Journal of Vertebrate Paleontology 27(1):87–98, March 2007

ARTICLE

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 itemirensis*, gen. et sp. nov. from Itemir and *Urbacodon* sp. from Dzharakuduk (Uzbekistan; Late Cretaceous: Cenomanian and Turonian, respectively), and *Archaeornithoides* from Bayn Dzak and *Byronosaurus* from Ukhaa Tolgod (Mongolia; Late Cretaceous: Campanian); and (2) serrated teeth, present in *Sinornithoides* from Huamuxiao (China; Early Cretaceous) and *Sinornithoides*-like taxa from Khamryn Us (Mongolia; Early Cretaceous: Aptian-Albian), Shestakovo (Russia; Early Cretaceous: Aptian-Albian), and Sheikhdzheili (Uzbekistan; Late Cretaceous: Cenomanian); Troodontidae indet. from Kansai (Tajikistan; Late Cretaceous: Santonian) and Alymtau (Kazakhstan; Late Cretaceous: Campanian), *Saurornithoides* (Mongolia and China; Late Cretaceous: Campanian-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; Varricchio et al., 1997, 1999, 2002; Xu et al., 2002b; Makovicky et al., 2003; Varricchio 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; Osmólska, 1987; Barsbold and Osmólska, 1990; Kurzanov and Osmólska, 1991; Elzanowski and Wellnhofer, 1992, 1993; Currie and Peng, 1994; Russell and Dong, 1994; Varricchio, 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 *Lindholmemys elegans* Riabinin, 1935. In 1958, A. K. Rozhdestvensky visited the Itemir-Dzharakuduk depression and made collections (Rozhdestvensky, 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). Rozhdestvensky'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 Rozhdestvensky 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

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FIGURE 1. Map of Uzbekistan (top) with the position of the Itemir-Dzharakuduk depression marked by asterisk (modified from Archibald and Averianov [2005]) and sketch of the Itemir-Dzharakuduk escarpments (bottom) with the position of microvertebrate site IT-01 (modified from Nessov, 1984). **1**–Itemir well, **2**–Dzharakuduk wells, **3**–Kul'beke well, **4**–Bissekty well, **5**–Khodzhakhmet well.

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 Bissekty 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 (*Acrodus* sp., *Polyacrodus* sp., *Hybodus* sp., *Cretodus* sp., *Hispidaspis* sp., and *Scapanorhynchus* sp.), osteichthyans (*Belonostomus* sp., Pycnodontiformes indet., *Lepidotes* sp., Amiidae indet., Pholidophoriformes indet., Ichthyodectidae indet., and Albulidae indet.), salamanders (Scapherpetidae indet.), turtles (Trionychidae indet. and Macrobaenidae indet.), Crocodyliformes indet., pterosaurs (Ornithocheiridae indet.), and dinosaurs (Neosauropoda indet., Tyrannosauroidea indet., Troodontidae gen. et sp. nov., Hadrosauroidea indet., and *Asiaceratops salsopaludalis*). 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**, Paleoherpetological 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 *-odon* (Ionic variant of Greek *odous*), tooth.

URBACODON ITEMIRENSIS, 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* Osmólska, 1987 and *Tochisaurus* Kurzanov and Osmólska, 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 symphyseal 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, *Archaeornithoides* from the Campanian of Mongolia, is known from a single fragmentary, possible hatchling, specimen (Elzanowski and Wellnhofer, 1992, 1993; Currie, 2000). 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 posteroventral 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

