The tetrapod fauna of the upper Permian Naobaogou Formation of China: 3. *Jiufengia jiai* gen. et sp. nov., a large akidnognathid therocephalian from China

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ABSTRACT

Recent field trips to the Member III of the Naobaogou Formation, Nei Mongol, China resulted in new fossil~~s~~ discoveries that increased our knowledge of the late Permian continental fauna from China. We present here a new large therocephalian, *Jiufengia jiai* gen. et sp. nov., represented by a partial skull with mandibles and part of the postcranial skeleton. This is the second therocephalian recovered from the Naobaogou fauna and, in turn, the second akidnognathid from this fauna and from China. The new taxon shows clear differences with respect to *Shiguaignathus wangi*, the ~~previous~~ akidnogathid previously reported from the Naobaogou Formation: the presence of four upper postcanines; of a large suborbital vacuity, and the flat ventral surface of vomer, lacking a ventromedian crest. Update of a previous phylogeny of therocephalians allocate the new species in the base of Akidnognathidae after a basal polytomy including the other two Laurasian akidnognathids, *Shiguaignathus* and *Annatherapsidus*, adding evidence to the hypothesis of the early evolution of this group in Laurasia.

INTRODUCTION

The record of Chinese terrestrial strata of Permian age is well documented and had produced a good representation of amniotes (Li & Liu 2015; Li et al. 2008). In recent years, a meticulous collective effort in Permian localities resulted in a remarkable expansion of the knowledge of the faunal members of terrestrial ecosystems (Li & Liu 2013; Liu 2013; Liu & Bever 2015; Liu & Li 2013; Liu et al. 2014; Reisz et al. 2011; Xu et al. 2015) and also has been successful in the record for the first time of ~~member of~~ therocephalians in the Chinese Permian (Liu & Abdala 2017a; Liu & Abdala 2017b). The Naobaogou Permian fauna was recently expanded by the record of *Shiguaignathus wangi*, a medium-sized and well-preserved snout, identified as the first Permian ~~A~~akidnognathid therocephalian from China (Liu & Abdala 2017a) and of the pareiasaur *Elginia wuyongae*, which implied a very important expansion of the distribution of this parareptile (Liu & Bever 2018).

Therocephalians constitute a heterogeneous group in the Permian, represented by three speciose lineages. One of these is Akidnognathidae, first erected as Akidognathinae by Nopcsa (1928) to include *Akidnognathus parvus* Haughton 1918, represented by a small skull with a relatively broad snout from the *Cistecephalus* Assemblage Zone of South Africa~~ with a relatively broad snout~~, originally included in Scaloposauridae (Haughton 1918). Later, Akidognathidae was proposed to include *Akidnognathus*, *Cerdosuchoides*, *Scylacosaurus* and *Ictidosaurus* (Haughton & Brink 1954). The latter two genera are currently included in Scylacosauridae, a family including the most~~of~~ basal and oldest therocephalians (van den Heever 1994, Abdala et al., 2008). The Family Euchambersidae (Boonstra 1934; Haughton & Brink 1954) was proposed to include the bizarre skull of *Euchambersia mirabilis* Broom 1931, although the spelling was later corrected as

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Euchambersiidae (von Huene 1940). Several other taxa considered now as akidnognathids were previously included into Moschorhinidae, Annatherapsididae (Mendrez 1974a; Mendrez 1975) and Euchambersiidae (Hopson & Barghusen 1986). Nowadays Akidnognathidae, in a phylogenetic context, include the South African late Permian *Akidnognathus*, *Promoschorhynchus*, *Euchambersia* and *Cerdosuchoides*, the Permo-Triassic *Moschorhinus*, the Early Triassic *Olivierosuchus*; the Russian late Permian *Annatherapsidus* and the recently described Chinese *Shiguaignathus* (Huttenlocker & Smith 2017; Liu & Abdala 2017a).

Here we report the second akidnognathid ~~taxon~~ from China and only the third for Laurasia, which clearly indicates that this predominantly ~~Gondwanean~~ Gondwanic lineage of therocephalian also has a reasonable representation in the Permian from Laurasia. In fact, two of the three therocephalian taxa reported for the Chinese Permian are members of the Akidnognathidae.

