Late Permian terrestrial faunal connections invigorated: the first whaitsioid therocephalian from China

Jun Liu[1,2*] [§] & Fernando Abdala[3,4]

[1]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, People's Republic of China
[2]College of Earth and Planetary Sciences, University of Chinese Academy of Sciences, Beijing 101408, People's Republic of China
[3]Unidad Ejecutora Lillo, CONICET, Fundación Miguel Lillo, Miguel Lillo 251, Tucumán, Argentina
[4]Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa

Received 24 February 2023. Accepted 25 May 2023

The record of therocephalian therapsids from the late Permian of China has recently been greatly expanded by the discovery of several new taxa of Akidnognathidae, a group previously known principally from South Africa and Russia. Continuing this string of discoveries, we present here the first Chinese record of a whaitsiid therocephalian. This is also the first record published of a tetrapod from Jingtai, Gansu, a late Permian locality that also yields remains of other groups such as dicynodonts, captorhinids, and chroniosuchians. This is the third taxon of whaitsiid therocephalian recognized in North Pangea. The new therocephalian is similar to the Russian *Moschowhaitsia vjuschkovi* in overall appearance, and although they are only recovered as sister-taxa in 6 out of 30 most parsimonious trees in our phylogenetic analysis, it is tentatively referred to *Moschowhaitsia* as a new species, *M. lidaqingi*. The phylogeny obtained is largely similar to previous hypotheses, recovering three main lineages of Eutherocephalia: Akidnognathidae, Whaitsioidea and Baurioidea. However, it differs from previous analyses in finding Chthonosauridae (comprising the Russian *Chthonosaurus* and Zambian *Ichibengops*) to be deeply nested within Whaitsioidea. Therocephalians were among the largest carnivores in the late Permian of North China, and may have represented the top predators in some faunas.

Keywords: Pangaea, Therocephalia, Permian, Sunan Formation, China.

INTRODUCTION

Therocephalia is an important therapsid clade known from the middle Permian to the Middle Triassic, with the bulk of its diversity held in four major lineages: Scylacosauridae, Akidnognathidae, Whaitsioidea, and Baurioidea (Huttenlocker 2009; Huttenlocker & Smith 2017; Liu & Abdala 2017, 2022). Baurioids have been known from Chinese Triassic strata for a long time (Young 1952) and are represented by at least five species (Li & Liu 2015; Liu & Abdala 2015). More recently, akidnognathids have been reported from the late Permian Naobaogou Formation, and four species are now known from that unit (Liu & Abdala 2017, 2019, 2020, 2022). The other major therocephalian subclades, however, have heretofore proven elusive in the Chinese Permian, notably whaitsioids, which are common in southern African assemblages and are also well-represented in Russia (Huttenlocker & Smith 2017).

In 2020, an expedition led by Drs Li Da-Qing and Yi Hong-Yu led to the discovery of the first late Permian tetrapod fossils from Jingtai County in Gansu. Over the course of three field seasons, many fossil tetrapods were collected from this area, including therocephalians, dicynodonts, captorhinids, and chroniosuchians. Although this fauna is generally similar to that from the Naobaogou Formation in Nei Mongol, different taxa were also found, including a large partial skull of the first Chinese whaitsioid therocephalian. Here we describe this material and discuss its phylogenetic position.

GEOLOGICAL BACKGROUND

The fossil was preserved in a nodule (concretion) from a layer of maroon siltstone, interbedded with pale purple sandstones. The fossil bed had been referred to as the lower part of the Wufoshi Formation, unofficially established by Wang De-Xu in one unpublished report but later introduced by Cai (1993). However, the bed in question has the same lithological characters as the upper part of the late Permian Sunan Formation (Li 2000), and is referred to that unit here.

MATERIAL AND METHODS

The new Chinese whaitsioid specimen, IVPP V31741, consists of a cranial fragment including the snout, partial right orbital region, and partial left postorbital bar.

The following comparative materials of whaitsioid therocephalians were consulted: *Chthonosaurus velocidens*: PIN 521/1; *Microwhaitsia mendrezi*: SAM-PK-K10984, K10990; *Moschowhaitsia vjuschkovi*: PIN 1100/19, 20, 21, 30, 69, 74; *Theriognathus microps*: AM 4045; BP/1/9, 100, 104,

---

*Author for correspondence. E-mail: liujun@ivpp.ac.cn

***Palaeontologia africana* 56: 111–117 — ISSN 2410-4418 [Palaeontol. afr.] Online only**
ZooBank: urn:lsid:zoobank.org:pub:6704C1A3-926E-4A45-AAB3-D8B86039D6A0 (https://zoobank.org)
Permanently archived on the 21st of July 2023 at the University of the Witwatersrand, Johannesburg, South Africa.
This article is permanently archived at: https://hdl.handle.net/10539/35706

