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A new polyglyphanodontian lizard with a complete lower temporal bar from the Upper Cretaceous of southern China

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Polyglyphanodontians were a dominant terrestrial lizard group during the Cretaceous. They were mainly distributed across Laurasia but show their greatest diversity in the Upper Cretaceous deposits of China and Mongolia. Several of the Asian taxa were comparatively large, with robust skulls and a dentition specialized for herbivory. Two polyglyphanodontian genera, *Tianyusaurus* from China and *Polyglyphanodon* from North America, are unusual in having developed a complete, or near complete, lower temporal bar. Here we describe a third polyglyphanodontian with a complete lower temporal bar, *Yechilacerta yingliangia* gen. et sp. nov., from the Upper Cretaceous of Jiangxi Province, southern China. These deposits have also yielded specimens of *Tianyusaurus*, but the new genus differs from *Tianyusaurus* in several key aspects of skull and dental morphology, including the presence of coarse pustulate cranial sculpture, and the absence of maxillary caniniform teeth. Phylogenetic analysis places the new genus and species as the sister taxon to *Tianyusaurus*, with both taxa nested among East Asian gilmoreteiids. Previous phylogenetic analyses using morphological characters have mostly placed polyglyphanodontians close to extant teioid lizards, but our analyses, using a constraint tree for squamates based on published molecular phylogenies, placed Polyglyphanodontia closer to Iguania. However, a more comprehensive review is needed to resolve their relationships.

<http://zoobank.org/urn:lsid:zoobank.org:pub:53B9CE04-E600-48AE-AC98-7476A949BCBD>

Keywords: Squamata; Polyglyphanodontia; China; Cretaceous; skull

Introduction

The Polyglyphanodontia (= Borioteiioidea; Nydam et al., 2007) are a clade of Cretaceous lizards known predominantly from localities in North America, Europe, and Asia (e.g. Alifanov, 2000; Folie & Codrea, 2005; Nydam, 1999). Polyglyphanodontians seem to have reached their greatest diversity in the Late Cretaceous of eastern Asia, although the earliest records are from the Early Cretaceous of Japan (e.g. *Kuwajimalla*; Evans & Manabe, 2008) and, purportedly, South America (*Tijubina*, Crato Formation, Brazil; Simões, 2012). Recent research has also placed them in North Africa in the mid-Cretaceous (*Bicuspidon*; Vullo & Rage, 2018), penecontemporaneous with *Bicuspidon* taxa described by Nydam and Cifelli (2002) from the Cenomanian of Utah. Most Asian polyglyphanodontians come from localities in Mongolia or China. One of the most completely known taxa is *Gilmoreteius* (formerly *Macrocephalosaurus*, Gilmore, 1943, but the name was found to be preoccupied; Langer, 1998) which is represented by several skulls and skeletons (Sulimski, 1975). Adult *Gilmoreteius* specimens were the size of a large modern *Iguana* or *Tupinambis*. Other Asian

polyglyphanodontians include *Adamisaurus* (Sulimski, 1972); *Darchansaurus*, *Erdnetosaurus* and *Cherminisaurus* (Sulimski, 1975); and *Alticephalosaurus*, *Aprisaurus* and *Tuberocephalosaurus* (Alifanov, 2000), all from Mongolia; *Tianyusaurus* (Lü et al., 2008; Mo et al., 2009) and an unnamed taxon ('Jianxi'; Mo et al., 2009) from southern China; and probably *Funiusaurus* (Xu et al., 2014) from Henan Province, China. The bizarre Asian *Sineoamphisbaena* has also been linked to polyglyphanodontians (e.g. Kearney, 2003), but is not discussed further herein.

The phylogenetic position of polyglyphanodontians within Squamata is currently unresolved, with teioid and iguanian relationships having been supported by recent analyses (e.g. compare Reeder et al. [2015] to Simões et al. [2016, 2018]). Most polyglyphanodontian taxa fall into one of four broad morphological groupings which are the basis for both established taxon names and proposed subclades. The North American–European Polyglyphanodontidae (e.g. *Polyglyphanodon*, *Paraglyphanodon*, *Dicodon*, *Bicuspidon*) have large, transversely oriented teeth and were probably herbivorous (Nydam, 1999) or possibly omnivorous (insects and plants; Melstrom, 2017) in smaller

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individuals. The North American Chamopsiidae, assigned to Polyglyphanodontia by Longrich *et al.* (2012), are small and have tricuspid teeth. The Asian Gilmoreteiididae have teeth with spatulate, mediolaterally compressed, multicuspoid crowns like those of extant herbivorous iguanians (e.g. *Iguana*), scincids (e.g. *Corucia*) and lacertids (e.g. *Gallotia*), and several taxa have one or more caniniform teeth (e.g. *Tianyusaurus*, *Tuberocephalosaurus*, *Aprisaurus*). There are also smaller Asian taxa attributed to Polyglyphanodontia (e.g. *Gobinatus*, *Mongolochamops*, *Barungoia*) that have simpler conical teeth and may represent the ancestral condition for the group (e.g. Alifanov, 2000). Finally, the Asian *Adamisaurus* (Sulimski, 1972) has a reduced number of conical teeth that have been enlarged into broad cones, and *Funiusaurus* (Xu *et al.*, 2014) has chisel-like teeth and maxillary caniniforms.

Phylogenetic relationships aside, polyglyphanodontians are of interest for several reasons. Firstly, they appear to have been one of the most successful groups of terrestrial Late Cretaceous squamates, particularly in eastern Asia. Secondly, whereas true herbivory is rare among modern reptiles (Sues, 2000), it seems to have been widespread within this lizard group. Thirdly, polyglyphanodontians are one of only two known major Mesozoic lizard clades that did not cross the Cretaceous–Palaeogene (K–Pg) boundary, the other being the marine mosasaurs. Fourthly, two genera, *Tianyusaurus* (China: Lü *et al.*, 2008; Mo *et al.*, 2009) and *Polyglyphanodon* (North America: Simões *et al.*, 2016) are highly unusual among squamates in having developed a complete lower temporal bar. *Tianyusaurus* is known from several specimens in which the quadrate is firmly sutured to an extended posterior jugal ramus, as well as to an expanded squamosal dorsally and pterygoid medially. In *Polyglyphanodon*, however, the posterior jugal ramus, when present, seems to have been weakly attached to the quadrate through connective tissue (Simões *et al.*, 2016). Although this difference suggests the two genera acquired a complete bar independently, and for different reasons, Simões *et al.* (2016) hypothesized that a genetic or developmental change early in polyglyphanodontian evolution might have permitted these lizards to extend the posterior ramus of the jugal. Here we describe a third polyglyphanodontian taxon, from the same region as *Tianyusaurus*, that also has a complete lower temporal bar, lending some support to the proposal of Simões *et al.* (2016).

Material and methods

Institutional abbreviation

YLSNHM, The Yingliang Stone Natural History Museum, Shuitou, Fujiang, China.

Material

The new lizard is represented by two specimens from neighbouring localities in Ganzhou, China (Fig. 1). One specimen is a three-dimensionally preserved and fully prepared skull (YLSNHM01796) that is designated as the holotype. The other comprises a well-preserved skull (YLSNHM01791A) that was excavated together with parts of the forelimb skeleton (YLSNHM01791B) and a second block containing the greater part of a vertebral column with hind limbs and pelvis (YLSNHM01791C). These three components are complementary in terms of size and preserved elements, and probably belong to one individual, slightly larger than the holotype. In the manuscript, we use YLSNHM01791 to refer to these elements collectively. YLSNHM01796 and YLSNHM01791 share diagnostic skull features that distinguish them from other polyglyphanodontians. The two specimens are both housed in the collections of the Yingliang Stone Natural History Museum, Shuitou, Fujiang, China. Although YLSNHM01791, if a single individual, is skeletally more complete than YLSNHM01796, the overall condition of the skull is poorer than that of YLSNHM01796, with a greater degree of compression that complicates the differentiation of some sutures from cracks. Both specimens appear to be adult, based on features like the well-developed cranial sculpture and tight cranial sutures, but some features of the postcranial skeleton of YLSNHM01791 (e.g. incomplete fusion of humeral epiphyses) suggest it had some capacity for further growth.

The designated holotype (YLSNHM01796) was scanned with a Nikon Metrology XTH 225/320 LC dual source industrial micro-computed tomographic scanner, housed in the China University of Geosciences, Beijing (CUGB), China. The scan used a beam strength of 220 kV, and an absorption contrast and spatial resolution of 50 µm. However, the degree of resolution between matrix and bone was too poor to permit reconstruction of internal details, and the description that follows is based on externally visible morphology. The second specimen was not scanned. Images were taken with a digital camera (Canon EOS 5DS R, EF 24-105mm f/4L IS II USM Lens) and Helicon Focus was used to merge the depth of field.

Phylogenetic analysis

To explore the relationships of *Yechilacerta* among squamates, we used the matrix of Gauthier *et al.* (2012). Although there are some problems with aspects of this matrix (e.g. Simões *et al.*, 2017), it has a more extensive sampling of crown squamates, and more detailed, squamate-focused character definitions, than the alternative matrix of Simões *et al.* (2018), even as amended by