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SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905

THEROCEPHALIA Broom, 1903

EUTHEROCEPHALIA Hopson and Barghusen, 1986

AKIDNOGNATHIDAE Nopcsa, 1928

Jiufengia jiai gen. et. sp. nov.

Etymology—'Jiufeng", refers to the name of the mountain where the fossil was collected; 'Jia' after Jia Zhen-Yan, the technician who discovered the specimen.

Holotype—IVPP V 23877, a skull with mandibles, incomplete right pectoral girdle, and incomplete right forelimb.

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Type Locality and Horizon—Locality DQS 72, near Wuliangshitai, Gongshanwan, Tumd Right Banner, Nei Mongolia, China; base of Member III, Naobaogou Formation.

Diagnosis—~~a~~ large akidnognathid with the following autapomorphies: snout (preorbital region) longer than half of skull length; anteroposteriorly short temporal region with orbit being slightly larger than the temporal opening; jugal anterior process extends nearly to the level of the anterior margin of lacrimal; ventral surface of vomer flat, lacking a ventromedian crest; pterygoid transverse flange anterior to the center of the orbit; prootic without central process; anteroventral process of the squamosal forms the bar anterior to the pterygo-paroccipital foramen; jugal tall below the orbit, intermedium between the condition of *Moschorhinus* and the remaining Akidnognathids.

DESCRIPTION

The specimen consists of the skull, mandibles, left scapula, right coracoid, partial right humerus, proximal portion of the right radius and partial right manus. The skull is slightly crushed along the middle part of the dorsal surface, and some bones on its right lateral side and dorsal surfaces ~~were~~ are eroded ~~prior to be collected~~ (Figs. 1-3). The skull is ~~occluding~~ articulated with the mandibles. A list of standard cranial measurements is provided in Table 1.

Skull roof

A prominent feature is the long snout, which represents more than half (58%) the length of the skull (Fig. 1; see Table 1). The skull has a triangular outline in dorsal view, being slightly constricted behind the canine and wider posteriorly. The general morphology resembles that of *Annatherapsidus*, but the latter does not show a constriction behind the canine (Ivakhnenko, 2011: fig. 22a).

The laterally wide premaxilla features an eroded anterior tip and ascending processes. The anterior surface of the right side is also eroded exposing the roots of some incisors (Fig. 2). The premaxilla has a narrow exposure on the lateral side, covered by the anterior lamina of the maxilla (Fig. 1). The alveolar margin of the premaxilla upturns anteriorly. The dorsal surface of the bone forms the ventral rim of the external nares with overlapping septomaxilla, only preserved on the left side. On the palate, the premaxilla meets the vomer with a short trapezoid posteriorly-directed vomerine process (Fig. 3).

There are five upper incisors (Fig. 2). Although the lateral surfaces of the alveoli are eroded, the crowns of the left five incisors are still preserved whereas the crowns are nearly vanished on the right side. The incisors are narrow, sharp conical, slightly curved lingually and somewhat anteriorly directed from alveoli. In lateral view, the alveolar margin is nearly straight. The crown of the anterior four incisors ~~are~~ is similar in ~~the crown~~ height (ca. 2 cm), the fourth has the largest diameter, and the fifth is smaller.

The ~~maxillary~~ dorsal margin of the maxilla is incomplete, and most of the suture with the nasal is untraceable (Fig. 1). The maxilla contacts the prefrontal posterodorsally and the lacrimal and jugal posteriorly. It sends a triangular posterior process which contacts with the also triangular anterior process of the jugal. The maxilla is very high (height is close to 40% of the bone length) and long, forming the majority of the lateral region of the snout. It extends anteriorly to the position of the fourth incisor and contacts both the septomaxilla and premaxilla. Its height seems increasing posteriorly, and the margins of the maxillae from both sides nearly meet along the midline on the dorsal surface (Fig. 4), suggesting the presence of a very narrow nasal at that point of the skull. The maxilla also bears numerous longitudinal grooves and pits but no~~t~~ foramen on the external surface of the facial plate. In lateral view, the ventral margin of the maxilla is slightly convex and directed anterodorsally in front of the level of the canine, while the posterior part is nearly straight.

