Ornithomimidae (Dinosauria: Theropoda) from the Bissekty Formation (Upper Cretaceous:
Turonian) of Uzbekistan

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ABSTRACT

The stratigraphically oldest remains of ornithomimid theropod dinosaurs are known from the Cenomanian Khodzhakul Formation and the Turonian Bissekty Formation of Uzbekistan. The ornithomimid from the Bissekty Formation is documented by more than 800 isolated bones that represent much of the skeleton. It shows at least three unambiguous synapomorphies of Ornithomimidae: anterior cervical centra length three to five times greater than transverse width; low and rounded fibular crest of tibia; metatarsal III pinched between metatarsals II and IV; and proximal end of metatarsal III not visible in anterior view. Phylogenetic analysis, based on a dataset with 568 morphological characters and including all known ornithomimosaurian taxa, places the ornithomimid from the Bissekty Formation near the base of the ornithomimid radiation, between *Archaeornithomimus asiaticus* and *Sinornithomimus dongi*.

Keywords: Dinosauria, Theropoda, Ornithomimidae, Cretaceous, Uzbekistan

1. Introduction

Ornithomimidae is a clade of Ornithomimosauria, a group of coelurosaurian theropods closely related to the Maniraptora (Makovicky et al., 2004). Superficially resembling present-day large ground-dwelling birds, ornithomimids are characterized by a proportionately small skull with large orbits, edentulous jaws covered by a keratinous beak, a long neck, long forelimbs with immobile wrist joints and long, subequal grasping fingers, long, cursorially adapted hind limbs, and an “arctometatarsalian” metatarsus in which the proximal portion of metatarsal III is “pinched” between metatarsals II and IV (Osborn, 1917; Russell, 1972; Osmólska et al., 1972; Nicholls and Russell, 1985; Kobayashi et al., 1999; Norell et al., 2001; Makovicky et al., 2004;

Barrett, 2005; Longrich 2008). Deinocheiridae, the sister-taxon of Ornithomimidae, as well as more basal ornithomimosaurian taxa lack the “pinching” of the proximal portion of metatarsal III (Kobayashi and Barsbold, 2005a,b; Makovicky et al., 2010; Lee et al., 2014). Some basal ornithomimosaurs retain highly modified dentitions (Pérez-Moreno et al., 1994; Ji et al., 2003; Kobayashi and Barsbold, 2005a).

In the western region of Central Asia fragmentary skeletal remains of ornithomimids have been reported from the Cenomanian of Kyrgyzstan and Uzbekistan and from the Santonian-Campanian(?) of Tajikistan and Kazakhstan (Nesov, 1995; Alifanov and Averianov, 2006; Averianov, 2006, 2007). **L.A. Nesov and colleagues first collected ornithomimid bones from the Turonian Bissekty Formation at Dzharakuduk (Uzbekistan) between 1974 to 1994. Between 1997 and 2006, the Uzbek-Russian-British-American-Canadian (URBAC) paleontological expeditions recovered much additional material (Archibald et al., 1998).** Ornithomimid remains are among the most common dinosaurian fossils in from the Bissekty Formation, second only to those of hadrosauroid ornithopods. **This is comparable to the situation in the Upper Cretaceous (Campanian) Dinosaur Park Formation of Alberta (Canada) where ornithomimids are the most abundant smaller dinosaurs (Longrich, 2008).** There are currently 766 catalogued specimens in the CCMGE, ZIN, and USNM collections and several dozens of additional as yet uncatalogued fragmentary elements. The vast majority of these remains are dissociated postcranial bones. Among isolated theropod cranial remains from Dzharakuduk, only frontals can be confidently attributed to Ornithomimidae at present. **We did not find consistent** taxonomically significant morphological differences between corresponding bones **and thus tentatively** interpret all ornithomimid skeletal remains as representing a single taxon.

This paper provides a detailed description and assessment of the relationships of the ornithomimid remains from Dzharakuduk. **There still exists a major gap in the fossil record of dinosaurs between the Aptian-Albian and the diverse Campanian-Maastrichtian faunas. The dinosaurian remains from the middle to upper Turonian Bissekty Formation of Uzbekistan**

partially fill this gap and offer new insights into the evolutionary diversification of many Late Cretaceous dinosaurian groups (Sues and Averianov, 2009a,b; Averianov and Sues, 2012a,b; Sues and Averianov, 2013, 2014, 2015; Sues et al., 2015).

Sedimentary deposits of the Bissekty Formation are exposed along an approximately 8 km long escarpment near the small settlement of Dzharakuduk (variously given in the literature as Dzhar-Kuduk, Dzharakuduk, Dzhyrakuduk, Bissekty, and Kul'beke) in the central Kyzylkum Desert, 32 km SW of Mynbulak in the Navoi district, Uzbekistan (Nesov, 1995, 1997; Archibald et al., 1998). The escarpment extends from about 42°06'22.60" N and 62°37'09.00" E to 42°05'44.22" N and 62°41'06.49" E (Fig. 1). The Bissekty Formation is a succession of medium-grained, poorly lithified, cross-bedded fluvial sandstones and clast-supported, well-cemented infraformational conglomerates. It reaches up to 80 m in thickness.

1.1. Institutional abbreviations

CCMGE – Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; USNM — National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.; ZIN PH — Paleoherpertological Collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

1.2. Locality abbreviations

The locality information following catalog numbers uses prefixes established by Nesov for localities within the middle-upper and lower parts of the Bissekty Formation, respectively: CBI – Central (Kyzylkum) Bissekty; CDZH – Central (Kyzylkum) Dzharakuduk.

1.3. Measurements

General: L - length; GL - greatest length; MH - maximum height; MW - maximum width.

Vertebrae: ACH - anterior height of centrum (without hypapophysis); ACW - anterior width of centrum; ANW - anterior width of neural arch (between lateral margins of prezygapophyses); CL - centrum length (ventral, without odontoid process for axis); 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).

Metapodials and phalanges: L - length; PW - maximum width of proximal end; DW - maximum width of distal end.

Femur: L - length (from greater trochanter to lateral distal condyle); PW - width of proximal end (from greater trochanter to head); HD - anteroposterior diameter of head; MW - mediolateral width at mid-shaft; DW - width of distal end.

All measurements are in mm.

2. Systematic paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Coelurosauria Huene, 1914

Ornithomimosauria Barsbold, 1983

Ornithomimidae Marsh, 1890

Ornithomimidae gen. et sp. indet.

Figs. 2-25

- 1995 *Alectrosaurus* sp. [partim]: Nesov, p. 38, pl. 1, figs. 1, 19, 20
- 1995 *Archaeornithomimus*(?) *bissektensis*: Nesov, p. 40, pl. 3, fig. 7
- 1995 Ornithomimosauria [indet.]: Nesov, pl. 2, fig. 19
- 1995 Oviraptorosauria? or cf. *Gallimimus* sp.: Nesov, pl. 3, fig. 1
- 1995 Theropoda [indet.]: Nesov, pl. 1, fig. 21, pl. 3, fig. 3
- 1995 cf. *Dryptosaurus* sp.: Nesov, pl. 3, fig. 6
- 1995 Hadrosauridae [indet.]: Nesov, pl. 10, fig. 2
- 1995 *Alectrosaurus*(?) sp.: Nesov, pl. 10, fig. 10
- 1995 *Gilmoresaurus arkhangelskyi* [partim]: Nesov, pl. 10, fig. 13
- 1997 *Azhdarcho lancicollis* [partim]: Nesov, pl. 15, fig. 15

Locality and horizon. Dzharakuduk II, **central** Kyzylkum Desert, Uzbekistan; Bissekty Formation; **middle-upper Turonian (Upper Cretaceous)**.

Referred material used in this study. Frontals, cervical, dorsal, sacral, and caudal vertebrae, fragments of scapula, coracoid, humerus, and ulna, metacarpals, phalanges of manus and pes, fragments of ilium, complete femora, fragments of femora, tibiae, fibulae, and astragali, medial distal tarsal, and metatarsals.

