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A new borioteioid lizard with large caniniform tooth from the Upper Cretaceous of South China

Mengli Wang^{a,b}, Liping Dong^c, Juan Yu^d, Fasheng Lou^e, Wenjiang Qiu^f and Fenglu Han^{a,*}

^aSchool of Earth Sciences, China University of Geosciences, Wuhan, China; ^bXinjiang University of Technology, Xinjiang, China;

^cInstitute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; ^dJiangxi Geological Museum, Nanchang, China; ^eInstitute of Jiangxi Geological Survey and Exploration Institute, Nanchang, China; ^fBasic Geological Survey Institute of Jiangxi Geological Survey and Exploration Institute, Nanchang, China

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Borioteiioidea (Polyglyphanodontia) is a group of lizards that were abundant in China and Mongolia during the Late Cretaceous. Two borioteioid genera, *Tianyusaurus* and *Yechilacerta*, with complete lower temporal bars, have been reported from the Upper Cretaceous of South China. Here we report a new borioteioid fossil lizard, *Caninosaurus ganzhouensis* gen. et sp. nov., based on an incomplete skull and mandible from the Upper Cretaceous Tangbian Formation of Ganzhou Basin, Jiangxi Province, South China. The new lizard differs from other Late Cretaceous lizards by possessing a unique combination of features, including nasal process of the premaxilla constricted at the base; elongated posterodorsal projection of the maxillary facial process; no articulation between the nasal and prefrontal; a prefrontal with a fossa on its lateral surface; elongated frontals with sculptured dorsal surface and a waisted orbital margin; tooth crowns with no denticles and cusps; and a large and caniniform fourth maxillary tooth. Phylogenetic analyses based on two recent data matrices both recover *Caninosaurus* within Borioteiioidea. In the unconstrained analyses, *Caninosaurus* is placed in a clade with *Tianyusaurus* and *Yechilacerta*. *Caninosaurus* is the third borioteioid lizard discovered from the Upper Cretaceous of the Jiangxi Province, increasing the diversity of borioteioid lizards found in eastern Asia. The small body size and possible omnivorous diet of *Caninosaurus* suggest it occupied a different ecological niche to *Tianyusaurus* and *Yechilacerta*.

<https://zoobank.org/urn:lsid:zoobank.org:pub:3F0B9E9D-E1FC-407D-8126-8ABBF63F8437>

Keywords: lizard; Boreoteiioidea; caniniform tooth; Cretaceous; China

Introduction

Borioteiioidea is a collection of herbivorous and omnivorous lizards known from the Late Cretaceous of North America, Europe, Asia and South America (Celerino de Carvalho & Santucci, 2024; Evans & Manabe, 2008; Folie & Codrea, 2005; Longrich et al., 2012; Nydam, 1999, 2013; Nydam et al., 2007; Sulimski, 1972; Xing et al., 2023; Xu et al., 2014). The extant clade Teiioidea (Teiidae and Gymnophthalmidae), from North and South America, is hypothesized to be the sister group of Borioteiioidea (Conrad, 2008; Scarpetta, 2020; Vitt & Pianka, 2004). Borioteioid lizards were first described by Gilmore (1942, 1943) from the Upper Cretaceous North Horn Formation of Emery County, Utah. Later, more material was reported from various Upper Cretaceous deposits of North America (e.g. *Bicuspidon* and *Dicodhodon*), as well as of Asia (*Adamisaurus*, *Gilmoreteius*, *Gobinatus* and *Tianyusaurus*) (Evans et al., 2002; Gao & Norell, 2000; Lü et al., 2008; Nydam & Voci, 2007; Sulimski, 1972). Early studies proposed that borioteioids originated in

North America and then migrated to Asia and beyond (Nydam, 1999; Nydam et al., 2007). However, the purported borioteioid *Kuwajimalla* from the Barremian of Japan suggested the group might have originated in eastern Asia during the Early Cretaceous (Evans & Manabe, 2008; Evans & Matsumoto, 2015).

Borioteiioidea is a highly diverse clade and contains Polyglyphanodontidae, Adamisauridae, Gilmoreteiidae and some basal taxa (Nydam et al., 2007). The majority of Late Cretaceous borioteioid lizards from North America are represented by isolated elements, particularly dentaries and maxillae (except *Polyglyphanodon* and *Paraglyphanodon*), whereas more complete skeletons and skulls were mainly found from the Upper Cretaceous of Mongolia and China (Gao & Norell, 2000; Nydam & Cifelli, 2002; Nydam et al., 2007). Polyglyphanodontidae is mainly distributed in North America and is characterized by transversely expanded teeth (Gilmore, 1942; Nydam & Cifelli, 2002; Nydam et al., 2007). Borioteioids from the Upper Cretaceous of Mongolia and China (Gao & Norell, 2000; Sulimski, 1972, 1975)

*Corresponding author. Email: hanfl@cug.edu.cn

encompass a diverse assemblage (e.g. Adamisauridae, Gilmoreteiidae) and include some small teiid-like taxa (e.g. *Gobinatus*). The dentitions of the Asian taxa are more diverse and at least four tooth morphotypes were recognized: (1) leaf-shaped, polycusate tooth (e.g. in *Gilmoreteius*); (2) large, bulbous, conical tooth (e.g. in *Adamisaurus*); (3) obliquely oriented, polycusate, blade-like tooth (e.g. in *Cherminisaurus*); (4) presence of canini-form tooth (e.g. in *Tianyusaurus*) (Gao & Norell, 2000; Lü et al., 2008; Nydam, 1999).

Four species of lizards have been established from the Upper Cretaceous of Ganzhou Basin, namely *Conicodontosaurus kanhsienensis* (Young, 1973), *Chianghsia nankangensis* (Mo et al., 2012), *Tianyusaurus* sp. (Mo et al., 2010) and *Yechilacerta yingliangia* (Xing et al., 2023). The holotype of *C. kanhsienensis* is only a partial dentary with a tooth imprint (Young, 1973), which is too poor to be assigned to *Conicodontosaurus* (Gao et al., 2021). *Tianyusaurus* was first described from the Upper Cretaceous of Luanchuan Basin, Henan Province (Lü et al., 2008), and more specimens of *Tianyusaurus* were reported from the Ganzhou Basin later (Mo et al., 2010). This genus is regarded as a borioteioid (Mo et al., 2010). *Chianghsia nankangensis* is a large predatory lizard of the Monstersauria (Anguimorpha) (Mo et al., 2012). *Yechilacerta yingliangia* is the second borioteioid from the basin; it was recovered as the sister taxon of *Tianyusaurus* and has a relatively large skull with coarse pustulate cranial sculpture (Xing et al., 2023).

Here we describe a new lizard from the Late Cretaceous of Ganzhou City, Jiangxi Province, South China. In terms of overall morphology, the new lizard shows a greater resemblance to some borioteioids based on cranial features (Gao & Norell, 2000). This is the fifth species and the third borioteioid reported from the Ganzhou Basin of Jiangxi, increasing the diversity of lizards in the Late Cretaceous of South China. The body size difference and the different tooth morphology suggest a niche differentiation among the borioteioids in the Ganzhou Basin at the time.

Geological setting

The specimen was found 2 km south-east of Ganzhou Railway Station, Zhanggong District, Ganzhou City, Jiangxi Province, China, and is from the Upper Cretaceous Tangbian Formation of Ganzhou Basin. Ganzhou Basin is one of the classic areas in the study of continental Cretaceous vertebrate fossils (He et al., 2017). The earliest studies of the vertebrates from this basin date back to the 1960s (Young, 1965), and subsequent extensive excavations have yielded a relatively rich

assemblage, including dinosaurs, turtles, crocodylians, lizards and mammals (He et al., 2017; Hu & Han, 2021; Li et al., 2019; Mo et al., 2010; Tong & Mo, 2010; S. Wang et al., 2013; Xing et al., 2022; Young, 1973). Situated within the southern segment of the South China Block, the Ganzhou Basin was formed owing to subduction of the palaeo-Pacific plate beneath the South China Block (J. Wang et al., 2022). Ganzhou Basin is a NE-trending faulted basin controlled by the Dayu-Nanchang Fault in the south-east margin, covering an area of about 1261.85 km² (He et al., 2017). There are well-exposed outcrops of the Upper Cretaceous successions of fluvial and lacustrine red beds in the Ganzhou Basin, which consist of five formations (in ascending order): the Maodian Formation, Zhoutian Formation, Hekou Formation, Tangbian Formation, and Lianhe Formation. The lower two formations are grouped as the Ganzhou Group, whereas the upper three are grouped as the Guifeng Group. The Tangbian Formation comprises a set of brick-red thick-giant bedded fine-grained sandstone sedimentary strata (Fig. 1), and was suggested to be littoral-shallow lake facies. The age of the Tangbian Formation was estimated as Santonian–Campanian according to palynology (F. Wu et al., 2017).

Material and methods

The specimen studied herein (CUGW VH110) preserves the anterior half of the skull and mandible of a small lizard which is exposed in right lateral view (Figs. 1–3; Supplemental Fig. S1). The left side of the skull is not exposed and is buried in the matrix. The specimen is deposited in the fossil lab of the China University of Geosciences (Wuhan). The skull and mandible were prepared by Mengli Wang, using a tungsten steel pick needle under a stereoscopic microscope, and were photographed using a Canon EOS 6D camera.