145, 153, 160, 163, 164, 182, 512, 655, 717, 719, 724, 747, 785, 844, 870, 891, 1202, 1567, 4093, 4123; CGS GHG137, K274, K280, WB261; GPIT-PV-60909 (formerly GPIT/RE/7142; K65), 116187 (formerly GPIT/RE/7143; K10), 117093 (formerly GPIT/RE/7144; K44), 117147 (formerly GPIT/RE/7154; K45), 117140 (formerly GPIT/RE/7161; K84), 117089 (formerly GPIT/RE/9277; K135), 117091 (formerly GPIT/RE/9278; K50), 117098 (formerly GPIT/RE/9279; K119); NHMUK PV OR 47065, R 5694, R 5698, R 5699, R 5748; NMQR 1549, 3375; RC 108/L2, 211, 213, 214, 380; SAM-PK-4006, K5263, K6984, K7453, K7511, K10429, K10981; TM 264, 258, 280; UCMP 42675, 42676; UMZC T.357, T.898, T.900, T. 901, T.902, T.903, T.904, T.994 (see Huttenlocker & Abdala 2015); *Viatkosuchus sumini*: PIN 2212/13.

SYSTEMATIC PALAEONTOLOGY

Therocephalia Broom, 1903
Eutherocephalia Hopson & Barghusen, 1986
Whaitsiidae Haughton, 1918

Moschowhaitsia Tatarinov, 1963

Type species. *Moschowhaitsia vjuschkovi* Tatarinov, 1963.

Diagnosis. Therocephalian with five upper incisors of which the fifth is much smaller than the others; seven small upper postcanines; rugose bone surface on orbital margin, with rugosities forming prefrontal boss; maxillary ventral margin with a distinct notch; maxillovomerine bridge present (also in *Theriognathus*).

***Moschowhaitsia lidaqingi* sp. nov.**

Figures 1, 2

LSID. urn:lsid:zoobank.org:act:D782B253-A028-4855-9F41-234106C3B118

Holotype. IVPP V31741, a snout, partial right orbital region, and partial left postorbital arch.

Type locality and horizon. Kushuiquan, Xiwan, Wufo Township, Jingtai County, Gansu Province, China; Sunan Formation (Lopingian, Permian).

Etymology. Dedicated to Dr Li Da-Qing, for his contribution to the discovery of late Permian tetrapods from Jingtai.

Diagnosis. Differentiated from *M. vjuschkovi* by larger size; lacrimal low and long, forming only the anteroventral orbital margin; more-developed notch on maxillary ventral margin anterior to the canine; vomerine ventral surface smooth and relatively flat, except for a short, shallow ridge at the posterior interchoanal portion.

DESCRIPTION

The bone surfaces of the partial skull are well preserved with distinct sutures (Figs 1, 2). The snout is slightly distorted, so the left side is narrower and higher than the right side. A small piece of bone seems to be missing between the two preserved portions (Fig. 1B,D).

The preserved portion (from the tip of the snout to the posterior margin of the right orbit) is ~21 cm. Based on comparisons with the corresponding portion of PIN 1100/20, the complete skull is estimated to be at least 35 cm in length, longer than the largest known skull of *Theriognathus* (Huttenlocker & Abdala 2016).

The premaxilla lies at the anterior tip of the skull, and is composed of distinct dorsal, maxillary, and vomerine processes (Figs 1, 2A). It forms the anterior portion of the anterolaterally-facing external naris. The dorsal process extends anterodorsally, then curves backwards and wedges between the anterior processes of the nasals. Its posterior end terminates anterior to the level of the posterior margin of the external naris. The rostral surface bears one (on the left side) or two (on the right side) anterior premaxillary foramina (Fig. 2A). Lateral to them, a few smaller nutrient foramina are observed on the right premaxilla.

On the palatal surface there are five alveoli for the incisors, with the most distal one being considerably smaller than the others (Fig. 1B). Another small (paired) posterior premaxillary foramen lies immediately posterior to the first incisor alveolus, as in *Moschowhaitsia vjuschkovi* (Ivakhnenko 2011), but it is unclear whether the median palatal foramen is present as in *Theriognathus microps* (Huttenlocker & Abdala 2015). The vomero-premaxillary suture is indistinct. The vomerine process of the premaxilla appears to form most of the medial wall of the anterior portion of the internal naris (which is confluent with the paracanine fossa).

The septomaxilla has a long, narrow facial exposure between the nasal and maxilla and a broad footplate (Figs 1, 2A). Its footplate is roughly trapezoidal on the lateral surface of the premaxilla, with a slightly concave medial process forming the posteroventral wall of the naris. On the anterior tip of the medial process, a short, round process points anterodorsally. The septomaxillary foramen is situated on the posterior margin of the footplate, just below the posterior portion of the external naris.

