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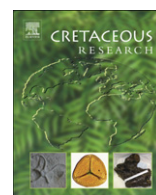
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Skeletal remains of Tyrannosauroida (Dinosauria: Theropoda) from the Bissekty Formation (Upper Cretaceous: Turonian) of Uzbekistan

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ABSTRACT

There exists a major gap in the fossil record of tyrannosauroid theropod dinosaurs spanning the early part of the Late Cretaceous. We report on skeletal remains referable to Tyrannosauroida indet. from the Turonian Bissekty Formation at Dzharakuduk in the central Kyzylkum Desert of Uzbekistan. Phylogenetic analysis of the hypodigm places the Bissekty tyrannosauroid as a non-tyrannosaurid tyrannosauroid more basal than the Campanian tyrannosauroids *Appalachiosaurus* and *Bistahieversor* from North America.

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1. Introduction

Some 60 localities yielding dinosaurian skeletal remains in the Late Cretaceous continental deposits of the Kyzylkum Desert in Uzbekistan have been recorded to date (Nessov, 1995, 1997; AA, unpublished data). The most common fossils found at almost all of these localities are isolated teeth of tyrannosauroid theropods. Other skeletal elements, including a variety of cranial and post-cranial bones or fragments of such bones, are found only in strata of the Turonian Bissekty Formation at Dzharakuduk, about 80 km west of Uchkuduk in the Navoi Viloyat (district) of Uzbekistan (Fig. 1). Sosedko (1937) referred the earliest finds of tyrannosauroid remains from Dzharakuduk to *Allosaurus* sp. Later Efremov (1944) attributed these materials to “Deinodontidae” (an old name for Tyrannosauridae). In 1958 Anatoly K. Rozhdestvensky (Paleontological Institute of the Soviet Academy of Sciences, Moscow) collected an excellently preserved theropod braincase from Dzharakuduk that Kurzanov (1976) later described in detail and designated as the holotype of a new taxon *Itemirus medullaris*. *Itemirus* has sometimes been classified as a tyrannosauroid (e.g., Holtz, 2004), but newly collected material indicates that it is, in fact, referable to Dromaeosauridae (Sues and Averianov, in preparation).

Nessov (1995) identified the Bissekty tyrannosauroid as *Alectrosaurus* sp. and referred to it numerous labiolingually compressed tyrannosauroid teeth from other Late Cretaceous

localities in the Kyzylkum Desert. He also noted the similarities of certain femora, a tibia, metatarsals, and astragali recovered from Dzharakuduk to those of the holotype of *Alectrosaurus olseni* from the Iren Dabasu Formation of Inner Mongolia, China (Gilmore, 1933; Perle, 1977; Mader and Bradley, 1989). Most of these bones, however, are referable to Ornithomimosauria, and a fragment of a maxilla (CCMGE 600/12457) has been re-identified as belonging to a dromaeosaurid (Sues and Averianov, in preparation). Nessov (1995) also identified some isolated teeth from Dzharakuduk as cf. *Aublysodon* sp. and noted that certain high-crowned, mesiodistally short teeth with transversely wide bases (e.g., Nessov, 1995, pl. 1, figs 3, 7, 10, 11) differ from those he had attributed to *Alectrosaurus* sp.; thus, he classified them as Theropoda indet. The latter possibly represent anterior maxillary or anterior dentary teeth of the same taxon, which had short anterior alveoli at least in the maxilla. Finally, Nessov identified premaxillary teeth without denticles as cf. *Aublysodon* sp.; we here assign these teeth to Tyrannosauroida indet.

Between 1997 and 2006 the joint Uzbek-Russian-British-American-Canadian expeditions (URBAC) to the Kyzylkum Desert greatly increased the known fossil record of dinosaurs from the Bissekty Formation at Dzharakuduk (Archibald et al., 1998). The aim of this paper is to describe all skeletal remains referable to Tyrannosauroida from Dzharakuduk and elucidate the phylogenetic position of the Bissekty tyrannosauroid.

Institutional abbreviations. CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; USNM,

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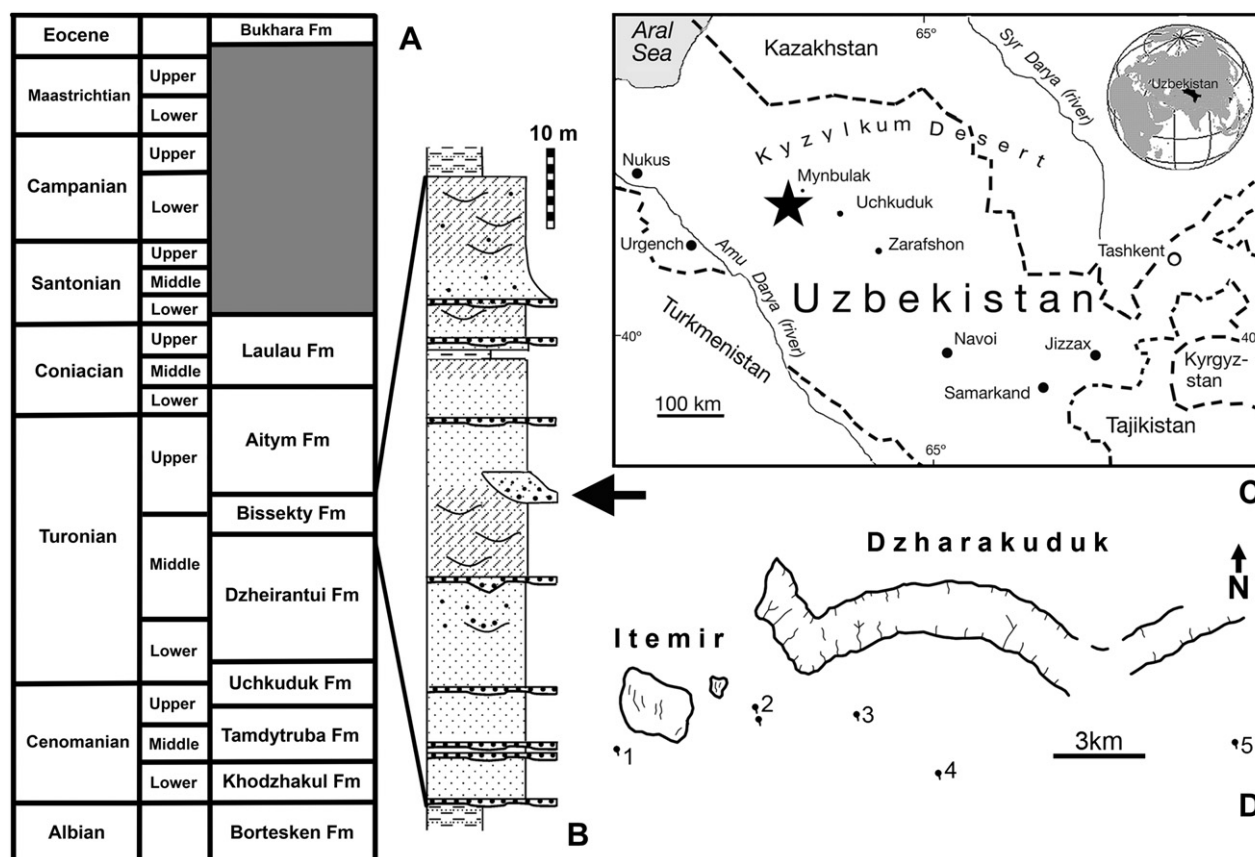


Fig. 1. Stratigraphic and geographic setting for the Dzharakuduk locality complex, Kyzylkum Desert, Uzbekistan. Stratigraphic succession of the Cretaceous formations (A) and section of the Bissekty Formation (B) at Itemir-Dzharakuduk depression are modified from unpublished work by C. King and colleagues. Arrow in B denotes position of the CBI-14 site, one of the most productive localities for microvertebrate remains. The outline map of Uzbekistan (C), with the position of the Itemir-Dzharakuduk depression marked by a star, and sketch of the Itemir-Dzharakuduk escarpments (D) are modified from Averianov and Sues (2007). 1, Itemir well; 2, Dzharakuduk wells; 3, Kul'beke well; 4, Bissekty well; 5, Khodzhakhmet well.

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Locality abbreviations. CBI, Central [Kyzylkum] Bissekty; CDZH, Central [Kyzylkum] Dzharakuduk. This prefixes were used by Nessov for the localities within upper-middle and lower parts of the Bissekty Formation, respectively.

Measurements. Tooth crowns: BW, basal width; FABL, fore-aft basal length; TCH, tooth crown height. Vertebrae: ACH, anterior height of centrum (without hypapophysis); ACW, anterior width of centrum; ANW, anterior width of neural arch (between lateral margins of prezygapophyses); CL, centrum length (ventral); NAL, neural arch length (between anterior and posterior margins of dorsal roof of neural canal); NSL, neural spine length (maximum); PCH, posterior height of centrum; PCW, posterior centrum width; PNW, posterior width of neural arch (between lateral margins of post-zygapophyses). All measurements are in millimeters.

2. Systematic paleontology

- Dinosauria Owen, 1842
- Saurischia Seeley, 1887
- Theropoda Marsh, 1881
- Tyrannosauroida Osborn, 1905

Tyrannosauroida indet.
Figs. 2–12

1995 *Alectrosaurus* sp. [partim]: Nessov, p. 38, pl. 1, figs 2, 5, 6, 8, 9, 12, 15 [not fig. 1, (ornithomimosaur ungal) and figs 19, 20 (ornithomimosaur astragali)]

1995 Theropoda [indet.]: Nessov, pl. 1, figs 3, 7, 10, 11

1995 Dinosauria [indet.]: Nessov, pl. 3, fig. 4.

Material examined. Almost complete right maxilla, fragment of left maxilla, isolated frontals, distal end of left quadrate, fragment of right dentary, posterior fragments of mandibular rami with fused articular and surangular, isolated premaxillary and lateral teeth; cervical, dorsal and caudal vertebrae, ungual phalanges of manus and pes; possible fragment of astragalus.