3. Description

3.1. Skull

3.1.1. Frontal

There are several incomplete ornithomimid frontals from Dzharakuduk. ZIN PH 2304/16 is an almost complete right frontal of a juvenile individual (Fig. 2). It is longer than wide and thin. The frontal tapers anteriorly with a pointed anterior end. A long facet for contact with the prefrontal contributes extensively to the dorsal margin of the orbit. The free dorsal margin of the orbit is quite long, only slightly shorter than the facet for the prefrontal, as in other ornithomimids except *Gallimimus bullatus* (Makovicky et al., 2004: fig. 6.2C). Posterior to the orbital margin the frontal bears a relatively short groove for contact with the postorbital. The postorbital process of the frontal is poorly differentiated. The dorsal surface of the more posterior portion of the frontal is distinctly domed and inclined ventrally at the suture between the frontal and parietal, reflecting the impression of the large cerebral hemisphere. The dome of one frontal is separated from the other by a shallow depression on the dorsal surface, as in other ornithomimids. This differs from the condition in *Garudimimus brevipes*, where frontals form a single dome (Kobayashi and Barsbold, 2005b). The anteroventral impression for the olfactory bulb is small but distinct. An incomplete frontal of a larger individual (ZIN PH 340/16) has a relatively smaller impression of the cerebral hemisphere. The supratemporal fossa extends onto the posterodorsal aspect of the frontal, as best seen in ZIN PH 810/16 and 974/16. The posterior portion of the bone bordering the supratemporal fossa is nearly vertical.

3.2. Postcranial axial skeleton

3.2.1. Cervical vertebrae

Anterior cervical vertebrae differ from the posterior ones in the obliquely inclined articular surfaces of the centra, the anteroventrally directed prezygapophyses, and shorter postzygapophyses that do not extend beyond the centrum posteriorly. The anterior articular surfaces face anteroventrally whereas the posterior ones face somewhat posterodorsally. On the

posterior cervicals, the articular surfaces of the centra are almost vertical. On all cervical vertebrae, these surfaces are oval and somewhat compressed dorsoventrally. All cervical centra are longer than high. The parapophyses are low and placed on the ventrolateral margin of the centrum. Their articular surfaces are confluent with the anterior articular surface of the centrum. Dorsal and somewhat posterior to the parapophyses, there is a large pleurocoel of variable shape but usually anteroposteriorly elongated. The centra are distinctly constricted at mid-length. Their ventral surfaces are flat transversely (except on the posteriormost cervicals) and delimited laterally by ventrolateral crests that extend posteriorly from the parapophyses.

On the anterior cervicals, the neural arch has long, anteroventrally recurved prezygapophyses and shorter postzygapophyses (Fig. 3). The articular surfaces of the prezygapophyses are oval, long anteroposteriorly, distinctly convex, and face anterodorsally (Fig. 3B, H). The postzygapophyseal articular surfaces are more circular, deeply concave, and face posteroventrally (Fig. 3I). The relatively long but low neural spine is placed centrally or shifted somewhat posteriorly (Fig. 3G, H). The anterior interspinous recess is relatively small and has a ventral floor (intrazygapophyseal lamina). The posterior interspinous recess is much wider and deeper and also has a ventral floor. The bars for attachment of the interspinous ligaments are poorly developed. The prezygapophyses and postzygapophyses are connected by weak lateral ridges, which form small epipophyses above the postzygapophyses (e.g., ZIN PH 134/16; Fig. 3G, H). The diapophysis starts as a ventral ridge below the prezygapophyses. On the ventrolateral side of the neural arch, just posterior and above to the diapophyses, an oblique, elongated pleurocoel (Fig. 3E, I) is bordered ventrally by a distinct ridge, which extends laterally to the short posterior diapophyseal process (Fig. 3I). A similar process is present on the posterior cervicals of *Archaeornithomimus asiaticus* and *Ornithomimus edmontonicus* (Makovicky et al., 2004). On the lateral side of the centrum, a prominent oblique crest separates the anteroventral pleurocoel from a posterodorsal depression.

On more anterior cervicals (ZIN PH 134/16 and 135/16; Fig. 3H, I), the posterior border of the neural arch is straight but it is incised between the postzygapophyses on a more posteriorly situated anterior cervical (ZIN PH 637/16).

Presumably juvenile anterior cervical centra with open neurocentral sutures closely resemble specimens from Dzharakuduk that we assign to Therizinosauroida but differ in having one rather than two pleurocoels on either side. The smallest juvenile centrum has CL of 15.2.

On the posterior cervicals, the neural arch is longer, with longer postzygapophyses, which extend posteriorly beyond the centrum, and with anterodorsally directed prezygapophyses. The neural spine is lower, almost non-existent, and the posterior interspinous recess is much longer and deeper than that on the anterior cervicals (Fig. 4B). The prezygapophyseal articular surfaces are elongate and face dorsally and slightly medially. There is a weakly developed pleurocoel on the lateral aspect of the centrum dorsal and posterior to the parapophysis. The diapophysis is better developed with a complex system of laminae and recesses. None of the available neural arches of the posterior cervicals is complete enough to establish presence of a diapophyseal posterior process. The neural canal is relatively large and subcircular in end view (Fig. 4A, D). The vertebrae from the posterior end of the cervical series (ZIN PH 129/16; Fig. 4A-E) are similar to the anterior dorsals in having a higher and much shorter neural spine, with the posterior interspinous recess greatly increasing in length, and a strong keel extending along the centrum except in the flat or concave surface between the parapophyses (Fig. 4E). ZIN PH 1005/16 (Fig. 4F-I; ACH=27.3; ACW=33.6; CL=55.3; PCH=28.0; PCW=27.7) is perhaps the last cervical. It has rounded parapophyses placed at middle height of the anterior articular surface of the centrum, as on the anterior dorsals. The centrum is much constricted at mid-length and has an oval pleurocoel posterior to the parapophysis. The flattened anterior area on the ventral surface of the centrum is greatly reduced and most of the ventral surface bears a prominent ventral keel (Fig. 4I).

3.2.2. *Dorsal vertebrae*

Anterior dorsals are known from only a few complete specimens and differ from the posterior dorsals in the placement of the parapophysis at or below the neurocentral suture. The anteriormost dorsals also bear distinct hypapophyses. The most complete anterior dorsal vertebrae are ZIN PH 856/16 and ZIN PH 536/16 (Fig. 5; CL=35.4, 40.8, ACW=20.9, 25.0, ACH=19.1, 18.7, PCW=17.9, 19.5, PCH=16.7, 20.5; NSL= --, 9.2). The neurocentral suture is evident on both specimens. The centrum is elongated and considerably constricted at mid-length. The anterior articular surface of the centrum is roughly triangular in outline and dorsoventrally compressed in ZIN PH 536/16 (Fig. 5A). The posterior articular surface of the centrum is oval, transversely compressed, and has a flattened dorsal margin (Fig. 5D). The parapophysis is oval and vertically oriented. **It is situated** along the anterior margin of the centrum just below the neurocentral suture (ZIN PH 536/16; Fig. 5C) or extends somewhat dorsally onto the neural arch (ZIN PH 856/16). A weak ridge extends posteriorly from the ventral margin of the parapophysis to the center of the centrum. A slight depression is developed just above this ridge and close to the center of the centrum. On a juvenile centrum ZIN PH 811/16, a small pleurocoel in this depression opens into the central cavity. The centrum is narrow ventrally, with a prominent ventral keel (Fig. 5E). On the neural arch, two thin laminae support the transverse process ventrally and separate infraprezygapophyseal, infradiapophyseal, and infrapostzygapophyseal fossae (Fig. 5C). The transverse process was dorsolaterally directed, at an angle of about 45° to the sagittal plane. It is short proximodistally and wide anteroposteriorly (ZIN PH 116/16). A horizontal ridge divides the infrapostzygapophyseal fossa into a shallow dorsal and a deep ventral compartment in ZIN PH 536/16 (Fig. 5C) but not in ZIN PH 537/16 and ZIN PH 856/16. The low neural spine is short anteroposteriorly. The rugosities for attachment of the interspinous ligaments are well developed. The anterior interspinous recess opens anteriorly and is floored ventrally by a thin intrazygapophyseal lamina. The posterior interspinous recess was about twice

as long. The prezygapophyses are not preserved but evidently were well separated from the sagittal plane. The neural canal is relatively large and circular. ZIN PH 537/16 (ACH=21.6; ACW=21.5; CL=39.1; NSL=13.6; PCH=21.8; PCW=19.7), lacking the hypapophysis and having an infraprezygapophyseal fossa that is larger than the infrapostzygapophyseal fossa, is apparently from a more posterior position in the dorsal series compared to ZIN PH 536/16 and ZIN PH 856/16.

