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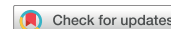
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A new anguimorph lizard from the Upper Cretaceous of Henan Province, China

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A new genus and species of anguimorph lizard, *Zhongyuanxi jiai* gen. et sp. nov., is described from the Upper Cretaceous (?Maastrichtian) Qiupa Formation of Henan Province, China. Its holotype specimen is represented by a three-dimensionally preserved partial skull and is described based on micro-CT scans of the overall skull and individual bones. Phylogenetic analyses using Bayesian inference place it as the sister taxon to the Mongolian *Aiolosaurus oriens* on the stem of Varanidae, whether or not a molecular constraint is applied. One of the more unusual features of *Zhongyuanxi jiai* is the presence of vomerine teeth, which have been recorded in a single living lizard (*Pseudopus*) and a small number of fossil anguimorphs, suggesting a more widespread distribution of this character among squamates, especially within Anguimorpha.

<http://zoobank.org/urn:lsid:zoobank.org:pub:830A9292-B0B9-4852-BAB5-AC1BCC46379C>

Keywords: Anguimorpha; Squamata; new taxon; Qiupa Formation; Asia; vomerine teeth

Introduction

The lizard clade Anguimorpha includes some of the most well-known lizards, such as the Komodo dragon (*Varanus komodoensis*), the Beaded lizard (*Heloderma horridum*) and the common slow worm (*Anguis fragilis*). They have also attracted a lot of scientific and public interest due to their proposed close relationship with snakes, as suggested by Camp (1923), and have a long evolutionary history with a rich fossil record (Estes, 1983). The earliest unambiguous anguimorph, or stem-anguimorph, is *Dorsetisaurus* from the Upper Jurassic of Europe and North America (Broschinski, 2000; Evans, 1994; Prothero & Estes, 1980); this clade appears to have been highly diversified during the Late Cretaceous in East Asia. At least 10 species, representing different anguimorph groups, are documented by well-preserved, three-dimensional fossils from the Gobi Desert of Mongolia and Chinese Inner Mongolia (Borsuk-Białynicka, 1984, 1985; Gao & Norell, 2000; Norell et al., 2007). Further Asian taxa have been reported from South China (Mo et al., 2012), South Korea (Park et al., 2015), Japan (Ikeda et al., 2021) and possibly Myanmar (Daza et al., 2018).

Here we report on a new anguimorph lizard based on a partially preserved skull from the Upper Cretaceous Qiupa locality, Henan Province, in the central region of China. It is the third lizard taxon reported from the locality, in addition to two polyglyphanodonts (*Tianyusaurus* and *Funiusaurus*, Lü, Ji, et al., 2008; Xu et al., 2014), thereby enriching the local squamate diversity at that time, as well as Late Cretaceous anguimorph diversity.

Institutional abbreviations

HNHM (HGM), Henan Natural History Museum/Henan Geological Museum, Zhengzhou, China; **IGM**, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; **STNM**, Shandong Tianyu Natural Museum, Linyi, China.

Geological setting

The fossil site (Fig. 1) is near Haoping village, within the Tantou Basin, Luanchuan County, Henan Province, China. The lizard specimen was recovered from the

