A new captorhinid reptile, *Gansurhinus qingtoushanensis*, gen. et sp. nov., from the Permian of China

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Abstract Captorhinids, a clade of Paleozoic reptiles, are represented by a rich fossil record that extends from the Late Carboniferous into the Late Permian. Representatives of this clade dispersed from the equatorial regions of Laurasia into the temperate regions of Pangea during the Middle and Late Permian. This rich fossil record shows that there was an evolutionary trend from faunivorous to omnivorous and herbivorous feeding habits within this clade. The discovery of well-preserved captorhinid materials in the Middle Permian of China allows us to determine that the new taxon, *Gansurhinus qingtoushanensis*, gen. et sp. nov, is a member of Moradisaurinae, a clade of captorhinids with multiple tooth rows arranged in parallel. The presence of this moradisaurine in the Middle Permian of south central Asia leads us to suggest that paleogeographic changes during the Permian, with part of what is today China becoming a large peninsula of Pangea, allowed these early reptiles as well as other terrestrial vertebrates to extend their geographic ranges to this region of the Late Paleozoic supercontinent.

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Introduction

Captorhinids were a diverse group of basal early reptiles, which ranged from the Late Carboniferous into the latest Permian, corresponding to a temporal range of more than 50 million years (Müller and Reisz 2005) making them the longest lived clade of reptiles confined to the Paleozoic. Their evolutionary history is particularly interesting and important because they represent the first pulse of reptilian diversification and geographic dispersal in terrestrial vertebrate evolution (Reisz 1997; Sues and Reisz 1998; Reisz and Sues 2000), but one that appears to have terminated by the Permo–Triassic boundary. Captorhinids were relatively small faunivorous reptiles during their initial stages of diversification, and known only from North America and Western Europe, but by the Middle Permian they consisted of mainly medium to large omnivorous and herbivorous animals, and had spread across much of Pangea, with representative taxa present in what is now Russia (Vjuschkov and Tchudinov 1957; Ivakhnenko 1990), central Europe (Sues and Munk 1996), India (Kutty 1972), Zimbabwe (Gaffney and McKenna 1979), Niger (de Ricqlès and Taquet 1982), Morocco (Jalil and Dutuit 1996), and South Africa (Modesto and Smith 2001).

The earliest known captorhinids were small reptiles, up to about 30 cm in snout-vent length, and with a single tooth row on the maxilla and the dentary. However, during the late Early Permian, some captorhinids increased in size and

several taxa evolved multiple tooth rows on the maxilla and mandible. New evidence suggests that the multiple tooth rowed condition evolved several times in captorhinid history (Kissel et al. 2002), but only the moradisaurine captorhinids appear to have combined the multiple tooth rowed condition and large body size (Modesto et al. 2007). The multiple tooth rowed condition in captorhinids can be associated with some form of dental occlusion, as evidenced by tooth wear, and indicates an omnivorous or herbivorous diet (Sues and Reisz 1998; Reisz 2006).

Captorhinid material was first reported from China by Li and Cheng (1997). The fragmentary material from the Upper Permian Naobaogou Formation of Inner Mongolia consists of partial maxillary and dentary dental plates that have been preserved in occlusion. Only the labial and lingual teeth are exposed, and the presence of multiple tooth rows can be inferred from the roots of teeth that have been exposed by erosion on the dorsal surface of the maxilla and the ventral surface of the dentary. The fragmentary nature of this material and the unusual morphology of the dentition made identification of this specimen tentative, and this report was largely ignored by subsequent workers. We report here on the partial, articulated skeletal remains of an older captorhinid reptile from the Middle Permian Dashankou fauna and discuss its phylogenetic and paleogeographic significance.

Systematic paleontology

Eureptilia Olson 1947

Captorhinidae Case 1911
    Moradisaurinae de Ricqlès and Taquet 1982
    Gansurhinus gen. nov.
    Gansurhinus qingtoushanensis sp. nov.

Diagnosis

Medium-sized moradisaurine captorhinid characterized by the presence of a long diastema between the single anterior tooth and the multiple tooth-rowed region of the upper dentition. Differs from other moradisaurines in having a maximum of five tooth rows on the maxillary and dentary dental plates, with individual teeth bearing a cusp-like emargination on the posterior aspect of the crown.

Etymology

Generic designation refers to the Gansu region of China, and *rhinus* (latinized from Greek for nose), a common epithet for this clade of reptiles. Specific designation refers to the locality name where the holotype was discovered, Qingtoushan.

