The tetrapod fauna of the upper Permian Naobaogou Formation of China: 10. Jimusaria monanensis sp. nov. (Dicynodontia) with an unique epipterygoid

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Abstract

Jimusaria is the first reported Chinese dicynodont, previously only known from Xinjiang. Here we refer two specimens from the Naobaogou Formation, Nei Mongol, China to *Jimusaria* for the following features: squamosal separated from supraoccipital by tabular, tabular contacting opisthotic, sharp and thin lateral dentary shelf expanding anteriorly into a thick swelling, nasals fused as single element, rod-like medial bar formed by footplate of epipterygoid connecting to the parabasisphenoid and periotic medially. A new species, *J. monanensis*, is named based on the diagnostic characters on these two specimens such as distinct caniniform buttress lacking posteroventral furrow, naso-frontal suture forming an anterior directed sharp angle, and converging ventral ridges on posterior portion of anterior pterygoid rami. In *Jimusaria*, the epipterygoid posteromedially contacts the parabasisphenoid and the periotic as a rod-like bar, a unique morphology unknown in any other dicynodonts. This structure probably increases the stability of the palatal complex. A similar structure might also appear in other dicynodonts as a cartilage connection. The new occurrence of *Jimusaria* increases the diversity of the tetrapod assemblage from the Naobaogou Formation, and further strengthens the connection between the tetrapod faunas from Nei Mongol and Xinjiang. Based on the current record, *Jimusaria* is a rare tetrapod genus which survived the end-Permian mass extinction.

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Introduction

During the Sino-Swedish expedition, Yuan P. L. collected some dicynodont fossils from Xinjiang, China. *Dicynodon sinkianensis* is the first named species from those specimens, and is the first record of Chinese Permian-Triassic tetrapods (Yuan & Young 1934). Later, this species was transferred to a new genus, *Jimusaria*, resulting in a new combination, *J. sinkianensis* (Sun, 1963). Three incomplete skulls from Turpan, Xinjiang were also referred to this genus as *J. taoshuyuanensis* (Sun 1973). King (1988) proposed *Jimusaria* as a junior synonym of *Dicynodon*, resuming the name *D. sinkianensis* and creating a new combination, *D. taoshuyuanensis*. Lucas (1998, 2001) and Li et al. (2008) followed this opinion. Kammerer et al. (2011) completed a comprehensive phylogenetic analysis on *Dicynodon*-related species; they revalidated *Jimusaria*, and regarded *J. taoshuyuanensis* as a junior synonym of *J. sinkianensis*.

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Abundant tetrapod fossils have been collected from the Naobaogou Formation of Nei Mongol, and they are referred to diverse clades such as Chroniosuchia, Captorhinidae, Pareiasauria, Dicynodontia, and Therocephalia (Li & Cheng 1997; Liu 2021; Liu 2023; Liu & Abdala 2020; Liu & Bever 2018; Liu & Chen 2021; Zhu 1989). This assemblage is dominated by the dicynodonts including *Daqinshanodon limbus* and *Turfanodon jiufengensis*. *Turfanodon* is the first described dicynodont genus shared by Nei Mongol and Xinjiang and distributed across both tropical and temperate zones (Liu, 2021). As mentioned but not described in Liu (2019), other than *Turfanodon*, *Jimusaria* was also produced from the Naobaogou Formation. Here we describe two specimens and propose a new species of *Jimusaria*.

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Materials & Methods

IVPP V26034, a nearly complete skull with mandible, six cervical vertebrae and an incomplete right scapula articulated with an incomplete bone (? coracoid); the skull basal length is 223mm (Figs. 1 and 2). IVPP V31929, an incomplete skull with complete mandible; the skull basal length is 143mm (Figs. 3, 4A, 4E and 5).

Phylogenetic analysis

The matrix is based on the recent works of Angielczyk, et al. (2021), Kammerer and Ordoñez (2021) and Liu (2022). The final data set consists 199 characters (23 continuous and 176 discrete-states) and 120 species (OTUs). Continuous characters were treated as additive, and eight discrete-state characters were treated as ordered (characters 56, 81, 84, 102, 163, 173, 189 and 199). The data were analyzed using parsimony in TNT v1.6 (Goloboff and Morales 2023) using New Technology search parameters, starting at level 65 and forced to find the shortest tree at least 50 times checking every five hits. Then using the traditional search method analysis trees produced from New Technology search. Symmetric resampling values were calculated based on 10000 replicates.