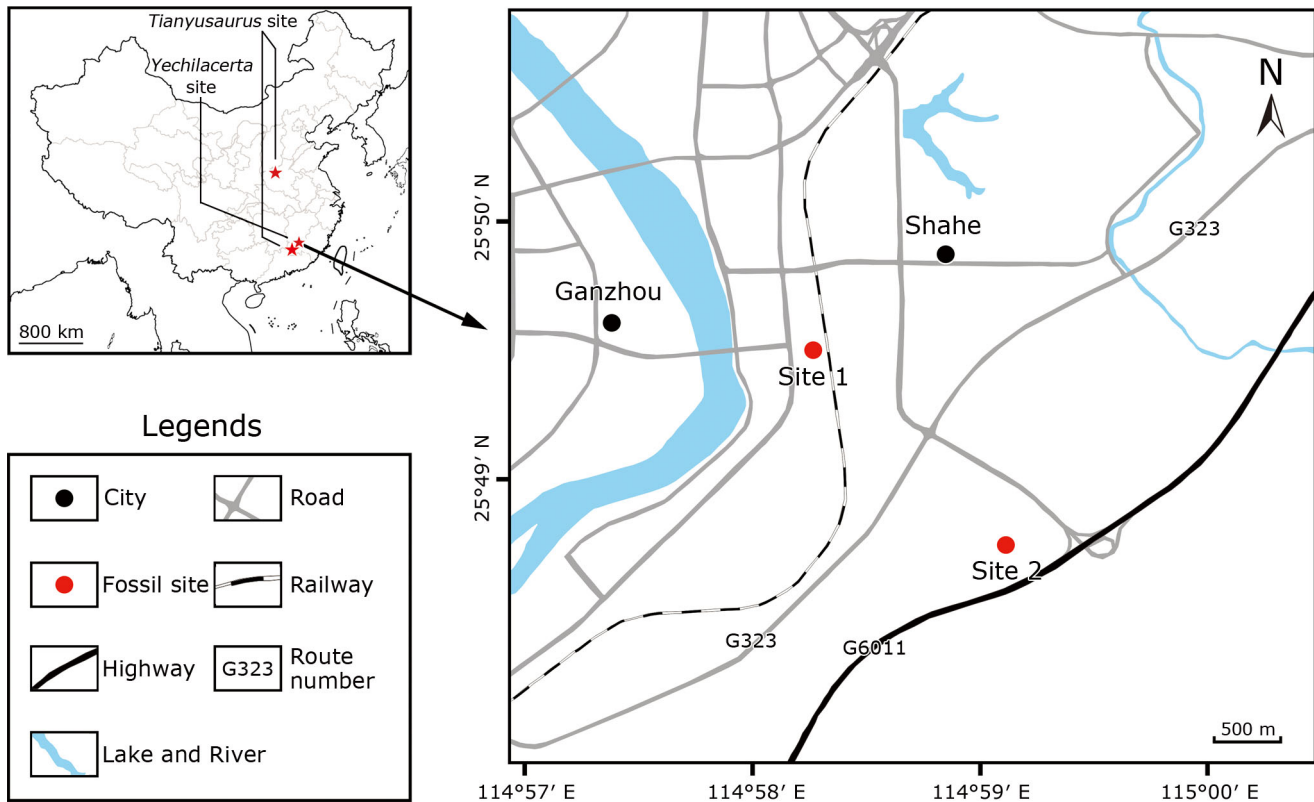


Figure 1. Map of China showing the localities for *Tianyusaurus* (Henan and Jianxi provinces) and *Yechilacerta yingliangia* gen. et sp. nov. (Jianxi Province), with an enlargement showing the two localities from which the holotype of *Yechilacerta yingliangia*, YLSNHM01796 (site 1), and the second specimen, YLSNHM01791 (site 2), were recovered.

Griffiths et al. (2021), Ford et al. (2021) and Talanda et al. (2022). Nonetheless, we ran an alternative analysis using a modified version of the matrix in Talanda et al. (2022), details of which can be found in the [Supplemental material](#). In their analysis of *Tianyusaurus*, Mo et al. (2009) used a slightly extended version of Conrad (2008), and this was re-used by Simões et al. (2016). The latter authors amended some of the Conrad (2008) character codings for polyglyphanodontians, but many of these changes had already been incorporated into Gauthier et al. (2012). For that reason, we did not run additional analyses with the updated Conrad (2008) matrix.

To the original Gauthier et al. (2012) matrix we added characters and amendments (as applicable) from Reeder et al. (2015, 80 mainly soft part characters, numbered 611–691) and Longrich et al. (2012, 11 tooth and jaw characters, here numbered 692–702). Over the decade or so since the original matrix was published, further Jurassic and Early Cretaceous taxa have been added to it, bringing the total of taxa included to 212. The original matrix included five polyglyphanodontian taxa: *Tchingisaurus*, *Gobinatus*, *Gilmoretius*, *Adamisaurus* and *Polyglyphanodon*, to which we added a further

nine: *Yechilacerta*; *Tianyusaurus* (Lü et al., 2008; Mo et al., 2009); *Aprisaurus*, *Tuberocephalosaurus*, *Dzhadochtasaurus* and *Barungoia* (Alifanov, 2000); and *Chermisaurus*, *Darchanosaurus* and *Erdenetosaurus* (Sulimski, 1975). *Funiusaurus* (Xu et al., 2014) was not included as the specimen is crushed and difficult to compare with more complete taxa, nor did we include genera like *Bicuspidon* (Nydam & Cifelli, 2002) that are represented only by dental material (e.g. Longrich et al., 2012). Coding for some character states was emended from that of Gauthier et al. (2012), based on subsequent work by Longrich et al. (2012), Fontana (2014) and Simões et al. (2015) (see [Supplemental material](#)).

We ran parsimony analyses using TNT v. 1.5 (Goloboff & Catalano, 2016), using a New Technology search with Ratchet (set to 20 iterations) and RAM (300 addition sequences), followed by a Traditional search with Tree Bisection Reconnection (TBR). The basal rhynchocephalian *Gephyrosaurus* was the designated outgroup, and for most analyses we enforced topological constraints. The basic molecular backbone constraint tree included 24 taxa and 18 positive nodal constraints, with the topology based on a consensus of the molecular

trees of multiple authors (e.g. Burbrink *et al.*, 2020; Karin *et al.*, 2020; Mount & Brown, 2022; Pyron, 2017; Pyron *et al.*, 2013; Reeder *et al.*, 2015; Singhal *et al.*, 2021; Streicher & Wiens, 2017; Townsend *et al.*, 2004; Vidal & Hedges, 2004, 2005; Zheng & Wiens, 2016). The only major differences in the tree topologies of these molecular-based analyses are the positions of Dibamidae and Gekkota relative to one another and to other crown-squamates, and the relationships of the three toxiciferan clades – Serpentes, Anguimorpha and Iguania – to one another. Our basic constraint tree left these nodes as unconstrained polytomies. However, we ran three additional analyses, following Mount and Brown (2022), in each of which we added an extra constraint to test possible resolutions of toxiciferan relationships.

Designated clades within the basic backbone constraint tree were:

1. (*Sphenodon*, *Kallimodon*)
2. (*Dibamus*, *Anelytropsis*)
3. (*Delma*, *Gekko*, *Coleonyx*)
4. (*Xantusia*, *Cordylus* [*Scincus*, *Acontias*])
5. ([*Tupinambis*, *Pholidobolus*] [*Lacerta*, *Rhineura*])
6. ([*Anilius*, *Python*][*Uromastix*, *Anolis*][(*Varanus salvator*, *Shinisaurus*) (*Heloderma*, *Xenosaurus grandis*, *Anniella*)])

These were arranged as follows: (1,(2,3,(4,(5,6))))). All other taxa were designated as floating.

We ran the analysis several times – with and without enforced constraints; with equal weighting or implied weighting ($k=3$); and with or without ordering (as in Gauthier *et al.* [2012], except for Ch. 155, complete lower temporal bar, which was left unordered). See [Supplemental material](#) (section 6) for individual tree figures.

Systematic palaeontology

Squamata Opperl, 1811

Polyglyphanodontia Alifanov, 2000

Gilmoreteiidae Langer, 1998

Genus *Yechilacerta* gen. nov.

(Figs 2–7)

Type species. *Yechilacerta yingliangia* sp. nov.

Diagnosis. A large lizard (head length ~ 100 mm) characterized by: coarse tuberculate cranial sculpture; sculpture on the posterolateral surface of the mandible; asymmetrical multicuspoid marginal teeth; a robust jugo-quadrate bar; strong sutural joints between the jugal, quadrate, squamosal and pterygoids; and a reduced interpterygoid vacuity.

Differential diagnosis. *Yechilacerta* is distinguished from other polyglyphanodontians by: the combination of a complete jugo-quadrate bar; a relatively short, broad frontal with little orbital emargination; a strongly reduced interpterygoid vacuity with apposition of the pterygoid palatal processes; sutural contacts between the quadrate, pterygoid, squamosal and jugal; a parietal that is emarginated by the upper temporal fenestrae; a shelf rather than a lateral fossa for the superficial adductor muscles on the surangular; ornamentation on the posterolateral surface of the mandible; and 30 presacral vertebrae. With many gilmoreteiids and *Polyglyphanodon*, *Yechilacerta* shares: the contact or near contact of the vomer and pterygoid; the hypertrophied splenial extending to, or almost to the symphysis; the jugal fully exposed and deep below the orbit; the lower temporal fenestra extending below the posterior half of the orbit (due to the placement and orientation of the postorbital process of the jugal); the elongated posterior process of the postorbital; and a maxillary facial process that is both dorsoventrally and anterolaterally deep. With *Tianyusaurus* and some specimens of *Polyglyphanodon*, *Yechilacerta* shares a complete lower temporal bar, and with *Tianyusaurus* further shares the strong sutural contacts between the quadrate, jugal, squamosal and pterygoid (*contra Tuberocephalosaurus*, *Aprisaurus*, *Darchansaurus*, *Cherminsaurus*, *Erdenetosaurus*, *Gilmoreteius* and all other known polyglyphanodontian and non-polyglyphanodontian lizards) and the possession of a mandibular shelf to accommodate the superficial adductor insertion. *Yechilacerta* differs from *Tianyusaurus*, *Aprisaurus*, *Tuberocephalosaurus*, *Darchansaurus*, and *Gilmoreteius* in: lacking caniniform teeth in the anterior maxilla; the broad, vertically oriented squamosal; the broader frontal; the reduced entry of the postfrontal into the supratemporal fenestra; and the short laterally (rather than posterolaterally) oriented supratemporal processes of the parietal. With *Tuberocephalosaurus* but not *Tianyusaurus*, *Yechilacerta* shares an almost complete closure of the interpterygoid vacuity except in its most posterior part, and the possession of thick tuberculate sculpture on the skull roofing bones, extending along the orbital margins of the prefrontal and postfrontal, although the sculpture is more developed in *Yechilacerta*. *Yechilacerta* differs from *Polyglyphanodon*, *Adamisaurus* and *Funiusaurus* in, and shares with other gilmoreteiids, the possession of multicuspoid teeth that are spatulate and not labiolingually expanded.