In palatal view, the maxilla has a broad exposure medial to the canine alveoli, approaching the wide anterior margin of the vomer. The maxilla exposure on the palate is constricted behind the canine, and its alveolar buccal margin is laterally concave. The maxilla houses two precanines, one canine, and four postcanines. The two small precanines are conical; the canine is cylindrical, with a diameter of 10 mm. The apex of the canine is ~~, with the apex~~ lost, and the preserved crown ~~having~~ has more than 3 cm in height. The canine extends below the ventral margin of the lower jaw (Fig. 1). The canine is slightly curved posteriorly, and its crown surface is covered by regular stripes. A wide diastema is present posterior to the canine. The postcanines are conical, with a wide massive base, posteriorly curved crown, which is slightly flattened labiolingually. The ~~late~~ two more posterior postcanines bear ~~crowns are~~ bigger crowns than the first two. The third postcanine is more strongly curved posteriorly when compared with the other postcanines.

Only the posterior portion of ~~T~~the nasals is~~are~~ preserved, ~~only the posterior portion~~ close to the prefrontals. ~~Its~~ The dorsal surface of the nasal on the left side is relatively well-preserved. The suture between the nasal and the frontal is unclear. If the posterior extension of the nasal is at level of the anterior margin of the orbit as in *Annatherapsidus*, the length of this bone is almost ~~equals to~~ half of the skull length. No mid~~-~~sagittal crest is observed on the nasal.

Only the left orbit is preserved (Figs. 1, 4). The orbit is rounded in dorsal view, and has an anteroposterior length of 44 mm ~~of anteroposterior length~~. The anterior wall of the orbit is formed by the prefrontal and lacrimal; the relatively deep suborbital bar is formed by the jugal, and maxilla only anteriorly; and the moderate postorbital arch is formed by the jugal and postorbital. The dorsal roof of the left orbit is incomplete. The lacrimal sutures with the prefrontal dorsally and the jugal ventrally. It is a rectangular bone in lateral view (Fig. 1). The triradiate jugal has a long anterior process, which ~~is~~ reaches nearly ~~at~~ the level of the anterior margin of the lacrimal. The jugal also

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extends anteriorly beyond the anterior margin of the orbit in *Akidnognathus* and *Annatherapsidus*, but it does not extend as far anteriorly~~, approach the anterior margin of the lacrimal~~ (Ivakhnenko 2011). Posteriorly, it contacts the anterior process of the squamosal approximately midway beneath the temporal fenestra, forming the zygomatic arch.

The prefrontal is roughly triangular in dorsal view (Fig. 4). It ~~borders~~ contacts medially with the nasal and frontal. The frontal is poorly preserved. The postorbital ~~sends~~ has a long ventral process ~~to~~ that covers the lateral surface of the jugal and partially forms the suborbital bar. The anterodorsal portion of the postorbital is missing, and the posterior process is short, forming the anterio~~r~~ lateral surface of the temporal fenestra, below the parietal crest (Fig. 5).

The temporal fenestra is roughly quadrangular (Figs. 1, 4). It is only slightly longer the orbit anteroposteriorly~~with its anteroposterior length only slightly longer than the orbit length~~.

The parietal is short, forming most of the narrow intertemporal region (Fig. 4). It forms a parietal crest which is longer than half of the temporal fenestra length. There is no evidence of the parietal foramen due to the poor preservation. The parietal forms the ~~median~~middle region of the lambdoidal crest, which is mostly eroded in the specimen and also extends ventrally to contact the interparietal on the occiput (Fig. 6).

