

New discoveries from the *Sinokannemeyeria-Shansisuchus* Assemblage Zone: 2. A new species of *Nothogomphodon* (Therapsida: Therocephalia) from the Ermaying Formation of Shanxi, China

LIU Jun^{1*} Fernando ABDALA²

(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, China

*Corresponding author: liujun@ivpp.ac.cn)

(2 Evolutionary Studies Institute, University of the Witwatersrand Private Bag 3, WITS 2050, Johannesburg, South Africa)

Abstract A new therocephalian specimen collected from the upper part of the Ermaying Formation of Liulin, Shanxi, China is named as *Nothogomphodon sanjiaoensis* sp. nov. This new species is differentiated from the type species *Nothogomphodon danilovi* by the following characters: dentary lower margin uneven; canine base is ovate rather than rounded; distinct diastema present between canine and first postcanine; absence of accessory cutting cusps on posterior border of the postcanines. *Nothogomphodon* has a postcanine morphology that resembles that of sectorial toothed basal cynodonts, which is the only evidence of therocephalians having developed this kind of complex sectorial dentition. Faunal analysis between the Russian *Eryosuchus* fauna and the Chinese *Sinokannemeyeria-Shansisuchus* Assemblage indicates that only *Nothogomphodon* is common to both faunas, whereas there is no common genus shared between the Chinese Ermaying and Karamayi formations. Therocephalians were present at a moderate level of diversity in Middle Triassic faunas from Laurasia, whereas nonmammaliaform cynodonts are only represented by two taxa. Conversely, in Gondwana cynodonts experienced an explosion in diversity in the Middle Triassic with the evolution of Gomphodontia, while therocephalians were scarcely represented in faunas of this age.

Key words Liulin, Shanxi, China; Middle Triassic; Ermaying Formation; therocephalians

1 Introduction

Therocephalia was a major therapsid lineage that reached its greatest species richness and morphological disparity during the Permian, but attained maximum dental complexity in the Triassic subclade Baurioidea. Representatives of this group were the latest-surviving therocephalians and went extinct in the Middle Triassic (Abdala et al., 2008; Ivakhnenko, 2011). Therocephalian monophyly has been debated. Abdala (2007) and Botha et al. (2007) proposed paraphyly for the group, based on phylogenetic analyses that recovered

cynodonts as a sister group of *Theriongnathus*. It must be noted, however, that the analyses by these authors were primarily focused on cynodont interrelationships, with limited taxon sampling in Therocephalia. In contrast, Huttenlocker and colleagues obtained a monophyletic Therocephalia based on an extensive sampling of characters and therocephalian taxa (Huttenlocker, 2009; Huttenlocker et al., 2011; Sigurdson et al., 2012).

Middle Triassic therocephalians exhibit low diversity in southern Africa; a recent taxonomic revision recognized only two species (*Bauria cynops* and *Microgomphodon oligocynus*) in the Olenekian-Anisian of South Africa and Namibia (Abdala et al., 2014). Triassic therocephalians are more diverse in Laurasia, with two Middle Triassic species from Russia (i.e., *Antecosuchus ochevi* and *Nothogomphodon danilovi*; Ivakhnenko, 2011; Tatarinov, 1974) and four species from the latest Early Triassic (i.e., *Hazhenia concave*, *Ordosiodon lincheyuensis*, *O. youngi*, and *Yikezhaogia megafenestrala*) and one from the Middle Triassic (i.e., *Traversodontoides wangwuensis*) of China (Hou, 1979; Li, 1984; Li et al., 2008; Sun and Hou, 1981; Young, 1961, 1974). Among the Middle Triassic Russian species, *N. danilovi* was based on an incomplete skull, PIN 2865/1, from the fauna of the *Eryosuchus* Assemblage Zone of eastern Europe (Shishkin et al., 2000; Tatarinov, 1974). This taxon was diagnosed by combining a relatively small size (estimated skull length ~10 cm) with very long (>2 cm), almost “saber-shaped” canines and tall, labiolingually flattened postcanines, whereby the upper and lower teeth obviously formed a cutting system but did not occlude (Ivakhnenko, 2011). When Tatarinov (1974) described this taxon, the skull and lower jaw were in occlusion and the dentition was only partially exposed (see Tatarinov, 1974: pl. VIII, fig. 1a, b). A new family, Nothogomphodontidae, was proposed within the infraorder Bauriamorpha, as defined by Watson (1917), for this taxon (Tatarinov, 1974). Later, its rank was assigned to the subfamily Nothogomphodontinae Tatarinov, 1974 within the family Bauriidae Broom, 1911 (Battail and Surkov, 2000). Recently, Ivakhnenko (2011) proposed a monotypic superfamily, Nothogomphodontoidea, within the suborder Scaloposaurida for *Nothogomphodon* and *Watsoniella* from the Middle Triassic of South Africa. However, *Watsoniella* has more recently been recognized as a junior synonym of *Microgomphodon* and thus a true bauriid (Abdala et al., 2014).