Material

Holotype: partial skull (partial left premaxilla, dental plate of right maxilla, partial braincase, right pterygoid) and some postcranial materials [Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences] IVPP V15989, Fig. 1a, b.

Referred specimen: IVPP V12026, dental plate of right maxillary and right dentary (Li and Cheng 1997).

Locality and horizon

IVPP V15989—Xidagou Formation, Qingtoushan (Dashankou) locality near Yumen, Gansu Province, China, Middle Permian. IVPP V12026—Naobaogou Formation of Baotou, Nei Mongol, China, Late Permian.

Anatomical description

The fragmentary premaxilla (not illustrated) is 10 mm in length and 15 mm in height, and distorted antero-posteriorly. Although much of its anatomy is missing, it is possible to discern the presence of three teeth, which are labio-lingually compressed with a pointed tip. As in other captorhinids, the first tooth is the largest in the series, much larger than the other premaxillary teeth, the other two teeth being sequentially smaller in size. Although three teeth are clearly present, the incomplete preservation and crushing of the bone precludes precise determination of the total number of premaxillary teeth. It is possible that there may have been an additional fourth tooth in this species. A small resorption pit is present on the lingual side of first tooth, an uncommon feature in captorhinids. A posteroventrally directed sulcus is present on the inner upper side of the bone.

The left maxillary (Fig. 2) is flat dorsoventrally and measures 60 mm in length and 20 mm in maximum width. The dorsal surface is smooth and seems to preserve at least part of the original surface. As in *Labidosaurikos* and *Moradisaurus* (Dodick and Modesto 1995), the strongly curved margin of the dental plate is identified as the lingual side and the relatively straight margin is the labial side. The posterior end of the bone appears to be incomplete; it is possible that the tooth rows may have been longer in the species. It is therefore difficult to compare this specimen with the better known *Labidosaurikos* or *Moradisaurus*, but the size of the individual teeth and the width of the maxilla indicate that *Gansurhinus* was substantially smaller than the former taxa, although still a relatively large captorhinid. A slender conical tooth stands close to the lingual side on the anterior of the plate, and a diastema of 13 mm separates it from the posterior teeth. This is also observed in IVPP V12026 although the tooth is stouter in

Fig. 1 *Gansurhinus qingtoushanensis* gen. et sp. nov., IVPP V15989, material described in this study. Note that these photographs show the skeleton in partial articulation. The various elements of this skeleton have since been disarticulated for more detailed study. Anatomical abbreviations: *c2* cervical vertebra 2, axis; *cl* clavicle; *dv* dorsal vertebra; *m* maxilla; *pm* premaxilla; *sc* scapula; *u* ulna
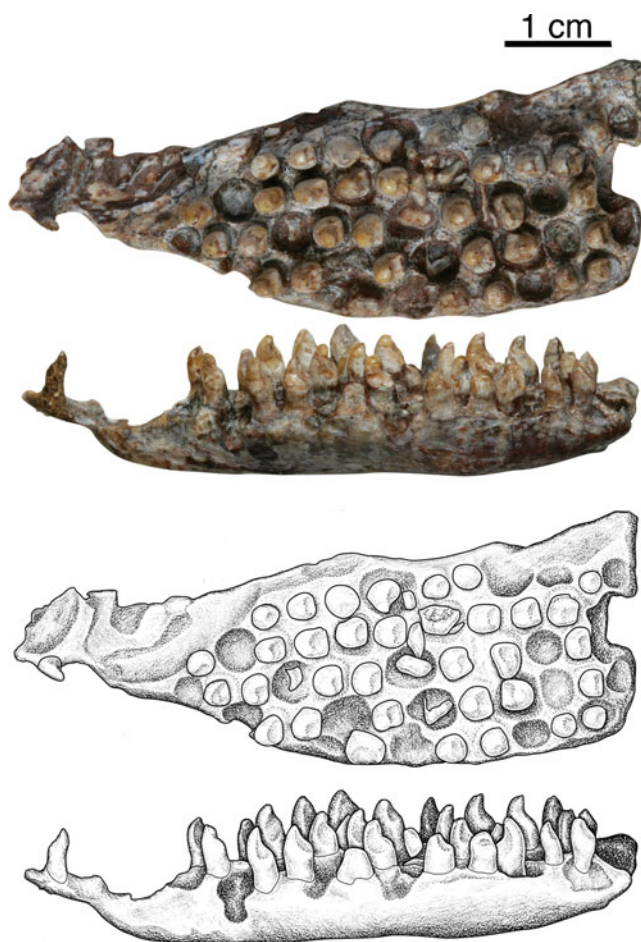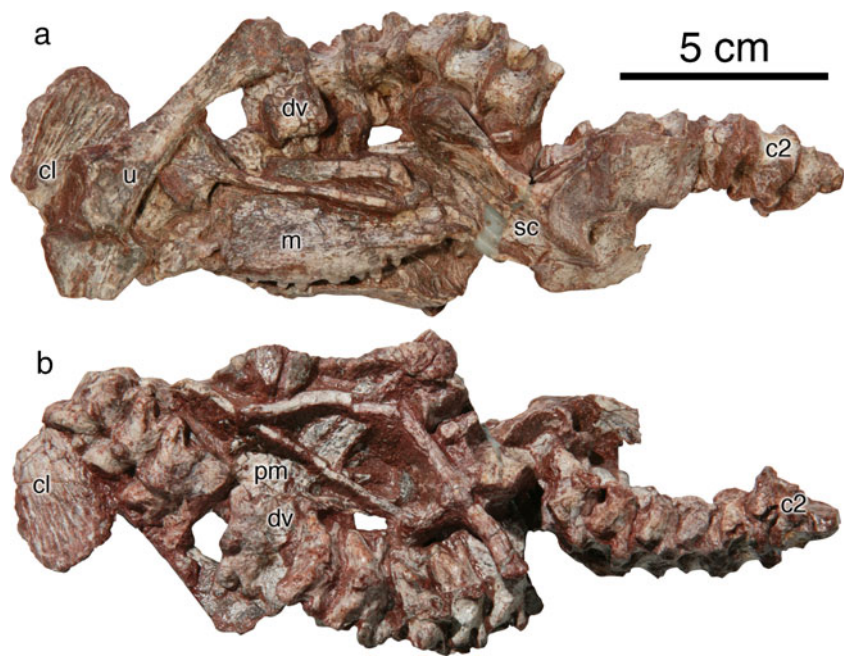