Posterior dorsal vertebrae are known from several specimens. The best preserved is ZIN PH 535/16 (ACH=29.9; ACW=27.3; CL=53.7; PCH=30.4; PCW=28.3; Fig. 6). The parapophysis is situated at or above the neurocentral suture (Fig. 6D). On some of the neural arches, the parapophysis is indistinct. The centrum is elongate and laterally constricted, but, in contrast with the anterior dorsals, the ventral keel is weak or absent. In some specimens, possibly from more posterior positions in the series, the ventral surface of the centrum is remarkably flat, especially posteriorly. The lateral surface of the centrum is concave but lacks the marked depression present on anterior dorsals. The infraprezygapophyseal and infradiapophyseal fossae are variably developed but usually deep; the former is always deeper and larger than the latter. On some isolated neural arches (e.g., ZIN PH 111/16), the bony roof of the neural arch protrudes posteriorly far beyond the pedicels of the arch and forms a distinct hyposphene. The infrapostzygapophyseal fossa is large and deep on these specimens. On other, possibly more posteriorly situated vertebrae (ZIN PH 108/16 and ZIN PH 535/16), the infrapostzygapophyseal fossae are confluent on both sides and form a marked depression between the roof of the neural canal and the postzygapophyses (the latter are not preserved on either specimen). The transverse process is directed posterolaterally and slightly dorsally. The prezygapophyses are closely placed, with small circular, flat, dorsally facing articular facets. The postzygapophyseal articular surfaces are distinctly concave and face ventrally. The neural arches have prominent anterior and posterior interspinous recesses with extensive ventral floors (the posterior interspinous recess is lacking in the specimens with the confluent infrapostzygapophyseal fossae). The neural spine is

tall, longer than on the anterior dorsals, and placed closer to the posterior end of the neural arch. Scars for the interspinous ligaments terminate at the apex of the neural spine (ZIN PH 110/16).

3.2.3. *Sacral vertebrae*

The incomplete sacrum CCMGE 474/12457 comprises four coalesced vertebrae (Fig. 7E-G). However, the posterior articular surface of sacral 4 has an articular surface for the sacral rib, indicating that one additional sacral vertebra was originally present but was only loosely connected to the other sacrals, as in *Archaeornithomimus asiaticus* (Gilmore, 1933: fig. 2). The individual sacral centra are relatively short, without marked differences in width. They lack pleurocoels and ventral sulci. Centrum height progressively decreases from the first to the fourth sacral. The height differential between the anterior and posterior articular surfaces of the centrum is more pronounced in ZIN PH 866/16 (Fig. 7A-D) than in CCMGE 474/12457. The first sacral vertebra resembles the dorsals, with widely spaced prezygapophysis and an open anterior interspinous recess, which is floored ventrally by a thin intrazygapophyseal lamina. The prezygapophyses of other sacrals appear to be fused with the postzygapophyses of the preceding vertebrae (Fig. 7A, E). The articular surface for the first sacral rib is relatively small and situated high on the neural arch (Fig. 7C). The articular surface for the second sacral rib is much deeper dorsoventrally but still confined to the diapophysis of the corresponding vertebra (Fig. 7C, F). The S-shaped articular surface for the third sacral rib is the largest and occupies the diapophysis of sacral 3 and the articular surfaces of the centra of sacrals 2 and 3 (Fig. 7C). A pair of laminar struts (centrodiapophyseal ridges) supporting ventrally the transverse process is developed on sacrals 1, 2, and 4 and obscured by the rib articulation facet on sacral 3. The neural spines are completely fused ventrally but, more dorsally, they are separated by remnants of the clefts between them (Fig. 7C, F). Most likely, fenestrae were present between the individual sacral neural arches, as in *Gallimimus bullatus* (Osmólska et al., 1972: fig. 9A).

3.2.4. Caudal vertebrae

Anterior caudals differ from the more posterior ones in the presence of transverse processes, distinctly shorter prezygapophyses, and distinct rather than ridge-like neural spines. The centrum is hollow on the more proximal anterior caudals but not on the more distal anterior and the posterior caudal vertebrae.

On the anterior caudals, the centrum is elongated, constricted at mid-length, with subcircular articular surfaces, and compressed laterally on the more anterior vertebrae and dorsoventrally in posterior ones. The ventral surface of the centrum is flattened, rarely with a weak ventral keel and usually with a triangular depression at the posterior margin, sometimes continuing anteriorly as a shallow ventral groove. The transverse processes are thin, blade-like, and more or less level with the neural canal. In the most anterior caudals, the transverse process is relatively short anteroposteriorly, with two variably developed ventral centrodiaepophyseal laminae separating the shallow infraprezygapophyseal, infradiaepophyseal, and infrapostzygapophyseal fossae (e.g., ZIN PH 80/16; Fig. 8A-E; ACH=34.6; ACW=31.3; ANW=17.0; CL=49.5; NAL=46.0, PCH=31.3; PCW=~29.0). Bony crests or laminae (prezygapophyseal ridge) link the transverse processes are linked to the prezygapophyses. On most vertebrae of this type, there is also a short transverse ridge on the dorsal surface of the transverse process at the middle of the neural arch. The hyosphene is usually well developed. On more posterior anterior caudals, these laminae disappear and the base of the transverse processes is much wider (e.g., ZIN PH 435/16, Fig. 8F-J). Variably expressed longitudinal ridges connect the pre- and postzygapophyses on these vertebrae. The prezygapophyses extend slightly beyond the anterior end of the centrum. Their articular surfaces are long and face dorsomedially. The postzygapophyseal articular surfaces are much smaller and face ventrolaterally; they are concave on the more anterior caudals. The neural spine is long and relatively tall. The anterior

interspinous recess is long and has a well-developed ventral floor. The posterior interspinous recess is completely confined below the neural arch. The lateral surface of the neural spine, dorsal to the transverse process, **bears** a low vertical ridge and a depression behind it (Fig. 8B, C). A similar depression on the neural spine of the anterior caudals, bordered by anterior and posterior ridges, was considered a diagnostic trait for *Garudimimus brevipes* (Kobayashi and Barsbold, 2005b: fig. 10B, C).

On the posterior caudals, the centrum is less constricted at mid-length, and its anterior and posterior articular surfaces are considerably compressed dorsoventrally (e.g., ZIN PH 960/16, Fig. 8K-T). The ventral surface of the centrum is more flat, with remnants of a ventral keel on the more anterior vertebrae and a longitudinal groove on the more posterior vertebrae. Some vertebrae may bear spur-like remnants of transverse processes. The neural spine is long, longer than on the anterior caudals, and quite low, decreasing in height on the more posterior vertebrae. The prezygapophyses are long, triangular in transverse section, without well-delimited articular surfaces and with variably excavated lateral surfaces, which sometimes bear a deep furrow. The postzygapophyses are shorter and spine-like, with better developed, ventrolaterally facing articular surfaces. The interspinous recesses are shorter than on the anterior caudals; the anterior recess has a ventral floor. The ridge between the pre- and postzygapophyses is usually pronounced, sometimes in form of two ridges extending between the opposite ends of the centrum. One posterior caudal has an apparently pathologically modified posterior end. Another posterior caudal centrum with a blunt, spherical posterior articular surface (USNM 538188) is possibly from the distal end of the caudal series.

