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TITANOSAURIA (DINOSAURIA, SAUROPODA) FROM THE UPPER CRETACEOUS (TURONIAN) BISSEKTY FORMATION OF UZBEKISTAN

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ABSTRACT—Exposures of the Bissekty Formation (Upper Cretaceous: middle-upper Turonian) at Dzharakuduk in the central Kyzylkum Desert of Uzbekistan have yielded abundant dinosaurian remains. We report here on cranial and postcranial remains that can be attributed to titanosaurian sauropods. This material is of considerable interest in view of the relative scarcity of sauropod fossils from the Upper Cretaceous of Central Asia. An incomplete braincase originally assigned to the ceratopsian *Turanoceratops tardabilis* actually belongs to a derived titanosaurian. It shares a number of features (including broad basal tubera and presence of wide depression between basal tubera) with braincases of various derived titanosaurian taxa from Asia and South America. Computed tomographic (CT) scanning of the braincase permitted digital reconstruction of a partial endocast. Overall, this endocast resembles those of other sauropods, although the pituitary fossa is considerably swollen. As in other derived titanosaurians, the abducens nerve passed lateral to the pituitary fossa. The inner ear resembles that of some other titanosaurs in having a very short lateral semicircular canal and that the anterior semicircular canal is only slightly longer than the posterior one. Isolated sauropod teeth from Dzharakuduk have slender, 'pencil-shaped' crowns, which often bear high-angle apical wear facets. The caudal vertebrae are gently opisthoccelous rather than procoelous, as is typically the condition on at least the anterior caudals in many other titanosaurs. An anterior caudal vertebra shows extensive pneumatization of its neural arch. The sauropod remains from the Bissekty Formation establish the presence of titanosaurians in Central Asia during the Turonian.

INTRODUCTION

Sauropod dinosaurs include the largest animals that ever lived on land and ranged in time from the Late Triassic to the Late Cretaceous (Upchurch, 1998; Wilson and Sereno, 1998; Upchurch et al., 2004). The most diverse clade, Titanosauria, is represented by numerous Cretaceous-age taxa across the globe, especially from the Southern Hemisphere (Powell, 2003; Wilson and Upchurch, 2003; Upchurch et al., 2004; Curry Rogers, 2005). It includes forms with osteoderms (such as *Saltasaurus*) and others that attained enormous size (such as *Argentinosaurus*).

The sauropod remains reported in the present paper were recovered from strata of the Upper Cretaceous (Turonian) Bissekty Formation of Uzbekistan (Nessov, 1995; Archibald et al., 1998). This unit is extensively exposed along an approximately 8 km long escarpment near the small settlement of Dzharakuduk (variously given in the literature as Dzhara-Kuduk, Dzhirakuduk, Dzhyrakuduk, Bissekty, and Kul'beke) in the central Kyzylkum Desert, 32 km southwest of Mynbulak in the Navoi District. The Bissekty Formation comprises an up to about 80 m thick succession of medium-grained, poorly lithified, cross-bedded fluvial sandstones and clast-supported, well-cemented infraformational conglomerates. These deposits have been interpreted as an aggradational 'lowstand' system. The infraformational conglomerates represent flooding surfaces resulting from regional changes in depositional regime following drops in eustatic sea level (Redman and Leighton, 2009).

In 1932, A. F. Sosedko and V. S. Smirnova visited Dzharakuduk and collected numerous dinosaurian remains, including caudal vertebrae and a humerus, which they attributed to sauropods and identified as '*Brontosaurus*' (Sosedko, 1937). The current whereabouts of these specimens are unknown. From 1974 until 1994, Lev A. Nessov collected and studied numerous dinosaurian remains from Cretaceous strata in the southwestern Kyzylkum Desert. From 1997 until 2006, the Uzbek-Russian-British-American-Canadian (URBAC) expeditions under the direction of J. David Archibald, A.A., and H.-D.S. continued this work, with focus on the particularly fossiliferous exposures at Dzharakuduk.

Nessov (1995) noted that teeth of sauropod dinosaurs are quite common at Dzharakuduk, especially at site CBI-14, which has yielded a wealth of small vertebrate remains, but bones of these animals are rarely found. Like most skeletal remains of vertebrates from this locality complex (Archibald et al., 1998), all sauropod bones and teeth reported here were dissociated. During our review of the extensive collections of dinosaurian specimens from Dzharakuduk, we identified a number of cranial and postcranial remains referable to Sauropoda. In view of the scarcity of Late Cretaceous remains of these dinosaurs from Central Asia, we present here descriptions of this material and assess its affinities.

The nomenclature for vertebral laminae (including abbreviations) follows Wilson (1999) and that for vertebral fossae follows Wilson et al. (2011). Otherwise, the standard nomenclature of comparative anatomy is employed.

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Institutional Abbreviations—CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; ISI, Indian Statistical Institute, Kolkata, India; IZANUZ, Institute of Zoology, Uzbekistan Academy of Sciences, Tashkent, Uzbekistan; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; ZIN PH, Paleoherpetological Collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Abbreviations for Measurements—For various bones: MW, maximum width. Vertebrae: ACW, anterior width of centrum; ANW, anterior width of neural arch (between lateral margins of prezygapophyses); CL, centrum length (ventral); NAL, neural arch length (between anterior and posterior margins of dorsal roof of neural canal); NSL, neural spine length (maximum); PCH, posterior height of centrum; PCW, posterior centrum width; PNW, posterior width of neural arch (between lateral margins of postzygapophyses).