Nomenclatural acts. The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are

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Systematic palaeontology

Anomodontia Owen, 1860

Dicynodontia Owen, 1860

Dicynodontoidea Olson, 1944

Genus *Jimusaria* Sun, 1963

Type species. *Jimusaria sinkianensis* (Yuan and Young, 1934)

Revised diagnosis. A medium-sized dicynodontoid with narrow intertemporal bar and squamosal zygomatic and quadrate rami forming an acute angle. It is also differentiated from other dicynodontoids by squamosal separated from supraoccipital by tabular and contacting opisthotic; sharp and thin lateral dentary shelf expanding anteriorly into a thick swelling; distinct medium-sized caniniform process; nasals fused as single element; rod-like medial bar formed by footplate

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of epipterygoid, connecting to the parabasisphenoid and periotic medially.

Jimusaria monanensis sp. nov.

Etymology. ‘Monan,’ means “south of the Gobi Desert of Mongolia”.

Holotype. IVPP V26034, a nearly complete skull with mandible, 6 cervical vertebrae, an incomplete right scapula articulated with an incomplete bone (? coracoid) (Figs. 1 and 2).

Type locality and horizon. Tumed Right Banner, Nei Mongol, China; Member I, Naobaogou Formation.

Referred material. IVPP V31929 Shiguai, Baotou, Nei Mongol, China. Member I, Naobaogou Formation, an incomplete skull with complete mandible (Figs. 3, 4A, 4E and 5).

Diagnosis. Differentiated from type species by distinct caniniform buttress lacking posteroventral furrow, naso-frontal suture forming an anterior directed sharp angle, and converging ventral ridges on posterior portion of anterior pterygoid rami.

Description

Skull

IVPP V26034 and V31929 are different in size. IVPP V26034 may represent an adult. Its skull is slightly crushed and both postorbital bars are broken; while the left ramus of the mandible is broken. In IVPP V31929, the incomplete skull has a weathered roof, and the right zygomatic arc and left squamosal are missing (Figs. 3, 4A, 4E and 5). The following description is based on

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both specimens if not specified.

The short snout has a smoothly curved dorsal surface, and its anterior surface formed by the premaxilla is low and relatively flat. Its ventral margin has a shallow middle notch (Fig. 3B). The snout region around the external nares is well-sculptured in IVPP V26034, but is only slight rugose in IVPP V31929 (Figs. 1A, 2A, 3B and 5).

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The premaxilla forms most of the secondary palate. On the palatal surface, there are a pair of parallel anterior ridges and a posterior ridge. The anterior ridges extend to the anterior premaxillary margin. The narrow posterior ridge extends anteriorly to the level of the tusk, and posteriorly to the vomer, which has nearly the same width (Figs. 1B and 3A).

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The septomaxilla lies within the anterodorsal concavity of the maxilla and forms the posterior margin of the naris. It contacts the premaxilla anteriorly and the nasal dorsally (Figs. 2A, 5A and 5B). In IVPP V31929, a septomaxillary foramen lies on the right side of the septomaxilla-maxilla junction (Fig. 5A). The postnarial region does not bear an excavation.

In lateral view, the maxilla contacts the septomaxilla and the premaxilla anteriorly, the nasal and the lacrimal dorsally, the jugal posterodorsally, and the squamosal posteriorly (Figs. 2A, 5A and B). It forms a regular-sized caniniform process as in most Permian dicynodonts. The caniniform process expands laterally as a distinct buttress, which bears a flat posterior surface without a lateral furrow as in *J. sinkianensis* (Kammerer et al. 2011). The anteroventral edge of the caniniform process lies at the level of posterior margin of the naris. The round tusk is curved

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posteriorly, and the base is directed anteroventrally while the tip is directed posteroventrally.

The nasals are well-fused without a median suture, same as in *J. sinkianensis* (Yuan & Young 1934) (Figs. 1A and 4A). The nasal boss is developed as a median swelling, forming the posterodorsal margin of the naris. The nasal contacts the prefrontal posterolaterally and the frontal posteriorly, the naso-frontal suture has two straight segments which form a sharp angle (Figs. 1A, 4A and 4C).

