A NEW TROODONTID (DINOSAURIA: THEROPODA) FROM THE CENOMANIAN OF UZBEKISTAN, WITH A REVIEW OF TROODONTID RECORDS FROM THE TERRITORIES OF THE FORMER SOVIET UNION

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ABSTRACT—Based on a review of troodontid specimens from the territories of the former Soviet Union, including new discoveries from Uzbekistan, two dental morphotypes can be distinguished among Troodontidae from the Cretaceous of Asia: (1) unserrated teeth, present in Mei from Lujiatun (China; Early Cretaceous: Hauterivian-Barremian), an unnamed taxon from Hövöör (Mongolia; Early Cretaceous: Aptian-Albian), Urbacodon itemirenensis, gen. et sp. nov. from Itemir and Urbacodon sp. from Dzharakuduk (Uzbekistan; Late Cretaceous: Cenomanian and Turonian, respectively), and Archaeornithoides from Bayn Dzak and Byronsaurus from Ukhaa Tolgod (Mongolia; Late Cretaceous: Campanian-Turonian, respectively), and (2) serrated teeth, present in Sinornithoides from Huanuxiao (China; Early Cretaceous) and Sinornithoides-like taxa from Khamryn U’s (Mongolia; Early Cretaceous: Aptian-Albian), Shestakovo (Russia; Early Cretaceous: Aptian-Albian), and Sheikhdzheili (Uzbekistan; Late Cretaceous: Cenomanian); Troodontidae indet. from Kansai (Taijikistan; Late Cretaceous: Santonian) and Abyntau (Kazakhstan; Late Cretaceous: Campanian), Saurornithoides (Mongolia and China; Late Cretaceous: Cenomanian-Maastrichtian), and Troodon from Kakanaut and Blagoveshchensk (Russia; Late Cretaceous: Maastrichtian).

INTRODUCTION

Troodontid theropods are among the rarest dinosaurs in the fossil record. Nine troodontid genera are currently recognized (Makovicky and Norell, 2004; Xu and Norell, 2004; Xu and Wang, 2004), with only Troodon formosus being represented by relatively abundant material from Campanian-to-Maastrichtian-age strata in western North America (e.g., Sternberg, 1932; L. S. Russell, 1948; D. A. Russell, 1969; Sues, 1977; Currie, 1985, 1987, 2004; Wilson and Currie, 1985; Currie and Zhao, 1994). Troodontidae have numerous bird-like features, and study of this group has substantially contributed to our understanding of the origin of birds (e.g., Currie, 1987; Varricchio, 1993, 1997; Varrichio et al., 1997, 1999, 2002; Xu et al., 2002b; Makovicky et al., 2003; Varrichio and Jackson, 2004; Xu and Norell, 2004). With the exception of Troodon, all named troodontid genera and at least one unnamed taxon are endemic to Asia (Osborn, 1924; Barsbold, 1974; Barsbold et al., 1987; Osmolska, 1987; Barsbold and Osmolska, 1990; Kurzanov and Osmolska, 1991; Elzanowski and Wellnhofer, 1992, 1993; Currie and Peng, 1994; Russell and Dong, 1994; Varrichio, 1997; Norell et al., 2000; Currie and Dong, 2001; Xu et al., 2002b; Makovicky et al., 2003; Makovicky and Norell, 2004; Xu and Norell, 2004; Xu and Wang, 2004). Troodon is now known from both western North America and the Far East of Russia. Despite this impressive list of taxa, we intend to demonstrate in this paper that the diversity of troodontids in Asia has been underestimated. Recent discoveries indicate that two dental morphotypes were present among Cretaceous Troodontidae from Asia, one with serrated and the other with unserrated teeth.

In this article, we describe a new troodontid with unserrated teeth from the Cenomanian-age Itemir locality in the central Kyzylkum Desert, Uzbekistan. A similar species is also represented at the nearby Turonian-age locality Dzharakuduk. The Itemir-Dzharakuduk depression contains strata of several Cretaceous formations that span the time interval from the Aptian-Albian to the Santonian (Fig. 1; Pyatkov et al., 1967; Sochava, 1968; Martinson, 1969; Nessov, 1995, 1997; King et al., in press). The first dinosaurian bones from Dzharakuduk were collected in 1914 by the Russian geologist A. D. Arkhangelsky (Arkhangelsky, 1916; Riabinin, 1931). During the 1930s, the locality was repeatedly visited by geologists (Sosedko, 1937). The best find made during that period was a complete turtle shell, the holotype of Lindhofemys elegans Riabinin, 1935. In 1958, A. K. Rozhestvensky visited the Itemir-Dzharakuduk depression and made collections (Rozhestvensky, 1964). Unfortunately, he erroneously claimed that Dzharakuduk (Bissekty) and Itemir represented the same locality, whereas these two sites are actually separated by several kilometers, expose Cretaceous strata of different ages (Albian-Cenomanian at Itemir and Turonian-Santonian at Dzharakuduk), and have yielded different vertebrate assemblages (Nessov, 1997). Rozhestvensky’s claim was accepted by Kurzanov (1976), who applied the generic nomen Itemirus to a new taxon of theropod dinosaur based on a braincase from Dzharakuduk that was collected by Rozhestvensky in 1958. The erroneous synonymy of the two localities, Itemir and Dzharakuduk, is still occasionally repeated in the secondary literature (e.g., Unwin and Bakhurina, 2000). Compounding the confusion is the fact that the richest vertebrate-bearing level at the Itemir locality, producing the holotype of the new troodontid described herein, is stratigraphically situated in the Cenomanian Dzharakuduk Formation (Martinson, 1969), a designation that...
reflects the scarcity of geographic place-names available for stratigraphic units in the Kyzylkum Desert. From 1977 to 1994, L. A. Nessov worked the Itemir and Dzharakuduk localities extensively (Nessov, 1995, 1997, and references therein). From 1997 to 2000 and from 2002 to 2004, these localities were explored by the international expeditions with Uzbek, Russian, British, American, and Canadian participants (Archibald et al., 1998). As a result, the Turonian-age vertebrate assemblage from the Bisskety Formation at Dzharakuduk is now among the richest known Cretaceous faunas in the world, with over 70 taxa currently identified. At present, the mammals and turtles are the best studied components of this assemblage (see Archibald and Averianov [2005] and Danilov and Parham [2005] for recent reviews of these two groups), but monographic studies of materials for other groups of vertebrates (e.g., dinosaurs) are still in preparation.