METHODS

R.C.R. and L.M.W. scanned the braincase CCMGE 628/12457 described in this paper at O'Bleness Memorial Hospital in Athens, Ohio, using a General Electric (GE) LightSpeed Ultra Multislice computed tomography (CT) scanner. It was scanned helically at a slice thickness of 625 μ m, 120 kV, and 200 mA, with a bow-tie filter (to decrease beam-hardening artifacts) and the Extended Hounsfield option engaged (to extend the dynamic range of images as much as 16-fold, improving resolution of detail from dense objects such as this fossil). The raw scan data were reconstructed using a bone algorithm, producing 209 slices. Data were output from the scanner in DICOM format and then imported into Amira 4.1.2 (VGS, Burlington, Massachusetts) for viewing, analysis, and visualization. The individual DICOM files are publicly accessible at Figshare (http://dx.doi.org/10.6084/m9. figshare.895015) and Ohio University (http://www.oucom.ohio. edu/dbms_witmer/CT_Data/Uzbekistan_titanosaur_braincase_ DICOM.zip). Structures of interest (cranial endocast, cranial nerves, vasculature, etc.) were highlighted and digitally extracted using Amira's segmentation tools for quantification and visualization. Surface renderings were generated and used to illustrate this article. Following Witmer et al. (2008), we will refer to the digital casts of structures as if they were the actual structures (e.g., 'optic nerve' rather than 'digital cast of canal for optic nerve').

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842 SAURISCHIA Seeley, 1887 SAUROPODA Marsh, 1878 NEOSAUROPODA Bonaparte, 1986 TITANOSAURIFORMES Salgado, Coria, and Calvo, 1997 TITANOSAURIA Bonaparte and Coria, 1993 Gen. et sp. indet. (Figs. 1–3, 4A–C, 5–10)

Material—CCGME 628/12457, incomplete braincase (Figs. 1, 2); numerous isolated teeth in ZIN PH collection (of which ZIN PH 253/16, ZIN PH 254/16, ZIN PH 255/16, and ZIN PH 256/16 are illustrated in Fig. 5); IZANUZ 335, fragment of cervical vertebra; IZANUZ 611 and USNM 538133 (Fig. 6), dorsal vertebral centra; USNM 538127, anterior caudal vertebra (Fig. 7); ZIN PH 962/16, posterior caudal vertebra (Fig. 8); ZIN PH 1462/16, fragment of proximal portion of right ulna; ZIN PH 278/16, manual phalanx V-1 (Fig. 9A, B); IZANUZ 248 and IZANUZ 636, metatarsalia I; IZANUZ 27 and ZIN PH 672/16 (Fig. 9C–F), metatarsalia II; CCMGE 663/12457 and ZIN PH 280/16

(Fig. 10), ungual phalanges of pedal digit I; ZIN PH 480/16, ungual phalanx of pedal digit II or III.

DESCRIPTION

Braincase

Osteology—Nessov (1995:fig. 5) originally attributed the partial braincase CCGME 628/12457 (Figs. 1, 2) to the ceratopsian *Turanoceratops tardabilis*, but it clearly differs from other known ceratopsian braincases in its structure. Much of the outer surface of the specimen has been damaged by erosion, probably due to prolonged exposure on the desert surface. The occipital condyle and most of both paroccipital processes were broken off.

The braincase is short anteroposteriorly but deep dorsoventrally. Most of its constituent bones are indistinguishably fused to each other, suggesting that the specimen represents a subadult or adult individual. The broken base of the occipital condyle suggests that the condyle was deflected posteroventrally when the supraoccipital region of the braincase is aligned vertically, as in Malawisaurus (Gomani, 2005) and Isisaurus but unlike in most other sauropods (Wilson et al., 2009). The foramen magnum is ovoid, taller than wide (28 mm vs. 23 mm), and apparently less wide than the occipital condyle. Lateral to the dorsal portion of this opening a slight prominence probably marks the point for contact with the proatlas. Proatlantal facets are variably present in titanosaurians and other sauropods (Knoll et al., 2013). The occipital surface dorsal to the foramen magnum, which presumably is formed by the supraoccipital, bears a broad, low, and transversely convex nuchal prominence, which is set off from the adjoining occipital surface by a depression on either side and extends dorsally to the level of the skull roof. Ventrally, the nuchal prominence divides into ridges that bound the dorsal and lateral margins of the foramen magnum. The nuchal prominence becomes convex dorsally where it meets the skull roof. Just lateral to the midpoint of the prominence, a crest extends laterally onto the paroccipital process. The left parietal is preserved. It is rather short anteroposteriorly and wide transversely, convex anteroposteriorly, and slopes anteroventrally. The parietal forms the medial margin of an anteroposteriorly narrow supratemporal fossa. Such pronounced compression of the supratemporal fossa characterizes titanosaurs generally (Paulina Carabajal et al., 2008; Knoll et al., 2013). Posteriorly, a distinct crest curves posteromedially toward the nuchal ridge and marks the posterior edge of the skull roof.