Derivation of name. The genus combines the Chinese for leaf-toothed (Yechi), reflecting the somewhat leaf-like shape of the teeth, with ‘*lacerta*’ (Latin, lizard). The specific epithet *yingliangia* refers to The Yingliang

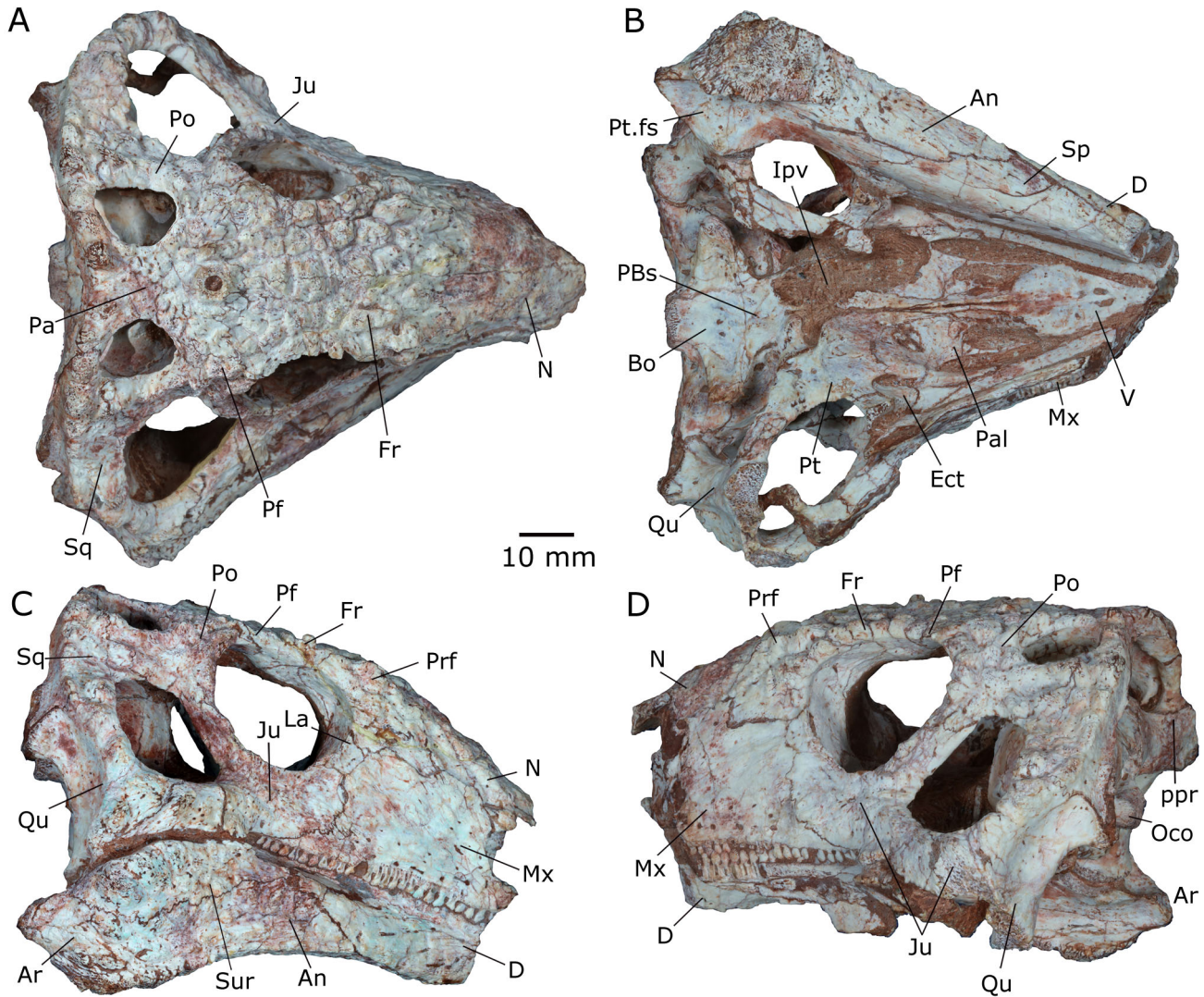


Figure 2. The holotype skull of *Yechilacerta yingliangia* gen. et sp. nov., YLSNHM01796, in (A) dorsal, (B) ventral, (C) right lateral, and (D) left lateral views. **Abbreviations:** An, angular; Ar, articular; Bo, basioccipital; D, dentary; Ect, ectopterygoid; Fr, frontal; *ipv*, interpterygoid vacuity; Ju, jugal; Mx, maxilla; N, nasal; Oco, occipital condyle; Pa, parietal; Pal, palatine; PBs, parabasisphenoid; Pf, postfrontal; Po, postorbital; ppr, paroccipital process; Prf, prefrontal; Pt, pterygoid; Pt.fs, pterygoideus fossa; Qu, quadrate; Sp, splenial; Sq, squamosal; Sur, surangular; V, vomer.

Stone Natural History Museum, operated by the philanthropic programme of its founder (Mr Liang Liu).

Holotype: YLSNHM01796 (Figs 2, 3, 5, 6), an almost complete skull missing a small part of the rostrum, housed in The Yingliang Stone Natural History Museum, Shuitou, Fujiang, China.

Type locality. Huadong Cheng Construction, Zhanggong District, Ganzhou City, Gansu Province, China (25.8123°N, 114.9709°E) (Fig. 1, site 1).

Stratigraphical horizon. Hekou Formation, part of the Guifeng Group. The holotype skull YLSNHM01796

(Figs 2, 3) was recovered from the Huadong Cheng Construction site, Zhanggong District, Ganzhou City. The second specimen, YLSNHM01791 (Fig. 4), was found near the Ganzhou Train Station, Zhanggong District, Ganzhou City (Fig. 1, site 2).

The Hekou Formation consists of channelized, fining-upward conglomerates, sieve deposits, and alternating sandstone and mudstone beds. The depositional setting is interpreted as primarily fluvially derived within a proximal alluvial fan system. Mud cracks and caliche deposits are common, and the prevailing palaeoclimate is interpreted as having been sub-humid. The formation has thus far yielded fossil algae, plants (Wen et al.,

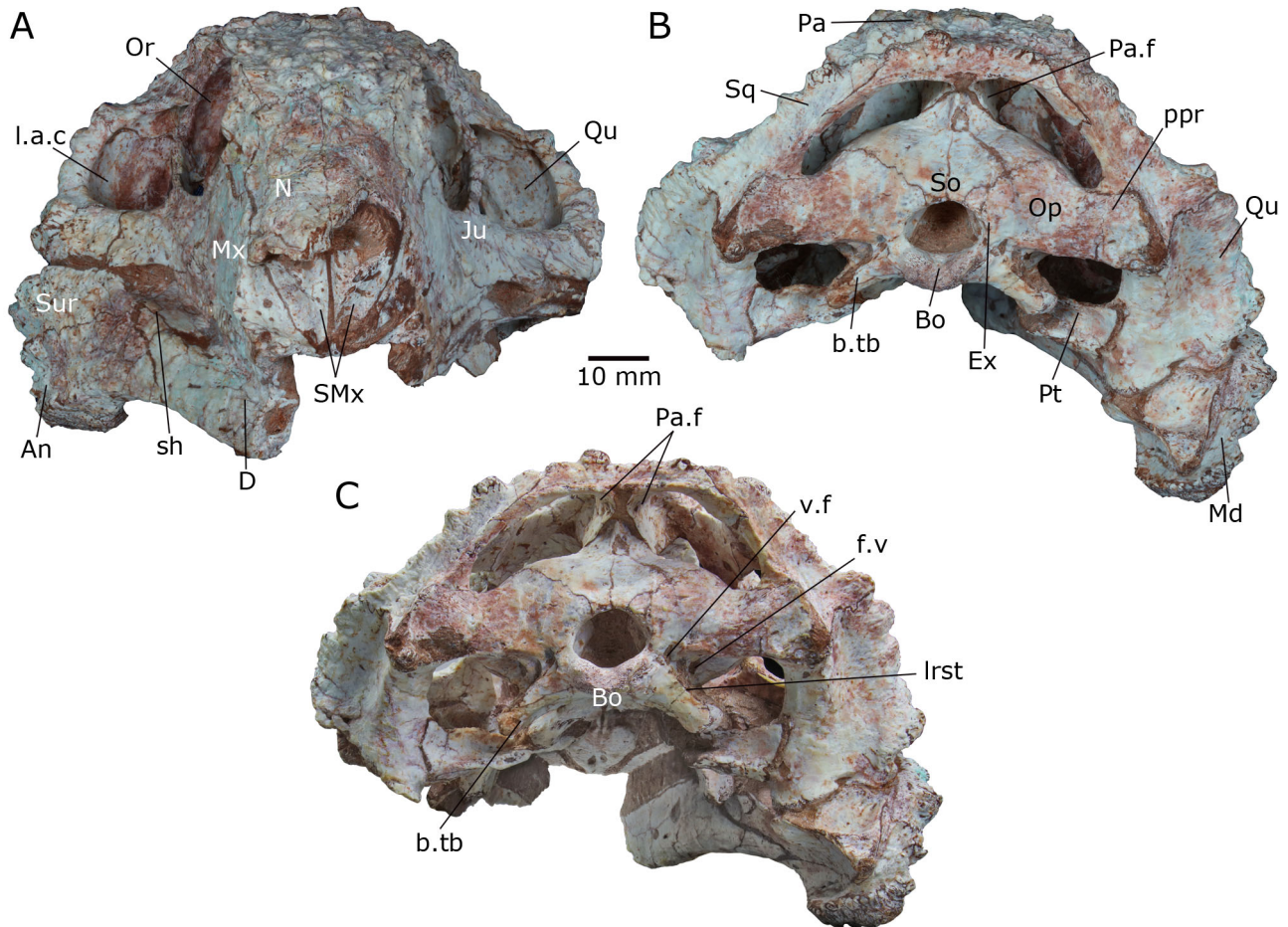


Figure 3. The holotype skull of *Yechilacerta yingliangia* gen. et sp. nov., YLSNHM01796, in (A) frontal, (B) occipital, and (C) oblique occipital views. **Abbreviations:** An, angular; b.tb, basal tubera; Bo, basioccipital; D, dentary; Ex, exoccipital; f.v, fenestra vestibuli; Ju, jugal; l.a.c, lateral adductor chamber; lrst, lateral opening of the recessus scalae tympani; Md, mandible; Mx, maxilla; N, nasal; Or, orbit; Pa, parietal; Pa.f, parietal foramen; ppr, paroccipital process; Pt, pterygoid; Qu, quadrate; sh, shelf; SMx, septomaxilla; So, supraoccipital; Sq, squamosal; Sur, surangular; v.f, vagus foramen.

2016), dinosaur bones (Xing, Niu, Wang *et al.*, 2021), trackways (Xing *et al.*, 2019, 2020) and dinosaur eggs (Peng, 2020; Xing *et al.*, 2020, 2022; Xing, Niu, Ma *et al.*, 2021), some with embryos (Xing, Niu, Ma *et al.*, 2021; Xing *et al.*, 2022). Palaeomagnetic studies have dated the host Guifeng Group to 71.4–65.0 Ma, Maastrichtian (Gu, 1991; Zuo, 1999). The dinosaur assemblage implies the Guifeng Group is penecontemporaneous with the red beds of the nearby Nanxiong Group (Xing *et al.*, 2022). The Hekou Formation is thought to correlate with the Dafeng and Yuanpu Formations of the lower Nanxiong Group (Zhang *et al.*, 2021).

Description

General features. The holotype (YLSNHM01796; Figs 2, 3, 5, 6) is a well-preserved skull missing the tip of

the rostrum and most of the right mandible, with the symphyseal region of the lower jaws having been detached. The skull is ~93.6 mm in midline length from the preserved tip of the snout to the back of the parietal but is estimated to have been 97–100 mm when complete (based on proportions of the second specimen). It is covered by coarse tuberculate sculpture, especially on the dorsal roofing bones (nasals, frontals, parietals) and along the bones surrounding the orbit (prefrontals, postfrontals, postorbitals, jugal postorbital ramus). The upper and lower temporal fenestrae are fully framed. The smaller upper temporal fenestra is ovoid with the long axis directed anteroposteriorly; the larger lower fenestra is also ovoid, but with the long axis running from posterodorsal to anteroventral. As is common in polyglyphodontians, the anterior part of the lower temporal fenestra extends below the posterior edge of the orbit, due to the oblique angle of the jugal postorbital process.