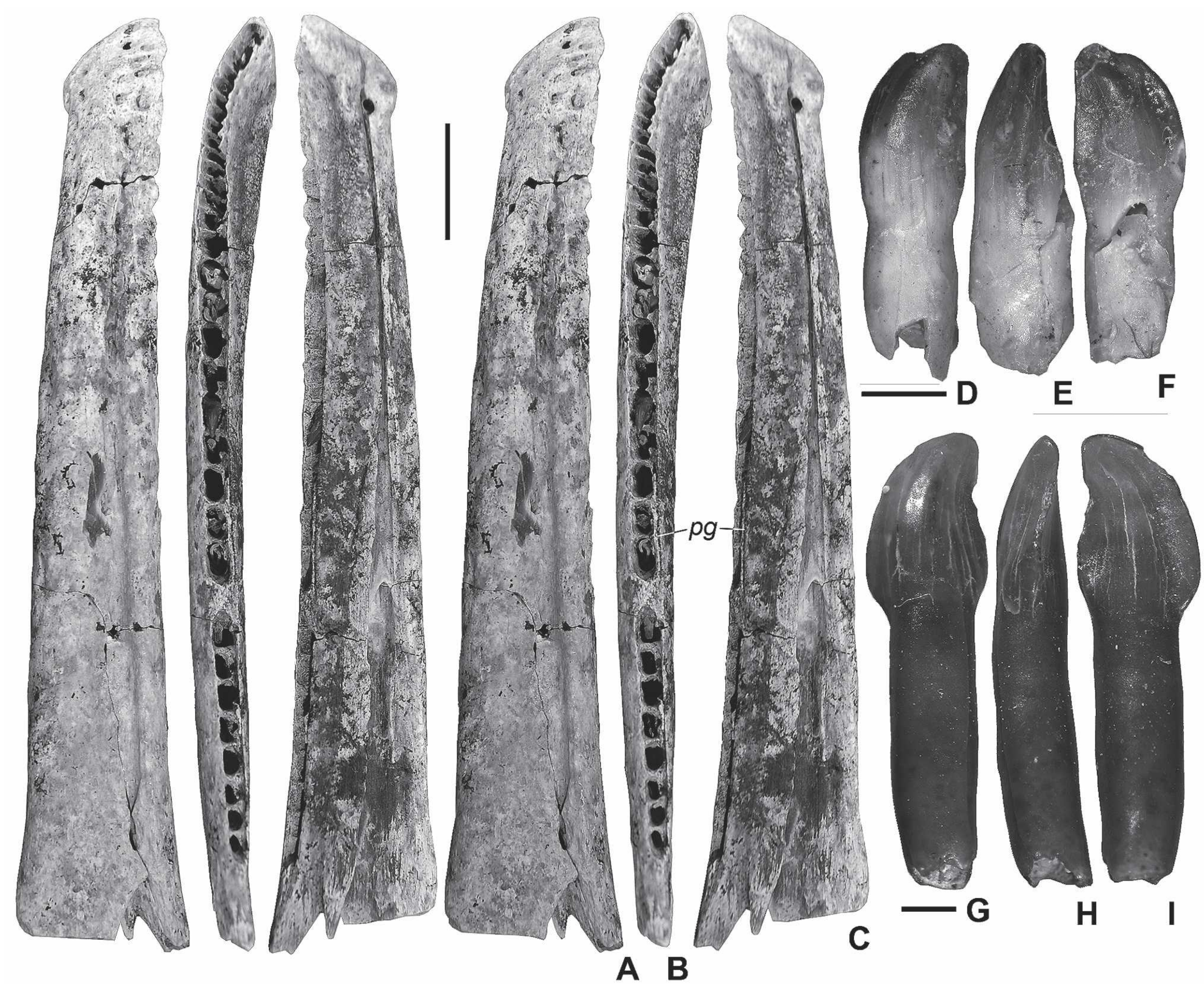

FIGURE 2. Left dentary (**A–C**, stereophotographs) and anterior dentary tooth **(D–F)** of *Urbacodon itemirensis*, gen. et sp. nov. (ZIN PH 944/16, holotype) from the Cenomanian Dzharakuduk Formation at Itemir and left anterior dentary tooth of *Urbacodon* sp. (ZIN PH 265/16) from the Turonian Bissekty Formation at Dzharakuduk, Itemir-Dzharakuduk Depression, central Kyzylkum Desert, Uzbekistan **(G–I)**. Dentary in **(A)** lateral, **(B)** dorsal, and **(C)** medial views; teeth in **(D, G)** labial, **(E, H)** distal, and **(F, I)** lingual views. Scale bars equal 10 mm **(A–C)** and 1 mm **(D–I)**, respectively. Abbreviation: **pg**, paradental groove.

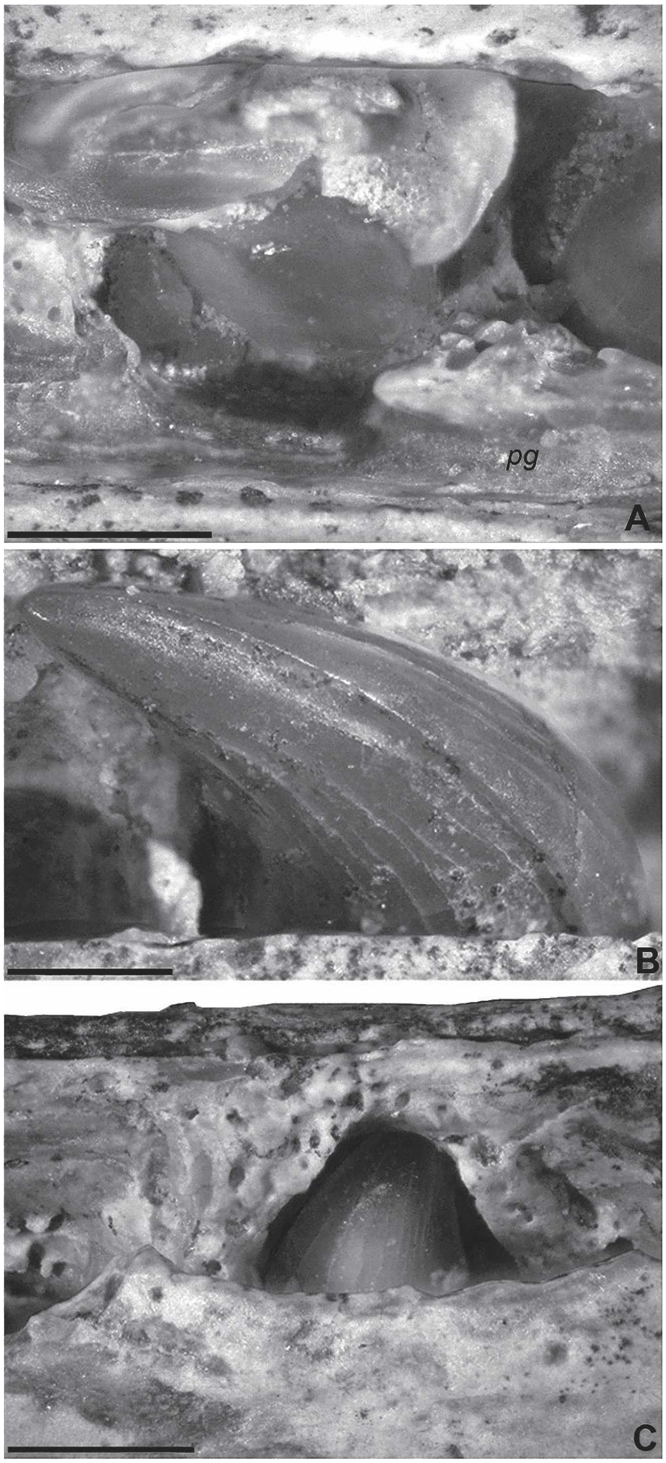

FIGURE 3. Close-up of the left dentary of *Urbacodon itemirensis*, gen. et sp. nov. (ZIN PH 944/16, holotype), showing replacement teeth in tooth positions 17 (**A**, occlusal view), 20 (**B**, lingual view), and 23 (**C**, labial view). Scale bar equals 1 mm. Abbreviation: **pg**, paradental groove.

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.

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).

REVIEW OF TROODONTID RECORDS FROM THE TERRITORIES OF THE FORMER SOVIET UNION

Shestakovo

A number of vertebrate-bearing localities around the Shestakovo settlement in Kemerovo 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. Weishampel (1990) and Weishampel and colleagues (2004) incorrectly placed this locality complex in the Gorno-Altai Republic. 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 denticle: 0.19 mm), and distinctly hooked. The first metacarpal and caudal from Shestakovo 1 will be described elsewhere.

Khodzhakul and Sheikhdzheili

These two closely spaced localities are situated within the lower Cenomanian Khodzhakul Formation in the southwestern Kyzylkum Desert in Karakalpakistan (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 labiolingually 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 Sheikhdzheili (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 labiolingually compressed crowns of the teeth, unserrated 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 diagnostic at the generic level. We follow Makovicky and Norell (2004:186) in considering *Troodon asiamericanus* Nessov, 1995 a nomen dubium.

Itemir

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.

Dzharakuduk

This locality in the Itemir-Dzharakuduk depression (see Fig. 1) 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 Deinonychosauria or Mammalia(?). The tooth has a slight constriction between the crown and root, unserrated 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.