Micro Computed Tomography

The holotype of the new taxon was scanned at the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences (KLVEHO, CAS) in Beijing, China, using the Nano-CT system (Phoenix X-ray, GE Measurement & Control) with a beam energy of 115 kV and a flux of 85 mA. A total of 1903 slices were obtained at a pixel resolution of 8.445 µm and checked in the commercial software Mimics 16.0 (and 3-matic Research). Although it is difficult to segment the fossil due to the low greyscale contrast between the matrix and the fossil, the data provide some anatomical details (Supplemental Fig. S2).

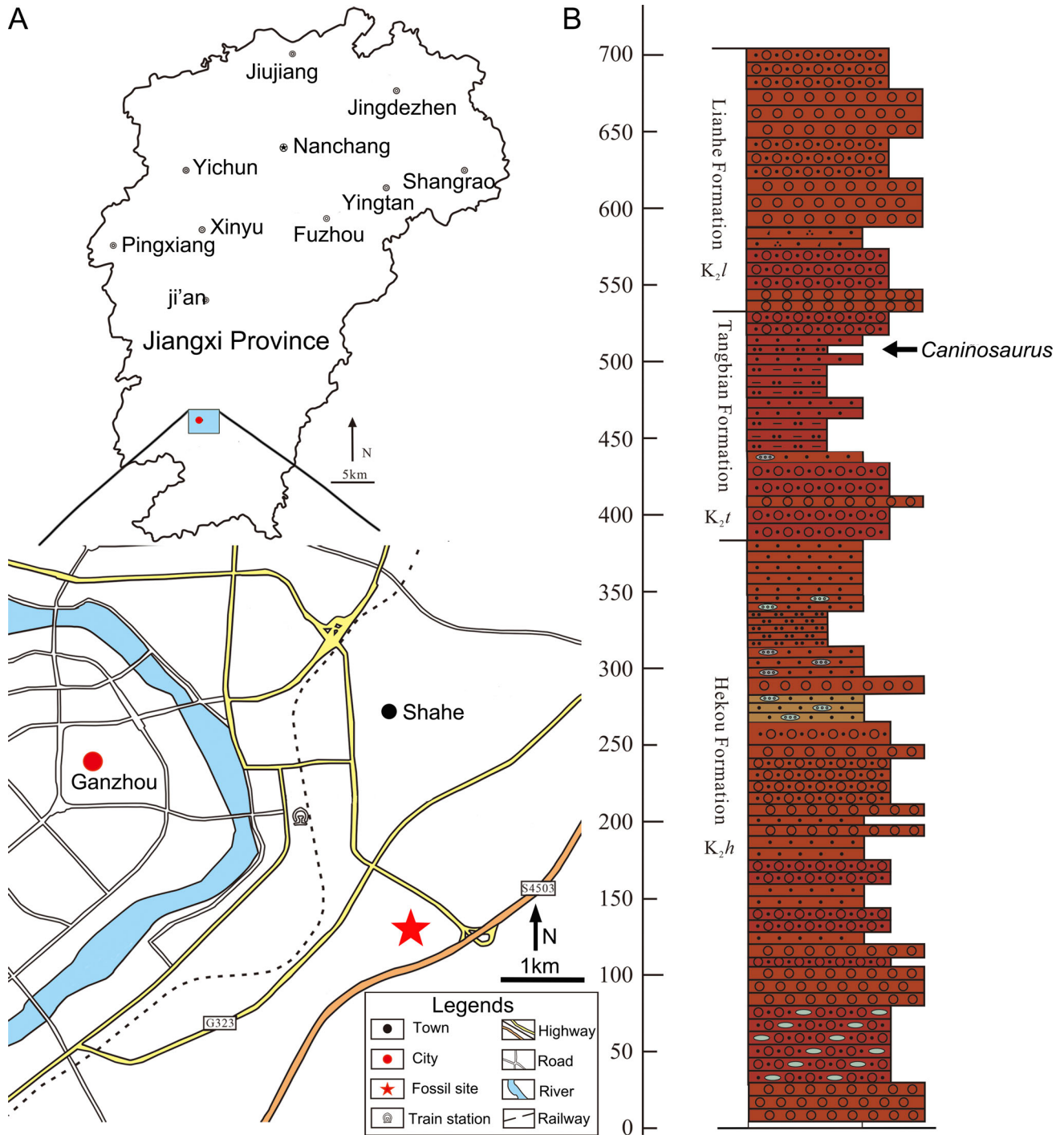


Figure 1. A, map of the locality showing where the holotype of *C. ganzhouensis* gen. et sp. nov., was collected. The red star marks the fossil locality. B, lithostratigraphy of the Upper Cretaceous Tangbian Formation.

Phylogenetic analysis

To obtain the phylogenetic position of the new lizard among squamates, we used two recent data matrices. One (referred to as the Simões-derived matrix) is that of

Simões et al. (2017), which was originally from Conrad (2008), and the other (referred to as the Čerňanský-derived matrix) is the matrix of Čerňanský et al. (2022), which was derived from those of Gauthier et al. (2012) and

Reeder et al. (2015). We added six extinct taxa into the first matrix: *Tianyusaurus*, *Aprisaurus*, Jiangxi-2, *Tuberocephalosaurus*, *Funiusaurus* and *Yechilacerta* (Lü et al., 2008; Mo et al., 2010; Xing et al., 2023; Xu et al., 2014), and our new taxon *Caninosaurus*, totaling 227 terminal taxa. Of 363 characters, 20 characters were set as ordered as in Conrad (2008) and 65 can be scored for *Caninosaurus* (17.9%). In the analysis based on the Čerňanský et al. (2022) matrix, we added four extinct taxa: *Tianyusaurus* (Henan and Jiangxi material) (Lü et al., 2008; Mo et al., 2010), *Funiusaurus* (based mainly on figures and description) (Xu et al., 2014), *Yechilacerta* (Xing et al., 2023) and *Caninosaurus*, resulting in a total of 208 terminal taxa and 691 characters. We ran 151 characters ordered as in Gauthier et al. (2012), and 67 characters can be scored in *Caninosaurus* (9.7%).

The data matrices were edited in Mesquite v. 3.03 and saved in the TNT format for parsimony analysis. Parsimony analyses were performed in the software TNT v. 1.6 (Goloboff & Morales, 2023), using *Rhynchocephalia* and *Gephyrosaurus bridensis* as the outgroup in the analysis of the Simões-derived matrix and Čerňanský-derived matrix, respectively, and ordered characters were set when needed as in Simões et al. (2017) and Čerňanský et al. (2022). Four different analyses were conducted on the Čerňanský-derived matrix, using unordered or ordered characters, with or without molecular constraints, to check what changes these settings can make (see Supplemental data 2 for the TNT scripts and full strict consensus trees of each analysis). The constraints were set according to the tree (*Gephyrosaurus bridensis* (*Dibamus novaeguineae* (*Gekko gekko* *Eublepharis macularius*))((*Cordylosaurus subtessellatus* *Scincus scincus* *Xantusia vigilis*))(((*Tupinambis teguixin* *Pholidobolus montium*)(*Lacerta viridis* (*Bipes biporus* *Rhineura floridana*)))(*Python molurus* *Cylindrophis ruffus*) (*Oplurus cyclurus* *Uromastyx aegyptia*) (*Varanus salvator* *Shinisaurus crocodilurus*))))), following the set of Dong et al. (2023),

which is based on the molecular phylogenetic study of Pyron et al. (2013). All other taxa were set as floating.

We employed the New Technology search option with sectorial search (default settings), ratchet (20 iterations), drift (default settings), tree fusing (default settings) and a minimum length tree to be found in 20 replicates. Tree bisection and reconnection was followed to find more maximum parsimony trees. Definition of phylogenetic clade names in this study can be seen in Table 1.

Systematic palaeontology

Order **Squamata** Opperl, 1811
 Borioteiioidea Nydam, Eaton et Sankey, 2007
 Polyglyphanodontidae Gilmore, 1942
 Genus ***Caninosaurus*** gen. nov.

Diagnosis. As for the type and only species.

Caninosaurus ganzhouensis gen. et sp. nov.

(Figs. 2–3)

Etymology. The genus name ‘Canino’ indicates long canine-like teeth; ‘saurus’ is derived from the Greek word *sauros*, meaning a lizard. The species name ‘ganzhou’ denotes the city where the fossil locality of this specimen is found.

Holotype. CUGW VH110, an incomplete skull with mandibles.

Locality and horizon. 2 km south-east of Ganzhou Station, Ganzhou City, Jiangxi Province; Tangbian Formation, Santonian–Campanian, Upper Cretaceous (F. Wu et al., 2017).

Diagnosis. A small-sized lizard, with a skull about 30 mm long across the dorsal midline, differs from all other borioteioids in the following combination of derived characters (autapomorphies are marked by *): nasal process of the premaxilla constricted at the base*, tall maxillary facial process (unlike that of

Table 1. Phylogenetic definitions of clade names used in this study.