Both maxillae are nearly complete and are the largest bones of the snout. The maxilla has distinct canine buttresses that would have housed large canines. Near the anterior margin of the maxilla, a shallow fossa lies below the septomaxillary foramen. As in *Moschowhaitsia*, there is a gentle medial constriction of the snout posterior to the canine buttress visible in ventral view. The dorsal lamina of the maxilla is tall and medially curved, with a wide exposure in dorsal view. Above the canine buttress, the lateral surface of the dorsal lamina bears a swollen, pitted area, on whose ventral margin are located a few nerve foramina. The jugal process tapers posteriorly, contacting the lacrimal and jugal, and extends further posteriorly along the medial surface of the jugal, below the orbit.

A short diastema is present between the fifth incisor and the canine. In lateral view, a marked notch is present anterior to the canine on the maxillary ventral margin (Fig. 1C,D). This notch lies within the diastema on the left side, and near the range of the canine alveolus on the right side. The right area of the diastema forms a convex ventral margin. The canine alveolus is large and located anteriorly. Its posterior portion is filled by spongy alveolar bone. This may be the position of the replaced canine. Posteriorly, there are seven postcanine alveoli on the left

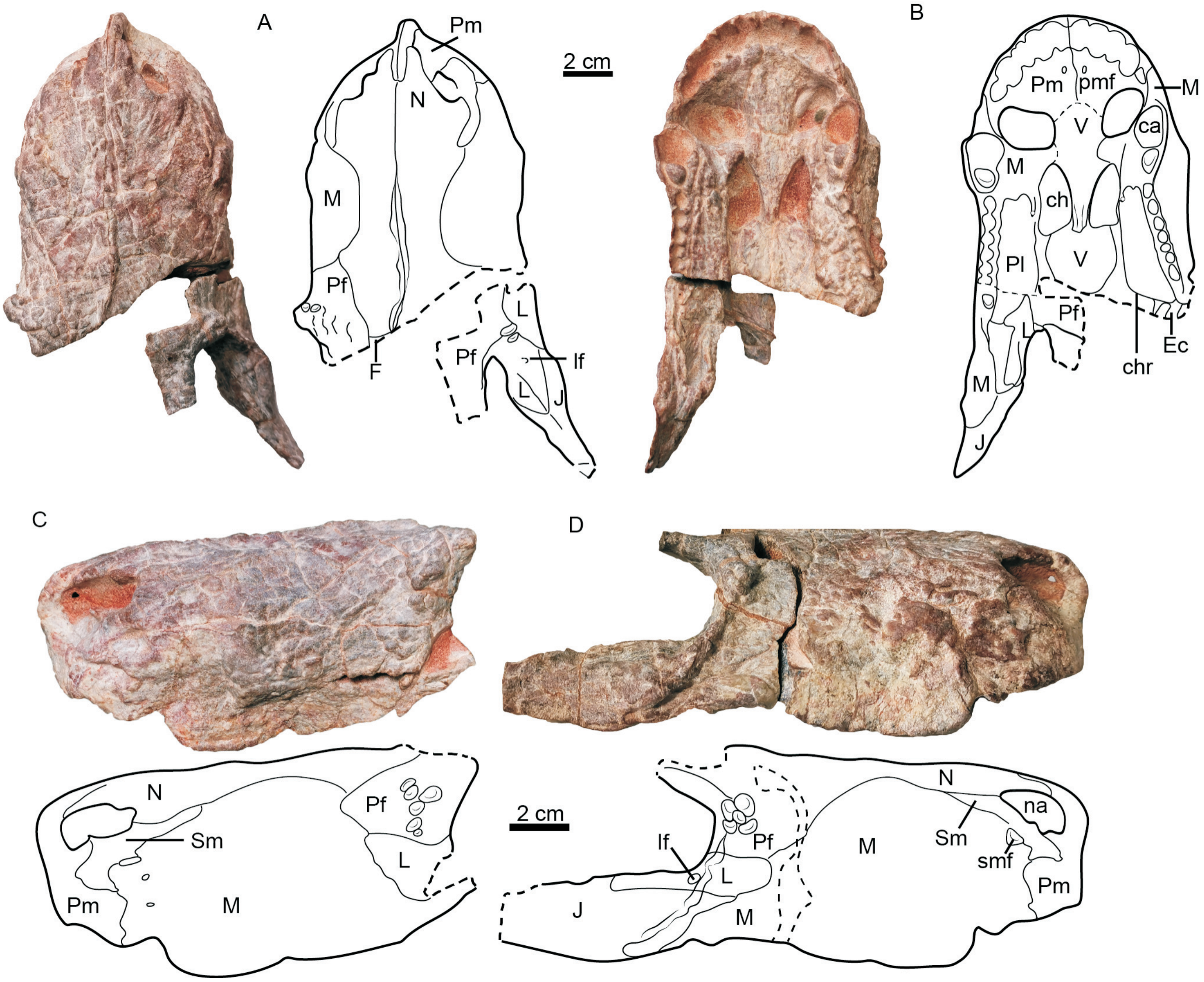

Figure 1. *Moschowhaitsia lidaqingi* sp. nov. photographs and interpretive drawings in dorsal (**A**), ventral (**B**), left lateral (**C**), and right lateral (**D**) views. ca, canine alveolus; ch, choana; chr, choanal ridge; Ec, ectopterygoid; F, frontal; J, jugal; L, lacrimal; lf, lacrimal foramen; M, maxilla; N, nasal; na, naris; Pf, prefrontal; Pl, palatine; Pm, premaxilla; pmf, premaxillary foramen; Sm, septomaxilla; smf, septomaxillary foramen; V, vomer.

upper jaw. Although there is a gap on the right side, there also appear to be seven postcanine alveoli, and the missing portion is very narrow. The anterior alveoli are generally larger than the posterior ones.

