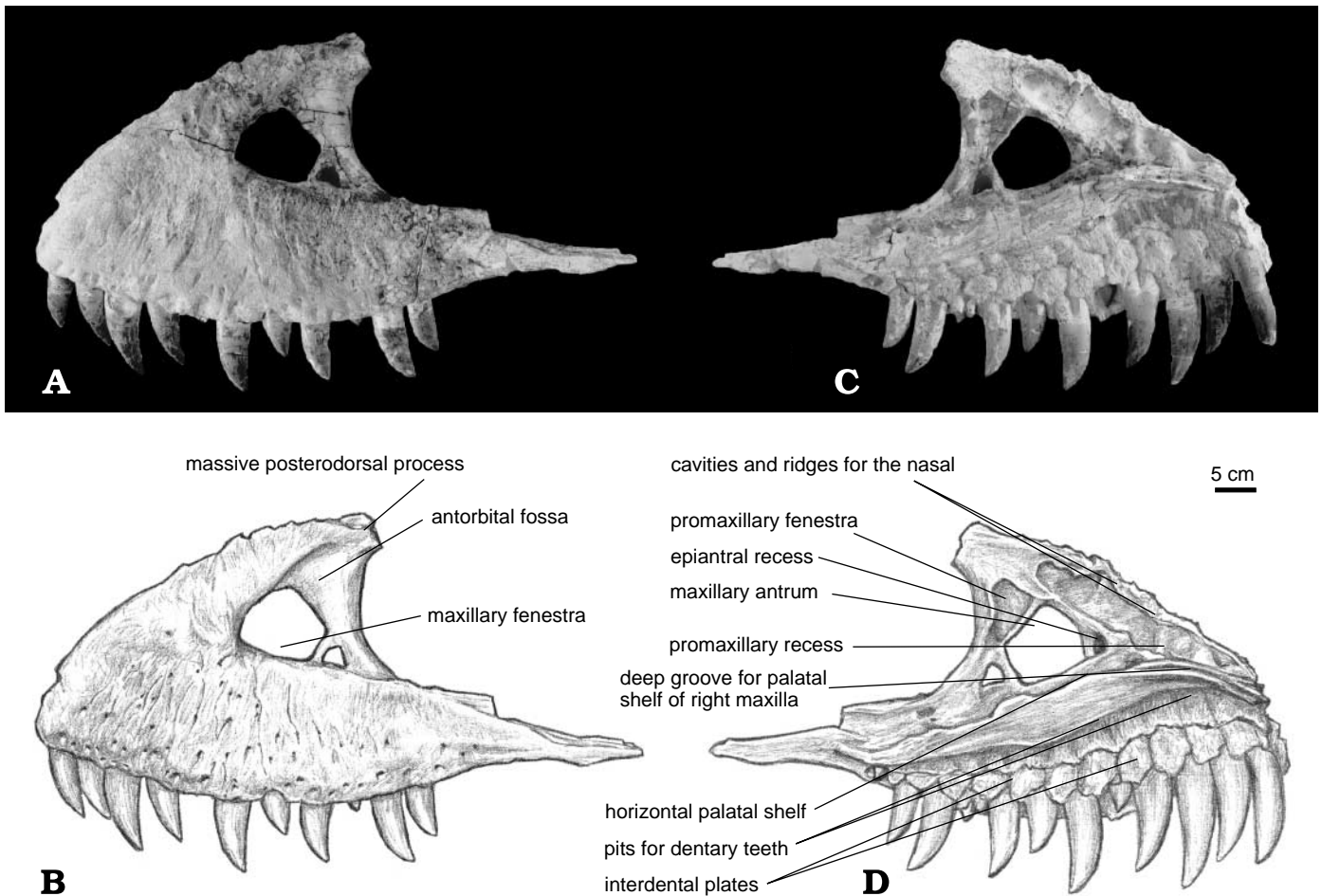


Fig. 4. Left maxilla of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A, B) and medial (C, D) views.

anterior part of the palatal shelves along the midline of the skull. This is especially evident in ZPAL MgD-I/3, which has been broken to the right of the midline. A similar situation occurs in *T. rex*. The palatal shelf is smooth, but there are several pits or depressions for dentary teeth in its proximal part, where it merges into the medial surface of the main body of the maxilla. This medial (lingual) surface bears a row of shallow grooves, against which the dentary teeth probably fitted. Further ventrally, covering the replacement teeth and bases of functional teeth, are the interdental plates. They have rough surfaces and are not fused together.

The medial surface of the maxilla shows several suboval chambers (accessory cavities or sinuses), situated along the nasal margin and anterodorsally from the maxillary fenestra. A thin layer of bone covered these chambers, but now it is broken. They follow the same pattern as described for *Gorgosaurus libratus* by Witmer (1997: fig. 30), with a promaxillary recess anteriorly and a maxillary antrum posteriorly (epiantral recess + maxillary antrum). The excavatio pneumatica within the ascending ramus of the maxilla is not observed. The epiantral recess is larger than in *G. libratus*, expanded dorsally and partly covered mediadorsally by the postantoral strut. The promaxillary recess is deeper, but of the

same general shape as in *G. libratus*, with two main cavities. Molnar (1991: fig 2, cavities a and b) described the same general shape for *T. rex*. The promaxillary fenestra is visible in medial view and is situated in the dorsal part of the promaxillary strut. On the ventral part of the promaxillary strut in the contact with the palatine part of the maxilla, the fenestra communicans opens between the posterior part of the promaxillary recess and the anterior part of the maxillary antrum.

In *Ta. bataar* the shape and size of the maxilla and its foramina are very much the same as in other tyrannosaurids (Carpenter 1990). The maxilla of "*Maleevosaurus*" would also fit within this variability range, except for the extremely elongated dorsal ramus as restored by Maleev (1974).

Nasal (Fig. 5).—As in other tyrannosaurids, the nasals of *Ta. bataar* are fused along the midline into a strong, elongated element, slightly compressed in the middle. The dorsal surface is convex in transverse section and rugose, with several round pits that open along both sides of the midline, especially just behind the nares and near the posterior end. The rugose texture is more pronounced in larger specimens and in the middle part of the nasals and is typical of mature speci-

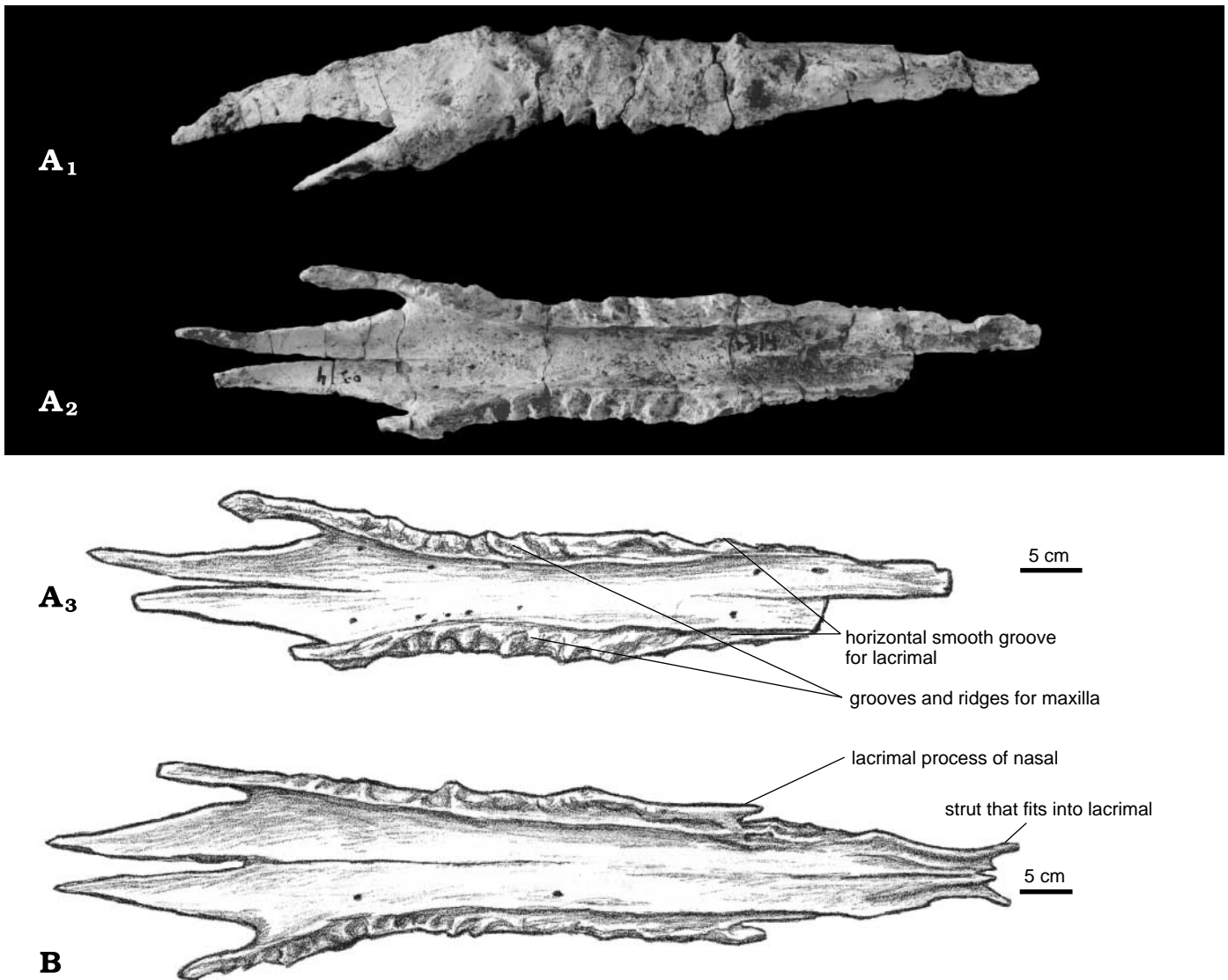


Fig. 5. **A.** Nasal of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A_1) and ventral (A_2 , A_3) views. **B.** Ventral view of the nasal of *Tyrannosaurus rex* BHI-3033.

mens (Carr 1999). The ventral surface is smooth and markedly concave in transverse section. There are several pits on the ventral surface of the bone. The first pair of pits is placed behind the nares and slightly medially from their rear end. The first pair of pits is also seen in *T. rex* (BHI-3033), but due to preservation only one more pit can be observed. Along their ventrolateral margins, the nasals contact the maxillae. Grooves and ridges perpendicular to the sagittal plane strengthen the contact. They extend along the whole maxillary contact, while Molnar (1991) stated that in *T. rex* they are restricted to the anterior one third. In the *T. rex* specimen available to us, BHI-3033, the ridges extend as far as in *Ta. bataar*, but they are less prominent (Fig. 5B).

In the anterior part, the nasals are widest just behind the external nares. The premaxillary processes of the nasal form the posterodorsal margin of each naris. The subnasal process is about half the length of the upper one, and contacts the

dorsolateral process of the premaxilla. The nasals are separated along the midline by a thin fissure, extending backwards from the contact with the premaxilla to the widest point (i.e., within anterior 1/4 to 1/3 of their length). The suture between the nasals is visible also in its posterior part, especially on the ventral surface and in the smaller individuals. This suture extends anteriorly to the level of the lacrimal-maxilla contact. The nasal contacts the frontal posteriorly along a W-shaped suture, and in its lateroposterior—with the lacrimal. The suture against the anterior ramus of the lacrimal differs considerably in *Ta. bataar* and *T. rex*. In *Ta. bataar* it is an almost horizontal, smooth groove. In *T. rex* the complex articulation between the anterior ramus of the maxilla and lacrimal seen in *Ta. bataar* is shifted to the nasal. Between the main body of the nasal and a posteriorly oriented lacrimal process (Fig. 5B), a robust groove is present for the anteriorly bifurcated, blunt end of the lacrimal. This lacrimal process of the nasal causes

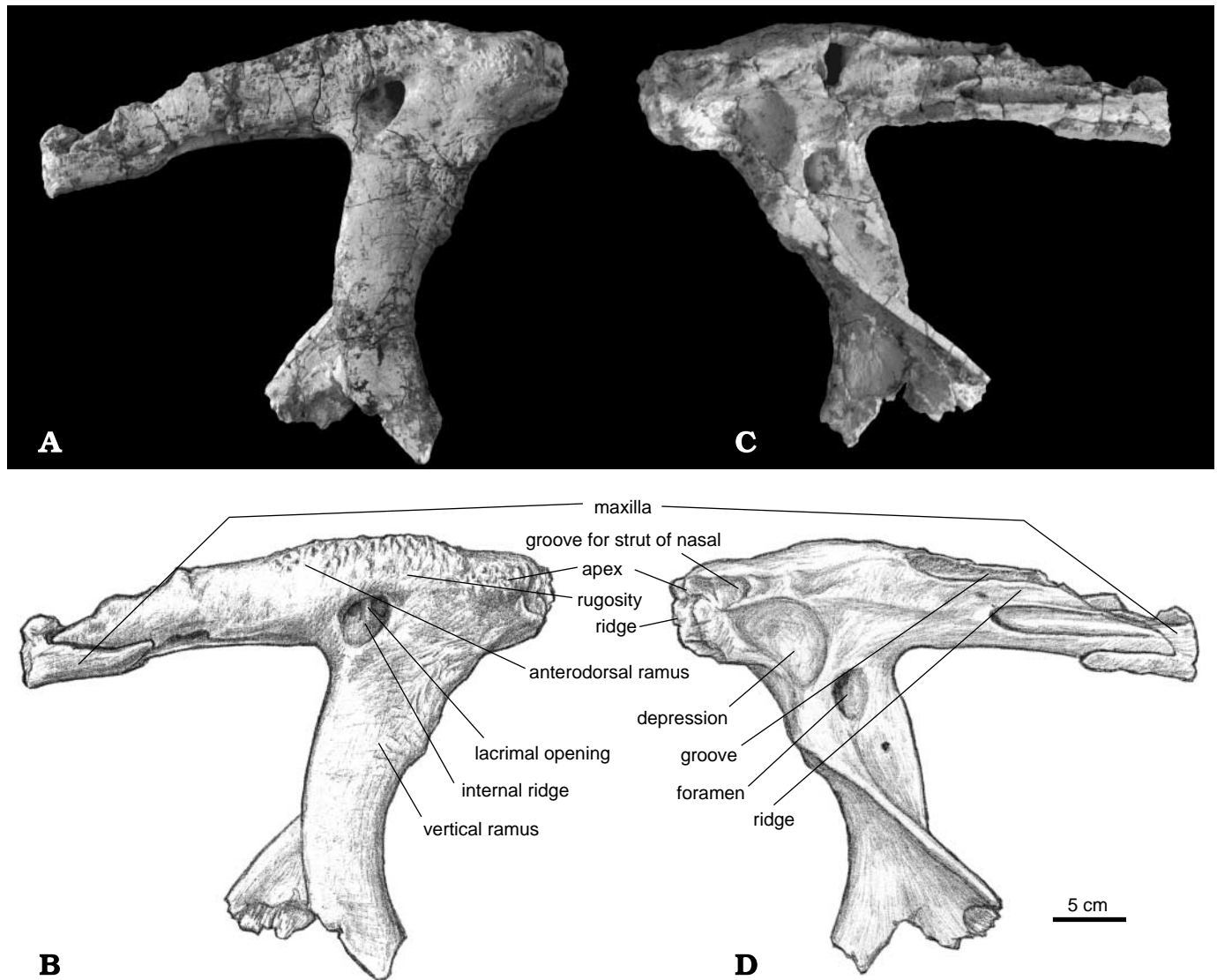


Fig. 6. Left lacrimal of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A, B) and medial (C, D) views.

the nasal bone to be wider in *T. rex* than in *Ta. bataar* and thus in dorsal aspect the nasals of *Ta. bataar* are more slender than in *T. rex*, *Albertosaurus* (Carr 1999: fig. 5) and *Daspletosaurus* (Russell 1970). The lack of expansion and lack of lacrimal process on the nasal might be synapomorphies of *Ta. bataar*, but may be present in *Alioramus*, too. In more primitive theropods like *Sinraptor* (Currie and Zhao 1993: figs. 3, 5) and *Allosaurus* (Madsen 1976: fig. 5b, c), the expansion is less prominent than in North American tyrannosaurids, but a small lacrimal process of the nasal is present (see discussion).