The paroccipital processes are for the most part broken off close to their proximal bases, but enough is preserved to suggest that they extended transversely. The basal tubera are distinct and extend ventrolaterally, more or less parallel to the occipital plane. They lack the distal foramen present in Lirainosaurus (Díez Díaz et al., 2011). The thickened lateral edges of the tubera suggest that they may have contacted the quadrates laterally, as in Nemegtosaurus (Wilson, 2005) as well as in Jainosaurus and Rapetosaurus (Wilson et al., 2009). A distinct ridge extends from each tuber to the occipital condyle. The basal tubera are separated by a wide depression ventral to the occipital condyle; a round pit forms the center of this depression. A similar depression or fossa is present in Jainosaurus (Wilson et al., 2009), Muvelensaurus (Calvo et al., 2007a), and Pitekunsaurus (Filippi and Garrido, 2008) and on the braincase of an unidentified titanosaurian from the Upper Cretaceous (Campanian-Maastrichtian) Allen Formation of Río Negro, Argentina (Garcia et al., 2008). Lirainosaurus lacks this feature (Díez Díaz et al., 2011). A low ridge linking the basal tubera bounds the depression ventrally. A small pit marks the midpoint of this ridge. Below the ridge and just medial to each tuber, a foramen marks the posterior entrance of the internal carotid artery on either side. Between the two carotid foramina is the median aperture of the craniopharyngeal canal, leading to the pituitary



FIGURE 1. Partial braincase of a titanosaurian sauropod (CCMGE 628/12457) from the Bissekty Formation at Dzharakuduk, Uzbekistan. \mathbf{A} , left lateral view; \mathbf{B} , posterior view; \mathbf{C} , right lateral view; \mathbf{D} , anterior view. Scale bar equals 3 cm.



fossa. The lumen of the pituitary fossa is visible through breaks on both sides of the braincase. Only the basal portion of the left basipterygoid process is preserved, but it indicates that the basipterygoid processes extended ventrolaterally and sharply diverged from one another, as in *Jainosaurus* (Wilson et al., 2009). The process is separated from the posterolateral portion of the basal tuber by a small notch, as in *Jainosaurus*. The (mostly broken) parasphenoid crest extended ventrally to a point just anterior to the basipterygoid processes.

The crista prootica forms a distinct lateral flange. A lateral depression extends onto the anterior surface of this flange and houses a large, dorsoventrally elongate foramen for passage of the trigeminal nerve (V). Just behind the crista prootica and bordered posteriorly by the ridge connecting the basal tuber to the occipital condyle, a deep recess contains the fenestra vestibuli (ovalis), the metotic foramen (or jugular foramen; for passage of cranial nerves IX–XI and internal jugular vein), and a small foramen for passage of an anterior branch of the hypoglossal nerve (XII). A lateral ridge extending from the base of the paroccipital process to the basal tuber separates the latter foramen from a more posterior opening for the hypoglossal nerve lateral to the occipital condyle, but CT scanning reveals that these two hypoglossal canals converge medially to open in the same endocranial region as in most other dinosaurs (Fig. 3C).

Cranial Endocast-CT scanning of CCGME 628/12457 has facilitated digital reconstruction of a partial endocast (Figs. 3, 4). Although the bony braincase is incomplete, it is very well preserved and undistorted, allowing almost fully resolved representation of its internal anatomy. Much like most sauropod endocasts, the cranial endocast is not particularly 'brain-like' in that gross regions of the brain (e.g., optic lobes, cerebellum) are not clearly demarcated, presumably due to the presence of overlying venous sinuses intervening between the neural tissue and the loosely fitting dura (Hopson, 1979; Witmer et al., 2008; Knoll et al., 2012, 2013; Paulina Carabajal, 2012). The cerebral region of this endocast is missing the anterior portion, but the preserved posterior portion is deep, short, and transversely wide. It overhangs the optic nerves (II), which would be situated well below the level of the olfactory peduncles, which are missing here (Fig. 3). The region of the forebrain is deeper and wider than long. It is set off from the remainder of the endocast by a slight constriction. Posterior and somewhat dorsal to the optic nerve is the small trochlear nerve (IV), ventral to which is the somewhat larger oculomotor nerve (Hopson, 1979; Witmer et al., 2008; Paulina Carabajal, 2012).

The pituitary (hypophysis) has a short infundibular stalk expanding posteroventrally as a large and swollen pendulous structure (Fig. 3A, B, E). No other known titanosaurians approach the extent of hypophyseal swelling exhibited here, although this swelling resembles the condition in some diplodocids (Janensch, 1935; Witmer et al., 2008). This swollen region housed the carotid arterial system and portions of the cavernous venous sinus as well as the pituitary gland itself (Witmer et al., 2008). We are currently unable to state definitively whether expansion of the vasculature or of the pituitary gland itself was responsible for the observed structure, although Edinger (1942) argued reasonably that the size of the hypophyseal fossa in the endocast reflects the size of the pituitary gland itself. A narrow passage connecting the ventral terminus of the pituitary region with the roof of the mouth probably represents the craniopharyngeal canal (Figs. 2C, 3A-C, E). The infundibular region has an unusual posterior expansion situated between the ventral swollen region and the dorsal narrow region (Fig. 3A, B). This posterior expansion is not discretely present in other sauropods. A median canal connects this posterior expansion with the ventral longitudinal venous sinus of the hindbrain region. This canal is present in a variety of sauropods, ranging from basal taxa such as Spinophorosaurus (Knoll et al., 2012) to other titanosaurs such as Jainosaurus (ISI R162; unpublished WitmerLab data) and Bonatitan (Paulina Carabajal, 2012), as well as some other sauropods, such as Camarasaurus (Witmer et al., 2008). Paulina Carabajal (2012) interpreted the median canal as the passage for the basilar artery, which is plausible, but we suggest a venous origin is more likely in that its almost haphazard phylogenetic distribution is more typical of variation in the venous system. Moreover, the arteries supplying the brain in extant amniotes tend to be closely associated with the brain tissue. The internal carotid arteries enter the pituitary fossa laterally at its posteroventral end. The abducens nerve (VI) extended lateral to the pituitary fossa rather than passing through it, which is a derived character state for titanosaurians (Paulina Carabajal, 2012; Knoll et al., 2013).