Description

Skull

Frontal: There are several isolated unfused frontals from younger specimens of Tyrannosauroida. The most complete of these frontals (ZIN PH 2330/16; Fig. 2) is triangular with an anteroposterior length 1.5 times greater than its transverse width. Its anterior end bears three facets for the overlapping nasal prongs, as in other

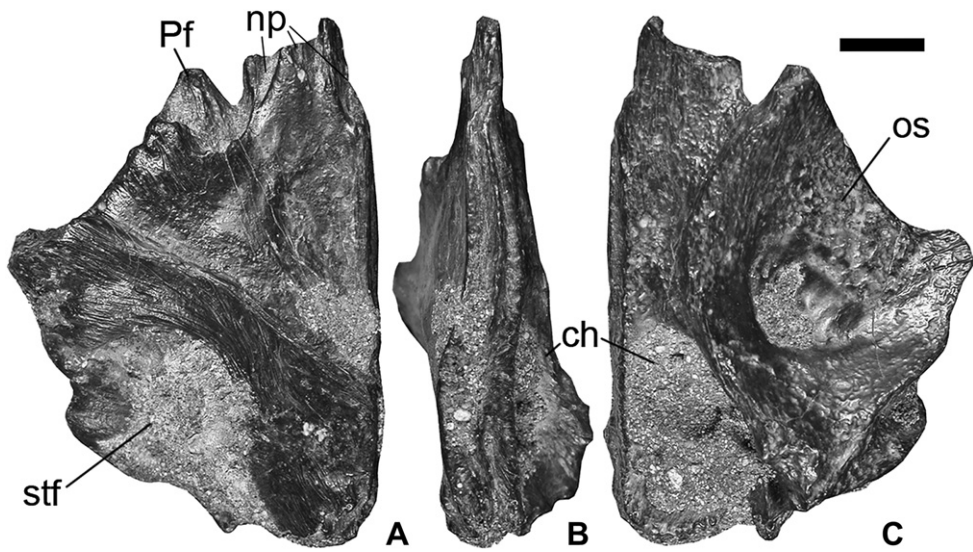


Fig. 2. ZIN PH 2330/16, juvenile left frontal of *Tyrannosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in A, dorsal, B, medial and C, ventral views. ch, impression of cerebral hemisphere; np, facets for nasal prongs; os, orbital surface; Pf, facet for prefrontal; stf, supratemporal fossa. Scale bar represents 1 cm.

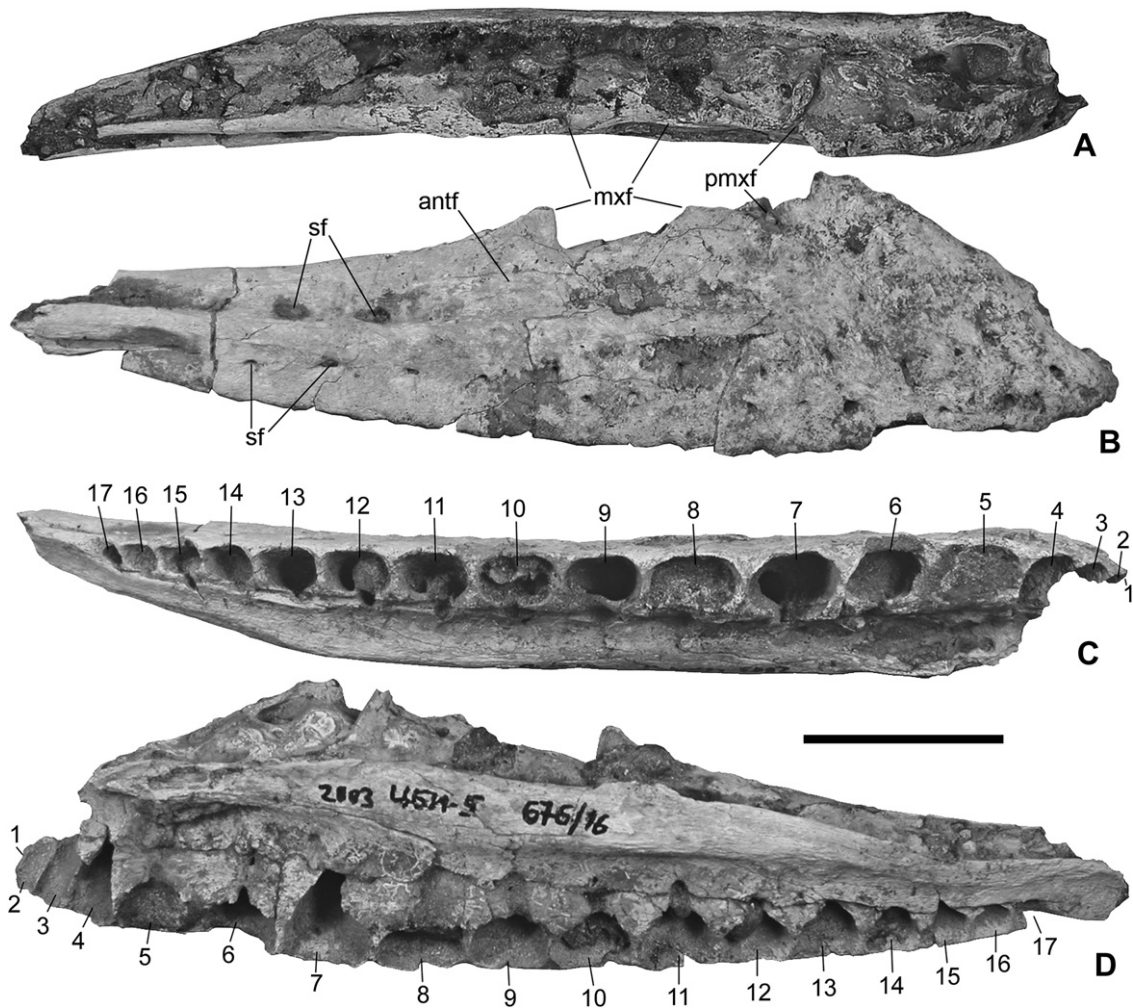


Fig. 3. ZIN PH 676/16 (CBI-5, 2003), right maxilla of *Tyrannosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in A, dorsal, B, lateral, C, ventral and D, medial views. antf, antorbital fossa; mxf, maxillary fenestra; pmxf, promaxillary fenestra; sf, supralabial foramina. Alveoli are numbered in ventral and medial views (1–17). Scale bar represents 5 cm.

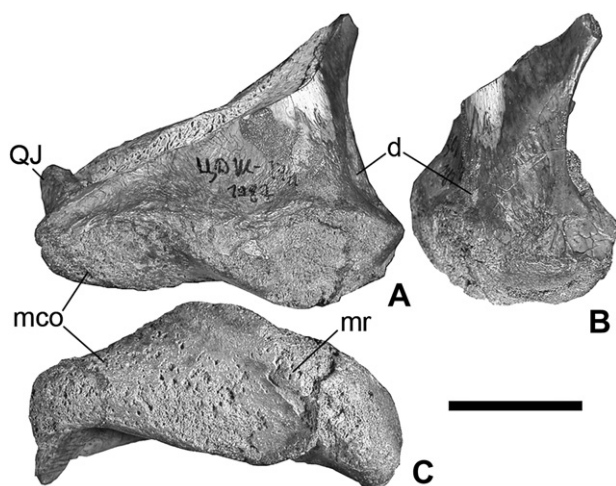


Fig. 4. ZIN PH 2296/16 (CDZH-17a, 1987), distal end of a left quadrate of *Tyrannosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in A, posterior, B, medial and C, ventral views. d, depression; mco, mandibular condyle; mr, median ridge; QJ, facet for quadratojugal. Scale bar represents 3 cm.

tyrannosauroids (Currie, 1987). The facet for the prefrontal is situated just lateral to that for the nasal and is similar in size; it extends further posteriorly compared with the nasal facet. The articular contact between the prefrontal and frontal is socket-like as the posterior portion of the facet for the prefrontal is overlapped by the thin bony layer of the frontal, similar to the condition on a frontal identified as cf. *Aublysodon* sp. from the Judith River Group of Alberta, Canada (Currie, 1987, fig. 1f). (Currie, 2005, did not mention this material again in a more recent synopsis of theropods from Dinosaur Provincial Park in Alberta.) The lateral margin of the frontal was probably completely excluded from the dorsal rim of the orbit by the lacrimal and postorbital. As on the frontal illustrated by Currie (1987, fig. 1f) the frontal-postorbital contact is divided into two parts. Anteriorly both bones contact with no overlap whereas posteriorly the frontal overlaps the postorbital, in contrast to the North American taxa, where the frontal is broadly

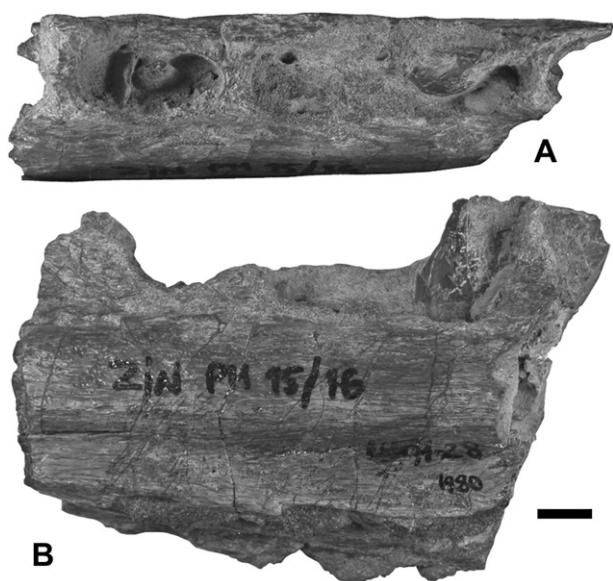


Fig. 5. ZIN PH 15/16 (CBI-28, 1980), fragment of right dentary of *Tyrannosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in A, dorsal and B, medial views. Scale bar represents 1 cm.

overlapped by the postorbital (Currie, 1987, fig. 1f–h). This unusual feature could be an ontogenetic trait as the sutural relationship between the frontal and postorbital changes during growth (Currie, 1987). Posterolaterally there is a distinct supratemporal fossa, which is bounded anteriorly by a raised subcircular ridge. The supratemporal fossa occupies a greater half of the dorsal surface of the bone and meets the opposite fossa along the midline. Posteriorly, the frontals were separated by a short anterodorsal process of the parietals. There is no sagittal crest, possibly owing to the juvenile nature of the specimen. The dorsal surface of the frontal anterior to the supratemporal fossa is flat and deepens medially. Along the posteromedial edge of the ventral surface of the frontal there is a broad articular surface for the laterosphenoid.