The round orbit faces more laterally than anteriorly (Fig. 3B). The orbit is formed by the flat prefrontal anterodorsally, the lacrimal anteriorly, the jugal ventrally, the postorbital posteriorly, the frontal dorsally, and the postfrontal posterodorsally (Figs. 1A, 2A and 5A). The lacrimal foramen lies close to the suture with the prefrontal. The jugal extends posteriorly behind the postorbital bar and contributes to the zygomatic arch, but it has a little contribution to the postorbital bar (Figs. 1B and 3A).

The frontals have distinct anteromedial processes (Figs. 1A and 4A). The left postfrontal can be identified in IVPP V31929, its surface is flat, without the groove as in IVPP RV341407 (Figs. 4A and 4C). The oval preparietal is flush with the skull roof, and forms the anterior margin of pineal foramen (Figs. 1A, 4A).

The left postorbital bar of IVPP V31929 is the only complete one. It is almost exclusively formed by the postorbital (Figs. 2A, 5A, B). The ventral portion of the postorbital bar is extremely anteroposteriorly expanded and mediolaterally flattened. The postorbital ascends

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dorsally and medially to join the skull roof, then extends posteriorly and forms the entire intertemporal bar with the parietal. The slender parietal also contributes to the narrow intertemporal bar, and it has a narrow dorsal exposure within the midline groove. The poor preservation prevents the judge on the presence of the sagittal crest (Fig. 1A). The postparietal contributes to the intertemporal bar but is covered by the postorbital dorsally.

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The right squamosal of IVPP V26034 is relatively complete unlike the others (Fig. 2A). The squamosal has a long zygomatic ramus, which has a flattened posterior portion, a long sutured area with the jugal, and bears a pointed anterior tip inserting the maxilla below the orbit. The lateral fossa formed by the zygomatic ramus and quadrate ramus of the squamosal can be observed in posterior view. The quadrate ramus of the squamosal descends ventrally with lateral expansion. The dorsal portion of the quadrate ramus is curved posteriorly. The quadrate ramus receives the fused quadratojugal and quadrate on its anteroventral surface (Figs. 2A, 5A). The quadrate foramen, between the quadrate and quadratojugal, faces anteromedially. The quadrate, articulating to the articular of the mandible, has a typical W-shape facet.

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The narrow vomer forms the septum and posterior margin of choana (Figs. 1B and 3A). The interpterygoid vacuity is formed by the vomer and the pterygoid. Its posterior margin is flush with the median pterygoid plate. The vomer raises dorsally above the choana as a vertical sheet which laterally clasps the parasphenoid (Figs. 5A and 5B).

The palatine widens anteriorly to form a rugose palatine pad, which contacts the premaxilla and the maxilla. Posteriorly, the palatine forms the lateral wall of the choana with the pterygoid. Laterally, the labial fossa is surrounded by the jugal laterally, the palatine medially, and the maxilla anteroventrally. The ectopterygoid also contributes to the labial fossa margin. The ectopterygoid contacts the maxilla anteriorly and the pterygoid posteriorly, extending posteriorly without exceeding the posterior margin of palatine pad in ventral view (Fig. 3A).

The pterygoid shows the typical X-shape of dicynodonts (Figs. 1B and 3A). The anterior ramus of the pterygoid touches the maxilla anteriorly, and the anterior pterygoid ridge extends on most portion of that; the posterior portion of that ridge converges posterior with the interpterygoid vacuity, differing from *J. sinkianensis* (Yuan & Young 1934) (Fig. 6). The median pterygoid plate has a distinct and thin crista oesophagea, which extends anteriorly to the posterior margin of interpterygoid vacuity and bifurcates into two low rami posteriorly.

The parabasisphenoid bears paired internal carotid canals, whose ventral openings locate near the suture with the pterygoid (Fig. 3A). The parabasisphenoid contributes to the anterodorsal margin of the basal tuber as a ridge in a very steep angle. The posterior portion of the basal tuber is formed by the basioccipital (Figs. 1B, 3A and 4E). The basal tuber is elongated anteroposterior and laterally directed with relatively narrow edges. The intertuberal ridge connects the paired basal tubera (Figs. 1B and 3A). The parabasisphenoid is well exposed in lateral view in IVPP V31929 (Figs. 5A and 5B). It contacts the periotic posteriorly, and extends anterodorsally. Its anterior portion supports the presphenoid dorsally, they are fused as a plate here. The

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orbitosphenoid is partly preserved, it separates into two wings which contact frontal dorsally.

The incomplete left stapes is preserved between the quadrate and the basal tuber in IVPP V31929 (Fig. 3A). The dorsal process is present. It has an "extra facet", similar to *Kingoria* (Cox 1959) and *Daptocephalus* (Ewer 1961).