There is no evidence of distinct optic lobes in the midbrain region of the endocast, suggesting that they were relatively modest in size and located dorsally where they were obscured by the overlying dural venous sinuses, as in most sauropods with the possible exception of Nigersaurus (Sereno et al., 2007; Witmer et al., 2008). A prominent, dorsoventrally elongated projection marks the passage of the trigeminal nerve (V) on either side. Just behind the ventral portion of the trigeminal root, the facial nerve (VII) passes ventrolaterally. Dorsal to the trigeminal root, there is a bulge on the endocast, on which a ridge presumably marks the course of the transverse sinus (a dural venous sinus), suggesting that the anterior portion of the middle cerebral vein exited the endocranium along with the trigeminal nerve, as in most other sauropods (Janensch, 1935, 1936; Witmer et al., 2008) and many other archosaurs (Sampson and Witmer, 2007). The bulge terminates dorsally in a peak-like dorsal feature that has been interpreted as space for a dural venous sinus (Witmer et al., 2008). This dural expansion resembles that in many other sauropods ranging from Spinophorosaurus (Knoll et al., 2012) to Camarasaurus (Witmer et al., 2008) in that it excavates the overlying skull roof and receives tributaries from diploic veins draining the bone as well as from the transverse sinus/middle cerebral vein system. A slight groove in the endocast anterior to the bulge probably corresponds to a medial ridge on the laterosphenoid (Paulina Carabajal et al., 2008; Wilson et al., 2009). The midportion of the endocast descends from the level of the forebrain to the short medulla and decreases in transverse width. Its dorsal surface bears a median ridge. As in other titanosaurians (e.g., Paulina Carabajal et al., 2008; Paulina Carabajal, 2012; Knoll et al., 2013) as well as other sauropods, there is no trace of a cerebellar flocculus. The opening for the combined passage of cranial nerves IX-XI is large. An anterior branch of the hypoglossal

 $[\]leftarrow$ FIGURE 2. CT-based surface renderings of a partial braincase of a titanosaurian sauropod (CCMGE 628/12457) from the Bissekty Formation at Dzharakuduk, Uzbekistan. **A**, left lateral view; **B**, anterior view; **C**, medial view of left side of sagittally sectioned braincase; **D**, posterior view. **Abbreviations: bptp**, basipterygoid process; **bt**, basal tuber; **car**, canal for cerebral carotid artery; **cpc**, craniopharyngeal canal; **evcm**, posterior (caudal) canal for middle cerebral vein; **de**, dural expansion; **ed**, endolymphatic duct; **fm**, foramen magnum; **fp**, fenestra perilymphatica (fenestra rotunda); **fv**, fenestra vestibuli (fenestra ovalis); **n**, notch between basal tuber and basipterygoid process; **oc**, occipital condyle (broken surface); **pfo**, pituitary (hypophyseal) fossa; **spha**, canal for Shenoid artery; **vls**, ventral longitudinal sinus; **II**, canal for N. opticus; **III**, canal for N. vestibulocochlearis; **IX**–**XI**, shared canal for Nn. glossopharyngealis, vagus, and accessorius and accompanying vessels; **XII**, canal for N. hypoglossus. Scale bar equals 2 cm.





А

В

FIGURE 4. Endosseous labyrinth of the left inner ears of A–C, CCMGE 628/12457; D–F, the titanosaurian *Jainosaurus septentrionalis* (ISI R162); G–I, the macronarian *Camarasaurus lentus* (CM 11338); and J–L, the diplodocoid *Diplodocus longus* (CM 11161) reconstructed from CT scans in lateral view (A, D, G, H), dorsal view (B, E, H, K), and posterior view (C, F, I, L). Abbreviations: crc, crus communis; csc, posterior (caudal vertical) semicircular canal; ed, endolymphatic duct; fp, fenestra perilymphatica (fenestra rotunda); fv, fenestra vestibuli (fenestra ovalis); I, lagena; lsc, lateral (horizontal) semicircular canal; rsc, anterior (rostral vertical) semicircular canal; ve, vestibule of inner ear. Scale bar equals 1 cm.

 $[\]leftarrow$ FIGURE 3. Partial 'virtual' endocast of CCMGE 628/12457 reconstructed from CT scans. **A**, left lateral; **B**, posterior; **C**, ventral; **D**, dorsal; and **E**, anterior views. Color scheme: cranial endocast, blue; endosseous labyrinth, pink; nerve canals (most of which also transmit veins), yellow; smaller venous canals, dark blue; arterial canals, red. **Abbreviations: car**, canal for cerebral carotid artery; **cer**, cerebral hemisphere; **cpc**, craniopharyngeal canal; **cvcm**, posterior (caudal) canal for middle cerebral vein; **de**, dural expansion; **fv**, fenestra vestibuli (fenestra ovalis); **lab**, endosseous labyrinth; **pfo**, pituitary (hypophyseal) fossa; **spha**, canal for sphenoid artery; **vls**, ventral longitudinal sinus; **II**, canal for N. opticus; **III**, canal for N. oculomotoricus; **IV**, canal for N. trochlearis; **V**, canal for N. trigeminus; **VI**, canal for N. abducens; **VII**, canal for N. facialis; **IX–XI**, shared canal for Nn. glosso-pharyngealis, vagus, and accessorius and accompanying vessels; **XII**, canal for N. hypoglossus. Scale bar equals 2 cm.