Maxilla: ZIN PH 676/16 is a nearly complete right maxilla, lacking only most of the ascending (dorsal) process (Fig. 3). Its preserved length is 261 mm, but possibly a small piece of the bone is missing at the anterior end. The maxilla is rather shallow, elongate, and straight, with a slightly convex alveolar margin. The ratio of curvature depth to the tooth row length is about 8% (the figure is approximate because the first alveolus is not completely preserved). The maximum depth of the curvature occurs at the eighth alveolus. The angle between the anterodorsal and ventral margins of the bone is quite low, as in *Alioramus* (Brusatte et al., 2009). It is 47° to the ventral margin of the first maxillary alveoli and 25° to the line between first and last maxillary alveoli. The posterior end of maxilla is slightly deflected laterally. The maxilla has 17 alveoli, as in *Alioramus* (Brusatte et al., 2009); possibly a small additional alveolus was present in the missing anteriormost portion. The first preserved alveolus is incomplete but obviously small. The mesiodistal length of the second through fourth alveoli rapidly increases from 5 to 12 mm. Evidently the anterior three or four maxillary teeth were different in shape from the more posterior ones, perhaps more similar in shape to the premaxillary teeth. The middle alveoli are rather constant in length (the largest is alveolus 7 with a length of 19.5 mm); starting at the thirteenth alveolus, they gradually decrease in size posteriorly. The triangular interdental plates are well developed. They do not contact each other and are separated by a groove that presumably housed the dental lamina. On the lateral aspect of the maxilla, two rows of supralabial foramina extend dorsal and parallel to the alveolar margin. The ventral row of these openings extends to the posterior end of the bone. Its posteriormost foramen is slit-like. The dorsal row of supralabial foramina is confined to the anterior half of the maxilla, but an additional dorsal row of supralabial is present within the antorbital fossa (Fig. 3D). This unusual condition is also present in a subadult specimen of *Tyrannosaurus rex* (T.D. Carr, pers. comm.). The antorbital fossa is extensive, extending well below the ventral margin of the antorbital fenestra and continuing to the posterior end of the maxilla. The width of the posterior extent of the antorbital fossa gradually decreases posteriorly. Here its depth is almost equal to the depth of the horizontal ramus below it. Its surface is smooth and delimited by a distinct rim from the surrounding more rugose lateral surface of the maxilla. The maxillary fenestra is rather large and has a straight ventral margin. It lies well within the antorbital fossa, with its anterior margin terminating about 20 mm behind the anterior margin of the antorbital fossa. The minimum distance between the maxillary fenestra and the ventral margin of the antorbital fenestra is 17 mm; it is located at the posterior end of the fenestra. The promaxillary fenestra is very small, but apparently it was visible in lateral view. The intermaxillary suture has three prominent ridges separated by deep grooves above the fourth to sixth maxillary teeth. In *Gorgosaurus* the intermaxillary contact is placed further anteriorly, above the first four maxillary teeth (Currie, 2003). The palatal shelf is narrow and flat, without a distinct articular surface for the palatine. The intermaxillary process does not extend

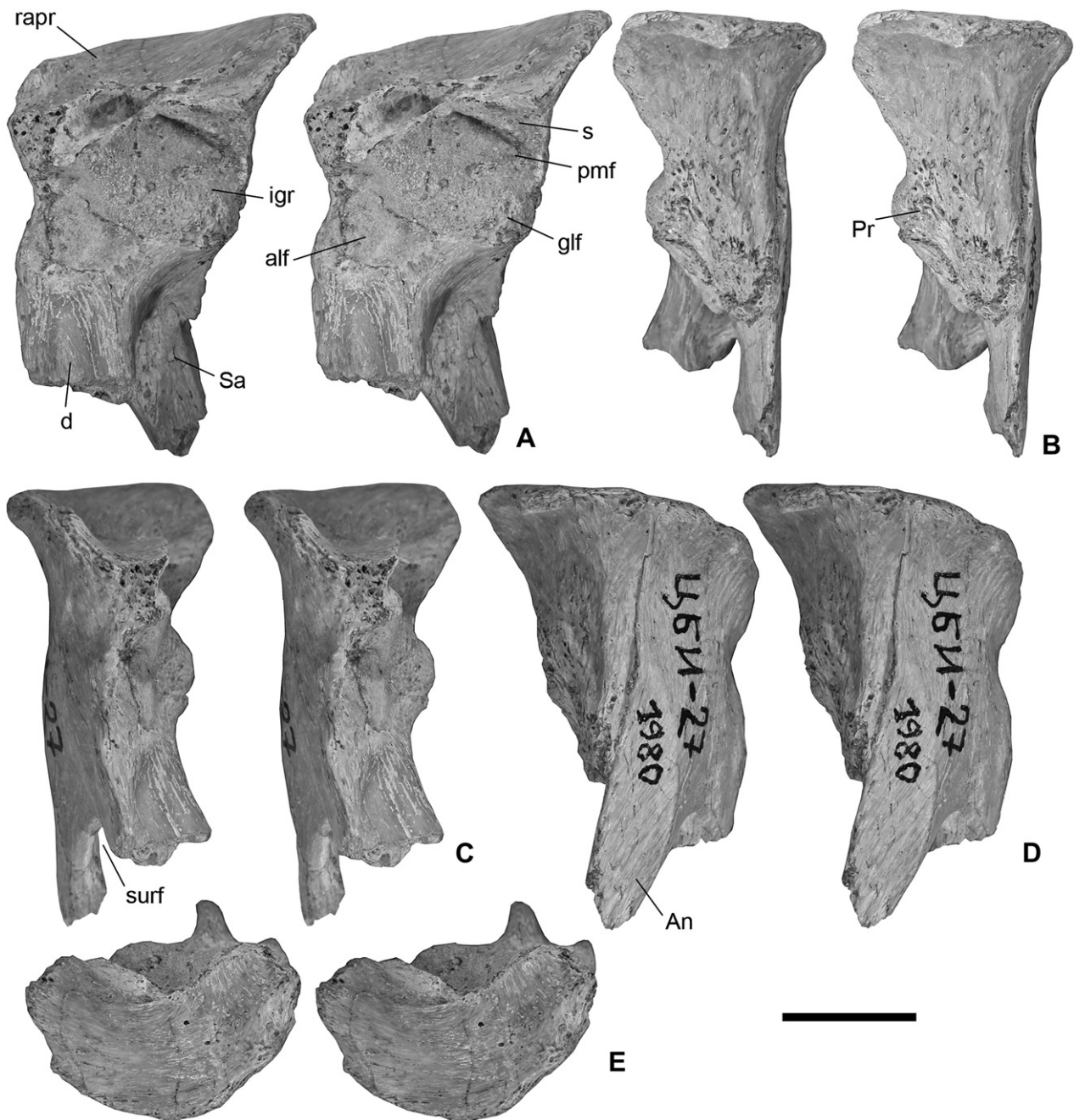


Fig. 6. ZIN PH 1239/16 (CBI-27, 1980), right fused articular and part of surangular of juvenile individual of *Tyrannosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in A, dorsal, B, medial, C, lateral, D, ventral and E, posterior views (stereopairs). alf, anterolateral fossa; An, facet for angular; d, depression; glf, glenoid fossa; igr, interglenoid ridge; pmf, posteromedial fossa; Pr, facet for prearticular; rapr, retroarticular process; s, sulcus; Sa, surangular; surf, surangular foramen. Scale bar represents 1 cm.

medial to the palatal process, as in subadult specimens of *Alioramus* and *Tyrannosaurus* (T.D. Carr, pers. comm.). Along the ventral surface of the palatal shelf there are very shallow depressions for the tips of the dentary teeth.

A fragment of a left maxilla (ZIN PH 2/16; preserved length: 105 mm) preserves the six posterior alveoli, the first of which is incomplete. The alveoli decrease in size posteriorly, and are separated by bony septa, which are expressed as more or less triangular interdental plates between successive alveoli in lingual view. The alveolar margin is gently convex in labial view. A row of supralabial foramina extends just dorsal and parallel to the alveolar margin of the first four alveoli and terminates in an anteroposteriorly

elongate posterior opening above the penultimate preserved alveolus. A gentle step in the lateral surface of the maxilla represents the ventral rim of the antorbital fossa, which extends to the abraded posterior end of the bone. This specimen belonged to an individual slightly larger than that represented by ZIN PH 676/16: the length of the posterior five alveoli is 82 versus 57 mm.

Quadrate: ZIN PH 2296/16 (Fig. 4) is a distal end of a left quadrate preserving the complete mandibular condyle. The condyle is 2.4 times wider mediolaterally than long anteroposteriorly. It has an oblique median ridge extending from the anteromedial corner of the condyle towards the middle of its posterior side. This crest

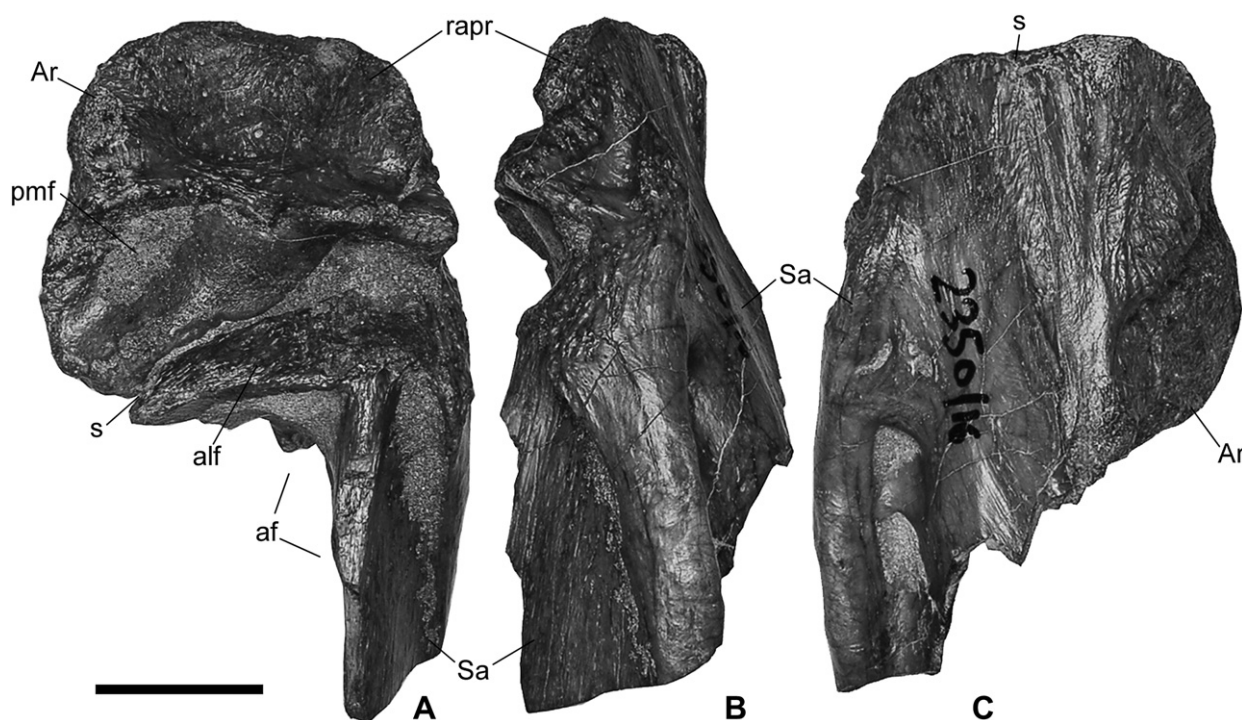


Fig. 7. ZIN PH 2350/16, left fused articular and part of surangular of adult individual of *Tyrannosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in A, dorsal, B, lateral and C, ventral views. Af, adductor fossa; alf, anterolateral fossa; Ar, articular; pmf, posteromedial fossa; rapr, retroarticular process; s, suture between articular and surangular; Sa, surangular. Scale bar represents 3 cm.