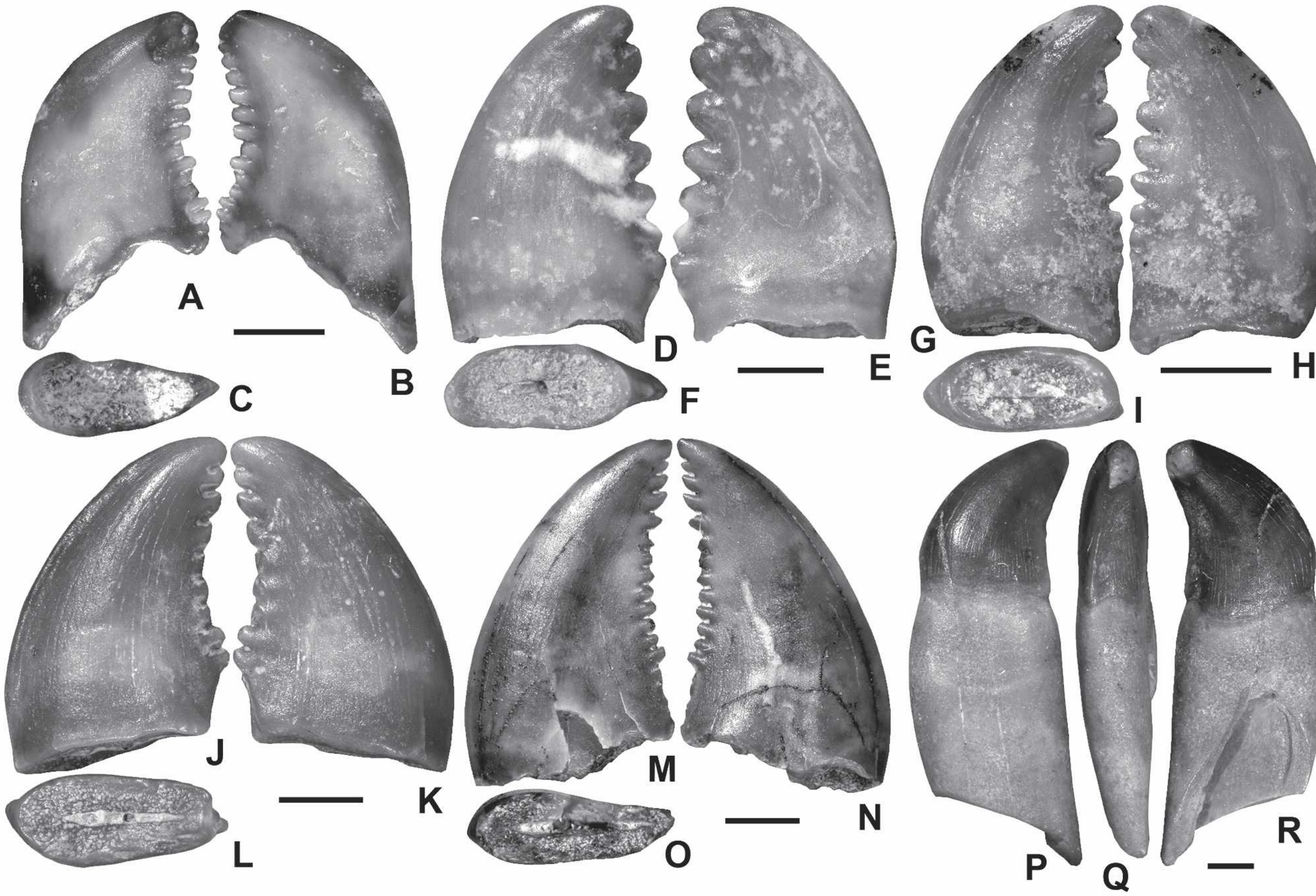

FIGURE 5. Teeth of Troodontidae indet. **(A–O)** and *Urbacodon* sp. **(P–R)** from the Aptian-Albian Ilek Formation at Shestakovo, Kemerovo Province, Western Siberia, Russia **(A–C)**, the Cenomanian Khodzhakul Formation at Sheikhdzheili, southwestern Kyzylkum Desert, Karakalpakistan, Uzbekistan **(D–O)**, and the Turonian Bissekty Formation at Dzharakuduk, central Kyzylkum Desert, Uzbekistan **(P–R)**. **A-C**, PM TGU 16/5-124, maxillary or posterior dentary tooth in **(A, B)** side and **(C)** basal views; **D–F**, ZIN PH 1886/16, left anterior dentary tooth in **(D)** labial, **(E)** lingual, and **(F)** basal views; **G-I**, ZIN PH 1885/16, left anterior dentary tooth in **(G)** labial, **(H)** lingual, and **(I)** basal views; **J–L**, CCMGE 49/12176, holotype of *Troodon asiamericanus* Nessov, 1995, right posterior dentary tooth in **(J)** lingual, **(K)** labial, and **(L)** basal views; **M–O**, ZIN PH 1888/16, maxillary(?) tooth in **(M, N)** side and **(O)** basal views; **P–R**, ZIN PH 1899/16, maxillary or posterior dentary tooth in **(P)** labial, **(Q)** distal, and **(R)** lingual views. Scale bar equals 1 mm.

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 *Byronosaurus* (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 mediolaterally 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 *Urbacodon 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 labiolingually 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 Kyzylpilyal' (= 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 Osmólska, 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.