The squamosal extends ~~medially~~ to contact the parietal medially and ~~posteriorly~~ the tabular posteriorly. In occipital view, it reaches the post-temporal fossa and forms ~~the~~ its dorsolateral corner ~~of the fossa~~ (Fig. 6). The squamosal extends ventrally to encase the lateral surface of the paroccipital process of the opisthotic, which forms a rudimentary mastoid process (Fig. 3). The posteroventral margin of the squamosal forms a vertical notch to accommodate the quadrate and quadratojugal. Anteromedially, it has a long ventral process which contacts the quadrate process of the pterygoid and the paroccipital process. The squamosal sends an anteroventral process to contact the prootic medially and the epipterygoid anteroventrally (Figs. 4, 5). This process completely forms the bar anterior to the pterygo-paroccipital foramen.

Palate

The choana is confluent with the fossa for the lower canine, and it extends anteriorly to the level of last incisor and posteriorly to the level of the third postcanine (Fig. 3). The choana is bordered laterally by the maxilla and palatine, anteriorly by the premaxilla, medially by the vomer, and posteriorly by the vomer and palatine.

The unpaired vomer is wide anteriorly contacting the vomerine process of the premaxilla. The suture between these bones lies posterior to the level of the anterior margin of the choanae. Its anterior width is greater than half of the vomer length between choanae. The vomer is narrow at the

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level of the posterior margin of the choana, but it is much wider than in several akidnognathids, with the exception of *Moschorhinus* (Liu & Abdala 2017a). The greatest width of the vomer is at the level of the posterior margin of the choanae, and progressively reduces its width posteriorly until the contacts with the pterygoid, which is posterior to the level of anterior margin of the suborbital vacuity, as in *Oliverosuchus parringtoni* (Botha-Brink & Modesto 2011). The posterior plate of the vomer is ventrally concave, lacking a ventromedian crest. In most akidnognathids, the ventromedian crest is developed on both anterior and posterior plates of the vomer, and only on the posterior plate in *Oliverosuchus* (Botha-Brink & Modesto 2011; Liu & Abdala 2017a:fig. 6).

The palatine has a slightly curved medial suture with the vomer. Its lateral suture with the maxilla ~~extends~~ is almost parallel ~~with~~ to the lateral margin of the skull (Fig. 3). The posterolateral process of the palatine extends to the middle~~way~~ of the lateral margin of the suborbital vacuity. The posteromedial side covers the pterygoid. The medial portion of the palatine almost lies on the same plane ~~to~~ than the nearly flat lateral portion, and the posterior part of the crista choanalis is a crest on a nearly flat surface. The crista choanalis turns laterally behind the posterior margin of the choanae, and ~~it directs~~runs to the notch on the anterior margin of the suborbital vacuity. On the lateral portion, the palatine bifurcates ~~as~~ in two short anterior processes located lateral and medial to the maxillo-palatine foramen. The maxillo-palatine foramen lies at the level of the anterior margin of the first postcanine.

The suborbital vacuity is large, slightly longer than wide (Fig. 3). The vacuities in the specimen have different size, but the left one seems to be less distorted and closer to the natural size. The vacuity is formed anteriorly by the palatine, medially and posteriorly by the pterygoid, posterolaterally by the ectopterygoid. On the medial margin of the vacuity, the palatine and the pterygoid form two parasagittal crests, which become two tuberosities. Between them, a prominent ventromedial tuber lies anterior to the interpterygoid fossa, similar to the morphology observed in *Promoschorhynchus* (Mendrez 1974b). The lateral lamina of the pterygoid is poorly developed.

The transverse process extends laterally and terminates in a swollen tuberosity (Fig. 3) as in *Annatherapsidus* (Ivakhnenko 2011)~~,~~ and *Oliverosuchus* (Botha-Brink & Modesto 2011). The transverse process is more or less horizontal on the medial side, but it turns nearly vertical ~~on the lateral side~~laterally.

The ectopterygoid is contacted ventrally and anteriorly by the palatine, and it expands dorsoventrally ~~for~~ at the posterior portion. The ectopterygoid forms a fossa on the posterolateral corner of the suborbital vacuity.