Fig. 2 *Gansurhinus qingtoushanensis* gen. et sp. nov., IVPP V15989, photographs and illustrations of left maxilla in ventral and medial views

the latter specimen. Five tooth rows lie roughly parallel to the labial margin. The teeth appear to be subthecodont in implantation and appear to grow in distinct sockets. The available evidence suggests that after a tooth is lost, a round socket remains. Some erupting teeth are present in some of these sockets. This is an unusual condition for a captorhinid; only basal members of this clade exhibit tooth replacement. As such, this may represent an autapomorphy for this taxon or may indicate that this is a very juvenile individual. Functional teeth are ankylosed to the jaw, filling completely the sockets. The crown of each tooth is single cusped distally, with a slightly recurved tip and a round, somewhat bulbous base. A triangular, slightly concave facet is formed below the cusp and is bounded laterally by two longitudinal ridges. The antero-posterior diameter of the teeth is similar or slightly larger than the mediolateral diameter. The teeth differ only slightly in height and diameter. Most teeth are recurved posteriorly, but a new erupting tooth, the seventh tooth on the fourth row, is recurved anteriorly. No obvious wear facets are present, although the tips of a few teeth are blunt.

The unusual configuration of the teeth and the pattern of replacement merit description. The numbers of preserved tooth positions are 10, 11, 12, 10, and 8, respectively, from labial to lingual side for five rows. In first labial row, the first, second, third, fifth, sixth, and ninth teeth are functional teeth; the third one is the largest and their size decreases both anteriorly and posteriorly. The ninth tooth is smallest and is the only conical tooth. A replacement tooth in the fourth tooth socket is lower but stouter than the third tooth. The base of a replaced tooth lies behind this tooth, and its crown lies behind the sixth tooth of the second row.

