Therizinosauroida (Dinosauria: Theropoda) from the Upper Cretaceous of Uzbekistan

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Abstract

Skeletal remains of indeterminate therizinosauroid dinosaurs are present in the Cenomanian Khodzhakul Formation and common in the Turonian Bissekty Formation of Uzbekistan. At least two taxa were present in the Bissekty Formation based on different frontal and humerus

morphotypes. Phylogenetic analysis based on a dataset with 348 morphological characters and including all known therizinosaurian taxa places the Bissekty taxa as derived non-therizinosaurid therizinosauroids. The Bissekty therizinosauroids are more derived than *Alxasaurus elesitaiensis* in the extensive pneumatization of the postcranial axial skeleton, the absence of teeth in the anterior portion of the dentary, the weak development or even absence of pits for the collateral ligaments on the manual phalanges, and the subtriangular medial aspect of the distal end of the humerus, with the entepicondyle positioned well medial to the ulnar condyle. They are less derived than Therizinosauridae in the presence of a basisphenoid recess, the absence of pneumatic openings on the anterior caudal vertebrae, the distal end of metacarpal III not being ginglymoid in dorsal view, and the separation of the femoral head from the neck of that bone by a raised ventral rim.

1. Introduction

Therizinosauroids are distinctive theropod dinosaurs with various features suggestive of herbivorous habits such as a broad pelvic girdle (indicating a large abdominal cavity), small, closely spaced teeth with lanceolate crowns, and the presence of a lateral shelf on the dentary indicative of an oral vestibule possibly bound by ‘cheeks’ (Clark et al., 1994, 2004; Zanno, 2010a,b). In contrast with the other common group of presumably plant-eating theropods, the toothless ornithomimids, the dentition in derived therizinosauroids was only lost on the anterior portions of the jaws, with formation of a rhamphotheca (Lautenschlager et al., 2014). In most Cretaceous dinosaurian assemblages from Asia, therizinosauroids are found along with ornithomimids, which suggests that the two groups differed in their feeding habits. Unlike ornithomimids and other cursorial theropods, therizinosauroids have functionally tetradactyl feet and, based on their limb structure and proportions, were likely slowly moving animals. The most distinctive feature of therizinosauroids are their sickle-like manual and pedal unguals; the most

extreme example are the greatly elongated, scythe-like manual unguals of the geologically youngest member of the clade, *Therizinosaurus cheloniformis* from the Maastrichtian of Mongolia (Maleev, 1954; Barsbold, 1976). The stratigraphically oldest undisputed therizinosauroids are known from the Early Cretaceous of East Asia and western North America (Xu et al., 1999; Clark et al., 2004; Kirkland et al., 2005b; Pu et al., 2013). The therizinosaurian affinities and the provenance of the enigmatic taxon *Eshanosaurus deguchiianus*, which is known only from a single dentary from allegedly Early Jurassic strata in Yunnan (China; see Barrett [2009]), are problematical. Therizinosauroids were most diverse in the first half of the Late Cretaceous of Asia and North America and drastically declined in the second half of the Late Cretaceous. The stratigraphically youngest records of this clade are known from the Campanian and Maastrichtian of East Asia (Maleev, 1954; Barsbold, 1976; Dong, 1979) and possibly from the Campanian of North America (Currie, 2005).

The Upper Cretaceous strata in the central Kyzylkum Desert, Uzbekistan, span the Cenomanian - Turonian interval, which represents the acme of therizinosauroid diversity. At Dzharakuduk (Fig. 1), therizinosauroids are the most common theropod dinosaurs after the ornithomimids in terms of skeletal remains other than teeth (Sues and Averianov, 2016). Currently there are 295 catalogued therizinosauroid specimens in the CCMGE, ZIN, IZANUZ, and USNM collections and several hundred mostly still uncataloged isolated teeth from the microvertebrate samples. In contrast with ornithomimids, there are more cranial fragments referable to therizinosauroids. Nesov (1995) first identified therizinosauroid remains from the Upper Cretaceous of the Kyzylkum Desert and published a brief account on some specimens. In this paper we provide a detailed description of the therizinosauroid bones and teeth from the Cenomanian and Turonian-age formations of Uzbekistan.

The most fossiliferous strata are those of the Bissekty Formation, which crop out along an approximately 8 km long escarpment near the small settlement of Dzharakuduk (variously given in the literature as Dzharakuduk, Dzharakuduk, Dzharakuduk, Bissekty, and Kul'beke) in the

central Kyzylkum Desert, 32 km SW of Mynbulak in the Navoi district, Uzbekistan (Nesov, 1995, 1997). This 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 comprises medium-grained, poorly lithified, cross-bedded fluvial sandstones and clast-supported, well-cemented infraformational conglomerates. It attains a thickness of up to 80 m.

1.1. Institutional abbreviations

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

1.2. Locality abbreviations

The locality information following catalog numbers uses prefixes established by Lev 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: GL - greatest length; MH - maximum height; MW - maximum width.

Vertebrae: ACH - anterior height of centrum (without hypapophysis); ACW - anterior width of centrum; 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: PW - width of proximal end (from greater trochanter to head); HD - anteroposterior diameter of head; MW - mediolateral width at midshaft; DW - width of distal end.

All measurements are in mm.

2. Systematic paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Therizinosauria Russell, 1997

Therizinosaurioidea Maleev, 1954

Therizinosaurioidea indet.

Figs. 2-26

1981 Pachycephalosauria? [indet.]; Nesov, fig. 10-14

1995 Segnosauria indet. [partim]; Nesov, p. 36, pl. 2, figs 1-4, 6, 12

1995 *Kuszholia* sp. (?) or Theropoda [indet.]; Nesov, pl. 2, fig. 18

1995 Theropoda(?) [indet.] or Aves [indet.]; Nesov, pl. 2, fig. 7

1997 Theropoda [indet.]; Nesov, pl. 20, figs 14-15

1997 Sauropoda indet.; Nesov, pl. 58, fig. 8

Localities and horizons. Sheikhdzheili, southwestern Kyzylkum Desert, Uzbekistan; Khodzhakul Formation (Upper Cretaceous: lower Cenomanian).

Dzharakuduk II, central Kyzylkum Desert, Uzbekistan; Bissekty Formation (Upper Cretaceous: middle-upper Turonian) and Aitym Formation (Upper Cretaceous: upper Turonian - ?Coniacian).

Referred material used in this study. Isolated teeth, fragments of humeri, and manual ungual from the Khodzhakul Formation; frontals, maxilla, braincase, and dentary fragments, isolated teeth, cervical, dorsal, sacral, and caudal vertebrae, cervical ribs, scapulocoracoid, humerus, femur, and tibia fragments, metacarpals, metatarsals and phalanges from manus and pes from the Bissekty Formation; fragmentary coracoid from the Aitym Formation.

Comment. Zanno (2010b) credited authorship of the name Therizinosauroida to Russell and Dong (1994). However, Russell and Dong (1994, p. 2108) merely changed the rank of that taxon and correctly cited Maleev (1954) as the author (based on the Principle of Coordination of the International Code of Zoological Nomenclature; ICZN 1999, Article 36.1). Maleev (1954, p. 108) originally proposed a family-level taxon Therizinosauridae for the reception of *Therizinosaurus cheloniformis*.

3. Description

3.1. Skull

3.1.1. Maxilla

A small fragment of the alveolar portion of a right maxilla (ZIN PH 1243/16, Fig. 2) is remarkably flat, with the lateral and medial sides of the bone meeting at an angle of about 115° at the alveolar margin. Eleven alveoli are preserved in an open groove. They are small, about 2 mm in anteroposterior diameter, closely packed, and laterally inclined. As the medial alveolar border is broken the presence of interdental plates cannot be confirmed. The alveolar row has a concave lateral margin. The medial margin of the maxilla is slightly convex and smooth. It apparently formed the lateral border of the internal narial opening. On the lateral side, close to the lateral edge, a prominent foramen opens medially into a large longitudinal groove that extends along the dorsal side of the bone and probably carried part of the maxillary ramus of the trigeminal nerve (V_2) and associated vessels. The groove is bordered laterally by a broken ridge, which probably represents the base of the ascending process of the maxilla. It is open dorsally in contrast with *Erlikosaurus andrewsi*, where a canal is completely enclosed in the body of the maxilla (Lautenschlager et al., 2014, fig. 4G, H). A slightly concave surface extending lateral from this ridge to the lateral margin of the bone represents the ventral floor of the antorbital fenestra. The angle between this floor and the lateral surface of the bone is about 70° .

3.1.2. Frontal

Six complete and partial frontals can be attributed to Therizinosauroidae. ZIN PH 978/16 (GL=23.8) represents a very young, possibly neonate individual. It has a well-developed facet for the prefrontal. The larger specimens ZIN PH 18/16 and 979/16 resemble each other in size and are almost identical in structure. The most complete is ZIN PH 18/16 (Fig. 3; GL=48.0). In dorsal view, it is twice as long as wide and forms an elongate triangle. Anterolaterally, it overlies the prefrontal and is overlapped by the nasal. The facet for the prefrontal is triangular and occupies the anterior extremity of the ventral surface. The facet for the nasal forms a narrow strip along the anterolateral margin of the frontal. The dorsal surface of the frontal is gently concave

between the upturned, apparently anteroposteriorly convex orbital margin (which is damaged) and the slightly raised medial edge of the bone. On the ventral side, a series of relatively large foramina is present along the preserved rugose orbital margin (Fig. 3C). The supratemporal fossa does not extend onto the posterodorsal aspect of the frontal. The posterior margin of the frontal is obliquely oriented, indicating that an anteromedian process of the parietals extended forward between the frontals, in contrast with *Erlikosaurus andrewsi*, where the frontoparietal contact is nearly transverse (Lautenschlager et al., 2014: fig. 7A, B). The crista cranii is low and close to the medial edge of the bone. The impression for cerebral hemisphere is triangular and only slightly larger than the elongate impression for the olfactory bulb. In ZIN PH 979/16, the anterior margin of the supraorbital rim is indented.