divides the condyle into two unequal portions; the lateral part is twice as wide as the medial one and is transversely concave whereas the medial portion is convex. The quadrate shaft is anteriorly concave and posteriorly convex. The lateral and medial edges of the shaft are sharp. On the posterior side of the shaft along the medial edge and above the condyle there is a markedly rugose, oval depression (with its long axis in a vertical direction). A larger, oval depression (with its long axis horizontally oriented) is present immediately above the condyle on the anterior side. It occupies the entire lateral half of the shaft, but it is deepest at its medial corner. On the posterior side along the lateral edge of the shaft and just above the condyle a fragment of the rugose articular surface for the quadratojugal is preserved. The bone of the quadrate is quite dense and shows no traces of pneumatization.

ZIN PH 2333/16 is a more complete, but poorly preserved distal end of the quadrate of a juvenile, which is similar to that bone in *Daspletosaurus* (Currie, 2003, fig. 28). It has a distinct flattened facet for contact with the quadratojugal.

Mandible

Dentary: ZIN PH 15/16 (Fig. 5) is a poorly preserved fragment of a right dentary, with three alveoli (two of which contain replacement teeth in different stages of eruption) and a partial alveolus each at the anterior and posterior end. The mesiodistal length of the largest complete alveolus in this fragment is 22 mm. Smaller unidentified jaw fragments have even larger alveoli (26 mm in ZIN PH 677/16). All alveoli are distinctly narrow labiolingually.

Articular and surangular: The posterior end of the mandibular ramus is known from four specimens with fused articular and surangular; three are of presumably adult size and one is a much smaller, juvenile fragment (ZIN PH 1239/16; Fig. 6). The description

is based on the latter specimen and on ZIN PH 2350/16 (Fig. 7), the best preserved adult specimen. The posterior end of the mandibular ramus closely resembles that in *Tyrannosauridae* (Brochu, 2003; Currie, 2003) in overall structure, but it is not hollow and lacks a pneumatic opening medial to the glenoid fossa (foramen aereum). The saddle-shaped glenoid area is divided into anterolateral and posteromedial fossae by a low but broad ridge. The ridge is separated from the retroarticular process by a distinct mediolateral groove in ZIN PH 1239/16 but not in ZIN PH 2350/16. In the former the groove is narrowest at the middle and expands medially and laterally. Surprisingly, the suture between the articular and surangular is most clearly evident on the larger specimen; within the glenoid fossa it extends parallel to the ridge separating the anterolateral and posterolateral fossae (Fig. 7A). The retroarticular process is short and posteromedially directed. It is a broadly concave, U-shaped plate, which faces posterodorsally. Anterior to the anterolateral portion of the glenoid fossa there is a triangular depression, which is separated from a more extensive medial depression (adductor fossa) by a tall, longitudinal ridge. A deep pit is present at the bottom of the adductor fossa in ZIN PH 1239/16. In ZIN PH 2350/16 there is a much smaller foramen in this position. The adductor fossa is bordered medially by the rugose area for contact with the prearticular. Ventral to the latter, in ZIN PH 1239/16 there is a flat, elongated area for contact with the angular on the ventral side of the surangular. The areas for contact with the angular and prearticular are separated by a narrow groove, which extends to the posterior margin of the retroarticular process. In ZIN PH 1239/16, the posterior margin of a surangular foramen is evident on the lateral side of the bone, just dorsal to the contact for the angular.

Teeth

Premaxillary teeth: Some premaxillary teeth have crowns that are distinctly D-shaped in transverse section (Fig. 8). Most of them are

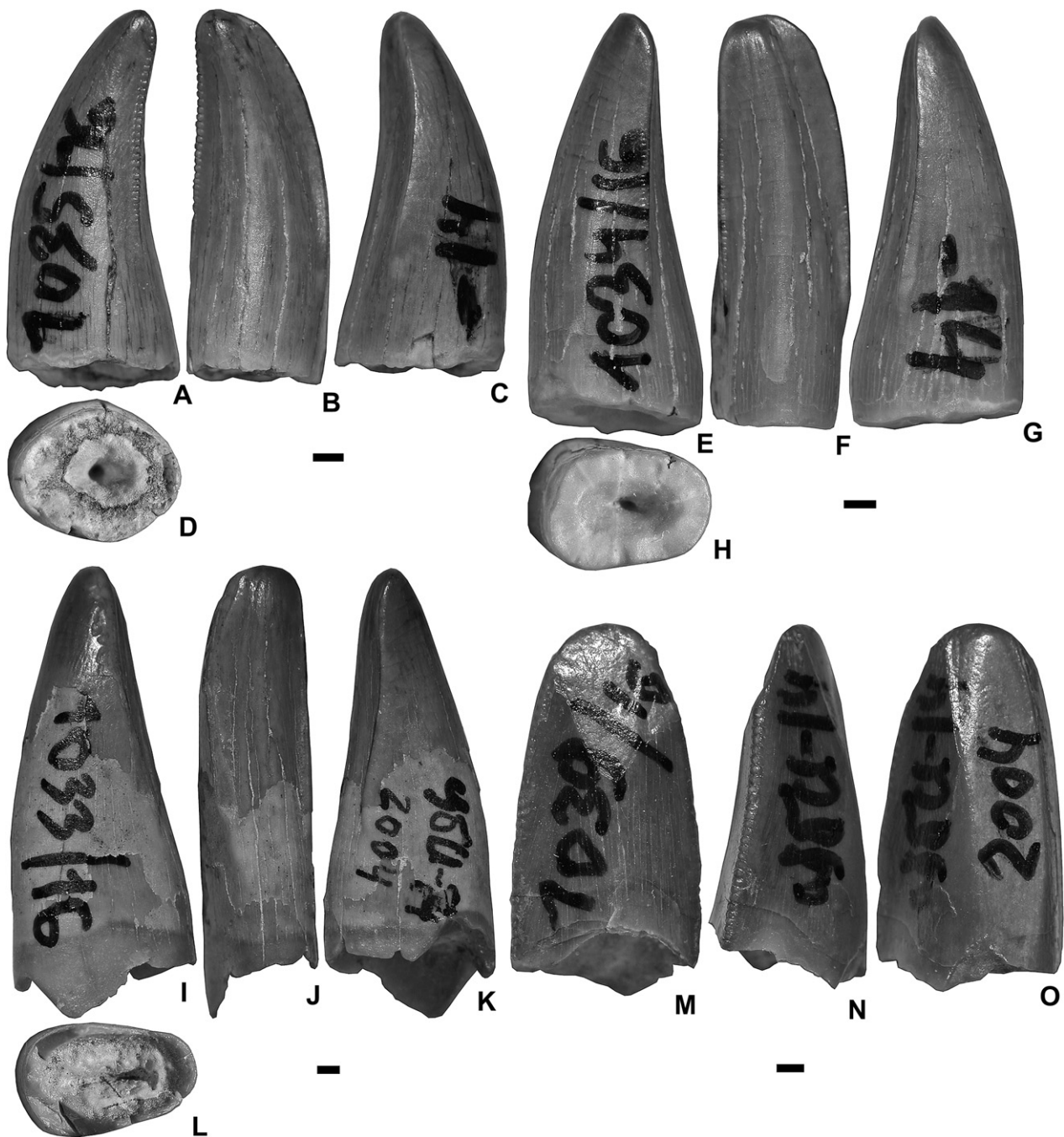


Fig. 8. Isolated premaxillary teeth of *Tyrannosauroidae* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A–D, ZIN PH 1035/16 (CBI-14), in A, distal, B, lingual, C, mesial and D, basal views. E–H, ZIN PH 1034/16 (CBI-14), in E, distal?, F, lingual, G, mesial? and H, basal views. I–L, ZIN PH 1033/16 (CBI-14, 2004), in I, distal?, J, lingual, K, mesial? and L, basal views. M–O, ZIN PH 1039/16 (CBI-14, 2004), in M, lingual, N, distal? and O, labial views. Scale bars represent 1 mm.

small (TCH = 5.3–19.2, FABL = 1.6–5.8, BW = 2.0–8.2) and were recovered through screen-washing of matrix. The tooth crown is slightly to moderately asymmetrical in labial or lingual view, with the mesial side convex, the distal side straight or concave, and the apex recurved distally. It is D-shaped in transverse section, with flat mesial, distal, and lingual sides, and a strongly convex labial side (BW/FABL = 1.00–1.52, $M = 1.33 \pm 0.03$, $n = 18$). A prominent longitudinal ridge on the lingual aspect of the crown is flanked by distinct grooves mesially and distally. The denticles are variably developed. On smaller teeth, both carinae lack denticles. On larger teeth, denticles may be absent on the mesial carina, but they are

always present on the distal carina. When present on both carinae, the denticles are larger on the distal carina (17.5–27.5 denticles per 5 mm). In ZIN PH 1039/16, wear facets are developed on both the labial and lingual sides of the crown (Fig. 8M, O).