Figure 4. The skull of the second specimen of *Yechilacerta yingiangia* gen et sp. nov., YLSNHM01791, in (A) frontal, (B) dorsal, (C) right lateral, and (D) left lateral views.

As seen clearly in an anterior view of the skull (Fig. 3A), the lower temporal fenestrae flare out laterally beyond the line of the orbits, creating a large ventrolateral adductor chamber (l.a.c).

YLSNHM01791 (Figs 4, 7) represents a slightly larger individual than YLSNHM01796 (skull length ~105 mm) and, as noted above, seems to comprise both a complete skull (Fig. 4) and components of the postcranial skeleton (axial skeleton and ribs, parts of both fore- and hind limbs, Fig. 7). The proximal epiphysis of the humerus is ossified but detached and the distal epiphysis is attached but not fully co-ossified with the humeral head (part of the epiphysial line remains visible), suggesting a potential for further growth.

Skull. The skull description is based primarily on the holotype, unless otherwise specified (Figs 2, 3, 5). The nasals of both specimens are incomplete anteriorly but appear to have been rather oblong in shape (not

triangular as in many gilmoreteiids) and were roughly half as wide as they are long. They have an irregular median suture and an interdigitating suture with the frontals well anterior to the orbits. The frontals are also paired with a tight median suture, tuberculate sculpture, and strong interdigitating sutures posteriorly with the single parietal. Laterally each frontal is flanked by the prefrontal anteriorly and postfrontal posteriorly but makes a small contribution to the orbital margin between these elements. The parietal is perforated by a circular parietal foramen just posterior to the fronto-parietal suture. The parietal is widest at this point, but then narrows between the small upper temporal fenestrae, before expanding again posteriorly into short lateral processes that meet the squamosals. Ventrally, the parietal bears deep medial flanges that clasp the anterior tip of the supraoccipital to either side of the midline.

The premaxilla is missing, apart from a fragment associated with the detached symphyseal region of the

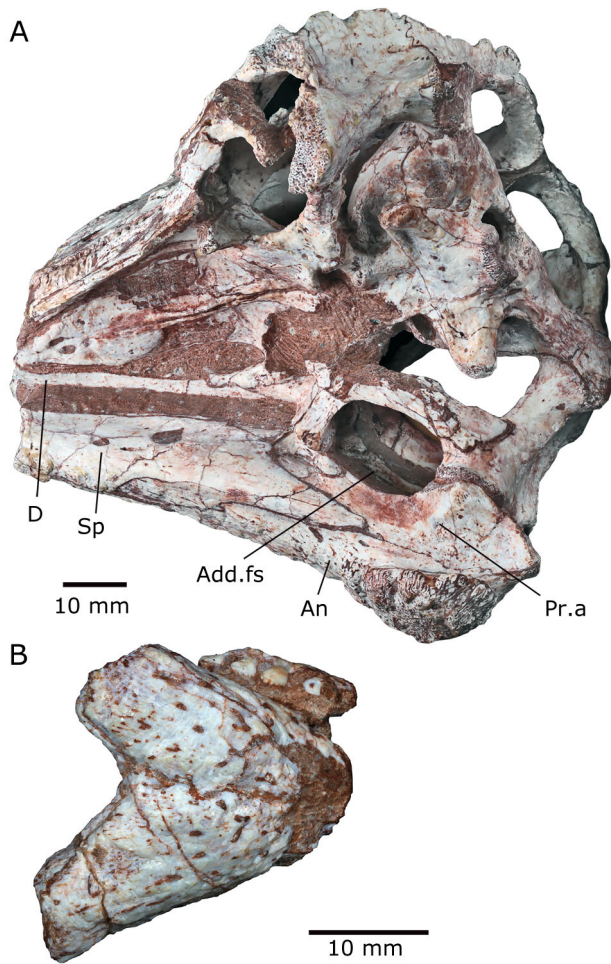


Figure 5. The holotype skull of *Yechilacerta yingliangia* gen. et sp. nov., YLSNHM01796 (A) in oblique ventral view to show the medial aspect of the right mandible, and (B) in ventral view to show the detached dentary symphysis and a fragment of premaxillary dentition. **Abbreviations:** Add.fs, adductor fossa; An, angular; D, dentary; Pr.a, prearticular; Sp, splenial.

mandibles, and an anterior view into the nasal cavity (Fig. 3A) shows large triangular plate-like septomaxillae flooring the nasal cavity and supported on each side by the maxillae. As in other polyglyphanodontians, the maxilla has a large vertical facial process that forms most of the lateral wall of the preorbital skull. It makes a broad contact with the nasal anterior to the prefrontal-nasal suture. The jugal process is very short and extends less than halfway across the orbit. Twenty-five teeth/tooth positions are preserved on the right maxilla, and 19 on the more damaged left maxilla. The maxilla meets the large nasal and broad prefrontal dorsally, and the expanded orbital ramus of the jugal posteriorly. The premaxillary process is not preserved on the holotype skull but is present on the left side of the second specimen. It is of similar length to the jugal process, bears four

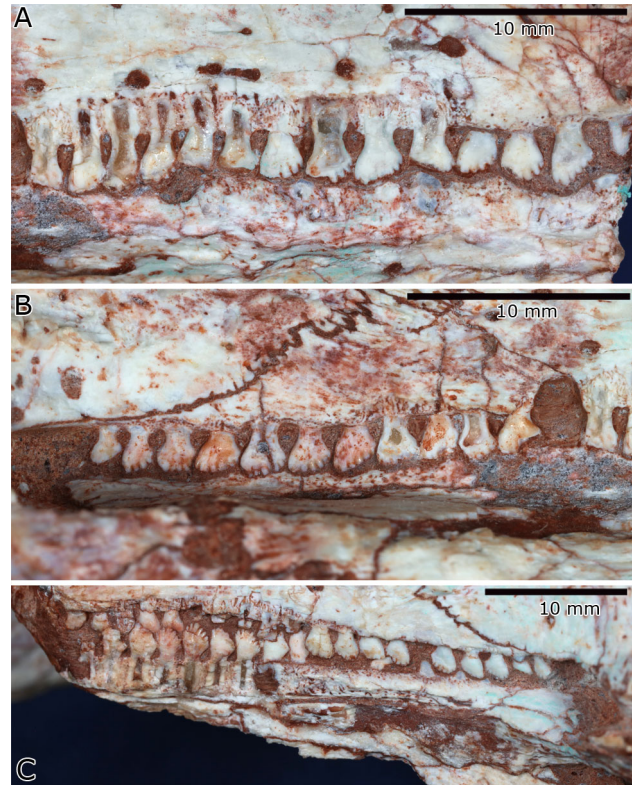


Figure 6. The holotype skull of *Yechilacerta yingliangia* gen. et sp. nov., YLSNHM01796. (A) and (B), right maxillary dentition with (A) anterior region and (B) posterior section, and (C) left maxillary and dentary dentition.

well-spaced teeth, and is slender and anteromedially directed. The superior alveolar foramen lies at the junction between the facial process and the premaxillary process.

The prefrontal is large with a strong facial component and a broad orbital flange that braces the anteroventral lamina of the frontal. It bears tuberculate sculpture along its orbital margin, terminating in a small lateral fossa just dorsal to its junction with the lacrimal and maxilla. Wedged between the prefrontal, maxilla, and jugal is a small semicircular lacrimal. The single lacrimal foramen lies between the lacrimal itself and the descending orbital flange of the prefrontal. The jugal is triradiate. A deep orbital ramus forms the ventral and anteroventral margins of the orbit, meeting the lacrimal dorsally and having a long almost vertical suture with the facial process of the maxilla. The narrower oblique postorbital ramus bears sculpture and has a tight dorsal suture with the postorbital bone, whereas the thick posterior ramus has a firm oblique suture with the expanded ventral margin of the quadrate. There is no quadratojugal.

The postfrontal and postorbital are both strongly sculptured, partially obscuring the suture between them.

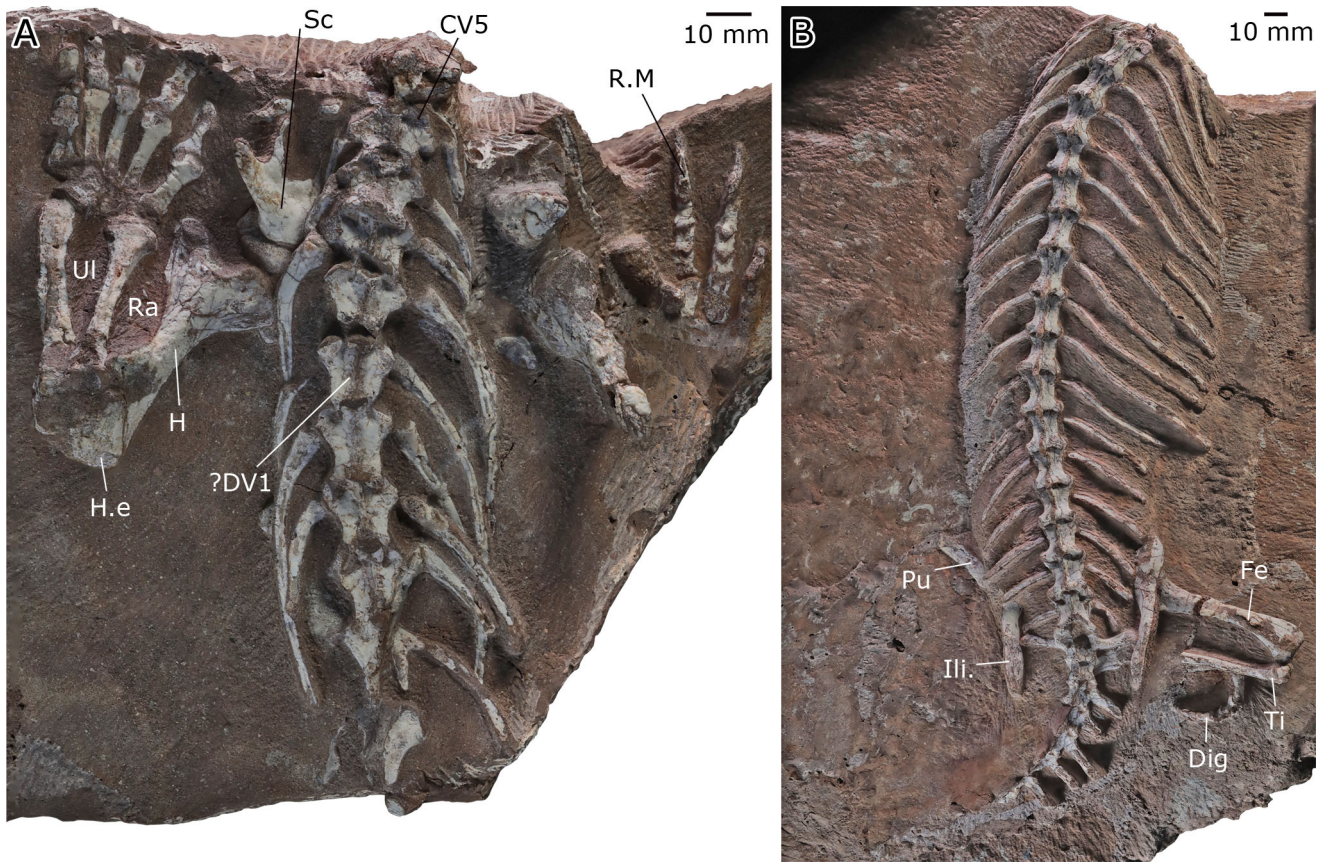


Figure 7. The postcranial skeleton of the second specimen of *Yechilacerta yingiangia* gen et sp. nov., YLSNHM01791 in dorsal view. **A**, pectoral region, forelimbs and anterior vertebral column; and **B**, dorsal, sacral and anterior caudal vertebrae, pelvic girdle, and hind limbs. **Abbreviations:** CV5, fifth cervical vertebra; **Dig**, digit (probably digit 4); **?DV1**, interpreted position of first dorsal vertebra; **Fe**, femur; **H**, humerus; **H.e**, humeral epiphysis; **Ili.**, ilium; **Pu**, pubis; **Ra**, radius; **R.M**, right manus; **Sc**, scapula; **Ti**, tibia; **UI**, ulna.