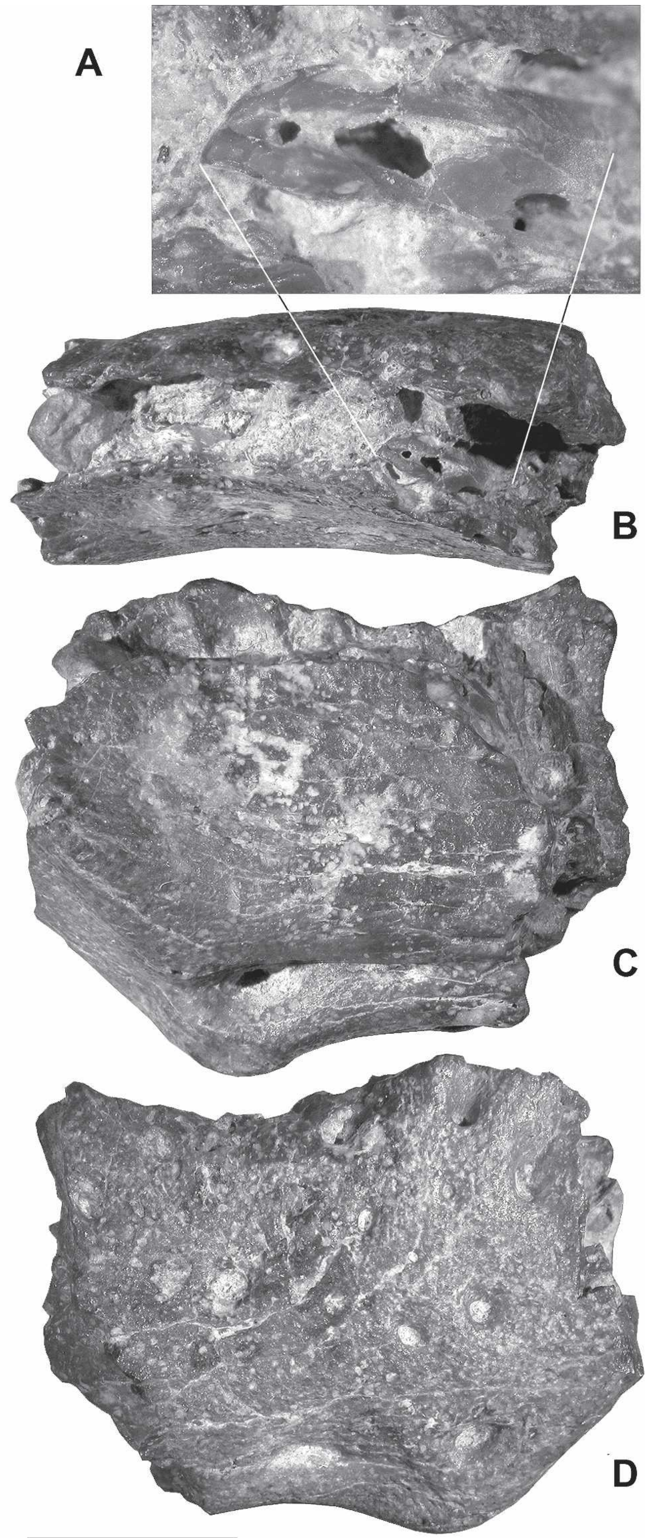

FIGURE 6. Fragment of the anterior portion of a right dentary (ZIN PH 2/66) of Troodontidae indet. from the Santonian Yalovach Formation at Kansai, northern Fergana Depression, Tajikistan. **(A)**, close-up view of replacement tooth; **(B)**, dorsal view; **(C)**, medial view; **(D)**, lateral view. Scale bar equals 5 mm.

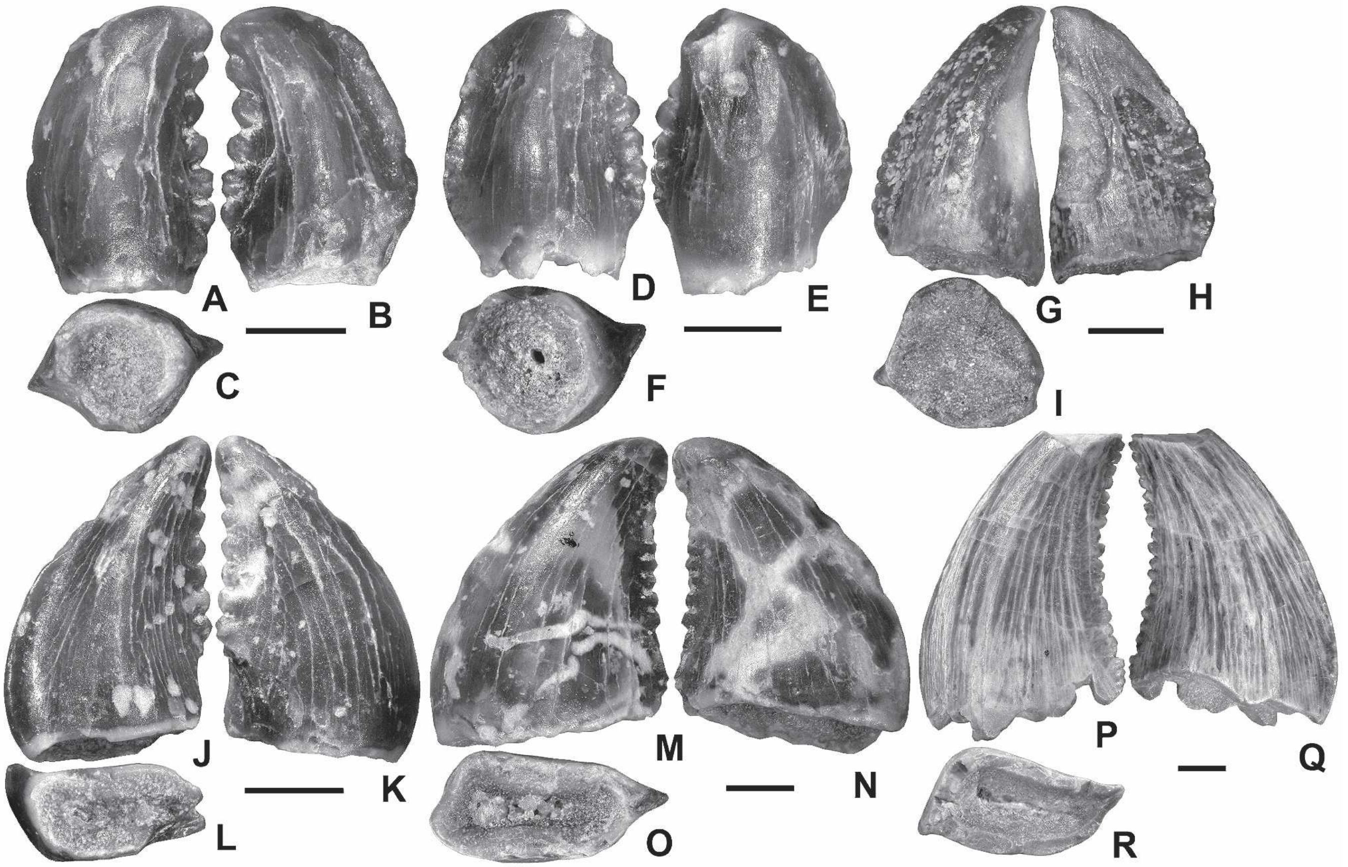

FIGURE 7. Teeth of Troodontidae indet. from the Santonian Yalovach Formation at Kansai, northern Fergana Depression, Tajikistan. **A–C**, ZIN PH 1/66, left anterior dentary tooth in **(A)** labial, **(B)** lingual, and **(C)** basal views; **D–F**, ZIN PH 3/66, right anterior dentary tooth in **(D)** lingual, **(E)** labial, and **(F)** basal views; **G–I**, ZIN PH 8/66, right premaxillary tooth in **(G)** labial, **(H)** lingual, and **(I)** basal views; **J–L**, ZIN PH 7/66, right posterior dentary tooth in **(J)** lingual, **(K)** labial, and **(L)** basal views; **M–O**, ZIN PH 5/66, posterior ?maxillary tooth in **(M, N)** side views and **(O)** basal view; **P–R**, ZIN PH 4/66, anterior ?maxillary tooth in **(P, Q)** side views and **(R)** basal view. Scale bar equals 1 mm.

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 = 1.9–4.6, M = 3.12 ± 0.48, BW = 1.2–2.4, M = 1.84 ± 0.20, TCH = 2.9–5.6, M = 4.24 ± 0.51 (n = 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 = 0.67 ± 0.09, n = 4. The distal denticles are relatively larger than in the tooth sample from Kansai (1.82–3.33, M = 2.42 ± 0.24 denticles per mm, n = 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).