Maxillary and dentary teeth: Isolated, usually incomplete tooth crowns referable to *Tyrannosauroidae* are quite common at Dzharakuduk (Fig. 9). They reach FABL of up to 26.6 mm and TCH of over 60 mm (the largest complete tooth has TCH = 65.2 mm, but there are fragments of even larger teeth). The tooth crowns are recurved, distinctly flattened labiolingually, and have serrated

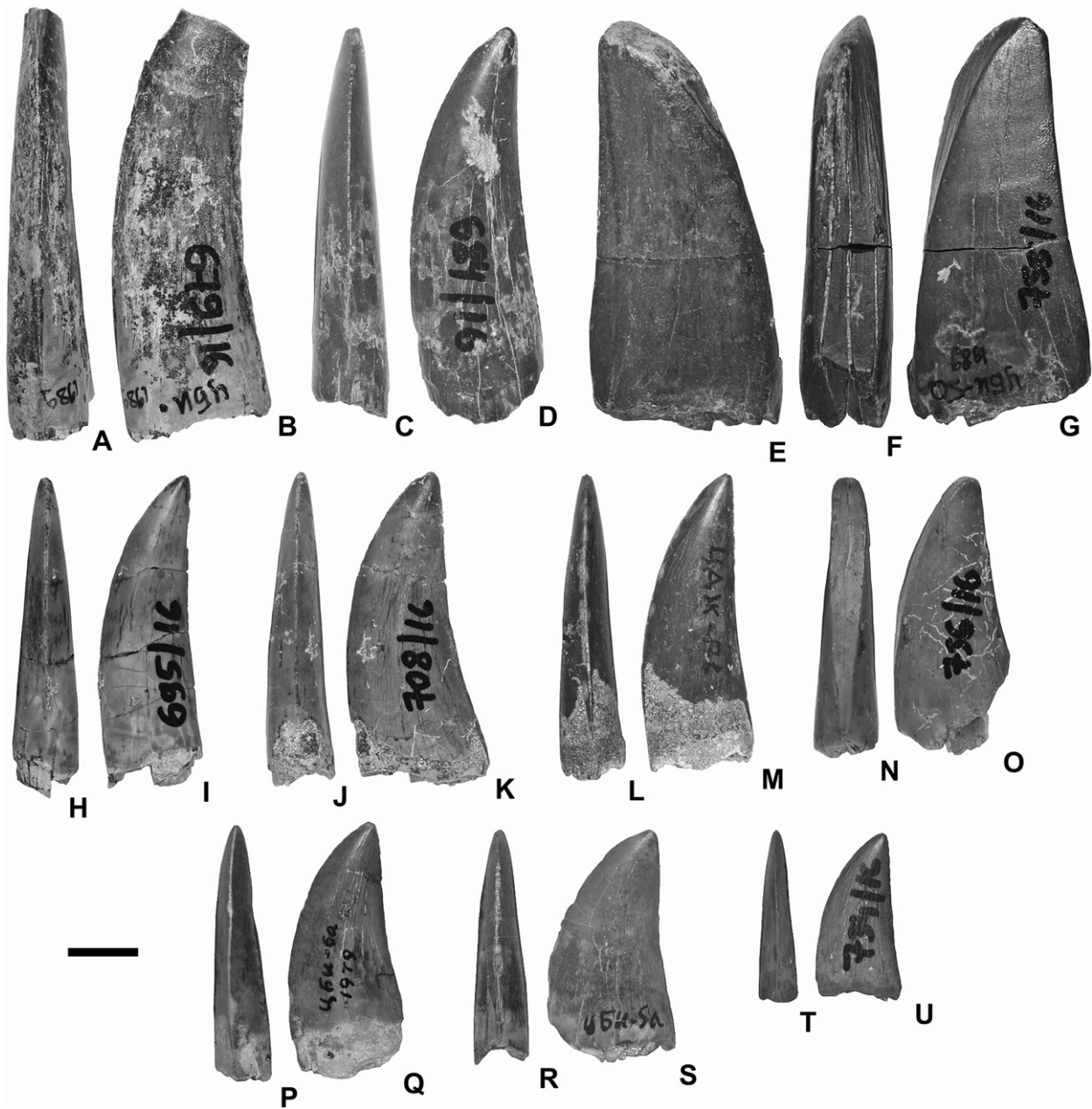


Fig. 9. Isolated maxillary or dentary teeth of *Tyrannosuroidea* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in anterior (A, C, F, H, J, L, N, P, R, T) and side (B, D, E, G, I, K, M, O, Q, S, U) views. A, B, ZIN PH 679/16 (1989). C, D, ZIN PH 684/16 (CBI-14, 1987). E–G, ZIN PH 755/16 (CBI-50, 1989). H, I, ZIN PH 695/16 (1989). J, K, ZIN PH 708/16 (CBI-14, 1991). L, M, ZIN PH 693/16 (CDZH-17v). N, O, ZIN PH 756/16 (CBI-14, 1987). P, Q, ZIN PH 733/16 (CBI-6a, 1979). R, S, ZIN PH 737/16 (CBI-5a). T, U, ZIN PH 734/16 (CBI-14). Scale bar represents 1 cm.

mesial and distal carinae. Some crowns are blade-like, but others are taller and narrower mesiodistally. The degree of labiolingual flattening can be expressed by the BW/FABL index, which is 0.41–0.70, $M = 0.51 \pm 0.07$, $n = 77$. There are 14–26 denticles per 5 mm of carina length on the middle third of the mesial carina ($M = 18.90 \pm 0.66$, $n = 19$) and 12–22 denticles per 5 mm on the middle third of the distal carina ($M = 17.50 \pm 0.52$, $n = 19$). The size of denticles is strongly negatively correlated with the crown size (expressed by FABL), being smaller in larger tooth crowns ($r = -0.67$ and -0.73 for mesial and distal carina denticles, respectively; correlation significant at $p < 0.05$). There are several tooth crowns with variously chipped-off tips and/or mesial edges, probably representing breakage incurred during feeding.

A small sample of tyrannosauroid teeth from the slightly older (Cenomanian) Khodzhakul Formation in the Kyzylkum Desert of Uzbekistan does not show any significant differences from the Bissekty teeth. The tooth crowns are similarly flattened labiolingually (BW/FABL index 0.44–0.67, $M = 0.54 \pm 0.02$, $n = 9$).

Vertebral column

Cervicals: A centrum of an anterior cervical is referable to *Tyrannosuroidea* (ZIN PH 671/16; Fig. 10A–C; CL = 79, ACH = 42, ACW = 56.5). Most of the neural arch is broken off, and the cervical ribs were not fused. The centrum is short and deeply opisthocoealous, with oblique anterior and posterior articular surfaces. Its

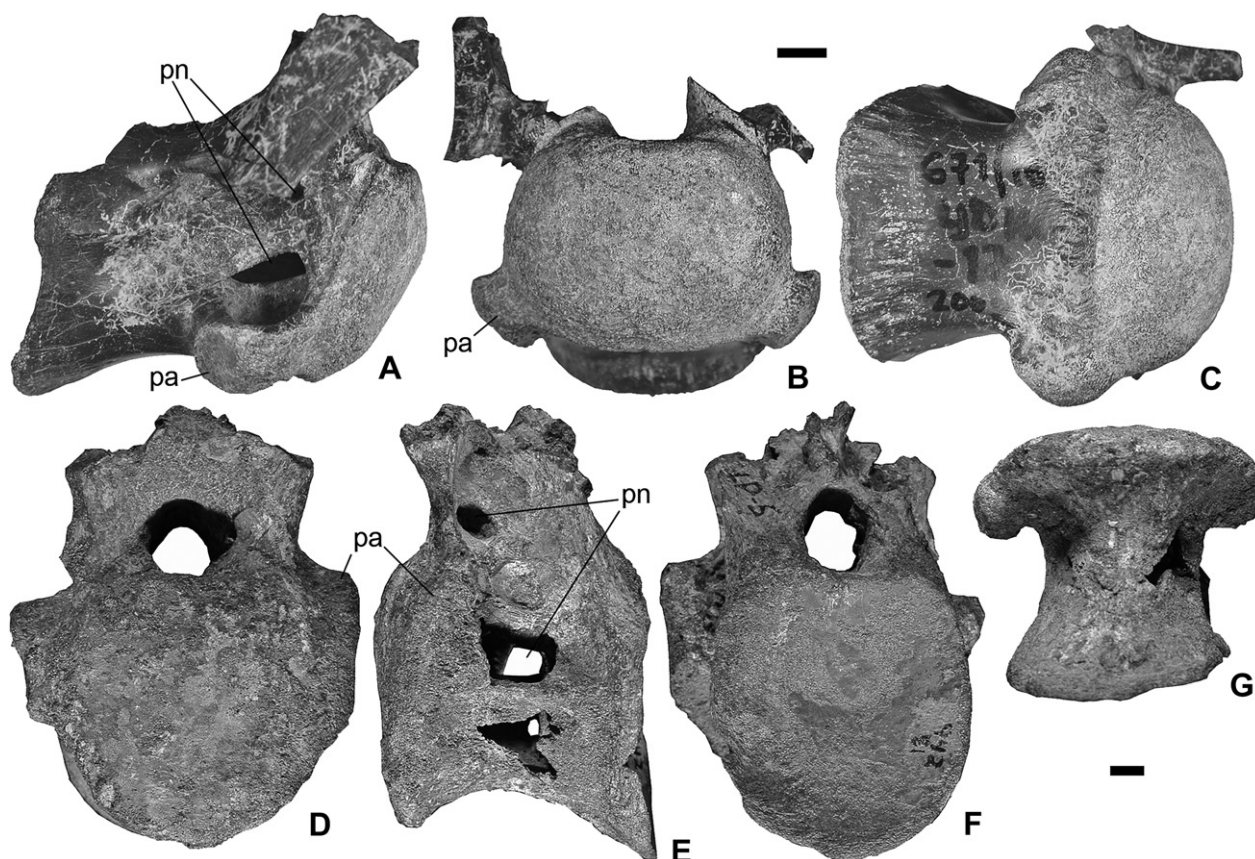


Fig. 10. Cervical vertebrae of *Tyrannosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A–C, ZIN PH 671/16 (CDZH-17, 2002), anterior cervical, in A, lateral, B, anterior and C, ventral views. D–G, USNM 538131 (2006), posterior cervical, in D, anterior, E, lateral, F, posterior and G, ventral views. pa, parapophysis; pn, pneumatic opening. Scale bars represent 1 cm.

ventral surface is flat. Laterally, two large pneumatic foramina open in the pleurocoel depression, below the base of the diapophysis and dorsal to the parapophysis; they are separated by a low horizontal ridge. The prediapophyseal lamina is well developed. The parapophysis is located ventrally, close to the anterior articular surface of the centrum. Its dorsal surface is extensively excavated by a pneumatic depression, which is ventrally divided by a low ridge. The centrum has a cancellous internal structure, with large spaces separated by thin struts.