FIGURE 5. Titanosaurian teeth from the Bissekty Formation at Dzharakuduk, Uzbekistan. A-C, ZIN PH 253/16, in labial (A), mesial or distal (B), and lingual (C) views. D-F, ZIN PH 254/16, in labial (D), mesial or distal (E), and lingual (F) views. G-I, ZIN PH 255/16, in side (G, I) and mesial or distal (H) views. J-L, ZIN PH 256/16, in labial (J), mesial or distal (K), and lingual (L) views. Scale bar equals 1 cm.

nerve (XII) extends immediately posterior to it, and this anterior hypoglossal branch is smaller in diameter than the posterior one. In some other titanosaurians, only a single root for XII has been reported (Paulina Carabajal, 2012; Knoll et al., 2013).

The 'virtual' endocast of the endosseous labyrinth of the inner ear has a short, conical lagena (Fig. 4A–C). The anterior semicircular canal is only slightly taller than the posterior one, and having anterior and posterior canals of subequal length—rather than having the anterior canal markedly taller and longer—is emerging as a potential synapomorphy of titanosaurians (Paulina Carabajal, 2012; Knoll et al., 2013). The horizontally extending lateral semicircular canal is the shortest of the three. The vertical planes of the anterior and posterior semicircular canals enclose an almost right angle between them. There is no trace of distinct ampullae, which is the situation in other sauropods as well (Fig. 4D–L).

Teeth

Isolated teeth of sauropods are common at Dzharakuduk, especially at locality CBI-14 (Fig. 5). All closely resemble each other and thus are described together. The teeth represent a considerable size range, with crown width ranging from about 2 to 8.5 mm. Their crowns are long, straight or gently curved, narrow mesiodistally, and have smooth mesial and distal carinae that extend parallel to each other for most of the height of the crown. The ratio of crown height to maximum crown width (slenderness index of Upchurch, 1998) exceeds 5.0, similar to that for teeth of *Nemegtosaurus* (Nowinski, 1971). The apical regions of the tooth crowns are more or less 'D'-shaped in transverse section, with a distinctly convex labial and a slightly flattened lingual surface. When unworn, the crown is lanceolate in outline in labial/lingual view, and the carinae converge toward



FIGURE 6. Dorsal centrum of a juvenile titanosaurian (USNM 538133) from the Bissekty Formation at Dzharakuduk, Uzbekistan. **A**, anterior; **B**, lateral; **C**, posterior; and **D**, ventral views. **Abbreviation**: **pl**, pleuro-coel. Scale bar equals 3 cm.

its apex. The apices of the tooth crowns (e.g., ZIN PH 253/16; Fig. 5A–C) become increasingly chisel-shaped with wear, and steeply angled, often almost vertical, and planar wear facets (exposing light-colored dentine) extend asymmetrically along the labial or (probably mostly) lingual surface of the crowns. Several larger and thicker tooth crowns (e.g., ZIN PH 254/16; Fig. 5D–F) have 'V'-shaped apical wear with steep mesial and distal facets. This combination of types of tooth wear is also present in *Nemegtosaurus* (Nowinski, 1971) and some other titanosaurians. The tooth crowns from Dzharakuduk have rather smooth enamel covering, which either bears only faint wrinkling or lacks wrinkles altogether. The tooth root is more or less circular in transverse section and increases slightly in diameter toward the crown.

Cervical Vertebra

IZANUZ 335 is a badly eroded fragment of a cervical centrum. Nessov (1995:19) estimated its original length at between 38 and 40 cm. It has a well-developed posterior centrodiapophyseal lamina and a large depression ventral to the latter. The base of the broken parapophysis extends for about half of the preserved length of the centrum. The ventral surface of the centrum is slightly concave anteroposteriorly. The convex anterior articular surface of the centrum is mostly eroded, revealing an internal structure comprising large cancellar spaces separated by thin bony lamellae, as is commonly the case in presacral vertebrae of Titanosauriformes (Upchurch, 1998).

Dorsal Vertebrae

Two dorsal vertebrae, IZANUZ 611 and USNM 538133, are represented by their distinctly opisthocoelous centra (USNM 538133: ACH = 42 mm, CL = 63 mm, PCH = 36 mm, PCW = 40 mm; Fig. 6). Open neurocentral sutures indicate that these vertebral centra belonged to immature individuals. The ventral surface of each centrum is concave anteroposteriorly and gently convex transversely. A deep, elliptical pleurocoel occupies much of the dorsolateral surface (Fig. 6B). It is undivided and does not contain pneumatopores. The ventral floor of the neural canal is slightly constricted at midlength.

Anterior Caudal Vertebra

A well-preserved anterior (proximal) caudal vertebra (USNM 538127; Fig. 7) is distinctive in its structure, especially the intricate lamination and pneumatization of the neural arch (ACH = 156 mm, ACW = 183 mm, ANW = 141 mm, CL = ca. 93 mm, PCH = ca. 168 mm). Unfortunately, parts of the centrum are still covered by iron-oxide-impregnated matrix that could not be removed without risking damage to the underlying bone; however, the neural arch and spine were largely cleaned of adhering sediment.