The postfrontal is relatively small and is wedged dorsally between the frontal anteriorly, the parietal medially, and the postorbital both ventrolaterally and posteriorly (Fig. 2A). It appears to make only a very small contribution to the posterodorsal corner of the orbit and the anterior margin of the upper temporal fenestra, between the parietal and the postorbital. The postorbital is larger and biradiate. Its ventral process meets the jugal to complete the postorbital bar and its wide posterior process forms the entirety of the upper temporal bar, contacting the squamosal at the posterior margin of the upper temporal fenestra.

The quadrate is massive with a wide tympanic crest that expands into a deep anteroventral tuberosity that is sutured to the jugal. It also expands ventromedially where it has a sutural contact with the posterior tip of the pterygoid. The quadrate is sutured dorsally to the squamosal (interdigitating suture seen clearly on the left side) and posterodorsally to the paroccipital process of the oto-occipital. The squamosal is large and almost vertical. It is strongly sutured to the quadrate ventrally, to

the parietal posterodorsomedially via a dorsal process, and to the posterior process of the postorbital anteriorly. Posteromedially, the quadrate and squamosal form a recess for the paroccipital process of the oto-occipital. There is no supratemporal. A narrow vertical bar of bone lying in the matrix medial to the left lower temporal bar and anterolateral to the endocranium may be part of the epipterygoid.

The palatal surface (Fig. 2B) shows the characteristic features of the polyglyphanodontian palate – notably posterior extension of the vomers resulting, in *Yechilacerta*, in a midline contact of the vomers and pterygoids; the reduction in size of the suborbital fenestra due to the expansion of surrounding elements; and the absence of palatal teeth. The vomers form an elongate triangular plate that tapers anteriorly towards the missing premaxillae, and widens posteriorly towards the articulation with the palatines, before narrowing again into spine-like processes that meet the pterygoids in the midline, separating the palatines completely. At no point does the vomer contact the maxillae (palaeochoanate

palate), with long slender choanae extending the full length of the rostrum and confluent with the opening for the vomeronasal organs. The anterior half of the vomerine plate is flat, perforated bilaterally by small ovoid fenestrae. Farther posteriorly, the medial borders are developed into low ridges that flank a long narrow median recess. On either side of these ridges, the bone is damaged, but it is clear from the preserved lateral edges of the bone that each vomer bore an elongate ovoid recess to either side of the midline. The palatines are short and broad, with a short wide choanal recess on the palatal surface and a large lateral process that contacts the maxilla anterolaterally and the ectopterygoid posterolaterally. Between the palatine, ectopterygoid and pterygoid, the suborbital fenestra is very restricted in size.

The pterygoids bear broad palatal plates that meet or nearly meet along the midline for most of their length so that the interpterygoid vacuity is restricted to a small triangular space anterior to the parabasisphenoid. This is clearer on the left side of the palate where the margin of the pterygoid is complete (Fig. 2B). Laterally, the pterygoid flanges are thick and robust, meeting the ectopterygoids anteriorly in a strong suture and forming the posterior margin of the small suborbital fenestrae. The combined ectopterygoid/pterygoid flange is robust but does not extend medially below the base of the coronoid in the lower jaw. The posterior portion of each pterygoid meets the basiptyergoid process medially and then narrows into the posterolaterally directed quadrate process that is sutured to the medial margins of the quadrate.

In palatal view, the short parabasisphenoid is damaged but preserves a small flared left basiptyergoid process that abutted the pterygoid as described above. It seems unlikely that any movement occurred at this joint. Posterior to the parabasisphenoid, the basioccipital is short and broad, with large laterally flared basal tubera and an eroded occipital condyle. In occipital view (Fig. 3B, C), the braincase is seen to be robust. The sutures between the supraoccipital and oto-occipitals remain patent, whereas those between the opisthotics and exoccipitals (together forming the oto-occipital) are completely obliterated. The anterior margin of the supraoccipital is flexed dorsally and is clasped by paired ventral parietal flanges as described above, but the rest of the supraoccipital is not crested. Bilaterally, the thick horizontal paroccipital processes of the oto-occipitals fit tightly between the squamosal and quadrate. The foramen magnum is relatively small. Below it, the kidney-shaped occipital condyle is flanked by strong ventrolaterally directed basal tubera, each with a well-developed crista tuberalis. One hypoglossal foramen is visible perforating each of the exoccipitals, but it is difficult to determine whether a second was also present.

The massive squamosal and quadrate make it difficult to visualize the braincase, but an oblique view of the left side (Fig. 3C) shows the presence of the vagus foramen between the ascending ramus of the exoccipital and the opisthotic, a circular fenestra vestibuli and, between them, a slit-like lateral opening of the recessus scalae tympani. However, it is unclear whether the apparent reduction in the lateral opening is natural or due to damage. In palatal view a flared crista prootica is exposed on the prootic to the left of, and above, the parabasisphenoid, and strong alar processes are visible through the upper temporal fenestrae. The braincase is therefore typically squamate in its morphology.

Mandible. The mandible is best preserved on the right-hand side of the skull (Fig. 2C, 5A). It comprises the dentary, splenial, and coronoid, surangular, and a partially fused angular and prearticular-articular. As seen in ventral view, the mandible appears fairly linear. However, the depth of the posterior part of the mandible and its relationship to the temporal region is shown clearly in the anterior view of the skull (Fig. 3A). This view also shows a feature not obvious in lateral view, namely the presence of a horizontal shelf on the posterolateral surface of the dentary that probably provided a surface of insertion for superficial fibres of the external adductor (*M. adductor mandibulae externus superficialis* [MAMES]). This shelf floors the expanded ventrolateral part of the adductor chamber described above and resembles the deep gutter present in *Tianyusaurus* (Mo *et al.*, 2009). A large superficial adductor muscle mass seems to have been accommodated medial to the lower temporal bar, but the bar prevented the muscle from extending down the lateral face of the surangular (as it does in many other polyglyphanodontians). As seen in lateral view (Fig. 2C, D), the articular surface for the quadrate lies below the level of the tooth row.

A relatively short, moderately deep dentary is preserved on the right side of the head, but the teeth are obscured. The posterior border of the dentary is not developed into dorsal and ventral processes. Instead, it has an oblique posterodorsal to anteroventral suture with the postdentary bones (surangular, angular). The left dentary is damaged but does reveal a row of eight anterior teeth and the tips of a few posterior ones. The symphyseal region has been detached and shows a long, firm, and probably immobile symphyseal suture (Fig. 5B). A small fragment of the right maxillary or premaxillary dentition is associated with this detached portion. Medial to the dentary and forming much of the ventral surface of the mandible anteriorly, is a large splenial. This element extends anteriorly towards the symphysis and posteriorly beyond the level of the coronoid (Fig. 5A) where it tapers to a point between the oblique margin of

the prearticular and the horizontal margin of the angular. As preserved, the splenial contains two openings, these could be the anterior mylohyoid foramen (smaller anteroventral opening) and anterior inferior alveolar foramen (larger posterodorsal opening) but their uneven shapes leave some uncertainty as to whether they are natural anatomical structures. The coronoid is partially obscured by the pterygoid flange but is relatively small. A short anteromedial process meets the dorsal margin of the splenial, with the remaining medial and posteromedial margins clasped by the prearticular. The posterior margin of the coronoid forms the anterior border of the mandibular adductor fossa but the lateral part of the coronoid and its dorsal process are obscured. The post-dentary bones are partially fused to one another. The prearticular component forms the medial wall of the short but deep mandibular adductor fossa and is fused without suture to the articular. A crack, or suture, separates the prearticular from the ventral angular component that wraps around the posteroventral margin of the mandible, contributing to both the ventrolateral and ventromedial surfaces. Laterally, the angular forms more than half the depth of the posterior mandible where it has a long horizontal dorsal suture with the surangular. Surangular foramina are not visible, possibly because of the sculpture. In ventral view (Fig. 2B), the retroarticular process is seen to be short and tapering. It is sharply divided into medial and lateral halves by a crest. The smooth medial portion of the process is continuous anteriorly with a ventromedially concave prearticular flange that probably accommodated the superficial part of the *M. pterygoideus* (with the deep part inserting above the flange). However, unlike most polyglyphanodontians, including *Tianyusaurus*, coarse sculpturing on the lateral mandibular surface provides a sharp demarcation line that shows the *M. pterygoideus* to have been restricted to the ventromedial aspect of the jaw (Fig. 2).

Dentition. Portions of the maxillary dentition are preserved on both sides of the skull, with a short length of the dentary dentition on the left side (Fig. 6). The breakage through the bone on the left dentary (Fig. 2D) and the right maxilla (Fig. 2C) shows the teeth to have cylindrical roots with a modified pleurodont implantation (i.e. attached to the apicolingual wall of the jaw), and anteroposteriorly expanded multicuspid crowns. The crowns are asymmetrical and slightly offset so that successive teeth slightly overlap one another. In the dentary, the mesial margin of the crown is longer than the distal one, so that the teeth appear to be tilted backward. However, there are fewer cusps along the mesial edge, and they are placed apically, whereas the distal cusps extend further down the oblique distal edge of the crown. Thus, the cutting edge of the dentary teeth is mostly posterior. The maxillary teeth have the opposite

arrangement, with the greatest number of cusps along the oblique mesial margin of each tooth. A short section of the upper tooth row is associated with the detached symphyseal portion of the dentary but it is not clear whether these are anterior maxillary or posterior premaxillary teeth. Either way, they are the same as the maxillary dentition, asymmetrical with the cusps along the leading edge. Given the massive robust skull, the teeth are surprisingly delicate, a feature seen in some other gilmoretids.