The most posterior part of the nasal bone is not preserved in the studied specimen (ZPAL MgD-I/4) of *Ta. bataar*, but it is well preserved in *T. rex* BHI-3033. From comparisons of the medial side of the lacrimal (see Fig. 5B) it is likely that the same structure is present in both. The most posterior part of the nasal in *T. rex* is a thin posterodorsal strut that bends slightly laterally. This process fits into a small pocket in the lacrimal.

Lacrimal (Fig. 6).—The anterodorsal ramus (anterior process of Currie 2003) of the lacrimal borders the antorbital opening from above, while the vertical ramus (descending or jugal ramus, or postorbital bar of Currie 2003) separates this opening from the orbit. The apex protrudes slightly backwards and meets the frontal. In larger specimens the apex and the dorsal margin is very rugose, but the pronounced lacrimal horn, found in most North American tyrannosaurids and in *Allosaurus*, is lacking. In *T. rex* (Fig. 7A) the apex is more inflated than in *Ta. bataar*. The posterior surface forming the suture to the frontal and prefrontal is divided vertically by a rugose ridge in *Ta. bataar*, but in *T. rex* (BHI-3033) this surface is nearly smooth. There is no contact between the postorbital and lacrimal in the described specimen of *Ta. bataar*, but see Currie (2003). The suture resembles that in *T. rex*, but it differs from that of *Albertosaurus* because of the more anteriorly positioned prefrontal in this genus (Carr 1999: fig. 5).

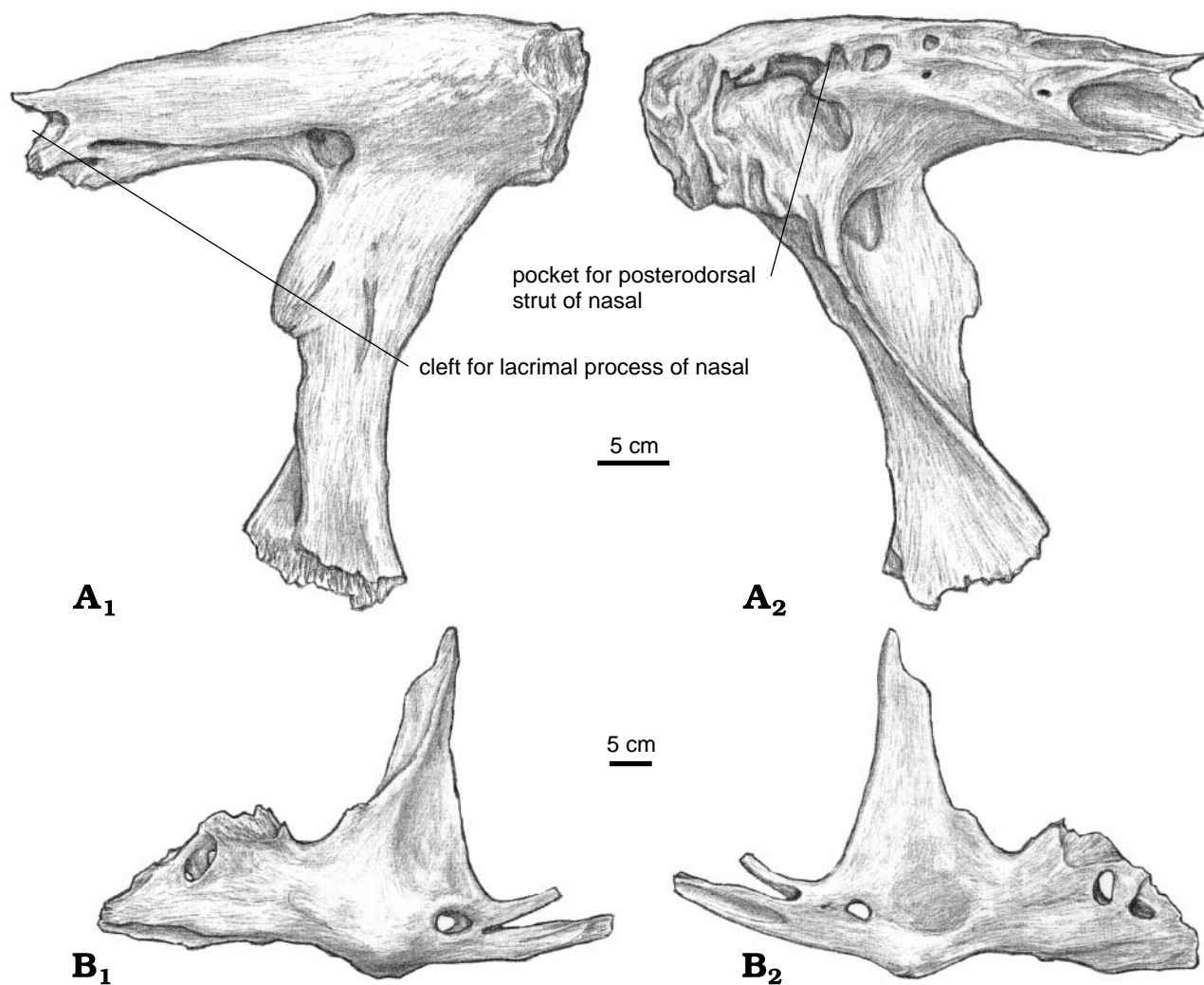


Fig. 7. *Tyrannosaurus rex* BHI-3033. **A.** Left lacrimal in lateral (A_1) and medial (A_2) views. **B.** Left jugal in lateral (B_1) and medial (B_2) views.

On the lateral side, just above and behind the posterodorsal corner of the antorbital fenestra, there is an oval or reniform lacrimal opening, which leads to interior sinuses, divided by an internal ridge. In *T. rex* the dorsal ramus contains a large sinus that is at least three-chambered in its apical moiety (Molnar 1991: fig. 3). In *Ta. bataar* the extent of the lacrimal sinus is similar, and fills most of the anterodorsal ramus and part of the vertical ramus.

The orbital margin of the vertical (= descending) ramus of the lacrimal is convex anteriorly, while the antorbital margin is straighter, only lightly bent in midheight. The lower third of this ramus widens ventrally, where it contacts the jugal; the anterior margin of the bone forms a ridge that continues ventrally (slightly posteriorly) on the lateral side of the lacrimal. A triangular flap of bone protrudes anteroventrally from behind the ridge (anterior process of the jugal suture). A crest separates two shallow concave areas on the medial side of the vertical ramus. The anterior area widens upwards, while the posterior area widens downwards. At least the upper part of the ramus is hollow, containing the lacrimal duct and probably a sinus extending downwards (in *T. rex* the descending

ramus appears to be solid; Molnar 1991). The contact between the jugal and lacrimal is similar in *Ta. bataar* and *T. rex* with the anterior process of the lacrimal medial to the jugal and the posterior process with a groove for the jugal.

The horizontal ramus is longer and less inflated in *Ta. bataar* (ZPAL MgD-I/4) than in *T. rex* (BHI-3033). The horizontal ramus narrows gradually towards its anterior end, where it is divided by a short mediolateral cleft. The cleft process fits into the robust posterior end of the maxilla, and separates the antorbital fenestra from the nasal. In *T. rex* this anterior process of the lacrimal is more clearly bifurcated (Fig. 7A), the cleft fits into the nasal and the contact with the maxilla is limited to a shallow groove in the anteroventral part. In *Gorgosaurus libratus* (TMP 91.36.500; Carr 1999: fig. 5) the suture is similar to that in *T. rex*, while in *Ta. bataar* the suture is like that of *Alioramus* (Kurzanov 1976: fig. 1).

The medial side of the horizontal ramus contacts the constricted, posterior part of the nasal. The contact surface is excavated longitudinally. In the anterior half there are two deep, parallel grooves, divided by a thin ridge that runs along the mediadorsal part of the ramus. A large foramen for blood ves-

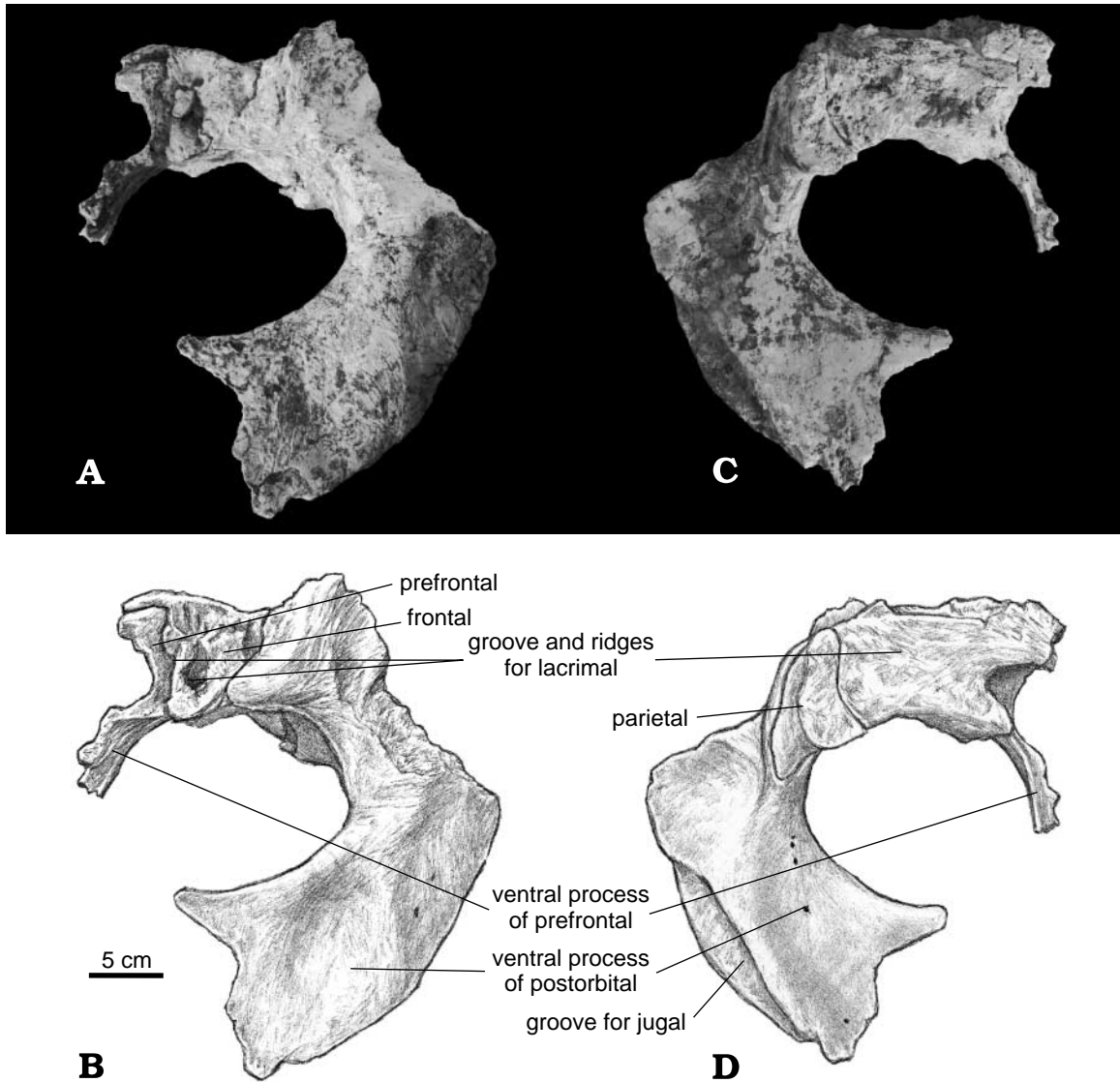


Fig. 8. Left prefrontal, frontal, postorbital and parietal of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A, B) and medial (C, D) views.

sels is situated in the middle of the ramus in *Ta. bataar*, and more anteriorly in *T. rex* (BHI-3033). More posteriorly, one horizontal ridge continues, and separates the lower, smooth and concave part of the medial surface from more sculpted upper part, contacting the nasal and anterior parts of the frontal. Medially, the apex has a large depression, which is absent in *T. rex*. Dorsal to this depression a small groove fits the position of the groove for the posterior hook of the nasal in *T. rex*. The horizontal ramus is hollow almost to the front end.

Prefrontal (Fig. 8).—Maleev (1974) described the prefrontal as a small triangular bone on the skull roof, surrounded by frontal, lacrimal, nasal, and postorbital. A similar bone is shown in the dorsal reconstruction of *T. rex* skull (Osborn 1912), and in *Daspletosaurus torosus* (Russell 1970). Molnar (1991) did not mention the bone in his detailed cranial osteology of *T. rex*, but did figure it in his thesis (Molnar 1973), and Rozhdhestvensky (in Maleev 1974) noted that the triangular outlines visible on

the skull roof could actually be the fractured posterolateral processes of the nasals.

The bone is clearly visible, lateral to the anterior process of the frontal, in dorsal and lateral view in the two disarticulated skulls studied (*Ta. bataar* ZPAL MgD-I/4 and *T. rex* BHI-3033). The lateral side of the prefrontal has several ridges for the attachment of the lacrimal, and supports most of the posteromedial side of the latter bone. A ventrally directed process of the prefrontal fits along the posterodorsal part of the medial side of the lacrimal. It makes the dorsal 1/4 of the medial ridge on the vertical ramus of the lacrimal in *Ta. bataar*. This ventral process of the prefrontal is smaller in *T. rex*. The bone can also be seen in *Ta. bataar* ZPAL MgD-I/38, where the nasals are absent, and both prefrontals are separated from the frontals by a wide fissure.