In 2004, a left dentary (ZIN PH 944/16; Figs. 2A–F, 3), designated as the holotype of a new troodontid taxon herein, was collected by the URBAC expedition at a newly discovered microvertebrate site IT-01 in the Dzharakuduk Formation at Itemir (Figs. 1, 4; geographic coordinates: 42°06′18″ N, 62°34′49″ E). The vertebrate assemblage from site IT-01 and adjacent localities comprises chondrichthyans (Acrodon sp., Polycrados sp., Hybodus sp., Cretodus sp., Hipsidaspis sp., and Scapanorhynchus sp.), osteichthyans (Belenoostomus sp., Pycnodontiformes indet., Lepidotes sp., Amiidae indet., Pholidophoriformes indet., Ichthyodectidae indet., and Albulidae indet.), salamanders (Scapherpetidae indet.), turtles (Trionychidae indet. and Macrobaenidae sp.), Crocodiliformes indet., pterosaurs (Ornithocheiridae indet.), and dinosaurs (Neosauropoda indet., Tyrannosauroidea indet., Troodontidae gen. et sp. nov., Hadrosauridae indet., and Asiaceratops subsupalvidalis). The vertebrate assemblage from the Dzharakuduk Formation is essentially the same as that for the Khodzhakul Formation in the southwestern Kyzylkum Desert of western Uzbekistan, which has been dated as early Cenomanian (Nessov, 1993, 1997; Nessov et al., 1994; King et al., in press). This allows determination of the age of the Dzharakuduk Formation as Cenomanian, which is consistent with data from the invertebrate fossils from this formation (Pyatkov et al., 1967; Sochava, 1968; Martinson, 1969; King et al., in press).

**Tooth Measurements**—BW, basal width of tooth crown; FABL, fore-aft basal length of tooth crown; TCH, tooth crown height. All measurements are in mm.

**Abbreviations**—CCMGE, Chernyshev’s Central Museum of Geological Exploration, Saint Petersburg; PM TGU, Paleontological Museum, Tomsk State University, Tomsk; URBAC, Uzbek/Russian/British/American/Canadian Joint Paleontological Expeditions; ZIN PH, Paleonherpetological Collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg; ZIN PO, Paleornithological Collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

**SYSTEMATIC PALEONTOLOGY**

**THEROPODA Marsh, 1881**

**MANIRAPTORA Gauthier, 1986**

**TROODONTIDAE Gilmore, 1924**

**URBACODON, gen. nov.**

**Type Species**—Urbacodon itemirensis, sp. nov.  
**Diagnosis**—As for type and only species.  
**Etymology**—Combination of the acronym URBAC for the international joint expeditions to the Kyzylkum Desert and -odont (Ionic variant of Greek odous), tooth.

**URBACODON ITEMIRENIS, sp. nov.**

**Holotype**—ZIN PH 944/16, left dentary (Figs. 2A–F, 3). Found by Anton S. Rezvyi on September 9, 2004.  
**Etymology**—From the name of the type locality, Itemir, and -ensis, Latin suffix denoting a place or country.  
**Type Locality and Horizon**—Site IT-01, Itemir locality, Itemir-Dzharakuduk Depression, central Kyzylkum Desert, Navoi Viloyat, Uzbekistan. Dzharakuduk Formation (Upper Cretaceous: Cenomanian).

**Diagnosis**—Distinguished from *Troodon* Leidy, 1856, Saurornithoides Osborn, 1924, Sinornithoides Russell and Dong, 1994, Sinovenator Xu et al., 2002b, Sinusonasus Xu and Wang, 2004, and an unnamed troodontid from Khamryn-Us (Barsbold et al., 1987) by the absence of serrations on the teeth, from *Byronosaurus* Norell et al., 2000 by the presence of fewer neurovascular foramina in the lateral groove on the dentary and by more bulbous anterior dentary crowns, and from *Mei* Xu and Norell, 2004 by much larger size.

**Comments**—Urbacodon cannot currently be compared to *Borogovia* Osmolska, 1987 and *Tochiariosaurus* Kurzanov and Osmolska, 1991 from the Upper Cretaceous (Maastrichtian) of Mongolia because both of the latter taxa are known only from hindlimb elements.

Urbacodon, with a rather straight dentary bearing 32 teeth, is more plesiomorphic than the clade comprising *Troodon* and *Saurornithoides*, which is characterized by the medially deflected symphylar region of the dentary and 35 dentary teeth (Currie, 1987; Makovicky et al., 2003). A diastema in the posterior part of the tooth row has not been previously reported for any troodontid and might prove diagnostic for the new taxon unless it merely represents an individual variation.