A posterior cervical (USNM 538131; Fig. 10D–G) lacks most of the neural arch (ACH = 67; ACW = 79; CL = 71; PCH = 71; PCW = 65). Its centrum is distinctly opisthocoealous. The anterior articular surface of the centrum is heart-shaped, with a concave dorsal margin. The posterior articular surface of the centrum is more oval in outline (with a vertical long axis) and its dorsal margin more incised than that of the anterior articular surface. The centrum is distinctly constricted between the articular ends and bears a prominent ventral ridge. A large oval parapophyseal facet (with a vertical long axis) is located immediately behind the anterior articular surface of the centrum and below the neurocentral suture. Posterior to this facet a large oval pneumatic foramen (with a horizontal long axis) opens into a prominent cavity inside the centrum. The pneumatic foramen extends posteriorly to the midlength of the centrum. The neural canal is relatively small and oval (with its long axis oriented vertically). The voluminous infradiapophyseal fossa occupies almost the entire preserved lateral side of the neural arch below the transverse process. It is delimited anteriorly and posteriorly by distinct laminae that ventrally support the transverse process. The anterior lamina extends almost vertically whereas the posterior one

extends anterodorsally from the dorsal margin of the posterior articular surface of the centrum. At the base of the anterior lamina there is a relatively large, oval pneumatic opening. A pneumatic foramen of similar size is present on the posterior surface of the posterior spur lateral to the prominent (mostly damaged) hyposphene. Only a small ventral portion of the infraprezygapophyseal fossa is preserved.

Dorsals: A well-preserved dorsal vertebra (CCMGE 432/12457, Fig. 11; ACH = 99, ACW = 99, ANW = 46.5, CL = 93, NAL = 90, NSL = 60, PCH = 99, PCW = 102.5, PNW = 48) lacks only the left transverse process and adjoining structures. The neural spine is low and narrow transversely; its dorsal edge is anteroposteriorly convex. It bears narrow but deep anterior and posterior grooves for interspinous ligaments. The right transverse process projects laterally and dorsally at a low angle and has a flat dorsal surface. A pronounced ventral lamina extends to the pedicle, giving the process a triangular outline in transverse section. It expands medially into a lamina that delimits the infradiapophyseal fossa posteriorly. The infradiapophyseal fossa is divided by a low, anteroposteriorly extending crest, below which there is a large, round pneumatic opening. The parapophysis is situated on the neural arch and level with the prezygapophyseal facet. The prezygapophysis projects only slightly anterior to the anterior articular surface of the centrum. Its facet faces dorsally and slightly medially. The deep infraprezygapophyseal fossa is subtriangular in lateral view. The large postzygapophyseal facets face ventrally and slightly laterally. The large, posterolaterally facing infrapostzygapophyseal fossa is delimited anteriorly by the ventral lamina of the transverse

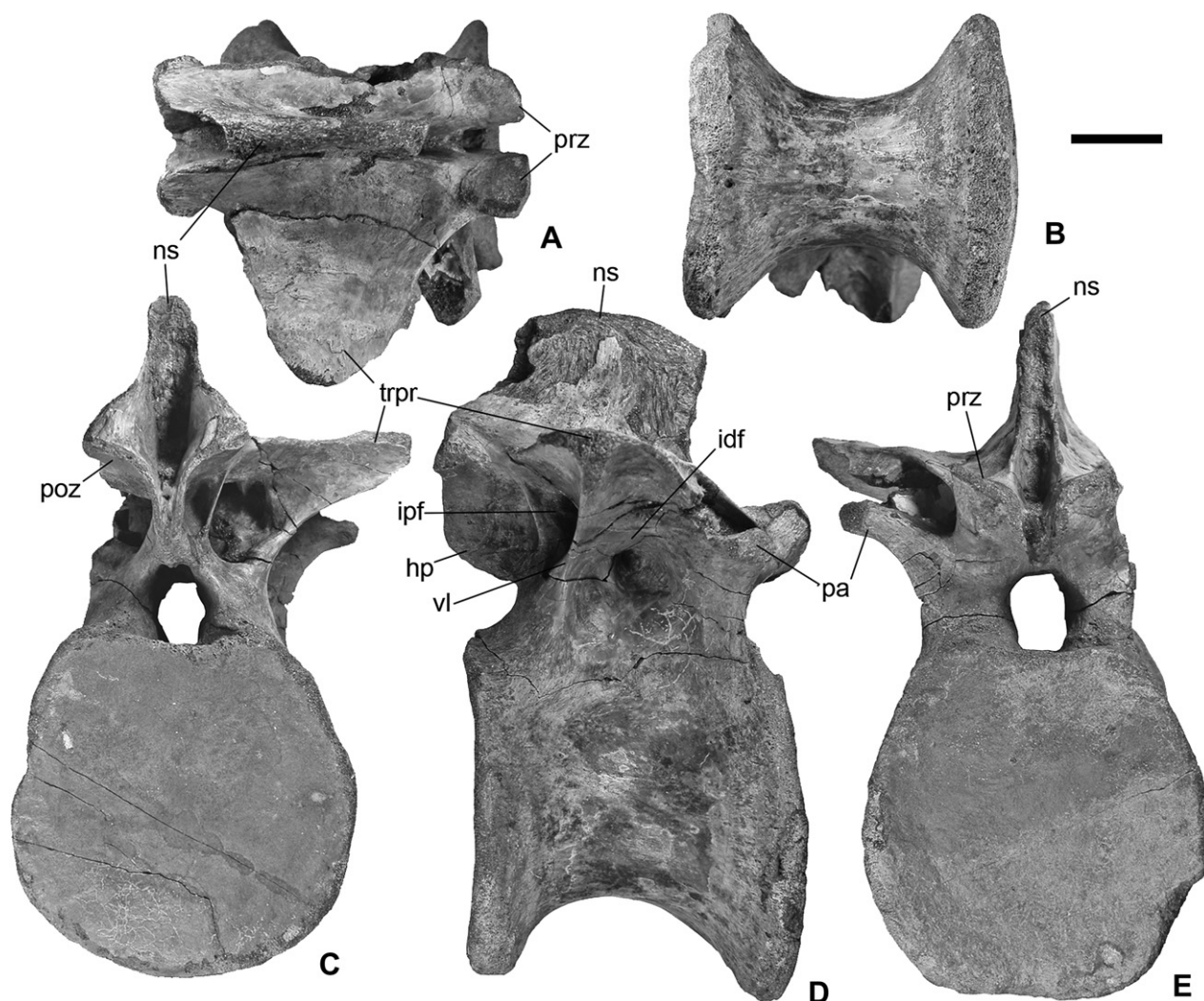


Fig. 11. CCMGE 432/12457 (CBI-5a, 1980), dorsal vertebra of *Tyrannosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in A, dorsal, B, ventral, C, posterior, D, lateral and E, anterior views. hp, hyposphene; idf, infradiapophyseal fossa; ipf, infrapostzygapophyseal fossa; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; trpr, transverse process; vl, ventral lamina. Scale bar represents 3 cm.

process, dorsally by the postzygapophysis, and medially by the pronounced hyposphene. It is divided by a thin, posterolaterally extending septum into a small medial recess and a large lateral fossa with a complex internal structure. The centrum is spoon-shaped and amphicoelous. Laterally, it bears a prominent, elliptical depression on either side just below the (obliterated) suture between the neural arch and centrum. Two small foramina are situated at the posterior end of this depression, but there is no large pneumatic opening.

A juvenile dorsal neural arch (USNM 538123; ANW = 22.3, NAL = 34.8, PNW = 24.4) differs from CCMGE 432/12457 in having a large, rounded parapophysis located on the neural arch ventral to the prezygapophysis. It has a prominent combined infraprezygapophyseal/infradiapophyseal fossa and a stout centrodiaepophyseal lamina. The infrapostzygapophyseal fossa is extensive but shallow. The hyposphene is rather small. The anterior groove for interspinous ligaments on the neural spine has a deep fissure at the base of the spine.

USNM 538132 (NAL = 37; NSL = 22) is the neural arch of an adult anterior dorsal. The large parapophysis is situated mostly above the neurocentral suture. The infradiapophyseal fossa is not as deep as in USNM 538123. The completely preserved neural spine is

much shorter anteroposteriorly than in CCMGE 432/12457. There is no trace of a hyposphene.

Two anterior dorsal centra (ZIN PH 2311/16 and 2312/16) each have a very large and deep pleurocoel extending between the anterior and posterior articular surfaces. The pleurocoels are medially separated only by a thin bony septum.

Several fragments of neural arches and neural spines of dorsal vertebrae (e.g., ZIN PH 105/16) may also be referable to *Tyrannosauroida*. The robust neural spines have strongly rugose surfaces extending along much of the length of the anterior and posterior grooves for interspinous ligaments, as is typical for *Tyrannosauridae* (e.g., [Lambe, 1917](#), fig. 15). The apices of the (in lateral view subrectangular) spines are distinctly capitate posteriorly. One specimen (ZIN PH 106/16) has a pathologically modified neural spine.