Clade name/author	Definition	Reference
Borioteiioidea	The most recent common ancestor of the clade containing <i>Chamops</i> , <i>Prototeius</i> , and the clade containing <i>Polyglyphanodon</i> , <i>Dicathodon</i> , and <i>Penetieus</i> , and all of its descendants.	Nydam et al. (2007)
Polyglyphanodontidae	<i>Adamisaurus magnidentatus</i> , <i>Gilmoreteus ferruginous</i> , <i>Gobinatus arenosus</i> , <i>Polyglyphanodon sternbergii</i> , and all descendants of their last common ancestor.	Conrad (2008)
Polyglyphanodontinae	All taxa sharing a more recent common ancestor with <i>Polyglyphanodon sternbergii</i> than with <i>Adamisaurus magnidentatus</i> or <i>Teius teyou</i> .	Conrad (2008)
Tuberocephalosaurinae	All taxa sharing a more recent common ancestor with <i>Tuberocephalosaurus</i> than with <i>Polyglyphanodon</i> and <i>Adamisaurus</i> .	Mo et al. (2010); Xu et al. (2014)
Scleroglossa	All descendants of the last common ancestor of <i>Gekko gekko</i> , <i>Scincus scincus</i> , and <i>Anguis fragilis</i> .	Conrad (2008)

Tchingisaurus and *Gobinatus*), a long and tapering post-erodorsal projection of the maxilla (similar to *Polyglyphanodon* but unlike that of all other borioteioids), lacking nasal-prefrontal contact (similar to *Polyglyphanodon*, *Tchingisaurus* and *Gobinatus*, but unlike that of all other borioteioids), sculpturing on the dorsal surface of the frontals (unlike those of *Adamisaurus* and *Paleochelco*), prefrontal with a fossa on its lateral surface (similar to *Funiusaurus* and *Yechilacerta*, but distinct from all other borioteioids), elongate and waisted frontals (differs from those of *Polyglyphanodon* and *Yechilacerta*), anterolateral process of the frontal tapering between the nasal and maxilla*, tooth crown chisel-like with no denticles and cusps (similar to *Funiusaurus*, but unlike those of other borioteioids), and a large caniniform tooth at the fourth maxillary tooth position*.

Remarks. Although the holotype displays a limited number of morphological features, the combination of the characters (tall maxillary facial process, deep mandible but a small coronoid without a labial process, a caniniform maxillary tooth) suggests its affinity to borioteioids. A few characters of this species occur in some other lizard groups. For example, waisted frontals, a tall facial process

of the maxilla, a prefrontal boss, and caniniform maxillary teeth also occur in some iguanians (Evans, 2008), and the former two characters also occur in teiids and lacertids (Čerňanský & Syromyatnikova, 2019). However, *Caninosaurus* differs from iguanians in having a post-frontal embracing the frontoparietal suture with long frontal and parietal processes, a frontal contacting the maxilla, and a deep mandible (Evans, 2008); from teiids in having a parietal foramen and lacking a well-developed labial process of the coronoid bone (Evans, 2008; Gauthier et al., 2012), and from lacertids in having a post-frontal with a distally bifurcated end but not a posterior expansion, and lacking a well-developed labial process or grooves that mark the overlying scales (Čerňanský & Syromyatnikova, 2019; Gauthier et al., 2012).

Description

The holotype preserves the anterior half of the skull and mandible (Figs. 2–3). The preserved skull appears long and deep, with a pointed snout. However, due to the strong lateromedial compression during burial and the incomplete nature of the specimen, the general shape of

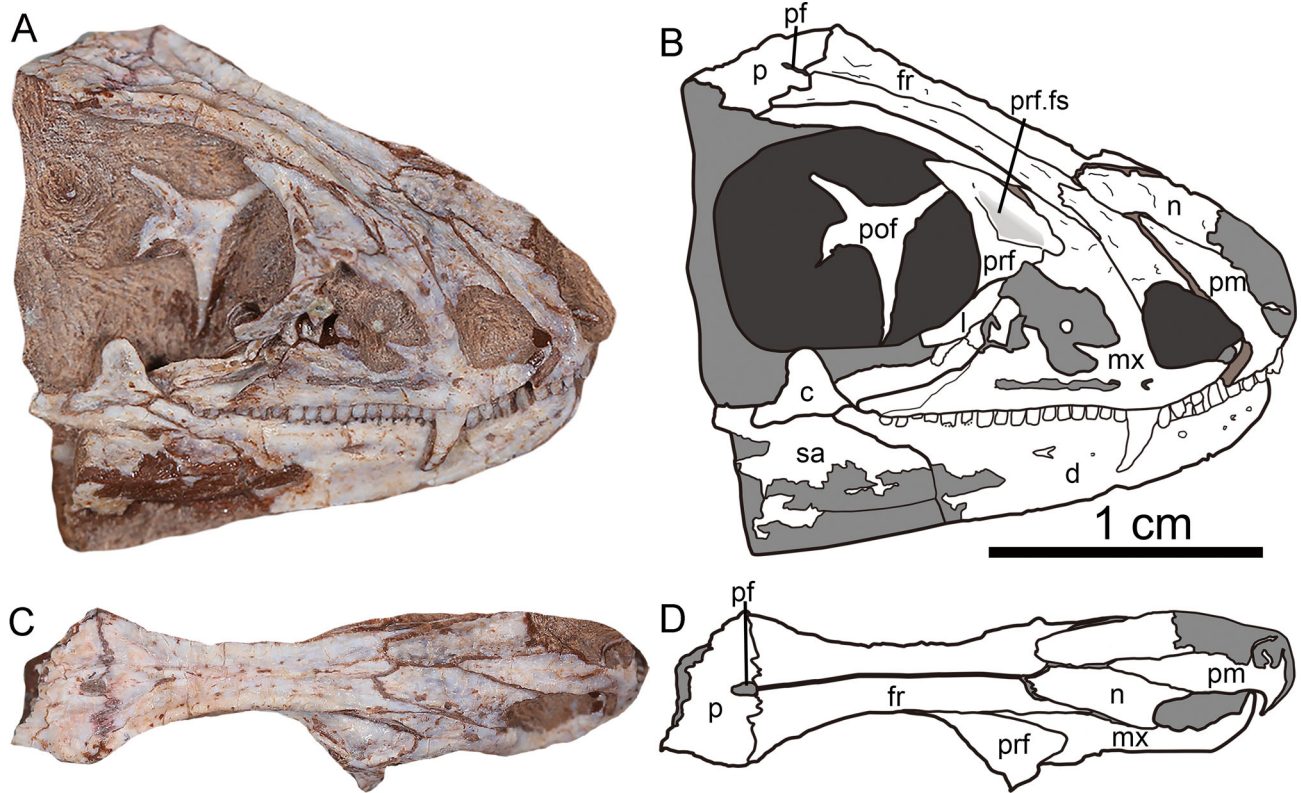


Figure 2. Photographs (A, C) and line drawings (B, D) of the holotype of *C. ganzhouensis* gen. et sp. nov. in right lateral view (A, B) and dorsal view (C, D). **Abbreviations:** c, coronoid; d, dentary; fr, frontal; l, lacrimal; mx, maxilla; n, nasal; p, parietal; pf, parietal foramen; pm, premaxilla; pof, postfrontal; prf, prefrontal; prf.fs, prefrontal fossa; sa, surangular.

the skull is uncertain. The external naris is large, nearly round, and facing laterally. The orbit is large and sub-circular and faces more dorsally than laterally. As preserved, the orbital region is nearly as long as the antorbital snout. The preserved external surface of the bones is slightly ornamented with rugosities (e.g. premaxilla, nasal, and frontal) (Fig. 2).

Premaxilla

The premaxilla is well preserved, with the left tip of the alveolar plate obscured by the matrix. It consists of a long nasal process and the alveolar plate is rather short (much less than half the nasal process) (Fig. 2). The nasal process ascends from the alveolar plate at an angle of about 60°, indicating the skull might be tall. The long nasal process of the premaxilla is slightly constricted at its base, widens gradually to reach its broadest at its midpoint, and tapers to a point posteriorly. At the base of the nasal process at either side, there is a small notch for the medial ethmoidal branch of the ophthalmic and ethmoidal nerve (trigeminal nerve) and ethmoidal artery to exit, as in *Polyglyphanodon* (Gilmore, 1942). The tapering posterior half intervenes between the two nasals, and terminates at the mid-length of the nasals, far away from the frontals. In anterior view, the alveolar plate is roughly a low triangle with a tapering lateral maxillary process. The lateral process was completely overlapped by the anterior premaxillary process of the maxilla, suggesting the premaxilla-maxilla articulation was of an overlapping type. The premaxilla was excluded from the ventral narial margin by the long anterior ramus of the maxilla. The preserved anterior surface of the premaxilla is smooth and lacks any of the foramina seen in *Tchingisaurus multivagus* and *Gobinatus arenosus* (Gao & Norell, 2000).

Maxilla

The maxilla is a large and sub-triangular bone in lateral view, and consists of a long anterior premaxillary process, a facial process, and a short posterior process. The premaxillary process tapers anterodorsally and terminates at the base of the nasal process of the premaxilla, forming the entire ventral margin of the external naris. The anterior end of the premaxillary process was probably broad, but it is unknown whether it was forked and whether there was a premaxilla-maxillary aperture. Although the facial process is broken, it is large and tall, extending posterodorsally, as in *Polyglyphanodon* (Gilmore, 1942). The facial process arises from the premaxillary process at a steep angle (almost vertical) and therefore forms most of the posterior margin of the external naris. The facial process gradually deflects onto the skull roof when contacting the nasal and

extends posterodorsally as a long projection between the frontal and prefrontal, therefore completely separating the nasal from the prefrontal. Although broken, it is known that the facial process posteriorly overlaps the prefrontal, the lacrimal, and probably the anterior end of the jugal, and its posterior margin slopes more gently than the anterior margin into a short posterior process. The posterior process of the maxilla terminates halfway below the orbit and includes a short edentulous region. The posterior part of the palatal shelf on the maxilla is seen due to the displacement and breakage of the jugal. It is broad and clearly displays a facet for the jugal on the dorsal surface. The maxillary dentition also extends for a distance below the orbit. The lateral surface of the maxilla is pierced by two large labial foramina facing anteroventrally (Fig. 2). The anterior one is located above the large caniniform tooth position, and the posterior one is located at the level above the 6th tooth position. Dentition is described in a separate section below.