The neural arch, transverse processes, and centrum of USNM 538127 are indistinguishably fused to each other. The left transverse process, part of the neural spine, and the left ventrolateral margin of the posterior articular surface of the centrum are not preserved. Furthermore, the left half of the neural spine was displaced forward along a vertical fracture. The gently opisthocoelous centrum is distinctly shorter anteroposteriorly and wider transversely than tall dorsoventrally. In lateral view, its concave posterior articular surface is positioned more ventrally than the nearly flat anterior one. The lateral and ventral surfaces of the centrum are concave anteroposteriorly. There are no pleurocoels or even depressions on the lateral surfaces, unlike in many other Titanosauriformes (Whitlock et al., 2011). Due to tightly adhering matrix, it cannot be definitely ascertained whether there are chevron facets or a ventral groove. The transverse process (caudal rib) rises from both the centrum and the neural arch just above the midheight of the centrum. It is triangular and its dorsal margin extends ventrolaterally, as in most sauropods but unlike in Flagellicaudata and some rebbachisaurid taxa (Whitlock et al., 2011). The (slightly abraded) lateral end of the process is thickened and curves slightly backward. The transverse process is connected to the prezygapophysis by the prezygodiapophyseal lamina (prdl). It bears two large, shallow fossae on its anterior surface immediately lateral to the prezygapophyseal facet; the dorsal fossa is the larger one and extends dorsomedially. On the right side of the neural arch, a short lamina separates these recesses, but this feature is not as distinct on the left side. Delicate bony crests further divide the floors of these fossae. The neural arch is taller than the centrum and is indistinguishably fused to the latter. It shows bilateral asymmetry in the development of some features, especially the various presumably pneumatic fossae. The prezygapophyses and postzygapophyses rise immediately from the neural arch and only slightly project beyond the respective articular surfaces of the centrum. Their articular surfaces are inclined at an angle of about 60° to the vertical plane. The prezygapophyseal surfaces face dorsomedially and are nearly flat. Two large pneumatic fossae are situated along the posterior margin of each prezygapophyseal facet on the anterior surface of the basal portion of the neural spine; the ones on the right side are deeper and more distinct. These depressions are separated from the prominent prespinal lamina (prsl) by a bony crest. In Neuquensaurus, the anterior surface of



FIGURE 7. Anterior caudal vertebra of a titanosaurian (USNM 538127) from the Bissekty Formation at Dzharakuduk, Uzbekistan. **A**, posterior; **B**, anterior; and **C**, lateral views. **Abbreviations:** ns, neural spine; **p**c, pneumatic cavity; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **podl**, postzygapophyseal spinodiapophyseal fossa; **posl**, postzygapophyseal spinodiapophyseal fossa; **posl**, postzygapophyseal lamina; **poz**, postzygapophysis; **prdl**, prezygodiapophyseal lamina; **prsl**, prespinal lamina; **prz**, prezygapophysis; **spdl**, spinodiapophyseal lamina; **tr**, transverse process. Scale bar equals 10 cm.

the neural spine is marked by numerous foramina (Salgado et al., 2005). Two ridges, probably corresponding to centroprezygapophyseal laminae (cprl), border the more dorsal portion of the neural canal laterally before merging in to the anterior surfaces of the pedicles of the neural arch. Situated just lateral to the dorsal apex of the neural canal, the postzygapophyseal surfaces face ventrolaterally and are slightly concave. The neural canal is relatively narrow transversely and almost pear-shaped in end view. The neural spine is slightly inclined posteriorly and has an anteroposterior length close to that of the centrum for most of its height. It bears prominent prespinal (prsl) and postspinal laminae (posl). The distinctly expanded apex of the neural spine is thick and convex transversely and (to a lesser extent) anteroposteriorly. At least the dorsal region of the neural spine contains a large pneumatic cavity with a complex internal structure comprising variously sized chambers (which are visible on the betterpreserved right side of the spine; Fig. 7B), similar to the condition in Futalognkosaurus (Calvo et al., 2007b). In lateral view, the prezygodiapophyseal lamina (prdl) joins the spinodiapophyseal lamina (spdl), the postzygodiapophyseal lamina (podl), and the transverse process in a cruciform structure (Fig. 7C). Just anterior to the postzygapophyseal facet, ventral to the postzygodiapophyseal lamina (podl) and anterior to the short centropostzygapophyseal lamina (cpol), two depressions correspond in their position to the postzygapophyseal centrodiapophyseal fossa (pocdf) recognized by Whitlock et al. (2011) in Alamosaurus and Mendozasaurus. The spinoprezygapophyseal lamina (sprl) extends from the posterolateral corner of the prezygapophyseal facet to the apex of the neural spine, and the spinopostzygapophyseal lamina (spol) forms the posterolateral edge of the neural spine. A prominent, deep postzygapophyseal spinodiapophyseal fossa (posdf) is bounded by the spinodiapophyseal lamina (spdl) anteriorly, the spinopostzygapophyseal lamina (spol) posteriorly, and the postzygodiapophyseal lamina



FIGURE 8. Posterior caudal vertebra of a titanosaurian (ZIN PH 962/ 16) from the Bissekty Formation at Dzharakuduk, Uzbekistan. **A**, anterior; **B**, posterior; **C**, dorsal; **D**, lateral; and **E**, ventral views. Scale bar equals 1 cm.

(podl) ventrally (M.D.D'Emic, pers. comm.; Fig. 7C). It contains four foramina on the left and three openings on the right side; a pair of these foramina is situated at the base of the fossa just dorsal to the postzygodiapophyseal lamina (podl). Similar openings are present in *Dongyangosaurus* (Lü et al., 2008).