The larger frontals CCMGE 462/12457, ZIN PH 1242/16, and ZIN PH 980/16 are similar to each other and differ somewhat from smaller frontals in their structure. CCMGE 462/12457 (Fig. 4; GL=81.8) is complete. It is not as narrow as frontals of the first morphotype. The orbital margin is more sigmoidal in dorsoventral view, with a laterally projecting postorbital process. The anterior margin of the supraorbital rim is not indented. The part of the crista cranii bordering the ventral impression for the cerebral hemisphere is sharp and forms a sutural contact with the orbitosphenoid. The crista cranii bordering the impression for the olfactory bulb is lower and more rounded. The facet for the prefrontal is similar in position to that on the previously described frontals. It is shallow and irregular in CCMGE 462/12457 and deeper and pocket-like in ZIN PH 980/16. There is no distinct facet for the nasal. Dorsally along the posterior margin in CCMGE 462/12457, a shallow, circular depression bordered anteriorly by a distinct oblique ridge forms part of the supratemporal fossa.

3.1.3. Braincase

ZIN PH 1805/16 is a fragmentary braincase lacking most of the basisphenoid (Fig. 5). It is highly pneumatized and apparently preserved only because it is partially covered by hard ferruginous matrix, which obscures some important details of the structure. The preserved bones are indistinguishably fused without any evidence of sutures between them. The braincase is short anteroposteriorly and deep dorsoventrally. The foramen magnum is large, approximately twice as high as the occipital condyle, and ovoid with pointed dorsal margin (MH=20.0, MW=19.8). There is a distinct oval depression on the dorsal surface of the basioccipital just anterior to the occipital condyle. The occipital condyle is low and crescent-shaped (MH=11.5, MW=17.2) and has a well developed neck. There is no subcondylar recess, which is well developed in *Falcarius utahensis* but absent in more derived therizinosauroids (Clark et al., 1994; Smith et al., 2011; Lautenschlager et al., 2014). The posterior surface of the basioccipital is at least twice as wide as the occipital condyle. It extends vertically from the condyle and bears a prominent horizontal ridge close to preserved ventral margin and a short, low median vertical ridge, extending half distance from the horizontal ridge toward the occipital condyle. A similar horizontal ridge is present in *Erlikosaurus andrewsi* (Clark et al., 1994, fig. 7). The vertical ridge is flanked on either side by a slight depression. The basal tubera are indistinct and form a slight bilateral convexity on the horizontal ridge. The basisphenoid extends immediately ventral to the horizontal ridge, in the same vertical plane as the posterior surface of the basioccipital. Medial to the basal tubera and ventral to the horizontal ridge, there are partially preserved openings of the basisphenoid recess (Fig. 5C, D). Ventrolateral to the occipital condyle, a slight depression probably housed the exits of the hypoglossal and vagus nerves; however, both sides are filled by tightly adhering matrix. The broken anterior surface of the basioccipital-basisphenoid reveals a highly pneumatized structure, with spaces separated by delicate struts and septa. In the middle, close to the anterior end of the preserved fragment, there is a deep triangular depression of the basisphenoid sinus with pointed anterior end.

The exoccipital is distinctly depressed lateral to the foramen magnum. The paroccipital process is broken off on both sides; its broken base reveals a prominent dorsal (posterior) tympanic recess that occupied at least the entire proximal portion of the paroccipital process. The dorsal tympanic recess is connected to the middle ear cavity by a large opening (Fig. 5B, E). The lateral recess is not preserved on the left side and filled in by matrix on the right side. The lateral side of the braincase is dominated by a strong oblique ridge (prootic-basisphenoid crest or flange; Sues, 1997). The anterior surface of this ridge bears two large foramina leading to a large cavity that probably housed the Gasserian ganglion of the trigeminal nerve (V). Dorsal of these openings are foramina for passage of the maxillary ramus of the trigeminal nerve (V_2), and there is a ventral foramen for the mandibular ramus of this nerve (V_3). The maxillary ramus extended dorsolaterally in a short groove. On the medial side of the braincase, the trigeminal opening is a single large foramen with a distinct notch at its anterodorsal corner, possibly for passage of the middle cerebral vein, with exits the endocranial cavity through the same opening. The ophthalmic ramus of the trigeminal nerve (V_1) passed from the cavity for the Gasserian ganglion anteriorly for a short distance and then exited through a small foramen in the anterior wall of the braincase. On the anterior surface of the braincase, it extends laterally and then dorsally in a deep groove.

On the flattened anterior surface of the braincase, possibly representing the orbitosphenoid, two small foramina are situated ventral to the opening for V_1 . These openings cannot be readily identified. Ventral to the anterior surface of the braincase, a large, bean-shaped opening connects the now broken pneumatic spaces of the paroccipital process and the basisphenoid. This is possibly part of the canal for passage of the internal carotid artery.

The endocranial cavity is mostly filled in by hard matrix. A prominent eminence of the vestibular pyramid is visible. Although the dorsal roof of the braincase is eroded, enough is preserved to establish that the supratemporal fenestrae were widely separated and that the intervening dorsal surface of the parietals was rather flat and wide mediolaterally. On the right

side, a distinct horizontal groove, possibly for the dorsal cerebral vein, extends along the posterodorsal margin of the supratemporal fenestra. The eroded surface of the supraoccipital and parietals reveals cancellous bony structure, with numerous small spaces separated by irregular, thin bony septa. It is not clear whether the supraoccipital bore a median crest.

3.1.4. Dentary

Two excellently preserved anterior portions of dentaries probably represent young individuals based on the distinctive bone grain (Fig. 6). ZIN PH 16/16 preserves three complete alveoli and part of a fourth. ZIN PH 1153/16 is much smaller but preserves twelve complete alveoli. The alveoli are round anteriorly and rectangular more posteriorly. The bony septa separating the alveoli decrease in thickness posteriorly. These partitions are lingually exposed as triangular interdental plates between adjoining alveoli. In ZIN PH 1153/16, the alveoli abruptly decrease in size (especially in width) posteriorly. In ZIN PH 1153/16, the tooth row turns more lingually in the posterior portion and, starting at the fifth tooth position, is bordered labially by the dentary shelf (Fig. 6A). Alveoli 1, 6, and 9 contain crowns of erupting teeth. The dentary turns sharply medially just anterior to the first alveolus so that the mandible had a broadly U-shaped outline in dorsal view. The symphyseal portion in ZIN PH 1153/16 is distinctly shorter than in ZIN PH 16/16. It is distinctly deflected ventrally and increases in depth toward the midline. Its labial surface is dorsoventrally convex. The dorsal margin of this region of the ramus is edentulous and forms a sharp crest (which does not reach the symphysis in ZIN PH 1153/16). The labial surface of the bone in ZIN PH 16/16 bears two round foramina and, anteromedial to the latter, a large, elliptical opening just below the dorsal crest. ZIN PH 1153/16 has similar but much smaller openings. More posteriorly, the labial surface of the dentary bears smaller, scattered foramina, which are probably neurovascular in origin. The posterodorsally inclined symphyseal contact area (greatest height 17 mm in ZIN PH 16/16 and 9 mm in ZIN PH 1153/16)

is narrow anteroposteriorly and rugose. The ventral edge of the dentary is sharp, and the anterior end of the deeply incised Meckelian groove extends just medial to this edge and terminates at the anterior exit of the infraalveolar canal, which is connected to the three large openings below the symphyseal cutting edge.

There are two fragments of mid-portions of dentaries (ZIN PH 1154/16 and 1155/16; Fig. 7), with an extensive dentary shelf and a posteriorly deep Meckelian groove. The lingual alveolar margin is complete in ZIN PH 1154/16 and appears to lack interdental plates.

3.1.5. Teeth

Isolated teeth of therizinosauroids are frequently recovered in screen washing samples from the Bissekty Formation at Dzharakuduk (Fig. 8). There are two general types of teeth: those with more conical crowns, possibly representing anterior maxillary and dentary teeth, and those with more lanceolate crowns, which may represent posterior maxillary and dentary teeth (based on comparisons with *Erlikosaurus andrewsi*; Clark et al., 1994; Lautenschlager et al., 2014). On the more conical teeth, the crown is taller and slightly asymmetrical, with a convex mesial edge and a distal edge that is convex basally and concave apically. The labial surface of the crown is convex, and the lingual surface is more flat. Both carinae are denticulated, but the mesial carina is distinctly shorter. The apex of the crown is formed by a large denticle and inclined distally. On the more lanceolate teeth, the crown is less tall, with a slightly recurved or straight apex, with less difference in length between the denticulated carinae, and a less concave lingual surface. Some lanceolate tooth crowns are thick near their bases and then gradually taper toward the apex more distally, whereas other tooth crowns are more flattened labiolingually. On the majority of lanceolate teeth, the carinae are mesial and distal in position, but on a few teeth (e.g., ZIN PH 266/16; Fig. 8J-L) both carinae are positioned on the lingual side of the crown. Most of the teeth

have a slight constriction between the crown and root. The root is subcircular in transverse section and up to three times longer than the crown is tall. The enamel is smooth.

A few therizinosauroid teeth from the Khodzhakul Formation do not differ in structure from those from the Bissekty Formation.