The interpterygoid fossa is quite small, as in *Annatherapsidus* (Ivakhnenko 2011). It lies at the base~~s~~ of the transverse processes. The very short edges of the interpterygoid fossa meet ~~behind the posterior edge of the transverse process~~ to form a posteromedial crest which is connected with the high and sharp parasphenoid keel. The basisphenoid process of the pterygoid extends posteriorly to

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form the lateral~~ly~~ margin of the external opening of the internal carotid canal with the parabasisphenoid. The lamina between the quadrate process and the basisphenoid process is strongly concave ventrally, bordered laterally by the strong crest of the quadrate process. ~~The quadrate process of the pterygoid extends posterolaterally.~~

The dorsal portion and possible partial ventral portion of the right quadrate is preserved. It is an expanded lamina located adjacent to the anterior surface of the squamosal. There is no evidence of the quadratojugal.

Braincase

The parabasisphenoid features ~~an~~ anteriorly the parasphenoid keel and a wide, deep groove located between the strong spheno-occipital tubercles (Fig. 3). The parabasisphenoid forms the majority of the anterior margin of the fenestra ovalis, while ~~–~~the basioccipital form the medial margin of the fenestra ovalis.

The posterior portion of the basicranium is incomplete with part of the basioccipital and exoccipitals eroded (Fig. 3). Anteriorly, the basioccipital participates in the formation of the spheno-occipital tubercle; laterally, it contacts the opisthotic and, posterolaterally, it sutures with two exoccipitals forming the ventral margin of the foramen magnum (Fig. 6).

The exoccipital forms the lateral portion of the occipital condyle and the foramen magnum (Fig. 3). The bone is nearly triangular in occipital view (Fig. 6). Its medial side forms the lateral wall of the foramen magnum, and its ventral side contributes to the roof of the large jugular foramen. The exoccipitals do not meet along the midline.

The occiput is inclined posteriorly (Fig. 3). In the occiput, the supraoccipital is fairly broad. It participates in the upper margins of the foramen magnum, separating the exoccipitals (Fig. 6). Anteriorly, it is also exposed in the temporal fossa (Fig. 5). From the margin of the foramen magnum, the supraoccipital has a ridge extending dorsolaterally that continues on the~~–~~ tabular, as in *Moschorhinus* (Durand 1991). The area between these ridges ~~is~~ has a deep indentation, mainly on the interparietal and the supraoccipital, for the attachment of the supravertebral cervical muscles. The supraoccipital has a short lateral extension between the opisthotic and the tabular.

The rectangular interparietal is a broad but low bone, with a short median ridge (Fig. 6). The high tabular forms a substantial portion of the lambdoid~~al~~ crest. It extends ventrally to contact the dorsolateral corner of the supraoccipital. Its ventral tip forms part of the dorsal border of the post-temporal fenestra.

The opisthotic consists of a robust paroccipital process, which forms the ventral border of the post-temporal fenestra in the occiput (Fig. 6). A shallow notch divides the mastoid process from the

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longer quadrate process (ventral flange). The mastoid process only has a rudimentary extension posteriorly, along with the posterior flange of the squamosal. A well-developed posterodorsal process of the opistothic contacts the tabular dorsolaterally and the supraoccipital dorsomedially, and forms half of the dorsal margin of the post-temporal fenestra. The internal process forms a lamina between the fenestra ovalis and the jugular foramen.

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The left prootic is well preserved. Its basal area is in contact with the parabasisphenoid posteriorly and it forms the lateral side of the anterior border of the fenestra ovalis (Fig. 3). Its anteroventral and anterodorsal processes are not well-exposed, partially covered by the epipterygoid (Fig. 5). Dorsally, the prootic contacts the supraoccipital, and posterior to the epipterygoid there is a triangular incisure, interpreted as a venous foramen. The long posterodorsal and posteroventral processes contact the squamosal and nearly form the entire dorsal and ventral margins of the posttemporal fenestra. There is no central process as described in *Promoschorhynchus* (Mendrez 1974). In ventral view, the suture between the prootic and the opisthotic runs medially towards the fenestra ovalis and continues on the dorsal border of the fenestra.