Prefrontal

The prefrontal is large and well preserved (Fig. 2). The bone is roughly triangular, consisting of a broad anterior lamina, a short frontal process, and an orbitonasal flange. Anteriorly, the prefrontal is overlapped by the facial process of the maxilla. The orbitonasal flange curves downward from the anterior lamina to form the anterior wall of the orbit, and it articulates with the lacrimal laterally enclosing a foramen for the lacrimal duct between them. Medially the prefrontal sutures with the frontal along the lateral margin of the frontal and forms the anteromedial edge of the orbit (as the frontal process), and with the long posterodorsal projection of the maxilla, and therefore lacks contact with the nasal as in *Polyglyphanodon*, *T. multivagus* and *G. arenosus* (Gao & Norell, 2000; Gilmore, 1942). In dorsal view, the orbital and the lateral margins of the prefrontal are raised as distinct ridges that enclose a large depression. The junction between the two ridges forms a boss like that in iguanians (Fig. 2; Supplemental Fig. S1) (Evans, 2008).

Lacrimal

The lacrimal is elongated and rectangular in outline, as in *Polyglyphanodon* (Gilmore, 1942). It is a relatively large bone located lateral to the prefrontal, bordering the orbit anterolaterally. The lacrimal is anterolaterally overlapped by the well-developed facial process of the maxilla, and encloses a lacrimal foramen with the prefrontal (see above). The lacrimal formed a wide articulation with the posterior region of the maxilla. Posteriorly, the lacrimal contacts the dorsal surface of the anterior ramus of the jugal.

Postfrontal

The right postfrontal is adequately preserved within the orbit, but it is detached from its original position, losing connections with the surrounding bones and rotating clockwise 90°. The postfrontal body is square in shape and bears four processes. The long medial two, diverging widely from each other at a wide angle, clasp the frontoparietal suture, whereas the short lateral two, forming a lateral narrow notch, receive the postorbital lateroventrally, as in *T. multivagus* (Gao & Norell, 2000).

Nasal

The nasals are elongated and rectangular in outline, with a ratio of nasal length to frontal length of about 0.55 (Fig. 2), which is similar to that of *Polyglyphanodon*, whereas the nasals are relatively short in *Tianyusaurus* and *Adamisaurus* (nasal-frontal length ratio 0.4 and 0.48, respectively) (Lü et al., 2008; Mo et al., 2010; Sulimski, 1972). They meet along the midline but are separated by the nasal process of the premaxilla for the anterior half of the nasals and intervened by the short anteromedial process of the frontal posteriorly. The anterior margin of the nasal is probably concave, being the dorsal half of the posterior margin of the external naris. Laterally the nasal sutures firmly with the facial process of the maxilla anteriorly and the anterolateral process of the frontal posteriorly. The nasal is separated from the prefrontal, as described above. Posteriorly the nasofrontal suture is W-shaped in dorsal view (Fig. 2). The short posterior processes of the nasals invade onto the frontal. The dorsal surface of the nasals bears obvious nodular sculpturing.

Frontal

The frontals are well preserved with a clear midline suture (Fig. 2; Supplemental Fig. S1). The frontals are long, moderately narrow, and they together have a weak constriction in their midlength in dorsal view (i.e. curved interorbital margins of frontals). The frontal expands posteriorly, reaching its greatest width at the frontoparietal suture which is more than twice the interorbital width and almost twice that of the nasofrontal suture (e.g. as in *G. arenosus*). Anteriorly, the frontal has a short and irregular anteromedial process, and a much longer and tapering anterolateral process. The midline suture is a distinct ridge, and the ridge bifurcates into two ridges which enclose a triangular depression anterior to the parietal foramen. The frontoparietal suture is interdigitated, and laterally there is a parietal lappet to support the parietal. The dorsal surface of the frontals is ornamented with rugosities, the complexity of which increases posteriorly close to the frontoparietal suture (e.g. *T. multivagus* and *G. arenosus*) (Gao & Norell, 2000). In lateral view, the frontal is arched slightly and the postfrontal facet is clearly visible (Fig. 2A).

Parietal

Only the anterior part of the parietal is preserved. It is single, with an anterior expansion. The parietal foramen is oval, lying on the frontoparietal suture as in *Polyglyphanodon* (Gilmore, 1942) and *Gilmoreteius chulsanensis* (Sulimski, 1975).

Mandible

The right mandible is exposed in lateral view, whereas the left one is buried within the matrix and is not seen. The right mandible is well preserved *in situ*, articulating with the cranium, but it lacks the posterior end (Fig. 2; Supplemental Fig. S1). The preserved mandible is deep but lateromedially thin, with a slightly convex lateral surface and a convex ventral margin.

The dentary is slightly bowed laterally. It is deep posteriorly and narrows anteriorly but does not taper to a tip. The anterior region deflects dorsally in lateral view. Although the distal end of the dentary is missing, a short groove on the anterior region of the coronoid suggests the dentary may have a coronoid process, overlapping part of the lateral surface of the coronoid. The lateral surface of the dentary is smooth and at least six alveolar foramina are observed (Fig. 2). These foramina are all situated anterior to the orbit and well below the alveolar margin. They are arranged generally in a row. The anterior three foramina are close to one another, but the others are well separated from each other. The posteriormost foramina is the largest and faces anteriorly.

The coronoid is relatively small, with a prominent dorsal process, but no labial process. The broad ventral margin of the bone is roughly straight in lateral view. Its dorsal margin is rounded (rather than pointed as in *Tianyusaurus*) with roughly parallel anterior and posterior margins, and inclines slightly posteriorly, therefore forming a concave posterior margin. The posterior process is developed and exposed in lateral view.

The preserved surangular is shown to support the coronoid bone and sutures anteriorly with the dentary, but other details are unknown.

Dentition

The premaxillary, maxillary, and dentary teeth are preserved although most of the dentary teeth are obscured by the maxillary teeth. The dentition is heterodont, with anterior cylindrical teeth, a caniniform tooth, and posterior chisel-like teeth along the maxilla (Fig. 3). The cylindrical and chisel-like teeth are small and closely packed. These teeth are attached on the lingual side of the maxilla inferred by the horizontal section of the CT scan data, and therefore are regarded as the pleurodont type (Supplemental Fig. S2). Most of the crown tips are

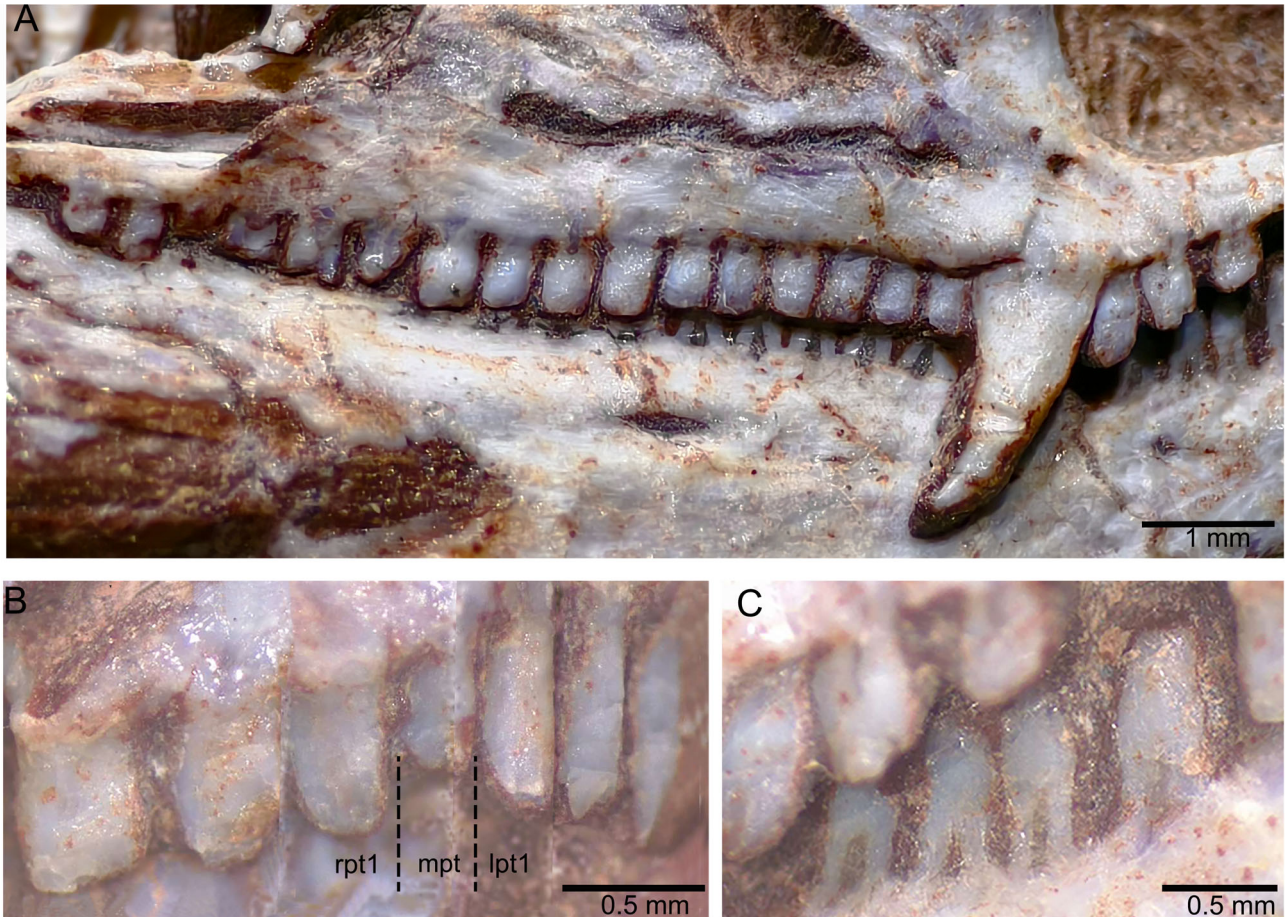


Figure 3. Images of the dentition of *Caninosaurus*. **A**, maxilla teeth in lateral view; **B**, premaxilla teeth in lateral view; **C**, dentary teeth in lateral view. **Abbreviations:** **lpt**, left premaxillary tooth; **mpt**, middle premaxillary tooth; **rpt**, right premaxillary tooth.

eroded or obscured and therefore the crown morphology is unknown. No denticles or cusps are observed.