3.2. Postcranial axial skeleton

All vertebrae are highly pneumatized. Their centra are composed of coarsely cancellous bone, especially near the articular ends.

3.2.1. Cervical vertebrae

Therizinosauroid cervicals from Dzharakuduk are represented mostly by isolated centra of juvenile individuals. However, the neurocentral sutures remain open even in larger specimens (e.g., ZIN PH 56/16 and 57/16 with CL=68.5 and 68.3, respectively). The cervicals are divided here into the anterior and posterior ones based on the relative width of the centrum. On anterior cervicals, the centrum is narrow and high, with the anterior and posterior articular surfaces that are higher than wide. On posterior cervicals, the centrum is low and wide, with the anterior and posterior articular surfaces that are wider than high. Anterior cervical centra are usually relatively longer (e.g., the elongate juvenile centrum ZIN PH 136/16 with CL=86.2; Fig. 9), whereas the posterior cervical centra are shorter.

Among the anterior cervicals, ZIN PH 2298/16 is nearly complete (ACH=42; ACW=44; CL=80; NAL=73; NSL=50; PCH=38; PCW=43; Fig. 10). The centra are long, longer than high, and more or less amphicoelous or amphiplatyan. They show pronounced angling of the articular surfaces. The flat or slightly concave anterior articular surface faces anteroventrally and the more concave posterior articular surface faces posterodorsally, and thus the centrum appears

trapezoidal in lateral view. The centrum is somewhat constricted at mid-length. Its lateral surface is concave anteroposteriorly and dorsoventrally, with typically two moderately deep pneumatic fossae, an anterior one dorsal to the parapophysis and a posterior one posterior and slightly dorsal to the anterior opening. Each depression contains several pneumatic foramina; these openings are highly variable in shape and size even on opposite sides of the same centrum. In addition to the pneumatic fossae, the centra have smaller foramina of variable position and size that might be pneumatic or vascular in origin. The centra reach their greatest transverse width anteriorly, where there are laterally and slightly ventrally projecting, large parapophyses. ZIN PH 52/16 apparently preserves a fragment of the capitulum of a cervical rib still attached to the left parapophysis. A prominent longitudinal ridge extends posteriorly from the parapophysis along the ventrolateral margin of the centrum on either side. The two ventrolateral ridges delimit the nearly flat ventral surface of the centrum. Only ZIN PH 142/16 has a slight midventral keel on the ventral surface closer to the posterior end of the centrum.

The neural arch on anterior cervicals (best preserved in ZIN PH 2298/16 and 52/16; Fig. 10) is lower than the centrum and wide. Its pre- and postzygapophyses are well separated. The robust postzygapophyses have large, “flexed” facets that face ventrally and slightly posterolaterally. These facets are situated lateral to the centrum. The epipophysis surmounting the complete right postzygapophysis forms a low ridge. The neural spine is low but rather long, and its base is deeply excavated by triangular interspinous recesses anteriorly and posteriorly. There is a distinct hyposphene. The neural canal is nearly circular in end view. An isolated prezygapophysis (ZIN PH 2242/16) is medially deflected. The prezygapophyseal articular surface is oval in outline (with its long axis anteroposteriorly), flat, and face dorsomedially.

Posterior cervicals are represented only by isolated centra. They closely resemble the anterior cervicals except that their centra are wider than high and the parapophyses are usually larger. The ventral surfaces of the centra are either concave (ZIN PH 55/16; Fig. 11A-E), or slightly convex (ZIN PH 57/16 and 1163/16; Fig. 11F-J). A markedly shortened centrum ZIN

PH 1163/16 (CL~59.5; Fig. 53F-J) could represent the last cervical, as in *Neimongosaurus yangi* where there is an abrupt shortening of the last cervical centrum (Zhang et al., 2001); it apparently lacks a hypapophysis or medioventral keel. The posterior articular surface on this centrum is almost vertical (rather than oblique as on other cervicals), further supporting its interpretation as the last cervical. A slight hypapophysis is present on the incomplete centrum ZIN PH 2237/16.

3.2.2. Cervical ribs

There are several isolated cervical ribs apparently representing different regions of the cervical column (Fig. 12). On all of them the capitular articular surface exposes the cancellous bony tissue, suggesting that these ribs were fused to the vertebrae.

ZIN PH 1257/16 is the most anterior rib in the sample (Fig. 12A-D). Its capitulum is large and globular. The tuberculum is much smaller and placed close to the capitulum from which it is separated by a slit-like groove. The body of the rib is a dorsoventrally expanded plate. The medial side of this plate has an extensive depression, starting from a groove between the capitulum and tuberculum and divided by a thin septum into two unequal parts. The anterior process is short and extends anteriorly.

ZIN PH 1256/16 is a more posterior anterior cervical rib (Fig. 12E-H). Its capitulum is relatively larger. The tuberculum is not preserved but apparently was close to the capitulum. The body of the rib consists of two plates: a dorsoventrally expanded lateral plate and a mediolaterally expanded medial plate, which is perpendicular to the former. On the dorsal surface of the medial plate there is an extensive but shallow, teardrop-shaped depression posterior to the capitulum.

ZIN PH 1258/16 is a posterior cervical rib with capitulum and tuberculum (not preserved) widely separated (Fig. 12I-L). The capitulum is relatively smaller than in anterior cervical ribs and placed on a distinct neck. The body of the rib consists of two perpendicular

plates, much as in the previously described rib, but the medial plate is greatly reduced. The capitulum and tuberculum were connected by a ridge. Anterior to this ridge there is a triangular depression. The anterior process is directed anteriorly and plate-like, similar in height to the body of the rib.

3.2.3. *Dorsal vertebrae*

All dorsal centra are subequal in height and length or slightly longer than high and somewhat constricted at mid-length. They are amphicoelous and have only a single pneumatic fossa on either side. The ventral margin of the centrum is concave anteroposteriorly in lateral view.

Anterior dorsals bear a well-developed, anteroventrally situated hypapophysis, which is continued posteriorly by a medioventral keel (Fig. 13). ZIN PH 97/16 with parapophysis on the anterodorsal corner of the centrum is one of the more anterior dorsals, and ZIN PH 101/16, without parapophysis on the centrum but with a distinct hypapophysis and a medioventral keel, is possible one of the posterior anterior dorsals. On other anterior dorsals, the parapophysis has a large concave facet and is situated on the neurocentral suture. The pneumatic fossa is variably developed, ranging from a shallow depression without any foramina in ZIN PH 93/16 and 1165/16 to a large pneumatic opening in ZIN PH 97/16 and 101/16. The anterior and posterior articular surfaces of the centra are flat or slightly concave and triangular in end view due to the well-developed hypapophysis and medioventral keel. The neural arch is fused to the centrum in ZIN PH 1165/16 (CL=33.5) whereas the neurocentral suture is still open in ZIN PH 97/16 (CL=59.8). The neural arch is tall, with high pedicles below the zygapophyses (the latter are not preserved on any of the anterior dorsals). The neural canal is teardrop-shaped, especially at the posterior end; dorsally, it is bordered by converging struts that support the robust hyposphene. The deep infrapostzygapophyseal fossa extends anteriorly almost to the level of the middle of the

parapophysis. The infradiapophyseal fossa is shallow and the infraprezygapophyseal fossa is small or absent. The base of transverse process is oblique, with its dorsal surface facing anterodorsally.

Posterior dorsals lack a hypapophysis and a medioventral keel; the ventral surface of the centrum is rounded transversely. The anterior and posterior articular surfaces of the centrum are circular or slightly laterally flattened. A small, oval pneumatic fossa is situated below the neurocentral junction near the anterior rim of the centrum or more posteriorly. On two large posterior dorsal vertebrae, this depression is large and vertically oriented in ZIN PH 1167/16 and small, slit-like, and variably developed on either side in ZIN PH 1166/16. The neural arch (incompletely preserved on ZIN PH 1166/16 and 1167/16) is tall, with high pedicles below the zygapophyses and a relatively small neural canal. The prezygapophyses (preserved on ZIN PH 1167/16) are large and placed close to each other, with only a slit-like anterior interspinous recess separating them. The prezygapophyseal facet is flat and inclined at about 45° to the vertical plane. On the posterior side of the neural arch (best preserved on ZIN PH 1166/16; Fig. 14), the postzygapophyses are nearly vertical, with strong infrapostzygapophyseal laminae converging ventrally and meeting just above the neural canal. The scar for interspinous ligaments is flanked laterally by alternating relatively large foramina on the sides of the posterior interspinous recess. The infrapostzygapophyseal fossa is small in ZIN PH 1166/16 but is much larger and divided into two depressions by a thin septum in ZIN PH 1167/16.

3.2.4. *Sacral vertebrae*

Several low, unfused sacral centra (CL=18.0-75.7) that are probably referable to Therizinosauroida (Fig. 13). Their anterior and posterior articular surfaces are semicircular, with a flat dorsal and a convex ventral margin. The lateral surface of the centrum bears a slit-like pneumatic opening of variable depth. Its ventral surface is flat, bearing a weak median ridge or

shallow grooves anteriorly and posteriorly. On the dorsal surface of the centrum, two pairs of oval depressions are situated near the ends: a larger transverse pair at the anterior? end and a smaller longitudinal at the posterior? end. The neural arch is pierced by a groove for the spinal nerve at the posterior? end.

3.2.5. *Caudal vertebrae*

All caudals referred hereto Therizinosauroida have transverse processes and, if the neural arch is preserved, a neural spine. Thus, the standard criteria for distinguishing between anterior and posterior caudals as in other theropod dinosaurs are not applicable here. The vertebrae with centra that are higher than long are considered anterior caudals and those with centra that are longer than high are interpreted as posterior caudals. The caudals are not pneumatized, unlike the cervicals and dorsals. They have only a shallow depression in place of a pneumatic foramen (more pronounced on an anterior caudal). An exception is an anterior caudal neural arch (USNM 538146) with a large pneumatic opening on the medial side of the base of the prezygapophyseal process. This opening leads to a chamber occupying most of the prezygapophysis and part of the base of the transverse process.

