Therocephalian (Therapsida) and chroniosuchian (Reptiliomorpha) from the Permo-Triassic transitional Guodikeng Formation of the Dalongkou Section, Jimsar, Xinjiang, China

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Abstract

The Guodikeng Formation represents an important Permo-Triassic transition sequence. This formation crops out extensively in the Dalongkou section, Jimsar, Xinjiang, yielding the dicynodonts Jimusaria and Lystrosaurus. This paper reports therocephalians and chroniosuchians from the Dalongkou section for the first time, which are also the first records of these two groups from the Guodikeng Formation. The newly discovered therocephalian is designated as Dalongkoua fuae. Its diagnostic characters include: the outer margin of the postcanine alveolus of the maxilla being dorsally concave; incisors spatulated and rounded; faint serrations on incisors and canines; a prominent adductor fossa on the coronoid process of the dentary; a subtriangular reflected lamina with two smooth concavities. The Guodikeng Formation is now represented by 3-4 genera of dicynodonts, 1 genus of therocephalian, and 1 genus of chroniosuchian, a discovery that increases its diversity. All these groups survived the end-Permian mass extinction, only disappearing in the Middle to Late Triassic.

Full Text

Therocephalian (Therapsida) and chroniosuchian (Reptiliomorpha) from the Permo-Triassic transitional Guodikeng Formation of the Dalongkou Section, Jimsar, Xinjiang, China

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Abstract The Guodikeng Formation encompasses the terrestrial Permo-Triassic transition sequence in China. This formation crops out in the Dalongkou section, Jimsar, Xinjiang where remains of the dicynodonts *Jimusaria* and *Lystrosaurus* were found. We are describing here a therocephalian and a chroniosuchian from the Dalongkou section, which are the first records of these groups for the Guodikeng Formation. Diagnostic characters of the new therocephalian, *Dalongkoua fuae* gen. and sp. nov., include maxillary ventral margin strongly concave in lateral view; incisors spatulated and rounded; incisors and canines with faint serrations; coronoid process of the dentary with a marked external adductor fossa; triangular reflected lamina of the angular with two smooth concavities. Chroniosuchians are represented by several postcranial elements and the vertebral morphology is similar to *Bystrowiana* and *Bystrowiella*. These remains are interpreted as representing a Bystrowianidae indeterminate. The new findings increase the diversity of the Guodikeng Formation that is now represented by three or four dicynodonts, one therocephalian and one chroniosuchian. All these groups survived the massive P-T extinction but disappear from the fossil record in the Middle to Upper Triassic.

Key words Dalongkou, Xinjiang; Permian; Triassic; Guodikeng Formation; chroniosuchian; therocephalian

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1 Introduction

Dalongkou section, Jimsar, in Xinjiang is a famous terrestrial section with Permo-Triassic transitional sequences. The southern limb Dalongkou anticline section (SLS) has been suggested as a candidate for the global non-marine Permian-Triassic boundary (PTB) reference section (Cheng and Lucas, 1993, Liu, 1994). This section was originally known by its fossil

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vertebrate bearings. This formation produced the dicynodonts *Jimusaria sinkianensis* and the first specimen of *Lystrosaurus* from China (Sun, 1963; Yuan and Young, 1934a, b), later the co-occurrence of these taxa on the same horizon of the Dalongkou section were noticed (Cheng, 1993). The lowest occurrence of *Lystrosaurus* at the SLS is at the base of bed 63 or 54 of the measured lithostratigraphic section (Fig. 1), ~65 m below the base of the Jiucaiyuan Formation (Cheng, 1993; Liu et al., 2002). The exact position of the holotype of *Jimusaria sinkianensis* is unknown, but Cheng (in Yang et al., 1986) suggested it could lies within the top 20 m of the Guodikeng Formation. This is perhaps the reason why Kozur and Weems (2011) located the stratigraphic position of this dicynodont 15 m below the base of the Jiucaiyuan Formation. Besides dicynodonts, the procolophonid *Santaisaurus yuani* and the archosauriform *Chasmatosaurus yuani* were discovered from horizons of the Jiucaiyuan Formation at the Dalongkou section (Koh, 1940; Li et al., 2008; Young, 1958, 1963).

The PTB in the Junggar Basin was traditionally positioned at the base of the Jiucaiyuan Formation, but a joint team of the Chinese Academy of Geological Sciences and the Xinjiang Bureau of Geology and Mineral Resources first proposed the PTB within the Guodikeng Formation (Yang et al., 1986). They tentatively located the PTB at the uppermost Guodikeng Formation; one major reason for this decision was the position of the lowest occurrence of *Lystrosaurus*. For a long time, *Lystrosaurus* was a Triassic index fossil, and its lowest occurrence marked (or at least approximate) the base of the Triassic (cf. Lucas, 1998).