The premaxilla has seven tooth positions (Fig. 3B; Supplemental Fig. S1). The premaxillary teeth are small (their height is similar to that of the non-caniniform maxillary teeth) and cylindrical-like in outline. The middle premaxillary tooth is relatively short. The three left premaxillary teeth are cylindrical, whereas the right premaxillary teeth are relatively wide and chisel-like. The maxilla bears 20 tooth positions and all teeth are preserved (Fig. 3A). The fourth one is caniniform, extremely large, pointed, and slightly recurved. Its height is larger than half the depth of the dentary, and about four times the height of other maxillary teeth. A caniniform tooth is seen in many Asian Borioteiioidea (e.g. *Tianyusaurus*, *Funiusaurus* and *Gilmoreteius*), but is located at different tooth positions (Gao & Norell, 2000; Lü et al., 2008; Mo et al., 2010; Xu et al., 2014). There are minor variations among the non-caniniform maxillary teeth although they are mostly chisel-like in shape and similar in size. The first three teeth increase

in size gradually, and the tooth just posterior to the caniniform tooth is as small as the 1st tooth, and the following ones increase in size again, to a lesser extent. The 10th post-caniniform tooth is wider than the other post-caniniform teeth and is almost square in lateral view. Starting from the 11th post-caniniform tooth, the tooth size decreases, with the last four teeth smaller than the anterior maxillary teeth although they are not complete. The dentary tooth row has the first four teeth exposed, and only the first one is completely visible (Fig. 3C). The first tooth is conical and seems more slender than the maxillary teeth.

Phylogenetic analyses

The phylogenetic analysis based on the Simões-derived matrix produces a consensus tree with a relatively low resolution. *Caninosaurus* is grouped with *Yechilacerta*, *Jiangxi_2*, *Aprisaurus* and *Tuberocephalosaurus*, although many borioteioids form a polytomy with

Lacertidae, Teiidae, Gymnophthalmidae and Xantusiidae (Supplemental data 2, Tree 5). The group of *Caninosaurus*, *Yechilacerta*, *Jiangxi_2*, *Aprisaurus* and *Tuberocephalosaurus* is supported by the M-shaped nasofrontal suture (23/0), maxillae contact at midline behind the nasal process of premaxilla (27/1), subpalpebral fossa of the prefrontal present (40/1), parietal tabs on frontals absent (69/0), parietal without transverse posterior margin between the supratemporal processes (82/1), palatines separate at midline (121/0), no dentary symphysis (167/1), and caniniform teeth present (215/1).

Within the clade, *Caninosaurus* and *Yechilacerta* were closely related as sister taxa, which is supported by the presence of the prefrontal supraorbital ridge (35/1) and paired frontals contacting at midline (36/1). These two synapomorphies are preserved in *Caninosaurus* (35/1, 36/1).

In the phylogenetic analyses derived from Čerňanský et al. (2022), *Caninosaurus* was recovered as a borioteioid lizard except in the analysis with ordered characters and molecular constraints. The constrained analysis with all characters unordered (Supplemental data 2, Tree

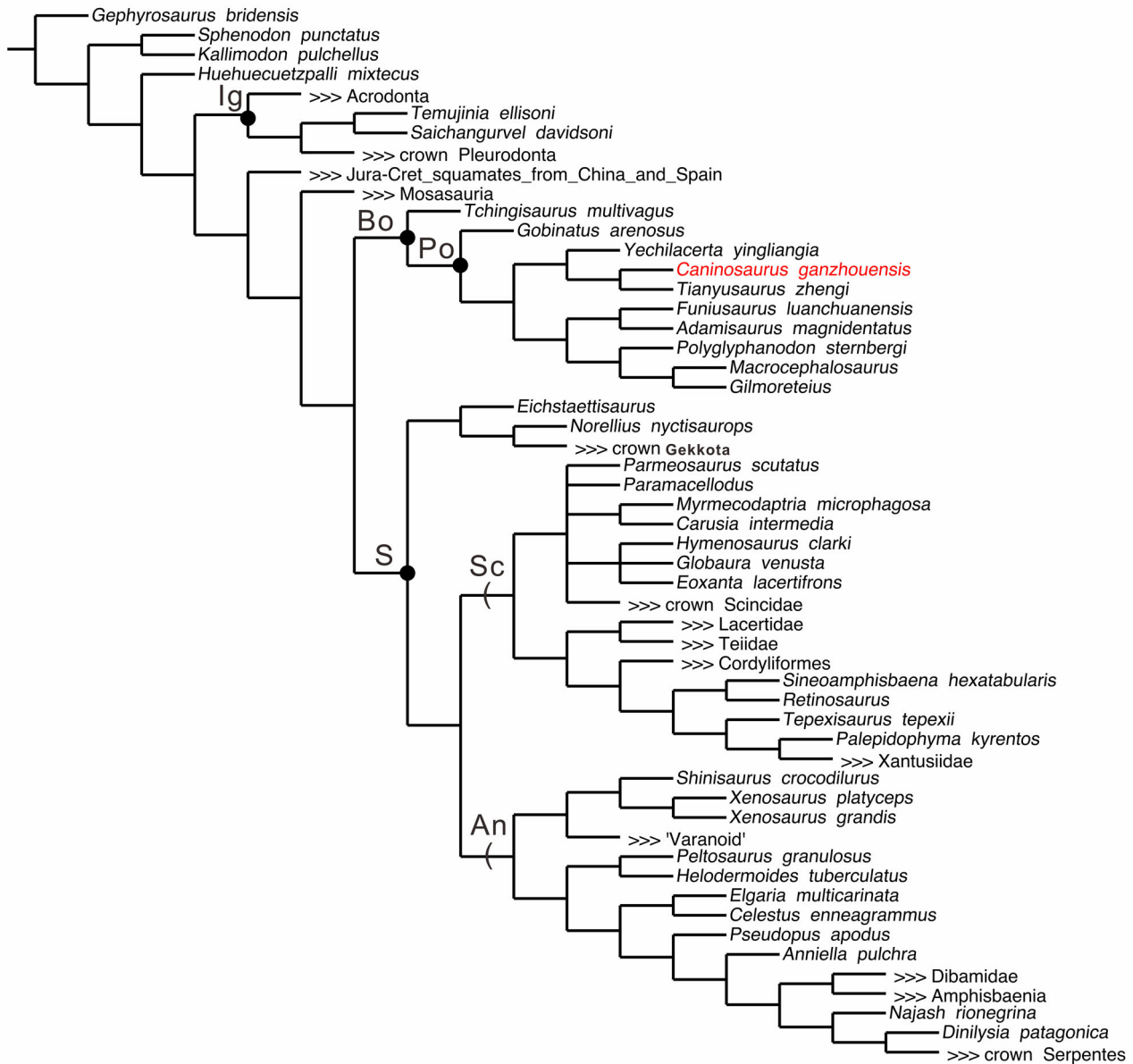


Figure 4. Simplified strict consensus tree from the ordered and unconstrained analysis based on Čerňanský-derived matrix. For the full tree see Supplemental Data 2, Tree 1. **Abbreviations:** An, Anguimorpha; Bo, Borioteiioidea; Ig, Iguania; Po, Polyglyphanodontidae; S, Scleroglossa; Sc, Scincomorpha.

4) recovered the borioteioid clade as a polytomy except the *Polyglyphanodon-Gilmoreteius* clade, and therefore the relationship of *Caninosaurus* with other borioteioids is not clear. The analysis with ordered characters (Supplemental data 2, Tree 2) does not group all the assumed borioteioids, including *Caninosaurus*, together, except for a clade consisting of *Funiusaurus*, *Adamisaurus*, *Polyglyphanodon* and *Gilmoreteius*.