ZIN PH 1001/16 (Fig. 16; NAL=83.6; NSL=44.2; PCH=67.8; PCW=55.4) is the only more or less complete anterior caudal. Its centrum is distinctly higher than long and laterally compressed, especially dorsally where it bears marked lateral depressions. It is amphicoelous, with the anterior articular surface more concave than the posterior one. Both articular surfaces are oval in outline. The deepest point of the articular surface is at the center on the anterior surface and near the dorsal border on the posterior surface. The centrum bears a deep ventral groove. The neural canal is relatively large and rhomboidal in outline in end view. The infraprezygapophyseal fossa is small but deep and well-defined on the left side but nearly indistinct on the right side. The base of the transverse process is remarkably wide

anteroposteriorly, and the transverse process was confined to the posterior edge of the neural arch. The neural spine is tall and has a concave dorsal border. It is highest above the postzygapophyses. The anterior and posterior grooves for interspinous ligaments are narrow. The bases of the prezygapophyses are stout and bear high prezygapophyseal ridges diverging from the anterior end of the neural spine and delimiting a deep and narrow anterior interspinous recess laterally. The postzygapophyses are not preserved in ZIN PH 1001/16. There is a prominent hyposphene, which does not extend posteriorly beyond the centrum. A relatively deep and narrow posterior interspinous recess is present between the hyposphene, neural spine, and medial walls of the postzygapophyses.

On more posterior caudals (e.g. ZIN PH 2214/16, ACH=51.8; ACW=43.1; CL=77.4; NSL=72.4; PNW=35.7; PCH=52.3; PCW=49.7), the centrum is distinctly longer than high, up to 1.8 times centrum height in some specimens (ZIN PH 2220/16). The centrum is more constricted at mid-length than on the anterior caudal. A shallow groove occupies most of the ventral surface of the centrum (ZIN PH 2216/16, 2217/16 and 2221/16), is confined to the posterior end (ZIN PH 2220/16 and 2215/16, Fig. 17G), or absent altogether (ZIN PH 2218/16). The chevron facets are usually well developed. The neural arch is very similar to that of the anterior caudal, with an anteroposteriorly wide transverse process connected by a strong lateral ridge to the base of the prezygapophysis. ZIN PH2216/16 (Fig. 17A-E) has a distinct oval prezygapophyseal facet, whereas the complete prezygapophysis on ZIN PH 2215/16 (Fig. 17F-J) lacks a distinct facet. In contrast to the anterior caudal, a hyposphene is lacking. The postzygapophyseal facets are well-defined, oval, and face ventrolaterally. The posterior interspinous recess is as deep as or shallower than on the anterior caudal. The neural spine is distinctly depressed in the middle, separated into the anterior and posterior alae (completely preserved on ZIN PH 2214/16 and 2217/16).

3.3. Appendicular skeleton

3.3.1. *Pectoral girdle*

There are two fragments of fused scapulocoracoids (Fig. 18) and several fragments of coracoids, including one from the Aitym Formation; they are identical in preserved structure. The coracoid portion of the glenoid facet is about half as large as the scapular contribution. A prominent biceps tubercle is situated close to glenoid. Anterodorsal to this tubercle, a ridge divides the lateral surface into two planes. A large coracoid foramen is located dorsal to this ridge, anterior to and at some distance from the glenoid. On the medial side, the coracoid canal opens near the contact between the coracoid and scapula, posterodorsal to the lateral opening. The coracoid canal is rather short; in ZIN PH 1240/16, its smaller medial opening is visible through the larger lateral opening (Fig. 18C). On the juvenile specimen ZIN PH 897/16, the coracoid canal is fully exposed due to breakage. The anteroventral coracoid process is deflected medially at an angle of 35° to 40° relative to the axis of the glenoid. The medial surface of the coracoid is deeply concave. Dorsal to the glenoid, the scapulocoracoid becomes very thin (Fig. 18A).

3.3.2. *Forelimb*

The humerus is known only from proximal and distal ends (Fig. 19). Both ends are considerably expanded transversely and flattened dorsoventrally. The head of the humerus extends across the proximal end and forms a distinct rounded articular surface that overhangs the dorsal surface of the bone. The prominent medial (internal) tuberosity has a slightly dorsally deflected apex. On the dorsal surface, a weak ridge extends distally from this tuberosity. The medial tuberosity is proximodistally wider in ZIN PH 33/16 (from the Khodzhakul Formation; Fig. 19A-C) and ZIN PH 2274/16 (from the Bissekty Formation; Fig. 19D-F) than in ZIN PH 31/16 (from the Bissekty Formation; Fig. 19G-I). The deltopectoral crest is missing on all

available specimens. The shaft is most completely preserved on the distal fragment ZIN PH 1290/16, where DW (incomplete) is more than 2.7 times greater than the minimum transverse width of the shaft. The largest distal end of a humerus from the Bissekty Formation (ZIN PH 34/16) has a greatest width of 115. On the ventral (anterior) surface of the distal end of the humerus, the hemispherical radial (medial) and ulnar (lateral) condyles are separated by a distinct but narrow flexor groove. The ulnar condyle is larger than the radial one. The well-developed entepicondyle is larger than the ectepicondyle. The ventral aspect of the ectepicondyle bears a tuberosity. On ZIN PH 34/16 and 35/16, this tuberosity is flanked dorsolaterally by a narrow groove, possibly for carpal and/or digital extensor muscles. In these specimens, a prominent ridge-like tubercle (ZIN PH 35/16) or ridge (ZIN PH 34/16) is present along the medial edge of the ventral side proximal to the entepicondyle (Fig. 19J, K) and possibly was a site of attachment for *M. brachialis*.

Metacarpal I is known from four complete specimens and one distal fragment (ZIN PH 27/16 is the largest; L=64.5; PW=27.5; DW=27.5; Fig. 20). The proximal articular end is more or less triradiate. The large, flat or slightly excavated triangular surface on the lateral aspect of the bone was in contact with metacarpal II. The dorsomedial side is slightly convex and the ventral side is concave. The long axis of the distal ginglymus of metacarpal I extends obliquely medially. The medial condyle is larger than the lateral one, which is offset distally from the former. The distal end of the metacarpal lacks distinct pits for the collateral ligaments.

The long, nearly symmetrical metacarpal II is known only from several distal ends (Fig. 21A-E). Its distal ginglymus is only slightly asymmetrical, with the lateral condyle extending slightly farther distally and somewhat deflected laterally. The ginglymus is about 1.3 times wider ventrally than dorsally. The lateral and medial condyles are narrow and separated by a wide intercondylar groove. There are no pits for the collateral ligaments, and the distal and medial surfaces of the ginglymus are flat. Some specimens of metacarpal II articulate perfectly with

manual phalanges II-1, which have slightly asymmetrical proximal articular ends. DW=16.5-28.5; there are also somewhat larger specimens with incomplete condyles.

Metacarpal III is represented by five fragments with distal articular ends (Fig. 21F-J). It is a rather long and gracile bone. The shaft is triangular in transverse section proximally and becomes more circular towards the distal end. The lateral surface is flat and the medial and ventral surfaces are slightly convex. The distal articular end is mediolaterally narrow and parallelogram-shaped, with oblique dorsal and ventral margins. Its lateral condyle is slightly smaller than the medial one. The medial condyle projects ventrally beyond the level of the lateral condyle and is deflected medially. The intercondylar groove is shallow. The lateral pit for the collateral ligament pit is deep whereas the medial one is shallow. DW=10.1-21.0.

Manual phalanx I-1 is known from four complete specimens and one fragment (Fig. 21K-P). The largest specimen is ZIN PH 1177/16 (L=79.4; PW=29.3; DW=23.0). The proximal end is more expanded dorsoventrally than the distal end. Its proximal articular surface is deeply concave and divided by a vertical, slightly oblique ridge into two almost symmetrical facets (of which the lateral is somewhat larger). The distal articulation is ginglymoid with well-developed, more or less symmetrical condyles separated by a shallow intercondylar groove. There are shallow depressions on both sides in place of the pits for the collateral ligaments; only ZIN PH 30/16 has distinct pits. The phalangeal shaft has a rather flat ventral surface, with a shallow depression immediately proximal to the ginglymus.

Eight specimens represent manual phalanges II-1 or II-2 (Fig. 21Q-V). The largest are ZIN PH 51/16 and 53/16 (L=61.1, 69.5; PW=30.0, 24.6; DW=28.5, 26.5, respectively). Some phalanges are more elongated whereas others are short and have wider proximal and distal ends. All phalanges have deeply concave proximal articular facets separated by a slightly oblique ridge into two asymmetrical parts and distinct proximoventral heels. Because of this heel the ventral surface is deeply concave proximodistally and flat mediolaterally. On the distal end, the well-

developed condyles of the ginglymus (the medial one being somewhat larger) are separated by a wide intercondylar groove. There is no pit for the collateral ligament on either side.

Manual phalanx III-1 is short and has a prominent proximoventral heel and asymmetrical proximal articular surface (ZIN PH 1244/16; L=27.4, PW=18.8; DW=19.5; Fig. 21W-Z). The lateral half of the proximal articular surface is smaller and projects more posteriorly than the medial half, matching the shape of the distal articular surface of metacarpal III. The distal articulation is ginglymoid, with the lateral condyle projecting more distally than the medial one. There is no pit for the collateral ligament on either side.