A troodontid with unserrated teeth, *Archeornithoides* from the Campanian of Mongolia, is known from a single fragmentary, possible hatchling, specimen (Elzanowski and Wellnhofer, 1992, 2002b, 2003).
It has a distinct small anterior alveolus on the dentary (Elzanowski and Wellnhofer, 1992:fig. 1c), which is absent in *Urbacodon*.

**Description**

**Dentary**—ZIN PH 944/16 is an excellently preserved left dentary, which lacks only the tip of the posterodorsal process (Fig. 2A–C). The length of the dentary along the dorsal margin is 79.2 mm. There are 32 alveoli arranged in two series separated by a diastema: an anterior series comprising 24 alveoli and a posterior series of eight alveoli. Alveolar size is largest near the diastema and decreases anteriorly and posteriorly. The interdental ridges are confluent only ventrally, separating the tooth roots but not the crowns. There are no interdental plates as in other troodontids (Currie, 1987; contra Varricchio, 1997). The labial wall of the alveolar row is higher than the lingual wall. The alveolar row is flanked medially by a distinct narrow paradental groove (which is only partially preserved), which becomes a line of shallow pits near the anterior end of the dentary (Fig. 2B, C). This groove represents a dorsal opening of a narrow vertical cleft lying medial to the tooth row. The ventral part of this cleft intersects the interdental ridges lingually and visible when the dorsal border of the lingual side of dentary is broken off (e.g., Fig. 3A; compare with Currie [1987:fig. 3b]). Only the anterior portion of dentary, encompassing the anterior nine teeth, gently curves medially. The remaining portion of dentary forms a perfectly straight tooth row. The dorsal and ventral margins of the dentary converge anteriorly.

The mandibular symphysis is more lightly built than in *Troodon* (Currie, 1987). The symphyseal facet is well defined and only slightly rugose, situated at an angle of approximately 45º to the horizontal. The posterior opening of the inferior alveolar canal is at the level of alveolus 24. Posterior to this opening there is an extensive depression for the Meckelian canal, which is roofed over dorsally by a thin plate of the dentary. Anterior to this opening, the Meckelian canal is confluent with the narrow, cleft-like Meckelian groove. The Meckelian groove extends toward the mandibular symphysis and continues on the symphyseal surface almost to the anterior end of dentary. Just
posterior to the symphysis and ventral to the Meckelian groove, a small foramen is confluent with the inferior alveolar canal. The splenial facets dorsal and ventral to the Meckelian groove can be traced forward to the level between alveoli 18 and 19. The splenial facet is deeper posteriorly and covers almost the entire posterior end of the dentary.

On the labial side of the medially curved anterior portion of dentary, near the dorsal margin, there is a row of six vascular foramina. Posteriorly, the dorsal row of foramina forms a groove, which extends posteriorly toward the end of the dentary. At the level of the most posterior alveolus, this groove is roofed by a bony bar. A second, ventral row of vascular foramina extends along the ventral border of the dentary. The foramina in the ventral row are closely spaced anteriorly and widely spaced posteriorly; the last of these openings is situated at the level of the diastema.

**Dentition—** Roots of teeth are preserved in alveoli 16 and 17 and crowns of erupting teeth in positions 17, 20, and 23 (Fig. 3). Although there is an unworn anterior tooth, its exact position cannot be established (Fig. 2D–F; it dropped out of an alveolus when the dentary was cleaned of adhering matrix). All four teeth have unserrated mesial and distal carinae. An anterior dentary tooth has a relatively straight crown with a distally curved apex and slight constriction between the crown and root. The labial side of the crown is more convex than the lingual side. Both carinae are flanked by grooves on the lingual side. Tooth 17 was in the process of eruption at the time of death lingual to the root of the functional tooth (Fig. 3A). The crown of the partially erupted tooth 20 is strongly curved distally, with its mesial carina displaced lingually (Fig. 3B). Tooth 23 is represented by a crown germ placed in a crypt in the lingual wall of the dentary lingual to the (not preserved) functional tooth (Fig. 3C).

**Comments—** The term ‘paradental groove’ is used here for the groove extending between the lingual side of dentary and interdental plates, following Elzanowski and Wellnhofer (1992, 1993). Currie (1987) suggested that this groove housed a blood vessel, but it more likely contained the dental lamina as in other vertebrates (Edmund, 1957). Holtz (2000) confusingly used the term ‘paradental groove’ to describe implantation of dentary teeth in a groove rather than in individual sockets (his Character 134). Primitively in theropods the paradental groove is shallow and extends level with the root bases; it bears openings along its entire length connecting the dental lamina with the tooth germs (e.g., Lamanna et al., 2002:fig. 2B), similar to the ‘special foramina’ in ornithischians (Edmund, 1957). The structure of the paradental groove in ZIN PH 944/16 is quite distinct. It forms a deep cleft immediately lingual to the tooth row, the ventral part of which intersects the interdental ridges and connects with the tooth germs and the dorsal part of which forms a narrow groove parallel to the tooth row along the dorsal margin of the lingual surface of the dentary. It is not clear whether this feature is unique to *Urbacodon* or whether the dorsal border of the lingual dentary side is incompletely preserved in other known troodontid dentaries. In *Troodon* and *Archaeornithoides*, the paradental groove intersects the interdental ridges (Currie, 1987: fig. 3b; Elzanowski and Wellnhofer, 1992:fig. 1c; Elzanowski and Wellnhofer, 1993:fig. 4B), but this might merely represent the ventral portion of the groove, with the dorsal portion missing. If this unique structure of the paradental groove is shared by all troodontids, it might represent an important autapomorphy for this group, possibly related to some change in tooth replacement.