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The epipterygoids are not so well preserved, a dorsal end is observed on the right side of IVPP V26034 (Fig. 2A) and a left footplate rests on the quadrate ramus in IVPP V31929. Posteriorly, the footplate extends medially forming a rod-like medial bar, contacting the parabasisphenoid and the periotic suture (Figs. 3A and 7A). Examining the holotype of *J. sinkianensis*, the epipterygoid also contacts the braincase laterally at the parabasisphenoid-periotic suture (Fig. 7B). This character is not reported in any other dicynodonts.

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In IVPP V31929, the periotic is composed of the prootic and the opisthotic (Figs. 4E and 5A), while the occipital elements are separated. In the holotype, it is unknown if the occipital elements are fused to the periotic due to the poor preservation (Fig. 2B). In IVPP V26034, the rod-like pila antotica rises anterodorsally from the periotic and forms a deep V-shaped notch for the trigeminal nerve (Fig. 2A); the notch for the vena capitis dorsalis is partly preserved on the periotic anterior edge. Laterally, the supraoccipital separates the periotic from the parietal (Fig. 2A).

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No bone suture can be identified on the occipital plate of the holotype, but some sutures are traceable on IVPP V31929 (Fig. 4E). The postparietal is exposed on the occipital plate. It is supported by the supraoccipital ventrally, and contacts the tabular laterally. The supraoccipital is a large element forming the dorsal half margin of the foramen magnum. The tabular separates the supraoccipital from the squamosal, it extends ventrolaterally to the margin of the post-temporal fenestra, contacting the periotic ventromedially. The post-temporal fenestra is almost completely formed by the periotic medially and the squamosal laterally. The paired exoccipitals meet on the midline and forms the ventral half of the foramen magnum, they join the basioccipital to form the tri-radiate occipital condyle. The facet for the proatlas is developed on the dorsal margin of the exoccipital, the jugular foramen lies near the occipital condyle in exoccipital.

Mandible

The mandible is articulated with the skull, and there is one relatively complete ramus in each specimen (Figs. 2A, 5B and 5C). The dentary symphysis forms an upturned beak, with a smooth anterior surface (Figs. 2A, 3B and 5C). The anterior surface has a clear border with the lateral surface. The dorsal surface of the dentary symphysis comprises a medial groove and two lateral tables, on which the medial edge is higher than the lateral one. The posterior dentary sulcus is narrow. Laterally, a distinct, thin lateral dentary shelf locates on the dorsal edge of mandibular fenestra. It extends for almost the entire length of that the fenestra and its anterodorsal portion is swelling (Fig. 5C). The dentary posteroventral process extends on the lateral surface of the angular, ventral to the mandibular fenestra. The angular joins the symphysis with its anterior tip.

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It also contributes to the ventral margin of the mandibular fenestra (Figs. 1B, 2A, 3A and 5C). The reflected lamina is small, more elongated than rounded, without ornamentation on the surface; its posterior margin is widely separated from the articular. A ridge runs dorsoposteriorly from the base of the reflected lamina to the surangular (Figs. 2A and 5C). The surangular lies dorsal to the angular and contacts the dentary anteriorly (Figs. 2A and 5C). The articular provides an articular facet with the quadrate, which allows the parasagittal movement.

The splenial forms the posteroventral portion of the symphysis. It can be observed in medial or ventral view. The prearticular extends anteriorly from the articular, forming the ventral portion of the mandible ramus on the medial surface, it contacts the surangular dorsally, the dentary anterodorsally, and splenial anteriorly (Figs. 1B and 3A).

Postcranial bones

The holotype preserved seven articulated cervical vertebrae, beginning with the atlas, an incomplete right scapula, and possibly part of the coracoid (Fig. 2C). The exact number of the cervicals in *Jimusaria monanensis* cannot be determined with certainty. However, given that the cervical number is no more than seven in anomodonts (Fröbisch & Reisz 2011; Liu 2021), the preserved vertebrae in the holotype of *Jimusaria monanensis* are considered to represent all cervicals.