3.3. Appendicular skeleton

3.3.1. Pectoral girdle

There are several fragments of scapulae, the most complete of which are ZIN PH 470/16 and ZIN PH 597/16. The scapula is considerably curved in the transverse plane. Its blade is long and narrow. Its glenoid facet faces posterolaterally. A shallow depression is present close to the posterior edge of the scapula and above the prominent supraglenoid buttress on the lateral side. This feature is pronounced in some specimens, including the smallest known specimen ZIN PH 793/16, but is small and shallow in others. This fossa is distinctly larger in *Beishanlong grandis* and placed more anteriorly and more proximal to the glenoid (Makovicky et al., 2010: fig. 2d). The anterior edge of the scapula forms a prominent convexity ("acromion") ventrally.

The coracoid (ZIN PH 2203/16, Fig. 9) is short dorsoventrally and long anteroposteriorly. Its lateral surface is convex, and its medial surface is deeply concave. The postglenoid process is prominent and relatively long. The depression for *M. coracobrachialis brevis* on the dorsal surface of the postglenoid process is shallow, with a ligamentous pit that is variously developed or absent. There is no deep notch between the postglenoid process and infraglenoid buttress on the medial side (Fig. 9C), unlike in *Beishanlong grandis* (Makovicky et al., 2010: fig. 2f). Along the dorsal margin of the postglenoid process, a ridge extends anteriorly to the large biceps (or coracoid) tubercle (Fig. 9B). The large coracoid foramen is situated close to the suture between the scapula and coracoid anterior to the glenoid. The deep coracoid portion of the glenoid faces posterolaterally and has a prominent infraglenoid buttress (Fig. 9A, B). The coracoid facet of the glenoid surface is roughly equal to the scapular contribution. The infraglenoid buttress is offset laterally from the posterior process. The medial opening of the coracoid foramen is smaller and placed anterior and somewhat dorsal to the lateral opening.

3.3.2. Forelimb

The proximal end of the humerus (Fig. 10; the largest specimen is ZIN PH 2204/16 with PW=72.3) has a distinct head that overhangs the dorsal surface of the bone. It is only about twice

as wide as the shaft. The head of the humerus is oval in proximal view (Fig. 10A, F). The lateral tuberosity is at approximately the same level as the head and about twice as large as the more distally situated medial tuberosity. The medial tuberosity is confluent with the humeral head. The weakly developed deltopectoral crest is placed close to the proximal articular end. Proximally, it is linked to the lateral tuberosity by a ridge and, distally, it merges rapidly into the humeral shaft (Fig. 10D). The shaft of the humerus is straight.

There are several partial ulnae, all of which lack the distal end (e.g., ZIN PH 984/16 and 985/16). The ulna is straight in the anteroposterior plane and slightly bowed medially. The olecranon process is not completely preserved on any **available** specimen. The anteromedial process is longer and thinner than the anterolateral process. A deep recess between these processes received the proximal end of the radius. The proximal articular surface of the ulna is undivided. The ulnar shaft is hollow and oval in transverse section, with a more flat anterior surface and convex remaining surfaces.

The manus is represented by isolated metacarpals and phalanges. Metacarpal I is known from several distal fragments. The most complete is ZIN PH 560/16 (DW=18.5; Fig. 11). The shaft of metacarpal I is strongly deflected medially in its distal half, with a concave medial and a convex lateral margin. The shaft is triangular in transverse section, with sharp medial and lateral edges and a ridge along the ventral side close to the lateral edge. The dorsal and ventromedial surfaces of the shaft are flat or slightly convex, whereas the ventrolateral surface is concave. On the preserved fragment there is no facet for contact with metacarpal II. The distal articular end is ginglymoid and asymmetrical. The lateral distal condyle is much larger than the medial one and has a more extensive pit for the collateral ligament. The medial condyle is positioned more proximally than the lateral condyle.

The shape of metacarpal II is ontogenetically variable. On smaller specimen, ZIN PH 1011/16 (L=66), the distal end is distinctly deflected laterally whereas on the largest specimen, ZIN PH 146/16 (L=93) it is perfectly straight. The intermediate-size specimen ZIN PH 152/16

(L=78; Fig 12) has a laterally deflected distal end but to a lesser extent than on the smaller specimen. On the medial side of ZIN PH 1011/16, a distinct facet for metacarpal I is bordered by sharp ridges anteriorly and posteriorly. It occupies 59% of the length of metacarpal II. Taking into account that the distal end of metacarpal I likely did not contact that of metacarpal II, metacarpal I was **clearly** subequal in length to metacarpal II. The proximal articular surface of metacarpal II is trapezoidal in outline, with a long anterior and a short posterior side. The shaft has nearly flat dorsal and ventral surfaces. The distal condyle is non-ginglymoid, with the medial and lateral condyles separated only posteriorly. The medial distal condyle varies in size but is always smaller than the lateral one. The pits for the collateral ligaments are shallow on both condyles.

Metacarpal III (Fig. 13) has a triangular proximal articular surface. The proximal portion of the shaft is triangular in transverse section. The ventral surface of the bone is flat, and its dorsomedial and dorsolateral surfaces are slightly convex. The distal condyle is non-ginglymoid, with the medial and lateral condyles poorly separated posteriorly. The lateral condyle is only slightly larger than the medial one. The intercondylar groove and both collateral ligament pits are shallow. The greatest length of metacarpal III is 65 mm (ZIN PH 611/16, which is not from an adult specimen). ZIN PH 610/16 shows signs of a healed fracture.

There are four proximal fragments of manual phalanx I-1, the largest of which has PW of 25.6 (ZIN PH 2373/16). The proximal articular surface of this phalanx is oval (in smaller specimens) to trapezoidal in outline (in larger specimens) and concave, being slightly divided by a groove ventrally. Lateral and medial to this groove the proximal articular surface is extended into paired flexor processes, as in other ornithomimids (Sereno, 2001: fig. 9A). The shaft is slightly recurved.

Only one manual phalanx III-1 can be identified (ZIN PH 824/16; L=22.6; PW=13.5; DW=12.6). It is short, with an anteroposteriorly wide proximal end. The proximal articular surface is undivided, deeply concave, and roughly triangular. The flexor tubercle is well

developed. The lateral pit for the collateral ligament is more pronounced than the medial one. The distal articular end is non-ginglymoid and almost flat.

The distal preungual phalanges of digits II and III (Fig. 14) are elongated (L+37.0-60.5, n=7) and have a deeply incised proximal articular surface, which is divided by a longitudinal ridge into almost equal parts (Fig. 14A). There is a proximal dorsal process. The phalangeal shaft is more recurved in smaller (juvenile) specimens but almost straight in adult specimens (Fig. 14). On the ventral (posterior) side, the proximal half of the bone has a flat or slightly concave triangular area. The more distal portion of the ventral side is flat or has a slight longitudinal ridge. The distal articular end is ginglymoid, asymmetrical, with a slightly larger medial distal condyle. The pits for the collateral ligaments are well developed on both sides.

The manual ungual phalanges are moderately curved and flattened mediolaterally (Fig. 15). The proximal articular surface is rather symmetrical in end view and divided by a low ridge. A relatively small ventral flexor tubercle is situated distal to the proximal end by about a third of the total length of the ungual. Deep neurovascular grooves extend laterally from the region of the flexor tubercle to the distal tip; the ventral rims of these grooves protrude slightly. Some of the phalanges are straighter than others, as in *Anserimimus planinychus* (Barsbold, 1988) and some specimens of *Archaeornithomimus asiaticus* (Smith and Galton, 1990: fig. 2W, X). These straighter unguals are usually smaller and apparently represent younger individuals. The greatest length of manual unguals ranges from about 17 mm (ZIN PH 212/16) to 74 mm (ZIN PH 190/16).

3.3.3. Pelvic girdle

The ilium is represented by several fragments, mostly of the acetabular portion, which greatly vary in size but are similar in structure (Fig. 16). The most complete fragment is ZIN PH 166/16 (Fig. 16), which preserves the acetabulum region and part of the postacetabular process

of a left ilium. A brevis shelf bounds the shallow brevis fossa laterally. The medial edge of this fossa is not completely preserved on any available specimen. The ventral border of the brevis shelf is straight. Just distal to the acetabulum, part of the brevis shelf ventral border is more depressed than the more distal part, projecting more ventrally and having a sharp ventral edge. The lateral surface of the ilium dorsal to this distal part is rugose. Only the posterior part of the cuppedicus fossa along the ventral margin of the preacetabular process is preserved on some specimens. It is deep and bound laterally by a sharp crest. The pubic peduncle is longer than the ischial peduncle. The ischial peduncle is wedge-shaped and pointed in lateral view. The lateral edge of the supraacetabular crest has a lateral expansion.