Medial to the canine alveolus, the maxilla sends a stout medial process to suture with the lateral process of the vomer, separating the internal naris into an anterior choanal portion coalesced with the paracanine fossa and a posterior choanal portion. Posteriorly, at the level of the first postcanine, the maxilla is covered by the palatine ventrally and a small maxillopalatine foramen is present on the maxilla-palatine suture near the crista choanalis. The sharp crista choanalis extends from the level of the canine and continues further posteriorly along the palatine, almost parallel with the maxillary ventral margin.

The long nasal is bordered by the premaxilla and external naris anteriorly, the septomaxilla anterolaterally, the maxilla laterally, the prefrontal posterolaterally, and the frontal posteriorly. The midline suture is relatively straight except for the posterior portion, which may be due to distortion. A low buttress rises on the suture around the level of the posterior tips of the septomaxilla and forms the median frontonasal ridge. The nasal is very narrow near its centre due to the tall dorsal lamina of the maxilla. The frontonasal suture lies at the level of the anterior orbital margin.

Neither of the prefrontal bones are complete, but a nearly complete shape can be determined by combining information from both sides. A relatively long anterior process sutures with the nasal medially and the maxilla anteriorly. It forms the dorsal half of the anterior orbital wall. A rounded boss formed by rugose, nodular bone lies on the anterodorsal corner of the right orbit, slightly above the suture with the lacrimal.

The right lacrimal is completely preserved. It forms the anteroventral margin of the orbit. As in *Moschowhaitsia*, the bone surface is rugose with nodules. The lacrimal contacts the dorsal lamina of the maxilla anteriorly, the prefrontal dorsally, and the jugal ventrally and posteriorly. The lacrimal foramen lies inside the anterior wall of the orbit.

The jugals are partially preserved. The left one has only a small part of the suborbital portion, whereas the right one has almost the complete suborbital portion (Fig. 1C,D). It extends anteriorly slightly beyond the anterior border of the orbit and tapers anteriorly between the lacrimal and maxilla. The anterior suborbital bar, formed by the jugal, lacrimal, and maxilla, is deep and wide. The medial side of the left postorbital bar is missing. The rest of the bar shows lateral expansion and thinning. The jugal forms a scarf joint with the postorbital and is partially covered dorsolaterally by the latter (Fig. 2B).

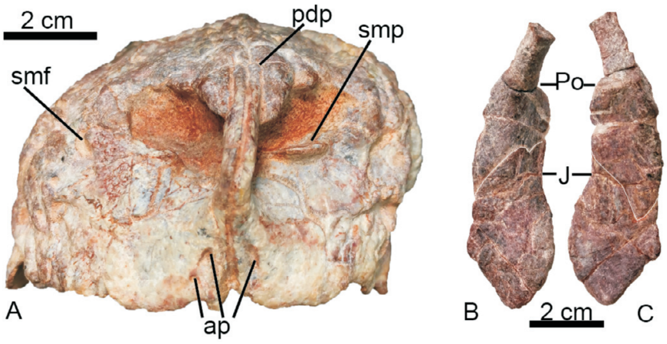

Figure 2. *Moschowhaitsia lidaqingi* sp. nov. snout in anterior view (**A**) and incomplete left postorbital arch in ventromedial (**B**) and dorsolateral views (**C**). ap, anterior premaxilla foramen; J, jugal; pdp, premaxillary dorsal process; Po, postorbital; smf, septomaxillary foramen; smp, septomaxillary medial process.

The vomer is almost complete except for the posterior tip. It is well exposed in palatal view (Fig. 1B). The anterior tip of the interchoanal process appears constrained by the premaxilla laterally. The interchoanal process reaches its widest point at the maxillo-vomerine bridge. The posterior portion of the interchoanal process is relatively wide, as in the other whaitsiids *T. microps* and *M. vjuschkovi* as well as the akidnognathid *Jiufengia jiai*. The ventral surface is almost flat, with only a low and short (<1 cm) ventral median ridge on the posteriormost portion of the interchoanal process. The postchoanal portion of the vomer is relatively wide and flat, with a maximum width at the middle, which is wider than the widest part of the interchoanal process. There is no ventromedian crest on the vomer between the palatines.