Based on palynomorph evidence, Ouyang and Norris (1999) placed the PTB at the base of Unit 3 in the uppermost Guodikeng Formation, ~50 m below the base of the Jiucaiyuan Formation. Hou (2004) discovered overlapping interval of sporomorphs from the middle part of the Guodikeng Formation at SLS, and placed the PTB at the base of Bed 51 of the measured lithostratigraphic section 1 (Fig. 1). Furthermore, Pang and Jin (2004) observed a distinct turnover in the ostracod assemblages between Bed 54 and 55 in the Guodikeng Formation (Fig. 1), approximately 10 m above the PTB suggested by the palynological analysis of Hou (2004). Foster and Afonin (2005) studied the abnormal pollen grains from Russia and China, and suggested that the latest Permian mass extinction level lies at the upper lower Guodikeng Formation, between Bed 63 to 65 on s1. Using conchostracan biostratigraphy, Kozur and Weems (2011) proposed the continental extinction event horizon at the middle part of the Guodikeng Formation at SLS; and they proposed that the first appearance datum (FAD) of *Falsisca verchojanica*, ~25 m below the base of the Jiucaiyuan Formation at SLS, correlates to the PTB. Based on the paleomagnetic data, Li et al. (2003) put the PTB between their Bed 41 and 42 at the SLS. Cao et al. (2008) suggested an isotopically defined PTB at the base of Bed 65 (Fig. 1).

In summary, there are distinct faunal and floral turnovers in the middle part of the Guodikeng Formation. As suggested by Kozur and Weems (2011), their

Fig. 1. Position of some vertebrate fossils and proposed PTB from the Guodikeng Formation in the SLS

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relationships with the end-Permian mass extinction need to be studied carefully, but they must not equate to the PTB.

A recent revision of *Dicynodon* restricted the name to two species from the African

Permian and *Jimusauria*, that was synonymized to *Dicynodon*, is considered as a valid taxon different of *Dicynodon* (Kammerer et al., 2011). The phylogeny presented by Kammerer et al. (2011:fig. 156) found *Jimusauria* as a basal form in a clade of Permian and Triassic dicynodonts. Metcalfe et al. (2009) points out the poor record of *Lystrosaurus* in the Guodikeng Formation in opposition to the rich representation of this taxon in the overlying Jiucaiyuan Formation. Considering the faunal composition of the Permo-Triassic transition in South Africa, they argue that the combined presence of *Lystrosaurus* and the *Jimusauria* is more likely representing levels of the Late Permian, in which the former taxon is poorly represented (Smith and Botha-Brink, 2014). As a result the PTB is interpreted on the top of the Guodikeng Formation, near the base of the Jiucaiyuan Formation. Recently, Gastaldo et al. (2015) reported a dicynodontoid skull of characteristically Permian aspect more than 10 m above the previous last occurrence of *Dicynodon* and a zircon age of (253.48 ± 0.15) Ma from a layer ~60 m below the current vertebrate-defined boundary from Karoo Basin. They suggested the PTB should be higher than that recognized by Ward et al. (2005). The work in Karoo Basin suggested an older occurrence of *Lystrosaurus*, and the PTB could be around the base of the Jiucaiyuan Formation in Junggar Basin.

Fig. 1 Position of some vertebrate fossils and proposed PTB from the Guodikeng Formation in the SLS
The stratigraphic column adapted from Cao et al. (2008). Subunits of lithological stratigraphy listed as s1 are from team work of 2000 (published in Li et al., 2003; Hou, 2004 and Pang and Jin, 2004), s2 from Yang et al. (1986)
C. IVPP V 23295, a chroniosuchian; J. the possible position of *Jimusaria sinkiangensis*; L. the lowest occurrence of *Lystrosaurus*; T. IVPP V 23296, the therocephalian *Dalongkoua fuae*. The continuous lines mean the exact position of PTB, while the dashed lines indicate unsure on the position