3.3.4. *Hind limb*

The femur is represented by three almost complete elements (one adult specimen, USNM 538119 [Fig. 17], and two juvenile specimens, CCMGE 479/12457 – the holotype of *Archaeornithomimus(?) bissektensis* – and ZIN PH 165/16). In addition, numerous proximal and distal ends of femora are available for study. The femur has a rather slender, laterally flattened shaft, which curves anteriorly and somewhat medially. Its proximal head projects somewhat dorsally on several specimens. A well-developed posterior hook bounds an oblique ligamentous groove on the posterior surface of the femoral head medially, as in other ornithomimids (e.g., Osmólska et al., 1972: pl. 51, fig. 1a). The greater trochanter is confluent with the femoral head; the combined articular surface slopes posteriorly and is weakly concave mediolaterally. The anterior (lesser) trochanter is situated proximally close to the greater trochanter. It forms a narrow, rather tall ridge that curves anteriorly and mediodistally and is separated from the greater trochanter by a notch. One or two foramina are present on the inner face of the crest just anterior to the notch. A short but well-developed accessory trochanter (Fig. 17C, D) continues anteriorly and distally from the apex of the anterior trochanter, from which it is separated by a slight notch.

A low mound on the lateral surface of the femur just distal to the notch between the greater and anterior trochanters served as the point of insertion of *M. iliofemoralis externus*, corresponding to the trochanteric shelf in other theropod dinosaurs (Hutchinson, 2001). The fourth trochanter forms a low but sharp crest and is situated proximal to the mid-length of the shaft. It is associated medially with a distinct scar for insertion of *M. caudifemoralis longus* (Fig. 17D, F). The distal articular end of the femur is rather narrow mediolaterally and bears mediolaterally flattened condyles. The lateral condyle is larger than the medial one and separated from it by a deep posterior groove. The lateral condyle is conical in shape and projects only slightly more distally than the medial condyle. On the anterior surface of the distal end of the femur, a sharp medial crest separates the origins of the external and internal/medial portions of *M. femorotibialis* (Hutchinson, 2001) and extends to the anteromedial corner of the medial condyle. Selected measurements: L=247 (USNM 538119), L=143 (CCMGE 726/12457), L=79 (ZIN PH 165/16); DW=48 (USNM 538119) and DW=21 (CCMGE 726/12457).

The tibia is represented only by incomplete proximal and distal ends, which represent a great range in size (Fig. 18). The proximal end is broadly convex medially and distinctly concave laterally anterior to the lateral condyle. The posterior and lateral proximal condyles are closely spaced; they are either subequal in size or the lateral condyle is larger (Fig. 18A). The cnemial crest is damaged in all available specimens but probably did not project much more proximally than the proximal surface of the posterior and lateral condyles. The cnemial crest occupies the proximal portion of the anteromedial edge of the tibia and protrudes anteriorly. Its anterior margin is slightly deflected laterally. The proximal portion of the tibial shaft is hollow and straight. The anterior side of the shaft is flat or slightly concave, the posterior side is greatly convex, and the lateral and medial sides are slightly convex. In ZIN PH 972/16, a series of vascular foramina is present on the lateral side of the cnemial crest at its distal end. The fibular crest extends along the anterolateral edge of the tibia, and its proximal end is approximately at the level of the distal end of the cnemial crest. The fibular crest is preserved only in two

specimens (ZIN PH 969/16 and ZIN PH 971/16, Fig. 18F-G), where it is high and sharp. There is no distinct trough for the fibula posterior to the fibular crest. In ZIN PH 969/16, a vascular foramen is present posterior to the proximal end of the fibular crest (Fig. 18G). This opening leads into a small canal in the bony wall, the internal opening of which can be traced for 12 mm further distally in the medullar cavity. The distal end of the tibia is expanded mediolaterally and flattened anteroposteriorly, with a clearly delimited surface for attachment of the ascending process of the astragalus (Fig. 18I). The outline of the distal articular surface of the tibia is an irregular parallelogram, with the medial edge longer than the lateral edge (Fig. 18J).

The fibula is definitely represented only by proximal ends (e.g., ZIN PH 6/16; Fig. 19). Its proximal end is flattened mediolaterally and expanded anteroposteriorly but rapidly tapers distally. The medial surface of the proximal end of the fibula bears a deep, vertical oval excavation for the reception of the fibular crest of the tibia. This excavation is deepest proximally and decreases in depth distally. The shaft of the fibula is hollow distal to this medial excavation.

The astragalus is known from several incomplete elements. One of these, ZIN PH 144/16 (width across trochlea: 47 mm; basal width of ascending process: 41 mm; Fig. 20A-E) lacks only the dorsal end of its ascending process. A wide sulcus divides the distal trochlea of the astragalus into two condyles, the medial one of which is larger and more robust than the lateral one, which is recessed laterally for contact with the small calcaneum. The medial condyle is sometimes separated from the anterior side by a small horizontal groove. A relatively large fibular facet on the lateral side between the lateral condyle and the ascending process (Fig. 20C) faces proximolaterally. Anterior and ventral to this facet, the entire lateral surface of the lateral condyle is occupied by the calcaneal facet (Fig. 20A, B). The ascending process is tall and blade-like, with a nearly straight lateral edge. Its anterior surface has a shallow, poorly delimited depression just above the trochlea.

The single distal tarsal referable to Ornithomimidae (ZIN PH 986/16; Fig. 20F, G) is flat and subtriangular. Specific interpretation of this bone is difficult due to the known variation in the structure of ornithomimid tarsals. In *Harpymimus okladnikovi* and *Archaeornithomimus asiaticus* the medial distal tarsal (distal tarsal 2) covers metatarsal III (Gilmore, 1933: fig. 7A; Smith and Galton, 1990: fig. 4H; Kobayashi and Barsbold, 2005a: fig. 6.10E) whereas the lateral distal tarsal (distal tarsal 3) covers metatarsal III in *Gallimimus bullatus* (Osmólska et al., 1972: fig. 16A3). If the former condition is used for identification, ZIN PH 986/16 would be a left medial tarsal, but, using the second condition, it would be a right lateral tarsal. The largest facet on the distal side in ZIN PH 986/16 is for metatarsal III, the smaller one is for either metatarsal II or metatarsal IV depending on which interpretation of the tarsal is used. The tarsal completely caps metatarsal III and covers only a small portion of the side of the metatarsal. The articular surfaces for the two metatarsals have a low anteroposterior ridge. The proximal articular surface of the bone is divided into a more gently sloping anterior and a steeper posterior part. Its posterior margin is convex. The North American ornithomimids have three distal tarsals, with a separate element covering metatarsal III (Marsh, 1890: pl. 1, fig. 2B; Lambe, 1902: fig. 11D).

Metatarsal II (Fig. 21) has a long, straight shaft and a subtriangular proximal articular surface. Its proximal portion has flat lateral and medial surfaces. The lateral margin of the proximal articular surface is gently concave and the medial margin is strongly convex. The posterior margin of the proximal articular surface forms a flange overhanging the shaft. The distal end of metatarsal II is known from several specimens. The largest fragment, ZIN PH 673/16, has DW=52.5. Its distal end is less curved laterally and has a mediolaterally less compressed distal articular surface compared to metatarsal IV. The lateral surface of the bone is flat and well delimited. The medial surface is convex, with a ventral ridge extending some distance proximal to the distal end. The distal condyle is not ginglymoid, with the condyles poorly separated only posteriorly. The distal articular surface is oblique in anteroposterior view, with the lateral condyle projecting more distally than the medial one. The medial distal condyle

is smaller than the lateral one but is more spine-like, projecting more ventrally, and deflected medially. The lateral pit for the collateral ligaments is large and deep, oval, with distinctly delineated margins. The medial pit is about half as large and much shallower.