There exists disagreement in the literature regarding the presence or absence of interdental plates in dromaeosaurid, spinosaurid, and troodontid theropods (e.g., Sues, 1977; Currie, 1987, 1995; Elzanowski and Wellnhofer, 1993; Charig and Milner, 1997; Varricchio, 1997; Norell et al., 2001b; Sues et al., 2002; Dal Sasso et al., 2005). In some specimens, highly vascularized bony walls between the alveolar margins and paradental groove have been interpreted as representing fused interdental plates (Currie, 1987: fig. 3d-f), whereas in other specimens, including ZIN PH 944/16, this vascularized area is absent and the space between the alveoli and the paradental groove is reduced to a narrow strip of bone. We interpret ZIN PH 944/16 as lacking interdental plates.
A number of vertebrate-bearing localities around the Shestakovo settlement in Kemerov Province, western Siberia (Russia), have produced an important faunal assemblage including fishes, amphibians, turtles, lizards, crocodyliforms, pterosaurs, dinosaurs, birds, and mammals (see Averianov et al., 2006 for the most recent review of the fauna). The vertebrate-bearing levels are confined to the Aptian-Albian Ilek Formation. A fragmentary troodontid skeleton, mentioned by Alifanov and colleagues (1999:492), was excavated at the Shestakovo 3 site by a commercial collector from Novosibirsk and was unfortunately unavailable for study. At the microvertebrate site Shestakovo 1, skeletal remains of troodontids are very rare. Several years of collecting by joint field crews from Tomsk State University and other Russian institutions have yielded only a single tooth, a first metacarpal, and a possible caudal vertebra referable to this group. The tooth, PM TGU 16/5-124 (Fig. 5A–C) is rather small (FABL = 2.1, WB = 1.0), with denticles present only on the distal carina. The denticles are small, with 5.7 per one mm (basal diameter of the largest dente: 0.19 mm), and distinctly hooked. The first metacarpal and caudal from Shestakovo 1 will be described elsewhere.

**Khodzhakul and Sheikhzheili**

These two closely spaced localities are situated within the lower Cenomanian-age Khodzhakul Formation in the southwestern Kyzylkum Desert of Uzbekistan. Their vertebrate assemblage includes fishes, amphibians, turtles, plesiosaurs, lizards, crocodyliforms, pterosaurs, dinosaurs, birds, and mammals (Nessov, 1997; Averianov and Archibald, 2005). Troodontidae are represented by rare postcranial bones and isolated teeth. The teeth are rather small (Fig. 5D–O), with FABL = 2.1–3.5, M = 2.92 ± 0.13, BW = 0.8–1.5, M = 1.17 ± 0.06, TCH = 3.5–5.7, M = 4.51 ± 0.24 (n = 10) and distinctly labioliually compressed, with a BW/FABL ratio 0.34–0.46 (M = 0.40 ± 0.01, n = 10). Five to 15 relatively large denticles are present on the distal carina (2.00–3.89, M = 3.03 ± 0.22 denticles per mm, n = 10); the mesial carina lacks denticles. The denticles are largest in the mid-portion of the distal carina, significantly decreasing in size towards the basal and apical ends. They are hooked distally, with their apices curved toward the crown apex (visible only on unworn denticles). CCMGE 49/12176 is unique in the sample in having its mesial carina displaced lingually and flanked distally by a distinct groove (Fig. 5J). In these respects it resembles a posterior dentary tooth of *Troodon* illustrated by Currie (1987:fig. 5u). In ZIN PH 1886/16 (Fig. 5D–F) and 1887/16, the lingual side of the tooth crown is flat; in the former specimen, there is also a vertical groove on the opposite convex side close to the mesial margin. Only ZIN PH 1886/16 shows a constriction between the crown and the root.

Nessov (1995:41) named *Troodon asiamericanus* on the basis of isolated teeth from Sheikhzheili (holotype: CCMGE 49/12176; Fig. 5J–L). He distinguished it from the North American type-species *T. formosus* Leidy, 1856 by the smaller size and more labioliually compressed crowns of the teeth, un serrated mesial carina, and narrower bases of the distal denticles. It is evident now that all of these features represent plesiomorphic character-states for troodontid teeth, which are also found in the Early Cretaceous Sinornithoides (Currie and Dong, 2001) and are thus not diagnostically at the generic level. We follow Makovicky and Norell (2004:186) in considering *Troodon asiamericanus* Nessov, 1995 a nomen dubium.

**Dzharakuduk**

This locality in the Cenomanian-age Dzharakuduk Formation in the central Kyzylkum Desert of Uzbekistan has yielded the holotype of *Urbacodon itemirensis*, gen. et sp. nov. The associated vertebrate assemblage is enumerated in the Introduction.

**Itemir**

This locality in the Cenomanian-age Dzharakuduk Formation in the central Kyzylkum Desert of Uzbekistan has yielded a very diverse vertebrate assemblage from the Turonian Bissekty Formation, currently comprising more than 70 taxa of fishes, amphibians, turtles, plesiosaurs, lizards, crocodyliforms, pterosaurs, dinosaurs, birds, and mammals (Nessov, 1997; Archibald et al., 1998; Archibald and Averianov, 2005; and references therein). Currently identified troodontid remains from Dzharakuduk include braincase and dentary fragments, isolated teeth, cervical, dorsal, and caudal vertebrae, first metacarpal, third metatarsal, and possibly some other postcranial bones. These specimens will be more fully documented in a monographic review of the dinosaurian faunas of the Kyzylkum Desert currently in preparation by the authors. All troodontid specimens from Dzharakuduk are currently identified as *Urbacodon* sp. For comparative purposes, we illustrate two troodontid teeth from Dzharakuduk herein (Figs. 2G–I and 5P–R) and briefly comment on some specimens previously reported by Nessov.