The palatine is a broad bone on the palate that borders the choana laterally and posteriorly. It is divided into two portions by the crista choanalis: a wide lateral portion and a narrow medial portion. The palatal surface of the lateral portion is rugose. The right palatine preserves the posterior portion, which contacts the lacrimal dorsally. This portion is exposed due to the missing ectopterygoid. The left ectopterygoid is only partially preserved (Fig. 1B).

DISCUSSION

The most distinct feature of this new therocephalian specimen is the maxillovomerine bridge, separating the anterior internal choana, coalesced with the paracanine fossa, from the posterior internal choana. This feature is restricted to only a few therocephalians, notably the whaitsiids *Theriognathus* and *Moschowhaitsia*, and questionably the chthonosaurid *Ichibengops* (Huttenlocker & Abdala 2015; Huttenlocker *et al*. 2015; Ivakhnenko 2011). The new specimen can be easily differentiated from *Theriognathus* by the presence of seven upper postcanines (all postcanines are absent in that taxon) and from *Ichibengops* by the presence of a median frontonasal crest. It is more difficult to differentiate from *Moschowhaitsia*, sharing several features with *M. vjuschkovi*: five upper incisors in which the fifth is much smaller than the rest, seven small upper postcanines, spongy alveolar bone posterior to the canine, rugose bone on the orbital anterior margin, and a maxillary ventral margin with a distinct notch. However, the new specimen can be distinguished from *M. vjuschkovi* by the shape of the lacrimal, which is low and long, only forming the anteroventral margin of the orbit. So a new species, *M. lidaqingi*, is here established within *Moschowhaitsia*.

The new species also shows some other minor differences from *M. vjuschkovi*. Although a distinct notch was not shown in reconstructions of this species (e.g. Ivakhnenko 2011: figs 15d, 17a), one can be observed lateral to the canine on both sides of the holotype, PIN 1100/20. By contrast, the notch is anterior to the canine in IVPP V31741 and is deeper. The jugal is restricted to the anterior margin of the orbit on the left side of PIN 1100/20 (Ivakhnenko 2011: fig. 15d), but it extends anteriorly beyond the anterior margin of the orbit on the right side in IVPP V31741. In IVPP V31741, the vomerine ventral surface is smooth and relatively flat, except for a short, weak ridge at the posterior interchoanal portion, but a distinct ridge is developed on this surface in PIN 1100/20. The rugose area on the orbital margin is better developed and the prefrontal boss formed by these rugosities is more distinct in IVPP V31741 than in PIN 1100/20. Some of these differences could be due to intraspecific variation, especially ontogenetic variation within the species (as has been shown in *Theriognathus*; Huttenlocker & Abdala 2015), but pending additional material showing variability, the position of the notch and morphology of the ridge on the vomerine ventral surface are proposed as additional diagnostic features for species within *Moschowhaitsia*.

The close relationships of these taxa are recognized by phylogenetic analysis, although the two species of *Moschowhaitsia* generally do not form a monophyletic group in our results (Fig. 3). The new species was coded for the most recent therocephalian matrix (Liu & Abdala 2022) (see Supplementary Material), and the matrix was analysed using the TNT 1.6 (Goloboff & Catalano 2016). The routine implemented consisted of 10 random addition sequences and TBR, saving 10 trees per replication, and a second search using the trees from RAM as a starting point and implementing TBR on those trees. It resulted in 30 most parsimonious trees (mpt) of 425 steps. The two species of *Moschowhaitsia* form a monophyletic clade only in 6 out of 30 mpts, where they are the sister group of *Chthonosaurus* plus *Ichibengops*.

The current analysis results in a well-resolved phylogenetic topology for Therocephalia. The strict consensus tree shows new positions for some taxa, although the major lineages and their interrelationships are mostly unchanged (Fig. 3). The major difference from previous hypotheses (e.g. Huttenlocker *et al*. 2015) is that the clade Chthonosauridae, formed by *Chthonosaurus* and *Ichibengops*, is recovered within Whaitsiidae. *Perplexisaurus*, which was recovered as sister taxon of Chthonosauridae at the base