The two unconstrained analyses obtained fully resolved but different topologies within borioteioids (Supplemental data 2, Trees 1, 3). In both, *Tchingisaurus* is at the base. The clade of *Yechilacerta*, *Tianyusaurus* and *Caninosaurus* is recovered. *Polyglyphanodon* and *Gilmoreteius* form sister taxa. In the ordered and unconstrained analysis (Fig. 4; Supplemental data 2, Tree 1), the borioteioid clade is supported by seven unambiguous synapomorphies: a moderately interdigitated frontoparietal suture (56/2), postfrontal with a bifid distal end (64/1), maxillae contact at midline excluding premaxilla from vomer (111/1), deep suborbital ramus of jugal (150/1), medial ridge on jugal pronounced (157/1), splenial extending anteriorly around a three-quarters the length of the dentary tooth row (375/3), anterior inferior alveolar foramen on splenial dorsal or posterodorsal to anterior mylohyoid foramen (379/1), bicuspid posterior teeth (434/2), and the absence of V-shaped wear facets of maxillary teeth on the lateral face of the dentary between teeth (436/1). Within the clade, *Caninosaurus* is grouped with *Yechilacerta* and *Tianyusaurus*, which is supported by six synapomorphies: nasal with subequal anterior and posterior width (18/1), postfrontal dorsally overlapping the parietal table (65/1), jugal not in contact with squamosal (154/1), jugal posterior process long enough to complete the lower temporal bar (155/0), jugal posterior process directed more ventrally (156/1), extensive quadrate-pterygoid overlap (182/0), teeth not swollen (437/0).

Discussion

Phylogenetic position of *Caninosaurus*

The number of characters that can be coded for *Caninosaurus* is relatively low, at 9.7% in Čerňanský et al. (2022) and 17.9% in Simões et al. (2017). This may be part of the reason why some of the phylogenetic analyses resulted in strict consensus trees with low resolution, failing to obtain a resolved relationship of the major clades of squamates or to group the borioteioids as a monophyletic group (in the Simões et al. (2017) analysis, and in the ordered and constrained Čerňanský-derived analysis).

The position of the borioteioid clade varies in unconstrained and constrained analyses, along with Iguania, Amphisbaenia, Dibamidae and Gekkota. The constrained and unordered tree groups Borioteiioidea and Iguania (as well as some Early Cretaceous species from China and Spain) in a more derived position, similar to the result of the constrained analyses in Xing et al. (2023). In the unconstrained trees, Borioteiioidea is more crownward than Iguania, being a sister taxon of 'Scleroglossa', similar to the result of Gauthier et al. (2012). The unconstrained and ordered tree displays a fully resolved topology within Borioteiioidea, which may show the close relationship between *Caninosaurus* and its contemporaries *Tianyusaurus* and *Yechilacerta* (Fig. 4) compared with an almost completely unresolved branch in the constrained and unordered tree. This result suggests the intra-relationships of this group are also influenced by the higher-level topology of Squamata and the character settings. More work is needed to get a stable phylogenetic framework for Borioteiioidea.

Comparison with other borioteioid lizards

Caninosaurus ganzhouensis can be ascribed to Borioteiioidea by retention of the parietal foramen, a large and tall facial process of the maxilla, relatively small premaxilla, postfrontal with long frontal process and parietal processes, and a bifid distal ramus (Gao et al., 2021; Nydam et al., 2007). *Caninosaurus* differs from other borioteioids and all other squamates in the following combination of derived characters: the frontals are narrow and waisted between the orbits; the anterolateral process of the frontal tapers between the nasal and maxilla; the facial process of the maxilla has a long and tapering posterodorsal projection; the 4th maxillary tooth is large and caniniform.

In comparison with North American borioteioid taxa, *C. ganzhouensis* resembles *Polyglyphanodon* (Gilmore, 1942) in having a tall facial process of the maxilla and a lacrimal, and in lacking nasal-prefrontal contact, while it differs in having the frontals waisted between the orbits (vs parallel in *Polyglyphanodon*), a large and caniniform maxillary tooth, mesiodistally broad posterior marginal teeth, and a dorsally rounded dorsal process of the coronoid (Conrad, 2008; Gilmore, 1942; Nydam & Cifelli, 2005; Simões et al., 2016). Moreover, in *Caninosaurus*, the base of the nasal process of the premaxilla is constricted (not constricted in *Polyglyphanodon*), the posterodorsal projection of the maxillary facial process is long and extensively contacts the frontal anterolateral process (short in *Polyglyphanodon*), and the lateral end of the postfrontal is notched (not notched in *Polyglyphanodon*). *Caninosaurus* resembles *Bicuspidon* in having a caniniform maxillary tooth, but differs from the latter in the

tooth crown with no obvious cusps (Folie & Codrea, 2005; Makádi, 2006; Nydam & Cifelli, 2002; Vullo & Rage, 2018). It differs from *Dicathodon* in the teeth not transversely expanded in occlusal view (Chavarría-Arellano et al., 2018; Nydam et al., 2007). It resembles *Paleochelco occultato* in having a lacrimal bone but differs from the latter in the facial process of the maxilla having a long dorsoposterior projection (Martinelli et al., 2021).

In comparison with Asian borioteioid taxa, *Caninosaurus* appears similar to *Gilmoretius*, *Aprisaurus* and *Tuberocephalosaurus* in bearing a caniniform maxillary tooth anteriorly. However, *Caninosaurus* differs from the latter genera in a long and tapering posterodorsal projection of the maxillary facial process that separates the nasal from the prefrontal (Langer, 1998; Mo et al., 2010; Sulimski, 1975; X. C. Wu et al., 1996; Xu et al., 2014), and further differs from *Gilmoretius* in having a distally tapering nasal process of the premaxillae (spatulate in *Gilmoretius*) (Gao & Norell, 2000). *Caninosaurus* differs from *Adamisaurus* in lacking nasal-prefrontal contact and having a longer nasal process reaching the midpoint of the nasal (not reaching in *Adamisaurus*) (Gao & Norell, 2000; Sulimski, 1972). *Caninosaurus* resembles *Tchingisaurus* and *Gobinatus* in having the anterior surface of the premaxillae smooth without foramina, lacking the nasal-prefrontal contact, and bearing sculpturing on the dorsal surface of the frontals (Gao & Norell, 2000). It differs from the latter two species in having a nasal process of the premaxilla constricted at the base and broadened in the middle and tapering distally, a maxilla with a long premaxillary process, and a parietal foramen lying on the frontoparietal suture. Moreover, the base of the tooth crown in *Tchingisaurus* is very narrow (cylindrical in *Caninosaurus*) (Gao & Norell, 2000). Small interdental gaps between teeth are present in *G. arenosus* (absent in *Caninosaurus*) (Gao & Norell, 2000).

Caninosaurus resembles *Tianyusaurus* and *Yechilacerta* in those borioteioid features, such as a tall maxillary facial process. However, *Caninosaurus* differs from the latter two in having a long and tapering posterodorsal projection on its facial process, tooth crowns without denticles or cusps, and a frontoparietal suture longer than the nasofrontal suture (Lü et al., 2008; Mo et al., 2010; Xing et al., 2023). Moreover, *Yechilacerta* has broad, rectangular frontals without anterolateral processes, rather than the narrow and waisted frontals with anterolateral processes in *Caninosaurus*.

Caninosaurus resembles *Funiusaurus* in having a caniniform maxillary tooth extending half the height of the dentary, but in *Funiusaurus*, the base of the nasal

process of the premaxilla is not constricted, the frontals are expanded to a greater degree at the frontoparietal suture, the caniniform maxillary tooth is the third one, there are fewer premaxillary teeth, the posterior teeth are bicuspid or tricuspid, and the dorsal process of the coronoid is sub-triangular and pointed dorsally (Xu et al., 2014).

Life and diet in borioteioids

The tooth crowns of *Caninosaurus* have no distinct cusps or denticles, like some large or noninsectivorous geckos (Melstrom, 2017; Sumida & Murphy, 1987). However, the presence of cusps could not be excluded, as the tooth crown morphology could change along ontogeny or due to wear.

In some lizards, there is a rather substantial ontogenetic change in tooth shape (Estes & Williams, 2010; Nydam & Cifelli, 2002). For example, the more pointed and recurved teeth in young individuals become rounded off when fully grown in *Varanus niloticus* (Boulenger, 1885; Estes & Williams, 2010); and the juvenile tricuspid teeth are replaced by multicuspid teeth in the adult in *Gallotia stehlini* (Barahona et al., 2000). It has also been suggested that adults have a slower replacement rate of posterior teeth than anterior teeth, which may cause their posterior teeth to become worn down with age (Cooper et al., 1970). In some borioteioids, tooth replacement was arrested later in ontogeny (e.g. *Dicathodon*) or is completely absent since early ontogeny (e.g. *Polyglyphanodon*), and therefore the teeth of the large individuals of these taxa may display more wear (Chavarría-Arellano et al., 2018; Folie & Codrea, 2005; Gilmore, 1942). Furthermore, grinding plant material wears down the cusps and may result in lower overall complexity. For example, the central cusp is often worn down and the tooth crown becomes relatively flat across the occlusal surface in *Amblyrhynchus cristatus*, which scrapes algae off rocks (Christensen & Melstrom, 2021).

However, the holotype of *Caninosaurus* bears rugosities on the bones suggesting that the individual was probably an adult or at least a subadult, so its dentition may not be the juvenile type of the species. There is no sign of wear visible in the lateral view of the dentary. Therefore, the uncusped posterior maxillary teeth, although broken, may represent the characteristic dentition of the species.

The fourth maxillary tooth is large and caniniform in *Caninosaurus*, perhaps serving to hold or aid in tearing food. It might represent a morphological adaptation to occasional vertebrate consumption (Christensen & Melstrom, 2021; Torres-Carvajal, 2007), although it could also be associated with territorial behaviour.