In 2000, some bones were collected from the SLS while digging a trench for paleomagnetic study. One specimen (IVPP V 23296) was produced from a green mudstone close to the yellow sandstone in Bed 40. All bones of this specimen are badly weathered, before being buried. Another specimen came from the red mudstone of Bed 70, including several vertebrae and a nearly complete humerus (IVPP V 23295). These materials were prepared and identified as a the-

rocephalian and a chroniosuchian. Therocephalian therapsids were important component of Middle Permian to Middle Triassic terrestrial faunas (Abdala et al., 2008, 2014; Huttenlocker et al., 2015; Ivakhnenko, 2011). In China, therocephalians are only known from the Triassic, including *Urumchia lii* recovered from the Jiucaiyuan Formation of Xinjiang, which was originally assigned as Late Permian (Li et al., 2008;

Young, 1952). The new discoveries represent, thus, the first report of a Permian therocephalian for China. Chroniosuchians is an enigmatic and a recent addition to the group of tetrapods. It was first reported in the Permian and Triassic of Russia (Golubev, 1998; Novikov and Shishkin, 2000; Shishkin et al., 2014), and later from the Permian of China (Li and Cheng, 1999; Young, 1979), and the Triassic of Kyrgyzstan and Germany (Schoch et al., 2010; Witzmann et al., 2008). The new material here presented is a new Permian record for China, and the first one from Xinjiang.

Abbreviation IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.

2 Systematic paleontology

Therapsida Broom, 1905

Therocephalia Broom, 1903

Eutherocephalia Hopson & Barghusen, 1986

***Dalongkoua fuae* gen. et sp. nov.**

Holotype IVPP V 23296, incomplete left premaxilla with three teeth, incomplete right premaxillae with four teeth, snout and part of the orbital region with the maxilla on both sides featuring functional and replacement canines, isolated vertebrae, left humerus, two phalanges and some bone fragments (Figs. 2–4).

Etymology 'Dalongkou', the name of locality; 'fu', dedicated to the preparator Ms. Fu Hua-Lin.

Diagnosis Maxillary ventral margin strongly concave in lateral view; incisors spatulated and rounded; incisors and canines with faint serrations; coronoid process of the dentary with a marked external adductor fossa; triangular reflected lamina of the angular with two smooth concavities.

Description Skull The skull is strongly deformed as a flat plate and broken into small blocks. The anterior portions of the premaxillae are separated from the rest of the skull (Fig. 2). Both premaxillae are represented as independent elements, with the right being better preserved. It forms a curved plate housing the alveoli for four incisors (Fig. 2C). Posteromedially, it has the process for contacting the vomer. The posterolateral side of the palatal surface curves dorsally, forming the anterior margin of the palatal fenestra for the lower canine (Fig. 2C). There are four preserved teeth, three of them with the main axis

Fig. 2 Holotype of *Dalongkoua fuae* gen. et sp. nov. (IVPP V 23296)

Figure 2: Fig. 2 Holotype of *Dalongkoua fuae* gen. et sp. nov. (IVPP V 23296)

of their bases oriented longitudinally, whereas the second is circular in section. The latter tooth, is completely preserved, presenting spatulated crown, concave lingually, and mesiolingual and distal smooth ridges (Fig. 2E). Remaining teeth are incomplete lacking any ridge at their bases, where the external surface is relatively smooth. Based on the preservation, we interpret the probable presence of at least five incisors. Two replacing teeth lie on the lingual side of the first and third functional incisors (Fig. 2C). The crown of the first replacement incisor show fainted

serrations on the medial margin. A tiny foramen lies posterior to the first replacing incisor. A long diastema separated the last incisor and the canine. The left premaxilla has three poorly preserved incisors and an extra alveolus for the fourth incisor, without tooth. There are pits with replacement teeth behind the second and third incisors.

The maxilla is a long bone with large facial plate. It extends anteriorly and covers the lateral surface of the premaxilla anterior to the canine. Ventrally, there is a concave ventral step. The maxilla is laterally expanded to encapsulate the canine, and the snout seems

Fig. 2 Holotype of *Dalongkoua fuae* gen. et sp. nov. (IVPP V 23296)
Skull, including premaxilla in left lateral (A), right lateral (B) and ventral (C) views; right premaxilla in dorsal view (D); the second preserved right incisor in lingual view (E)
Abbreviations: F. frontal; J. jugal; M. maxilla; N. nasal; Pf. prefrontal; Pm. premaxilla; Po. postorbital; r.c. replacing canine; t.f. temporal fenestra; V. vomer. Scale bar equals 1 cm

constricted behind the canine. On the right side, the facial plate is folded medially, and a remarkable longitudinal ridge is present, suggesting a well exposed maxillary platform. The platform is posteriorly concave in lateral view as in *Theriognathus microps* (Huttenlocker and Abdala, 2016). The root of the left canine is exposed posteriorly. An erupting replacing canine lies anteromedially to the canine on both sides. The maxillary ventral margin is strongly concave in lateral view. The postcanines are not observed on the skull, but some isolated teeth could be postcanines. Two of them preserved the base of the crown, and it is possible to see strong ridges on two margins without serration. One margin is remarkable concave, the other is straight to slightly concave. One preserved tip of postcanine have faint serrations on both margins of the cusp. The putative preserved postcanines are much smaller than the incisors.