A therocephalian partial lower jaw was collected from Shanxi, China in 2012 in an expedition led by the senior author. It was found in sandstone of the upper member of the Ermaying Formation and associated with the skeleton of a kannemeyeriid dicynodont and posteranial remains of an archosauromorpha. A tuff layer above this fossiliferous level produced a SHRIMP U-Pb zircon age of (243.1±3.9) Ma, defining the age for this unit as Middle Triassic (Liu et al., 2013). In this contribution, we describe and provide a taxonomic identification for this new therocephalian specimen from the Middle Triassic of China.

Institutional abbreviations IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

2 Systematic paleontology

Terocephalia Broom, 1905

Nothogomphodontidae Tatarinov, 1974

***Nothogomphodon* Tatarinov, 1974**

Type species *Nothogomphodon danilovi* Tatarinov, 1974.

Holotype PIN 2865/1, incomplete skull with lower jaws.

Type locality and horizon Orenburg Region, Sol'-Iletskii District, Berdyanka-2 Locality, Russia; Middle Triassic, Anisian–Lower Ladinian.

Revised diagnosis Skull short; anterior snout wide, without abrupt lateral bend at the transition to the zygomatic region; large orbit slightly shorter than the snout; bony vomeromaxillary bridge short, ending near the anterior one-third of the length of the postcanine tooth row; short osseous palate extending posteriorly only to the level of second postcanine; fused mandibular symphysis; dental formula: I 4/2 C1/1 PC 8/8; postcanines with cutting labiolingually-flattened crowns with main cusp directed backward; anterior border of crown with one or two cusps.

***Nothogomphodon sanjiaoensis* sp. nov.**

Etymology ‘Sanjiao’, the name of the locality.

Holotype IVPP V 20170, a partial jaw preserving an almost complete left dentary and the symphyseal portion of the right dentary.

Type locality and horizon Locality SX/B, Shapingze, Sanjiao Town, Liulin County, Shanxi Province, China; the Ermaying Formation, Middle Triassic.

Diagnosis Differentiated from *Nothogomphodon danilovi* by the following characters: dentary lower margin uneven; canine base is ovate rather than rounded; distinct diastema present between canine and first postcanine; absence of supplementary cutting cusps on posterior border of the postcanines.

Description The specimen is composed of nearly complete left dentary and anteriormost portion of right dentary, two canines, and seven left postcanines (Fig. 1). The thin dentary is 10 cm long. Its size is slightly larger than that of PIN 2865/1. The rami are fused at a tall symphysis, whose anterodorsal portion is incomplete. The external surface of the symphyseal region is rough, with many small nutrient foramina. The anterior margin of the bone is inclined posteroventrally, and joins the lower margin as a weak protuberance. The lower margin is uneven, but slightly thickened posteriorly. The anterior part is slightly curved dorsally (concave), the middle part is nearly straight, and the posterior part turns somewhat upwards (convex). The angular process is obtuse and without posterior projection. The alveolar margin of the dentary is widened mediolaterally to accommodate the teeth. Posterior to the position of alveoli, the ramus dentalis gently rises towards the coronoid process. The coronoid process is thickened along its anterior margin, directed more posteriorly than dorsally. It is relatively long

and low, but the dorsal tip is not preserved.

As reported in the bauriid *Microgomphodon* (Abdala et al., 2014), a fossa is present on the lateral surface of the dentary, similar to the masseteric fossa in cynodonts. A few nutrient foramina and many tiny pits are distributed on the lateral surface of the mentum, whereas the slightly concave posterior part of the lateral surface of the dentary is ornamented by long axial striae, which appear more prominent on the masseteric fossa. On the medial surface, a long slot for the postdentary bones runs posteriorly from the base of the canine. As inferred from the anterior position of the slot, the splenial may have had a small contribution to the mandibular symphysis, but do not likely meet its counterpart.