Postorbital (Figs. 8, 9).—The postorbital is a triradiate bone, with the largest ramus extending ventrally to meet the jugal

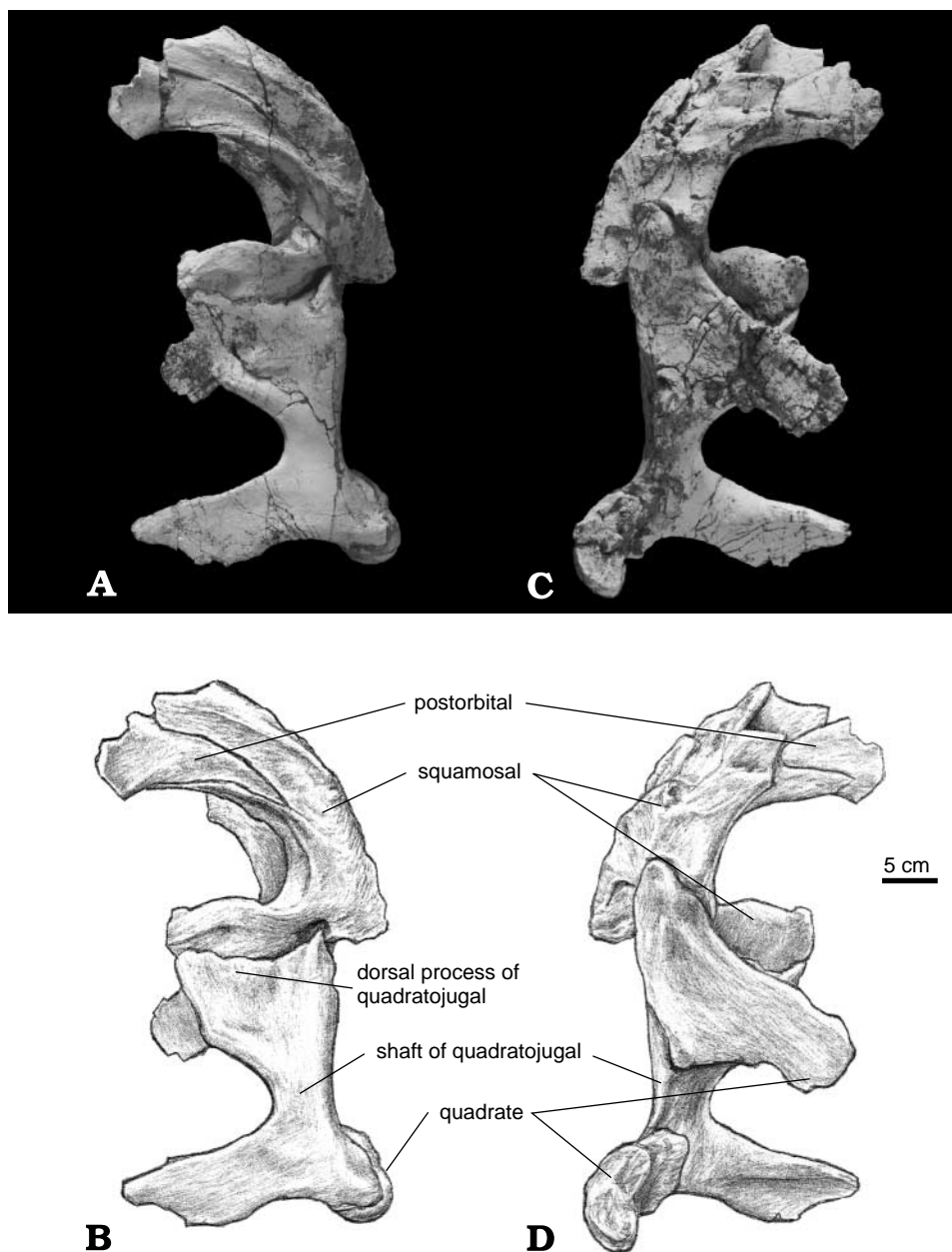


Fig. 9. Left squamosal, quadrate, quadratojugal, postorbital of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A, B) and medial (C, D) views.

bone. The posterior (intertemporal of Currie 2003) ramus meets the squamosal, and the medioventral ramus joins the frontal and possibly the parietal and laterosphenoid (see Currie 2003). The orbital margin of the postorbital is strongly arched and a protruding rugosity extends parallel to its upper part, forming a crescent-shaped postorbital horn. This anteriorly concave crescent is most rugose and pronounced in the largest specimens, but can be seen in all specimens studied. Molnar (1991) described a groove rimmed with tubercles along the dorsal margin of the orbit as typical of the *T. rex* postorbitals (Fig. 11B). Such a feature has not been observed in *Ta. bataar*. Instead, there is a rim that runs along the posterior edge of the orbit, and flanks a smooth surface perpendicular to the lateral plane. This surface is widest in the posteriormost part of the orbit and narrows ante-

riorly, where the rim fades away into a vertical sheet of bone, protruding into the orbit. The position and curvature of this smooth, concave surface seems to fit the posterior part of the eyeball and its muscles.

The lower part of ventral ramus forms an anteroventrally oblique contact surface with the jugal. A thin, vertical sheet of bone extends further anteriorly into the orbit, which is a typical feature of most large specimens of tyrannosaurids (see discussion in Currie 2003).

Squamosal (Figs. 9, 10).—The squamosal is a large bone and consists of a hollow thin-walled body with anteroventral (quadratojugal), anterodorsal (postorbital or intertemporal ramus), and mediadorsal processes. In lateral view the bone oc-

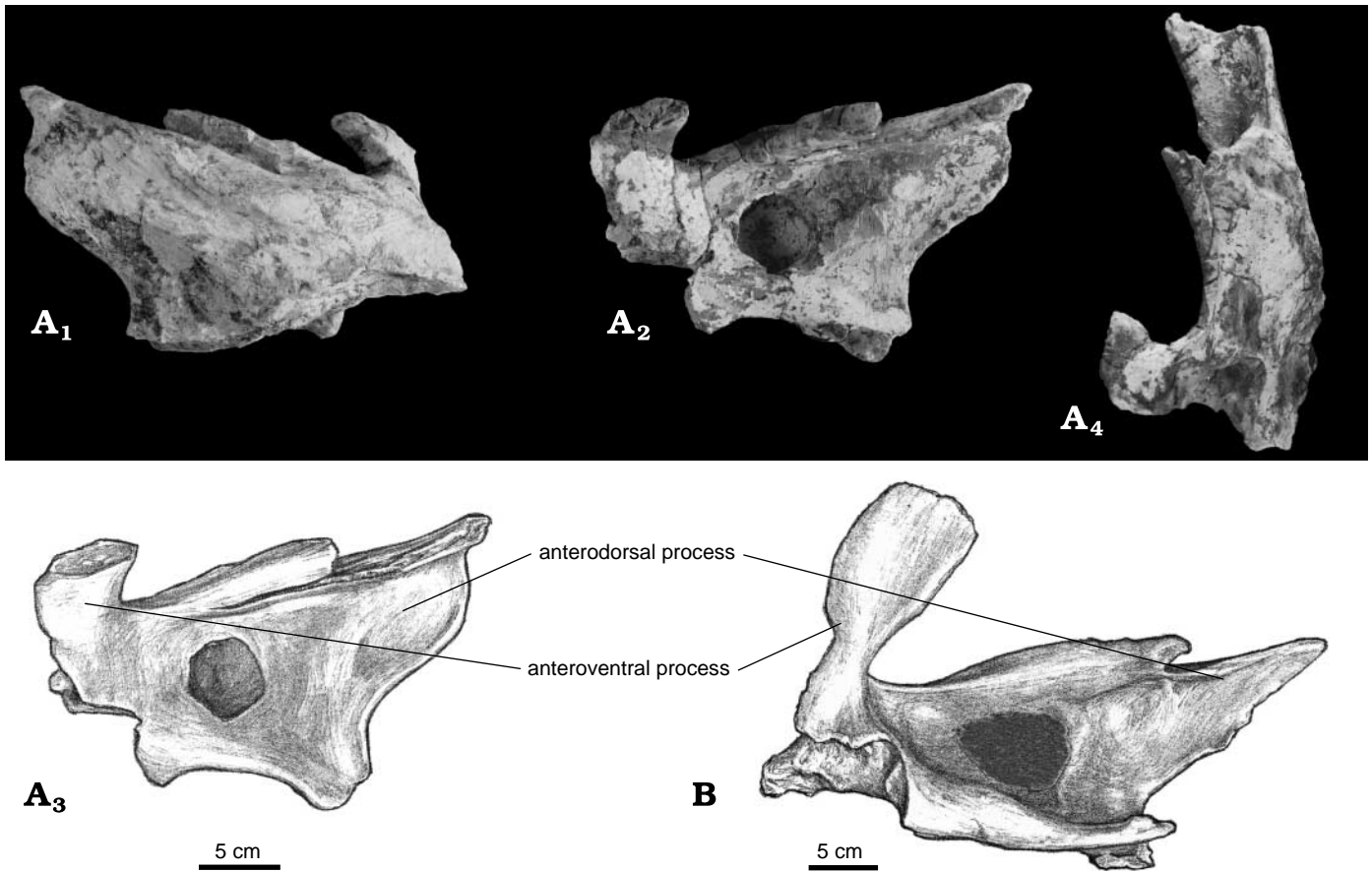


Fig. 10. **A.** Right squamosal of *Tarbosaurus bataar* ZPAL MgD-I/4 in dorsal (A_1), ventral (A_2 , A_3), and lateral (A_4) views. **B.** Mirrored left squamosal of *Tyrannosaurus rex* BHI-3033 in ventral view. A_1 – A_3 and B, anterior is up.

cupies the posterodorsal corner of the side of skull, and borders the upper part of the lower temporal fenestra posteriorly. The squamosal forms a long, deep groove for the postorbital along the anterodorsal process. The bone meets the quadratojugal on the ventral surface of its anteroventral process and the quadrate in a deep groove on its posteriormost end. The anteroventral process of the squamosal is almost horizontal and is flexed slightly downwards in its distal part in ZPAL MgD-I/4. It almost divides the lower temporal fenestra into separate openings. The process extends along the dorsal margin of the quadratojugal, which partly overlaps it laterally in the anterior and posterior part of the contact area. This overlapping of the quadratojugal is greater than in *Albertosaurus*, *Gorgosaurus*, and *Daspletosaurus*, and is more like that of *T. rex* BHI-3033.

In lateral view, the anterodorsal process is inclined at an angle of 45 degrees to the anteroventral process and is curved (convex dorsolaterally). This process is deeper than the anteroventral one, overlaps medially the posterior ramus of the postorbital, and surrounds its end from above and below. Within the angle between the anterodorsal and the anteroventral processes of the squamosal, there is a thin “flap” of bone, offset slightly medially from both processes. This forms a gently arching posterior margin of the upper part of the lower temporal fenestra.

The body and the anterodorsal process of the squamosal are deeply concave anteromedially. The nuchal process extends along the posterior edge of the upper temporal fenestra towards the nuchal crest and joins the parietal. This vertically deep part of squamosal lies almost in the plane of nuchal crest. Posteriorly, the body of the squamosal is covered by the exoccipital/opisthotic. Generally, the squamosal of *Ta. bataar* ZPAL MgD-I/4 is very similar to that of *T. rex*, as described and figured by Osborn (1912) and Molnar (1991). It differs from that of *Albertosaurus* and *Daspletosaurus* (Russell 1970; Carr 1999), where the anteroventral process is more curved and about the same thickness as the anterodorsal process. The body and mediadorsal processes of the squamosals in *Albertosaurus* and *Daspletosaurus* are located more posteriorly in respect to nuchal crest, but this may be an allometric difference.

Jugal (Fig. 12).—The jugal is compressed and consists of three rami in the parasagittal plane. The bone is only slightly concave on the medial side. In ventral view, *T. baatar* lacks the strong lateral flexure observed in *T. rex*. Molnar (1991) concluded that in some specimens of *T. rex* (illustrated in Osborn 1912) this flexure is an artefact, but in the specimen available to us (BHI-3033) the flexure is real (Fig. 7B). The jugal extends from the antorbital fenestra to the anteroventral

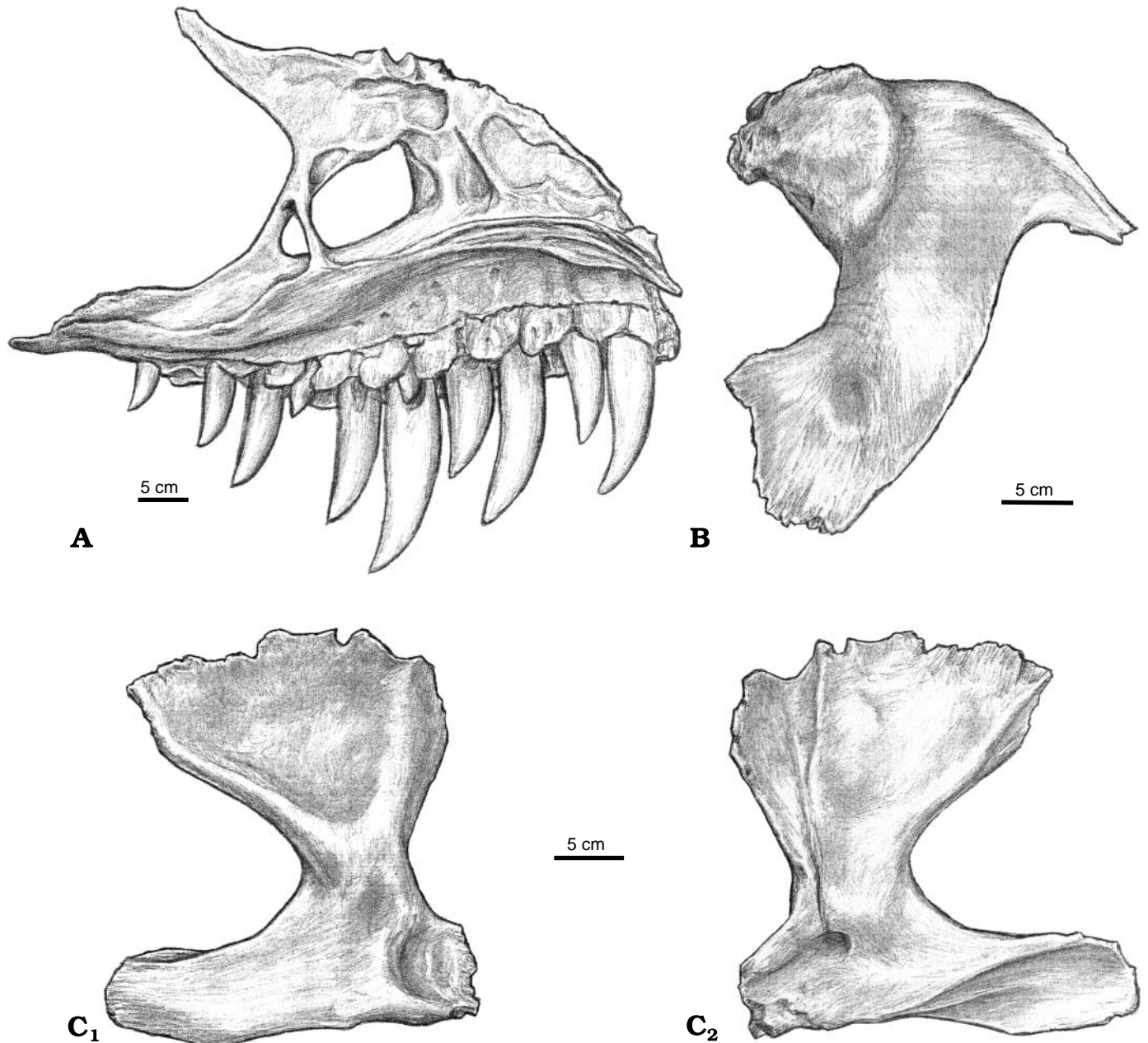


Fig. 11. *Tyrannosaurus rex* BHI-3033. **A.** Maxilla in medial view. **B.** Postorbital in lateral view. **C.** Quadratojugal in lateral (C_1) and medial (C_2) views.

corner of the lower temporal fenestra. The lateral side of the jugal has a round opening (jugal foramen), located below the posterior margin of the orbit. This opening led to internal chambers (sinuses). Generally, the surface of the jugal is mostly smooth; only the slightly protruding part of it, the cornual process, situated ventrally to the jugal foramen, is rugose in larger specimens. There are two small foramina situated at the border between the ascending and posterior rami on the lateral side. In *T. rex* there is one large foramen or two smaller foramina. On the dorsal side, at the base of the ascending ramus, there is one foramen.