CCMGE 71/12455 is a premaxillary tooth originally figured by Nessov (1993:fig. 6-2) and tentatively referred to either Deinonychosauroidea or Mammalia(?) The tooth has a slight constriction between the crown and root, un serrated mesial and distal carinae displaced on the lingual side of the crown, a flat lingual side of the crown with a median ridge flanked by mesial and distal grooves, a strongly convex labial side of the crown, and a distally curved apex.

ZIN PH 256/16 is an anterior dentary tooth (Fig. 2G–I). It is distinctly larger than but almost identical in structure with an anterior dentary tooth of *Urbacodon itemirensis*.

ZIN PH 1899/16 (Fig. 5P–R) is a posterior dentary or maxillary tooth with a slight constriction between the crown and root.

**FIGURE 4.** Outcrop of the Dzharakuduk Formation at the microvertebrate site IT-01 at Itemir, central Kyzylkum Desert, looking west, with Anton Rezvyi standing approximately at the site where he found ZIN PH 944/16 (photograph by A.O. Averianov).
The crown is strongly curved distally. Both carinae are devoid of serrations. The lingual side of the root has a resorption pit containing the crown of a replacement tooth.

CCMGE 2/11822 (Nessov, 1981:fig. 10-12; Nessov, 1995:pl. 2, fig. 10) is a tooth, originally identified as Theropoda indet., with an unserrated crown similar to the specimen described above, but the mesial carina is displaced lingually.

CCMGE 466/12457 is a braincase fragment that was originally attributed to a small, possibly dromaeosaurid theropod (Nessov, 1995:pl. 2, fig. 17). It is referable to the Troodontidae because the foramen magnum is much larger than the occipital condyle and the reduced basal tubera are situated directly below the occipital condyle and separated by a narrow groove (Xu et al., 2002b; Makovicky et al., 2003). The foramen magnum is pear-shaped and about twice as high as the occipital condyle, which is relatively larger than that in Troodon (Currie and Zhao, 1994) but smaller than that in Byrornosaurus (Makovicky et al., 2003).

ZIN PO 4608 (Nessov, 1992:pl. 2, fig. 1; Nessov, 1997:pl. 19, fig. 1) is a dentary fragment preserving 12 alveoli and the erupting unserrated crown in alveolus 7 (counting from the preserved anterior end), which was not noted in the original description. On the labial side, there are two rows (dorsal and ventral) of closely spaced, cleft-like neurovascular foramina, with at least some of the dorsal foramina united to form a groove. Originally, ZIN PO 4608 was assigned to the Ichthyornithiformes. However, as Nessov (1992:21) correctly noted, this bone, in contrast with the dentary of Ichthyornis (Clarke, 2004), is not fused with the splenial and bears two rather than one lateral rows of neurovascular foramina. These features are typical for troodontid dentaries. ZIN PO 4608 is similar in most respects to the holotype of Urbacodon itemirensis, but it is about one third the dorsoventral depth and has a relatively more open Meckelian groove, which might represent an ontogenetically variable trait. It is interpreted here as a juvenile specimen of Urbacodon sp.

CCMGE 475/12457 (Nessov, 1995:pl. 3, fig. 2) is an elongate caudal vertebra originally identified as Ornithomimidae? indet. However, it is relatively more elongate than the ornithomimid posterior caudals from Dzharakuduk, and the centrum is medially rather than dorsoventrally flattened. It bears a long, low, and ridge-like neural spine on the transversely concave dorsal surface of the neural arch, and the centrum has a longitudinal ventral groove. This vertebra could be a ‘mid’-caudal of a troodontid, which already lacks transverse processes but still retains a low neural spine. In the collections from Dzharakuduk, there are a number of more posterior troodontid caudals, each of which has a shallow dorsal groove on the neural arch without a
neural spine and circular pits dorsal to the neural canal for the insertion of interspinous ligaments (cf. Varricchio, 1997).

Kansai

This important lower Santonian vertebrate locality in the Yalovach Formation of the northern Fergana Depression in northern Tajikistan has produced skeletal remains of fishes, amphibians, turtles, lizards, crocodyliforms, pterosaurs, dinosaurs, birds, and mammals (Alifanov and Averianov, 2006). Troodontids are represented only by a dentary fragment and isolated teeth. ZIN PH 2/66 is a fragment of the anterior portion of a right dentary (Fig. 6). It is generally similar to the dentary of *Umbacodon itemirensis* but is larger and relatively more massive. There is also a distinct foramen on the Meckelian groove at the symphysis. The labial side is covered by numerous relatively large neurovascular foramina that are not clearly arranged into the rows. The fragment preserves nine confluent alveoli. At the posterior end of the fragment, a replacing tooth is preserved; it has a slight constriction between the crown and root (Fig. 6A). The only exposed carina of this crown is broken and it cannot be determined whether it was serrated or not.