The atlas consists of two separate neural arches, the transverse process has a high dorsoventral

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expansion. The axis has an anteroposteriorly expanding neural spine, the articular facet of its postzygapophysis faces more laterally than ventrally. The odontoid partly exposes in dorsal view, it fuses with the axis centrum. The 3rd vertebra has a nearly vertical neural spine, which narrows in anteroposterior width dorsally. Its postzygapophysis has a more or less horizontal articular facet. In the 5-6th vertebrae, the neural spines expand in width and incline slightly posteriorly. All centra are amphicoelous.

The bowed scapula is incomplete, with broken anterior and dorsal margins. Posteriorly, a rugose portion can be observed on base of scapula, which represents the origination of the scapular head of M. triceps.

Discussion

In previous study, IVPP V26034 was proposed to be closely related to *Jimusaria sinkianensis* (Liu 2019). IVPP V26034 and V31929 can be referred to *Jimusaria* by the distinct medium-sized caniniform process, the sharp and thin lateral dentary shelf expanding anteriorly into a thick swelling, and fused nasals. However, these specimens show the following features which differentiate them from *J. sinkianensis*: anteriorly directed naso-frontal suture (Figs. 1A, 4A and 4B), caniniform process without posterolateral furrow, and keel of anterior rami of pterygoid converging posteriorly (Figs. 3A and 6). Hence, based on these diagnostic characters, a new species, *J. monanensis*, is proposed to include them.

Jimusaria taoshuyuanensis was considered as a junior synonym of *J. sinkianensis* by

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Kammerer et al. (2011). The referred specimens (IVPP V3240) bear the diagnostic features of *J. sinkianensis*, but are clearly different from the new species proposed here, supporting their conclusion. All specimens have a distinct caniniform process with a posterior furrow (Fig. 6), V3240.1 and V3240.2 expose a relative straight naso-frontal suture (Figs. 4C and 4D), V3240.2 and V3240.3 show paired, parallel ventral ridges on the posterior portion of the anterior pterygoid rami (Fig. 6).

The holotype of *Jimusaria sinkianensis* shows that the tabular contacts the periotic, and separates the squamosal from the supraoccipital; the footplate of the epiptergoid elongates medially and contacts both the parabasisphenoid and the periotic as in *J. monanensis* (Figs. 4F, 7B), so those characters are autapomorphies of *Jimusaria*. In *J. sinkianensis*, the parietal is narrowly exposed within the shallow groove of the intertemporal bar, and whether the postparietal contributes to the intertemporal bar is unknown in holotype (Fig. 4C), and the diagnosis of this species should be revised from Kammerer et al. (2011).

Phylogenetic analysis

The phylogenetic position of *Jimusaria* is highly unstable within Dicynodontoidea in previous studies. It was recovered outside the clade of Lystrosauridae plus Kannemeyeriiforme (Angielczyk et al. 2017; Angielczyk et al. 2021; Cox & Angielczyk 2015; Kammerer et al. 2011; Kammerer et al. 2013; Kammerer & Smith 2017), as the sister group of *Gordonia*, and forming a

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clade with *Sintocephalus* plus *Euptychognathus* (Angielczyk & Kammerer 2017; Kammerer 2018), or being part of the monophyletic group (*Jimusaria* + *Gordonia*) as the sister group of Kannemeyeriiformes (Kammerer 2019a; Kammerer 2019b; Kammerer et al. 2019; Liu 2021). It also was recovered closely related to *Dicynodon* than *Lystrosaurus* (Olivier et al. 2019). Recent analyses recovered it in a relatively basal position within Dicynodontoidea (Kammerer & Ordoñez 2021; Liu 2022).

Jimusaria monanensis was scored based on IVPP V26034 and V31929 for the recent character list (Angielczyk et al. 2021; Kammerer & Ordoñez 2021; Liu 2022), some scorings of *J. sinkianensis* were revised (Supplemental Data 1). Finally, one most parsimonious tree of length 1273.225 was recovered (Fig. 8).

The topology is basically the same as in Liu (2022) and Kammerer & Ordoñez (2021), but different with that obtained by Angielczyk et al. (2021) (Fig. 8). *Kunpania* was recovered as one of the basal members of Bidentalia. *Jimusaria* was recovered at the same position that in Liu (2022) and Kammerer & Ordoñez (2021), there is no monophyletic *Jimusaria* + *Gordonia*.

The epipterygoid morphology of *Jimusaria*

The posterior portion of footplate send the rod-like medial bar to the parabasisphenoid and periotic medially in IVPP V31919 (Fig. 7A). Ventrally, this rod seems like a connection between the quadrate ramus of the pterygoid and the lateral braincase wall in the pterygo-paroccipital

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foramen (Fig. 3A).