Both epipterygoids are preserved, but only the left one is complete (Figs. 3-5). It is a flat, blade-like bone (Fig. 5). It expands dorsally to contact the parietal, and its posterodorsal process contacts the supraoccipital posteriorly. It has a posterior apophysis ~~posterior~~ to the posterior foramen, which overlaps the anterodorsal process of the prootic. The basal part expands anteroposteriorly to cover nearly half length of the quadrate ramus of the pterygoid. The posteroventral process contacts the squamosal, and a foramen [f in Figs. 3, 4] is separated from the large cavum epiptericum.

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Mandible

Both mandibles are preserved, but the right one is more complete (Figs. 1, 7). The dentary is long and deep, and the well-developed coronoid process has a straight terminal end. The horizontal ramus is constricted in height behind the canine, and distinctly expands posteriorly to the last postcanine (Fig. 7). A tall unfused symphysis forms a deep anterior chin. It is smoothly convex anteriorly in lateral view, forming an angulation of 110° with the dentary ventral margin. The dentary lateral surface is convex outwards, lacking any fossa. The dentary angle, anterolateral to reflected lamina, is rounded and slightly convex.

The dentary contains three or four incisors, one canine and five or six postcanines. It seems to be four incisors in CT image, with the fourth being smaller and located laterally to the others. Five inclined posteriorly postcanines are counted on the left, but six on the right. However, the first right postcanine could be a replacing canine too. The first left postcanine is smaller than the others, whereas the last right postcanine (4 mm) is less than half the size of the previous teeth.

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The splenial is an elongated bone (Fig. 3). Anteriorly, it meets the counterpart and participates in the formation of the lower part of the symphysis. It reaches the highest point below the second postcanine where its dorsal border is closer to the upper margin of the dentary, and decreases ~~the~~ in height from there until the level of the last postcanine, from where it extends posteriorly as a slender rod. It contacts the angular posteriorly, behind the level of the transverse process, but the ~~exact~~ suture is not clearly visible. The ventral margin of the splenial is nearly confluent with that of the dentary near the symphysis, but it gradually rises posteriorly.

The postdentary fossa is elongated and formed by the surangular, prearticular, and angular (Fig. 7). The surangular is a narrow strip, having a concave ventral margin as the dorsal border of the mandibular fenestra. The mandibular fenestra is exposed laterally posterior to the dentary. The angular forms the ventral border of the fenestra on the lateral side. The angular reflected lamina has a wide 'U'-shaped notch posteriorly, which is most posteriorly than dorsally directed. The lateral surface of the reflected lamina is ornamented by ridges, grooves and corrugations. The prearticular is a narrow, splint-like bone, which extends anteriorly to the level of the transverse process (Fig. 3). It forms the ventral margin of the mandibular fenestra on the medial side. A triangular coronoid forms the anterior margin of the mandibular fenestra on the medial side. The articular is partially preserved but with no features to mention.

Postcranial skeleton

Some disarticulated postcranial bones were preserved with the skull. The following are the only identifiable elements.

Pectoral girdle. Only part of the ventral portion of the right scapula (Fig. 8A) ~~was~~ is preserved. The right coracoid is complete, and a small piece of procoracoid is fused to it (Fig. 8B, C). The glenoid fossa seems to be only formed by the coracoid and scapula. The coracoid is expanded ventrally and curved inwards towards the midline. The tuberosity for the coracoid head of the triceps~~'~~ ~~coracoid head~~ lies posteroventral to the glenoid and far from it, as in *Promoschorhynchus* (Huttenlocker et al. 2011) and other therocephalians (Kemp 1986). A small fossa lies on the posterodorsal side of the medial surface of the coracoid, just below the articular surface, and some longitudinal striations are observed anterior to this fossa. This might be the area for attachment of the muscle subcracoideus.

Forelimb. The right humerus lost most of its proximal and distal ends (Fig. 8D, E). The proximal half of the bone curves dorsally relative to the distal half. The proximal half is broad, with a smoothly concave ventral surface limited anteriorly by the deltopectoral crest and posteriorly by a ridge. The middle diaphysis is short and approximately circular in cross section, beyond which the

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bone expands to form the wide distal region. A large entepicondylar foramen lies in the posterior face and opens anteriorly into a deep trough on the ventral surface.