Some unidentified manual preungual phalanges possibly belong to manual digit III (e.g., ZIN PH 118/16). They differ from the preungual phalanges of digit II in being more gracile and elongate and lacking a well-developed proximoventral heel. However, these phalanges are not as long as phalanx I-1. The distal ginglymus is almost symmetrical, with well-developed condyles separated by a wide intercondylar groove and with only shallow depressions in the place of the pits for the collateral ligaments. L=43.7-59.6, PW=15.5-20.4, DW=14.8-18.6.

Manual and pedal ungual phalanges of therizinosauroids from Dzharakuduk cannot always be confidently distinguished from each other (Fig. 22). Some unguals with less developed and more distally placed ventral flexor tubercles possibly belong to the pes (e.g., ZIN PH 356/16 and 1189/16, Fig. 22D-G, J, K). Other larger unguals with larger and proximally projecting ventral flexor tubercle clearly are manual elements (e.g., CCMGE 454/12457 and ZIN PH 19/16, Fig. 22A-C). However, there are specimens with flexor tubercles that are intermediate in size and position between these two extremes, making clear distinction between manual and pedal unguals impossible. All ungual phalanges are greatly flattened mediolaterally and strongly curved. Each has a robust flexor tubercle ventral to the proximal articular facet. Lateral grooves for the claw sheath extend close to the ventral edge distally from just below the proximal articular facet of the ungual to its distal tip (ZIN PH 45/16). Distally, the grooves are slightly asymmetrically arranged. The proximal articular facet lacks a posterodorsal projection on all

available well-preserved unguals. It is deeply concave in side view, and its surface is divided by a median ridge. The facet is clearly delimited by bony rims, especially dorsally and more ventrally. The largest ungual in our sample is ZIN PH 19/16 (Fig. 22A, B), with a greatest proximal depth of 62 mm and height of the proximal articular facet of 32 mm.

3.3.3. *Hind limb*

The femur ZIN PH 775/16 (PW=108, HD~44, MW=41; Fig. 23) represents a not yet skeletally mature individual. Its proximal end is shaped like a figure eight in proximal view, with the large greater trochanter and medially directed head. The articular surface of the head bears a small posteromedial tubercle, which is bounded by a notch anteriorly and posteriorly. Lateral and somewhat distal to the posterior notch, the posterior surface of the bone bears a presumably vascular groove. The proximal surface of the greater trochanter is damaged, but apparently it was placed somewhat ventrally to the proximal surface of the femoral head. The greater trochanter is separated from the femoral head by a constriction in proximal view. The posterior half of the lateral surface of the greater trochanter is rugose. The lesser trochanter is spike-like and much smaller than the greater trochanter. It terminates dorsally well below the proximal surface of the latter. The fourth trochanter forms a prominent ridge along the posteromedial edge of the bone. Just medial to it a slight scar marks the insertion of *M. caudifemoralis longus*.

Two isolated femoral heads, ZIN PH 776/16 (HD~67) and 2068/16, represent larger individuals. They have prominent foramina on the posterior side adjacent to the proximal articular surface. A juvenile femur (ZIN PH 777/16; PW=42, HD=17) resembles the larger femur with similarly developed lesser and fourth trochanters.

The distal end of the femur is known from two fragments. The lateral condyle does not extend laterally beyond the lateral margin of the shaft. It is directed almost ventrally whereas the medial condyle is directed medioventrally. The distal end is U-shaped in distal view, with a deep

intercondylar fossa separating the lateral and medial condyles posteriorly. The anterior groove separating the condyles is very shallow. The lateral condyle is distinctly narrower mediolaterally than the medial one, with a pointed posterior edge (tibiofibular crest). In both specimens, especially in ZIN PH 1396/16, the posterior intercondylar fossa is rather deep and bordered proximally by a prominent step-like eminence.

The tibia is known from two proximal fragments, one from a juvenile and the other possibly from an adult (ZIN PH 600/16, Fig. 24A-E), and several distal pieces (Fig. 24F-J). The shape of the triangular proximal end is distinctive among theropods but similar to at least some other therizinosauroids in being unusually wide mediolaterally, with the cnemial crest projecting slightly anteriorly and dorsally. The mediolateral width of the proximal end of ZIN 600/16 (44.3) is 68% of its anteroposterior length (65.6). The cnemial crest is oblique rather than vertical, with its tip slightly deflected laterally. The lateral condyle is large, triangular, and directed posteriorly. Its posteriormost point is continued distally as a short and blunt vertical ridge. The posterior condyle is less than half the size of the lateral one and situated anterior to the latter. The anterolateral margin of the proximal surface, which contacts the fibula, is concave, whereas it is convex in other known theropod taxa. The anteromedial and posterior surfaces of the tibia are concave proximally but become convex distally. The shaft is hollow with rather thin bony walls. There is no fibular crest on this fragment.

The largest distal tibial fragment (ZIN PH 1428/16) has the mediolateral width of over 140. Its distal end is greatly expanded mediolaterally, with the lateral malleolus about twice as wide as the medial malleolus and projecting further distally. The anterior surface of the distal end is slightly concave, sometimes with a distinct articular facet for the astragalus. The posterior surface has a prominent vertical ridge closer to the medial edge. It is flat medial and lateral to this ridge except for a slight concavity on the posterior surface of the lateral malleolus whose lateral edge is slightly turned posteriorly.

Metatarsal I is represented by several complete and fragmentary specimens. The largest is ZIN PH 59/16 (L=84.3, DW=33.7; Fig. 25A-F). Its proximal end bears a deep, concave lateral depression for contact with the presumably convex medial surface of the proximal end of metatarsal II. The narrow, crescentic proximomedial articular surface of metatarsal I was in contact with the tarsus. The shaft of the bone has a flattened ventral surface. The asymmetrical distal articular end of metatarsal I forms a bulbous dorsal surface. It is oblique in dorsoventral view with the lateral condyle projecting far more distally. This suggests that the first pedal digit was medially offset from the other digits. Ventrally, its condyles are separated by a deep pit just proximal to the articular surface. The distal end of the metatarsal bears shallow lateral pits for the collateral ligaments; the lateral pit is deeper than the medial one.

Metatarsal II is known from three distal fragments, the most complete of which is ZIN PH 1348/16 (Fig. 25G-K) with DW=55.3. The distal ginglymus is asymmetrical, with a much larger lateral condyle and a narrow medial condyle. Ventrally, both condyles project proximally as narrow prongs separated by wide and deep depression. The medial prong is much longer and more prominent in ZIN PH 1195/16 than in ZIN PH 492/16 and 1348/16. There is a shallow depression in place of the pit for the collateral ligament on either side.

Phalanx 1 of pedal digit I is represented by several specimens (Fig. 25L-Q). ZIN PH 1432/16 is the largest (L=72.5; PW=58.1; DW=41.0). The proximal articular surface forms a prominent ventrolateral “heel,” which is evident in dorsal view and projects considerably laterally. It is oblique in dorsoventral view, corresponding to the oblique distal articulation of the first metatarsal. As on the other preungual pedal phalanges, the ventral and dorsal margins are concave in side view. The distal end of the phalanx has well-developed condyles separated by wide intercondylar groove. The lateral condyle is somewhat larger and projects farther distally than the medial one. The pits for the collateral ligaments are variably developed, ranging from shallow depressions (ZIN PH 64/16) to distinct pits (ZIN PH 65/16).

Several phalanges have non-ginglymoid proximal articular ends, similar to the phalanx I-1 described above, but the ventral “heel” protrudes slightly laterally or not at all. They probably represent proximal phalanges of pedal digits II-IV. Some are rather elongate whereas others are short. Most of these phalanges have a marked depression at the middle of the dorsal surface just proximal to the distal condyle. The pits for the collateral ligaments are weakly developed or absent.

Several rather symmetrical preungual phalanges represent elements of pedal digits II-IV (Fig. 25R-W). The proximal articular surface is deeply ginglymoid, with almost symmetrical proximal articular facets, a distinct dorsal lip, and an even more prominent ventral heel. The ventral and dorsal sides are concave in side view. The distal articular end has well developed and slightly asymmetrical condyles. On some specimens the distal condyles are directed distally in medial/lateral view. The pit for the collateral ligament is usually well developed. Some shorter phalanges lacking collateral ligament pits possibly represent pedal phalanges IV-2 or IV-3.

4. Phylogenetic position of Bissekty therizinosauroids

Zanno (2010b) provided the most recent comprehensive phylogenetic analysis of Therizinosauria, to which Pu et al. (2013) added *Jianchangosaurus yixianensis*. It would appear that there are two therizinosauroid taxa in the Bissekty Formation of Uzbekistan (see discussion below). However, the therizinosauroid material from this formation does not vary in terms of the characters listed by Zanno (2010b). Thus we treat the Bissekty therizinosauroids as a single terminal taxon in order to get a preliminary assessment of their phylogenetic relationships. The material can be scored for 108 out of 348 characters (31.0%) in the dataset by Zanno (2010b; see Appendix 1 for the character-taxon matrix). Some of the characters and original scorings in this dataset require comments. The order of characters follows that in the supplemental information to Zanno (2010b).

Character 41: *Falcarius utahensis* was coded as having frontals narrow anteriorly as a wedge between the nasals (41(0)) and *Erlikosaurus andrewsi* as having frontals end abruptly anteriorly, with the suture with the nasal transversely oriented (41(1)). However, the condition of this character is not much different in these taxa and the nasal suture in *Erlikosaurus andrewsi* is oblique rather than transverse (Lautenschlager et al., 2014, fig. 7A). This suture also extends obliquely on both frontal morphotypes from the Bissekty Formation (Figs. 3A, 4D). All these taxa are coded here for the plesiomorphic state for this character.