The anterior ramus widens anteriorly and is divided distally by a deep incision into medial and lateral flaps, the latter

being subdivided into smaller upper and larger lower processes. The narrowing, posterior tip of the maxilla fits between them and continues along the ventral edge. The anterior ramus abuts the lower ramus of the lacrimal dorsally, and the ectopterygoid ventromedially. The ascending process of the jugal abuts the postorbital along a shelf in the upper 3/4 of its oblique anterior margin, and its posterior, subvertical margin forms most of the anterior border of the lower temporal fenestra. The jugal-postorbital contact in *Ta. bataar* is a straight, oblique line (in *Daspletosaurus* and *Albertosaurus* the line is distinctly bent; Russell 1970). A large indistinct depression covers most of the lateral side of the ascending process. This depression is notably smaller in *T. rex*

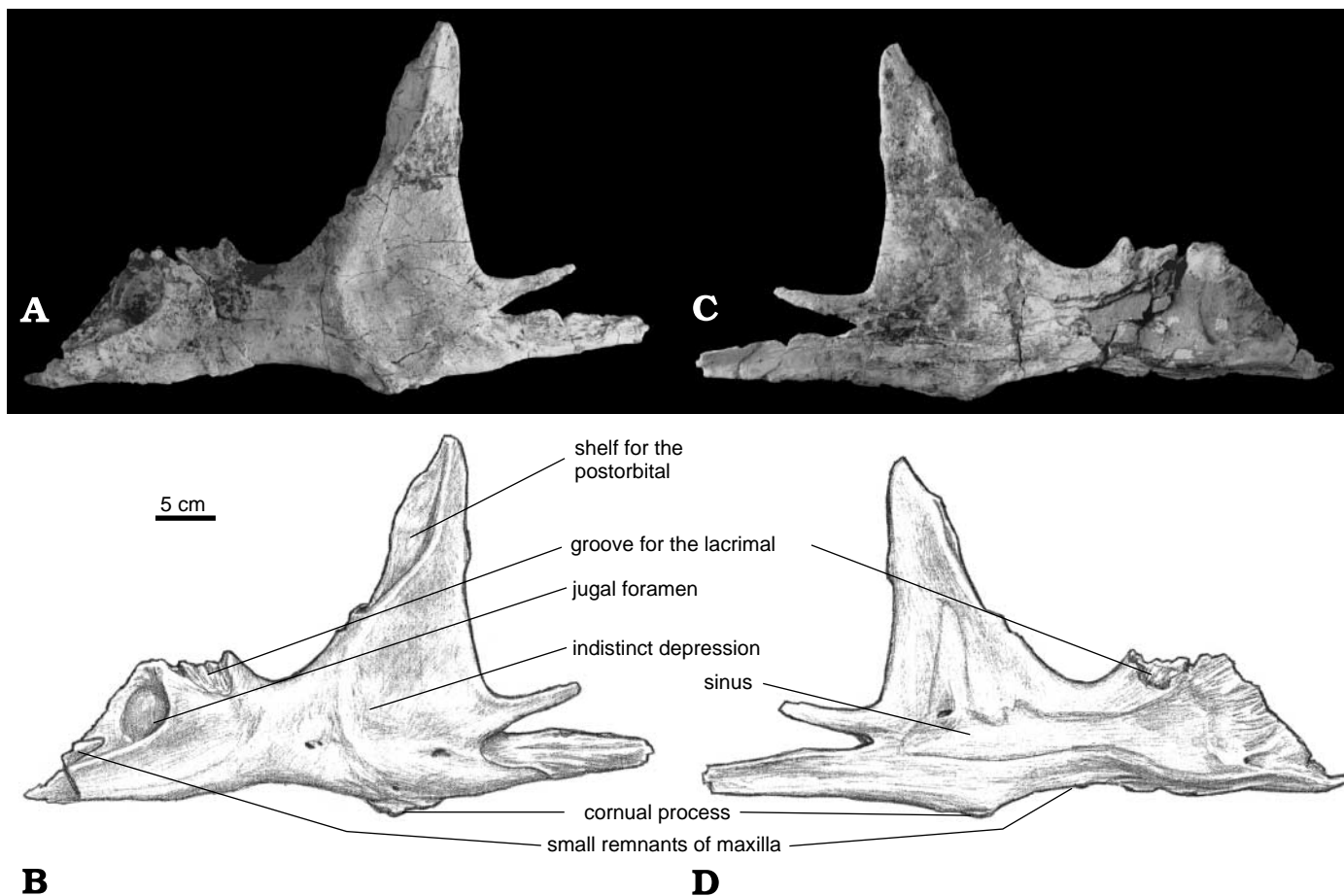


Fig. 12. Left jugal of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A, B) and medial (C, D) views.

(BHI-3033; Fig. 7B). The posterior ramus (subtemporal process of Currie 2003) is divided by a triangular notch into two processes, of which the dorsal is markedly smaller than the ventral. They embrace the anterior end of the quadratojugal, which laterally overlaps almost the entire ventral process of the posterior ramus. The ventral process is thickest on the ventral side but thins dorsally. In *T. rex* (BHI-3033, Fig. 7B) the process is more convex and of even thickness.

Quadratojugal (Fig. 9).—The quadratojugal is oriented vertically. In lateral aspect, it is wide ventrally, narrow in midheight, and wide dorsally. The elongated dorsal process overlaps the anteroventral process of the squamosal laterally and the quadrate posteromedially. The ventral process extends anteriorly to fit between the forked posterior ramus of the jugal and overlaps most of the ventral one. The posterior part of ventral process of the quadratojugal overlaps the quadrate just anterodorsally to the quadrate condylus and in the posterodorsal corner of the bone. The bone covers the quadrate laterally, but it joins it only in the upper and lower part of the thicker, posterior margin of the quadrate (“shaft” in Molnar 1991). The middle part of the quadratojugal (consisting only of the shaft) is thus separated from the quadrate by an opening (paraquadrate foramen), which is lens-shaped in posterior view. The shaft of the quadratojugal in *Ta. bataar* is more slender than it is in *T. rex*

(BHI-3033; Fig. 11C). The main difference pertains to the articulation between the jugal and the anteroventral process of the quadratojugal. In both taxa the quadratojugal fits between the forked posterior part of the jugal, with a dorsal thickening of the process, but the shape is different. In *Ta. bataar* the process is almost straight but slightly bent laterally in the anteriormost part. In *T. rex* (BHI-3033) it is extremely concave medially and covers a larger part of the posterior ramus of the jugal laterally.

Palatine (Fig. 13).—The palatine is roughly triangular in both dorsal and lateral view. The bone is hollow, thin-walled with a smooth surface, except for rugose patches on the inflated dorsal surface.

There are four processes protruding from the triangular main body, the anterolateral maxillary process, the dorso-medial vomeropterygoid process (vomery process of Currie 2003), the ventroposterior pterygoid process, and the dorsoposterior jugal-lacrimal process. The dorsal side of the palatine contains two large openings (palatine recesses) placed laterally along the deep groove for the maxilla. A smaller foramen is placed more medially. In *T. rex* (BHI-3033) the large openings are similar in shape to those in *Ta. bataar*, while the medially placed foramen is larger.

The maxillary margin is slightly convex anterolaterally, with a deep groove for the posterior part of the palatine pro-

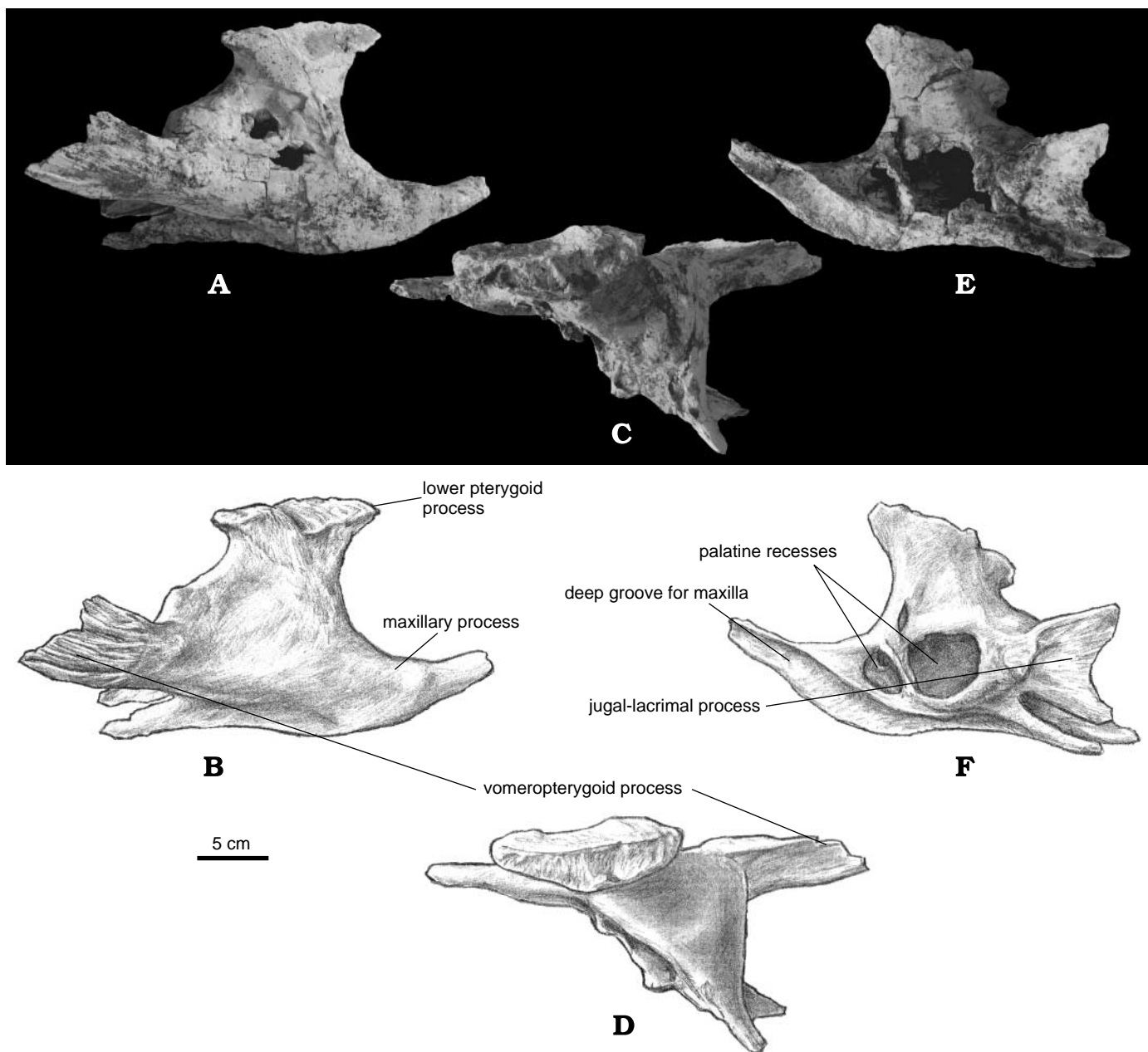


Fig. 13. Left palatine of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A, B), dorsal (C, D), and medial (E, F) views.

cess of the maxilla. There is a deep pocket where the dorsal process surface meets the maxillary groove anteriorly. This is absent in *T. rex* (BHI-3033). In both *Ta. bataar* and *T. rex* the palatine extends to the level of the fifth alveolus from the back. In *Ta. bataar* the medial side of the pterygoid process has several small ridges, while in *T. rex* this surface is almost smooth with a central ridge on the most anterior part of the surface. The vomeropterygoid process is very similar in both, while the jugal process is deeper in *Ta. bataar*.

The curvature of the choanal margin of the palatine of *Ta. bataar* is more pronounced than in *T. rex* and the posterior margin of the choana is almost perpendicular to the long axis of the skull. This resembles the situation in *Daspletosaurus*

torosus (and to some extent in *Allosaurus fragilis*, Madsen 1976: pl. 2B), but the choanae are broader and shorter in *Ta. bataar* than in all above species. The shape of the choanae is, however, variable within a single individual (GIN 107/1). Also, the palatine-ptyergoid contact in relation to the vomer is more like in *Albertosaurus* and *Daspletosaurus* (Russell 1970) than in *T. rex* (Molnar 1991). Another feature shared by *Ta. bataar* and *Daspletosaurus* while barely present in *T. rex* is the pterygopalatine fenestrae. They are markedly smaller than the choanae in *Ta. bataar*, as in *Daspletosaurus*. The palatopterygoid fenestra in *Ta. bataar* seems to be broader posteriorly, while it is anteriorly broader in *Daspletosaurus*. They are contained exclusively between the

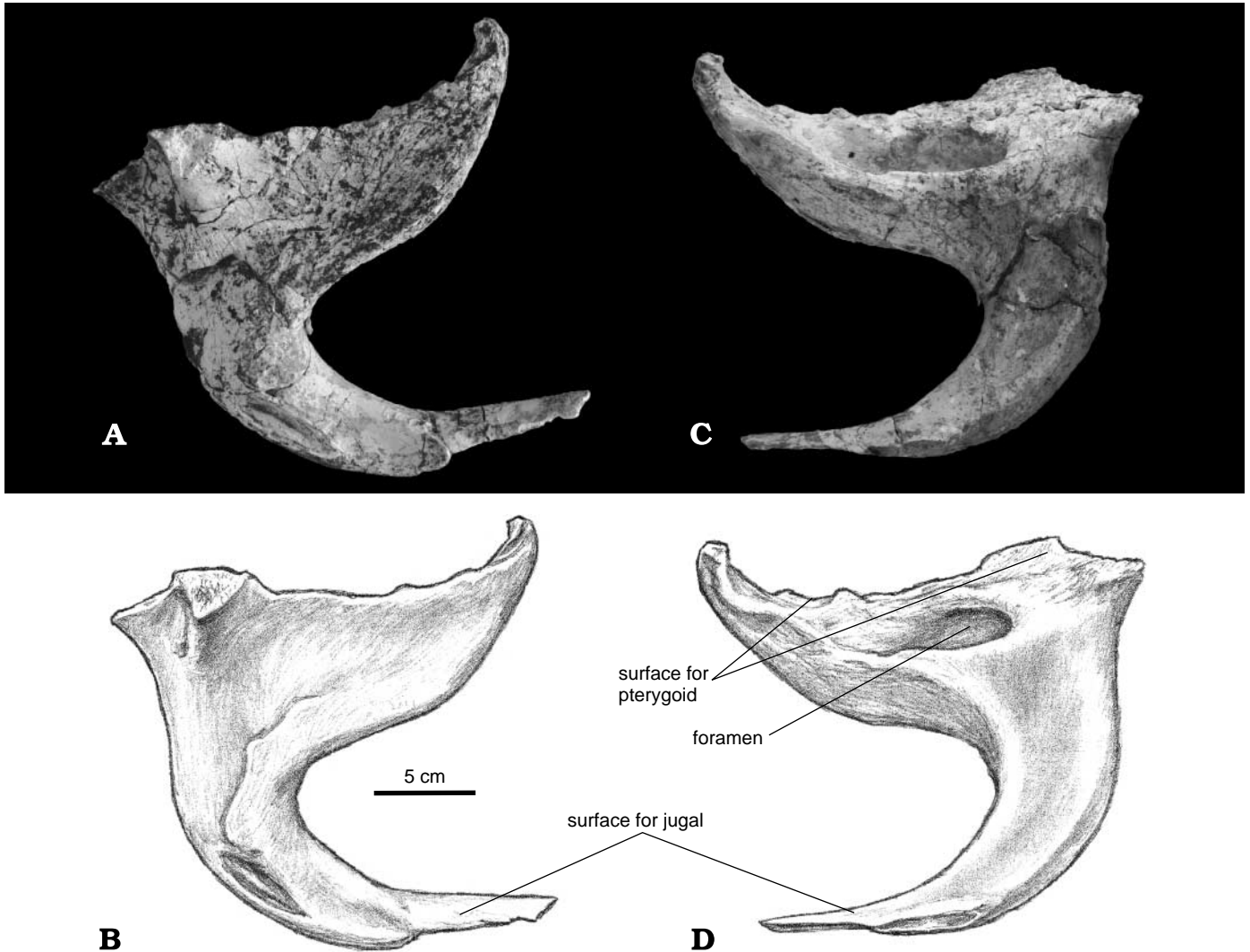


Fig. 14. Left ectopterygoid of *Tarbosaurus bataar* ZPAL MgD-I/4 in dorsal (A, B) and ventral (C, D) views.

palatines and pterygoids, and situated anteromedially from the suborbital fenestra. The suborbital fenestrae are bigger and, as in *Allosaurus*, also the ectopterygoids, jugals and maxillae participate in forming their posterolateral margins.