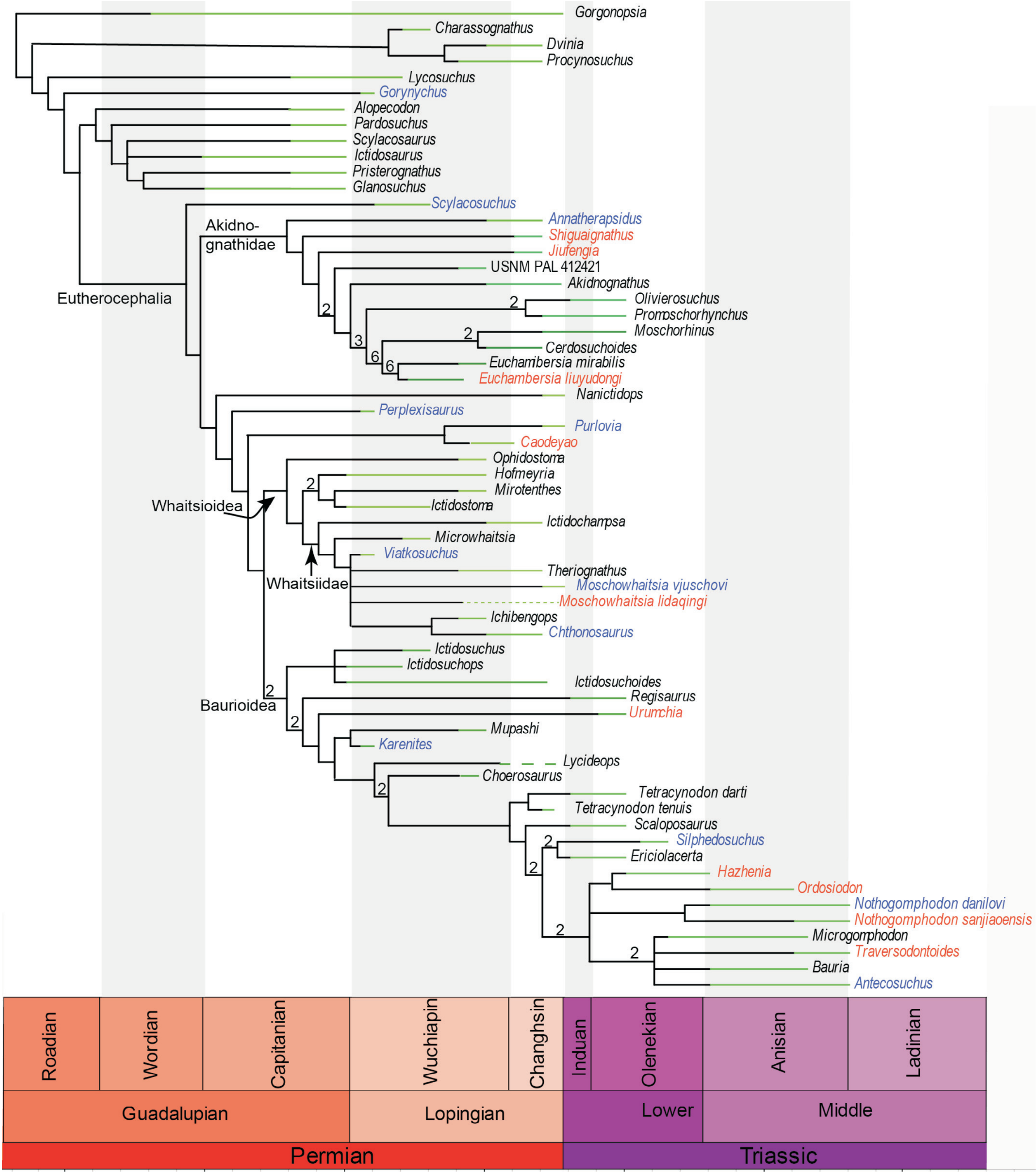

Figure 3. Calibrated strict consensus tree of Therocephalia. Therocephalian taxa from China shown in red, Russia in blue, and Africa in black. Green lines show temporal ranges of the taxa. Main therocephalian lineages indicated. Numbers above of branches represent Bremer Support.

of Akidnognathidae in our previous phylogenetic hypothesis (Liu & Abdala 2022), is now recovered outside of a major lineage formed by (*Purlovia* + *Caodeyao*), Whaitsioidea, and Baurioidea.

Moschowhaitsia lidaqingi is the first tetrapod to be described from the new locality of Jingtai and the first whaitsiid therocephalian reported for the late Permian of China. Its age is roughly contemporaneous with the tetrapod fauna of the Naobaogou Formation, where four therocephalians have been reported, including three akidnognathid species and the aberrant *Caodeyao liuyufengi* (Liu & Abdala 2017, 2019, 2020, 2022). The new find expands the Laurasian record of Whaitsioidea and strengthens the idea that the three major lineages of Eutherocephalia had a global distribution in the late Permian of Pangea.

Only a few species of eutherocephalians had skull sizes greater than 30 cm, and the maximum basal skull length is

35 cm (Huttenlocker 2014). Estimations from the preserved parts of IVPP V31741 suggest that the new taxon has one of the largest skulls known among eutherocephalians. Although therocephalians did include some large carnivores, they generally were not the top predators of their time. In South Africa and Russia, therocephalian species are generally smaller than either the dinocephalians (in the middle Permian) or gorgonopsians (in the late Permian) that coexisted with them. This applies to the largest middle and late Permian therocephalian taxa such as *Glanosuchus*, *Lycosuchus*, and *Theriognathus* (Huttenlocker 2014; Day & Rubidge 2020; Day & Smith 2020; Viglietti, 2020), albeit not to the medium-sized therocephalians *Gorynychus* and *Viatkosuchus* from the Kotelnich Fauna (Kammerer & Masyutin 2018) in which therocephalians form the bulk of the known predators.