The contact between the footplate of the epipterygoid and the parabasisphenoid is a common character in dicynodonts, but that suture connection occurs between the anterior ramus of the footplate and the basipterygoid process, as observed in basal dicynodonts, such as *Eodicynodon*, *Diictodon*, and *Pristerodon* (Barry 1968; Barry 1974; Sullivan & Reisz 2005), and bidentalians (Cluver 1971; Keyser 1973). This type of connection is quite different from that of *Jimusaria*.

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A contact between the epipterygoid and the prootic is a relatively "derived" feature in therapsids. Some therocephalians possess a dumb-bell-shaped epipterygoid, and that dorsal expanding portion of the ascend ramus of the epiptergoid contacts the prootic (Barry 1965; Durand 1991; Huttenlocker et al. 2011; Liu & Abdala 2022). Some therocephalians and some cynodonts have plate-like epipterygoid which sutures with the prootic posteriorly and forms part of the lateral wall of the braincase (Barry 1965; Kemp 1972; Olson 1944). Some dinocephalians have an expanding epipterygoid which meets the periotic posteriorly, too (Olson 1944). However, none of those junction are rod-like or originate from the footplate of epipterygoid (Barry 1965; Olson 1944).

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Some therocephalians show a similar structure in a comparable region as in *Jimusaria*, but the sheet-like structure just anterior to the post-temporal fenestra is formed by the otic process of the squamosal, the anteroventral process of the squamosal, or both. Although the epipterygoid also sends a ramus to that process (Durand 1991; Kemp 1972; Liu & Abdala 2019; van den Heever

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1994). van den Heever (1994) deduced the function of the sheet-like process as protecting the neurovascular elements which pass through the post-temporal fenestra.

The location and shape of the rod-like medial bar of the epipterygoid in *Jimusaria* are quite different, and quite unlikely had the same function. One possible function of the rod-like medial bar of the epipterygoid might be an additional auditory conduction medium, as some authors presumed that fossorial dicynodonts used the skull roof sense the quake from the ground when they lived in underground burrows (Cox 1972; Laaß 2015). Under this situation the sound conducts through the skull roof to the inner ear, and the slender epipterygoid with the medial connection to the periotic could act an efficient transmit route. However, the shape of naso-frontal suture and the horizon orientation of stapes do not support a fossorial habit for *Jimusaria* (Kammerer 2021; Laaß 2015). Another possible function of the rod-like medial bar of the epipterygoid is increasing the stability of the palatal complex. In dicynodonts, the ventrolateral ridge of the parabasisphenoid is presumed to provide the attachment for M. protractor pterygoidei, which connects the parabasisphenoid and the quadrate ramus of the pterygoid, and keeps the palatal complex in proper position (Surkov & Benton 2004). In *Jimusaria*, the ventrolateral ridges of the parabasisphenoid are present, indicating M. protractor pterygoidei is developed, suggesting the demand of stabilizing the palatal complex in proper position. The epipterygoid in tetrapods generally has the function of stabilizing the palatal complex and connecting it to the skull roof (Romer 1956). It could be hypothesized that the rod-like medial

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The epipterygoid ossified from palatoquadrate cartilage, representing an element of splanchnocranium, in early tetrapods it connects to the quadrate frequently (Barry 1965). In dicynodonts, the unossified palatoquadrate cartilage should be present dorsal to the pterygoid, from the plate of the pterygoid to the quadrate ramus of the pterygoid; as cartilage still links the epipterygoid and the quadrate in some living lizards (Jollie 1960). This hypothesis can explain the variable position of the footplate of the epipterygoid in dicynodonts (Barry 1974; Ewer 1961; Maisch 2002; Surkov & Benton 2004). Therefore, there are two possible scenarios for the osteogenesis of the rod-like medial connection of the epipterygoid to the lateral wall of braincase: (1) the palatoquadrate has a unique medial projection and that portion ossify as part of the epipterygoid in *Jimusaria*; or (2) a cartilaginous connection persists between the quadrate ramus of the pterygoid and the lateral wall of braincase in most, if not all dicynodonts, but ossification occurred in *Jimusaria*. The second scenario seems more advantageous considering the inferred function of the epipterygoid. The cartilaginous connection would provide a weaker but similar function.