The greatest surprise was the dorsoposterior jugal-lacrimal process visible on the skull in lateral view. The process lies medially to the most anteroventral part of the lacrimal and fits into the concave area of the bone. This is a similar situation to that described for *Gorgosaurus* (Currie 2003).

Ectopterygoid (Fig. 14).—This stout, triangular bone has a protruding, hook-like lateral process, posteriorly bent and reaching the anteromedial part of jugal with the convex side of its tip. The medial part of the bone articulates with the pterygoid. The body of the ectopterygoid in *Ta. bataar* is hollow as in other tyrannosaurids, but the oval opening on its ventral surface is smaller than in *T. rex* (BHI-3033).

The anterior edge of the ectopterygoid “hook” forms the posterior margin of a triangular suborbital fenestra. The fenestra is bordered medially by the pterygoid, and antero-

laterally by the outer part of the posterior edge of the palatine as well as the ventral side of the anterior end of the jugal arch (the posteriormost part of the maxilla and anteriormost part of jugal). The shape, size, and position of this foramen is very similar to that in *T. rex* BHI-3033, but it differs from that of *Daspletosaurus*, where it is less triangular and more curved. In *Allosaurus* the foramen is triangular, but proportionally larger than in the tyrannosaurids.

In dorsal view the ectopterygoids of *Ta. bataar* ZPAL MgD-I/4 and *T. rex* BHI-3033 are somewhat different. A ridge placed in the root of the hook is directed medially in *T. rex*, while in *Ta. bataar* it starts in two grooves on the distal part of the hook and turns posteromedially. In the posterior end of the main body the articulation to the pterygoid differs. A large groove in *T. rex* is equivalent to two small grooves divided by a ridge in *Ta. bataar*. In ventral view the bone is very similar in the two.

Vomer (Fig. 15).—The vomer of *Ta. bataar* consists of a large rhomboid plate at the anterior end (recognized as an autapo-

morphy of Tyrannosauridae by Molnar 1991) and long, laterally flattened stem which is bifurcated posteriorly. The shape of the vomer is similar to that of *T. rex* (Molnar 1991: fig. 5). The bone is not preserved in *Ta. bataar* ZPAL MgD-I/4, partial in ZPAL MgD-I/3, but is well preserved in GIN 107/1. In the latter, the anterior rhomboid plate, ca. 20 cm long and almost 10 cm wide, is distorted and has been displaced towards the right side of the skull. This displacement shows that the palatal shelves of the maxillae meet anteriorly on the midline, and the vomer would normally overlap them ventrally. The anterior tip of the vomer definitely extends ventrally well onto the palatal surface of premaxillae, a situation not obvious in *T. rex* (Molnar 1991). The stem of the vomer in *Ta. bataar* lacks two pits (?dental fossae) observed in one specimen of *T. rex* (Molnar 1991). There is a long medial groove, representing the suture line of vomers, on its ventral side, extends over the rhomboid plate, but vanishes anteriorly. The posterior ends of the vomer are overlapped in the sagittal plane by the vomerine processes of the pterygoids. Immediately in front of this contact and just behind the internal nares, the vomers extend to the medial portion of the palatine.

Pterygoid (Fig. 15).—The pterygoid is not preserved in ZPAL MgD-I/4, but is seen in other specimens (GIN 107/1, GIN 107/2, GIN 100/70, PIN 551-2, ZPAL MgD-I/3). The general form of the pterygoid in *Ta. bataar* is similar to that of *T. rex* described by Molnar (1991). It consists of a flat, horizontal palatal plate and a vertical, plate-like quadrate process. From the posterior part of the palatal plate a short, blunt, posterior process protrudes to contact the basisphenoid and a triangular lateral process to contact the ectopterygoid, while the medial margin of the palatal plate extends anteriorly to form a vomerine process. The vomerine process is thin, gently curved and its proximal part is inclined anteromedially, but the distal part is oriented anteriorly. Thus the gap between the vomerine processes of the contralateral pterygoids narrows anteriorly (though they do not meet). The process starts as a ridge on the proximal part, but flattens laterally and lies in the same plane as the palatal plate.

The posterior process of the pterygoid is short and inclined slightly mediadorsally, to meet the basiptyergoid processes of basisphenoids. The ventral side of the palatal plate is flatter than illustrated by Maleev (1974) and, thus it is very similar to that of *T. rex* BHI-3033 (Fig. 15B₂, B₃). There are, however, differences in their shape with the medial margin in *Ta. bataar* being more sigmoidal and gently curved laterally in the anterior part. As in *T. rex*, the lateral margin is concave. A marked difference between the pterygoids of *Ta. bataar* and *T. rex* is the shape of the anterior edge of the palatal plate. In *T. rex* it is an oblique line, inclined slightly anteromedially-posterolaterally, joining the vomerine process at an angle of about 130 degrees (Molnar 1991: fig. 6). In *Ta. bataar* the edge is curved, anteriorly convex. Thus it recedes medioposteriorly and meets the vomerine process at an angle of about 50–70 degrees to the long axis of the skull, so the medial part of anterior edge of the palatal plate of the pterygoid does not contact the

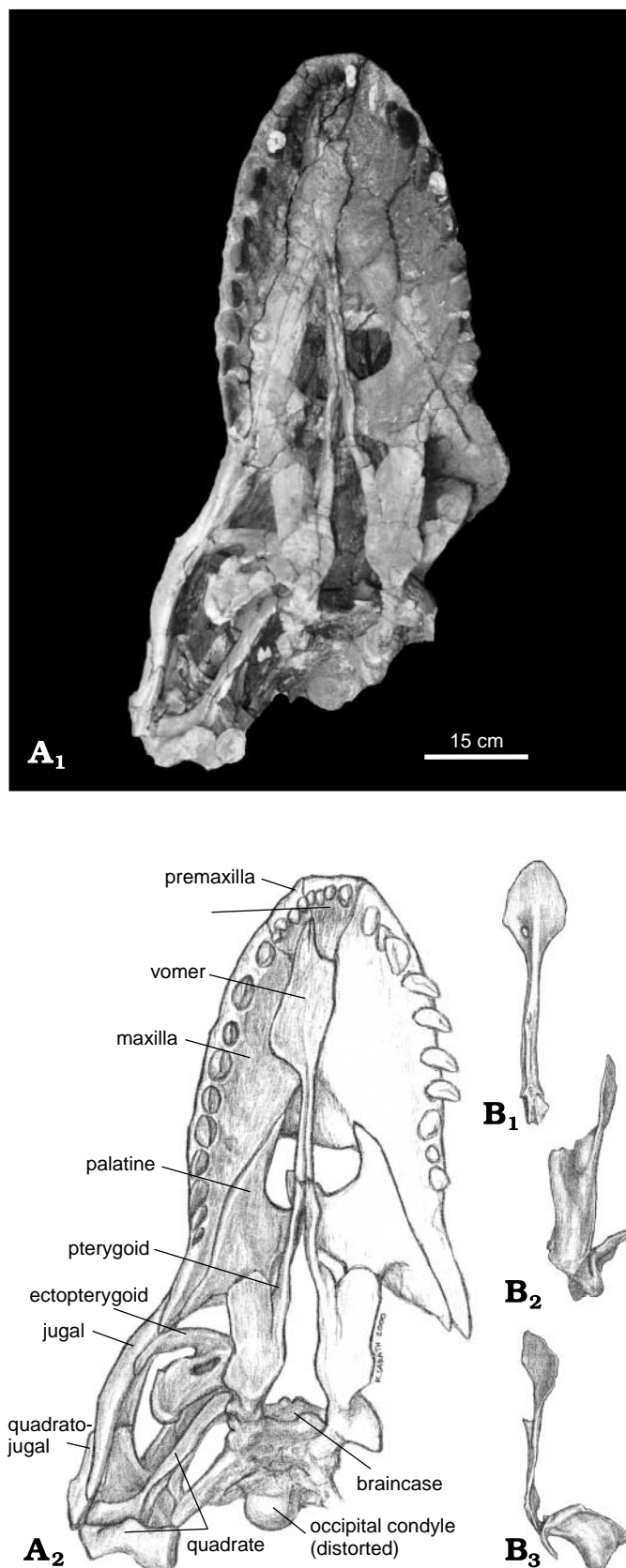


Fig. 15. A. Ventral view of the skull of *Tarbosaurus bataar* GIN 107/1 (A₁) and explanatory drawing of the same (A₂). B. *Tyrannosaurus rex* BHI-3033; lateral view of vomer (B₁), lateral view of pterygoid (B₂), dorsal view of pterygoid (B₃). Not to scale.

palatine. A triangular pterygopalatine fenestra opens between the pterygoid and palatine, bordered posteriorly by the medial part of the palatal plate, medially by the lateral side of the vomerine process and anterolaterally by the palatine.

The vertical, quadrate process of the pterygoid is compressed at the base and then very wide dorsally. It is inclined posterolaterally, so that it is parallel to the quadrate. It broadly underlaps the anteromedial part of the quadrate. The posterior margin of that process is less curved than in *T. rex* as reconstructed by Molnar (1991).

Epipterygoid (Fig. 16).—Maleev (1974) did not mention the epipterygoid, though it is often preserved in *Ta. bataar* where it articulates with the quadrate process of the pterygoid along a planar joint. The bone is preserved in ZPAL MgD-I/4 and also seen in ZPAL MgD-I/3 and GIN 100/70. The epipterygoid is thin and forms a vertically elongated triangle with a rod-like upper part. In *Ta. bataar* the basal part of the epipterygoid is flat, with slightly concave lower margin, and it overlaps the dorsal part of the vertical process of pterygoid, just anterior to the area overlapped by the quadrate. The epipterygoid narrows dorsally. The anterior edge of the rod-like process is slightly bent posterodorsally where it forms a ridge on the distal, swollen part. This tapers gently to form a tip oriented dorsally and slightly posterolaterally.

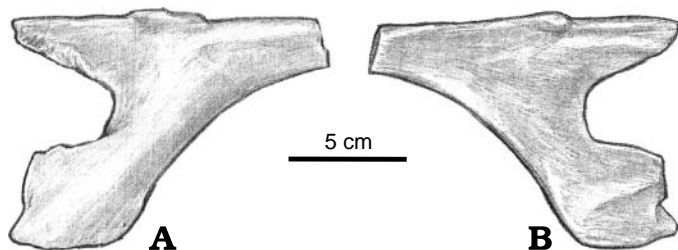


Fig. 16. Left epipterygoid of *Tarbosaurus bataar* ZPAL MgD-I/4 in lateral (A) and medial (B) views.

Molnar (1991) suspected that in *T. rex* the distal (upper) end of the epipterygoid contacted the laterosphenoid. In *Ta. bataar* there is no evidence for such a contact. If the quadrate and pterygoid are properly oriented in GIN 100/70, and in ZPAL MgD-I/3, then the upper end of the articulated epipterygoid points slightly away from the braincase. Only a rotation of quadrate and pterygoids to make them incline more mediodorsally would allow a contact between the epipterygoid and the laterosphenoid.

Quadrate (Fig. 9).—The quadrate is broken in ZPAL MgD-I/4, but the dorsal part of it contacting the squamosal and the articulation surface for the articular is well preserved. The middle part of the quadrate is separated from the quadratojugal by the large paraquadrate foramen. The upper contact surface between the quadrate and quadratojugal is almost vertical and lies in the parasagittal plane, while the lower is oblique, as the quadrate bulges medially in its ventral part, forming a large condyle. A slightly widened, con-

cave posteroventral end of the quadratojugal overlies the lateral surface of the condylar part of the quadrate.

The condyle itself is massive, and its two convex elliptical articular surfaces are separated by an oblique groove, as in other large theropods (*A. fragilis*, *T. rex*). The dorsal end of the quadrate has a saddle-like articular contact surface for the squamosal as in *T. rex* (Molnar 1991). The quadrate extends anteriorly into a deep, thin, flat pterygoid process, which distally bends slightly medially, and contacts the quadrate process of the pterygoid. The proximal part of the pterygoid process of the quadrate bears two concavities medially. These are separated by a rounded ridge oriented anterodorsally and merging into the flat medial surface of the anterior process of quadrate. Above the condyle there is a large, dorsoventrally elongated foramen in the anteromedial wall of the bone, leading to the internal sinus.

In lateral view, the bone is hardly visible, being hidden behind the quadratojugal. Only the posterior end of the condyle can be seen.

Braincase

Frontal (Fig. 17, Table 1).—The frontals are surrounded anteriorly by the nasals and prefrontals, laterally by the lacrimals and postorbitals, and posteriorly by the parietals. Their ventral surface forms the roof of the brain cavity (the telencephalic part), and joins with the parasphenoid ventrally, surrounding the brain from below. The smooth dorsal surface of the frontals is flat between the lacrimals, but further back it slopes down, along a semicircular anterior border of the upper temporal fenestra. The fenestrae are separated by the sagittal crest. Its anterior part is formed by the frontals, and the posterior part by the parietals. The interfrontal suture and sutures with parietals and postorbitals are indistinct and hardly traceable on the skull surface. Only the anterior part of the interfrontal suture is clearly visible, especially in younger individuals. The frontal is separated from the orbit by the lacrimal-postorbital contact. The sutural contact of the postorbital/frontal consists of a complex pattern of ridges and grooves common to both *Ta. bataar* and *T. rex*. In *Ta. bataar* two ridges divide the groove for the posterior part of the lacrimal, while this groove is deep and smooth in *T. rex*. This difference is also reflected in the shape of the posterior apex of the lacrimal (see lacrimal description). The contribution of the frontals to the skull roof and the shape of the frontal in dorsal view are both size related traits, and newly collected specimens of *Ta. bataar* show the changing trend (Currie 2003).

Table 1. Measurements of *Tarbosaurus bataar* (ZPAL MgD-I/4) and *Tyrannosaurus rex* (BHI-3038) frontals (in mm). Measured: ¹ on midline at front of supratemporal fossa; ² from most posterior end of the frontoparietal suture to dorsal junction of the frontal, nasal and prefrontal; ³ from midline to medial edge of slot between lacrimal and postorbital.