Based on the preserved alveoli, there seem to be four incisors present between the two canines, the same number of lower incisors as *Nothogomphodon danilovi* (PIN 2865/1; Ivakhnenko, 2011). The canine is very long, only slightly more slender than that of PIN 2865/1 and with the canine base being ovate rather than rounded as PIN 2865/1. No wear is observable

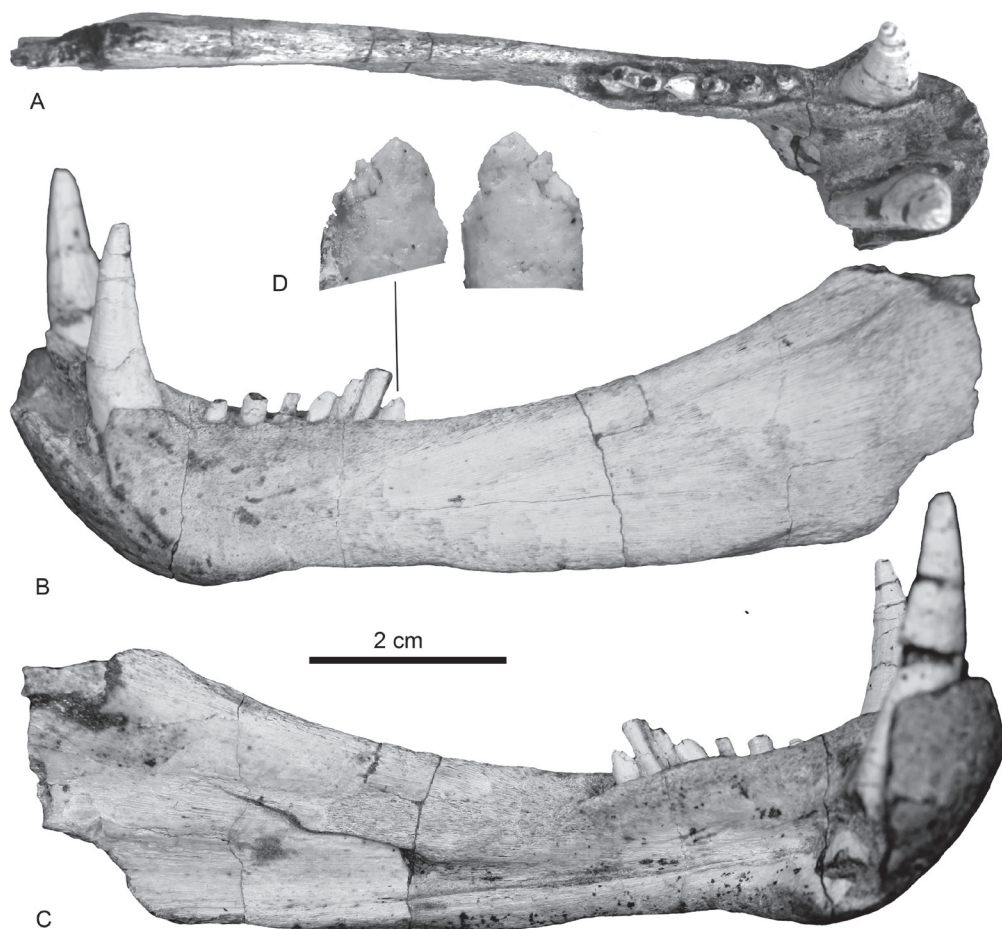


Fig. 1 Left dentary of *Nothogomphodon sanjiaoensis* sp. nov., holotype, IVPP V 20170
A-C. in dorsal, lateral and medial views; D. the enlarged seventh postcanine in lateral and medial views

and the tips of the canines on both sides are broken. There is a small diastema between the canine and the postcanines. Seven postcanine teeth are preserved on the left side, followed by one empty alveolus; therefore the postcanine number is eight, as in PIN 2865/1. The crowns of most postcanines except the fourth and seventh are lost. The anterior three postcanines are separated by a short space, while the last four are positioned close to each other so that their tooth edges come in contact. The anterior teeth are slightly inclined posteriorly, while the posterior teeth are distinctly slanted posteriorly, as in the postcanines of PIN 2865/1. The sixth one is the tallest. The fourth and seventh postcanines appear as newly erupted teeth, and have no distinct tooth neck. The tooth necks of the other postcanines are high, longitudinally ovate in section and slightly flattened labiolingually. The postcanine teeth are slightly smaller than those of PIN 2865/1 and their crowns look like a flat cutting blade. The anterior and posterior edges of the crown have sharp longitudinal crests. No denticle is observed on the anterior crest of the fourth postcanine, but the apex is broken and the posterior edge contacts the fifth postcanine. Two anterior denticles are fused in an integral bicuspid crest on the seventh postcanine as in *N. danilovi*, whereas no denticle is present on the posterior edge. Wear facets are not observed.