The teeth from Kansai (Fig. 7) are similar in size to the troodontid teeth from the Khodzhakul Formation, with FABL = 1.3–4.6, M = 2.47 ± 0.33, n = 10, BW = 1.0–2.4, M = 1.61 ± 0.15, n = 10, and TCH = 2.1–4.6, M = 3.39 ± 0.30, n = 7, but less labiobuingly compressed, apparently due to the larger proportion of premaxillary and anterior dentary teeth in the sample (BW/FABL ratio is 0.44–1.08, M = 0.72 ± 0.08, n = 10). The Kansai teeth have distinctly larger distal denticles (2.63–6.67, M = 3.52 ± 0.34 denticles per millimeter, n = 11) than those from the Khodzhakul Formation. At least three teeth have a serrated mesial carina, but the mesial denticles are distinct enough to be measured only on one of these specimens (3.75 denticles per millimeter). Some teeth show lingual displacement of the mesial carina.

A single unserrated possible troodontid tooth from Kansai (ZIN PH 13/60) may indicate that troodontids with serrated and unserrated teeth coexisted at this site. The only other known locality where the two dental morphotypes are found together is the Campanian-age Ukhaa Tolgod locality in Mongolia (Norell et al., 2000; Makovicky et al., 2003; Norell and Hwang, 2004).

Nessov (1995:43, pl. 3, fig. 12) named *Troodon isfarensis* based on what he considered a left frontal (CCMGE 484/12457) from the Santonian Yalovach Formation at Kyzylpylai (Isfara 2) in the Fergana Depression of Tajikistan. We were unable to locate this specimen in the CCMGE collections, but, judging from the published photograph, the bone is not a frontal but rather closely resembles hadrosaurid prefrontals. Thus, *Troodon isfarensis* is not a valid troodontid taxon (see also Makovicky and Norell, 2004:186).

Shakh-Shakh

This designation denotes a series of localities in the upper Santonian to lower Campanian Bostobe Formation in the northeast Aral Sea area of Kazakhstan. The vertebrate fauna recovered so far includes fishes, turtles, crocodyliforms, pterosaurs, and dinosaurs (Nessov, 1997; Averianov, in press; and references therein). Nessov (1995:105; 1997:109) cited the presence of Troodontidae for this locality complex with reference to a personal communication from D. A. Russell. Particularly, he noted that this identification is based on “fused tibiale and fibulare having features of Troodontidae.” Co-ossification of the astragalus and calcaneum, however, is also known in some other theropod groups (Currie, 1987; Barsbold and Osmolska, 1990; Varricchio, 1997; Makovicky and Norell, 2004). Although the presence of troodontids in the Shakh-Shakh vertebrate assemblage would not be unexpected, it cannot be confirmed with reference to specific material at the present time.
Alymtau (=Kyrkkuduk II)

This vertebrate-bearing locality in the lower Campanian portion of the Darbasa Formation on the northern slope of the Alymtau Range in southern Kazakhstan has yielded remains of fishes, amphibians, turtles, lizards, crocodyliforms, pterosaurs, dinosaurs, and mammals (Averianov and Nessov, 1995; Averianov, 1997; Nessov, 1997). Troodontids are represented by isolated teeth previously identified as cf. *Troodon* sp. (Averianov and Nessov, 1995; Nessov, 1995). The teeth are somewhat larger than the troodontid teeth from Kansai, with FABL/H11505 1.9–4.6, M/H11505 3.12 ± 0.48, BW/H11505 1.2–2.4, M/H11505 1.84 ± 0.20, TCH/H11505 2.9–5.6, M/H11505 4.24 ± 0.51 (n/H11505 5). There is a smaller percentage of the premaxillary teeth in the available sample, and the BW/FABL ratio is 0.52–0.89, M/H11505 0.67 ± 0.09, n/H11505 4. The distal denticles are relatively larger than in the tooth sample from Kansai (1.82–3.33, M/H11505 2.42 ± 0.24 denticles per mm, n/H11505 7). Mesial denticles are present on a single specimen (Fig. 8A–C; 3.33 denticles per millimeter compared with 2.33 distal denticles per millimeter in this specimen). The mesial carina is usually displaced lingually.