In the second row, the first, third, sixth, eighth, ninth, and 10th tooth positions are functional teeth; the fifth tooth is lower than other teeth but similar in diameter. It still does not fill the socket and is not fused with the jaw. The second tooth position is a round socket. The seventh tooth position is a socket with an erupting tooth preserved in it. The posteriormost position is broken. In the third row, the socket of the posteriormost position is also broken and no tooth is preserved. The second, third, fifth, sixth, eighth, and 11th tooth positions have functional teeth of similar size. The ninth tooth position has an erupting tooth and is similar in size to functional teeth, but still does not fill the socket completely. Its tip is recurved to the labial side, not the posterior side as is the case for most of the other teeth. We interpret this as a potential post-mortem modification because it is difficult to envisage how or why the tooth would rotate before becoming ankylosed to the maxilla. The first and 10th tooth positions are round sockets without teeth. The fourth and seventh tooth positions have newly erupting teeth with horizontal cusps which are directed lingually in the former but posteriorly in the latter. In the fourth row, the second, third, fourth, sixth, and ninth positions have functional teeth. The seventh tooth position has an erupting tooth similar to that of the ninth tooth position in the third row. Again, this tooth is recurved anteriorly rather than posteriorly. In fifth and eighth positions, it is a round socket with a newly erupting tooth whose tip points lingually. In the lingual tooth row, only five teeth are preserved; they lie on the second, fourth, fifth,

seventh, and eighth positions. The crown of the second tooth is broken, and the seventh and eighth teeth are slender. The first, third, and sixth teeth have been apparently shed, and there is no evidence of any replacement teeth (Fig. 3).

The maxilla of IVPP 12026 is slightly smaller than that in IVPP 15896, but the individual teeth are similar in shape. The overall similarities between these maxillae is striking, and despite the potential age difference merits assignment to the same taxon. The maxilla of IVPP 12026 is a fan-shaped bone with five rows of teeth. The tooth rows are nearly parallel, and the third one is apparently the longest, based on the exposed roots of the teeth. Details of the overall dentition cannot be discerned, but the labially and lingually exposed teeth are posteriorly recurved. The lingual and labial teeth of the bone identified as the dentary have also been exposed and, surprisingly, all identifiable teeth are anteriorly recurved rather than posteriorly. Although the maxilla and dentary bones are tightly occluded, probably by post-mortem crushing, there is no evidence of any dental wear.

Only a small fragment of the braincase of IVPP 15896 is preserved (not illustrated), consisting of a small part of the exoccipital and opisthotic. Their anatomy is poorly preserved, but is generally consistent with the pattern seen in moradisaurine captorhinids (Dodick and Modesto 1995).

The preserved portions of the postcranial skeleton (IVPP 15896) provide clear evidence of the captorhinid affinities of this reptile. There are 16 vertebrae preserved in three

Fig. 3 *Gansurhinus qingtoushanensis* gen. et sp. nov., IVPP V15989, photographs and illustrations of vertebrae 14–16 in right and left lateral, and ventral views. The presence of neural spine alternation is most evident in dorsal view
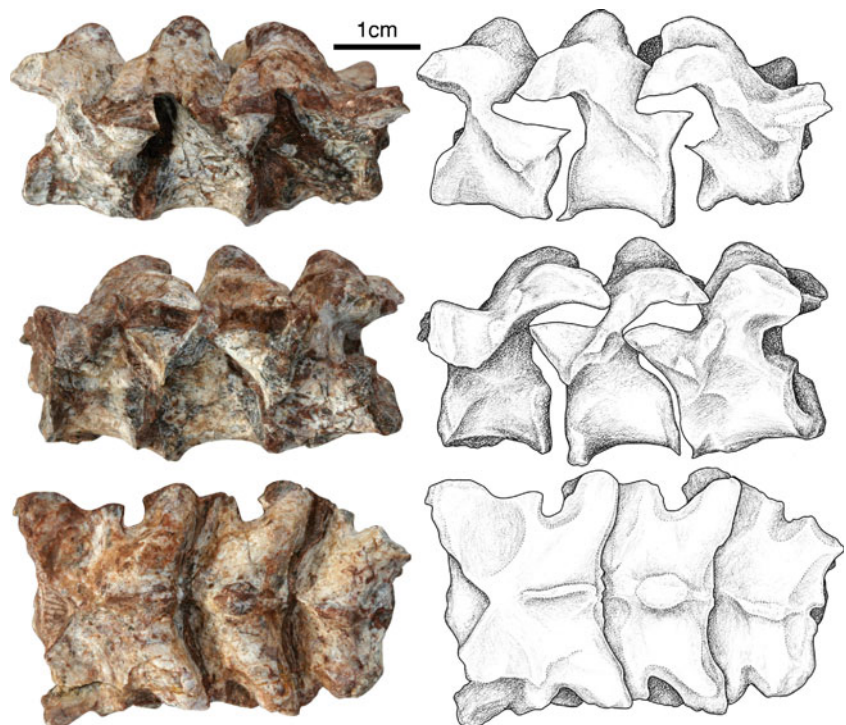
segments that were slightly separated from each other, but presumably formed a single series that extended posteriorly from a fragment of the atlas centrum to the 16th vertebra. Only a ventral fragment of the atlantal vertebra is preserved, and the axial vertebra is damaged, especially in the region of the neural spine. The preserved portion does, however, show the typically expanded, posteriorly massive postzygapophyseal buttresses, as in *Captorhinus laticeps* (Heaton and Reisz 1980; Dilkes and Reisz 1986; Sumida 1990). The other vertebrae of the series are well preserved and show the typical captorhinid morphology of rounded ventral surfaces of the centra, swollen neural arches, with the swelling being modest in the cervical series, but pronounced in the dorsal series. The dorsal vertebrae are relatively short and wide, with the zygapophyses extending far laterally. As in captorhinids where the vertebral anatomy is well known, the articulated series of vertebrae in *Gansurhinus* show clear evidence of neural spine height alternations (Heaton and Reisz 1980; Dilkes and Reisz 1986; Sumida 1990).