Discussion This lower jaw belongs to a typical late baurioid therocephalian, and is very similar to *Nothogomphodon danilovi* in the following shared features: fused symphysis, lower dental formula of $i2\ c1\ pc8$; sectorial postcanines with labiolingually flattened crowns; anterior border of crown with few cusps. However it is differentiated from *N. danilovi* and we recognize the new species *N. sanjiaoensis*, presenting some particular characters only recorded in therocephalian representatives from Laurasia. It is interesting to highlight two key features that seem to have developed only in the geologically younger therocephalians (e.g., bauriids and allies). First is the presence of a noticeable masseteric fossa on the lateral surface of the dentary, which is known only in *Nothogomphodon* and in *Microgomphodon* (Ivakhnenko, 2011; Abdala et al., 2014). Second is the development of complex postcanine crowns. It was previously known that the complexity of the bucco-lingually expanded postcanines of bauriid therocephalians developed in parallel, during late Olenekian-early Anisian, with the gomphodont/traversodont dentition of non-mammalian cynodonts (Abdala and Ribeiro, 2010). The sectorial dentition recorded in *Nothogomphodon*, however, is a novelty for therocephalians. Tricuspid postcanines are known in the record of therocephalians from the Middle Permian through Triassic, but these are mostly restricted to small specimens and are formed by a main cusp with smaller anterior and posterior accessory cusps (Boonstra, 1954; Ivakhnenko, 2011; Mendrez-Carroll, 1979). However *Nothogomphodon* is the only taxon that developed complex sectorial postcanines with curvature of cusps that has some resemblance to those of basal cynodonts such as *Galesaurus*.

3 Biostratigraphic implications of *Nothogomphodon* from the Ermaying Formation of China

The *Sinokannemeyeria-Shansisuchus* Assemblage of the Ermaying Formation is an abundant and heterogeneous fauna in which archosauromorphs and dicynodonts are well represented. The latter is the most diverse lineage of the fauna with at least nine known species (Li et al., 2008; Liu, 2015). Besides these groups, both non-mammaliaform cynodonts and proclophionids are represented by one taxon each. *Nothogomphodon sanjiaoensis* is the second therocephalian taxon known from this fauna, other than *Traversodontoides wangwuensis*. In contrast, the contemporaneous fauna of the Karamayi Formation is depauperate, known primarily from a few dicynodonts (best known from the famous “Nine Dragon Wall”; Sun, 1978) and archosauromorphs (Sun, 1980; Young, 1973a, b). The *Sinokannemeyeria-Shansisuchus* Assemblage was formerly correlated to the Russian *Eryosuchus* fauna based on their tetrapods (Rubidge, 2005; Sun, 1980), most likely because of the dominance and diversity of dicynodonts represented by kannemeyeriids and shansiodontids (Shishkin et al., 2000), even though there were no common components at the generic level. The coeval faunal assemblage of the Karamayi Formation has yielded the Russian erythrosuchian archosauromorph, *Vjushkovia* (Young, 1973b). This Chinese archosauromorph, however, was renamed as *Youngosuchus*, whereas the Russian form was considered synonymous with the coeval *Garjainia* (Kalandadze and Sennikov, 1985); both these conclusions have been accepted by recent workers (Gower and Sennikov, 2000; Gower, 2000; Ezcurra et al., 2013; Nesbitt et al., 2013). Two common genera, *Turfanosuchus* and *Parakannemeyeria* (Li et al., 2008; Sun, 1980), were traditionally considered shared by the Ermaying and the Karamayi formations, but recent works challenged the taxonomic identifications of the materials. The species of *Turfanosuchus* represented in these formations (Wu, 1982; Young, 1973a) were found to represent distinct clades, and therefore they are not congeneric (Sookias and Butler, 2013). *Parakannemeyeria brevirostris* from the Xinjiang locality (Karamayi Formation) was renamed as *Xiyukannemeyeria brevirostris* (Liu and Li, 2003). Later, a new species *Parakannemeyeria chengi* was named for a specimen from Dalongkou, Xinjiang in levels of the Karamayi Formation (Liu, 2004). Recent reanalysis of this specimen by the senior author suggests that it does not belong to *Parakannemeyeria* because its caniniform process extends laterally rather than almost vertically as is typical of *Parakannemeyeria* (Sun, 1963). Therefore, recent taxonomic studies show the absence of common archosauromorphs or dicynodonts between these two Chinese units. The lack of taxonomic commonality between the Middle Triassic Russian and Chinese faunas and even between the Chinese Ermaying and Karamayi formations indicate high endemism in terrestrial faunas of the Middle Triassic of Laurasia. This pattern is contrary to that of the Early Triassic faunas, in which at least *Lystrosaurus* had a worldwide distribution, being also represented in Chinese and Russian faunas; and suggests an increasing differentiation and endemism of tetrapods from the Early to Middle Triassic, concordant with