Character 97: The coding of *Jianchangosaurus yixianensis* as having a carotid process on the cervical centra (97(1)) is likely in error. This character is not described in the text nor visible on the published figures (Pu et al., 2013).

Character 102: *Jianchangosaurus yixianensis* is coded as having anterior dorsal vertebrae without prominent hypapophyses (102(0)). However, the anterior dorsal centra are completely obscured by matrix or ribs (Pu et al., 2013, figs. 5C, 6A). Thus, scoring of the character-state for this taxon is changed to unknown.

Character 135: Some therizinosaurian taxa are coded as having the scapula and coracoid as distinct bones (135(0)), others as having fused scapulocoracoid (135(1)). Such ontogenetically correlated characters should be avoided in a phylogenetic analysis. *Nothronychus graffami* shows bilateral variation of this character in a single individual (Hedrick et al., 2015). This taxon is coded here for the apomorphic state. All other taxa coded originally by plesiomorphic state are coded here as unknown.

Character 138: The coding of *Suzhousaurus megatheroides* and *Therizinosaurus cheloniformis* is changed to 138(0), articular surface of glenoid fossa restricted from external aspect of scapula (Barsbold, 1976, figs. 1, 2; Li et al., 2008, fig. 3(1)).

Character 188: The coding of *Segnosaurus galbinensis* and *Nothronychus graffami* is changed to 188(0), accessory trochanteric crest distal to anterior trochanter absent (Zanno, 2010b, fig. 4F; Hedrick et al., 2015, fig. 30A).

Character 225: In the original matrix, *Erlikosaurus andrewsi* and *Nothronychus mckinleyi* are coded for the state 2, which is not specified in the character description. We assume that this state means absence or reduction of basal tubera, as character-state 254(2).

Character 252: Two therizinosaurian taxa have been coded for this character, *Falcarius utahensis* (252(1)) and *Erlikosaurus andrewsi* (252(0)). The subcondylar recess is absent (252(0)) in the Bissekty therizinosauroid (Fig. 5d) and in *Nothronychus mckinleyi* (Smith et al., 2011, fig. 5A).

Character 269: The coding of *Jianchangosaurus yixianensis* is changed to 269(1), ventral surface of cervical centra with prominent ventral depression. The definition of this character-state is that the ventral surface of the cervical centra is deeply concave rather than bears an actual depression, and all therizinosauroids are similar in this respect.

Character 270: All therizinosaurian taxa except *Jianchangosaurus yixianensis* are coded as having prominent crests along posterolateral margins of ventral cervical centra (270(1)). This region in *Jianchangosaurus yixianensis* does not differ from those in other therizinosaurian taxa and the taxon should be coded for the same state.

Character 292: The coding of *Suzhousaurus megatheroides* is changed to 292(0), entepicondyle on posterolateral margin of humeral shaft (Zanno, 2006, fig. 2B) absent (Li et al., 2007, fig. 3(4)).

Character 296: The coding of *Suzhousaurus megatheroides* is changed to unknown because metacarpal III is unknown for this taxon (Li et al., 2007; Li et al., 2008).

Character 323. In the original matrix only two of 77 taxa were scored for this character, *Velociraptor mongoliensis* (323(0)) and *Jianchangosaurus yixianensis* (323(1)). The femoral head is demarcated from the neck by a raised ventral rim (323(0)) in the Bissekty therizinosauroids (Fig. 23C, E), *Beipiaosaurus inexpectus* (Zanno, 2010b, fig. 2F), *Falcarius utahensis* (Zanno, 2010a, fig. 15B, D), and *Suzhousaurus megatheroides* (Li et al., 2008, fig. 8a, b). The femoral head confluent with the neck without evident transition (323(1)) in *Erliansaurus*

bellamanus (Xu et al., 2002, fig. 2C), *Neimongosaurus yangi* (Zhang et al., 2001, pl. 3, fig. L), *Nothronychus graffami* (Hedrick et al., 2015, fig. 30A, C), and *Segnosaurus galbinensis* (Zanno, 2010b, fig. 4F).

Character 324: In the original dataset *Falcarius utahensis* was coded as having the ligament groove on the posterior surface of the femoral head moderate to deeply formed, bounded medially by a well developed caudal lip (324(0)). *Neimongosaurus yangi*, *Nothronychus graffami*, and *Segnosaurus galbinensis* are coded as having this groove absent to poorly developed (324(1)). Other therizinosaurian taxa have unknown state for this character. The groove is present in the Bissekty therizinosauroids (Fig. 23E), *Jianchangosaurus yixianensis* (Pu et al., 2013, fig. 1), *Neimongosaurus yangi* (Zhang et al., 2001), and *Suzhousaurus megatheroides* (Li et al., 2008, fig. 8b).

Character 327: The coding of *Alxasaurus elesitaiensis* and *Segnosaurus galbinensis* is changed to 327(0), anteroposterior length of proximal tibia exceeds transverse width (Perle, 1979, fig. 6; Russell and Dong, 1994, fig. 12B).

As in the previous analyses of this dataset (Zanno, 2010b; Pu et al., 2013), 20 characters were made additive (27, 37, 40, 68, 76, 78, 97, 106, 113, 157, 163, 168, 253, 303, 308, 309, 310, 334, 342, and 345), and two characters were deactivated (165 and 215; Pu et al. (2013) excluded character 125 instead of 215 apparently by mistake). We also excluded from the dataset the poorly known taxon “*Nanshiungosaurus*” *bohlini* because it has no unique character combinations (Zanno, 2010b). The parsimony analysis performed is similar to that in Zanno (2010b): using the heuristic search algorithm of TNT (Tree analysis using New Technology), version 1.1 (Goloboff et al., 2008), with 1,000 replicates of Wagner trees, random addition sequences, and TBR (tree bisection-reconnection) swapping methods holding 10 trees per replicate. All characters were equally weighted. The default memory was increased to hold 10,000 trees (a maximum available option). The analysis produced 1,520 most parsimonious trees with the length of 1,279 steps, consistency index of 0.34, and retention index of 0.69.

Zanno (2010b) did not specify what memory size was used in her analysis. If the default setting (100 trees) was used, this might explain the smaller number of most parsimonious trees recovered in that analysis. The fragment of the strict consensus tree relevant to Therizinosauria is shown in Fig. 26. The phylogenetic relationships of derived therizinosauroids are not resolved on this cladogram and a monophyletic Therizinosauridae, as defined by Zanno (2010b), is not supported.

The Bissekty therizinosauroids have the following unambiguous synapomorphies of Therizinosauria:

- 13(1) Basipterygoid processes abbreviated or absent;
- 90(1) Dentary with interdental plates medially between teeth;
- 113(2) Pneumatic openings present on all sacrals;
- 118(1) Neural spines of caudal vertebrae separated into anterior and posterior alae throughout much of caudal sequence;
- 269(1) Ventral surface of cervical centra with prominent ventral depression;
- 270(1) Posterolateral margins of ventral cervical centra with prominent crests;
- 295(1) Ventrolateral aspect of proximal surface of metacarpal I with rectangular buttress which underlies ventromedial surface of metacarpal II;
- 326(1) Lateral fossa of proximal tibia (incisura tibialis) wide and shallow, nearly absent;
- 335(0) Shafts of metatarsals not appressed.

Therizinosauroidae is defined as the least inclusive clade containing *Beipiaosaurus inexpectus* and *Therizinosaurus cheloniformis* (Zanno, 2010b). The Bissekty therizinosauroids have the following unambiguous synapomorphies of Therizinosauroidae:

- 86(0) Serration denticles on dentary and maxillary teeth large;
- 87(1) Distal and often mesial edges of teeth with large, hooked denticles that point toward the tip of the crown;

266(1) Dentary and maxillary teeth (excluding anteriormost dentary teeth) nearly symmetrical in labial view;

339(1) Greater trochanter and femoral head bridging region depressed.

The Bissekty therizinosauroids are more derived than *Beipiaosaurus inexpectus* in having a dorsally inclined femoral head, extending at an obtuse angle from the long axis of the femur (320(1)). They are more derived than *Alxasaurus elesitaiensis* in having extensive axial pneumatization, extending through more than half of the dorsal vertebrae (106(2)), anterior end of dentary edentulous (220(3)), ligament pits on the manual phalanges weakly developed or absent (302(1)), and medial aspect of distal portion of the humerus expanded and subtriangular in anterior view and entepicondyle located well medial to ulnar condyle (343(1)).

The Bissekty therizinosauroids are less derived than a clade of Late Cretaceous therizinosauroids from Asia and North America in having a basisphenoid recess between the basisphenoid and basioccipital (9(0)), the absence of pneumatic features on the anterior caudal vertebrae (279(0)), metacarpal III distally not ginglymoid in dorsal view (296(0)), and femoral head demarcated from the neck by a raised ventral rim (323(0)). The last plesiomorphic state is also present in *Suzhousaurus megatheroides*.

Zanno (2010b) defined Therizinosauridae as the least inclusive clade containing *Nothronychus graffami*, *Segnosaurus galbinensis*, *Erlikosaurus andrewsi* and *Therizinosaurus cheloniformis*. She listed Enigmosauridae and Nanshiungosauridae among the subjective junior synonyms of Therizinosauridae, although the type genera of those families were not included in Therizinosauridae. She considered *Suzhousaurus* and *Enigmosaurus* outside Therizinosauridae “based on the recovery of these genera as sister-taxa to the clade in the agreement subtree of all most parsimonious trees, or when the labile taxon *Therizinosaurus* is pruned from the analysis” (Zanno, 2010b, p. 520). However, the nominal genus of Therizinosauridae should not be pruned from the analysis because it must be an internal specifier for that clade. Detailed discussion of this and related issues is beyond the scope of this study (Fig. 26).