Postcranial skeleton overview. The components of the postcranial skeleton are preserved in dorsal view in YLSNHM01791 (Fig. 7). As noted in the introduction, this specimen was excavated in three parts from the same site and probably, but not certainly, pertains to a single individual. The first part bears the skull and parts of four cervical vertebrae (Fig. 4). The second section bears eight complete and two damaged vertebrae, as well as part of the left pectoral girdle (scapula and part of coracoid incompletely exposed), an almost complete left forelimb (missing the distal phalanges), and the proximal and distal parts of the right forelimb, including the distal parts of three digits (probably 3–5) (Fig. 7A). The larger third block bears 16 complete dorsal vertebrae preceded by another partial vertebra, then two sacrals, and six anterior caudals, as well as parts of both pelves (not fully exposed), the right femur and tibia, and parts of a digit (Fig. 7B). Between the three blocks, there are therefore eight cervical and 22 dorsal vertebrae, giving a slightly extended presacral count of at least 30. However, it is possible there were more than this in missing parts of the original specimen.

Vertebral column. There are four vertebral elements in association with the back of the skull, the second of which has the longest neural arch and is here interpreted as the axis. Anterior to this are bone fragments that likely present the atlantal neural arches. The fourth vertebra bears a short deep headed rib on the right side, and therefore CV4 is probably the first rib-bearing cervical. On the second matrix block, the first four complete vertebrae are relatively short (ranging from 6.67 to 10 mm along the anterior to posterior midline of the neural arch (L)) and are wider (W) anteriorly than they are long (L) in dorsal view ($L/W = 31\text{--}50\%$). There are bone fragments anterior to the first complete vertebra, but these do not seem to represent a complete element. The fifth vertebra on this block is intermediate in length and width ($L = 11.67\text{ mm}$, $L/W = 66.7\%$), and the remaining vertebrae are almost as long as they are wide ($L = 15\text{ mm}$, $L/W = 90\%$). We therefore interpret the first four complete vertebrae preserved as cervicals (giving an estimated total of eight cervicals), with the fifth

probably representing the first dorsal (giving a total of six anterior dorsals on this block). All these vertebrae bear ribs. The ribs of the first three vertebrae on the block (CV5–7) are too short to have reached the sternum. The rib of the fourth preserved vertebra (CV8) is longer. All the following ribs are long. The last dorsal on this block has lost most of its neural arch, providing a glimpse of the underlying centrum, which is prococious as in other polyglyphanodontians. The third, large block bears a fully articulated series of 16 dorsal vertebrae (with a partial vertebra + rib at the anterior end, probably where the smaller pectoral-forelimb block was detached). These dorsal vertebrae are more elongated than those of the cervical region, although they shorten towards the sacrum. The neural spines are low, and they bear zygosphenes and zygantra. All dorsal vertebrae bear ribs, including the last, although it is not clear whether the last dorsal rib is free or fused. There is a distinct decrease in rib length in the last seven dorsals. The two sacral vertebrae have been disarticulated and rotated, so that they are preserved in anterior view. The sacral transverse processes are not fused at their tips and the transverse process of the second sacral seems to be more robust than that of the first. The anterior caudals have long transverse processes but are otherwise poorly preserved in dorsal view.

Pectoral girdle and forelimb. The pectoral girdle is preserved on the left-hand side, represented by a partial scapula that is short and robust and has a distinct dorsal emargination. The coracoid is obscured by matrix. The forelimbs are relatively short and strongly built. The left is almost complete and fully articulated. The humerus is robust ($L = 62.5$ mm), with a roughly 60° twist between the expanded proximal and distal heads ($W = 25.8$ mm for both heads). The ossified proximal epiphysis has detached and lies within the glenoid fossa of the scapulocoracoid. The distal epiphysis (Fig. 7A, H, e) is attached, but the epiphysal line is partly visible, suggesting co-ossification had begun but was not complete. Both the radius and ulna are preserved ($RL = 36.7$ mm; $\sim 58.7\%$ of humeral length), although their proximal heads are damaged, and it is not possible to determine whether or not an olecranon process was ossified on the ulna. The distal head of the radius is broader than its proximal head, but the reverse is the case for the ulna. Both appear to have an at least partially co-ossified distal epiphysis. The carpals are ossified but damaged. They probably represent a large ulnare and several other elements, but these cannot be identified with confidence. The left manus preserves metacarpals 1–5. These are relatively short and robust, with the third ($L = 21.7$ mm) slightly longer than the second ($L = 18.3$ mm) and fourth ($L = 19.2$ mm), and the first ($L = 15$ mm)

and fifth ($L = 12.5$ mm) shortest. The digits are incompletely exposed, with a proximal phalanx and partial ungual on the first digit, two very short phalanges ($L = 7$ mm) on the second, one on the third, two on the fourth, and two on the fifth. The right forelimb preserves only the proximal part of the humerus, a fragment of either radius or ulna, and the distal ends of three digits – apparently digits 3–5. Of these, the fifth is badly damaged, but the fourth appears to preserve the proximal end of the metacarpal with four very short phalanges and a longer, curved ungual. The third is similar, but with three short phalanges and an ungual. This suggests the original phalangeal formula for the manus was 2:3:4:5:3/4.

Pelvic girdle and hind limb (Fig. 7B). The pelvis is not fully exposed and only the dorsal margin of the ilium and pubis are visible. In this view, the iliac blade is long and rather narrow, meeting the sacral ribs well posterior to the level of the acetabulum, although this may not be natural. There is no evidence of an anterior iliac tubercle.

The right femur is complete (estimated $L = \sim 73$ mm, allowing for the partly obscured proximal head). It is sigmoid and, like the humerus, is robust and relatively short compared to presacral body length (head + presacral column). The distal epiphysis is attached (proximal epiphysis not visible). The tibia is in articulation ($L = 50$ mm). There is a bony nodule on its proximal end, but whether this is a partly detached tibial epiphysis or a patella is unclear and it was not included in the length measurement. One pedal digit is visible as a curved structure deep to the tibia, with four short phalanges, and so is probably the fourth digit. A long, curved digit (digit 4) in roughly the same position is illustrated for the holotype of *Gilmoreteius* (*'Macrocephalosaurus'*) *chulsanensis* (Sulimski, 1975, fig. 6).

Taken overall, *Yechilacerta* has a relatively long body and short robust limbs. The humerus is 4.2 mid-dorsal vertebral lengths (DVL), and the femur is 4.87 vertebral lengths. Amongst extant lizards, this femoral length is similar to normal limbed extant lizards with unspecialized body plans and of large body size (e.g. *Varanus niloticus* [5 DVL], *Uromastyx* sp. [5.23 DVL], *Gallotia* sp. [4.3 DVL]).

Results of phylogenetic analysis

The position of *Yechilacerta* within Polyglyphanodontia

In all analyses using the updated and extended Gauthier *et al.* (2012) matrix, constrained or unconstrained, ordered or unordered, and with equal or implied

weighting, *Yechilacerta* nested with large Asian polyglyphanodontians, as the sister taxon to *Tianyusaurus*. The ingroup relationships of the other polyglyphanodontian taxa are rather unstable, but this likely reflects the fact that: (1) only four (*Gilmoreteius*, *Yechilacerta*, *Polyglyphanodon*, *Adamisaurus*) have any substantial postcranial material; (2) the skulls of many taxa are incompletely known (e.g. braincase or palatal features); and (3) no other Euramerican polyglyphanodontid or chompsiid taxa were included as none is represented by significant non-dental material. A comprehensive review of the in-group relationships of Polyglyphanodontia is needed but is beyond the scope of this work where our main aim was to place the new taxon within squamate phylogeny.

Figures 8A and B display summary consensus trees. Figure 8A shows a minimal level of resolution that is compatible with the results of all analyses. Figure 8B shows a more resolved topology that is compatible with the majority of constrained analyses. *Adamisaurus* was usually but not always placed stemward of *Polyglyphanodon*. Gilmoreteiidae was usually monophyletic, but *Polyglyphanodon* was placed as the sister taxon to *Cherminisaurus* when the analysis was run with implied weighting ($k=3$), both unordered and ordered, with both taxa stemward of *Gilmoreteius* in the latter analysis (see Supplemental material section 6, for tree data).

The position of Polyglyphanodontia within Squamata

As in Gauthier et al. (2012), analyses run without molecular constraints (whether characters were ordered or unordered) placed Polyglyphanodontia on the stem of a clade including Mosasauria + the traditional Scleroglossa (Gekkota, Anguimorpha, Scincomorpha, Serpentes). With enforced constraints (see Methods), and either equal or implied weighting, Polyglyphanodontia was frequently placed as the sister group of Iguania within Toxicofera (Iguania, Anguimorpha, Serpentes) but with some variation:

- Constrained (basic), ordered and equal weights: the strict consensus of 1728 trees after TBR was poorly resolved but the 70% majority rule tree (MRT) placed Polyglyphanodontia (and a sub-set of unstable Jurassic/Early Cretaceous taxa) as the sister group to Iguania.
- Constrained (basic), ordered and implied weights ($k=3$): single tree, Polyglyphanodontia was placed as the sister group to Iguania.
- Constrained (basic), unordered, and equal weights: the strict consensus of 17,711 trees was poorly

resolved, but a 70% MRT placed Polyglyphanodontia as the sister group of Iguania and a small suite of Early Cretaceous taxa.

- Constrained (basic), unordered, and implied weighting ($k=3$): a single tree resulted in which Polyglyphanodontia was placed as the sister group of Iguania + (Serpentes, Mosasauria).
- Constrained, ordered, with an extra constraint linking Anguimorpha and Serpentes, equal weighting (strict consensus and 70% MRT of 192 trees) and with implied weighting ($k=3$, single tree): Polyglyphanodontia was placed as the sister group to Iguania.
- Constrained, ordered, with an extra constraint linking Iguania and Serpentes. Strict consensus (equal weighting) was poorly resolved due to the instability of *Tchingisaurus* (moving between Iguania and Polyglyphanodontia) and *Huehuecuetzpalli* (moving between squamate stem and Iguania), but 70% MRT placed Polyglyphanodontia as sister group of Iguania, as did implied weighting ($k=3$).
- Constrained, ordered, with extra constraint linking Iguania and Anguimorpha, equal weighting: in all 52 trees resulting from an initial NT search, Polyglyphanodontia was placed as the sister group of Iguania, but both the strict consensus tree and 70% MRT (after TBR: 12,496 trees) were poorly resolved due to the movement of the Early Cretaceous Mexican *Huehuecuetzpalli* between the squamate stem and the stem of Iguania. When *Huehuecuetzpalli* was deactivated, the strict consensus of 8560 trees after TBR placed Polyglyphanodontia as the sister group to Iguania, as did the single tree using implied weighting.

Figure 8C shows a summary of squamate phylogeny with alternative positions of Polyglyphanodontia: the teioid placement favoured by many previous authors (e.g. Estes, 1969, 1983; Nydam et al., 2007) and the sister-group relationship with Iguania found in the majority of the analyses herein using the Gauthier et al. (2012) matrix (see also Discussion).