Specimen	Length ¹	Width ²	Depth ³
ZPAL MgD-I/4	120	105	80
BHI-3033	140	117	75

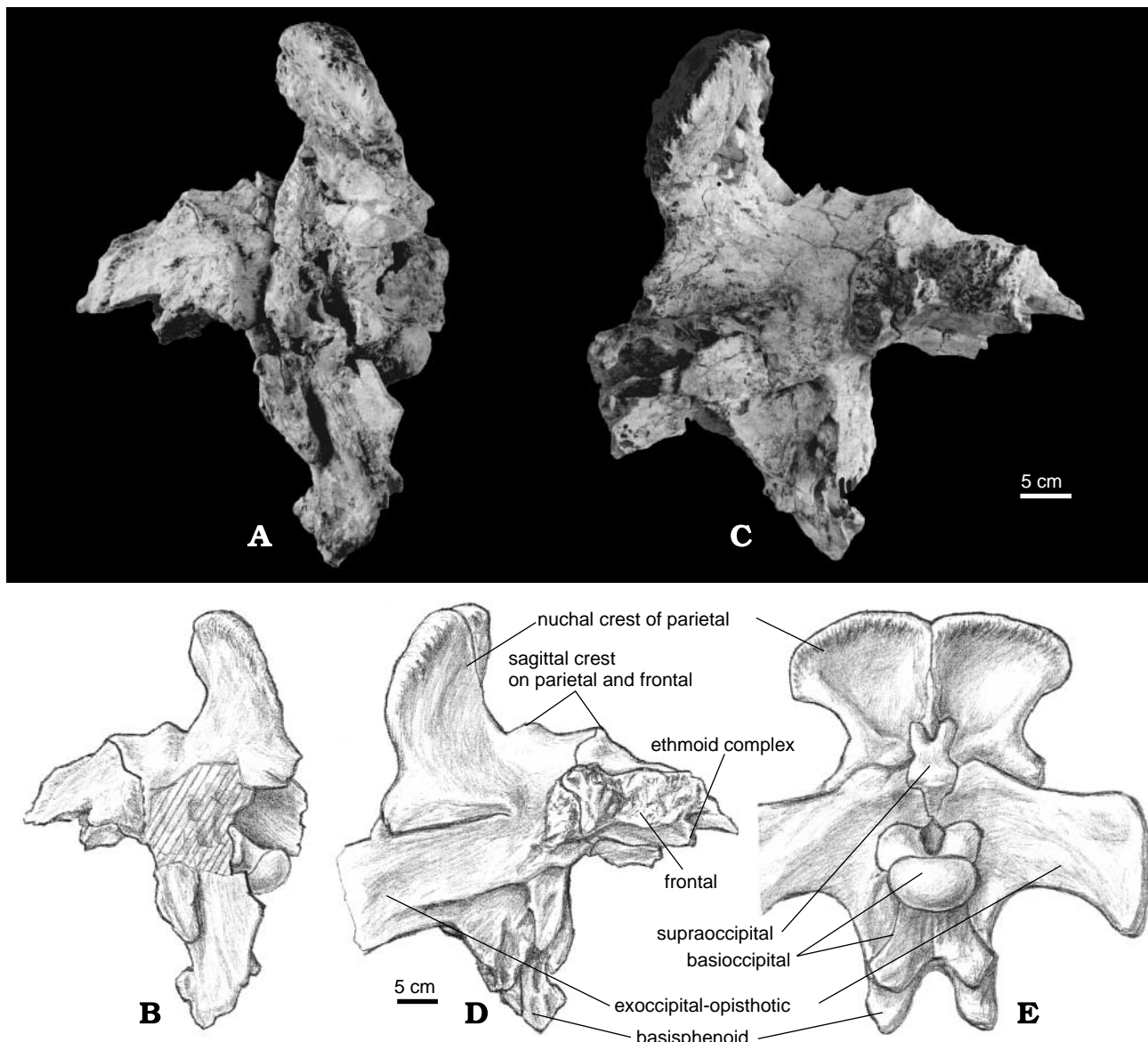


Fig. 17. Brainscase of *Tarbosaurus bataar* ZPAL MgD-I/4. A, B. Lateral view, left side. C, D. Lateral view, right side. E. Partly reconstructed occipital view.

Parietal (Fig. 17, Table 2).—Both parietals are fused together along the sagittal crest, which merges posteriorly with the transverse nuchal crest. The profile of the sagittal crest is concave, with the lowest point at the level of maximum lateral constriction of parietals when seen in dorsal view. The posterior part of the sagittal crest rises more steeply than the anterior part. The crest is thin, sharp, and its sides are almost parallel. They slope steeply downwards, especially in the isthmus between the upper temporal fenestrae. The nuchal crest is rather massive, higher than the sagittal crest and can be divided into two symmetrical alae, separated by a medial groove. Each is laterally expanded and has rounded edges; the dorsal edge is thick and convex in posterior aspect, while the lateral is thinner and concave. Along the dorsal edge the surface is rugose and the pattern extends onto the external and posterior side of the edge. The posterior wall of the ala is

slightly concave. The size and shape of the nuchal crest depends on the age of the individual. Thus in a juvenile specimen of *Ta. bataar*, the alae in dorsal view are slightly recessed posteriorly (GIN 100/70), while in adults (e.g., GIN 107/2) they lie exactly in a transverse plane, as they do in *T. rex* and *Nanotyrannus* (in *D. torosus* and *G. libratus* they are

Specimen	Width ¹	Width ²	Height ¹	Height ²
ZPAL MgD-I/4	320	190	240	130
BHI-3033	410	309	260	98

slightly concave. The size and shape of the nuchal crest depends on the age of the individual. Thus in a juvenile specimen of *Ta. bataar*, the alae in dorsal view are slightly recessed posteriorly (GIN 100/70), while in adults (e.g., GIN 107/2) they lie exactly in a transverse plane, as they do in *T. rex* and *Nanotyrannus* (in *D. torosus* and *G. libratus* they are

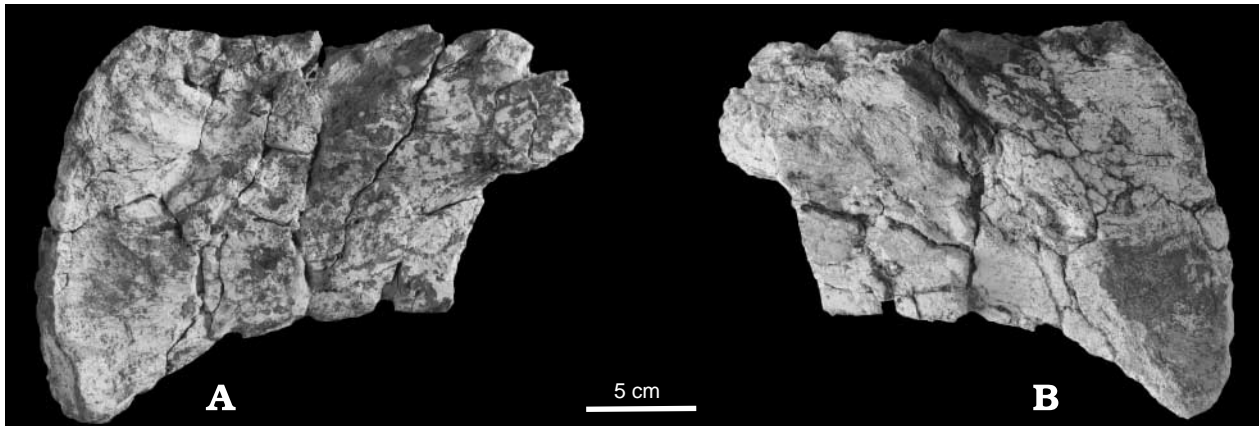


Fig. 18. Left exoccipital-opisthotic of *Tarbosaurus bataar* ZPAL MgD-I/4 in occipital (A) and medial (B) views.

inclined forward). In GIN 107/2, which probably represents a fully adult individual, they are not only thicker and more rugose, but also relatively smaller with regard to the whole occipital part of the skull. This is also true in large specimens of *T. rex* (e.g., BHI-3033). GIN 100/65 has two pronounced ridges on the posterodorsal side of the parietals. The ridges form a V-shape with its apex facing forward, and extending between the posterior 1/4 part of the sagittal crest and the upper edge of each nuchal crest. In other specimens (right side of GIN 100/2) such structures are hardly visible or absent.

The parietals occur evenly anterolaterally to meet the frontals along the transverse flexure marking the anterior part of the upper temporal fossae and where the parietals form their concave anterior walls. Maleev (1974) described the parietals as fitting into incisions in the squamosal, but this is not the case and they are barely in contact with the squamosal.

Ethmoid complex (Fig. 17).—The ethmoid extends along its midline of the skull roof, below the frontals. It reaches the parasphenoid posteroventrally and is partly overlapped by the nasals anterodorsally. The ethmoid bone of *Ta. bataar* ZPAL MgD-I/4 fits the description and figure of *T. rex* given by Osborn (1912: fig. 8). It is not preserved in BHI-3033. The ventral side of the bone is transversely concave and bears a sagittal septum in its anterior part. The ethmoid is wider and shallower anteriorly. The bone is also visible in front of the braincase in ZPAL MgD-I/3. No contacts with lacrimals have been observed.

Exoccipital-opisthotic (Figs. 17, 18).—As in all theropods, these bones are completely fused in tyrannosaurids. The exoccipital-opisthotics lie dorsolaterally from the basioccipital. The major part of each exoccipital-opisthotic is a plate extending laterally from the foramen magnum and bordered dorsally by the supraoccipital, parietals and squamosals. The plate is inclined posterolaterally. In *T. rex*, it contains an internal sinus occupying a dorsolateral portion of the exoccipital-opisthotic (Russell 1970; Molnar 1991). The exoccipital formed the posterior part of the braincase and is perforated by the foramina for cranial nerves IX–XII (Maleev 1974: fig. 12).

Maleev (1974) described separate “exoccipitalia” and “paroccipitalia, or opisthotica”, but did not mention that they are fused. The lateral parts of the exoccipital-opisthotic form large, winglike paroccipital processes, extending posteroventrally.

Basioccipital (Fig. 17).—The dorsal part of the basioccipital forms most of the occipital condyle (except most of its dorsal surface). In juveniles, the condyle is subspherical in shape, but in adults becomes reniform with a flattened dorsal part. The foramen magnum above the condyle is pear-shaped, elongated dorsally in ZPAL MgD-I/3, and rounded. It is proportionally smaller in larger specimens.

The ventral part of the basioccipital forms a rectangular plate descending on the posterior surface of the basisphenoid. The descending part of the basioccipital is slightly concave transversely. Ventrally, the descending part of the basioccipital broadens and forks into two basitubera. Dorsolaterally, it is not possible to see the suture to the exoccipital-opisthotics.

Supraoccipital (Fig. 17).—The supraoccipital is situated dorsal to the foramen magnum. The bone forms a triangle with its apex oriented ventrally, and an incision in the middle of the dorsal, thickened edge. Ventrolaterally, it fuses with the exoccipitals-opisthotics. Dorsally, it has a deep groove for the medioventral part of the parietal. The posterior surface of the supraoccipital bears a vertical medial ridge in its dorsal part. In *Ta. bataar* ZPAL MgD-I/4 the transverse width of the supraoccipital is less than the transverse width of the occipital condyle, while it is wider in *T. rex* BHI-3033.

Basisphenoid (Fig. 17).—The basisphenoid extends as a subtriangular plate in the transverse plane. Its posterodorsal edge is sutured to the ventral edge of the paroccipital processes and ventrolateral edges form the basiptyergoid processes. The processes have been broken in ZPAL MgD-I/4 and MgD-I/3, revealing internal sinuses. The fractured basiptyergoid process shows several oval sinuses separated by thin septa oriented anteromedially-posterolaterally. The presence of sinus chambers in the basisphenoid has been

noted in *T. rex* by Osborn (1912) and Molnar (1991), as well as in *G. libratus* by Russell (1970), who presented a diagrammatic reconstruction of the extent of those sinuses. In Russell's reconstruction (Russell 1970: fig. 4), only a large, single sinus is visible in the ventral part of the basisphenoid, while several are present in *Ta. bataar*.

Sclerotic ring.—The sclerotic ring is only preserved in a subadult specimen with the skull length of about 0.8 metre, GIN 100/70. Here the sclerotic ring has an external diameter of about 65 mm and internal diameter of 30 mm. It consists of 15 plates. The sclerotic ring is still relatively large in this juvenile individual, and the orbit is almost oval. The “keyhole shape” of the orbit in adults defines the space for the eye at the upper end. The eye in juveniles would also occupy proportionally more of the orbit.

Mandible

The mandibles of *Ta. bataar* and *T. rex* were recently described by Hurum and Currie (2000). Here we repeat some of their observations and add a more thorough description of each bone. In *Ta. bataar*, as in all tyrannosaurids, the posterior part of the mandible is deep and connected with the dentary by an intramandibular joint. The posterior part deepens progressively in ontogeny. The posterior end is transverse, without a retroarticular process, though in the largest specimens a stout posteromedial process may develop on the articular. There is a small anterior surangular foramen. The mandibular fenestra is also small and becomes dorsoventrally compressed in ontogeny.

Dentary (Fig. 19, Table 3).—The ventral margin of the dentary is almost straight, slightly concave. The symphyseal margin ends below the third tooth and rises anteriorly and obliquely to reach the anterior end of the tooth row. It is slightly convex in lateral view and its transition into the ventral margin of the dentary varies from gentle curvature (as in ZPAL MgD-I/4), to a rather sharp flexure (like in PIN 551-3, or GIN 107/1; where a rugosity exists at that point on the left dentary). A rugose zone extends on the mesial margin of symphyseal surface. In lateral view, the dentary of *Ta. bataar* (ZPAL MgD-I/4) is more pointed anteriorly than in *T. rex* (BHI-3033), but this might be an allometric difference.

The dentary bears a row of circular pits parallel to the tooth row along the labial margin, some 2–3 cm below the teeth, and spaced each 1–2 cm (slightly more than one per tooth) in the posterior part and more frequent in the anterior end. Other, less numerous pits open below at the external surface of the dentary. On the lingual side at the level of tooth 2 to 12, it bears a gently down-curved Meckel's groove at 1/3 of its height from its ventral edge. At its anterior end this groove is the same as in *T. rex* (BHI-3033), but its posterior part is moved dorsally. The Meckel's groove runs below, and parallel to, a more prominent groove, marking the lower margin of the supra-dentary. The dentary is rather stout and massive in its anterior part, bearing larger teeth. The posterior part is rather thin,

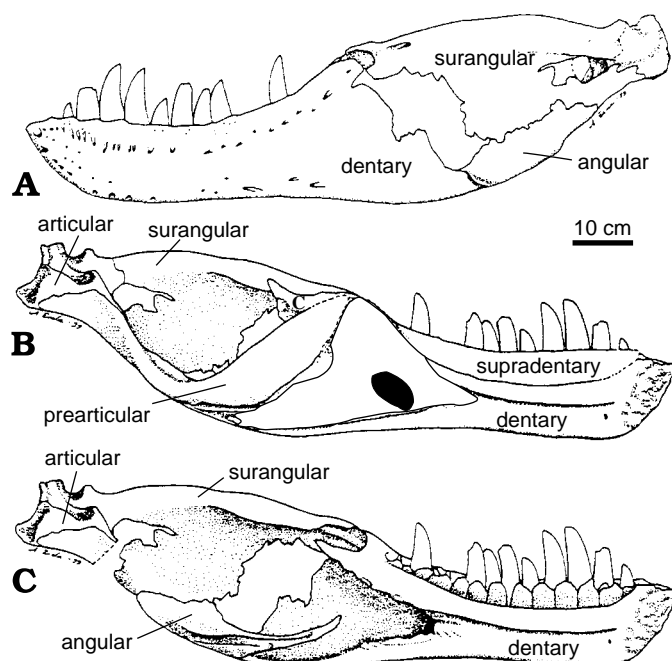


Fig. 19. Mandible of *Tarbosaurus bataar* ZPAL MgD-I/4. A. Lateral view, B. Medial view. C. Medial view with prearticular and splenial removed. Based on Hurum and Currie (2000), except for a new reconstruction of the splenial.