In contrast to late Permian assemblages elsewhere, therocephalians may have been the top predators in North China at that time. Among late Permian tetrapod records from North China, known carnivores include therocephalians, chroniosuchians, and embolomeres (Liu 2021; Liu & Chen 2021; Chen & Liu 2023). Only one gorgonopsian specimen was recently reported from the late Permian of Xinjiang (Liu & Yang 2022), but no definitive gorgonopsians are known from North China, except for a canine tentatively identified as gorgonopsian (Liu *et al*. 2014). Independent of its taxonomy, its size does not indicate a large predator. Chroniosuchians were widely distributed in China, but their known skull sizes are all less than 30 cm. Only the embolomere *Seroherpeton yangquanensis* has a skull length longer than 30 cm (Chen & Liu 2020). However, like chroniosuchians, embolomeres were semi- or fully aquatic predators, and would not have competed directly with therocephalians in terrestrial food webs.

It is a pleasure and a privilege for us to present this contribution to a special issue in honor of Bruce Sidney Rubidge, who has contributed immensely to increasing and spreading knowledge of the fossil treasures of South Africa for more than 40 years. Both authors have had the opportunity to work with him and share unforgettable times on field trips to the classic *Tapinocephalus* Assemblage Zone of the Karoo. The 'Latino' F.A. is particularly grateful for the fantastic opportunity that Bruce provided for him to work at the Evolutionary Studies Institute (former Bernard Price Institute for Palaeontological Research), a renowned therapsid paradise in Johannesburg. The authors also thank the members of the field teams to Jingtai in 2020 and 2021, Su Ling-Nian and Fu Hua-Lin for fossil preparation, Guo Rui for improving line drawings and Lucinda Backwell for editing and improving the English. The comments from reviewers Christian Kammerer, Adam Huttenlocker, and Julia Suchkova significantly improved this work. This work was supported by Strategic Priority Research Program of Chinese Academy of Sciences (XDB2600 0000), the International Partnership Program of Chinese Academy of Sciences (132311KYSB 20190010), and the Chinese Academy of Sciences President's International Fellowship Initiative Grant (2022VCB0006) (to F.A.). F.A.'s research was financed by the CONICET of Argentina and the National Research Foundation of South Africa. This investigation is part of the PICT-2020-01498 grant awarded to F.A. and LJ.

ABBREVIATIONS

Institutional

AM	Albany Museum, Makhanda, South Africa;
BP	Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa;
CGS	Council for Geoscience, Pretoria, South Africa;
GPIT	Paläontologische Sammlung, Eberhard Karls Universität Tübingen, Tübingen, Germany;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China;
NHMUK	Natural History Museum, London, U.K.;
NMQR	National Museum, Bloemfontein, South Africa;
PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia;
RC	Rubidge Collection, Wellwood, South Africa;
SAM	Iziko South African Museum, Cape Town, South Africa;
TM	Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa;
UCMP	University of California Museum of Paleontology, Berkeley, U.S.A.;
UMZC	University Museum of Zoology, Cambridge, U.K.

§ORCID iDs

J. Liu: orcid.org/0000-0003-2205-9671
F. Abdala: orcid.org/0000-0001-9838-2497

REFERENCES

BROOM, R. 1903. On the classification of the theriodonts and their allies. *Report of the South African Association for the Advancement of Science* **1**, 286–294.

CAI, K-D. 1993. Triassic System in Gansu. *Acta Geologica Gansu* **1993** (suppl.), 50–100 (in Chinese).

CHEN, J. & LIU, J. 2020. The youngest occurrence of embolomeres (Tetrapoda: Anthracosauria) from the Sunjiagou Formation (Lopingian, Permian) of North China. *Fossil Record* **23**(2), 205–213.

CHEN, J. & LIU, J. 2023. A late Permian archosauriform from Xinjiang shows evidence of parasagittal posture. *The Science of Nature* **110**(1), 1. https://doi.org/10.1007/s00114-022-01823-8

DAY, M.O. & RUBIDGE, B.S. 2020. Biostratigraphy of the *Tapinocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**(2), 149–164.

DAY, M.O. & SMITH, R.M.H. 2020. Biostratigraphy of the *Endothiodon* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**(2), 165–180.

GOLOBOFF, P. & CATALANO, S. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32**, 221–238.

HAUGHTON, S.H. 1918. Investigations in South African fossil reptiles and amphibia. 11. Some new carnivorous Therapsida, with notes upon the brain-case in certain species. *Annals of the South African Museum* **12**, 175–215.

HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. **In:** Hotton, N., III, MacLean, P.D., Roth, J.J. & Roth, E.C. (eds), *The Ecology and Biology of the Mammal-like Reptiles*, 83–106. Washington, D.C., Smithsonian Institution Press.

HUTTENLOCKER, A. 2009. An investigation into the cladistic relationships and monophyly of therocephalian therapsids (Amniota: Synapsida). *Zoological Journal of the Linnean Society* **157**(4), 865–891.