Discussion

The phylogenetic position of *Yechilacerta*

Despite its heavily sculptured skull and complete lower temporal bar, *Yechilacerta* is diagnostically squamate based on characters of the temporal region (e.g. absence of the quadratojugal [Ch. 181,1], quadrate with lateral conch [Ch. 180,0]); braincase (e.g. fusion of exoccipital and opisthotic [Ch. 352,1]; subdivided metotic fissure

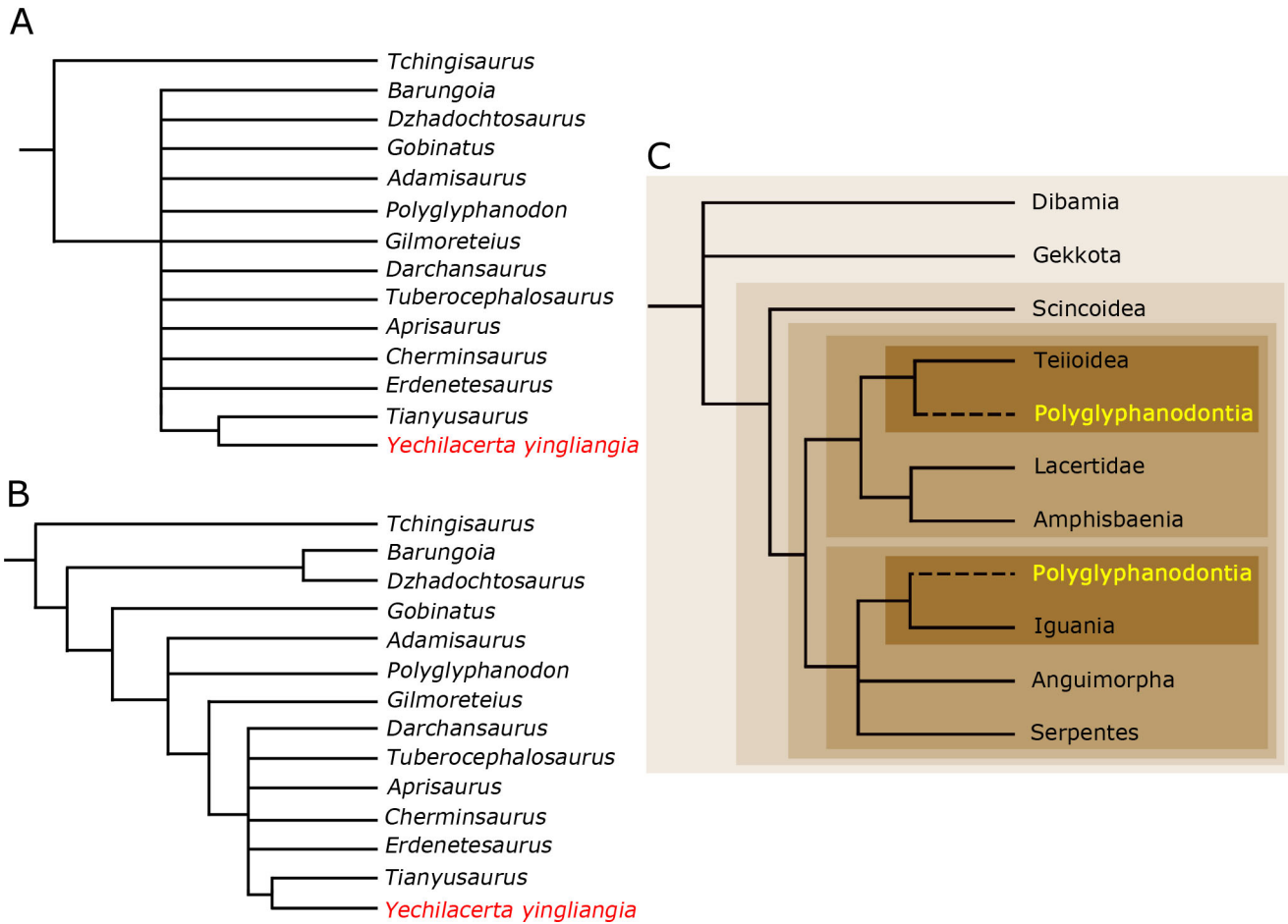


Figure 8. **A** and **B**, alternative consensus trees from a constrained TNT analysis of the emended Gauthier *et al.* (2012) data matrix, with different levels of resolution. **C**, a summary tree of squamate relationships, based on molecular data, with the two most common alternative positions of Polyglyphanodontia reported by previous authors and the current paper. See text for further details.

[Ch. 354,1]; prootic with well-developed alar process [Ch. 305,1] and crista prootica [Ch. 307,0]; vertebral column (procoelous vertebrae [Ch. 467,1], zygosphenozygantrum [Ch. 468,1]); and pectoral girdle (scapula emargination [Ch. 492,1]).

Within Squamata, *Yechilacerta* shares with polyglyphanodontian lizards the long, deep facial process of the maxilla; contact or near contact of the vomer and pterygoid in the palatal midline (Ch. 259,0); deep suborbital ramus of the jugal (Ch. 150,1), with prominent medial ridge (Ch. 157,1); large lower temporal fenestra that extends forward below the orbit; long posterior process of the postorbital; absence of palatine and pterygoid teeth (Chs. 255,1; 267,1); and hypertrophied splenial reaching, or nearly reaching, the symphysis (Ch. 375,3). Within Polyglyphanodontia, *Yechilacerta* shares a suite of cranial and dental characters with Asian taxa generally placed in the Gilmoreteiidae, including multicuspid

spatulate teeth (Ch. 434,3); reduced suborbital fossa and expanded ectopterygoid (Ch. 281,1); reduced dentary angular process (Ch. 368,2); and deep dentary with teeth that appear small relative to dentary size. However, *Yechilacerta* differs from most other gilmoreteiids in the development of a robust lower temporal bar and the sutural contacts between the quadrate and surrounding bones (pterygoid, jugal, squamosal). In this specialized morphology (Chs. 155,0; 177,2; 182,0) it resembles *Tianyusaurus*, specimens of which have also been recovered from the Ganzhou locality (Fig. 1). The two genera emerged as sister taxa in all phylogenetic analyses using the Gauthier *et al.* (2012) matrix, supported by additional characters including nasal and maxillary shape (Chs. 18,1; 31,0; 114,3; 116,0; 124,0); tooth asymmetry; posterior extension of the parietal over the braincase (Ch. 99,1); parallel vomerine ridges (Ch. 222,2); reduced crista tuberalis in braincase (Ch. 312,1);

and posterior extension of the splenial (Ch. 376,0); as well as long, laterally oriented basal tubera and a dorsal shelf on the surangular.

Yechilacerta differs from *Tianyusaurus* in the following characters: the squamosal is larger and more vertically oriented in *Yechilacerta*; the frontal is broader without a strong interorbital emargination (interorbital width/naso-frontal suture width 131% in *Lechisaurus* vs 47% in *Tianyusaurus*; interorbital width/midline frontal length 78% in *Yechilacerta* vs 18% in *Tianyusaurus*); the prefrontal has a long suture with the nasal (vs very short in *Tianyusaurus*); the supratemporal processes of the parietals are shorter and more laterally (vs postero-laterally) oriented; there is greater closure of the interpterygoid vacuity; the postfrontal is almost excluded from the supratemporal fenestra (vs widely exposed); the paroccipital processes are not distally expanded (vs expanded); the supraoccipital is uncrested (vs crested); the angular is fused to the prearticular and articular (vs unfused); and the M. pterygoideus muscle was restricted to the ventromedial surface of the mandible, as demonstrated by the lateral sculpture (vs winding onto the posteroventrolateral surface).

However, both specimens of *Yechilacerta* are larger (skull lengths of 97–100 mm and 105 mm) than those described for *Tianyusaurus* (e.g. skull lengths of 87.4 mm, 79.5 mm, 56 mm; Mo et al., 2009). This raises the question as to whether the cranial differences between *Tianyusaurus* and *Lechilacerta* could reflect ontogenetic variation and/or sexual dimorphism, male lizards often having larger heads than females (e.g. Anderson & Vitt, 1990; Herrel et al., 2002), especially where there is male-on-male aggression (e.g. Carothers, 1984). Ontogenetic variation seems unlikely. The largest skulls of *Tianyusaurus* are already strongly ossified, with thick bone and tight sutures, and they were certainly not juvenile. Moreover, there is a similar difference in head size between the largest *Tianyusaurus* described by Mo et al. (2009) and the holotype of *Yechilacerta* on the one hand, and the two specimens of *Yechilacerta* on the other. Ontogenetic variation could explain some differences in ornamentation, and some cranial features can vary substantially with age (e.g. frontal width, parietal shape; Klembara et al., 2017), but not between large individuals at, or close to, maturity. Moreover, other features of *Tianyusaurus* (e.g. the greater expansion of the paroccipital process and the presence of a supraoccipital crest) are the reverse of what would be expected in less mature individuals. Added to that, the presence of caniniform maxillary teeth in the (smaller) *Tianyusaurus* but not *Yechilacerta* renders both ontogenetic variation and sexual dimorphism unlikely. To our knowledge there is no instance of

caniniform teeth being present in an immature lizard but lost in the adult (rather the reverse; e.g. Christensen & Melstrom, 2021), and although caniniform teeth may be larger in some male lizards compared to females (e.g. J. S. Cooper et al., 1970), they are not completely absent in the females. We therefore feel justified in giving *Yechilacerta* and *Tianyusaurus* separate generic status.

The phylogenetic position of Polyglyphanodontia

The phylogenetic position of Polyglyphanodontia within squamates has remained problematic as many of these lizards show a combination of apparently ancestral features (e.g. pterygoid-vomerine contact or near contact, dorsal process on the squamosal, open upper temporal fenestra) with more derived features (e.g. a specialized dentition). The morphology-based analysis of Gauthier et al. (2012) placed polyglyphanodontians on the stem of ‘Scleroglossa’ (all squamates other than Iguania), but the monophyly of Scleroglossa is not supported in analyses using molecular or combined evidence data (e.g. Burbrink et al., 2020; Pyron et al., 2013; Streicher & Wiens, 2017; Vidal & Hedges, 2004, 2005; Zheng & Wiens, 2016). Many previous authors considered polyglyphanodontians to be closely related to Teiioidea (e.g. Alifanov, 1988, 1993a, 1993b, 1993c, 2000; Estes, 1969, 1983). A phylogenetic analysis by Nydam et al. (2007) found the Cretaceous ‘teiid’ taxa to form a monophyletic sister group to Teiioidea and erected the name Boreoteiioidea to encompass the North American and Asian fossil taxa, the name reflecting their apparently boreal (northern continent) distribution, and similar arrangements were recovered by Conrad (2008), Wiens et al. (2012), and Simões et al. (2016, 2018). However, Gilmore (1942) and Romer (1956) had a very different view of polyglyphanodontian relationships, placing them with iguanians. This pre-cladistic suggestion received support in the phylogenetic analysis of Lee (2009) and, more recently, the combined evidence analyses of Reeder et al. (2015) and Pyron (2017). Reeder et al. (2015), using likelihood, parsimony and Bayesian analyses, found strong support for an iguanian-polyglyphanodontian relationship. Pyron (2017) compared the results of combining a molecular data set with the morphological data set of either Conrad (2008) or Gauthier et al. (2012). In the first case (Conrad matrix), polyglyphanodontians were recovered as the sister group of teioids (as did Simões et al. [2016] using a modified version of the same matrix); in the second (Gauthier et al. matrix) they were placed with Iguania. This matrix-based ambiguity (teioid vs iguanian relationships) mirrors the results of our analyses, with all the analyses using the Gauthier et al. (2012) matrix, combined with that of Reeder et al. (2015), placing

polyglyphanodontians with, or close to, Iguania. The supplementary analyses (see [Supplemental material](#)) using an amended matrix of Simões *et al.* (2018) were less clear cut, with unconstrained analyses (using equal or implied weighting) placing polyglyphanodontians + the extant teiid *Teius* with iguanians, and analyses with enforced constraints placing polyglyphanodontians as the sister group either of Laterata as a whole (lacertids, amphisbaenians and teioids) or of teioids within Laterata.