more global patterns for dicynodonts recognized by Fröbisch (2009) and the provincialization of terrestrial tetrapod faunas of the southern hemisphere by the Middle Triassic (Sidor et al., 2013).

However, recent studies show that some dicynodont genera were wide-spread, represented in Laurasian and Gondwanan faunas of the Anisian and suggesting the absence of geographic barriers hampering migration of tetrapods between these sub-continentes during that time. Thus, *Shansiodon* was not limited to the Ordos Basin of China, but is also known from the Karoo Basin of South Africa (Hancox et al., 2013; Yeh, 1959). This long range extension of a dicynodont is in contrast with the record and diversity of eutheriodonts (therocephalians and cynodonts) in Laurasian and Gondwanan faunas. For example non-mammaliaform cynodonts are well represented and diversified in the Middle Triassic of Gondwana, at a time that was pivotal for the evolution of this group (Abdala and Ribeiro, 2010). On the contrary, in Laurasia there is a single record of this group in the Middle Triassic from China (and a second record, represented by an isolated lower postcanine, in the Middle Triassic of Germany; Hopson and Sues, 2006). The only putative gomphodont cynodonts from Russia (Tatarinov, 1974, 1988) were recently reassigned as bauriid therocephalians (Ivakhnenko, 2011; Abdala et al., 2014). On the other hand therocephalians are moderately represented in Laurasian Middle Triassic faunas from China and Russia (Ivakhnenko, 2011), whereas only two species are represented in Gondwana. This study extends the distribution of the peculiar *Nothogomphodon* from the Russian *Eryosuchus* fauna (Donguz Gorizont) to the Chinese *Sinokannemeyeria-Shansisuchus* Assemblage, representing thus far, the only generic communality between these two Laurasian faunas. This genus is the only therocephalian that possesses complex sectorial postcanines (including curved cusps) and one of the few with a masseteric fossa on the dentary. Despite the evidence from dicynodonts, in particular *Shansiodon*, for navigable migration pathways linking Laurasia with Gondwana, Middle Triassic eutheriodonts have a peculiar distribution that suggests increased endemism. This is demonstrated by contrasting diversity patterns, with a moderate diversity of therocephalians but low diversity of cynodonts in the Middle Triassic of Laurasia and the reverse dominance of non-mammaliaform cynodonts in corresponding faunas of Gondwana.

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中国肯氏兽——山西鳄组合带的新发现之二：山西二马营组幻阔齿兽(兽孔类：兽头类)一新种

刘俊¹ Fernando ABDALA²

(1 中国科学院古脊椎动物与古人类研究所, 脊椎动物演化与人类起源重点实验室 北京 100044)

(2 南非金山大学进化研究所 约翰内斯堡 WITS2050)

摘要：记述了2012年在山西柳林三交二马营组上部采集的一个兽头类下颌标本，将其命名为幻阔齿兽三交种(*Nothogomphodon sanjiaoensis* sp. nov.)。新种以下列特征区别于属型种*N. danilovi*：齿骨下缘起伏，犬齿基部卵圆形，犬齿与第一犬后齿间有显著间隙，犬后齿后缘无辅助齿尖。幻阔齿兽以其特殊的犬后齿形态与具裂齿的基干犬齿兽相似，它也是已知的唯一一类具有这种复杂裂齿齿系的兽头类。将俄罗斯的引鳄动物群与中国的肯氏兽-山西鳄组合带进行比较发现，幻阔齿兽是二者唯一共有的属，而中国的二马营组与克拉玛依组却没有共享的属。

关键词：山西柳林，中三叠世，二马营组，兽头类

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