Other elements of the postcranial skeleton, preserved in the holotype, are entirely consistent with the assignment of *Gansurhinus* to Captorhinidae. For example, the scapulo-coracoid is relatively short and stout; the head of the clavicle is moderately expanded and has the type of fluted surface that is seen in *Captorhinus*.

Taxonomic identity

The two captorhinid specimens from China apparently differ in age. IVPP V15896 was found in the Xidagou Formation, with the presumed age of Middle Permian (perhaps Roadian) (Liu et al. 2009). IVPP V12026, on the other hand, comes from the Naobaogou Formation, co-existed with *Daqingshanodon*, pareiasaurs, and therocephalians, and the presumed age is Late Permian (Li and Cheng 1997). These ages have been biostratigraphically determined and must be considered tentative. In both specimens, the maxillary dental plates are preserved, allowing us to propose that these two captorhinid specimens from China are taxonomically indistinguishable from each other despite their different ages. They are both characterized by their distinctly shaped dentition and the lack of tooth wear. These teeth are unusual for captorhinids, but not unique in shape. Most moradisaurine captorhinids have simple conical teeth with slightly swollen bases. However, in the unnamed moradisaurine material from the Argana Formation of Morocco (Jalil and Dutuit 1996), the apex of the tooth is pointed and posteriorly recurved. In addition, an undescribed specimen from Texas, FMNH UR 955, tentatively assigned to *Labidosaurikos*, has the same kind of cusp morphology as *Gansurhinus*. This mandibular fragment from North America has no diagnostic features beyond the unusual dentition and the presence of four

rows of teeth, but in contrast to the known specimens of *Gansurhinus*, the dentition shows extensive wear associated with propalinal jaw movement. The lack of dental wear in *Gansurhinus* is intriguing and suggests that this Middle to Late Permian captorhinid may have had a different feeding strategy from the Early Permian moradisaurines of North America.

Discussion

Phylogenetic analysis

Gansurhinus is confidently assigned to Captorhinidae on the basis of its dentary and maxillary dentition in the holotypic and referred specimen, and its vertebral morphology. The phylogenetic position of *Gansurhinus* within the Captorhinidae was evaluated relative to 15 other captorhinid taxa (Fig. 4), with *Paleothyris* and *Protorothyris* as outgroups (Müller and Reisz 2005). The captorhinid taxa in this analysis do not represent the entirety of this family. Several taxa are either based on fragmentary specimens or are being restudied, and require revision. Only three members of the captorhinid clade Moradisaurinae were therefore included in this analysis, *Moradisaurus*, *Labidosaurikos*, and *Rothianiscus*. The former two taxa were examined by two of the authors, and some of the data for *Rothianiscus* were kindly provided by Mr. Torsten Liebrecht, Humboldt University in Berlin. Seventy-four characters (see the Electronic supplementary material for character list and data matrix) were scored for the taxa, using previous data sets (Dodick and Modesto 1995; Müller and