The nasal is long and forms the dorsal surface of the snout. A middle ridge is present on the posterior portion of the nasal. It is sutured with the frontal on the level of the anterior margin of the orbit (Fig. 2A). Laterally, it contacts

Fig. 3 Holotype of Dalongkoua fuae gen. et sp. nov.

Figure 3: Fig. 3 Holotype of Dalongkoua fuae gen. et sp. nov.

the maxilla and the prefrontal. The prefrontal, frontal and postorbital form the dorsal margin of the orbit, whereas the postorbital bar is formed by the postorbital and jugal.

Lower jaw Dentary The symphyseal region and the posterior part of the left dentary is preserved, as well as the right reflected lamina of the angular (Fig. 3). The articular symphysis with the right dentary is broken, and the lower margin is incomplete (Fig. 3B). The symphyseal region bears a marked constriction lateral to the lower canine where the upper canine rests. The anterior part of this region bears pits and grooves, whereas the surface that will be contacting the medial side of the upper canine is smooth. The posteroventral portion of the dentary forms a thickened lower border that supports the angular in a trough on its medial surface (Fig. 3B). The posteroventral corner of the dentary forms an angle of 137°. The coronoid process is well developed, with a dorsal adductor fossa on the lateral surface (Fig. 3A). The posteroventral margin of the dentary, below the bulged ridge that limits ventrally the adductor fossa, forms a descending flange ending in a sharp ridge. Although the posterodorsal corner is incomplete, the preserved portion shows a nearly straight posterodorsal margin. Six teeth are preserved on the symphyseal region. The biggest one is the canine, and anteromedially there is a replacing canine that is partially wrapped by it (Fig. 3C). Faint serrations developed on the anterior margin of the replacing canine. There are four lower incisors, including three preserved teeth and one alveolus (Fig. 3C). A tiny tip of an erupting tooth lies immediately anterior to the canines. The last incisor is small and partially preserved; whereas two other incisors, medial to the later, are also preserved. One of them is faceted showing a well-developed ridge laterally (the medial side is not exposed). Very fine serrations, only visible under microscope magnification, are present on the margins of the larger two preserved incisors.

Angular The right angular is nearly complete. This bone is flat and elongated posteriorly with a triangular-like reflected lamina (Fig. 3D, E). The large reflected lamina bears a deep 'U' -shaped dorsal notch which is posterodorsally directed (Fig. 3D). The lateral surface of the reflected lamina is ornamented by fine, radiating ridges and grooves, and is divided into three

parts by large grooves directed ventrally and posteriorly (Fig. 3D).

Prearticular The prearticular lies on the medial side of the angular (Fig. 3E). It is an elongate element forming an anterior rod to contact the splenial. Posteriorly, it is a triangular plate, whose posterior process contacts the articular.

Fig. 3 Holotype of *Dalongkoua fuae* gen. et sp. nov. (IVPP V 23296) Symphysis and posterior portion of the left dentary in lateral (A) and medial (B) views; left dentary symphysis in dorsal view (C); right angular in lateral (D)

Fig. 4

Figure 4: Fig. 4

and medial (E) views
Abbreviations: a.f. adductor fossa; b.s. broken surface; f.a. facet on the dentary for the angular; i. incisor; m.f. mandibular fenestra; Pra. prearticular; r.c. replacing canine. Scale bars equal 1 cm

Vertebrae Two partial vertebrae including centra and a left partial neural arch are represented. The complete centrum in one of them, interpreted as dorsal vertebra, is amphicoelous, and deeply hollowed. The second element has an incomplete centrum and a clear suture between the centrum and the right partial neural arch shows lack of synostosis between them (Fig. 4A, B). The transverse process extends dorsolaterally and is angled posterolaterally, with a vertical flange on the ventral side. This is similar to the dorsal vertebra of *Promoschorhynchus platyrhinus* (Huttenlocker et al., 2011).