Metatarsal III (Fig. 22; DW=51 for ZIN PH 1347/16) has a broad, flat anterior surface to about mid-length where it begins to taper rapidly proximally. Its shaft is triangular in transverse section and wedged between those of metatarsals II and IV more proximally. Its distal condyle is non-ginglymoid, with the subequal lateral and medial condyles separated by a shallow groove posteriorly. In distal view the medial condyle is slightly more expanded anteroposteriorly than the lateral condyle. The lateral pits for the collateral ligaments are prominent. The distal articular surface of metatarsal is not sharply delimited on the posterior (ventral) surface of the bone.

Metatarsal IV is known from a few proximal and distal ends (e.g., ZIN PH 576/16; Fig. 23). Its proximal articular surface is trapezoidal in outline, with a concave medial edge. The anteroproximal end of the medial side has a triangular facet for the metatarsal II. The shaft of the metatarsal is flattened anteriorly and medially as well as rounded posterolaterally. The distal end of the bone is deflected laterally. Its medial side is flattened, with a sharp ridge along the ventral edge terminating some distance proximal to the distal condyle. The distal condyle is non-ginglymoid, with the condyles separated by a posterior groove. The distal articular surface of the metatarsal is considerably constricted mediolaterally and asymmetrical. The medial distal condyle is larger than the lateral one. The pits for the collateral ligaments are shallow, the medial one being slightly more prominent.

The proximal phalanges of the pedal digits have proximal articular surfaces with straight anterior margins. On the more distal preungual phalanges, the anterior margins are proximally incised. The proximal phalanx of pedal digit II (Fig. 24A-F) is long ($L=24.9-53.1$, $n=9$) and asymmetrical, with the shaft somewhat bent and the proximal end deflected medially. Its proximal articular surface is oval (with the long axis extending anteroposteriorly) and smoothly concave. There are two short ridges on the posterior side at the proximal end. The distal articular

end is ginglymoid and asymmetrical, with the medial condyle being slightly larger. The pit for the collateral ligament is deeper on the medial side.

The proximal phalanx of pedal digit III (Fig. 24G-L) is symmetrical and has a straight shaft ($L=41.1-60.8$, $n=8$). The proximal articular surface is oval (with the long axis extending mediolaterally) and smoothly concave. There are two short, widely separated ridges on the posterior side at the proximal end; the surface between them is flat. The distal articular end is weakly ginglymoid, almost flat, and symmetrical with subequal medial and lateral condyles. There is a shallow depression on the anterior side just proximal to the distal condyle. The pits for the collateral ligaments are equal in size on both sides. Both the lateral and medial sides of some pedal phalanges III-1 and III-2 have variably developed depressions at the posteroproximal corners (Fig. 24I, K). A similar depression, but present only on the lateral surface of phalanges III-1 and III-2, was considered diagnostic for *Garudimimus brevipes* (Kobayashi and Barsbold, 2005b: fig. 17C).

The proximal phalanx of pedal digit IV (Fig. 24M-R) is distinctly shorter than phalanx II-1 ($L=15.2-39.5$, $n=10$). Its proximal articular surface is oval (with the long axis extending anteroposteriorly), concave, and divided posteriorly by a notch into two unequal parts, corresponding to the shape of the distal articular end of metatarsal IV. The phalanx is anteroposteriorly constricted at the distal condyle. The distal articular end is ginglymoid and asymmetrical, with the medial condyle distinctly larger than the lateral one. The pit for the collateral ligament is deeper on the medial side.

Most of the preungual distal pedal phalanges (Fig. 24S-X, AF, AG) are short ($L=20.8-35.3$, $n=10$) and constricted at mid-length. They have deep ginglymoid distal ends. A few phalanges, possibly **representing** III-2 or III-3, are more elongate and have weakly divided proximal articular surfaces, but with a proximally incised anterior margin (ZIN PH 816/16 or 852/16).

The pedal ungual phalanges are more or less triangular in transverse section (Fig. 24Y-AE). They are straight or only slightly curved and have flat surfaces, especially more distally. The lateral neurovascular grooves are bounded ventrally by pronounced edges. A distinct flexor fossa is present on the ventral side of the ungual a short distance distal to the proximal articular facet. On some but not all ungual phalanges, this fossa contains a small median ridge or tubercle for insertion of a flexor tendon (e.g., ZIN PH 235/16; Fig. 24AB, AE; L=15.4-36.7, n=10).

4. Phylogenetic position of the Bissekty ornithomimid

To assess the phylogenetic position of the Bissekty ornithomimid we used the character-taxon matrix published by Choiniere et al. (2012) and focused on Ornithomimosauria, adding scorings **for the ornithomimid remains from the Bissekty Formation and for *Deinocheirus mirificus*** (Lee et al., 2014). The list of changes to the original matrix and the updated matrix can be found in the **Supplementary Information**. The material from the Bissekty Formation could be scored for 197 (34.7%) of the 568 characters from the character-taxon matrix. The coded characters are listed in the Supplementary Information.

Three analyses were performed. The first analysis was similar to that employed by Lee et al. (2014), using the heuristic tree search strategy of TNT version 1.1 (Goloboff et al., 2003) and performing 1,000 replicates of Wagner trees (using random addition sequences, RAS) followed by TBR branch swapping (holding 10 trees per replicate). This heuristic search yielded 150 most parsimonious trees, each with tree length of 2931 steps, a Consistency Index of 0.21, and a Retention Index of 0.61. The larger number of most parsimonious trees compared to that from the analysis by Lee et al. (2014) can be explained by the fact that we increased the maximum number of the trees held in memory from the default 100 to the maximum possible 10,000, whereas the cited authors used the default settings of TNT and recovered only six most parsimonious trees. A portion of the strict consensus of these trees, pertaining to

Ornithomimosauria, is illustrated in Fig. 25. The second analysis used NONA (Goloboff, 1999) with 10,000 ratchet replications. This analysis resulted in 838 most parsimonious trees, each with a length of 3052 steps, a Consistency Index of 0.22, and a Retention Index of 0.61. The tree length is likely unreliable, because NONA and TNT show different lengths for the same trees (the number generated by NONA being greater). The phylogenetic relationships within Ornithomimosauria shown in the strict consensus of these 838 most parsimonious trees are identical to those in the previous analysis (Fig. 25). The third analysis was run by PRAP (parsimony ratchet analysis using PAUP; Müller, 2007) and PAUP* 4.0b10 (Swofford, 2002). The equal weight analysis with 10,000 ratchet replications produced 5577 most parsimonious trees, each with a length of 2931 steps, a Consistency Index of 0.23, and a Retention Index of 0.61. A successive weighting analysis (Farris, 1969) was conducted to reduce possible phylogenetic noise from the highly homoplastic characters. Using PAUP, the characters were reweighted by the maximum value of rescaled consistency indices (RC) and a heuristic search with 10,000 random sequence addition replicates and TBR (tree bisection and reconnection) branch swapping was performed. During reweighting 510 characters (89.8%) got a weight of less than 1. The tree statistics stabilized after three successive runs of reweight analysis. The strict consensus tree of the three recovered most parsimonious trees is fully resolved, with *Pelecanimimus polyodon*, *Shenzhousaurus orientalis*, and *Beishanlong grandis* successively branching off. The remainder of the tree is identical to the cladogram in Fig. 25.

Our resulting cladogram (Fig. 25) is similar to the phylogenetic tree recovered by Lee et al. (2014) in dividing derived ornithomimosaurians into two clades, Deinocheiridae and Ornithomimidae. However, the content of Deinocheiridae is different, with *Harpymimus okladnikov* found as the basal member in our analysis and *Beishanlong grandis* in that position in the analysis by Lee et al. (2014). Our analysis implies that teeth were lost independently in Deinocheiridae and Ornithomimidae. Within Ornithomimidae the difference between the two cladograms concerns the position of *Anserimimus planinychus*. The analysis by Lee et al. (2014)

found *Anserimimus planinychus* as the sister-taxon to a clade comprising *Gallimimus bullatus* and the North American ornithomimids, whereas it is the sister-taxon to *Ornithomimus edmontonicus* in our analysis. We note that Choiniere et al. (2012) coded this taxon for several bones that have not been reported for the holotype. We do not know the source for these codings.