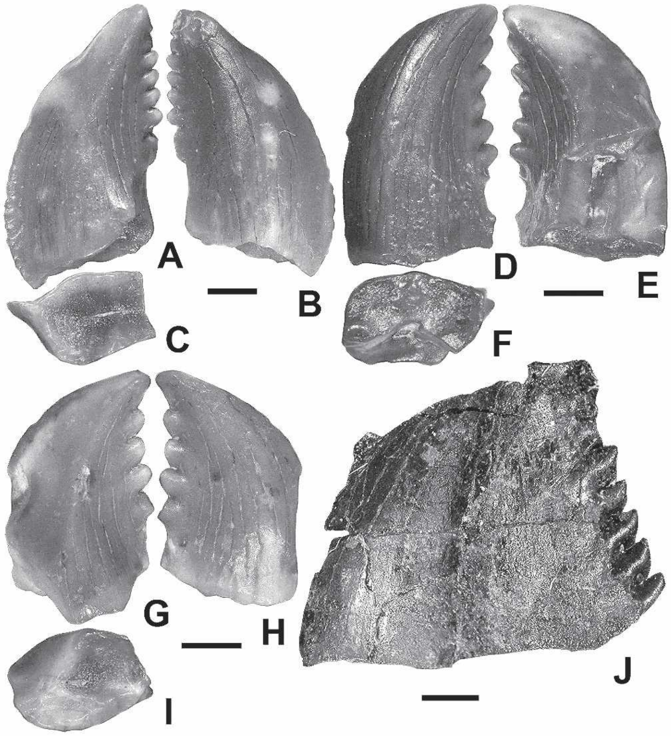

FIGURE 8. Teeth of Troodontidae indet. from the Campanian Darbasa Formation at Alymtau, southern Kazakhstan **(A–I)**, and *Troodon* cf. *T. formosus* from the Maastrichtian Kakanaut Formation at Kakanaut, Chukotka, Far East of Russia **(J)**. **A–C**, ZIN PH 2/67, left ?maxillary tooth in **(A)** lingual, **(B)** labial, and **(C)** basal views; **D–F**, ZIN PH 3/67, left posterior ?dentary tooth in **(D)** labial, **(E)** lingual, and **(F)** basal views; **G–I**, ZIN PH 4/67, right posterior ?dentary tooth in **(G)** lingual, **(H)** labial, and **(I)** basal views; **J**, ZIN PH 1/68, partially preserved tooth in ?labial view. Scale bar equals 1 mm.

Blagoveshchensk

This important vertebrate locality is in the upper(?) Maastrichtian Udurchukan Formation (Tsagayan Group) on the bank of the Amur River in the city of Blagoveshchensk 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 Blagoveshchensk is geographically much closer to the Mongolian localities with *Saurornithoides* 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 unserrated teeth, *Archaeornithoides deinosauriscus* 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 paradental groove and absence of interdental plates. Elzanowski and Wellnhofer (1993:248) considered the possibility that *Archaeornithoides deinosauriscus*, known only from a tiny skull fragment, represented a juvenile troodontid, specifically *Saurornithoides mongoliensis* from the same locality (Osborn, 1924). However, they rejected this identification primarily because of the unserrated teeth and broad palatal shelves of the maxillae. These objections are no longer valid because there are now troodontids with unserrated 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 *Saurornithoides*. 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 *Saurornithoides*. An alternative possibility, that *Archaeornithoides* is a juvenile dromaeosaurid, was proposed by Chiappe and colleagues (1996) based on an alleged dromaeosaurid embryo with unserrated teeth (Norell et al., 1994). However, this specimen was subsequently reidentified as an oviraptorid 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 unserrated 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 unserrated teeth is *Byronosaurus* from the Campanian-age Ukhaa Tolgod beds of Mongolia (which might be a lateral equivalent of the Djadokhta Formation; Kielan-Jaworowska et al., 2003). It was originally interpreted as an aberrant troodontid, and its unserrated teeth were considered autapomorphic for this taxon (Norell et al., 2000; Makovicky et al., 2003). The third troodontid with unserrated 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 unserrated teeth, *Urbacodon* gen. nov. from the Cenomanian and Turonian of Uzbekistan. Discoveries of two additional troodontid taxa with unserrated 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 unserrated 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 (Varricchio, 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 ornithomimosaurs, 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 unserrated teeth in troodontids may be exemplified by isolated teeth from the Aptian-Albian-age Hövöör (= 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 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 teeth 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 Shestakovo, this value is even smaller (0.19 mm).

A sample of troodontid teeth from the lower Santonian Yalovach 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 teeth, 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 Darbasa 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 Campanian, 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 heterochronic development of faunal complexes during the Cretaceous, 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]).

ACKNOWLEDGMENTS

We thank Dr. Sergei Leshchinskiy (TGU) for permission to study and publish on specimen PM TGU 16/5-124 in this paper. We gratefully acknowledge support for fieldwork from the National Geographic Society (grants 5901-97 and 6281-98 to J.D. Archibald and H.-D.S.), the National Science Foundation (grants EAR-9804771 and 0207004 to J.D. Archibald and H.-D.S.), the Navoi Mining and Metallurgy Combinat, and the Civilian Research and Development Foundation (RU-G1-2571-ST-04 to A.O.A.). The work of A.O.A. was supported by the President's of Russia grant MD-255.2003.04, by the Russian Fund of Basic Research grants 04-04-49113 and 04-04-49637, and by the Russian Science Support Foundation. An English translation of Nessov (1995) by Tatyana Platonova and edited by H.-D.S. is available from The Polyglot Paleontologist Web site (http://ravenel.si.edu/paleo/paleoglot/index.cfm).

LITERATURE CITED

Alifanov, V. R., and A. O. Averianov. 2006. [On the finding of ornithomimid dinosaurs (Saurischia, Ornithomimosauria) in the Upper Cretaceous beds of Tajikistan.] Paleontologicheskii Zhurnal 2006(1):98–102. [Russian]

Alifanov, V. R. and Y. L. Bolotsky. 2002. New data about the assemblages of the Upper Cretaceous carnivorous dinosaurs (Theropoda) from the Amur Region; pp. 25–26 in G. L. Kirillova (ed.), Fourth International Symposium of IGCP 434: Cretaceous Continental Margin of East Asia: Stratigraphy, Sedimentation, and Tectonic, Program and Abstracts. UNESCO-IUGS-IGCP, Khabarovsk.

Alifanov, V. R., M. B. Efimov, I. V. Novikov, and M. Morales. 1999. [A new psittacosaur complex of tetrapods from the Lower Cretaceous Shestakovo locality (southern Siberia).] Doklady Akademii Nauk 369(4):491–493. [Russian]

Archibald, J. D., and A. O. Averianov. 2005. Mammalian faunal succession in the Cretaceous of the Kyzylkum Desert. Journal of Mammalian Evolution 12:9–22.

Archibald, J. D., H.-D. Sues, A. O. Averianov, C. King, D. J. Ward, O. I. Tsaruk, I. G. Danilov, A. S. Rezvyi, B. G. Veretennikov, and A. Khodjaev. 1998. Précis of the Cretaceous paleontology, biostratigraphy and sedimentology at Dzharakuduk (Turonian?-Santonian), Kyzylkum Desert, Uzbekistan; pp. 21–28 in S. G. Lucas, J. I. Kirkland, and J. W. Estep (eds.), Lower to Middle Cretaceous Terrestrial Ecosystems. Bulletin of the New Mexico Museum of Natural History and Science 14.