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The ontogenetic variation of *Jimusaria*

IVPP V26034 differs from V31929 in size, and they are inferred to represent different

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ontogenetic stages. The smaller specimen (IVPP V31929) has a smoother snout region with only some pits and rugosities (Fig. 3B), while the larger specimen (IVPP V26034) has a distinctly rough snout (Figs. 1A and 2A). A similar pattern also occurs in *Jimusaria sinkianensis* (Figs. 4B-4D). The changing from pits to sculpture might indicate that the keratinous beak became heavier, as appeared in *Turfanodon bogdaensis* (Liu 2021).

Comparing the two specimens (IVPP V26034 and V31929), the interorbital region becomes relatively wider, and the intertemporal bar becomes narrower (although it might be caused by deformation); the pterygoid medial plate is relatively longer while the interpterygoid vacuity is relatively smaller. The smaller specimen (IVPP V31929) already has a distinct caniniform buttress, indicating that feature developed at a relatively young age in *Jimusaria monanensis*.

In *J. sinkianensis*, the three small specimens (IVPP V3240) show distinct caniniform buttresses and the indistinct posteroventral furrow continues dorsoposteriorly to the depressions in the maxilla; the larger specimen (IVPP RV341407) possesses fatter caniniform processes with distinct posteroventral furrows and stronger depressions (Fig. 6). The tusks are directed vertically in the larger specimen rather than anteroventrally as in the small specimens. So, the growth pattern of the caniniform process is different between these two species.

Paleobiogeographic and biostratigraphic implications

The tetrapod assemblage of the Naobaogou Formation is the most diversity tetrapod

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assemblage of Lopingian in China. The previous report of *Turfanodon jiufengensis* imply the Naobaogou Formation shares at least one common taxon with the Guodikeng Formation (Liu 2021). Several dicynodonts have been reported from the Guodikeng Formation of Xinjiang, including *Jimusaria sinkianensis*, *T. bogdaensis*, *Diictodon feliceps*, and some *Lystrosaurus* species (Li et al. 2008). The finding of *J. monanensis* enhances the connection between the faunas of Nei Mongol and Xinjiang. Same as *Turfanodon*, *Jimusaria* is the second reported dicynodont genus distributed across temperate and tropical zones.

Recent stratigraphic work placed the Permo-Triassic boundary at the base of Guodikeng Formation in Xinjiang (Yang et al. 2021). Based on the field observations, the horizon of the holotype of *J. sinkianensis* is the upper portion of the Guodikeng Formation, early Triassic in age (Angielczyk et al. 2022) while other specimens of this species also could be Triassic in age. Meanwhile, two specimens of *J. monanensis* were collected from Member I of the Naobaogou Formation, which possibly correlates with the Wuchiapingian (Shen et al. 2022; Shen et al. 2021). So, *Jimusaria* is a rare tetrapod record which survived the end-Permian mass extinction.

Conclusions

A new dicynodont species, *Jimusaria monanensis*, was discovered in the Naobaogou Formation. This record further increases the diversity of the Lopingian Daqingshan fauna and the connection between the North China and Xinjiang during the Lopingian, Permian. The peculiar

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rod-like medial bar of the epipterygoid in *Jimusaria* is inferred to have stabilized the palatal complex, and a similar structure may appear in many other dicynodonts as part of palatoquadrate cartilage remains. *Jimusaria* spanned from Wuchiapingian to Early Triassic in age.

Eliminado: perform stabilizing

Eliminado: function with the highest probability

Institutional abbreviations

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

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Fig. 1. *Jimusaria monanensis* sp. nov. from the Naobaogou Formation, holotype, IVPP V26034. (A) dorsal; (B) ventral views. Abbreviations: AN, angular; AR, articular; bt, basal tuber; BO, basioccipital; co, crista oesophagea; D, dentary; F, frontal; ipv, interpterygoid vacuity; J, jugal; L, lacrimal; la, lacrimal fossa; M, maxilla; N, nasal; P, parietal; PBS, parabasisphenoid; PE, periotic; PF, prefrontal; pif, pineal foramen; PL, palatine; PM, premaxilla; PO, postorbital; PP, preparietal; PRE, prearticular; PT, pterygoid; ptf, post-temporal fenestra; Q, quadrate; SP, splenial; SQ, squamosal; t, tusk; V, vomer. Scale bar represents 5 cm.