In our analysis Ornithomimidae is diagnosed by three unambiguous synapomorphies, all of which are present in the ornithomimid from the Bissekty Formation:

263(2): Anterior cervical centra length three to five times transverse width.

517(1): Shape of fibular crest: low and rounded.

554(1): Metatarsal III pinched between II and IV and not visible in anterior view proximally.

The clade comprising the ornithomimid from the Bissekty Formation and more derived ornithomimid taxa is diagnosed by four unambiguous synapomorphies:

316(0): Ventral surface of anterior caudals rounded.

399(1): Distal articular end of metacarpal II without ginglymus.

505(1): Lateral distal condyle of femur distally conical.

508(0): Cnemial crest proximal projection: approximately at the same level as posterior condyles.

There are two autapomorphies for the ornithomimid from the Bissekty Formation:

286(1): Anterior dorsal vertebrae, anterior and posterior infrazygapophyseal fossae: with one or more accessory centrodiapophyseal laminae dividing fossa into multiple chambers.

321(1): Centrodiapophyseal laminae on anterior caudal vertebrae prominent, as well developed as those on dorsal vertebrae.

Character-state 321(1) is unique among Ornithomimosauria but character-state 286(1) is shared by *Garudimimus brevipes*, *Deinocheirus mirificus*, and *Ornithomimus edmontonicus*.

Ornithomimids more derived than the taxon from the Bissekty Formation are united by two unambiguous synapomorphies:

302(4): Number of sacral vertebrae: six.

568(0): Form of flexor fossa on pedal unguals without development of flexor tubercle.

The stratigraphically oldest known skeletal remains referable to Ornithomimidae are from Cenomanian strata in Kyrgyzstan and Uzbekistan. Averianov (2006) reported a partial coracoid from the Tokubai Formation of Kyrgyzstan. The Khodzhakul Formation of the southwestern Kyzylkum Desert in Uzbekistan has yielded fragmentary ornithomimid remains. They include caudal vertebrae, scapula and coracoid fragments, manual preungual and ungual phalanges, fragments of ilium and astragalus, fragments of metatarsals II and III, pedal phalanges II-1 and IV-1, and preungual and ungual pedal phalanges. These bones are mostly indistinguishable from the corresponding elements from the Bissekty Formation. A possible distinct ornithomimid taxon was present in the Coniacian to Santonian(?) Kynyr Formation of Zhaldyrbas-Takyr in the central Kyzylkum Desert of Uzbekistan. An anterior caudal from this locality (ZIN PH 1901/16) differs from those from the Bissekty Formation in the presence of a strong ventral ridge. Indeterminate ornithomimid remains have also been recorded from the lower Santonian Yalovach Formation of Tajikistan (Alifanov and Averianov, 2006) and the Santonian to Campanian(?) Bostobe Formation of western Kazakhstan (Averianov, 2007).

5. Concluding remarks

Nesov (1995) based *Archaeornithomimus(?) bissektensis* on a small, presumably juvenile femur (CCMGE 726/12457) from the Bissekty Formation of Dzharakuduk. He attributed only immature specimens to this species, assigning all larger ornithomimid remains to Tyrannosauridae. Nesov tentatively referred the ornithomimid material to *Archaeornithomimus* based on its supposedly small size. In fact, some adult ornithomimid specimens from Dzharakuduk represent rather large animals, comparable in size to the Campanian *Gallimimus*. We consider *Archaeornithomimus(?) bissektensis* a nomen dubium in agreement with

Makovicky et al. (2004: 139). Although the ornithomimid material from the Bissekty Formation probably does represent a new taxon that can be diagnosed by a combination of characters and at least two autapomorphies, we refrain from naming it because of the lack of associated cranial and/or postcranial elements (see also Longrich [2008]). **We cannot conclusively rule out that the wealth of available bones represents more than one taxon. Some Campanian and Maastrichtian assemblages of dinosaurs include two or more ornithomimid taxa – for example, the Dinosaur Park Formation of Alberta (Canada; Longrich, 2008). We noted some minor variation in the descriptions of individual bones from the Bissekty Formation. However, growth series are not available for most ornithomimid taxa (Kobayashi and Lü, 2003), and thus it is impossible to assess whether the observed differences represent ontogenetic or sexual variation or indicate the presence of more than one taxon.**

The ornithomimid from the Bissekty Formation and *Archaeornithomimus asiaticus* from the Coniacian-Santonian Iren Dabasu Formation of Inner Mongolia (China) represent the basal ornithomimid taxa in the phylogenetic analysis (Fig. 25). They are followed in a crownward direction by *Sinornithomimus dongi* from the Ulansuhai Formation of Inner Mongolia (Kobayashi and Lü, 2003). The age of the Ulansuhai Formation is younger than Turonian based on a radiometric date of 92 Ma from the underlying Suhongtu Formation (Kobayashi and Lü, 2003). **In turn, these early taxa are followed by derived ornithomimids in Asia and western North America during the Campanian and Maastrichtian (Osmólska et al., 1972; Russell, 1972; Makovicky et al., 2004; Longrich, 2008). However, as Ji et al. (2003) noted, the presence of Early Cretaceous ornithomimosaur in Europe (see also Allain et al. [2014]) makes the identification of an Asian center of origin for Ornithomimidae problematical.**

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Figure legends

Fig. 1. Top: Location of the Dzharakuduk locality complex (indicated by star) on a map of Uzbekistan and neighboring countries (left) and on a more detailed map of the region around Mynbulak (right). Areas of vertical lines indicate salt flats (sor). Left illustration adapted and modified from <http://en.wikipedia.org/wiki/Uzbekistan>. Bottom: View of the exposures of Cretaceous strata along the Dzharakuduk escarpment, central Kyzylkum Desert, Uzbekistan, from an airplane with approximate boundaries between the Bissekty Formation and adjacent units. View toward North. Photo by A. Averianov.

Fig. 2. ZIN PH 2304/16 (CBI-17, 2006), right frontal of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, lateral view; B, ventral view; C, dorsal view; D, posterior view. Abbreviations: crc, crista cranii; ch, impression for cerebral hemisphere; ob, impression for olfactory bulb; Pf, facet for prefrontal; Po, facet for postorbital; stf, supratemporal fossa. Scale bar equals 1 cm.

Fig. 3. Anterior cervical vertebrae of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 130/16 (CBI-4, 1987), in (A) right lateral, (B) dorsal, (C) anterior, (D) left lateral, and (E) ventral views; F, ZIN PH 637/16 (CBI-, 2003), in lateral view. G-I, ZIN PH 134/16 (CBI-14, 1984), neural arch, in (G) lateral, (H) dorsal, and (I) ventral views. Abbreviations: dpp, diapophyseal posterior process; ep, epipophysis; ns, neural spine; pa, parapophysis; pl, pleurocoel; poz, postzygapophysis; prz, prezygapophysis. Scale bars equal 1 cm.

Fig. 4. Posterior cervical vertebrae of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 129/16 (CBI-14, 1987), in (A)

posterior, (B) dorsal, (C) lateral, (D) anterior, and (E) ventral views. F-I, ZIN PH 1005/16 (CBI-), in (F) anterior, (G) posterior, (H) lateral, and (I) ventral views. Abbreviations: pa, parapophysis; pl, pleurocoel. Scale bar equals 1 cm.

Fig. 5. ZIN PH 536/16 (CBI-5), anterior dorsal vertebra of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, anterior view; B, dorsal view; C, lateral view; D, posterior view; E, ventral view. Abbreviations: hp, hyposphene; hy, hypapophysis; idf, infradiapophyseal fossa; ipf, infrapostzygapophyseal fossa; iprf, infraprezygapophyseal fossa; ns, neural spine; pa, parapophysis. Scale bar equals 1 cm.

Fig. 6. ZIN PH 535/16 (CBI-6), posterior dorsal vertebra of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, ventral view; C, anterior view; D, lateral view; E, posterior view. Abbreviations: idf, infradiapophyseal fossa; iprf, infraprezygapophyseal fossa; pa, parapophysis. Scale bar equals 1 cm.