5. Discussion

Therizinosauroids were apparently abundant elements of the Cenomanian and Turonian dinosaurian communities on the western edge of the Asian landmass. The much smaller sample of skeletal remains from the Cenomanian Khodzhakul Formation does not provide evidence for presence of more than one therizinosauroid taxon. However, at least two taxa are present in the Turonian Bissekty Formation based on distinct morphotypes of frontals and humeri and on patterns of closure of the neurocentral sutures visible on the dorsal vertebrae at different sizes. Multiple sympatric therizinosauroid taxa have also been reported from the roughly coeval Bainshire and Iren Dabasu formations of the Gobi Desert (Zanno, 2010b). A humerus from the Khodzhakul Formation (ZIN PH 33/16; Fig. 19A-C), with a proximodistally wide, rectangular medial tuberosity, is similar to one of the two morphotypes from the Bissekty Formation (Fig. 19D-F) and may belong to the same or a closely related taxon. A similarly developed medial tuberosity is present in *Neimongosaurus yangi* (Zhang et al., 2001, pl. 2, figs. I, J). On the second humerus morphotype from the Bissekty Formation the medial tuberosity is proximodistally short and triangular in the anterior/posterior view (Fig. 19GH, I).

Frontals of the first morphotype, best exemplified by ZIN PH 18/16 (Fig. 3), resemble the corresponding element in *Erlikosaurus andrewsi* (Clark et al., 1994; Lautenschlager et al., 2014) in the elongate triangular shape, upturned orbital margin, highly rugose lateral edge immediately anterior to the postorbital, but differ in the less widely separated cristae cranii and smaller ventral impressions for the olfactory lobes and cerebral hemispheres.

Frontals of the second morphotype (Fig. 4) are more similar to the frontal of *Erlikosaurus andrewsi* in overall proportions, especially the sigmoidal orbital margin with a better developed postorbital process and in the depression of the supratemporal fossa posterodorsally.

The partial braincase ZIN PH 1805/16 is almost identical to the braincases of *Erlikosaurus andrewsi* (Clark et al., 1994; Lautenschlager et al., 2014) and *Nothronychus mckinleyi* (Kirkland et al., 2005a; Smith et al., 2011) in so far as comparisons are possible. It also resembles the braincase of the oviraptorosaur *Epichirostenotes curriei* (Sues, 1997) in certain features. Similarities to these taxa include the distinct depressions lateral to the foramen magnum, the crescentic occipital condyle, the absence of a ventral subcondylar recess (present in *Falcarius utahensis*; Smith et al., 2011), the presence of a prominent horizontal ridge on the posterior side of the basioccipital ventral to the occipital condyle that incorporates reduced basal tubera, the vertical ventral surface of the basisphenoid, and the prominent lateral depression in the otic region. ZIN PH 1805/16 differs from both *Erlikosaurus andrewsi* and *Epichirostenotes curriei* and resembles *Nothronychus mckinleyi* in having a foramen magnum that is relatively higher and larger than the occipital condyle. The most obvious structural difference between ZIN PH 1805/16 and *Erlikosaurus andrewsi* is the more dorsal position of the trigeminal foramen on the medial wall of the braincase in the former. ZIN PH 1805/16 also differs from *Erlikosaurus andrewsi* and resembles *Nothronychus mckinleyi* in the absence of a distinct nuchal crest.

Nesov (1995, p. 36) mentioned a highly pneumatized basisphenoid fragment (CCGME 719/12457) that is possibly referable to a therizinosauroid. This specimen is, however, too fragmentary for more precise taxonomic identification beyond Theropoda.

The anterior caudals are similar to those of *Nothronychus graffami*, *Erliansaurus bellamanus*, and other therizinosauroids (Kirkland and Wolf, 2001; Xu et al., 2002; Hedrick et al., 2015) in having a well-developed hyposphene, a bony web connecting the transverse process with the zygapophyses, and a posterior ventral groove on the centrum, but differ in the absence of pneumatic foramina. The apparent shift of the transitional point toward the most posterior caudals based on the available material suggests a rather short tail for the Bissekty therizinosauroids, much as in other therizinosauroid taxa. The caudal vertebrae generally resemble those of *Neimongosaurus yangi* (Zhang et al., 2001, pl. 2, fig. A). Some elongate

caudal centra from Dzharakuduk resemble the long posterior caudals of *Falcarius utahensis* (Zanno, 2010a: fig. 10) but appear to be proportionately shorter.

The scapulocoracoid is extremely thin dorsally, as in *Therizinosaurus cheloniformis* (Barsbold, 1976).

The humeri of the Bissekty therizinosauroids are characteristic for this group in having strongly expanded proximal and distal ends, a hypertrophied medial tuberosity on the proximal end, an entepicondyle on the distal end, small and ventrally displaced radial and ulnar condyles separated only by a narrow flexor groove, and a ventral tuberosity on the ectepicondyle (Zhang et al., 2001; Xu et al., 2002; Hedrick et al., 2015). They are more derived than the humeri of *Beipiaosaurus inexpectus* and *Erliansaurus bellamanus*, in which the flexor groove between the ulnar and radial condyles is broader (Xu et al., 2002). In the Bissekty therizinosauroids, the ectepicondyle is small compared to the greatly expanded entepicondyle, as in *Alxasaurus elesitaiensis* and *Segnosaurus galbinensis*. Possibly this represents the plesiomorphic condition because the ectepicondyle is more expanded in other therizinosauroids.

Unlike in *Erliansaurus bellamanus* (Xu et al., 2002, fig. 1F), the distal condyle of the metacarpal III in the Bissekty therizinosauroid material is not expanded mediolaterally relative to the shaft.

The tibia is similar to that in *Neimongosaurus yangi* (Zhang et al., 2001, pl. 3, fig. J) in the unusually broad, triangular proximal end with a reduced cnemial crest but differs in the position and orientation of the proximal condyles. In specimen ZIN PH 600/16, the lateral condyle is situated posterior to the posterior condyle and directed posteriorly, whereas in *Neimongosaurus* the lateral condyle is anterior to the posterior condyle and directed anterolaterally. In *Alxasaurus elesitaiensis* and *Erliansaurus bellamanus*, the cnemial crest is better developed (Russell and Dong, 1994, fig. 12B; Xu et al., 2002, fig. 2E). In ZIN PH 600/16, the fibular crest apparently was placed far ventral to the cnemial crest because it is not present on the preserved proximal fragment.

6. Conclusions

Therizinosauroid theropods are common and represented by two distinct morphotypes in the Upper Cretaceous (Turonian) Bissekty Formation of the central Kyzylkum Desert in Uzbekistan. However, the lack of associated material currently prevents more detailed taxonomic assessment. Based on the known skeletal remains, the Bissekty therizinosauroids are more derived than *Alxasaurus elesitaiensis* in the extensive pneumatization of the postcranial axial skeleton, the absence of teeth in the anterior portion of the dentary, weak development or absence of pits for the collateral ligaments on the manual phalanges, and the subtriangular medial aspect of the distal end of the humerus, with the entepicondyle positioned well medial to the ulnar condyle. The Bissekty taxa are less derived than Therizinosauridae in the presence of a basisphenoid recess, the absence of pneumatic openings on the anterior caudal vertebrae, the distal end of metacarpal III not being ginglymoid in dorsal view, and the separation of the femoral head from the neck of that bone by a raised ventral rim.

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Figure captions

Fig. 1. Location of the Dzharakuduk locality complex (indicated by star) on a map of Uzbekistan and neighboring regions (left) and on a more detailed map of the region around Mynbulak (right). Areas of vertical lines indicate salt flats (sor). Left illustration modified from a United Nations map. [intended for page width]

Fig. 2. ZIN PH 1243/16 (CBI-14, 1984), fragment of right maxilla of Therizinosauroida indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, lateral view; C, ventral view; D, anterior view; E, medial view. Abbreviations: af, ventral floor of antorbital fenestra; apr, ascending process (broken base); cm, choanal margin; lf, lateral neurovascular foramen; nc, neurovascular canal. Scale bar equals 1 cm. [intended for column width]

Fig. 3. ZIN PH 18/16 (CDZH-14a), left frontal of Therizinosauroides indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, medial view; C, ventral view. Abbreviations: ch, impression of cerebral hemisphere; f, foramen; N, facet for nasal; ob, impression for olfactory bulb; Prf, facet for prefrontal. Scale bar equals 1 cm. [intended for column width]

Fig. 4. CCMGE 462/12457 (CBI-14, 1980), left frontal of Therizinosauroides indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, medial view; B, ventral view; C, lateral view; D, dorsal view; E, posterior view. Abbreviations: ch, impression for cerebral hemisphere; Prf, facet for prefrontal; pop, postorbital process; stf, supratemporal fossa. Scale bar equals 1 cm. [intended for page width]

Fig. 5. ZIN PH 1805/16 (CBI), incomplete braincase of Therizinosauroides indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, ventral view; C, anterior view; D, posterior view; E, lateral view. Abbreviations: br, basisphenoid recess; bt, basal tuber; dtr, opening of dorsal (posterior) tympanic recess; ica, passage for internal carotid artery; oc, occipital condyle; vcd, vena capitis dorsalis; V₁₋₃, branches of trigeminal nerve. Scale bar equals 1 cm. [intended for page width]