The proximal portions of the right ulna and radius are preserved. The ulna has no olecranon process, and the proximal side is rough (Fig. 8F, G). In anterior view, the proximal articular facet is lateromedially expanded. Ventral to the proximal end is a fossa for the origin of extensor musculature~~muscle origin~~ (Fig. 8F). The radius has a thin shaft and expanded end. The proximal articulating facet is concave (Fig. 8H, I). A sharp ridge extends on the posterior side of the bone, below the facet for articulation to the ulna.

Elements of four digits of the right manus, identified as digit I-IV, are preserved together (Fig. 9). Their shape is similar to that of *Oliverosuchus* (Botha-Brink & Modesto 2011). Distal carpals 1 and 2 are preserved. The medial surface of the distal carpal 1 is strongly concave and the distal is articulated to the metacarpal I. A bone in contact with the metacarpal II is interpreted as an out of place distal carpal 2. The bone is relatively large and transversely expanded on one side. Metacarpals I-IV are nearly complete, measuring 7, 22, 29, and 30 mm respectively. The rectangular, wider than longer, metacarpal 1 is remarkably short and squat, differing of the quadrangular element of *Olivierosuchus* (Botha-Brink and Modesto, 2011: text-fig. 7). The other three metacarpals are long with expanded ends, and with similar length of the III and the IV, which are longer than the II. A s~~S~~imilar pattern of metacarpal lengths is represented in *Olivierosuchus* (Fontanarrosa et al, 2018: fig. 3B). The diaphysis of the metacarpal II is remarkably wider than ~~those~~ that of metacarpals III and IV (Fig. 9B). The phalanges preserved for each digit are 2-2-1-3, including three disarticulated phalanges from digit IV (Fig. 9C, D). The terminal (ungual~~a~~) phalange is narrow, pointed and claw-like, while the others are short, broad and squat.

DISCUSSION

The fossil record of therocephalian has been historically poorly represented in the extensive exposures of the terrestrial Chinese Permian. However, recent discovery of two new, definite, late Permian therocephalians (Liu and Abdala, 2017a, 2017b) are challenging this situation. The akidnognathid *Shiguaignathus wangi*, was the first therocephalian reported for the faunal association of the Naobaogou Formation. IVPP V 23877, here described as *Jiufengia jiai*, is the second therocephalian and, in turn, the second akidnognathid of the Naobaogou ~~fauna~~ assemblage ~~for~~ according to the following features: a septomaxilla well exposed outside of the external naris, broadly overlapping the premaxilla anteriorly; a very expanded vomer, broadly overlapping the vomerine process of the premaxilla; and contribution of the premaxilla and maxilla to a fossa for the lower canine on the palatal surface.

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Jiufengia jiai is different from the smaller *Shiguaignathus wangi* from the same horizon by the presence of four upper postcanines, presence of a large suborbital vacuity, and ventral surface of vomer flat, lacking a ventromedian crest.

The dental formula of *Jiufengia jiai* is I5:pC2:C1:Pc4/i4:c1:pc5. Only ~~some~~ *Moschorhinus* and *Olivierosuchus* (with three; Durand 1991; Botha-Brink & Modesto 2011)~~;~~ and *Euchambersia* (with none; Benoit 2016) have less postcanines than *Jiufengia jiai*. Remaining akidnognathids have from five (e.g., *Promoschorhynchus*) to a maximum of eight only recorded in the other Chinese Permian akidnognathid, *Shiguaignathus* (Liu and Abdala 2017b). *Jiufengia jiai* ~~It~~ can also be differentiated from other akidnognathids by the long snout which is more than half the skull length, the transverse process is anterior to the orbit, the ventral surface of the vomer is flat along the middle line, lacking a ventromedian crest, and anterior process of jugal nearly leveled to the anterior margin of the lacrimal. All these characters show that this specimen represents a new species within Akidnognathidae.