HUTTENLOCKER, A.K. 2014. Body size reductions in nonmammalian eutheriodont therapsids (Synapsida) during the end-Permian mass extinction. *PLOS ONE* **9**(2), e87553. https://doi.org/10.1371/journal.pone.0087553

HUTTENLOCKER, A.K. & ABDALA, F. 2015. Revision of the first therocephalian, *Theriognathus* Owen (Therapsida: Whaitsiidae), and implications for cranial ontogeny and allometry in nonmammaliaform eutheriodonts. *Journal of Paleontology* **89**(4), 645–664.

HUTTENLOCKER, A.K., SIDOR, C.A. & ANGIELCZYK, K.D. 2015. A new eutherocephalian (Therapsida, Therocephalia) from the upper Permian Madumabisa Mudstone Formation (Luangwa Basin) of Zambia. *Journal of Vertebrate Paleontology* **35**(5), e969400. https://doi.org/10.1080/02724634.2015.969400

HUTTENLOCKER, A.K. & SMITH, R.M.H. 2017. New whaitsioids (Therapsida: Therocephalia) from the Teekloof Formation of South Africa and therocephalian diversity during the end-Guadalupian extinction. *PeerJ* **5**, e3868. https://doi.org/10.7717/peerj.3868

IVAKHNENKO, M.F. 2011. Permian and Triassic Therocephals (Eutherapsida) of Eastern Europe. *Paleontological Journal* **45**(9), 981–1144.

KAMMERER, C.F. & MASYUTIN, V. 2018. A new therocephalian (*Gorynychus masyutinae* gen. et sp. nov.) from the Permian Kotelnich locality, Kirov Region, Russia. *PeerJ* **6**, e4933. https://doi.org/10.7717/peerj.4933

LI, J-L. & LIU, J. (eds) 2015. *Basal Synapsids*, Vol. 3. Beijing, Science Press.

LIU, J. 2021. The tetrapod fauna of the upper Permian Naobaogou Formation of China: 6. *Turfanodon jiufengensis* sp. nov. (Dicynodontia). *PeerJ* **9**, e10854. https://doi.org/10.7717/peerj.10854

LIU, J. & ABDALA, F. 2015. New discoveries from the *Sinokannemeyeria-Shansisuchus* Assemblage Zone: 2. A new species of *Nothogomphodon*

(Therapsida: Therocephalia) from the Ermaying Formation (Anisian, Middle Triassic) of Shanxi, China. *Vertebrata Palasiatica* **53**(2), 123–132.

LIU, J. & ABDALA, F. 2017. The tetrapod fauna of the upper Permian Naobaogou Formation of China: 1. *Shiguaignathus wangi* gen. et sp. nov., the first akidnognathid therocephalian from China. *PeerJ* **5**, e4150. https://doi.org/10.7717/peerj.4150

LIU, J. & ABDALA, F. 2019. The tetrapod fauna of the upper Permian Naobaogou Formation of China: 3. *Jiufengia jiai* gen. et sp. nov., a large akidnognathid therocephalian. *PeerJ* **7**, e6463. https://doi.org/10.7717/peerj.6463

LIU, J. & ABDALA, F. 2020. The tetrapod fauna of the upper Permian Naobaogou Formation of China: 5. *Caodeyao liuyufengi* gen. et sp. nov., a new peculiar therocephalian. *PeerJ* **8**, e9160. https://doi.org/10.7717/peerj.9160

LIU, J. & ABDALA, F. 2022. The emblematic South African therocephalian *Euchambersia* in China: a new link in the dispersal of late Permian vertebrates across Pangea. *Biology Letters* **18**(7), 20220222. https://doi.org/10.1098/rsbl.2022.0222

LIU, J. & CHEN, J. 2021. The tetrapod fauna of the upper Permian Naobaogou Formation of China: 7. *Laosuchus hun* sp. nov. (Chroniosuchia) and interrelationships of chroniosuchians. *Journal of Systematic Palaeontology* **18**(24), 2043–2058.

LIU, J., XU, L., JIA, S-H., PU, H-Y. & LIU, X-L. 2014. The Jiyuan tetrapod fauna of the Upper Permian of China—2. Stratigraphy, taxonomical review, and correlation with other assemblages. *Vertebrata Palasiatica* **52**(3), 328–339.

LIU, J. & YANG, W. 2022. A gorgonopsian from the Wutonggou Formation (Changhsingian, Permian) of Turpan Basin, Xinjiang, China. *Palaeoworld* **31**(3), 383–388.

TATARINOV, L.P. 1963. [A new Late Permian therocephalian]. *Paleontologicheskii Zhurnal* **1963**(4), 76–94.

VIGLIETTI, P.A. 2020. Biostratigraphy of the *Daptocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**(2), 191–206.

YOUNG, C-C. 1952. On a new therocephalian from Sinkiang, China. *Acta Scientia Sinica* **2**, 152–165.