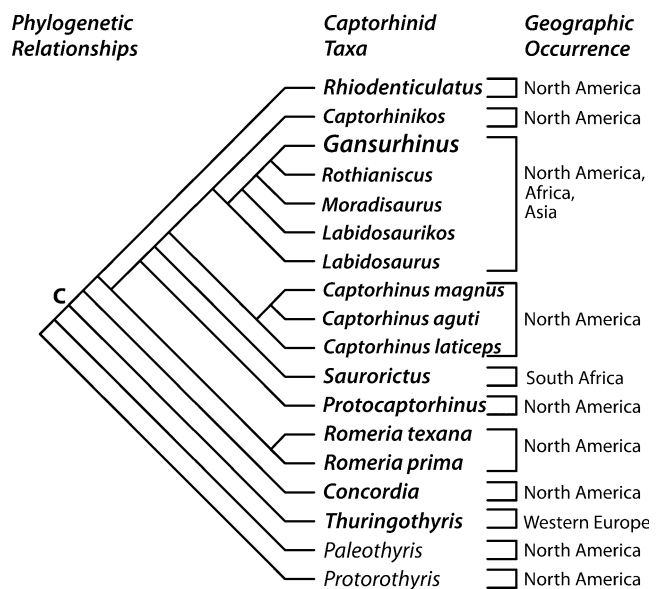| Phylogenetic Relationships	Captorhinid Taxa	Geographic Occurrence

Fig. 4 Hypothesis of captorhinid relationships (see text for discussion of analysis, and online supporting documentation for list of characters and data matrix). *C* denotes Captorhinidae

Reisz 2005, 2006; Modesto et al. 2007), but also additional cranial and postcranial characters were included; some of the dental characters were also modified in order to deal with variation in the multiple tooth-rowed taxa. The branch-and-bound search option in PAUP* (Swofford 2002) yielded a single most parsimonious tree (TL=142; CI=0.6690; HI=0.3380; RI=0.7883; RC=05274), with a tree topology similar to those in previous studies, but in which *Gansurhinus* nests within Moradisaurinae, as a sister taxon to *Rothianiscus*. Our analysis indicates that *Gansurhinus* from the Middle to Late Permian of China is a derived moradisaurine captorhinid reptile, with its closest sister taxon being a North American form. Our results also indicate that *Labidosaurus* is the sister taxon to a monophyletic Moradisaurinae (includes *Labidosaurikos*, *Rothianiscus*, *Moradisaurus*, and *Gansurhinus* in this analysis). This pattern of relationships (Fig. 4) is strongly supported, with bootstrap values of 99% and 100%, respectively, and decay indices of four steps in both. However, other potential moradisaurine captorhinids could not be included in this analysis because of their extremely fragmentary nature, being represented by fragmentary tooth plates or individual bones. Their inclusion in the analysis could not resolve their position within Moradisaurinae.

Paleogeographic implications The appearance of these derived captorhinids in China is consistent with the occurrence of other Permian reptiles in China and with the geographic reconstruction of Pangea. We have previously reported on the presence of bolosaurids in this faunal assemblage (Müller et al. 2008) and argued that *Belebey* was found in both Russia and China. Bolosaurids are part Parareptilia, a clade of reptiles that includes pareiasaurs and other enigmatic forms that are known from predominantly Middle and Upper Permian strata. Bolosaurids are unusual in this regard because they are the oldest known parareptiles and, like captorhinid reptiles, range in age from the latest Carboniferous to the Middle Permian. Captorhinids are part of Eureptilia, a clade of reptiles that includes diapsids (including extant squamates, crocodilians, birds, as well as dinosaurs and numerous other groups of extinct forms). Despite their wide taxonomic separation, bolosaurids and captorhinids present a synchronous evolutionary history with regards to their presence in China. Paleogeographic reconstructions of Pangea in the Late Carboniferous and Early Permian show China as large islands east of the Laurasian landmass, isolated from the Pangean mainland (Blakey 2007). In contrast, by the Middle Permian, the part of China that is represented by the Gansu province was a large peninsula attached to Laurasia (Scotese and Langford 1995; Li et al. 2004; Scotese 2004), thus allowing for biotic interchange. It is therefore reasonable to suggest that only by the Middle Permian were terrestrial reptiles such as bolosaurids and captorhinids able to expand their geographic range to the east, including China.

The presence of the new fossil material provides paleontological confirmation of the proposed connection between China and Pangea towards the end of the Paleozoic. In contrast to bolosaurids, whose paleogeographic distribution in the Paleozoic is restricted to the equatorial and subequatorial regions of Pangea, captorhinids have a much wider distribution. Members of the clade are present in higher northern latitudes of Laurasia, in central and southern Africa, and in India. Their presence in China expands their geographic range, raising the possibility that they are the first eureptiles to have gained a near global distribution.

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