The isolated arch is possible of a cervical vertebra, with its zygapophyses bearing more or less horizontal articulating surfaces (Fig. 4C, D). The transverse process is not preserved and should lie well down on the neural arches. The neural spine is robust and inclines anteriorly. This is similar to the cervical of *Olivierosuchus parringtoni* (Botha-Brink and Modesto, 2011).

Sternum A partial posterior margin of the sternum is preserved (Fig. 4G, H). It is a large plate with convex ventral surface and concave dorsal surface. There is no posterior notch, and a weak midline ridge is developed on the ventral surface, as in *Promoschorhynchus platyrhinus* (Huttenlocker et al., 2011).

Fig. 4 Holotype of *Dalongkoua fuae* gen. et sp. nov. (IVPP V 23296)
An incomplete dorsal vertebra in lateral (A) and posterior (B) views; an incomplete cervical neural arch in left lateral (C) and medial (D) views; two phalanges in dorsal (E) and ventral (F) views, distal to the top; sternum in ventral (G) and dorsal (H) views; left humerus in dorsal (I), anterior (J), ventral (K) and posterior (L) views. Scale bars equal 1 cm

Humerus The humerus is robust with expanded proximal end, missing the distal end and the deltopectoral crest (Fig. 4I–L). The proximal half is curved dorsally relative to the shaft (Fig. 4J, L). A low ridge lies on the rough posterodorsal side, possible representing part of the wide posteroventral ridge described by Kemp (1986). The long shaft is broken on the place of the entepicondylar foramen.

Phalanges Two phalanges are well preserved (Fig. 4E, F). A longitudinal middle groove develops on the ventral surface. They are nearly as wide as length. Nearly quadrangular phalanges are represented in several therocephalians including the Scylacosauridae *Glanosuchus*, the Akidnognathidae *Olivierosuchus*, the Hofmeyriid *Mirotenthes* and the Whaitsiidae *Theriognathus* (Attridge, 1956;

Boonstra, 1964; Botha-Brink and Modesto, 2011; Fourie and Rubidge, 2007; Abdala, pers. obs).

Chroniosuchia Tatarinov, 1972
Bystrowianidae Vjuschkov, 1957
Genus and species undetermined

Referred specimen IVPP V 23295, five vertebrae, rib, gastral scales, partial ilium, left femur, and partial fibula (Figs. 5, 6).

Description Vertebrae Three articulated vertebrae show two intercentra, two isolated pleurocentra are fused to the neural arches, and there are three isolated intercentra. Four larger vertebrae are tentatively identified as dorsals and the smallest as caudal.

The morphology of the vertebrae is very similar to that of *Bystrowiana sinica* or *Bystrowiella schumanni* (Liu et al., 2014; Witzmann et al., 2008) (Fig. 5).

The length of the large pleurocentrum is approximately 14 mm, whereas the length in the other two is 12 and 10 mm. The pleurocentrum are roughly twice as long anteroposteriorly as the intercentra. The height of the pleurocentra is about 10 mm. All pleurocentra are deeply amphicoelous with a round cross-section, and they are not perforated by the notochord. In

Fig. 5 Chroniosuchian specimen (IVPP V 23295) from Dalongkou section

Three dorsal vertebrae in anterior (A), left lateral (B), posterior (C), dorsal (D) and ventral (E) views; one caudal vertebra in anterior (F), left lateral (G), posterior (H), and ventral (I) views; J. gastral scales; caudal intercentrum in anterior (K), left lateral (L), and ventral (M) views

Abbreviations: dp. diapophysis; ha. haemal atch; ic. intercentrum; nc. neural canal; ns. neural spine; pc. pleurocentrum; pnc. paraneural canal; poz. postzygapophysis; pp. parapophysis; prz. prezygapophysis; tp. transverse process. Scale bar equals 1 cm

lateral view, the anterior and posterior margins of the pleurocentrum are curved but the ventral margin is nearly straight. A small knob (parapophysis) for the capitulum lies on the middle of the pleurocentrum anterior margin (Fig. 5B, E), and a longitudinal faint ridge runs posterior to it. The parapophysis is separated from the diapophysis by an anterodorsally directed incisure. On the larger pleurocentrum, the ventral surface is slightly convex to smooth (Fig. 5E). On the smallest pleurocentrum, two anteroposteriorly directed, low ridges delimit the faintly concave ventral margin (Fig. 5I) as in *Bystrowiella schumanni* (Witzmann et al., 2008).