Kakanaut

The Kakanaut locality is situated in the ‘middle’ Maastrichtian Kakanaut Formation on the Kakanaut River near Pekul’nei Lake in the Chukotka Autonomous Region of the Russian Far East. The vertebrate assemblage includes dinosaurs and possibly birds (Nessov and Golovneva, 1990; Nessov, 1992, 1995, 1997). It is currently the northernmost known locality with dinosaurian skeletal remains in the Eastern Hemisphere (Rich et al., 1997, 2002). Although “teeth and bones” of troodontids were mentioned by Nessov (1992:29), only a single incomplete tooth partially embedded in a block of tuff was found in the collection (ZIN PH 1/28, Fig. 8J). The troodontid from Kakanaut was previously identified as *Troodon* cf. *T. formosus* (Nessov and Golovneva, 1990; Nessov, 1992, 1995, 1997). This identification is provisionally retained here because *Troodon* is also known from Maastrichtian-age sites in Alaska (Clemens and Nelms, 1993; Rich et al., 1997, 2002; Gangloff, 1998; Fiorillo and Gangloff, 2000), now separated by approximately 1,600 km from the Kakanaut locality. However, it is not clear if isolated teeth are sufficiently diagnostic to distinguish *Troodon* from *Saurornithoides* (Currie, 1987). ZIN PH 1/28 is a rather large tooth, with FABL exceeding 6 mm. The distal denticles are strongly hooked with the pointed tips turned up towards the apex of the crown and relatively large (1.64 denticles per mm). Nevertheless, this value is slightly lower than that for *Troodon formosus*, which has about two distal denticles per mm (Currie et al., 1990; Baszio, 1997). Unlike in *T. formosus*, there are no distinct pits between the bases of the distal denticles. It is not clear if the mesial carina was serrated or not. *Troodon* is the only theropod identified from skeletal remains at the Kakanaut locality and is the most common theropod taxon in a vertebrate assemblage from Alaska (Fiorillo and Gangloff, 2000). This suggests that *Troodon* was well adapted to life at high paleolatitudes (Fiorillo and Gangloff, 2000).
Troodon, known only from a tiny skull fragment, from the same locality (Osborn, 1924). However, Archaeornithoides, a clade comprising Baryonyx, Spinosaurus, and Troodontidae, based on the presence of the parodental groove and absence of interdental plates. Elzanowski and Wellnhofer (1993:248) considered the possibility that Archaeornithoides deinosaursicus, known only from a tiny skull fragment, represented a juvenile troodontid, specifically Sauornithoides mongolensis from the same locality (Osborn, 1924). However, they rejected this identification primarily because of the unerrated teeth and broad palatal shelves of the maxillae. These objections are no longer valid because there are now troodontids with unerrated teeth, and wide palatal shelves are also known in troodontids (Currie, 2000; Makovicky et al., 2003). Currie (2000: 445) suggested that Archaeornithoides might be a juvenile of Sauornithoides. Elzanowski and Wellnhofer (1993:248), however, claimed that juvenile theropod teeth generally do not differ much from adult teeth and may have even larger denticles than adult teeth, and thus considered it unlikely that Archaeornithoides is a juvenile Sauornithoides. An alternative possibility, that Archaeornithoides is a juvenile dromaeosaurid, was proposed by Chiappe and colleagues (1996) based on an alleged dromaeosaurid embryo with unerrated teeth (Norell et al., 1994). However, this specimen was subsequently reidentified as an aberrant troodontid embryo with palatal ‘bumps’ that were initially misinterpreted as teeth (Norell et al., 2001a). Archaeornithoides might be a juvenile of the roughly coeval troodontid Byronosaurus, which also has unerrated teeth (see below). Until the diversity and ontogenetic variation of Mongolian troodontids become better understood, it is preferable to retain Archaeornithoides as a distinct taxon.

The second described troodontid with unerrated teeth is Byronosaurus from the Campanian-age Ukhha Tolgod beds of Mongolia (which might be a lateral equivalent of the Djadokht Formation; Kielan-Jaworowska et al., 2003). It was originally interpreted as an aberrant troodontid, and its unerrated teeth were considered autopomorphic for this taxon (Norell et al., 2000; Makovicky et al., 2003). The third troodontid with unerrated teeth is Mei from the Hauterivian- to Barremian-age lower part of the Yixian Formation in Liaoning Province, China (Xu and Norell, 2004). Here we place on record a fourth troodontid with unerrated teeth, Urbacodon gen. nov. from the Cenomanian and Turonian of Uzbekistan. Discoveries of two additional troodontid taxa with unerrated teeth were recently announced from the Early Cretaceous of China and the Campanian of Mongolia, respectively (Hwang et al., 2004). Together, these records indicate a much greater diversity of Troodontidae in Asia than previously assumed.

Published phylogenetic analyses of Troodontidae (Xu et al., 2002b; Makovicky et al., 2003; Makovicky and Norell, 2004) included only a single taxon with unerrated teeth, Byronosaurus; it is therefore unclear whether this feature characterizes a grouping within Troodontidae or whether it developed independently in different troodontid taxa. For many years, large marginal denticles were considered the most diagnostic attribute of troodontid teeth, suggesting possibly omnivorous (Nessov, 1995; Holtz et al., 2000) or insectivorous (Varrichio, 1997) habits. The complete absence of marginal denticles in Byronosaurus, Mei, and Urbacodon is thus unexpected. Among coelurosaurian theropods, teeth without serrations are also known in alvarezsaurids, basal ornithomimosaurids, basal oviraptorosaurs, and basal birds (Howgate, 1984; Weigert, 1995; Elzanowski, 2002; Xu et al., 2002a; Ji et al., 2003; Makovicky et al., 2003, 2004).

An early stage in the development of unerrated teeth in troodontids may be exemplified by isolated teeth from the Aptian-Albian-age Hövörö ( = Khovboor) locality in Mongolia, which were originally attributed to birds (Kurochkin, 1988:pl. 7, figs. 5,6). Nessov and Golovneva (1990:201) first suggested that

**Blagoveschensk**

This important vertebrate locality is in the upper(? ) Maastrichtian Udurchukan Formation (Tsagayan Group) on the bank of the Amur River in the city of Blagoveschensk in Amur Province, Far East of Russia. The vertebrate fauna includes turtles, crocodyliforms, and dinosaurs (Rozhdestvensky, 1957; Bolotsky and Moiseenko, 1988; Nessov, 1995, 1997; Moiseenko et al., 1997; Bolotsky and Godefroit, 2004; Godefroit et al., 2004). The occurrence of Troodontidae indet. (Bolotsky and Moiseenko, 1988; Nessov and Golovneva, 1990; Nessov, 1995), Troodon cf. formosus (Moiseenko et al., 1997), or Troodon sp. (Alifanov and Bolotsky, 2002) has been cited in previous accounts based on isolated teeth from this locality, but none of the specimens has been described. Despite the fact that Blagoveschensk is geographically much closer to the Mongolian localities with Sauornithoides than to the Chukotkan and Alaskan localities with Troodon, the latter identification seems plausible, because the rather diverse Maastrichtian hadrosaurid assemblage from the Amur River area suggests faunal exchange between East Asia and western North America (Godefroit et al., 2001, 2003, 2004; Bolotsky and Godefroit, 2004; see also Tumanova et al. [2004] concerning a possible record of nodosaurid ankylosaurs from the Kundur locality).