Posterior Caudal Vertebra

ZIN PH 962/16 is a well-preserved posterior (distal) caudal (Fig. 8; ACH = 39.2 mm, ACW = 40.5 mm, ANW = 30.2 mm, CL = 61.1 mm, NAL = 60.5 mm, NSL = 51.0 mm, PCH = 38.7 mm, PCW = 41.8 mm, PNW = 17.9 mm). Its centrum is gently opisthocoelous. Centrum height and width are almost equal at either articular surface. There is no ventral groove or hollow. The neural arch has short peduncles and is situated well forward of the posterior end of the centrum, which is diagnostic for Titanosauriformes (Upchurch et al., 2004: Curry Rogers, 2005). Its neural spine is low dorsoventrally. The spine-like prezygapophyses lack well-defined articular surfaces and extend forward beyond the anterior articular surface of the centrum. The postzygapophyses are indistinct. There are no traces of transverse processes.

Ulna

ZIN PH 1462/16 is a poorly preserved fragment of the proximal portion of a right ulna, lacking the olecranon process and



FIGURE 9. Manual and pedal bones of sauropods from the Bissekty Formation at Dzharakuduk, Uzbekistan. A–C, ZIN PH 278/16, right manual phalanx V-1 in proximal (A), lateral (B) and anterior (C) views; D–G, ZIN PH 672/16, left metatarsal II in proximal (D), medial (E), anterior (F), and lateral (G) views. Scale bars equal 1 cm.

the proximal articular surface. Its anteromedial process is thin transversely and twice as long as the laterally projecting anterolateral process. The latter is short and curves forward. There is a deep oval depression in the radial notch. The medial surface of the ulna is distinctly concave.

Manual Phalanges

Manual phalanx V-1 is represented by one complete bone (ZIN PH 278/16; Fig. 9A, B) and one fragmentary element. Its proximal articular surface is semicircular in outline and concave. The posterior surface of the phalanx is almost flat, and its anterior surface is convex. The lateral and medial edges of the bone extend parallel to each other. The distal articular surface is well developed and ginglymoid, with the lateral portion steeply turning proximally. This supports identification of the elements as manual phalanx V-1.

Metatarsals

We interpret the short and robust bones IZANUZ 248 and IZANUZ 636 as metatarsalia I. The more slender elements IZA-NUZ 27 and ZIN PH 672/16 probably represent metatarsalia II. ZIN PH 672/16 is the better preserved of the latter (Fig. 9C–F; L = 183 mm, proximal end MW = 91.5 mm, anteroposterior diameter = 116.5 mm, distal end MW = 99 mm). Its proximal condyle is kidney-shaped in outline, with a convex medial side and a shorter, concave lateral side. The long axis of this end is perpendicular to that of the distal end. The proximal articular surface slants medially. The distal end of the metatarsal is transversely elongated, deeply concave, and lacks pits for collateral ligaments.



FIGURE 10. Ungual phalanx of left pedal digit I of a sauropod (ZIN PH 280/16) from the Bissekty Formation at Dzharakuduk, Uzbekistan, in proximal (**A**), lateral (**B**), and medial (**C**) views. Scale bar equals 1 cm.

Pedal Ungual Phalanges

There are several more or less sickle-shaped ungual phalanges, which possibly belong to pedal digit I. ZIN PH 280/16 is the best preserved of these elements (Fig. 10). The ungual phalanges are flattened from side to side and lack a flat ventral surface. The proximal articular surface is poorly preserved on all known elements, and the presence of a dorsal intercondylar process cannot be established. It is expanded laterally so that the proximal end is triangular in outline in end view. Distally, along about a half of the ventromedial edge, the ungual has a raised, rugose edge. Anastomosing grooves and deep pits, presumably for nutrient vessels supplying the claw sheath, are restricted to the area beneath and lateral to this ridge and mark the surface covered by the keratinous claw sheath in life. On the medial side, along the proximal end of the rugose ridge, a distinct pit follows the groove for the claw sheath distally. These features are most prominent in CCMGE 663/12457 and much less distinct in ZIN PH 280/16. The ungual phalanx ZIN PH 480/16 is not sickleshaped and is relatively short. Its proximal articular surface is kidney-shaped in outline.

PHYLOGENETIC RELATIONSHIPS

In the absence of associated skeletal remains, it is impossible to ascertain whether the sauropod material from Dzharakuduk represents one or more taxa. Many Cretaceous-age continental strata have yielded two or more taxa of titanosaurian sauropods (Upchurch et al., 2004); thus, a similar situation cannot be ruled out for the material from the Bissekty Formation. The dissociated and often fragmentary nature of the available skeletal material constrains assessment of its relationships, yet some elements have phylogenetically informative features.

CCMGE 628/12457 shares the presence of transversely wide basal tubera (and a possible contact between the basicranium and quadrate) with Nemegtosaurus (Wilson, 2005) and various other derived titanosaurians (Calvo and Kellner, 2006; Wilson et al., 2009). Furthermore, it shares with Jainosaurus (Wilson et al., 2009), Muyelensaurus (Calvo et al., 2007a), Pitekunsaurus (Filippi and Garrido, 2008), and an unidentified titanosaurian from Río Negro, Argentina (García et al., 2008) the presence of a wide depression between the basal tubera, which extend more or less parallel to the occipital plane. CCMGE 628/12457 also resembles braincases assigned to Isisaurus from the Upper Cretaceous (Maastrichtian) of India and Pakistan (Wilson et al., 2005, 2009) in the distinct deflection of the occipital condyle relative to the skull roof. Based on these similarities as well as various features of the cranial endocast, it is attributable to a titanosaurian. The unusual structure of the hypophyseal region, including the posterior expansion of the infundibular region, may help determine the affinities of this specimen more precisely as titanosaurian endocranial structure becomes better known. As Wilson et al. (2009) noted, the cranial structure of many titanosaurian taxa is still poorly known; thus, the phylogenetic significance of particular features of the braincase remains uncertain.