Fig. 7. Partial synsacra of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-C, ZIN PH 866/16 (CBI-4, 1989), in (A) dorsal, (B) anterior, (C) lateral, and (D) ventral (D) views. E-G, CCMGE 474/12457 (CDZH-16), in (E) dorsal, (F) lateral, and (G) ventral views. Scale bars equal 1 cm.

Fig. 8. Caudal vertebrae of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 80/16 (CBI-5a), anterior caudal in (A) anterior, (B) dorsal, (C) lateral, (D) posterior, and (E) ventral views. F-J, ZIN PH 435/16 (CDZH-17a, 1991), anterior caudal in (F) posterior, (G) dorsal, (H) lateral, (I) anterior, and (J) ventral views. K-O, ZIN PH 960/16 (CBI-1116-3), posterior caudal in (K) anterior, (L) dorsal, (M) lateral, (N) posterior, and (O) ventral views. P-T, ZIN PH 429/16 (CBI-14, 1980), posterior

caudal in (P) posterior, (Q) dorsal, (R) lateral, (S) anterior, and (T) ventral views. Scale bars equal 1 cm.

Fig. 9. ZIN PH 2203/16 (CBI-5, 2006), incomplete right coracoid of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, lateral view; C, medial view. Abbreviations: bt, coracoid (biceps) tubercle; gl, glenoid facet; igb, infraglenoid buttress; pgp, postglenoid process. Scale bar equals 2 cm.

Fig. 10. Proximal portions of humeri of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 272/16 (CBI-7, 1997), right proximal end in (A) proximal, (B) posterior, (C) dorsal, (D) anterior, and (E) ventral views. F, ZIN PH 2204/16 (CBI-, 2006), left proximal end in proximal view. Abbreviations: dc, deltopectoral crest; h, head; lt, lateral tuberosity; mt, medial tuberosity. Scale bars equal 1 cm.

Fig. 11. ZIN PH 560/16 (CBI-28, 1980), distal fragment of right metacarpal I of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, distal view; B, proximal view; C, lateral view; D, anterior view; E, medial view; F, posterior view. Scale bar equals 1 cm.

Fig. 12. ZIN PH 152/16 (CBI-14, 1987), left metacarpal II of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, proximal view; B, distal view; C, medial view; D, anterior view; E, lateral view; F, posterior view. Scale bar equals 1 cm.

Fig. 13. ZIN PH 611/16 (CBI-14, 1987), right metacarpal III of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, proximal view;

B, distal view; C, lateral view; D, anterior view; E, medial view; F, posterior view. Scale bar equals 1 cm.

Fig. 14. ZIN PH 825/16 (CBI-14, 1982), distal preungual phalanx of manual digit II or III of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, proximal view; B, distal view; C, side view; D, anterior view; E, side view; F, posterior view. Scale bar equals 1 cm.

Fig. 15. ZIN PH 190/16 (CDZH-14a, 1980), manual ungual phalanx of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, side view; B, ventral view; C, side view. Abbreviations: ft, flexor tubercle; gr, groove. Scale bar equals 1 cm.

Fig. 16. ZIN PH 166/16 (CBI-5a, 1987), fragment of left ilium of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, lateral view; B, ventral view; C, medial view. Abbreviations: ac, acetabulum; bf, brevis fossa; bs, brevis shelf; cf, cuppedicus fossa; ip, ischial peduncle; pop, postacetabular process; pp, pubic peduncle; sac, supraacetabular crest. Scale bar equals 3 cm.

Fig. 17. USNM 538119 (CBI-14, 1997), left femur of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, proximal view; B, posterior view; C, medial view; D, anteromedial view; E, anterior view; F, lateral view. Abbreviations: act, accessory trochanter; at, anterior trochanter; ft, fourth trochanter; gt, greater trochanter; h, head; lc, lateral condyle; mc, medial condyle. Scale bar equals 5 cm.

Fig. 18. Tibial fragments of *Ornithomimidae* gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 1424/16 (CBI-14, 1987), right proximal

fragment in (A) proximal, (B) posterior, (C) lateral, (D) anterior, and (E) medial views. F-H, ZIN PH 969/16 (CBI-, 2003), right shaft fragment in (F) posterior, (G) lateral, and (H) anterior views. I, J, ZIN PH 625/16 (CBI-, 1998), left distal fragment in (I) anterior and (J) distal views.

Abbreviations: cc, cnemial crest; fc, fibular crest; lc, lateral condyle; pc, posterior condyle; vf, vascular foramen. Scale bars equal 1 cm.

Fig. 19. ZIN PH 6/16 (CBI-27, 1980), proximal fragment of left fibula of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, proximal view; B, lateral view; C, medial view. Scale bar equals 1 cm.

Fig. 20. Tarsal elements of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 144/16 (CBI-4, 1989), left astragalus in (A) anterior, (B) lateral, (C) posterior, (D) medial, and (E) ventral views. F, G, ZIN PH 989/16 (CBI-14, 1987), left medial or right lateral distal tarsal in (F) proximal and (G) distal views.

Abbreviations: asp, ascending process; Ca, calcaneal facet; Fi, fibular facet; lc, lateral condyle; mc, medial condyle; II, III, IV, contact surfaces for the second, third, and fourth metatarsals.

Scale bars equal 1 cm.

Fig. 21. Fragments of metatarsal II of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-D, ZIN PH 188/16 (CBI-51), right proximal fragment in (A) lateral, (B) posterior, (C) medial, and (D) proximal views. E-I, ZIN PH 490/16 (CBI-), left distal fragment in (E) distal, (F) medial, (G) anterior, (H) lateral, and (I) posterior views. Scale bars equal 1 cm.

Fig. 22. ZIN PH 126/16 (CBI-14, 1985), distal fragment of right metatarsal III of Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk,

Uzbekistan. A, medial view; B, posterior view; C, lateral view; D, anterior view; E, distal view.

Scale bar equals 1 cm.

Fig. 23. ZIN PH 576/16 (CBI-14, 1987), distal fragment of right metatarsal IV of

Ornithomimidae gen. et sp. indet. from the Bissekty Formation (Turonian) at Dzharakuduk,

Uzbekistan. A, lateral view; B, anterior view; C, medial view; D, posterior view; E, distal view.

Scale bar equals 1 cm.

Fig. 24. Pedal phalanges of Ornithomimidae gen. et sp. indet. from the Bissekty Formation

(Turonian) at Dzharakuduk, Uzbekistan. A-F, ZIN PH 214/16 (CBI-5a, 1989), left proximal

phalanx II-1 in (A) proximal, (B) distal, (C) medial, (D) anterior, (E) lateral, and (F) posterior

views. G-L, ZIN PH 217/16 (CBI-5a, 1987), proximal phalanx III-1 in (G) proximal, (H) distal

(I, K) side, (J) anterior, and (L) posterior views. M-R, ZIN PH 834/16 (CBI-5a, 1989), left

proximal phalanx IV-1 in (M) proximal, (N) distal, (O) medial, (P) anterior, (Q) lateral, and (R)

posterior views. S-X, ZIN PH 852/16 (CBI-14, 1989), distal phalanx III-2 or III-3 in (S) distal,

(T) proximal, (U) ventral, (V, X) side, and (W) dorsal views. Y-AB, ZIN PH 791/16 (CDZH-25,

1980), ungual phalanx in (Y) proximal, (Z) dorsal, (AA) side, and (AB) ventral views. AC-AE,

ZIN PH 235/16 (CBI-4), ungual phalanx in (AC) proximal, (AD) side, and (AE) ventral views.

AF, AG, ZIN PH 821/16 (CBI-14, 1987), distal preungual phalanx in (AF) anterior and (AG)

distal views. Abbreviations: d, depression; ft, flexor tubercle; gr, groove. Scale bars equal 1 cm.

Fig. 25. Extract of the strict consensus trees of 150 most parsimonious trees produced by

heuristic search option in TNT showing the relationships within Ornithomimosauria. Numbers

above nodes are Bremer support values calculated by TNT.

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