**DISCUSSION**

The first discovered troodontid taxon with unerrated teeth, Archaeornithoides deinosaursicus from the Campanian Djadokhta Formation at Bayn Dzak, Mongolia, was originally interpreted as the closest theropod relative of birds (Elzanowski and Wellnhofer, 1992, 1993). Elzanowski and Wellnhofer referred Archaeornithoides to a clade comprising Baryonyx, Spinosaurus, and Troodontidae, based on the presence of the parodental groove and absence of interdental plates. Elzanowski and Wellnhofer (1993:248) considered the possibility that Archaeornithoides deinosaursicus, known only from a tiny skull fragment, represented a juvenile troodontid, specifically Sauornithoides mongolensis from the same locality (Osborn, 1924). However, they rejected this identification primarily because of the unerrated teeth and broad palatal shelves of the maxillae. These objections are no longer valid because there are now troodontids with unerrated teeth, and wide palatal shelves are also known in troodontids (Currie, 2000; Makovicky et al., 2003). Currie (2000: 445) suggested that Archaeornithoides might be a juvenile of Sauornithoides. Elzanowski and Wellnhofer (1993:248), however, claimed that juvenile theropod teeth generally do not differ much from adult teeth and may have even larger denticles than adult teeth, and thus considered it unlikely that Archaeornithoides is a juvenile Sauornithoides. An alternative possibility, that Archaeornithoides is a juvenile dromaeosaurid, was proposed by Chiappe and colleagues (1996) based on an alleged dromaeosaurid embryo with unerrated teeth (Norell et al., 1994). However, this specimen was subsequently reidentified as an aberrant troodontid embryo with palatal ‘bumps’ that were initially misinterpreted as teeth (Norell et al., 2001a). Archaeornithoides might be a juvenile of the roughly coeval troodontid Byronosaurus, which also has unerrated teeth (see below). Until the diversity and ontogenetic variation of Mongolian troodontids become better understood, it is preferable to retain Archaeornithoides as a distinct taxon.

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these teeth may actually belong to troodontids. The teeth have a slight constriction between the crown and root, and the crown is strongly deflected distally. The mesial carina is unserrated whereas the distal carina bears some very small denticles. In overall structure, these teeth resemble those of Urbacodon sp. from Dzharakuduk (Fig. 5P–R).

According to Currie (1987) and Currie and Dong (2001), the maxillary and dentary teeth in Saurornithoides and Sinornithoides have denticles only on the distal carina, whereas the maxillary and anterior dentary teeth in Troodon also have mesial denticles. (Denticles are present on both carinae of the premaxillary teeth in all troodontids with serrated teeth.) The unnamed troodontid from the lower Cenomanian Khodzhakul Formation in Karakalpakistan appears to resemble Sinornithoides and Saurornithoides in having anterior dentary (Fig. 5D–I) and maxillary (Fig. 5M–O) teeth without mesial serrations. A possible maxillary tooth (Fig. 5M–O) is larger than the dentary tooth but has smaller distal denticles, as in Saurornithoides and Troodon (Barsbold, 1974; Currie, 1987). The Khodzhakul troodontid also resembles Sinornithoides in having relatively small distal denticles, with a basal diameter of approximately 0.3 mm (Russell and Dong, 1994; Currie and Dong, 2001). In a troodontid tooth from Shestakovoy, this value is even smaller (0.19 mm).

A sample of troodontid teeth from the lower Santonian Ya-

Lavoch Formation in the Fergana Depression (Kansai, Tajikistan) appears to represent another dental morphotype. Here the possible anterior (Fig. 7P–R) and posterior (Fig. 7M–O) maxillary teeth lack mesial denticles, as in Saurornithoides, Sinornithoides, and the Khodzhakul troodontid. But mesial denticles might be present on anterior dentary teeth (Fig. 7A–F), where they vary from slight undulations to distinct denticles, as in Troodon (Currie, 1987).

A third type of troodontid tooth, with serrated mesial carinae on the maxillary and anterior dentary teeth, is exemplified by the Campanian- to Maastrichtian-age Troodon from North America (Currie, 1987; Currie et al., 1990; Baszio, 1997). In Asia, a small sample of troodontid teeth from the lower Campanian Darbas Formation in southern Kazakhstan (Alymtau), with a probable maxillary tooth that has a serrated mesial carina (Fig. 8A–C), may be similar. Maastrichtian troodontids from the Russian Far East (Kakanaut and Blagoveshchensk localities) may also belong to a similarly derived taxon (cf. Troodon sp. or Troodon cf. formosus), but this identification remains to be confirmed by documentation of a larger sample of teeth.

It is interesting that troodontids with serrated teeth in the coastal plains of Middle Asia show a diversity of serration patterns during the time interval from the Cenomanian to the Cam-

pian, while the Campanian-Maastrichtian Saurornithoides from the conterminous but more inland Gobi Desert retained a more primitive dentition comparable to that of the Early Cretaceous Sinornithoides, with unserrated mesial carinae on the maxillary and dentary teeth. This observation is in accordance with the scenario developed by Nessov (1993, 1997) concerning the heterogeneous development of faunal complexes during the Cre-

taceous, where the origin and early diversification of certain important tetrapod groups took place on the coastal plains of Middle Asia (see also similar data on mammals summarized in Archibald and Averianov [2005]).

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