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Abstract

The Permian dicynodont records were previously rare in North China, but many dicynodont specimens have been collected from the Naobaogou Formation in Daqingshan area, Nei Mongol since 2009. Among these specimens, seven morphotypes have been identified, and they may represent seven different species: two of them are closely related to Daqingshanodon limbus, three or four are closely related to Jimusaria sinkianensis, and one may be closely related to Turfanodon. This study shows the dicynodonts also have a high diversity at the species level in North China.

Full Text

Preamble

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The Tetrapod Fauna of the Upper Permian Naobaogou Formation of China–4. The Diversity of Dicynodonts

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Abstract
Permian dicynodont records were previously rare in North China, but many di-

cynodont specimens have been collected from the Naobaogou Formation in the Daqingshan area, Nei Mongol since 2009. Among these specimens, seven morphotypes have been identified, and they may represent seven different species: two are closely related to *Daqingshanodon limbus*, three or four are closely related to *Jimusaria sinkianensis*, and one may be closely related to *Turfanodon*. This study shows that dicynodonts also have high diversity at the species level in North China.

Key words Daqingshan area, Nei Mongol; Permian; Naobaogou Formation; *Daqingshanodon*; *Jimusaria*; *Turfanodon*

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1 Introduction

Dicynodonts were first discovered in China during the Sino-Swedish Expedition, and *Dicynodon sinkianensis* was the first named Chinese dicynodont species (Yuan and Young, 1934). A new genus, *Jimusaria*, was established for this species due to its differences from the type species of *Dicynodon* (Sun, 1963). Later, *J. taoshuyuanensis* was named based on three incomplete skulls (Sun, 1973a), but this species is generally considered a junior synonym of *J. sinkianensis* (King, 1988; Kammerer et al., 2011) or related to *Delectosaurus* (Kurkin, 2012).

In addition to *Jimusaria*, at least three valid Permian dicynodont genera are known from Xinjiang: *Turfanodon*, *Kunpania*, and *Diictodon* (Sun, 1973a, b, 1978; Li and Liu, 2015). In contrast, Permian dicynodont records were scarce in the North China Stratum Area, with only one species from Gansu (*Dicynodon sunanensis* Li et al., 2000; *Turfanodon bogdaensis* by Kammerer et al., 2011; *T. sunanensis* by Li and Liu, 2015) and one species from Nei Mongol (Inner Mongolia) (*Daqingshanodon limbus*) (Zhu, 1989).

The Naobaogou Formation exceeds 1000 m in thickness and is divided into three lithological members (I, II, III) corresponding to three sedimentary cycles, each beginning with a thick conglomerate layer and dominated by purple siltstone. Although this stratum has a limited distribution within the Daqingshan area, it is highly fossiliferous (Zhu, 1989). Since 2009, we have recorded more than 80 tetrapod specimens from all three members of the formation. Among these, two therocephalian species and one pareiasaur species have been reported (Liu and Abdala, 2017, 2019; Liu and Bever, 2018). As in most other late Permian tetrapod faunas (Bernardi et al., 2017), dicynodonts represent the most abundant and diverse tetrapods from the Naobaogou Formation, with at least seven dicynodont morphotypes identified to date that may represent seven distinct species.

2 Materials

This paper briefly describes and compares seven new specimens from the Naobaogou Formation: IVPP V 23878, a skull lacking the left zygomatic arch, incomplete mandibles, and three vertebrae; V 23879, a snout; V 23880, an incomplete skull; V 26034, a nearly complete skull occluding with mandibles, some vertebrae, and a scapula; V 26035, an incomplete skull with some postcranial bones; V 26036, a flat skull with an incomplete snout; and V 26037, an incomplete skull with mandibles. The stratigraphic levels of these fossils are as follows: Member III contains V 23878 and V 26036; Member II contains V 23879, V 23880, V 26035, and V 26037; and Member I contains V 26034.

3 Description and Discussion

These new specimens can be easily differentiated from one another based on the following characters : (1) Posterolateral edge of the quadrate ramus of squamosal curls anteriorly at mid-height: absent (0) or present (1) (Kammerer et al., 2011); (2) Parietals well exposed on the skull roof and relatively flat (0), exposed in midline groove or channel (1), or with narrow dorsal exposure that is crest-like (2) (Angielczyk and Kammerer, 2017, discrete-state character 49); (3) Orientation of the temporal portion of the postorbital: relatively flat, with most of the exterior surface facing dorsally (0), or close to vertical, with most of the exterior surface facing laterally (1) (modified from Angielczyk and Kammerer, 2017, discrete-state character 51); (4) Caniniform process: flat (0) or rounded (1) (new); (5) Angle formed by zygomatic and quadrate rami of squamosal in lateral view: nearly right angle (0) or acute angle (1) (modified from Angielczyk and Kammerer, 2017, continuous characters 12); (6) Notch on dorsal edge of narial opening: absent (0), obtuse (1), or sharp (2) (modified from Angielczyk and Kammerer, 2017, discrete-state character 18); (7) Nasal boss: absent (0), present as a median swelling with a continuous posterior margin (1), or present as paired swellings near the posterodorsal margin of external nares (2) (modified from Angielczyk and Kammerer, 2017, discrete-state character 34); (8) Premaxillary midridge on dorsal surface: absent (0) or present (1) (new); (9) Sharp, blade-like lateral dentary shelf expanding anteriorly into a thick swelling: absent (0) or present (1) (Kammerer et al., 2011; modified from Angielczyk and Kammerer, 2017, discrete-state character 128); (10) Ratio of intertemporal bar length to orbital length in midline (new); and (11) Ratio of occipital width to height (new).