The intercentra are about as tall as the pleurocentra in lateral view. The articular intercentra show smooth periosteal bone, without haemal arch on the ventral surface. They appear wedge-like in articulation (Fig. 5B, E), but actually are ball-like (Fig. 5K–M). On three free caudal intercentra, the ventral

surface consists of slightly concave, smooth periosteal bone, and bears the ventrolateral bases of the hemapophyses as in *Bystrowiella schumanni* (Witzmann et al., 2008). The roughened dorsal surface of the intercentrum is convex and did not articulate

with the neural arch, forming part of the base of the neural canal. The largest intercentrum measures 9.7 mm long, while the others range from 8 to 9 mm. The exposed length of them in ventral view is nearly 5 mm.

All neural arches are fused to the pleurocentrum and the spines only preserved at their base. The zygapophyses are widely spaced (Fig. 5D, E) and the facets slope medially at a small angle to the horizontal plane in anterior view. There are two pairs of well-developed paraneural canals at the base of the zygapophyses, with the anterior openings of the dorsal pair being larger than those of the lateral pair (Fig. 5A). As in *Bystrowiana permira*, the number and shape of the openings on the two sides could be different (Liu et al., 2014). The neural canal is compressed dorsoventrally. The short transverse process lies on the upper half of the pleurocentrum, bearing small, unfinished diapophyses (Fig. 5A–C).

Rib and gastral scales A proximal rib fragment, and some gastral scales are preserved on a bone plate (Fig. 5J). The gastral scales are thin, some ending in a sharp point.

Ilium The preserved acetabular area of the right ilium is similar to that of *Dendrysecos helogenes* or *Chroniosaurus* (Clack and Klembara, 2009; Holmes et al., 1998; Schoch and Milner, 2014). The anterior margin is slightly concave (Fig. 6A). There is a distinct crescent supra-acetabular buttress, and, anteroventrally, a notch on the anterior margin of acetabulum. The iliac blade is only preserved as a narrow base above the acetabular rim. On the medial side, a strong iliac ridge runs dorsoventrally and divides the medial surface in two portions (Fig. 6B).

Femur The slender left femur is well-ossified and nearly complete (Fig. 6C–H). The general shape of the bone is same as that of *Chroniosaurus* (Clack and Klembara, 2009). The length of the bone is 73 mm, and the width is 21 mm for proximal and distal ends. The distal side deflects ventrally relative to the proximal part, so the bone is curved dorsally. The anterior margin is curved while the posterior margin is relatively straight. Differing from *Chroniosaurus dongusensis*, the articular surface on the proximal side is smoothly convex and dorsoventrally flattened (Fig. 6C). The dorsoventral height of the articular surface is near half its anteroposterior length (Fig. 6G). The proximal extensor surface of the femur bears some striations on the posterior side (Fig. 6C), indicating the insertion for the ischiotrochantericus.

On the anteroflexor side, the ventrally directed adductor blade demarcates the anterior side of the deep intertrochanteric fossa (Fig. 6D, E). The broken internal trochanter is separated from the femoral head by a narrow ridge, and it continues distally as a low crest, the fourth trochanter (Fig. 6D). The anterior surface of the adductor blade is rugose with deep muscle scars.

Fig. 6

Figure 5: Fig. 6

From the distal end of the fourth trochanter, the adductor crest follows a strongly diagonal course posteroventrally to a point distal to the middle of the shaft (Fig. 6E, F). A low ridge continues distally on the posterior side of the shaft ending on the distal posterior corner. This ridge does not seem to be for muscle attachment. In other groups such as captorhinomorphs, seymouriamorphs and temnospondyls, the adductor crest generally runs towards the popliteal area (Fox and Bowman, 1966; Klembara and Bartik, 2000; Pawley, 2007).

The popliteal area is pitted and concave on the flexor side (Fig. 6E). The fibular (posterior)

Fig. 6 Chroniosuchian specimen (IVPP V 23295) from Dalongkou section
Right ilium in lateral (A) and medial (B) views; left femur in extensor (C), anterior (D), flexor (E), posterior (F), proximal (G), and distal (H) views; left fibula in flexor (I); proximal (J) and extensor (K) views.
Abbreviations: ab. adductor blade; ac. adductor crest; asn. anterior supracetabular notch; cn. cnemial crest; cnt. cnemial trough; dip. dorsal iliac process; fc. fibular condyle; ff. fibula fossa; icf. intercondylar fossa; it. internal trochanter; itf. intertrochanteric fossa; mir. mesial iliac ridge; pa. popliteal area; pir. posterior intertrochanteric ridge; sab. supracetabular buttress; tc. tibial condyle; t4. fourth trochanter. Scale bar equals 1 cm.

condyle projects more distally than the tibial (anterior) condyle. Proximal to the fibular condyle is a narrow but deep fibular fossa. In extensor view, a deeply incised intercondylar fossa is oriented posteroventrally towards the midline of the fibular condyle (Fig. 6H).