Arkhangelsky, A. D. 1916. [Upper Cretaceous deposits of Turkestan. Part 1. Upper Cretaceous deposits of North-West Kyzylkum and Fergana.] Trudy Geologicheskogo Komiteta, Novaya Seriya 151: 1–198. [Russian]

Averianov, A. O. 1997. New Late Cretaceous mammals of southern Kazakhstan. Acta Palaeontologica Polonica 42:243–256.

Averianov, A. O. In press. Theropod dinosaurs from the Late Cretaceous of the northeastern Aral Sea area, Kazakhstan. Cretaceous Research.

Averianov, A. O., and J. D. Archibald. 2005. Mammals from the mid-Cretaceous Khodzhakul Formation, Kyzylkum Desert, Uzbekistan. Cretaceous Research 26:593–608.

Averianov, A. O., and L. A. Nessov. 1995. A new Cretaceous mammal from the Campanian of Kazakhstan. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1995:65–74.

Averianov, A. O., A. V. Voronkevich, S. V. Leshchinskiy, and A. V. Fayngertz. 2006. A ceratopsian dinosaur *Psittacosaurus sibiricus* from the Early Cretaceous of West Siberia, Russia. Journal of Systematic Palaeontology 4:359–395.

Barsbold, R. 1974. Saurornithoididae, a new family of small theropod dinosaurs from Central Asia and North America. Palaeontologia Polonica 30:5–22.

Barsbold, R., and H. Osmólska. 1990. Troodontidae; pp. 259–268 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. University of California Press, Berkeley.

Barsbold, R., H. Osmólska, and S. M. Kurzanov. 1987. On a new troodontid (Dinosauria, Theropoda) from the Early Cretaceous of Mongolia. Acta Palaeontologica Polonica 32:121–132.

Baszio, S. 1997. Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of southern Alberta, Canada. Courier Forschungsinstitut Senckenberg 196:33–77.

Bolotsky, Y. L., and P. Godefroit. 2004. A new hadrosaurine dinosaur from the Late Cretaceous of Far Eastern Russia. Journal of Vertebrate Paleontology 24:351–365.

Bolotsky, Y. L., and V. G. Moiseenko. 1988. [On Dinosaurs of the Amur River Region.] Amur KNII DVO AN SSSR, Blagoveshchensk, 38pp. [Russian]

Charig, A. J., and A. C. Milner. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. Bulletin of the British Museum (Natural History) Geology 53:11–70.

Chiappe, L. M., M. A. Norell, and J. M. Clark. 1996. Phylogenetic position of *Mononykus* (Aves: Alvarezsauridae) from the Late Cretaceous of the Gobi Desert. Memoirs of the Queensland Museum 39:557–582.

Clarke, J. B. 2004. Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and *Apatornis* (Avialae: Ornithurae). Bulletin of the American Museum of Natural History 286:1–179.

Clemens, W. A., and L. G. Nelms. 1993. Paleoecological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. Geology 21:503–506.

Currie, P. J. 1985. Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds. Canadian Journal of Earth Sciences 22:1643–1658.

Currie, P. J. 1987. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). Journal of Vertebrate Paleontology 7:72–81.

Currie, P. J. 1995. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). Journal of Vertebrate Paleontology 15:576–591.

Currie, P. J. 2000. Theropods from the Cretaceous of Mongolia; pp. 434–455 in M. J. Benton, M. A. Shishkin, D. M. Unwin and E. N. Kurochkin (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge.

Currie, P. J. 2004. Theropods, including birds; pp. 367–397 in P. J. Currie and E. B. Koppelhus (eds.), Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed. Indiana University Press, Bloomington.

Currie, P. J., and Z.-M. Dong. 2001. New information on Cretaceous troodontids (Dinosauria, Theropoda) from the People's Republic of China. Canadian Journal of Earth Sciences 38:1753–1766.

Currie, P. J., and J.-H. Peng. 1994. A juvenile specimen of *Saurornithoides mongoliensis* from the Upper Cretaceous of northern China. Canadian Journal of Earth Sciences 30:2224–2230.

Currie, P. J., and X.-J. Zhao. 1994. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. Canadian Journal of Earth Sciences 30:2231–2247.

Currie, P. J., J. K. Rigby, Jr., and R. E. Sloan. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada; pp. 107–125 in K. Carpenter and P. J. Currie (eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge.

Dal Sasso, C., S. Maganuco, E. Buffetaut, and M. A. Mendez. 2005. New information on the skull of the enigmatic theropod *Spinosaurus*, with remarks on its size and affinities. Journal of Vertebrate Paleontology 25:888–896.

Danilov, I. G., and J. F. Parham. 2005. A reassessment of the referral of an isolated skull from the Late Cretaceous of Uzbekistan to the stem-testudinoid turtle genus *Lindholmemys*. Journal of Vertebrate Paleontology 25:784–791.

Edmund, A. G. 1957. On the special foramina in the jaws of many ornithischian dinosaurs. Contributions of the Royal Ontario Museum, Division of Zoology and Palaeontology 48:1–14.

Elzanowski, A. 2002. Archaeopterygidae (Upper Jurassic of Germany); pp. 129–159 in L. M. Chiappe and L. M. Witmer (eds.), Mesozoic Birds: Above the Heads of Dinosaurs. University of California Press, Berkeley.

Elzanowski, A., and P. Wellnhofer. 1992. A new link between theropods and birds from the Cretaceous of Mongolia. Nature 359:821–823.

Elzanowski, A., and P. Wellnhofer. 1993. Skull of *Archaeornithoides* from the Upper Cretaceous of Mongolia. American Journal of Science 293-A:235–252.

Fiorillo, A. R., and R. A. Gangloff. 2000. Theropod teeth from the Prince Creek Formation (Cretaceous) of northern Alaska, with speculations on Arctic dinosaur paleoecology. Journal of Vertebrate Paleontology 20:675–682.

Gangloff, R. A. 1998. Arctic dinosaurs with emphasis on the Cretaceous record of Alaska and the Eurasian-North American connection; pp. 211–220 in S. G. Lucas, J. I. Kirkland, and J. W. Estep (eds.), Lower and Middle Cretaceous Terrestrial Ecosystems. Bulletin of the New Mexico Museum of Natural History and Science 14.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds; pp. 1–55 in K. Padian (ed.), The Origin of Birds and the Evolution of Flight. Memoirs of the California Academy of Sciences 8.

Gilmore, C. W. 1924. On *Troodon validus*, an orthopodous dinosaur from the Belly River Cretaceous of Alberta, Canada. Bulletin of the University of Alberta, Department of Geology 1:1–43.