Table 3. Measurements of *Tarbosaurus bataar* and *Tyrannosaurus rex* dentaries (in mm). ¹ length of the dentary tooth row; ² minimum lateral depth of the dentary at about midlength; ³ height of longest dentary tooth crown = enamel covered part.

Specimen	Length ¹	Depth ²	Tooth ³
ZPAL MgD-I/4	480	120	85
BHI-3033	580	170	100

though much deeper than the anterior one. It is strengthened by two bars of bone, forking at the level of 10th to 11th teeth. Here is the apex of a triangular fossa, separating dorsal and ventral bars on the labial side of dentary (the anterior end of Meckelian fossa), from which a groove continues anteriorly. The triangular Meckelian fossa between the bars is overlain by the splenial, which is only partially preserved in ZPAL MgD-I/4 and rarely preserved *in situ*.

The posterodorsal part of the dentary has a long medial process and a shorter lateral process separated by a deep pocket. The dorsolateral process (the intramandibular process of the dentary, Currie and Zhao 1993), fits into a slot on the medial side of the surangular (Hurum and Currie 2000).

The thin, ventroposterior margin of the dentary is often broken away. In better preserved specimens, like ZPAL MgD-I/4, it runs obliquely posteroventrally from behind the end of mandibular tooth row and ends on the ventral margin of the mandible, where the lower jaw is deepest. In *Ta. bataar*, the posteroventral part of the dentary has an abrupt, square end, concave medially in transverse section where it

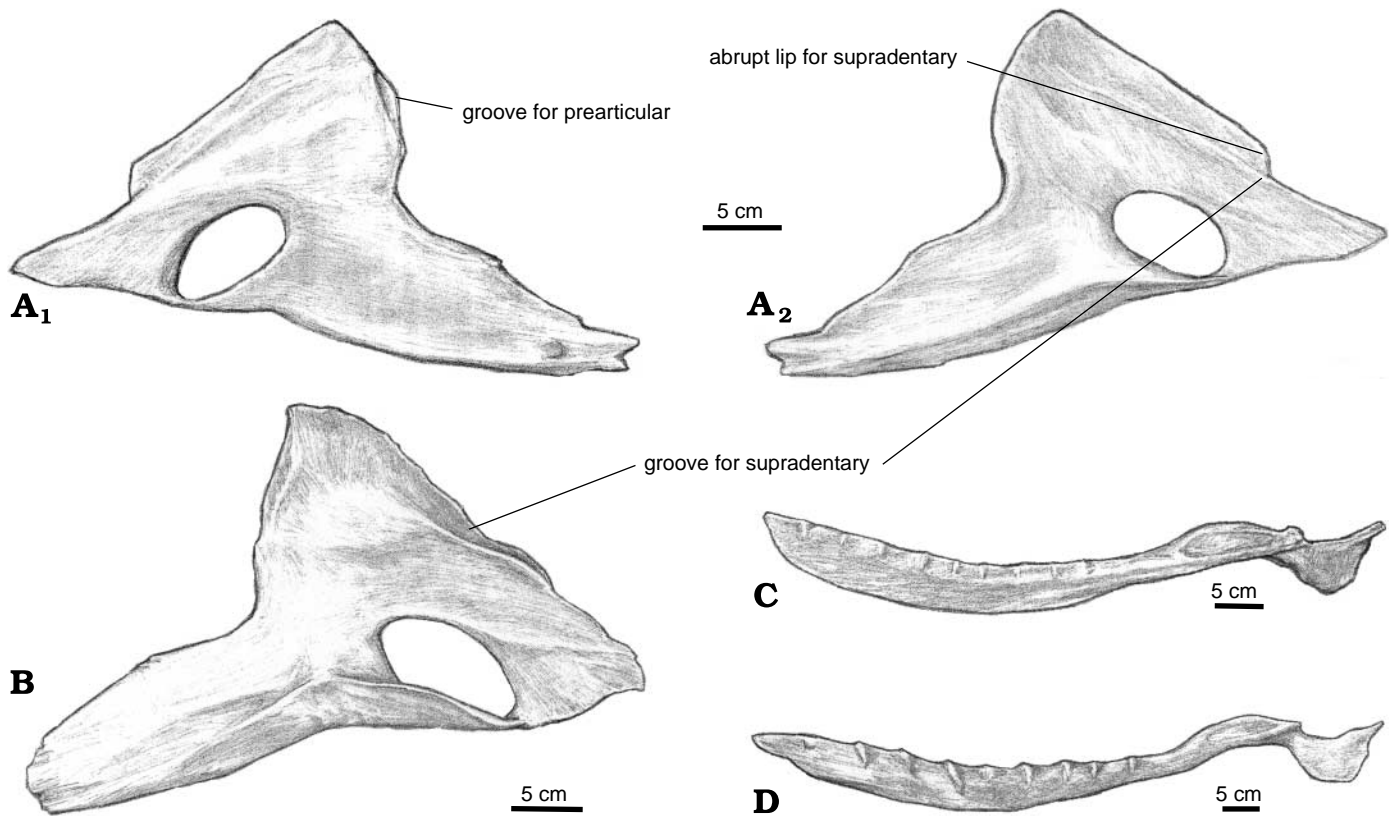


Fig. 20. **A.** Reconstructed splenial of *Tarbosaurus bataar* (based on both ZPAL MgD-I/34 and MgD-I/4) in medial (lingual) (**A₁**) and lateral (**A₂**) views. **B.** Lateral view of the left splenial of *Tyrannosaurus rex* BHI-3033. **C.** Medial view of the supraddentary of *Tarbosaurus bataar* ZPAL MgD-I/4. **D.** Medial view of the supraddentary of *Tyrannosaurus rex* BHI-3033.

meets the angular. Its posterior end articulates with a perfectly matched vertical ridge on the lateral surface of the angular. In *T. rex* and *G. libratus*, there is a smooth groove on the angular with no abutting ridge for the posteroventral end of the dentary (Hurum and Currie 2000).

Supraddentary/coronoid (Figs. 19, 20).—The supraddentary is a flat bone, extending on the labial side of the dentary along the tooth row. It covers the interdental plates. The lateral surface of the bone bears shallow concavities, corresponding to the interdental plates (Maleev 1974) and weak ridges that fit between the teeth (Hurum and Currie 2000). As in *T. rex*, the supraddentary of *Ta. bataar* extends backwards from the septum between the 2nd and 3rd teeth, to the end of the tooth row. Here it thins to fit between the last teeth bases, the splenial and prearticular, and is fused to the coronoid (Hurum and Currie 2000). The tyrannosaurid supraddentaries are bent ventrally as in *Allosaurus* (Madsen 1976: pl. 9D, erroneously labelled “C” on the drawing), but much deeper dorsoventrally, so that they resemble a “stretched crescent”, with the ventral edge more curved than the dorsal edge, rather than a strip of bone.

The coronoid of *Ta. bataar* is a small, thin, flat, triangular bone, clearly visible on the lingual side of the right mandible of ZPAL MgD-I/4 and GIN 107/1, fitting between the prearticular and surangular. Its shape, size and location corre-

spond strictly to that of *T. rex* as illustrated by Osborn (1912). The anterodorsal side of the triangle contacts the surangular, the large, flat medial surface is partially covered by the anterodorsal section of the prearticular (the sharp, elongated anterior apex of coronoid is squeezed between the two bones and bends slightly upwards). The posteroventral side is free and hangs over the Meckel’s groove and the surangular. Molnar (1991: 155) describes the coronoid as “lying at the anterodorsal angle of the Meckelian fossa”. This correctly describes the appearance of the coronoid in a fully articulated mandible, but it should be remembered, that the fossa extends much farther anteriorly and is covered by the prearticular and the splenial.

Splenial (Figs. 19, 20).—The splenial is only partially preserved in ZPAL MgD-I/4. A complete splenial is present in the right mandible of GIN 107/1, in ZPAL MgD-I/134 the main body of the right splenial is preserved, and only the dorsal part is missing in ZPAL MgD-I/5. The splenial is a triangular bone, flattened so that it lies in a parasagittal plane, with the long base oriented almost parallel to the ventral margin of dentary. In *T. rex* the ventral margin is more inclined and the anterior tip of the splenial is placed higher, because of the more dorsal position of the posterior part of the Meckel’s groove on the dentary. The lingual surface of the splenial lies at the same level as the lingual surface of the an-

terior part of the dentary. The ventral edge of the splenial is thicker than the rest of the bone and in close contact with the ventral bar of bone in the posterior part of the dentary. The anterodorsal edge contacts the dorsal bar of the dentary. Thus, the splenial tightly covers the triangular fossa, and the anterior part of the Meckelian fossa in the dentary, except for the foramen, adjacent to the ventral margin of splenial. The foramen is oval (ellipsoid) with its long axis oriented anteroventrally-posterodorsally. Its anterior end almost reaches the ventral bar of the dentary at the level of 11th tooth, while the posterior lies at the level of the last alveolus (and the posterior end of supradentary). The width of that foramen is about 2/3 of its length, and is roughly equal to the distance separating it from the anterodorsal margin of splenial. The posterodorsal edge of splenial is deeply convex, contacts the prearticular along its upper part and has a small groove for the prearticular. The dorsal apex is blunt. The posterior bifurcated tip of the posteroventral process meets the angular. The posteroventral process of ZPAL MgD-I/4 has a foramen directed dorsoventrally which is not seen in any other specimens. The anterodorsal side of the triangular splenial has a marked lip, and in lateral view this lip has a groove that fits the supradentary. The shape of the lip differs in different tyrannosaurids, the two extremes being the gradual, not very pronounced lip of *Tyrannosaurus* and the abrupt lip of *Tarbosaurus* (Fig. 20A₂, B).

Maleev (1974: fig. 19) illustrated the splenial of *Ta. bataar*, as the right side splenial of PIN 551-2 in lingual view. It is however the lingual view of a left splenial. In lateral view a longitudinal ridge along the ventral margin would be visible; the ridge marks the flexure between the flat surface of bone, and the obliquely sharpening “blade” of the contact surface for the ventral bar of the dentary, as can be seen in isolated splenials of ZPAL MgD-I/34. The facet is widest in the middle, and thins toward both ends, as the ridge that borders it is curved. Moreover, the anterior margin of the splenial illustrated by Maleev is uneven, because of fractures in the dorsal part and the tip of the anterior process is broken. The ventral margin of the bone below the splenial foramen is also incomplete, giving the impression of a wide gap, while the foramen, though much larger than in *Allosaurus* (Madsen 1976: pl. 9), does not break the ventral margin of bone. The longitudinal opening in the posterior process shown by Maleev seems to exaggerate the concavity of the splenial.

Angular (Fig. 19).—The angular in *Ta. bataar* consists of a posterior flat, wing-like plate, flaring posterodorsally in the parasagittal plane and of an anterior finger-like stem, oriented dorsoanteriorly. The posterior plate is slightly concave medially and convex ventrolaterally. In lateral aspect, it forms the posteroventral margin of the mandible and is bordered dorsally by the surangular and anteriorly by the dentary. In medial aspect, most of the posterior plate of the angular is hidden behind the prearticular. Only a small triangular part of the angular is visible near the flexure of the ventral margin of the mandible. The angular in medial aspect is bordered by

the prearticular dorsally and by the splenial anteriorly. The stem fits between the prearticular and the splenial which covers its distal part medioanteriorly. In its proximal part the lateral surface fits against the medial side of the posteroventral corner of the dentary. The vertical ridge on the lateral surface of the angular for the posteroventral end of the dentary is only seen in *Ta. bataar*. In *T. rex* and *G. libratus*, there is a smooth groove on the angular. In both *Ta. bataar* and *T. rex*, the anteromedial groove for the posteroventral part of the splenial is deep (Hurum and Currie 2000). A small groove dorsoanterior to the main splenial groove is only found in *Ta. bataar* and indicates the different shape of the medial side of the posteroventral part of the splenial.

The medial side of the angular in both *T. rex* and *Ta. bataar* contains two ventral ridges. One starts at the anterior end of the stem, separates the prearticular and splenial grooves and continues posteriorly as the ventral margin of the angular. The other is shorter and placed dorsal to the posterior part of the first ridge. Both ridges have corresponding grooves on the prearticular. The groove in the prearticular for the long ridge is smooth in *T. rex*, while in *Ta. bataar* it contains two notches into which grooves on the long ridge interlock.

Molnar (1991) described the angular of *T. rex* as being “much like that of *Allosaurus fragilis*”. The main difference between the tyrannosaurid and allosaur angular is the shape of its anterior part. In *Allosaurus* (Madsen 1976: pl. 7D, E) the anterior process of articular is an almost flat, blade-like triangle. In tyrannosaurids it forms a thin, fingerlike stem with a ridge along the medial side (Maleev 1976: fig. 17; Molnar 1991: pl. 15).

Surangular (Fig. 19).—The surangular is a large, flat bone forming most of the posterior part of the mandible in lateral aspect. It consists mostly of a thin plate oriented parasagittally. Its height is the reason why the mandible of tyrannosaurids is much deeper than in other theropods. It narrows anteriorly and posteriorly. The bone is slightly convex dorsolaterally, and the upper margin is bent medially to form a thick medial flange which dorsally borders the large Meckelian fossa on the labial side of the mandible. Another, shorter ridge runs on the lateral side in the posterior part of the bone between the dorsal margin and the surangular fenestra, close to the jaw articulation. The surangular fenestra perforating the bone near its posterior end, is elliptical and fully visible in lateral aspect. Thus it is not hidden by the hanging flange of the lateral ridge of the surangular as in *T. rex* (Osborn 1912: fig. 1), but less in BHI-3033. In tyrannosaurids the surangular is overlapped anteriorly by the dentary along an oblique (dorsoanterior-ventroposterior) line. The opposite was reconstructed by Carr (1999: figs. 5, 6).

The surangular has two anterodorsal processes, a large medial, and a smaller lateral process. The long medial process fits deeply into the pocket between the pair of posterodorsal processes of the dentary, thereby restricting the mediolateral movement between the two bones (Hurum and Currie 2000). The surangular is overlapped by the angular ventrolaterally.

Posteriorly the posterior, thickest part of surangular inter-fingers with the articular and medially it meets the pre-articular, forming the anterior part of the mandibular articular surface. It is possible to see the sutures, but impossible to prepare them apart in MgD-I/4. In *T. rex* (BHI-3033) the bones are less fused and it is possible to disarticulate them.

Prearticular (Fig. 19).—The prearticular consists of the posteroventral body and anterodorsally directed ramus, with approximately perpendicular axes, both lying in a parasagittal plane. The body occupies the posteroventral margin of the mandible. The body of the bone stretches obliquely from the area of the mandibular joint, where it partially fuses with the articular, along the ventral margin of the surangular. The bone is located medioventrally to both angular and surangular. The body of the bone is bar-like, oval in cross-section and thinnest in the mid-length. A low, blunt ridge runs along the body of the prearticular, on the lateral side. It begins on the dorsal side at the posterior end of the bone and forms a posteroventral rim of the Meckelian fossa. The ridge then continues anteroventrally towards the medial side, and near the lowest point of the bone on the medioventral side, its shape continues further on the ventral flexure of the angular.

The anterodorsal ramus is a mediolaterally flattened sheet of bone, ascending along the posterior end of splenial, covering the Meckelian fossa posteriorly to the splenial. The ramus is of even width in its proximal and medial part, but thins distally, and terminates dorsally near the upper edge of the mandible in contact with the coronoid. The posterodorsal part of the splenial covers the anterodorsal margin of the prearticular (Hurum and Currie 2000).