Fibula The proximal end of the left fibula is preserved (Fig. 6I–K). The head is convex to fit on the concave articular surface of the femur. Small striae distribute around the proximal articular surface (Fig. 6I, K), indicating the presence of cartilage or perhaps ligamentous connective tissue. The extensor surface is incised by a cnemial trough, which is bordered anteriorly by the prominent cnemial crest (Fig. 6J). Another crest is on the posterior surface of the bone. A striate area on the medial side of this ridge, distal to the proximal articular surface, provided attachment for muscles.

3 Discussion

The new therapsid specimen (IVPP V 23296) can be diagnosed as a therocephalian for the presence of palatal fenestra for the lower caniniform confluent with choana, and the

posterventral portion of the dentary forming a thickened lower border that ex-

tends below the angular bone and supports the latter in a trough on its medial surface. It has four lower incisors, and can be then diagnosed as an eutherocephalian (Huttenlocker, 2009). In addition, the shape of the reflected lamina, lacking an anterodorsal rounded portion in front of the notch that makes this structure circular in basal therocephalians is also an indication that the new species is member of Eutherocephalia.

Dalongkoua fuae show evidence of faint serrations in the margin of a replacement incisor and canine and on the tip of a postcanine. These findings are contrary to the assumed absence of serrations in the dentition of eutherocephalia (e.g. van den Heever, 1994; Abdala et al., 2008; Huttenlocker, 2009; and Huttenlocker et al., 2015, for incisors and Huttenlocker and Sidor, 2012 for anterior dentition). The serrations in the teeth of *Dalongkoua fuae* are exceedingly faint and it is clear that they will disappear with a minimum wear as demonstrated by the smoothly ridged crown of the preserved elements.

This specimen represents a new species on the basis of the following characters: maxillary ventral margin is strongly concave in lateral view; incisors spatulated and rounded; incisors and canines with faint serrations; coronoid process of the dentary with a marked adductor fossa; triangular reflected lamina with two concavities.

The maxillary ventral margin is convex or nearly straight in most therocephalians, but it is slightly concave in *Moschowhaitsia* (Ivakhnenko, 2011), and strongly concave in *Euchambersia* and *Theriognathus* (Broom, 1931; Huttenlocker and Abdala, 2016). Recent studies (e.g., Huttenlocker et al., 2015) indicate that spatulated incisors are restricted to a group of akidnognathids. In *Dalongkoua fuae* the completely preserved second left incisor is spatulated, whereas remaining left incisors, although incomplete, show the crown enough preserved to suggest the presence of rounded (non-spatulated) incisors. The adductor fossa is developed in the dorsolateral portion of the coronoid process, above of the through for the postdentary bones. This fossa is different to the one described on the lateral surface of the dentary in the bauriids *Microgomphodon oligocynus* (Abdala et al., 2014) and in the Russian *Notogomphodon danilovi* (Abdala, pers. obs.), as in these taxa there is no connection between the fossa and the through for the postdentary bones. The incomplete left dentary of *Urumchia lii* also seems to have an adductor fossa, although less developed than in *D. fuae* (Fig. 7). A triangular reflected lamina is also present in the holotype of *Tetracynodon darti*, but the lamina show a more complex lateral surface with several ridges and valley. In the lamina of *D. fuae* there is a posterior deep canal and a dorso-ventrally oriented shallow and wide depression.

Urumchia lii is the only known therocephalian from the Xinjiang, documented in the Jiucaiyuan Formation (Sun, 1991; Young, 1952). Diagnostic characters in this species are concentrated in the palate and in the postcanine morphology (Li et al., 2008; Sun, 1991). Unfortunately both palate and postcanines are incompletely preserved in *Dalongkoua fuae*, the postcanines only represented by

Fig. 7 *Urumchia lii* (IVPP V 702). Skull in dorsal (A) and right lateral (B) views; lower jaws in left lateral view (C). Showing the sharing characters with *Dalongkoua fuae*: 1. the mid-ridge between the posterior portions of the nasals and the anterior portions of the frontals; 2. depressed facial area of the maxilla; 3. adductor fossa on the dentary. Scale bars equal 1 cm