Godefroit, P., Y. L. Bolotsky, and V. R. Alifanov. 2003. A remarkable hollow-crested hadrosaur from Russia: an Asian origin for lambeosaurines. Comptes Rendus Palevol 2:143–151.

Godefroit, P., Y. L. Bolotsky, and J. Van Itterbeeck. 2004. The lambeosaurine dinosaur *Amurosaurus riabinini*, from the Maastrichtian of Far Eastern Russia. Acta Palaeontologica Polonica 49:585–618.

Godefroit, P., S. Zan, and L. Jin. 2001. The Maastrichtian (Late Cretaceous) lambeosaurine dinosaur *Charonosaurus jiayinensis* from north-eastern China. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 71:119–168.

Holtz, T. R., Jr. 2000. A new phylogeny of the carnivorous dinosaurs. Gaia 15:5–61.

Holtz, T. R., Jr., D. L. Brinkman, and C. L. Chandler. 2000. Denticle morphometrics and a possibly omnivorous feeding habit for the theropod dinosaur *Troodon*. Gaia 15:159–166.

Howgate, M. E. 1984. The teeth of *Archaeopteryx*, and reinterpretation of the Eichstätt specimen. Zoological Journal of the Linnean Society 82:159–175.

Hwang, S. H., M. A. Norell, Q. Ji, and K. Gao. 2004. A new troodontid from the lower Yixian Formation of China and its affinities to Mongolian troodontids. Journal of Vertebrate Paleontology 24(Suppl. to 3):73A–74A.

Ji, Q., M. A. Norell, P. J. Makovicky, K. Gao, S.-A. Ji, and C. Yuan. 2003. An early ostrich dinosaur and implications for ornithomimosaur phylogeny. American Museum Novitates 3420:1–19.

Kielan-Jaworowska, Z., J. H. Hurum, and D. Badamgarav. 2003. An extended range of the multituberculate *Kryptobaatar* and distribution of mammals in the Upper Cretaceous of the Gobi Desert. Acta Palaeontologica Polonica 48:273–278.

King, C., N. J. Morris, D. J. Ward, W. B. Braham, P. Doyle, and M. J. Hampton. In press. Cretaceous stratigraphy of the western and central Kyzylkum Desert, Uzbekistan. Cretaceous Research.

Kurochkin, E. N. 1988. [Cretaceous Mongolian birds and their significance for the study of bird phylogeny.] Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii 34:33–42. [Russian]

Kurzanov, S. M. 1976. [Structure of the braincase of carnosaur *Itemirus* gen. nov. and some questions of dinosaur cranial anatomy.] Paleontologicheskii Zhurnal 1976(3):127–137. [Russian]

Kurzanov, S. M., and H. Osmólska. 1991. *Tochisaurus nemegtensis* gen. et sp. n., a new troodontid (Dinosauria, Theropoda) from Mongolia. Acta Palaeontologica Polonica 36:69–76.

Lamanna, M. C., R. D. Martinez, and J. B. Smith. 2002. A definitive abelisaurid theropod dinosaur from the early Late Cretaceous of Patagonia. Journal of Vertebrate Paleontology 22:58–69.

Leidy, J. 1856. Notice of remains of extinct reptiles and fishes, discovered by Dr. F. V. Hayden in the Bad Lands of the Judith River, Nebraska Territory. Proceedings of the Academy of Natural Sciences Philadelphia 8:72–73.

Makovicky, P. J., and M. A. Norell. 2004. Troodontidae; pp. 184–195 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. Second Edition. University of California Press, Berkeley.

Makovicky, P. J., Y. Kobayashi, and P. J. Currie. 2004. Ornithomimosauria; pp. 137–150 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. Second Edition. University of California Press, Berkeley.

Makovicky, P. J., M. A. Norell, J. M. Clark, and T. Rowe. 2003. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). American Museum Novitates 3402:1–32.

Marsh, O. C. 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science (3) 21:417–423.

Martinson, G. G. 1969. [Biostratigraphy and fauna of the Cretaceous continental deposits of the Tajik Depression, Kyzylkum, and circum-Tashkent Chul]; pp. 18–51 in G. G. Martinson (ed.), [Continental deposits of the Eastern Regions of Middle Asia and Kazakhstan (Lithostratigraphy and Biostratigraphy).] Nauka, Leningrad. [Russian]

Moiseenko, V. G., A. P. Sorokin, and Y. L. Bolotsky. 1997. [Fossil Reptiles of the Amur River Area.] Amurskii Nauchnyi Tsentr DVO RAN, Khabarovsk, 54 pp. [Russian]

Nessov, L. A. 1981. [Cretaceous salamanders and frogs of the Kyzylkum Desert.] Trudy Zoologicheskogo Instituta AN SSSR 101:57–88. [Russian]

Nessov, L. A. 1984. [Preservation of organisms' remains and conditions of their burial in the Kul'beke Bed of Itemir]; pp. 62–76 in V. G. Ochev (ed.), [Taphonomy and Questions of Paleogeography.] Izdatel'stvo Saratovskogo Universiteta, Saratov. [Russian]

Nessov, L. A. 1992. [Review of localities and remains of Mesozoic and Paleogene birds of the USSR and the description of new findings.] Russkii Ornitologicheskii Zhurnal 1:7–50. [Russian]

Nessov, L. A. 1993. [New Mesozoic mammals from Middle Asia and Kazakhstan and comments on the evolution of mammal faunas of the Cretaceous coastal plains of Asia.] Trudy Zoologicheskogo Instituta RAN 249:105–133. [Russian]

Nessov, L. A. 1995. [Dinosaurs of Northern Eurasia: New Data about Assemblages, Ecology, and Paleobiogeography.] Izdatel'stvo Sankt-Peterburgskogo Universiteta, Saint Petersburg. 156 pp. [Russian]

Nessov, L. A. 1997. [Cretaceous Nonmarine Vertebrates of Northern Eurasia.] (Posthumous edition by L. B. Golovneva and A. O. Averianov.) Izdatel'stvo Sankt-Peterburgskogo Universiteta, Saint Petersburg, 218 pp. [Russian]

Nessov, L. A., and L. B. Golovneva, 1990. [History of the flora, vertebrates and climate in the late Senonian of the north-eastern Koriak Uplands]; pp. 191–212 in V. A. Krasilov (ed.), [Continental Cretaceous of the USSR.] Dal'nevostochnoe Otdelenie AN SSSR, Vladivostok. [Russian]

Nessov, L. A., D. Sigogneau-Russell, and D. E. Russell. 1994. A survey of Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological setting, age and faunal environment. Palaeovertebrata 23:51–92.

Norell, M. A., and S. H. Hwang, 2004. A troodontid dinosaur from Ukhaa Tolgod (Late Cretaceous, Mongolia). American Museum Novitates 3446:1–9.

Norell, M. A., J. M. Clark, and L. M. Chiappe. 2001a. An embryonic oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of Mongolia. American Museum Novitates 3315:1–17.