The suborbital vacuity of *Jiufengia jiai* is more similar to *Annatherapsidus* than other taxa in ~~the~~ its ~~big~~ large size, anterioposterior length greater than the width, long and relatively straight lateral margin which is more anteriorly than medially directed, and ~~the~~ posterior margin nearly laterally directed. But its anterior margin has a deep notch, but smoothly as the latter (Ivakhnenko 2011).

To reconstruct the phylogenetic position of *Jiufengia jiai*, we coded it in our previous matrix (Liu & Abdala 2017a) and we also included as a terminal the recently described Russian therocephalian *Gorynychus* (Kammerer & Masyutin 2018). The matrix was analyzed with TNT 1.5 (Goloboff & Catalano 2016), as in Liu & Abdala (2017a)~~:~~ the search for most parsimonious trees (mpt) consisted of 10 random addition sequences and TBR, saving 10 trees per replications, and a second search using the trees from RAM as starting point and implementing TBR on those trees. Seventeen multistate characters were considered as additives. The search resulted in 7560 mpt of 384 steps in which most of the major groups of Therocephalia are recovered as monophyletic (Fig. 10). The result is nearly identical to our previous analysis (compare the consensus tree in figure 10 with the right one in figure 7 of Liu & Abdala, 2017a). The only differences to report are in the placement of the two new terminals added in the current study. *Jiufengia jiai* is recovered as a basal akidnognathid, following a politomy at the base of this clade that include the other two Laurasian akidnognathids *Shiguaignathus* and *Annatherapsidus* (Fig. 10). Besides of the Laurasian most basal records of Akidnognathidae, the current evidence shows medium-to-large sized Permian akidnognathids in Laurasia. On the contrary, from the four late Permian akidnognathids in the Karoo Basin, only *Moschorhinus* at the end of the Permian shows a large size (maximum skull length 262 mm; Huttenlocker and Botha-Brink, 2013), with remaining taxa ranging between 107 and ~135 mm in skull length (Table 2). The youngest record of akidnognathid in the Karoo, represented by *Olivierosuchus* is the smaller representative of the linage. In contrast two of the

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three Laurasian akidnognathids show large sizes (above 200 mm, Table 2), and only *Shiguaignathus* is a medium-sized animal.

Although the current matrix is different from that of Kammerer & Masyutin (2018) in a few characters, the result is quite different regarding the placement of the Russian *Gorynychus* and *Perplexisaurus*. In our analysis *Gorynychus* is one of the basalmost therocephalians, recovered as sister taxon of *Lycosuchus* (altough only in the majority consensus tree; Fig. 10). Two characters are producing this monophyly: a deep suborbital bar and five or less upper postcanines in adults. *Perplexisaurus* is recovered as a basal member of the recently defined clade Chthonosauridae (Huttenlocker & Sidor, 2016). This group has only one synapomorphy: parietal crest in adults extends forward to include parietal foramen. However the score of this character is ~~a question mark~~not known in *Ichibengops*, therefore the only synapomorphy of the group is not strictly speaking a real one.

The differences between our results (that reflect mostly the hypothesis of Huttenlocker and coworkers) and that of Kammerer & Masyutin (2018) show~~s~~ unstability in current ~~hypothesis~~ hypotheses of therocephalian relationships, which is evident in the support values of monophyletic groups represented in Figure 10. Thus, supports are overall low and they are especially poor in basal Therocephalian, Eutherocephalia, Chtonosauridae, basal Akidnognathia, Whaitsoidea, Whaitsiidae, and Lycideopidae.

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Table 1 Measurements of IVPP V 23877 (in mm)

Dorsal skull length, from tip of the snout to posterior margin of squamosal/occiput	250
Basal skull length from tip of the snout to occipital condyle	225
Maximum skull width	~170
Snout (preorbital) length (left side)	145
Length from tip of the snout to anterior border of temporal fenestra	186
Breadth of rostrum at level of canines	68
Length of maxillary dentition	60
Total length of upper postcanine tooth row	32