Figure 6: Fig. 7 *Urumchia lii* (IVPP V 702). Skull in dorsal (A) and right lateral (B) views; lower jaws in left lateral view (C). Showing the sharing characters with *Dalongkoua fuae*: 1. the mid-ridge between the posterior portions of the nasals and the anterior portions of the frontals; 2. depressed facial area of the maxilla; 3. adductor fossa on the dentary. Scale bars equal 1 cm

isolated fragments including two crown bases and one tip. There are however a set of characters shared between these two species indicating perhaps

relationships (Fig. 7): medial margin of the frontal bones directed dorsally in *Dalongkoua fuae* indicating the presence of a central ridge in the posterior internasal and interfrontal sutures, the presence of a depressed facial area of the maxilla immediately above of the dental series, also described recently in *Ichibengops* of East Africa by Huttenlocker et al (2015), an apparent development of an adductor fossa, although clearly smaller, in the left dentary of *Urumchia lii*; and the presence of spatulated incisors. The putative relationship between these two taxa should be considered as a working hypothesis, whose validation will require finding of additional material.

Fig. 7 *Urumchia lii* (IVPP V 702)
Skull in dorsal (A) and right lateral (B) views; lower jaws in left lateral view (C). Showing the sharing characters with *Dalongkoua fuae*: 1. the mid-ridge between the posterior portions of the nasals and the anterior portions of the frontals; 2. depressed facial area of the maxilla; 3. adductor fossa on the dentary
Scale bars equal 1 cm

The new specimen of Reptiliomorpha (IVPP V 23295) is referred to chroniosuchian for the characteristic ball-and-socket joint between pleurocentra and intercentra (Ivakhnenko and Tverdokhlebova, 1980). It can be further assigned to Bystrowianidae for paired paraneural canals on the vertebrae (Novikov et al., 2000). The vertebrae show the similar morphology as other bystrowianids, and intercentra is similar to the figured for *Bystrowiella schumanni* (Novikov and Shishkin, 2000; Witzmann et al., 2008). The morphology of ilium, femur, and fibula is consistent with this taxonomic identity (Clack and Klembara, 2009; Ivachnenko and Tverdokhlebova, 1980). Unfortunately, no dermal scute was discovered, and no further identification could be made.

Chroniosuchian specimens in China were first reported from the Upper Permian Jiyuan fauna (Young, 1979), and then from the Middle Permian Dashankou fauna (Li and Cheng, 1999). The new findings here reported represent the latest occurrence of chroniosuchians in

China. This group however is known from the Middle/Upper Triassic Madygen Formation of Kyrgyzstan (Schoch et al., 2010), indicating their continued presence in Laurasia after the Permian extinction.

These new findings allow recognizing that the diversity of tetrapod near the Permo-Triassic boundary in China, and particularly in Xinjiang, was higher than previously recognized. Only dicynodonts were previously reported from the Guodikeng Formation, including *Lystrosaurus*, *Jimsaria*, *Turfanodon*, and possibly *Diictodon* (Li et al., 2008). Both chroniosuchians and therocephalians crossed the P-T boundary; therocephalians become extinct in the Middle Triassic (Abdala et al., 2014), whereas the youngest record of chroniosuchians is in the Middle or Late Triassic (Schoch et al., 2010).

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Newly discovered therocephalian and chroniosuchian from the Guodikeng Formation of the Dalongkou Section, Jimsar, Xinjiang

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Abstract: The Guodikeng Formation is an important Permo–Triassic transitional sequence. This formation is widely exposed at Dalongkou, Jimsar, Xinjiang, and has yielded two dicynodont taxa, *Jimsaria* and *Turfanodon*. This paper reports the first discoveries of therocephalian and chroniosuchian from the Dalongkou section, which also represent the first records of these two groups from the Guodikeng Formation. The newly discovered therocephalian is named *Dalongkoua fuae*. Its diagnostic features include: the posterior margin of the

postcanine alveolus on the maxilla is concave posteriorly; the incisors are round and blunt; the incisors and canine have weak serrations; the coronoid process of the dentary has a distinct masseteric fossa; the reflected lamina is nearly triangular, with two smooth depressions. At present, the Guodikeng Formation contains 3–4 genera of dicynodonts, 1 genus of therocephalian, and 1 genus of chroniosuchian; this discovery increases its diversity. These groups all survived the end-Permian mass extinction and did not disappear until the Middle to Late Triassic.

Key words: Dalongkou, Xinjiang; Permian; Triassic; Guodikeng Formation; Therocephalia; Chroniosuchia

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Note: Figure translations are in progress. See original paper for figures.