Norell, M. A., J. M. Clark, and P. J. Makovicky. 2001b. Phylogenetic relationships among coelurosaurian theropods; pp. 49–67 in J. A. Gauthier and L. E. Gall (eds.), New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom. Peabody Museum of Natural History, Yale University, New Haven.

Norell, M. A., P. J. Makovicky, and J. M. Clark. 2000. A new troodontid theropod from Ukhaa Tolgod, Mongolia. Journal of Vertebrate Paleontology 20:1–11.

Norell, M. A., J. M. Clark, D. Dashzeveg, L. M. Chiappe, A. R. Davidson, M. C. McKenna, and M. J. Novacek. 1994. A theropod dinosaur embryo, and the affinities of the Flaming Cliffs dinosaur eggs. Science 266:779–782.

Osborn, H. F. 1924. Three new Theropoda, *Protoceratops* Zone, Central Mongolia. American Museum Novitates 144:1–12.

Osmólska, H. 1987. *Borogovia gracilicrus* gen. et sp. n., a new troodontid dinosaur from the Late Cretaceous of Mongolia. Acta Palaeontologica Polonica 32:133–150.

Pyatkov, K. K., I. A. Pyanovskaya, A. K. Bukharin, and Y. K. Bykovskii. 1967. [Geological Structure of the Central Kyzylkum.] Fan, Tashkent, 177 pp. [Russian]

Riabinin, A. N. 1931. [Dinosaur remains from the Upper Cretaceous of the Amu-Darya River.] Zapiski Rossiiskogo Mineralogicheskogo Obshchestva 40(1):114–118. [Russian]

Riabinin, A. N. 1935. [Remains of a turtle from the Upper Cretaceous deposits of the Kyzylkum Desert.] Trudy Paleontologicheskogo Instituta AN SSSR 4:69–77. [Russian]

Rich, T. H., R. A. Gangloff, and W. R. Hammer. 1997. Polar dinosaurs; pp. 562–573 in P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego.

Rich, T. H., P. Vickers-Rich, and R. A. Gangloff. 2002. Polar dinosaurs. Science 295:979–980.

Rozhdestvensky, A. K. 1957. [On the locality of Late Cretaceous dinosaurs on the Amur River.] Vertebrata PalAsiatica 1:285–291. [Russian]

Rozhdestvensky, A. K. 1964. [New data on the localities of dinosaurs on the territory of Kazakhstan and Middle Asia.] Nauchnye Trudy Tashkentskogo Gosudarstvennogo Universiteta Imeni V.I. Lenina, Seriya Geologiya 234:227–241. [Russian]

Russell, D. A. 1969. A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta. Canadian Journal of Earth Sciences 6:595–612.

Russell, D. A., and Z.-M. Dong. 1994. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. Canadian Journal of Earth Sciences 30:2163–2173.

Russell, L. S. 1948. The dentary of *Troodon*, a genus of theropod dinosaurs. Journal of Paleontology 22:625–629.

Sochava, A. V. 1968. [Red-colored Cretaceous Sediments of Middle Asia.] Nauka, Leningrad, 122 pp. [Russian]

Sosedko, A. F. 1937. [Cemetery of vertebrates in the center of the Kyzylkum Desert.] Sotsialisticheskaya Nauka i Tekhnika 5:106–111. [Russian]

Sternberg, C. M. 1932. Two new theropod dinosaurs from the Belly River Formation of Alberta. Canadian Field Naturalist 46:99–105.

Sues, H.-D. 1977. Dentaries of small theropods from the Judith River Formation (Campanian) of Alberta, Canada. Canadian Journal of Earth Sciences 14:587–592.

Sues, H.-D., E. Frey, D. M. Martill, and D. M. Scott. 2002. *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. Journal of Vertebrate Paleontology 22: 535–547.

Tumanova, T. A., Y. L. Bolotsky, and V. R. Alifanov. 2004. The first finds of armored dinosaurs in the Upper Cretaceous of Russia (Amur Region). Paleontological Journal 38:73–77.

Unwin, D. M., and N. N. Bakhurina, 2000. Pterosaurs from Russia, Middle Asia and Mongolia; pp. 420–433 in M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge.

Varricchio, D. J. 1993. Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus.* Journal of Vertebrate Paleontology 13:99–104.

Varricchio, D. J. 1997. Troodontidae; pp. 749–754 in P .J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego.

Varricchio, D. J., and F. D. Jackson. 2004. Two eggs sunny-side up: reproductive physiology in the dinosaur *Troodon formosus*; pp. 215–233 in P. J. Currie, E. B. Koppelhus, M. A. Shugar, and J. L. Wright (eds.), Feathered Dragons: Studies on the Transition from Dinosaurs to Birds. Indiana University Press, Bloomington.

Varricchio, D. J., J. R. Horner, and F. D. Jackson. 2002. Embryos and eggs for the Cretaceous theropod dinosaur *Troodon formosus*. Journal of Vertebrate Paleontology 22:564–576.

Varricchio, D. J., F. D. Jackson, and C. N. Trueman. 1999. A nesting trace with eggs for the Cretaceous theropod dinosaur *Troodon formosus*. Journal of Vertebrate Paleontology 19:91–100.

Varricchio, D. J., F. D. Jackson, J. J. Borkowski, and J. R. Horner. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. Nature 385:247–250.

Weigert, A. 1995. Isolierte Zähne von cf. *Archaeopteryx* sp. aus dem Oberen Jura der Kohlengrube Guimarota. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1995:562–576.

Weishampel, D. B. 1990. Dinosaurian distribution; pp. 63–140 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. University of California Press, Berkeley.

Weishampel, D. B., P. M. Barrett, R. A. Coria, J. Le Loeuff, X. Xu, X.-J. Zhao, A. Sahni, E. M. Gomani, and C. R. Noto. 2004. Dinosaur distribution; pp. 517–606 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. Second Edition. University of California Press, Berkeley.

Wilson, M. C., and P. J. Currie. 1985. *Stenonychosaurus inequalis* (Saurischia, Theropoda) from Judith River (Oldman) Formation of Alberta: New findings on metatarsal structure. Canadian Journal of Earth Sciences 22:1813–1817.

Xu, X., and M. A. Norell. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. Nature 431:838–841.

Xu, X., and X.-L. Wang. 2004. A new troodontid (Theropoda: Troodontidae) from the Lower Cretaceous Yixian Formation of Western Liaoning, China. Acta Geologica Sinica 78:22–26.

Xu X., Y.-N. Cheng, X.-L. Wang, and C.-H. Chang. 2002a. An unusual oviraptorosaurian dinosaur from China. Nature 419:291–293.

Xu X., M. A. Norell, X.-L. Wang, P. J. Makovicky, and X.-C. Wu. 2002b. A basal troodontid from the Early Cretaceous of China. Nature 415:780–784.

Submitted March 9, 2006; accepted September 16, 2006.