The mesiodistally narrow, 'pencil-shaped' tooth crowns contacted either one or two teeth in the opposing jaw, producing high-angle and occasionally 'V'-shaped apical wear facets. This condition is found in both diplodocoids and 'narrow-crowned' titanosaurians, including *Nemegtosaurus* (Barrett et al., 2002; Wilson et al., 2005). As in diplodocoids and *Nemegtosaurus*, the apical wear facets are steeply inclined, often nearly vertical on the tooth crowns from Dzharakuduk. The teeth from Dzharakuduk most closely resemble those of *Nemegtosaurus* (Nowinski, 1971; Wilson, 2005), especially in their high slenderness index, and differ only in their much less pronounced enamel sculpturing.

Wilson (2005:312) observed that the anterior caudal vertebra USNM 538127 "may later be shown to have opisthocoelicaudiine affinities." This caudal differs from the anterior caudals of Opisthocoelicaudia skarzynskii from the Maastrichtian Nemegt Formation of Mongolia (Borsuk-Białynicka, 1977), which are distinctly opisthocoelous, have proportionately longer centra, long prezygapophyses, and simple, dorsoventrally low transverse processes, and their neural spines lack capitate apices. Most other titanosaurians have distinctly procoelous centra with a bowl-shaped anterior articular surface and a posterior articular condyle ('ball') on at least the anterior caudals (Curry Rogers, 2005; Whitlock et al., 2011). The poorly known titanosaurian Borealosaurus from the Upper Cretaceous Sunjiawan Formation of Liaoning (China) has opisthocoelous mid-distal caudals (You et al., 2004), and the titanosaurian Sonidosaurus from the Upper Cretaceous (Senonian) Erlian Formation of Inner Mongolia (China) has at least one opisthocoelous anterior caudal (Xu et al., 2006). Thus, You et al. (2004) suggested that Borealosaurus might be closely related to Opisthocoelicaudia. However, D'Emic et al. (2013) noted that these taxa have opisthocoely in different regions of the caudal column: Opisthocoelicaudia has distinctly opisthocoelous anterior caudal vertebrae but amphiplatyan mid-caudal vertebrae, whereas Borealosaurus has opisthocoelous mid-distal caudals.

Huabeisaurus from the Upper Cretaceous Huiquanpu Formation of Shanxi (China) has anterior caudal centra with nearly flat anterior and distinctly concave posterior articular surfaces (D'Emic et al., 2013). D'Emic et al. (2013) observed that this condition is also present in *Phuwiangosaurus* from the Lower Cretaceous (Hauterivian–Valanginian) Sao Khua Formation of Thailand and *Tangvayosaurus* from the Lower Cretaceous (Aptian–Albian) 'Grès supérieurs' of Laos. USNM 538127 shares this condition as well, and this may suggest a closer relationship between these sauropod taxa (M. D. D'Emic, pers. comm.).

The presence of paired depressions possibly homologous to the postzygapophyseal centrodiapophyseal fossa is a derived feature shared only with *Alamosaurus*, *Mendozasaurus*, and certain other titanosaurians (Whitlock et al., 2011). The distinctly expanded apex of the neural spine is elsewhere found in *Futalognkosaurus* (Calvo et al., 2007b). The triangular, ventrolaterally tapering transverse process is also shared with the aforementioned forms. USNM 538127 clearly has a distinctive combination of features and likely represents a new taxon. However, we do not consider a single vertebra an adequate basis for proposing a new binomen.

ACKNOWLEDGMENTS

H.-D.S. and A.A. thank A. V. Abramov, J. D. Archibald, G. O. Cherepanov, I. G. Danilov, S. Dominguez, C. King, N. Morris, C. M. Redman, A. S. Resvyi, C. Skrabec, P. P. Skutschas, E. V. Syromyatnikova, and D. J. Ward for their efforts in the field, scientific expertise, and camaraderie. The cooperation of the Zoological Institute of the National Academy of Sciences of Uzbekistan is greatly appreciated. I. Morrison carefully prepared USNM 538127. For assistance with CT scanning of CCMGE 628/ 12457, we thank H. Rockhold, RT, and O'Bleness Memorial Hospital, Athens, Ohio. We are indebted to M. D. D'Emic (Stony Brook University) and A. Paulina Carabajal (Museo Carmen Funes) for constructive reviews of a draft of the manuscript. H.-D.S. and A.A. gratefully acknowledge financial support from the National Science Foundation (EAR-9804771 and EAR-0207004 to J. D. Archibald and H.-D. Sues), the National Geographic Society (5901-97 and 6281-98 to J. D. Archibald and H.-D. Sues), the Navoi Mining and Metallurgy Combinat, the Civilian Research and Development Foundation (RU-G1-2571-ST-04 and RUB1-2860-ST-07), the Russian Fund of Basic Research (07-04-91110-AFGIRa) and the Russian Scientific Fund project 14-14-0015. L.M.W. and R.C.R. acknowledge support from the Ohio University Heritage College of Osteopathic Medicine and the National Science Foundation (IBN-0343744, IOB-0517257, IOS-1050154). The Ohio Supercomputing Center provided additional support.

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Submitted November 21, 2013; revisions received January 7, 2014; accepted January 18, 2014. Handling editor: Richard Butler.