Caninosaurus also shows features that may suggest a herbivorous diet, such as a deep skull, a short snout, and anteroposteriorly broad marginal non-caniniform teeth (Metzger & Herrel, 2005), but the lack of any distinct denticles or cusps indicates that *Caninosaurus* was not an effective plant-eating animal. Taken together, evidence indicates *Caninosaurus* was probably omnivorous.

Caninosaurus, *Yechilacerta* and *Tianyusaurus* lived in the same region during the Late Cretaceous (Mo et al., 2010; Xing et al., 2023). *Tianyusaurus* may have eaten turgid fleshy fruits (Mo et al., 2010), and the morphology of the tooth crown of *Yechilacerta* indicates a herbivorous (or ‘true herbivory’) diet of predominantly fibrous plant material (see Xing et al., 2023), based on the skull and mandible morphology, as well as the tooth morphology. *Caninosaurus* (skull length roughly 30 mm) is much smaller than *Tianyusaurus* (skull length over 87 mm) and *Yechilacerta* (skull length 97–100 mm), and bears quite different tooth crowns (lacking distinct denticles or cusps vs being multicuspid). Therefore, *Caninosaurus* might have employed a different diet and occupied a different ecological niche to avoid interspecific competition with the other two borioteioids.

Conclusions

In this paper, we describe and name a new lizard taxon (*Caninosaurus ganzhouensis*) from the Late Cretaceous Ganzhou Basin, Jiangxi Province, China, which is most similar to *Tianyusaurus* from the Henan and Jiangxi provinces. *Caninosaurus ganzhouensis* represents another taxon with caniniform teeth from Asia and appears to belong to Borioteiioidea. This is the fifth lizard taxon reported from the Ganzhou Basin of Jiangxi Province, thereby increasing the local diversity of the squamate and vertebrate assemblage.

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Supplemental material

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Data availability statement

The data that support the findings of this study are openly available in MorphoBank at <https://doi.org/10.7934/P5888> (M. Wang et al., 2025).

References

- Barahona, F., Evans, S. E., Mateo, J. A., García-Márquez, M., & López-Jurado, L. F. (2000). Endemism, gigantism and extinction in island lizards: The genus *Gallotia* on the Canary Islands. *Journal of Zoology*, 250(3), 373–388. <https://doi.org/10.1111/j.1469-7998.2000.tb00781.x>
- Boulenger, G. A. (1885). *Catalogue of the lizards in the British Museum (Nat. Hist.)*, Volume 2 xi + 382 London: British Museum (Natural History) order of the Trustees.
- Celerino de Carvalho, J., & Santucci, R. M. (2024). A new fossil Squamata from the Quiricó Formation (Lower Cretaceous), Sanfranciscana Basin, Minas Gerais, Brazil. *Cretaceous Research*, 154, 105717. <https://doi.org/10.1016/j.cretres.2023.105717>
- Čerňanský, A., & Syromyatnikova, E. V. (2019). The first Miocene fossils of *Lacerta cf. trilineata* (Squamata, Lacertidae) with a comparative study of the main cranial osteological differences in green lizards and their relatives. *PLOS ONE*, 14(8), e0216191. <https://doi.org/10.1371/journal.pone.0216191>
- Čerňanský, A., Stanley, E. L., Daza, J. D., Bolet, A., Arias, J. S., Bauer, A. M., Vidal-Garcia, M., Bevitt, J. J., Peretti, A. M., Aung, N. N., & Evans, S. E. (2022). A new Early Cretaceous lizard in Myanmar amber with exceptionally preserved integument. *Scientific Reports*, 12(1), 1660. <https://doi.org/10.1038/s41598-022-05735-5>
- Chavarria-Arellano, M. L., Simoes, T. R., & Montellano-Ballesteros, M. (2018). New data on the Late Cretaceous lizard *Dicodhodon bajaensis* (Squamata, Borioteiioidea) from Baja California, Mexico reveals an unusual tooth replacement pattern in squamates. *Anais da Academia Brasileira de Ciências*, 90, 2781–2795. <https://doi.org/10.1590/0001-3765201820170563>
- Christensen, K., & Melstrom, K. M. (2021). Quantitative analyses of squamate dentition demonstrate novel morphological patterns. *PLoS ONE*, 16(9), e0257427. <https://doi.org/10.1371/journal.pone.0257427>
- Conrad, J. L. (2008). Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American*

- Museum of Natural History*, 310, 1–182. <https://doi.org/10.1206/310.1>
- Cooper, J. S., Poole, D. F. G., & Lawson, R. (1970). The dentition of agamid lizards with special reference to tooth replacement. *Journal of Zoology*, 162(1), 85–98. <https://doi.org/10.1111/j.1469-7998.1970.tb01259.x>
- Dong, L., Wang, Y., & Evans, S. E. (2023). A new fossil lizard (Reptilia: Squamata) from the Lower Cretaceous of eastern Inner Mongolia, China. *Cretaceous Research*, 141, 105363. <https://doi.org/10.1016/j.cretres.2022.105363>
- Estes, R., & Williams, E. E. (2010). Ontogenetic variation in the molariform teeth of lizards. 4(1), 96–107. <https://doi.org/10.1080/02724634.1984.10011989>
- Evans, S. E. (2008). The skull of lizards and tuatara. In C. Gans, A. S. Gaunt, & K. Adler (Eds.), *The skull of Lepidosauria. Biology of the Reptilia*, 20, 1–347.
- Evans, S. E., & Manabe, M. (2008). An early herbivorous lizard from the Lower Cretaceous of Japan. *Palaeontology*, 51(2), 487–498. <https://doi.org/10.1111/j.1475-4983.2008.00759.x>
- Evans, S. E., & Matsumoto, R. (2015). An assemblage of lizards from the Early Cretaceous of Japan. *Palaeontologia Electronica*, 18(2), 1–36. <https://doi.org/10.26879/519>
- Evans, S. E., Prasad, G. V. R., & Manhas, B. K. (2002). Fossil lizards from the Jurassic Kota Formation of India. *Journal of Vertebrate Paleontology*, 22(2), 299–312. [https://doi.org/10.1671/0272-4634\(2002\)022\[0299:FLFTJK\]](https://doi.org/10.1671/0272-4634(2002)022[0299:FLFTJK])
- Folie, A., & Codrea, V. A. (2005). New lissamphibians and squamates from the Maastrichtian of Hateg Basin, Romania. *Acta Palaeontologica Polonica*, 50(1), 57–71.
- Gao, K., & Norell, M. A. (2000). Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bulletin of the American Museum of Natural History*, 249, 1–118. [https://doi.org/10.1206/0003-0090\(2000\)249](https://doi.org/10.1206/0003-0090(2000)249)
- Gao, K., Shang, Q., & Li, C. (2021). *Palaeovertebrata Sinica. Volume II. Fascicle 3 (Serial no.7)*. Science Press.
- Gauthier, J. A., Kearney, M., Maisano, J. A., Rieppel, O., & Behlke, A. D. B. (2012). Assembling the squamate tree of life: Perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History*, 53(1), 3–308. <https://doi.org/10.3374/014.053.0101>
- Gilmore, C. W. (1942). Osteology of *Polyglyphanodon*, an Upper Cretaceous lizard from Utah. *Smithsonian Miscellaneous Collections*, 92(3148), 229–265. <https://doi.org/10.5479/si.00963801.92-3148.229>
- Gilmore, C. W. (1943). Osteology of Upper Cretaceous lizards from Utah, with a description of a new species. *Proceedings of the United States National Museum*, 93(3163), 209–214.
- Goloboff, P. A., & Morales, M. E. (2023). TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics*, 39(2), 144–153. <https://doi.org/10.1111/cla.12524>
- He, F., Huang, X., & Li, X. (2017). Occurrence rule and buried characteristics of dinosaur fossils in the Ganzhou Basin, Jiangxi Province. *East China Geology*, 38, 250–254. <https://doi.org/10.16788/j.hddz.32-1865/P.2017.04.002>
- Hu, J., & Han, F. (2021). A new multituberculate, *Yubaatar qianzhouensis* sp. nov.: The first Late Cretaceous mammal from Ganzhou Basin, Jiangxi Province. *Acta Palaeontologica Sinica*, 60(4), 565–579. <https://doi.org/10.19800/j.cnki.aps.2020057>
- Langer, M. C. (1998). Gilmoretiidae new family and *Gilmoretius* new genus (Squamata, Scincomorpha): Replacement names for *Macrocephalosauridae* Sulimski, 1975 and *Macrocephalosaurus* Gilmore, 1943. *Comunicações do Museu Ciências e Tecnologia PUCRS*, 11, 13–18.
- Li, C., Wu, X.-C., & Rufolo, S. J. J. C. R. (2019). A new crocodyloid (Eusuchia: Crocodylia) from the Upper Cretaceous of China. *Cretaceous Research*, 94, 25–39. <https://doi.org/10.1016/j.cretres.2018.09.015>
- Longrich, N. R., Bhullar, B.-A. S., & Gauthier, J. A. (2012). Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary. *Proceedings of the National Academy of Sciences of the United States of America*, 109(52), 21396–21401. <https://doi.org/10.1073/pnas.1211526110>
- Lü, J. C., Ji, S. A., Dong, Z. M., & Wu, X. C. (2008). An Upper Cretaceous lizard with a lower temporal arcade. *Naturwissenschaften*, 95(7), 663–669. <https://doi.org/10.1007/s00114-008-0364-1>
- Makádi, L. (2006). *Bicuspideon* aff. *hatzegiensis* (Squamata: Scincomorpha: Teiidae) from the Upper Cretaceous Csehbánya Formation (Hungary, Bakony Mts). *Acta Geologica Hungarica*, 49(4), 373–385. <https://doi.org/10.1556/ageol.49.2006.4.5>
- Martinelli, A. G., Agnolin, F., & Ezcurra, M. D. (2021). Unexpected new lizard from the Late Cretaceous of southern South America sheds light on Gondwanan squamate diversity. *Revista del Museo Argentino de Ciencias Naturales*, 31(5), 57–80. <https://doi.org/10.22179/REVMACN.23.716>
- Melstrom, K. M. (2017). The relationship between diet and tooth complexity in living dentigerous saurians. *Journal of Morphology*, 278(4), 500–522. <https://doi.org/10.1002/jmor.20645>
- Metzger, K. A., & Herrel, A. (2005). Correlations between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis. *Biological Journal of the Linnean Society*, 86(4), 433–466. <https://doi.org/10.1111/j.1095-8312.2005.00546.x>
- Mo, J., Xu, X., & Evans, S. E. (2010). The evolution of the lepidosaurian lower temporal bar: New perspectives from the Late Cretaceous of South China. *Proceeding of the Royal Society B*, 277(1679), 331–336. <https://doi.org/10.1098/rspb.2009.0030>
- Mo, J., Xu, X., & Evans, S. E. (2012). A large predatory lizard (Platynota, Squamata) from the Late Cretaceous of South China. *Journal of Systematic Palaeontology*, 10(2), 333–339. <https://doi.org/10.1080/14772019.2011.588254>
- Nydam, R. L. (1999). Polyglyphanodontinae (Squamata: Teiidae) from the medial and Late Cretaceous, new records from Utah, USA and Baja California del Norte, Mexico. *Miscellaneous Publications Utah Geological Survey*, 99(1), 303–317.
- Nydam, R. L. (2013). Squamates from the Jurassic and Cretaceous of North America. *Palaeobiodiversity and Palaeoenvironments*, 93(4), 535–565. <https://doi.org/10.1007/s12549-013-0129-5>
- Nydam, R. L., & Cifelli, R. L. (2002). A new teiid lizard from the Cedar Mountain Formation (Albian–Cenomanian boundary) of Utah. *Journal of Vertebrate Paleontology*,