Fig. 2. *Jimusaria monanensis* sp. nov. from the Naobaogou Formation, holotype, IVPP V26034. (A) right lateral; (B) posterior views; (C) photo of vertebrae and scapula. Abbreviations: AN, angular; AR, articular; COR, coracoid; D, dentary; EPI, epipterygoid; F, frontal; fm, foramen magnum; J, jugal; L, lacrimal; la, lacrimal foramen; M, maxilla; mf, mandibular fenestra; N, nasal; ntn, notch for the trigeminal nerve; oc, occipital condyle; P, parietal; PBS, parabasisphenoid; PE, periotic; PF, prefrontal; PL, palatine; pla, pila antotica; PM, premaxilla; PT, pterygoid; ptf, post-temporal fenestra; PO, postorbital; pop, paroccipital process; Q, quadrate; QJ, quadratojugal; SA, surangular; SC, scapula; SM, septomaxilla; SO, supraoccipital; SQ, squamosal; t, tusk; V, vomer. Scale bars represent 5 cm.

Fig. 3. *Jimusaria monanensis* sp. nov. from the Naobaogou Formation, IVPP V31929. (A)

ventral; (B) anterior views. Abbreviations: AN, angular; AR, articular; BO, basioccipital; co, crista oesophagea; D, dentary; EC, ectopterygoid; EPI, epipterygoid; J, jugal; ic, internal carotid canal; ipv, interpterygoid vacuity; M, maxilla; PBS, parabasisphenoid; PE, periotic; PL, palatine; PM, premaxilla; PT, pterygoid; pr, posterior ridge of premaxilla; PRE, prearticular; Q, quadrate; ST, stapes; SP, splenial; SQ, squamosal; t, tusk; V, vomer. Scale bar represents 5 cm.

Fig. 4. *Jimusaria monanensis* sp. nov. from the Naobaogou Formation, (A) and (E) IVPP V31929. *J. sinkianensis* from the Guodikeng Formation, (B) V3240.1; (C) and (F) IVPP RV341407; (D) V3240.2. (A)-(D) in dorsal views; (E) and (F) in occipital views. Abbreviations: BO, basioccipital; EPI, epipterygoid; EO, exoccipital; F, frontal; jf, jugular foramen; N, nasal; P, parietal; PE, periotic; PF, prefrontal; POF, postfrontal; pop, paroccipital process; PP, postparietal; ptf, post-temporal fenestra; SO, supraoccipital; SQ, squamosal; TA, tabular. Scale bars represent 5 cm.

Fig. 5. *Jimusaria monanensis* sp. nov. from the Naobaogou Formation, IVPP V31929. (A) right lateral; (B) left lateral views; (C) drawing of mandible in left lateral view. Abbreviations: AN, angular; AR, articular; D, dentary; EC, ectopterygoid; F, frontal; J, jugal; L, lacrimal; lds, lateral dentary shelf; M, maxilla; mf, mandibular fenestra; N, nasal; OS, orbitosphenoid; PBS, parabasisphenoid; PE, periotic; PF, prefrontal; pif, pineal foramen; PL, palatine; PM, premaxilla;

PRS, presphenoid; PT, pterygoid; Q, quadrate; QJ, quadratojugal; SA, surangular; SM, septomaxilla; smf, septomaxilla foramen; SQ, squamosal; t, tusk; V, vomer. B, C share same scale bar. All scale bars represent 5 cm.

Fig. 6. Photos of all specimens of *Jimusaria sinkianensis* (A) IVPP RV341407; (B) V3240.1; (C) V3240.2; (D) V3240.3 in ventral views; the arrows indicate the autapomorphies of *J.sinkianensis* which are the caniniform process with posterior furrow and the parallel ventral ridge on posterior portion of anterior pterygoid rami. (B)-(D) share same scale bar. Scale bars represent 5 cm.

Fig. 7. Photos of (A) *Jimusaria monanensis* (IVPP V31929) and (B) *J. sinkianensis* (RV341407) in anterolateral views; the arrow indicates the connection between the epipterygoid and the lateral braincase wall. Abbreviations: EPI, epipterygoid; PE, periotic; PBS, parabasisphenoid. Scale bars represent 2 cm.

Comentado [LG8]: Please, also add an arrow pointing to this connection in figure 7A.

Fig. 8. Phylogeny of Bidentalia. *Jimusaria monanensis* in bold. Labeled clades: C, Cryptodontia; D, Dicynodontoidea. Numbers at nodes represent symmetric resampling values >45.

Comentado [LG9]: I recommend you label the node Bidentalia.