Fig. 6. Incomplete symphyseal portions of left dentaries of Therizinosauroides indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-C, ZIN PH 1153/16 (CDZH-17a, 2003) in (A) dorsal, (B) medial, and (C) labial views. D-F, ZIN PH 16/16 (CBI-14, 1987) in (D) dorsal, (E) lingual, and (F) ventral views. Abbreviations: f, foramen; ds, dentary shelf; idp, interdental plate; Mg, Meckelian groove; s, symphysis. Scale bars each equal 1 cm. [intended for page width]

Fig. 7. ZIN PH 1154/16 (CBI-5a, 1987), fragment of right dentary of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, medial view; C, lateral view; D, ventral view. Abbreviation: Mg, Meckelian groove. Scale bar equals 1 cm. [intended for column width]

Fig. 8. Teeth of *Therizinosauroides* indet. from the Khodzhakul Formation (Cenomanian) at Sheikhdzheili (A-C) and Bissekty Formation (Turonian) at Dzharakuduk (D-L), Uzbekistan. A-C, ZIN PH 1157/16 (SSHD-8, 1981), in (A, C) side and (B) distal? views. D-F, ZIN PH 1161/16 (CBI-14), in (D, F) side and (E) distal? views; G-I, ZIN PH 270/16 (CBI-14), in (G, I) side and (H) distal? views. J-L, ZIN PH 266/16 (CBI-14), in (J) mesial or distal, (K) lingual, and (L) labial views. Scale bars each equal 1 mm. [intended for page width]

Fig. 9. ZIN PH 136/16 (CBI-41), anterior cervical centrum of *Therizinosauroides* 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: p, pneumatic opening; pa, parapophysis. Scale bar equals 1 cm. [intended for column width]

Fig. 10. ZIN PH 2298/16 (CBI-14, 1980), anterior cervical of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, ventral view; C, posterior view; D, lateral view; E, anterior view. Abbreviations: di, diapophysis; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis. Scale bar equals 5 cm. [intended for page width]

Fig. 11. Posterior cervical centra of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 55/16 (CBI-5a, 1980) in (A) ventral, (B) dorsal, (C) anterior, (D) lateral, and (E) posterior views. F-J, ZIN PH 1163/16 (CBI) in (F)

ventral, (G) dorsal, (H) posterior, (I) lateral, and (J) anterior views. Abbreviations: p, pneumatic opening; pa, parapophysis. Scale bars each equal 1 cm. [intended for page width]

Fig. 12. Cervical ribs of *Therizinosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-D, ZIN PH 1257/16 (CDZH-17a), right anterior rib in (A) dorsal, (B) medial, (C) ventral, and (D) lateral views. E-H, ZIN PH 1256/16 (CBI-14, 1984), right anterior rib in (E) dorsal, (F) medial, (G) ventral, and (H) lateral views. I-L, ZIN PH 1258/16 (CBI-5a, 1989), left posterior rib in (I) dorsal, (J) lateral, (K) ventral, and (L) medial views. Abbreviation: ca, capitulum. Scale bars each equal 1 cm. [intended for page width]

Fig. 13. ZIN PH 93/16 (CBI-27, 1980), anterior dorsal vertebra of *Therizinosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, ventral view; C, anterior view; D, lateral view; E, posterior view. Abbreviation: pa, parapophysis. Scale bar equals 1 cm. [intended for column width]

Fig. 14. ZIN PH 1166/16 (CBI, 1987), posterior dorsal vertebra of *Therizinosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, ventral view; C, anterior view; D, lateral view; E, posterior view. Abbreviation: poz, postzygapophysis. Scale bar equals 3 cm. [intended for column width]

Fig. 15. ZIN PH 615/16 (CBI-14, 1980), sacral centrum of *Therizinosauroida* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, anterior? view; B, posterior? view; C, dorsal view; D, ventral view; E, lateral view. Scale bar equals 1 cm. [intended for column width]

Fig. 16. ZIN PH 1001/16 (CBI-15a, 1980), anterior caudal vertebra of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, dorsal view; B, anterior view; C, lateral view; D, posterior view. Scale bar equals 3 cm. [intended for column width]

Fig. 17. Posterior caudal vertebrae of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 2216/16 (CBI, 2006) in (A) dorsal, (B) ventral, (C) anterior, (D) lateral, and (E) posterior views. F-J, ZIN PH 2215/16 (CBI-5) in (F) dorsal, (G) ventral, (H) anterior, (I) lateral, and (J) posterior views. Scale bars each equal 1 cm. [intended for page width]

Fig. 18. ZIN PH 1240/16 (CBI-16, 1989), left scapulocoracoid fragment of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, lateral view; B, posterior view; C, medial view. Abbreviations: bt, biceps tubercle; cf, coracoid foramen; Co, coracoid; gl, glenoid; Sc, scapula. Scale bar equals 1 cm. [intended for column width]

Fig. 19. Humerus fragments of *Therizinosauroides* indet. from the Khodzhakul Formation (Cenomanian) at Sheikhdzheili (A-C) and the Bissekty Formation (Turonian) at Dzharakuduk (D-L), Uzbekistan. A-C, ZIN PH 33/16 (SSHD-8, 1998), fragment of proximal end of right humerus in (A) proximal, (B) dorsal, and (C) ventral views. D-F, ZIN PH 2274/16 (CBI-14, 2004), fragment of proximal end of right humerus in (D) proximal, (E) dorsal, and (F) ventral views. G-I, ZIN PH 31/16 (CBI-5, 1979), fragment of proximal end of right humerus in (G) proximal, (H) dorsal, and (I) ventral views. J-L, ZIN PH 35/16 (CBI-4, 1989), fragment of distal end of left humerus in (J) ventral, (K) dorsal, and (L) distal views. Abbreviations: dc, deltopectoral crest; ent, entepicondyle; h, head of humerus; mt, medial tuberosity; rc, radial condyle; uc, ulnar condyle. Scale bars each equal 1 cm. [intended for page width]

Fig. 20. ZIN PH 27/16 (CBI), right metacarpal I of *Therizinosauroides* 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. [intended for column width]

Fig. 21. Manual elements of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 66/16 (CBI-5a, 1989), distal portion of left metacarpal II in (A) lateral, (B) anterior, (C) medial, (D) posterior, and (E) distal views. F-J, ZIN PH 539/16 (CBI-5a, 1987), distal fragment of left metacarpal III in (F) lateral, (G) anterior, (H) medial, (I) posterior, and (J) distal views. K-P, ZIN PH 1177/16 (CBI-14, 1980), right proximal phalanx I-1 in (K) proximal, (L) distal, (M) lateral, (N) anterior, (O) medial, and (P) posterior views. Q-V, ZIN PH 51/16 (CBI-14, 1980), left phalanx II-1 or II-2 in (Q) proximal, (R) distal, (S) medial, (T) anterior, (U) lateral, and (V) posterior views. W-Z, ZIN PH 1244/16 (CBI-5a), left proximal phalanx III-1 in (W) medial, (X) anterior, (Y) lateral, and (Z) posterior views. Scale bars each equal 1 cm. [intended for page width]

Fig. 22. Ungual phalanges of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan, in side views and in (D) proximal and (E) dorsal views. A, B, ZIN PH 19/16 (CBI-16, 1989); C, CCMGE 454/12457 (CBI-16, 1979); D-G, ZIN PH 1189/16 (CBI); H, I, ZIN PH 40/16 (CBI-14, 1984); J, K, ZIN PH 356/16 (CBI-14, 1987). Abbreviations: ft, flexor tubercle; gr, groove. Scale bars each equal 1 cm. [intended for page width]

Fig. 23. ZIN PH 775/16 (CBI-16, 1989), proximal portion of right femur of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan. A, proximal view; B, lateral view; C, anterior view; D, medial view; E, posterior view. Abbreviations: at, anterior

trochanter; ft, fourth trochanter; gt, greater trochanter; h, head of femur. Scale bar equals 5 cm.

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Fig. 24. Fragments of tibiae of *Therizinosauroides* indet. from the Bissekty Formation

(Turonian) at Dzharakuduk, Uzbekistan. A-E, ZIN PH 600/16 (CBI-14, 1984), fragment of right proximal portion in (A) proximal, (B) lateral, (C) anterior, (D) medial, and (E) posterior views.

F-J, ZIN PH 1426/16 (CBI-27, 1980), fragment of right distal end in (F) lateral, (G) anterior, (H) distal, (I) medial, and (J) posterior views. Abbreviations: cc, cnemial crest; lc, lateral condyle; lm, lateral malleolus; mm, medial malleolus; pc, posterior condyle. Scale bars each equal 1 cm.

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Fig. 25. Pedal elements of *Therizinosauroides* indet. from the Bissekty Formation (Turonian) at

Dzharakuduk, Uzbekistan. A-F, ZIN PH 59/16 (CBI-20, 1980), right metatarsal I in (A) lateral, (B) anterior, (C) medial, (D) posterior, (E) proximal, and (F) distal views. G-K, ZIN PH 1348/16 (CBI), distal portion of left metatarsal II in (G) posterior, (H) medial, (I) anterior, (J) lateral, and (K) distal views. L-Q, ZIN PH 65/16 (CBI-28, 1980), left phalanx I-1 in (L) proximal, (M) distal, (N) medial, (O) anterior, (P) lateral, and (Q) posterior views. R-W, ZIN PH 1198/16 (CBI), preungual phalanx of digit II, III or IV in (R) proximal, (S) distal, (T, V) side, (U), anterior, and (W) posterior views. Scale bars each equal 1 cm. [intended for page width]

Fig. 26. Portion of the strict consensus tree of 1520 most parsimonious trees produced by TNT heuristic search analysis, showing relationships within Therizinosauria. Numbers above nodes are Bremer support values calculated by TNT. [intended for column width]

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