- 22(2), 276–285. [https://doi.org/10.1671/0272-4634\(2002\)022\[0276:Antlft\]2.0.Co;2](https://doi.org/10.1671/0272-4634(2002)022[0276:Antlft]2.0.Co;2)
- Nydam, R. L., & Cifelli, R. L. (2005). New data on the dentition of the scincomorph lizard *Polyglyphanodon sternbergi*. *Acta Palaeontologica Polonica*, 50(1), 73–78.
- Nydam, R. L., Eaton, J. G., & Sankey, J. (2007). New taxa of transversely-toothed lizards (Squamata: Scincomorpha) and new information on the evolutionary history of 'teiids'. *Journal of Paleontology*, 81(3), 538–549. <https://doi.org/10.1666/03097.1>
- Nydam, R. L., & Voci, G. E. (2007). Teiid-like scincomorph lizards from the Late Cretaceous (Campanian) of southern Utah. *Journal of Paleontology*, 41(2), 211–219. <https://doi.org/10.1666/03097.1>
- Pyron, R. A., Burbrink, F. T., & Wiens, J. J. (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13(1), 93. <https://doi.org/10.1186/1471-2148-13-93>
- Reeder, T. W., Townsend, T. M., Mulcahy, D. G., Noonan, B. P., Wood, P. L., Jr., Sites, J. W., Jr., & Wiens, J. J. (2015). Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. *Plos One*, 10(3), e0118199. <https://doi.org/10.1371/journal.pone.0118199>
- Scarpetta, S. G. (2020). Unusual lizard fossil from the Miocene of Nebraska and a minimum age for cnemidophorine teiids. *Royal Society Open Science*, 7(8), 200317. <https://doi.org/10.1098/rsos.200317>
- Simões, T. R., Caldwell, M. W., Palci, A., & Nydam, R. L. (2017). Giant taxon-character matrices: Quality of character constructions remains critical regardless of size. *Cladistics*, 33(2), 198–219. <https://doi.org/10.1111/cla.12163>
- Simões, T. R., Funston, G. F., Vafaeian, B., Nydam, R. L., Doschak, M. R., & Caldwell, M. W. (2016). Reacquisition of the lower temporal bar in sexually dimorphic fossil lizards provides a rare case of convergent evolution. *Scientific Reports*, 6, 24087. <https://doi.org/10.1038/srep24087>
- Sulimski, A. (1972). *Adamisaurus magnidentatus* n. gen., n. sp. (Sauria) from the Upper Cretaceous of Mongolia. *Results of the Polish–Mongolian Palaeontological Expeditions, Pt IV*, 27, 33–40.
- Sulimski, A. (1975). Macrocephalosauridae and Polyglyphanodontidae (Sauria) from the Late Cretaceous of Mongolia. *Palaeont Polonica*, 33, 25–102.
- Sumida, S. S., & Murphy, R. W. (1987). Form and function of the tooth crown structure in gekkonid lizards (Reptilia, Squamata, Gekkonidae). *Canadian Journal of Zoology*, 65(12), 2886–2892. <https://doi.org/10.1139/z87-438>
- Tong, H., & Mo, J. (2010). *Jiangxichelys*, a new nanhsiungchelyid turtle from the Late Cretaceous of Ganzhou, Jiangxi Province, China. *Geological Magazine*, 147(6), 981–986. <https://doi.org/10.1017/S0016756810000671>
- Torres-Carvajal, O. (2007). Heterogeneous growth of marginal teeth in the black iguana *Ctenosaura similis* (Squamata: Iguania). *Journal of Herpetology*, 41(3), 528–531. [https://doi.org/10.1670/0022-1511\(2007\)41\[528:HGOMTI\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2007)41[528:HGOMTI]2.0.CO;2)
- Vitt, L. J., & Pianka, E. R. (2004). Historical patterns in lizard ecology: What teiids can tell us about lacertids. In N. R. V. Pérez-Mellado, & A. Perera (Eds.), *The biology of lacertid lizards. Evolutionary and ecological perspectives* (pp. 139–157). Institut Menorquí d'Estudis, Recerca 8, Menorca.
- Vullo, R., & Rage, J.-C. (2018). The first Gondwanan borioteioid lizard and the mid-Cretaceous dispersal event between North America and Africa. *The Science of Nature*, 105(11), 61. <https://doi.org/10.1007/s00114-018-1588-3>
- Wang, J., Yuan, Y., Zhang, D., & Chang, S.-C. (2022). Detrital zircon geochronology of Late Cretaceous successions in the Ganzhou Basin, South China: Evidence of a major tectonic transition. *Geological Society, London, Special Publications*, 521, 225–236. <https://doi.org/10.1144/sp521-2021-168>
- Wang, M., Dong, L., Yu, J., Lou, F., Qiu, W., & Han, F. (2025). Data from: A new borioteioid lizard with large caniniform tooth from the Upper Cretaceous of South China. *MorphoBank*. <https://doi.org/10.7934/P5888>
- Wang, S., Sun, C., Sullivan, C., & Xu, X. (2013). A new oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of southern China. *Zootaxa*, 3640, 242–257. <https://doi.org/10.11646/zootaxa.3640.2.7>
- Wu, F., Huang, Z., Liu, Y., & Song, Z. (2017). *The regional geology of China, Jiangxi Province*. Beijing: Geological Press.
- Wu, X. C., Brinkman, D. B., & Russell, A. P. (1996). *Sineoamphisbaena hexatabularis*, an amphisbaenian (Diapsida: Squamata) from the Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China), and comments on the phylogenetic relationships of the Amphisbaenia. *Canadian Journal of Earth Sciences*, 33(4), 541–577. <https://doi.org/10.1139/e96-042>
- Xing, L., Niu, K., & Evans, S. E. (2023). A new polyglyphanodontian lizard with a complete lower temporal bar from the Upper Cretaceous of southern China. *Journal of Systematic Palaeontology*, 21(1), 2281494. <https://doi.org/10.1080/14772019.2023.2281494>
- Xing, L., Niu, K., Yang, T. R., Wang, D., Miyashita, T., & Mallon, J. C. (2022). Hadrosauroid eggs and embryos from the Upper Cretaceous (Maastrichtian) of Jiangxi Province, China. *BMC Ecology and Evolution*, 22(1), 60. <https://doi.org/10.1186/s12862-022-02012-x>
- Xu, L., Wu, X., Junchang, L., Jia, S., Zhang, J., Pu, H., & Zhang, X. (2014). A new lizard (Lepidosauria: Squamata) from the Upper Cretaceous of Henan, China. *Acta Geologica Sinica – English Edition*, 88(4), 1041–1050. <https://doi.org/10.1111/1755-6724.12271>
- Young, C. (1965). Egg fossils from Nanhsiung, Kwangtung and Kanchou, Kiangsi. *Vertebrata Palasiatica*, 9(02), 141–189.
- Young, C. (1973). On a Mesozoic lizard from Kanhsien, Kiangsi. *Vertebrata Palasiatica*, 11(01), 44–45. <https://doi.org/10.19615/j.cnki.1000-3118.1973.01.005>

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