Caudals: Several well-preserved caudal vertebrae are referable to *Tyrannosauroida*. They lack pleurocoels, but some have one large or numerous small foramina on the lateral surface of the centrum. In contrast with dorsals, even the anterior caudals lack a hyposphene. The largest anterior caudal is ZIN PH 1476/16 (ACH = 77.7, ACW = 83.2, CL = 80.4, NAL = 38.8, NSL = 32.4, PCH = 78.4,

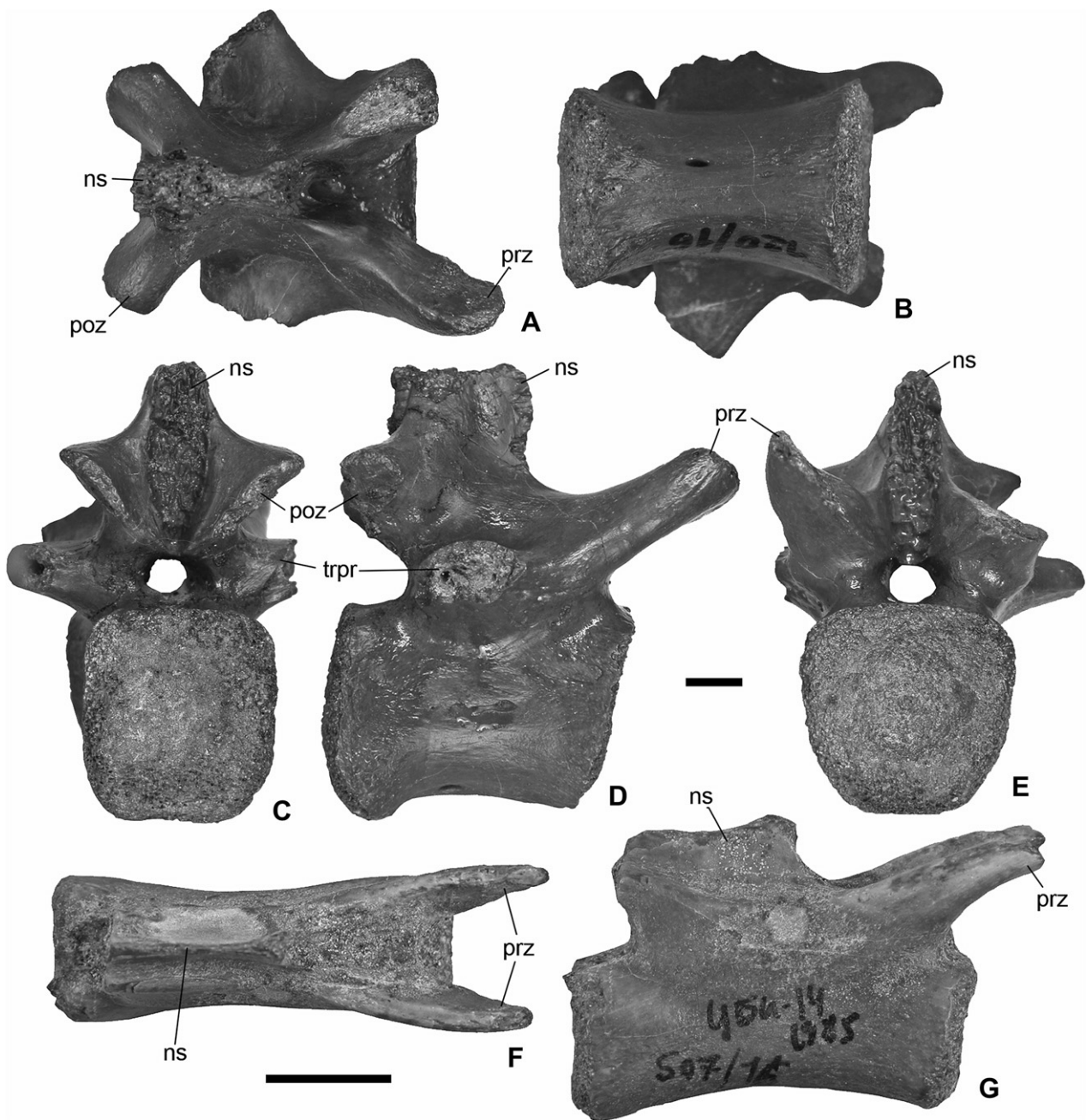


Fig. 12. Caudal vertebrae of *Tyrannosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A–E, ZIN PH 120/16 (CBI-14, 1984), anterior caudal, in A, dorsal, B, ventral, C, posterior, D, lateral and E, anterior views. F, G, ZIN PH 507/16, posterior caudal, in F, dorsal and G, lateral views. ns, neural spine; prz, prezygapophysis; trpr, transverse process. Scale bars represent 1 cm.

PCW = 78.3). One vertebra (ZIN PH 120/16; Fig. 12A–E; ACH = 36, ACW = 37, CL = 48, NAL = 22, NSL = 24.5, PCH = 37, PCW = 33, PNW = 41.5) has a well-developed, horizontal transverse process and is possibly derived from the middle of the caudal column. It has extensive, rather slender prezygapophyseal processes with long, dorsomedially facing facets and well-developed, posterolaterally projecting transverse processes (which are, for the most part, broken off). Anteriorly, at about mid-height, the caudal centrum has a small foramen on either lateral side, but there is no fossa. The articular surfaces of the centrum are subrectangular in end view; the anterior surface is concave, whereas the posterior surface is flat. The ventral groove on the centrum is relatively shallow. Paired, raised posteroventral areas served as attachment points for

a chevron element. There exists size-independent variation among the known vertebrae in the development of the anterior interspinous recess. Some caudals have an extensive dorsal roof over the neural canal starting well anterior the neural spine, whereas in others (e.g., ZIN PH 1476/16) this roof is absent and the neural canal is open dorsally anterior to the attachment area for interspinous ligaments. There are few vertebrae with the anterior dorsal roof of the neural canal intermediate between these two extremes.

There is no clear transition point in the caudal series; the neural spine disappears apparently several vertebral positions after the disappearance of the transverse processes. We identify vertebrae without a transverse processes as posterior caudals (e.g., ZIN PH 507/16; Fig. 12F, G; ACH = 12.0, ACW = 12.3, ANW = 12.4, CL = 29.7,

PCH = 11.6, PCW = 11.6). The neural spine is low and relatively long, shifted to the posterior half of the neural arch, or replaced by a longitudinal ridge. The prezygapophyseal processes are long and slender, projecting anteriorly well beyond the anterior margin of the centrum and diverging laterally.

Forelimb

Manual ungual phalanges: An isolated manual ungual phalanx I-2 is referable to Tyrannosauroida (ZIN PH 619/16; Fig. 13A–C). It is mediolaterally flattened and moderately curved. Its proximal articular surface is symmetrical and divided by a low ridge. A well-developed ventral flexor tubercle is situated close to the proximal end of the ungual. Deep lateral grooves for the keratinous sheath of the claw extend from the region of the flexor tubercle to the distal tip; the ventral rims of these grooves protrude slightly. The greatest length of the bone is 66.9 mm.

A similar bone, but with the flexor tubercle located closer to the more mediolaterally compressed proximal articular surface, might represent manual ungual phalanx II-3 (USNM 538181; Fig. 13D–F).

Hindlimb

Astragalus: *Nessov* (1995, p. 39) referred a number of isolated astragali (including CCMGE 447/12457 and CCMGE 448/12457) to the Bissekty tyrannosauroid, which he identified as *Alectrosaurus*. There are several partial astragali in the ZIN collection. Most only preserve the trochlea, but based on size and close resemblance to ornithomimosaur astragali, we consider it likely that the majority of these bones belong to Ornithomimosauria rather than to

Tyrannosauroida. One fragment of a large right astragalus (ZIN PH 121/16), however, is possibly referable to the latter group. The junction between the ascending process and trochlea is less pronounced on this specimen than on any of the smaller astragali.

Pedal ungual phalanges: A left pedal ungual phalanx (ZIN PH 124/16; Fig. 13G–I; greatest length, 58 mm) has the lateral groove placed slightly more dorsal than the medial one. It has raised rugosities lateral and medial to the proximal articular facet and another rugose area just distal to the ventral margin of the articular facet, but there is no distinct flexor tubercle.

USNM 538167 (Fig. 13J–L) is more asymmetrical than ZIN PH 124/16, with an asymmetrical proximal articular surface and the lateral groove placed distinctly more dorsal than the lateral groove. This phalanx is certainly from a lateral digit and possibly represents the left ungual of the second pedal digit (II-3).

3. Phylogenetic relationships of the Bissekty tyrannosauroid

We refer all tyrannosauroid specimens from the Bissekty Formation at Dzharakuduk to a single taxon because we have observed no variation within the available sample suggesting the presence of more than one. Furthermore, there are currently no other known local vertebrate assemblages containing more than one tyrannosauroid taxon (*Holtz, 2004*); indeed, it is rather unlikely that there would have been two or more closely related large predators existing sympatrically.

To assess the phylogenetic position of the Bissekty tyrannosauroid, we performed a cladistic analysis using the character-taxon matrix presented by *Brusatte et al. (2010)*. The Bissekty

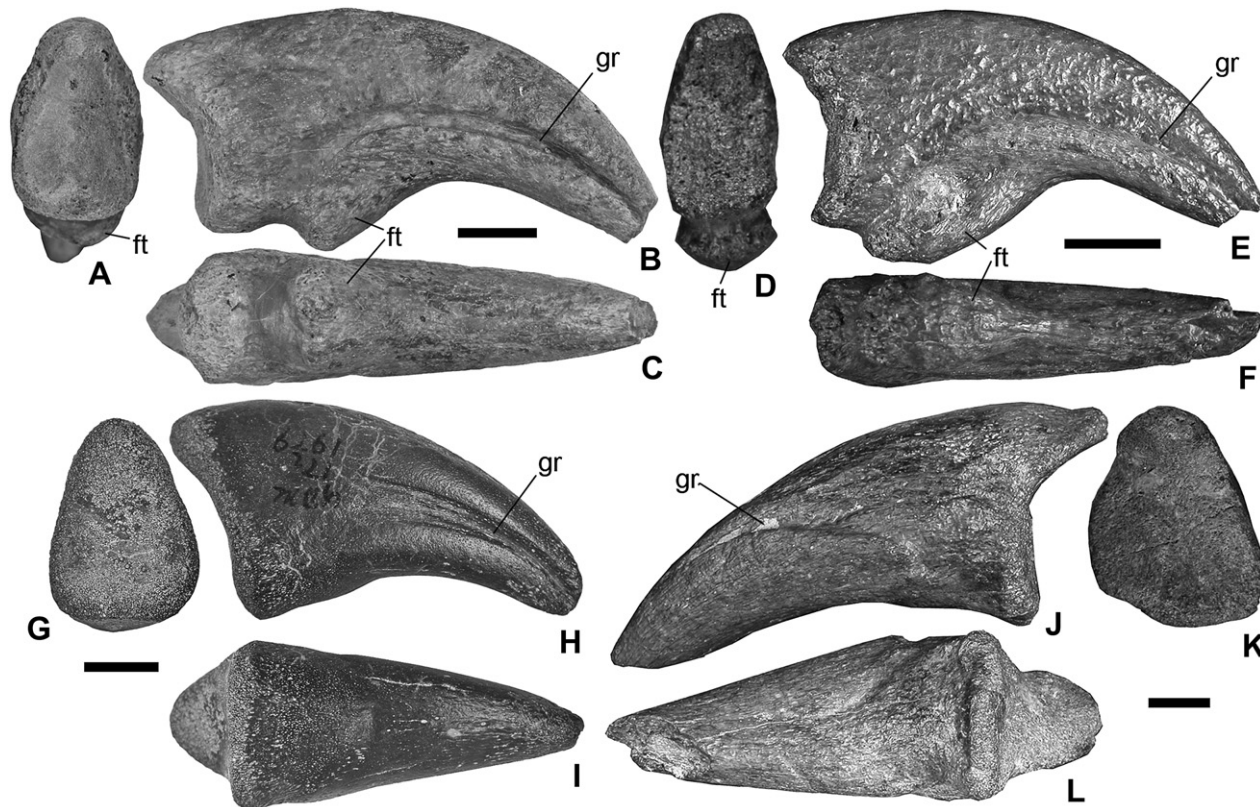


Fig. 13. Ungual phalanges of Tyrannosauroida indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A–C, ZIN PH 619/16, manual ungual I-2, in A, proximal, B, lateral or medial and C, ventral views. D–F, USNM 538181 (1997), manual ungual II-3(?), in D, proximal, E, lateral or medial and F, ventral views. G–I, ZIN PH 124/16 (CDZH-17g, 1979), left pedal ungual, in G, proximal, H, medial and I, ventral views. J–L, USNM 538167, left pedal ungual II-3(?), in J, lateral, K, proximal and L, ventral views. ft, flexor tubercle; gr, groove. Scale bars represent 1 cm.