A comprehensive review of polyglyphanodontian relationships is beyond the remit of this paper and requires more data (computer tomography (CT) scans and additional, more complete specimens), especially of early/less specialized members of the clade. Here, we do not advocate one hypothesis of relationship (iguanian) over another (teioid) but highlight this uncertainty as a basis for future work. Many of the characters that polyglyphanodontians share with iguanians (dorsal process on squamosal, large splenial, deep suborbital ramus of jugal) could be convergent (possibly functional) and/or result from the retention (or development) of apparently ancestral features. Moreover, some of these characters can also be found in teiids (open upper temporal fenestra, dorsal process of squamosal, expanded facial process of maxilla, large splenial, complex teeth), complicating analyses based on morphology. The Late Cretaceous Brazilian lizard *Pristiguana* (specimen apparently now lost) provides an interesting illustration of this problem. Although usually referred to Iguania (e.g. Estes, 1983), the original authors (Estes & Price, 1973) described *Pristiguana* as showing similarities to teiids as well as iguanids, noting points of resemblance with North American chamopsiids and with *Polyglyphanodon*. They even discussed whether Teiidae and Iguania might be related, with *Pristiguana* retaining features of a common ancestor. Although this hypothesis of relationship is no longer tenable, it does demonstrate that difficulties in determining whether fossil taxa are related to iguanians or to teiids are not new.

The lower temporal bar in *Yechilacerta*

For many years, it was widely accepted that the presence of a complete lower temporal bar, as found in the rhynchocephalian *Sphenodon*, was the ancestral lepidosaurian condition and that loss of that bar in the ancestors of squamates released the quadrate for squamate streptostyly (combined with reduction of quadrate-squamosal and quadrate-ptyergoid contacts). However, description of stem-lepidosaurs like *Marmoretta* (Evans, 1991; Griffiths *et al.*, 2021), *Sophineta* (Evans & Borsuk-Białynicka, 2009), *Paliguana* (Ford *et al.*, 2021), *Vellbergia* (Sobral *et al.*, 2020) and *Fraxinisaura*

(Schoch & Sues, 2018), and of early rhynchocephalians like *Gephyrosaurus* (Evans, 1980) and *Diphydontosaurus* (Whiteside, 1986), has shown that the last common ancestor of rhynchocephalians and squamates lacked a lower temporal bar (e.g. Curtis *et al.*, 2011; Evans, 2003; Evans & Jones, 2010; Jones, 2008; Moazen *et al.*, 2009). Moreover, revisions of several Permo–Triassic taxa over the last few decades suggest that the last common ancestor of Archosauromorpha and Lepidosauromorpha also lacked a lower temporal bar (Curtis *et al.*, 2011; Dilkes, 1998; Moazen *et al.*, 2009; Müller, 2003). Under that hypothesis, a complete lower bar arose independently in several lineages (rhynchosaur, archosauriforms, rhynchocephalians). Development of the bar in *Sphenodon* has been related to the need to brace the quadrate against feeding (compressive) stresses acting on the quadrate at the jaw joint (e.g. Curtis *et al.*, 2011; Jones & Lappin, 2009; Mo *et al.*, 2009; Moazen *et al.*, 2009), and a similar explanation probably applies to many other taxa.

Until recently, however, a complete lower temporal bar was unknown in any squamate, suggesting there might be a constraint against its development in this group. In many squamates, an extra posterior component of the MAMES, arising from the quadrate, extends onto the posteroventrolateral surface of the mandible and increases bite force (Rieppel & Gronowski, 1981; Schaerlacken *et al.*, 2008). The size and action of this muscle could potentially be limited by the presence of a complete lower temporal bar (Rieppel & Gronowski, 1981; Schaerlacken *et al.*, 2008), acting as a constraint on its development. The discovery, therefore, of several late Cretaceous polyglyphanodontian lizards with a complete jugo-quadrate bar (no quadratojugal) (Lü *et al.*, 2008; Mo *et al.*, 2009; Simões *et al.*, 2016; this paper) was unexpected.

In its possession of large body size, a deep skull, short retroarticular process, ventrally displaced jaw joint, and multicuspid spatulate teeth, *Yechilacerta* shows features considered indicative of ‘true herbivory’ (*sensu* W. E. Cooper & Vitt, 2002; Metzger & Herrel, 2005). In truly herbivorous lizards, such as many extant iguanas, the lacertid *Gallotia*, and the scincid *Corucia*, the diet is predominantly (~80%) made up of fibrous plant material (W. E. Cooper & Vitt, 2002; Metzger & Herrel, 2005). In these taxa, the short retroarticular process has been associated with slow jaw opening (small M. depressor mandibulae: Metzger & Herrel, 2005) whereas the ventrally displaced jaw joint reportedly improves lever action (e.g. Greaves, 1974; Jones, 2008; Reilly *et al.*, 2001) and makes it easier for the upper and lower teeth to meet simultaneously along the tooth row (Greaves, 1974; Jones, 2008). *Tianyusaurus* also shows adaptations to herbivory (Mo *et al.*, 2009), as does

Polyglyphanodon (Nydham, 1999). Herbivory, and the requirement to bite through tough plant material, might provide a partial functional explanation as to why a complete lower temporal bar arose within Polyglyphanodontia, except that many other Asian polyglyphanodontians were also herbivorous (based on dentition and skull shape) and lack the bar. Its development in *Tianyusaurus* and *Yechilacerta*, in association with firm pterygo-quadrate and quadrate-squamosal articulations, suggests that their diet and/or feeding mechanics differed in some way from those of other gilmoreteiids.

In *Polyglyphanodon*, although the elongated posterior process of the jugal extends to the quadrate, it seems to have had a ligamentous rather than sutural connection (Simões et al., 2016). Using *Iguana* as a model, Simões et al. (2016) performed a computer simulation to assess the effect of adding a lower temporal bar on the distribution of cranial strain. A similar computational analysis was run by Moazen et al. (2009) for *Tianyusaurus* (using *Uromastyx*), but Simões et al. also modelled a soft tissue connection between the jugal and quadrate to replicate the condition in *Polyglyphanodon*. Although they agreed that the sutured jugo-quadrate bar in *Tianyusaurus* (and therefore by implication also *Yechilacerta*) likely had a role in stabilizing the quadrate (Moazen et al., 2009), they concluded that the bar provided no obvious functional advantage in *Polyglyphanodon*. Instead, they proposed that the repeated development of a lower temporal bar in polyglyphanodontians might have been facilitated by a genetic mutation that removed a developmental constraint in polyglyphanodontian ancestry.

The presence of a distinct surangular crest in large gilmoreteiids like *Gilmoreteius* and *Tuberocephalosaurus* is evidence that the MAMES had expanded down the lateral surface of the mandible in these taxa, contributing to increased bite force. If the lower temporal bar limits this expansion (Rieppel & Gronowski, 1981), then it raises the question as to whether, or how, *Polyglyphanodon*, *Tianyusaurus* and *Yechilacerta* compensated for the proposed reduction in power. For *Polyglyphanodon*, Simões et al. (2016) suggested that an enlarged M. pterygoideus, in combination with large body size, provided sufficient total muscle mass to deal with fibrous plant material despite a proportionally smaller MAMES. In *Tianyusaurus* and *Yechilacerta*, however, the mandible bears a dorsolateral shelf or trough that partially floors an adductor chamber lying medial to the jugo-quadrate bar (Mo et al., 2009; this paper, Fig. 3A). It seems likely that the MAMES inserted into this dorsal shelf. Moreover, *Yechilacerta* shows further expansion of the ventrolateral part of the adductor chamber, with bowing of the jugo-quadrate bar. Medially, the mandibular adductor fossa is also deep (suggestive of a strong M. adductor mandibulae

posterior, as in lacertiids and teiids; Rieppel, 1980) and there is a deep ventromedial fossa on the prearticular indicative of a large M. pterygoideus (Jones et al., 2009; Throckmorton, 1978). However, unlike other gilmoreteiids (including *Tianyusaurus*), the superficial fibres of the M. pterygoideus apparently did not wind onto the ventrolateral or posterolateral part of the jaw, as evidenced by the dermal sculpture on this surface (which is indicative of direct contact with overlying skin). The M. pterygoideus may therefore have been less powerful. Mo et al. (2009) suggested that *Tianyusaurus* might have been adapted to biting hard with an open mouth (e.g. on tough buds, cones, or fruits), facilitated by its posterovertrally displaced jaw joint and apparently powerful M. pterygoideus. Given the differences in M. pterygoideus configuration and the deeper, more robust skull, *Yechilacerta* probably employed a different feeding strategy to *Tianyusaurus*. Whatever that strategy was, however, it must also have placed considerable strain on the jaw joint. This combination of a mechanically robust skull and relatively small teeth is paradoxical, but without an obvious modern analogue and/or greater knowledge of the contemporaneous local vegetation, and its material properties, it is difficult to speculate further.

Conclusions

Two new fossil lizard specimens from the Upper Cretaceous of southern China represent a new genus and species of polyglyphanodontian lizard, *Yechilacerta yingliangia*. Phylogenetic analysis places this new taxon with Asian gilmoreteiids like *Gilmoreteius*, *Tuberocephalosaurus*, *Aprisaurus* and *Tianyusaurus*. *Yechilacerta* and *Tianyusaurus* emerge as sister taxa but show sufficient morphological differences to support their separate generic status. Like other gilmoreteiids, they are interpreted as specialist herbivores, but their unusual skull morphology (firmly sutured quadrate, strong lower temporal bar, mandibular shelf for insertion of superficial external adductor) suggests there may have been differences in their diet or feeding strategy from those of other gilmoreteiids. The position of Polyglyphanodontia within Squamata remains controversial, although our analysis using the Gauthier et al. (2012) matrix supports iguanian rather than teioid affinities.

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The authors report that there are no competing interests to declare.

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