When the angular is removed, the body of the bone is covered by six slightly anterodorsally directed ridges and five grooves in lateral view. The most ventral ridge is the ventral guide for the groove for the long ridge observed on the angular. Anterior to the ridge is a notch that fits into the angular. Dorsal to the first ridge on the prearticular is the second ridge that forms the ventral border for the groove for the second, shorter ridge on the angular. A third short, but very prominent ridge on the prearticular marks the dorsal limit for the posterior part of the short ridge on the angular. There are three long, weaker ridges dorsal to the three prominent ridges that do not have any contact with other bones. The pattern of the three main ridges is the same in *T. rex*, except for the notch in front of the first ridge that is not present. The three dorsal, weaker ridges are not found in BHI-3033.

Articular (Fig. 19).—The articular is a short, stout bone, forming the posteriormost part of the mandible, including the transversely expanded facet of the mandibular joint. The glenoid fossa consists of two concave surfaces, separated by an oblique ridge. The articular is strongly fused with the prearticular anteromedially. Anterolaterally, the articular contacts the surangular. The posterior end is expanded into an oval (semicircular) shallowly concave surface, facing slightly medially.

The tyrannosaurids lack the retroarticular process. This is also the case of *Ta. bataar*, though in the large and probably gerontic specimen GIN 107/2, there are prominent ventromedially bent processes, protruding posteriorly from both articulars. This feature is however unique among the studied specimens and may be considered an individual variation, related to age or some pathology. Normally, only a low ridge or short medial process is observable on the medial edge of the posterior surface of the articular.

Dentition

The terms tooth counts, tooth positions, and numbers of alveoli are synonymized in the following description. Each premaxilla of *Ta. bataar* bears four teeth. The teeth are smaller than those of the maxilla and more slender. Each premaxillary tooth is compressed so that the longer axes of their D-shaped cross sections are perpendicular to the tooth row (the extrapolated long axes of the teeth cross sections would meet near the anterior end of the vomer).

The maxilla bears 12–13 teeth in *Ta. bataar*, 12 in ZPAL MgD-I/4. The tooth count may differ in both maxillae of the same individual (e.g., in GIN 107/1 there are 12 teeth in the left maxilla and 13 in the right). Such differences in tooth

Table 4. Measurements of the individual bones of *Tarbosaurus bataar* ZPAL MgD-I/4 (in cm); ¹ maximal anteroposterior length; ² maximal dorsoventral depth.

ZPAL MgD-I/4	Length ¹	Depth ²
The skull as a whole	110	43
Premaxilla	11	~16
Maxilla	63	36
Nasal	64	10
Lacrimial	35	29
Prefrontal	11	8
Postorbital	~20	27
Squamosal	27	15
Jugal	51	30
Quadratojugal	20	21
Vomer	–	–
Palatine	29	13
Ectopterygoid	18	6
Pterygoid	–	–
Epipterygoid	13	2
Quadrate	16	28
Frontal	12	8
Parietal	16	17
Exoccipital-opisthotic	~25	18
Dentary	73	23
Supradentary/coronoid	59	6
Splenial	reconstructed	
Angular	40	~12
Surangular	47	~23
Articular	13	11
Prearticular	49	24

number are independent of growth stage of the individuals, as noted by Russell (1970) for *Albertosaurus* and *Daspletosaurus*. In *T. rex* (BHI-3033) there are 11 teeth in the maxilla (11–12 in others).

In *Ta. bataar* the dentary bears 15 (rarely 14) teeth. The base of the mandibular dental row, occupying almost the whole upper edge of dentary, is concave. The anterior part is almost straight, while the posterior rises markedly. The teeth, however, are smaller in the posteriormost part of the row, so the tips of fully grown mandibular teeth lie on an almost straight line, sloping down at both ends (the first and last two teeth do not reach the medium level). The longest teeth are at the positions 3 to 9. There are 12–14 dentary teeth in *T. rex*.

In *Tarbosaurus bataar* (ZPAL MgD-I/4) the teeth have up to 85 mm long crowns. The serration count is 3 serrations per mm on the premaxillary teeth, 2 serrations per mm on the maxillary, and 2 serrations per mm on the dentary teeth. In *Tyrannosaurus rex* (BHI-3033) the teeth have up to 100 mm long crowns. The serration count is 3 serrations per mm on the premaxillary teeth, 2 serrations per mm on the maxillary, and 2 mm on the dentary teeth.

Table 5. Measurements of the individual bones of *Tyrannosaurus rex* BHI-3033 (in cm). ¹ maximal anteroposterior length; ² maximal dorsoventral depth.

BHI-3033	Length ¹	Depth ²
The skull as a whole	~140	57
Premaxilla	15	27
Maxilla	79	38
Nasal	81	9
Lacrimal	35	38
Prefrontal	9	10
Postorbital	33	37
Squamosal	40	30
Jugal	60	42
Quadratojugal	26	25
Vomer	44	7
Palatine	38	15
Ectopterygoid	22	12
Pterygoid	56	25
Epipterygoid	–	–
Quadrate	34	30
Frontal	9	13
Parietal	20	21
Exoccipital-opisthotic	25	17
Dentary	90	28
Supradentary/coronoid	72	6
Splenial	50	21
Angular	55	25
Surangular	65	25
Articular	20	14
Prearticular	57	37

Discussion

More attention has been paid to North American tyrannosaurines (NATs) than to their Asian relatives and until now they have all been considered to share the same general skull structure. The Asiatic tyrannosaurines have been assigned to various taxa (see Introduction) and discussions focused mainly on their validity and the possibility of them being growth series or ecomorphs. Little attention has been directed at the detailed relationships between the Asiatic forms and NATs. Since the pioneering work by Maleev (1955a, b, c, 1964, 1965, 1974), the best known Mongolian specimens were usually regarded as being closely related to, or even congeneric, with *Tyrannosaurus* and *Gorgosaurus* (including *Albertosaurus*). No detailed phylogenetic hypotheses were, however, put forward until recently (Holtz 2001; Currie et al. 2003).

The new material studied in this paper allows us to speculate if the tyrannosaurines can be divided into NATs and an Asiatic group. This is not a formal division, and more of a working hypothesis that needs to be addressed more thoroughly in a biomechanical analysis, which is beyond the scope of this paper.

NATs show a consistent pattern of the cranial joints with minor differences, described by Russell (1970), Bakker *et al.* (1988), Molnar (1991), and Carr (1999), but see *Daspletosaurus* described by Currie (2003) which may be a link between the Asiatic group and NATs. Of particular interest are the dorsal joints handling the dorsally directed impact on the maxilla. From anterior to posterior this impact line is formed by maxilla-nasal-lacrimal-frontal/prefrontal. From studies of the sutures between the bones in *T. rex* BHI-3033, it is evident that the stress must have been directed from the maxilla to the nasal via an immobile articulation of transverse ridges and grooves. The nasal has a lacrimal process in the posterior end for the anterior end of the lacrimal. The dorsoposterior end of the lacrimal is robust and fits into a large groove in the frontal and medially contacts the prefrontal. The lacrimal process of the nasal is present in all NATs, except a large specimen of *Daspletosaurus* (Currie 2003), while the complexity of the maxilla-nasal contact differs.

Studying the sutures in *Ta. bataar*, we noticed that there is an evolutionary shift to a direct route of the impact stress from the maxilla to the lacrimal. The anterodorsal end of the lacrimal bends more ventrally than in NATs and fits as a sheath around the massive, posterodorsal end of the maxilla. The posterodorsal end of the lacrimal is supported by a ridge and groove system in the prefrontal and frontal that locks the lacrimal more thoroughly to the basicranium than it does in NATs. The prefrontal contributes to a larger degree to the posteromedial articulation surface for the lacrimal, and has a long ventrally directed process that fits onto the medial side of the lacrimal. In NATs the posterodorsal end of the maxilla is thin and laterally compressed, and the prefrontal is smaller. The robust articulation between the maxilla and lacrimal and

lack of a lacrimal process on the nasal are also observed in *Alioramus* (Kurzanov 1976: figs. 1, 2). These robust articulations between maxilla-nasal-lacrimal-frontal/prefrontal are in contrast to the paper-thin dorsoposterior end of maxilla, especially in *T. rex*, that only covers a small portion of the anteriormost lacrimal.

The lacrimal process of the nasal for the anterior end of the lacrimal is widely distributed among theropods e.g., *Allosaurus* (Madsen 1976), *Sinraptor* (Currie and Zhao 1993) and *Carnotaurus* (Bonaparte et al. 1990). In *Eotyrannus* (Hutt et al. 2001) the process is not preserved (see also Currie et al. 2003). In *Allosaurus* the main stress distribution in the skull during maximum impact is between the maxilla and lacrimal (Rayfield et al. 2001); this is also the case in *Ta. bataar*, judging from the sutures. But the articulation of the maxilla-nasal-lacrimal is also similar in *Allosaurus* (Rayfield et al. 2001) to albertosaurines and NATs (Currie et al. 2003). The more primitive allosaurid double skull articulation provide, information on the plesiomorphic condition of an ancestor to both NATs and *Ta. bataar*/*Alioramus*. Both articulations were present in a common ancestor and the two different articulations were improved separately. Our new description of the skull morphology of *Ta. bataar* supports the relationship with *Alioramus*, but rejects the more traditional one, in which *Ta. bataar* with *T. rex* were placed together in the same genus (e.g., Holtz 2001). We believe that the similarities between *Tarbosaurus* and the more derived *Tyrannosaurus* may result from parallel evolution, as they shared tyrannosaurine synapomorphies and were subject to similar selective pressures as large, top predators in their respective palaeoecosystems.

Both Asiatic and North American latest Cretaceous tyrannosaurines hunted large prey, while also being opportunistic scavengers (Horner and Lessem 1993). However, the prey available to them were obviously different. Among the kinds of NATs, the adult *T. rex* was the largest animal in the ecosystem and probably specialized in bringing down large horned dinosaurs, like *Triceratops* (Erickson and Olson 1996), but this group was absent outside North America. Thus, the Mongolian tyrannosaurines were forced to feed on sauropods, hadrosaurs (also true for NATs, see Carpenter 2000), and perhaps also ankylosaurs. These differences in typical prey items might have exerted different selective pressures, concerning hunting strategy and mechanical requirements maximizing their success rate as predators. It is interesting to note that ontogenetically the tyrannosaurines probably passed through several niches, specializing in different prey categories at subsequent growth stages. It now seems that the adult *T. rex* reached a stage never attained even by the largest Mongolian tyrannosaurines, which have a "paedomorphic" appearance if the shape of their skull is compared. Such a difference in ecological niche would substantiate the separation of *T. rex* and *Ta. bataar* at the genus level. On the other hand, *Ta. bataar* had more rigid jaws than *T. rex*. We can only guess at its functional meaning. One possibility is that the lateral expansion of the posterior part of the skull in *T. rex* served to both increase the force of the crush-

ing bite and stereoscopic abilities. The latter was probably especially important in precise judgement of distance to the ceratopsian prey, armed with dangerous horns and also when hunting small prey. Other, less well-armed, large prey species, such as sauropods, probably did not require such a precision, and the crushing force could have been lower. The less kinetic upper jaw and mandible of Mongolian tyrannosaurines might partially compensate for their relatively weaker posterior parts of the skull when struggling with massive sauropod prey.

Conclusion

The skull of *Tarbosaurus bataar* differs from that of *Tyrannosaurus rex* in several important anatomical structures (*Tyrannosaurus rex* character states in parentheses):

- Maxilla: The massive, posterodorsal process of the maxilla has the anterior end of the lacrimal as a sheath around its posterior end (thin and plate-like).
- Nasal: The lack of lateral expansion and lack of a posteriorly oriented lacrimal process. The articulation to the lacrimal is only a smooth groove (lacrimal process).
- Lacrimal: The horizontal ramus narrows gradually towards its anterior end, where it is divided by a short mediolateral cleft. The clefted process fits into the robust posterior end of the maxilla. The posterior surface of the apex forming the suture to the frontal and prefrontal is divided vertically by a rugose ridge (anterior end of horizontal ramus clearly bifurcated and fits into the nasal).
- Prefrontal: The lateral side of the prefrontal has several ridges for the attachment of the lacrimal, and supports most of the posteromedial side of the bone (smaller contact area).
- Palatine: the dorsoposterior jugal-lacrimal process is in contact with the most ventral part of the lacrimal and visible in lateral view in the skull (not visible).
- Dentary: the posteroventral part has an abrupt, square end, concave medially in transverse section where it meets the angular. This posterior end articulates with a perfectly matched vertical ridge on the lateral surface of the angular (thin posteroventral end with no abrupt end)
- Angular: vertical ridge on the lateral surface for the articulation with the dentary (smooth groove on the angular with no abutting ridge).
- Splenial: an abrupt lip for the supradentary (not very pronounced lip).
- Dentition: 12–13 maxillary teeth, 14–15 dentary teeth (11–12 maxillary and 12–14 dentary).

Ta. bataar and *Alioramus* share specific mechanisms for transmitting stress acting on the jaws. The nasal is excluded from the major series of bones participating in deflecting the impact in the upper jaw, and the dentary-angular interlocking makes a rigid lower jaw. Such functional anatomical solutions may be regarded as their unique synapomorphy, not found in any other theropod group.

Acknowledgements

The comparative studies of tyrannosaurid material in Poland, USA, Canada, Russia and Mongolia were enabled by research grants from the Norwegian Research Council grant no. 122898/410 (to JHH) and from the Polish Committee for Scientific Researches (KBN) grant no. 407259101 (to Halszka Osmólska and KS). We wish to thank the following persons and institutions for allowing us to examine the specimens in their care: Dr. Altangerel Perle and Khishigjav Tsogbaatar (State Museum in Ulaanbaatar), Dr. Rinchen Barsbold (Geological Institute of the Mongolian Academy of Sciences, Ulaanbaatar), who also permitted the study Mongolian tyrannosaurid specimens temporarily exhibited at the Naturhistorisches Museum Wien, with kind cooperation from the Museum director, Dr. Heinz A. Kollmann, and Dr. R. Golebiewski; Dr. Mark Norrell (American Museum of Natural History in New York), Darren Tanke, who introduced us to the material at the Royal Tyrrell Museum of Palaeontology in Alberta, Drumheller, as well as in the Field Station in Brooks, Alberta, and on display in Edmonton; Dr. Thomas Carr and Dr. Hans-Dieter Süess (Royal Ontario Museum, Toronto), Dr. Sergey M. Kurzanov and Dr. Konstantin E. Mikhailov, who provided access to the holotype and paratypes of *Tarbosaurus* in the Orlov Palaeontological Museum, Paleontological Institute of Russian (then Soviet) Academy of Sciences in Moscow. Dr. Evgeny N. Kurochkin kindly provided photographs of the holotype of *Alioramus*. The cast of the skull of *Tyrannosaurus rex* (BHI-3033) was made available to us by the generous help of Peter Larson and Larry Hutson at the Black Hills Institute, South Dakota. We warmly thank Dr. Hans Arne Nakrem, Bjørn Lund, Øyvind Enger and Tomasz Sulej for their skilful help in the preparation and casting of the *Tarbosaurus* specimen. Dr. Mahito Watabe provided logistic support to KS during his stay in Mongolia. Dr. Thomas R. Holtz and Prof. Halszka Osmólska kindly reviewed an early draft of the paper and Prof. David L. Bruton helped improve our Polish/Norwegian English. Per Aas (Natural History Museum, University of Oslo, Norway) made the photographs and the drawings of the lower jaw were made by Annegi Eide. Finally, special thanks are due to Prof. Halszka Osmólska and Dr. Phillip Currie, for encouraging us to pursue the study of tyrannosaurids and for providing valuable comments during this study.

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