These new specimens and the holotype of *Daqingshanodon limbus* (V 7940) can be divided into three morphogroups and seven morphotypes.

Morphogroup I includes specimens IVPP V 7940, V 23878, and V 26037. Two of the new specimens are larger than V 7940 [Figure 1: see original paper]. All share a unique feature: the posterolateral edge of the quadrate ramus of the squamosal curls anteriorly at mid-height, which was suggested as an autapomorphy of *Daqingshanodon limbus* (Kammerer et al., 2011). However, the ridge

extending from the base of the zygomatic arch to the anterolateral edge of the caniniform process is only weakly developed in the two larger specimens [Figure 1: see original paper]. They also share common features such as parietals exposed in a midline groove and a relatively flat temporal portion of the postorbital. Despite slight differences, V 26037 could represent an adult specimen of *D. limbus*, similar to the case of *Pelanomodon* (Kammerer et al., 2015). Compared to V 7940 and V 26037, V 23878 has a much longer intertemporal bar, an undeveloped nasal boss, lacks a nasal mid-ridge, and has a premaxilla that contacts the frontal. This specimen represents a different morphotype and may constitute a new species closely related to *D. limbus*.

Morphogroup II includes specimens IVPP V 26034, V 26035, and V 26036. These three specimens have a crest-like parietal, and the exterior surface of the temporal portion of the postorbital faces laterally. V 26035 can be distinguished by the presence of a postcaniniform crest, a strongly curved snout, and a frontal mid-ridge. V 26036 can be distinguished by its long interparietal bar and low, wide occiput. These three specimens represent three morphotypes and perhaps three distinct species.

These specimens show many features in common with *Jimusaria sinkianensis*. Even two autapomorphies of *J. sinkianensis* proposed by Kammerer et al. (2011) can be observed in some specimens. The lateral dentary shelf is sharp, blade-like, and expands anteriorly into a thick swelling in V 26034. The caniniform process is short and rounded, with equivalent curvature anteriorly and posteriorly in both specimens, although it is less developed than in the holotype of *J. sinkianensis*. The diagnosis of *J. sinkianensis* also includes the following character combination: narrow intertemporal bar with no dorsal exposure of parietals, squamosals narrow in lateral view with the zygomatic and quadrate rami forming an acute angle, and prominent grooves arcing between the postfrontals and postorbitals (Kammerer et al., 2011). The narrow intertemporal bar has no dorsal exposure of parietals in V 26035, but has narrow exposure of parietals in the holotype of *J. sinkianensis* and V 26036; the condition is uncertain in V 26034 [Figure 2: see original paper]. The zygomatic and quadrate rami form an acute angle in all three specimens. V 26034 is similar to *Striodon magnus* in having a long and narrow intertemporal bar and rectangular temporal fenestra, but its occiput is narrow and high compared to that of *Striodon magnus* (Sun, 1978).

Morphogroup III includes specimens IVPP V 23879 and V 23880 [Figure 3: see original paper]. Both specimens have a distinct mid-ridge on the snout, a distinct notch on the dorsal edge of the narial opening, and anterior ridges on the palatal surface of the premaxilla exposed in lateral view. The mid-ridge extends only on the upper part of the premaxilla in V 23879 but covers at least the entirety of the premaxilla and nasal in V 23880. They represent two different morphotypes. V 23879 is similar to *Turfanodon* in the abrupt turning of the dorsal surface anterior to the orbit and could be closely related. V 23880 is generally similar to *Jimusaria* but differs significantly in having a well-developed

premaxillary median ridge and is tentatively identified as Bidentalia indet.

4 Comparison and Conclusion

In summary, including *Daqingshanodon limbus*, seven dicynodont morphotypes have been recognized from the Naobaogou Formation. Two morphotypes are closely related to *Daqingshanodon*, three or four are closely related to *Jimusaria*, and one may be closely related to *Turfanodon*. Further work is needed to determine how many new species are present and the exact phylogenetic relationships of each species.

In addition to these dicynodonts, at least three dicynodont species from three genera (*Turfanodon*, *Kunpania*, and *Diictodon*) are known from the late Permian of China. Around the same age, Russia produced the following dicynodonts: *Elph borealis* (Kurkin, 1999), *Interpresosaurus blomi* (Kurkin, 2001), *Australobarbarus* (*A. platycephalu* and *A. kotelnitschi*) (Kurkin, 2000), *Idelesaurus tataricus* (Kurkin, 2006), *Delectosaurus arefjevi* (Kurkin, 2001), *Vivaxosaurus trautscholdi* (Amalitzky, 1922; Kammerer et al., 2011), and *Peramodon amalitzkii* (Kammerer et al., 2011; Sushkin, 1926). Compared to the Russian record, some dicynodont clades remain absent from China. At present, no Chinese species appear closely related to *Elph*, *Australobarbarus*, or *Idelesaurus*.

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