tyrannosauroid material can be scored for 37 of the 307 characters (12.0%) listed by Brusatte et al. (2010): 15(0), 16(0), 17(0), 18(0), 19(0), 22(0), 24(0), 27(0), 28(1), 29(0), 30(0), 32(0), 33(1), 35(1), 36(0), 113(0), 114(1), 115(2), 116(1), 117(0), 118(0), 120(1), 121(1), 196(2), 198(2), 199(1), 200(0), 201(0), 202(1), 213(1), 214(0), 217(1), 219(0), 221(1), 222(2), 229(0), 231(0). One thousand repetitions of the parsimony ratchet (island hopper) algorithm of NONA version 2.0 (Goloboff, 1999) run with Winclada version 1.00.08 interface (Nixon, 1999) produced a single most parsimonious tree with a length of 558 steps, a consistency index of 0.64, and a retention index of 0.83 (Fig. 14). The Bremer support values were found by TNT version 1.1 (Goloboff et al., 2003).

Based on this analysis, the Bissekty taxon is a non-tyrannosaurid tyrannosauroid more derived than *Raptorex* (Sereno et al., 2009). It is placed basal to the North American tyrannosauroids *Appalachiosaurus* (Carr et al., 2005) and *Bistahieversor* (Carr and Williamson, 2010), which are basal to Tyrannosauridae. The analysis reveals no autapomorphies for the Bissekty tyrannosauroid. Among 24 synapomorphies for the clade comprising the Bissekty tyrannosauroid, *Appalachiosaurus*, *Bistahieversor* and Tyrannosauridae, three character states can be identified on the available material of the Bissekty tyrannosauroid:

Character 115(2): Frontal, supratemporal fossa, anteroposterior length compared to overall length of exposed portion of frontal on skull roof: between 50 and 60%. Calculated from the almost complete juvenile frontal ZIN PH 2330/16 where the supratemporal fossa occupies more than half of the dorsal surface of the bone.

Character 202(1): Axis and postaxial cervicals, anteroposterior length of centrum compared to dorsoventral height of posterior centrum face: less than or equal to each other. Calculated from the posterior cervical USNM 538131 (Fig. 10D, E).

Character 217(1): Cervical and dorsal vertebrae, rugose ligament attachment scars in pre- and postspinal fossae: present as prominent, rectangular flanges that extend outside of the fossae and are visible in posterior view, but only on the dorsal vertebrae. The rugose ligamentous scars are present on all dorsals or dorsal neural spines referred to the Bissekty tyrannosauroid. However, none of the known cervical vertebrae is preserved with the neural arch attached and thus it is unclear whether these ligamentous scars were also present on the cervical vertebrae (state 2 of this character) of the Bissekty tyrannosauroid.

4. Discussion

The Bissekty tyrannosauroid is middle–late Turonian in age (Archibald et al., 1998; King et al., unpublished data), some 10 Ma older than the oldest (middle Campanian) tyrannosauroid *Appalachiosaurus* from North America (Carr et al., 2005). Except for the late-surviving *Dryptosaurus* from the Maastrichtian of eastern North America (Carr et al., 2005; Brusatte et al., 2011), more basal tyrannosauroid theropods are known only from the Early Cretaceous deposits in Europe (Hutt et al., 2001) and Asia (Sereno et al., 2009; Li et al., 2010). Thus the Bissekty tyrannosauroid fills a major temporal gap in the fossil record of tyrannosauroids: the first half of the Late Cretaceous (Cenomanian–Santonian). The only other tyrannosauroid taxon described from this time interval (but see Van Itterbeeck et al., 2005) is *Alectrosaurus olseni* from the Iren Dabasu Formation of Inner Mongolia, China (Gilmore, 1933). It was originally described on the basis of forelimb and hindlimb bones, but subsequently it has been established that the forelimb actually belonged to a therizinosaur (Perle, 1977; Mader and Bradley, 1989; Zanno, 2010). In addition to the holotypic hindlimb, there are undescribed isolated cranial bones possibly referable to

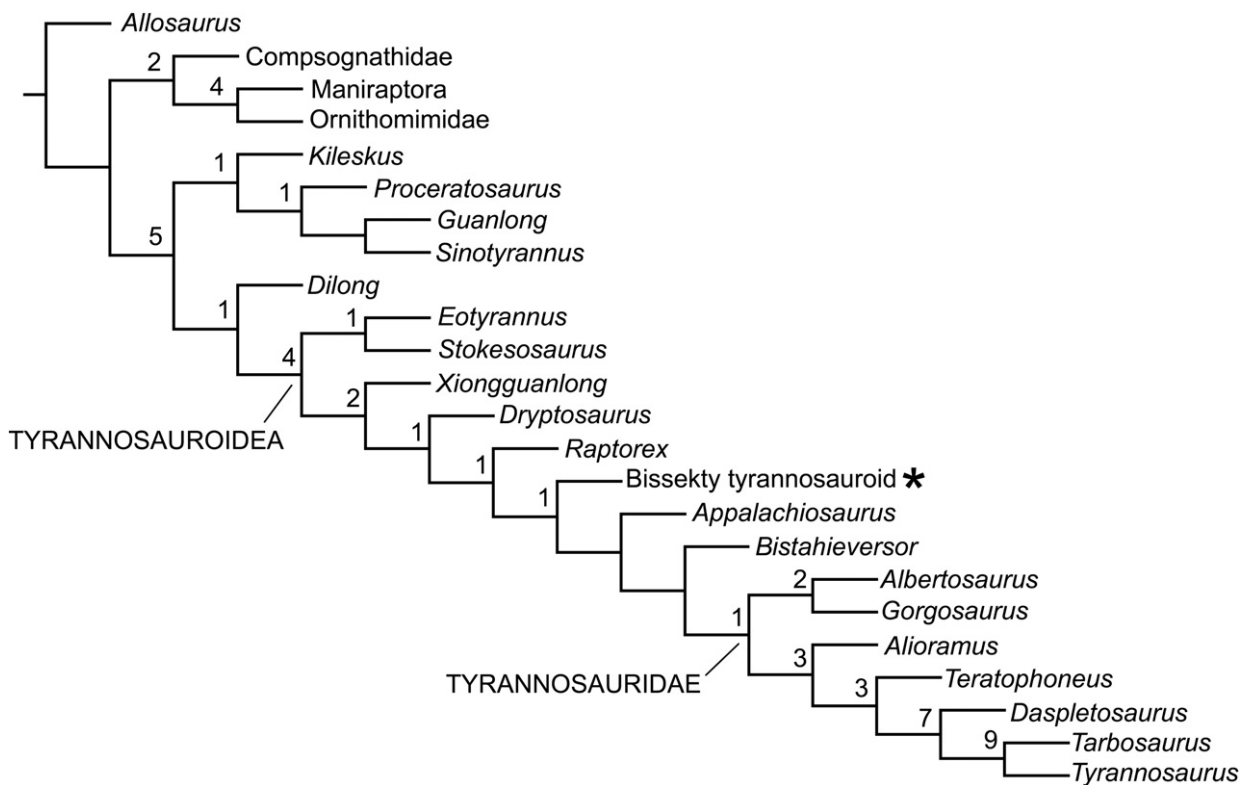


Fig. 14. The single most parsimonious tree recovered using of the parsimony ratchet (island hopper) algorithm of NONA version 2.0 and the character–taxon matrix compiled by Brusatte et al. (2010) with the addition of the Bissekty tyrannosauroid (highlighted by an asterisk). The Bremer support values are shown at the nodes.

Alectrosaurus from the Iren Dabasu Formation in the collections of the American Museum of Natural History (Brochu, 2003). Perle (1977) referred to *Alectrosaurus* a partial skeleton including a fairly complete skull from the correlative Bainshire Formation at Baishin Tsav, Mongolia. However, this specimen is not definitely referable to *Alectrosaurus* (T.D. Carr, pers. comm.). Currie (2000, fig. 22.7A) published a reconstruction of this skull and noted (p. 447) that it lacks denticles on the premaxillary teeth, but there is no such information in the original description by Perle (1977). According to Carr and Williamson (2004), non-denticulate premaxillary teeth probably belong to immature individuals.

The low, straight maxilla of the Bissekty tyrannosauroid resembles those of the Baishin Tsav skull (Perle, 1977). It is similar in the gently convex alveolar margin, high number of teeth (at least 17), smaller anterior maxillary teeth, two rows of supralabial foramina, and extensive antorbital fossa extending to the posterior end of maxilla posteriorly and anterior to the maxillary fenestra anteriorly. The phylogenetic significance of these similarities is uncertain because these plesiomorphic character states are also retained in juveniles of more derived tyrannosauroids. More meaningful comparisons of the Bissekty and Bainshire tyrannosauroid remains will only be possible when a more detailed description of the skull from Baishin Tsav finally becomes available. The abundance of tyrannosauroids during the first half of the Late Cretaceous in Asia is consistent with the hypothesis of an Asiatic center of origin for Tyrannosauridae.

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