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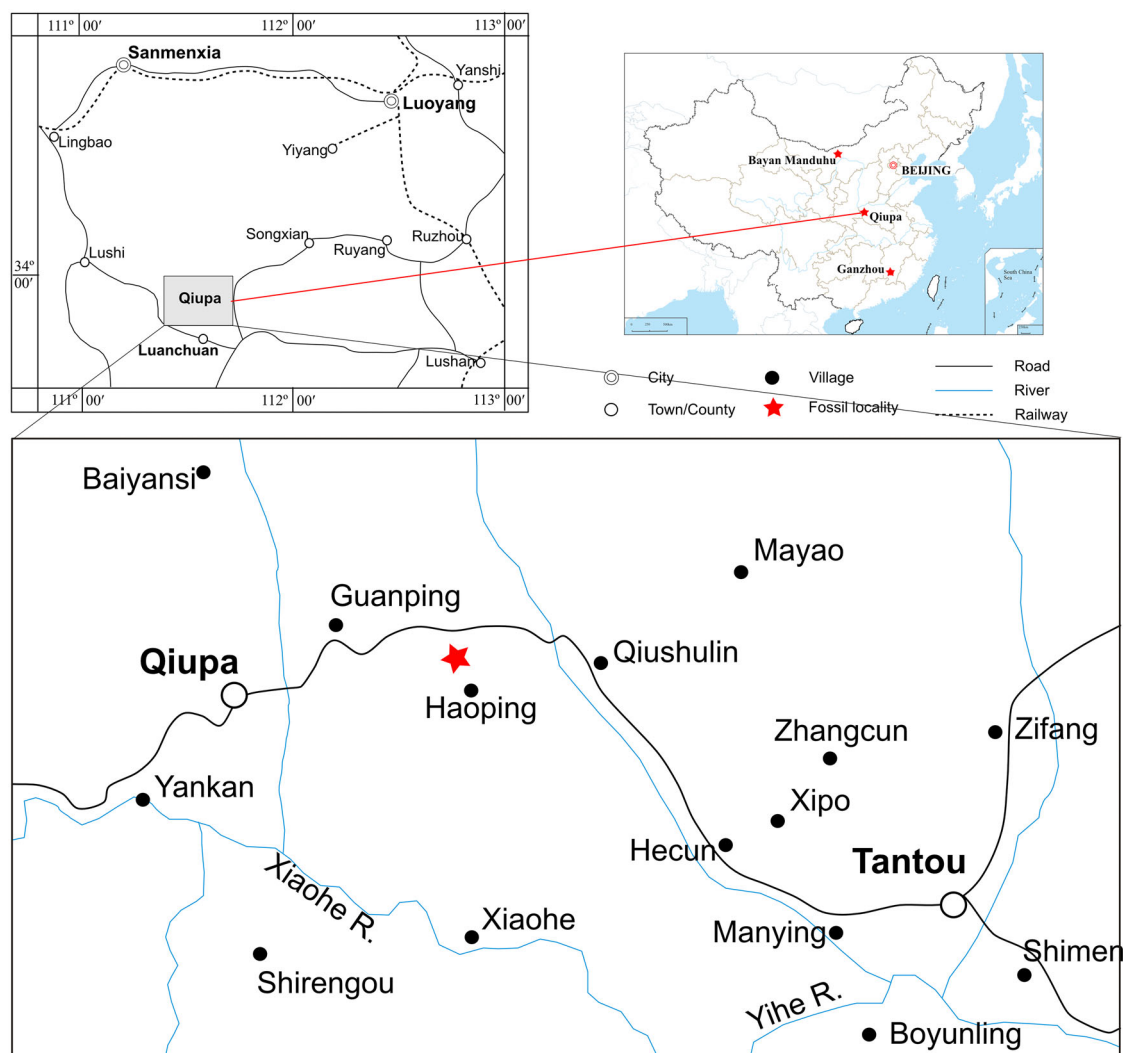


Figure 1. The geographical position of the fossil locality. The upper right map shows where the three main Late Cretaceous lizard fossil localities of China are, and the upper left map shows the position of the working area (the grey square) where Qiupa locality is.

Upper Cretaceous Qiupa Formation which is exposed along the northern margin of the basin. Various vertebrates, including several dinosaurs, mammals, birds and lizards, have been reported from the formation and are known collectively as the ‘Luanchuan Fauna’ (Lü et al., 2008; Wei et al., 2021). Two lizard specimens, the holotype (STNM-05-f702) of *Tianysaurus zhengi* (Lü et al., 2008) and that (HGM 41HIII-114) of *Funiusaurus luanchuanensis* (Xu et al., 2014) were described from the same horizon in a nearby region.

There is no absolute dating of the Qiupa Formation due to the lack of datable minerals. Wei et al. (2021) suggested the formation to be of late Campanian age, based on the similarity of the faunal assemblage to that of the Nemegt Formation of Mongolia (late Campanian

to early Maastrichtian). However, an earlier stratigraphical study in the Tantou Basin (Jiang et al., 2011) suggested that the K–T boundary lies between the top of the Qiupa Formation and the base of the Gaoyugou Formation. If their conclusion was correct, then the lizard described herein should be from, at the earliest, Maastrichtian age deposits, as the fossil-bearing horizon at the Haoping site lies in the upper part of Qiupa Formation.

At the time the Qiupa Formation was deposited, the paleoclimate was judged to have been tropical-subtropical semi-arid and semi-humid based on pollen data (Mao et al., 2013), but was more recently inferred to be humid or semi-humid based on weathering features and pollen data (Zhu et al., 2015).

Material and methods

The new specimen HNHM 41HIII0727 (Fig. 2A) was excavated in 2013 from the Haoping site and is now deposited in the Henan Natural History Museum in Zhengzhou City, Henan Province. It is a partial skull, three-dimensionally preserved in a reddish mudstone, with the dorsal and lateral parts exposed. To obtain more anatomical information, especially on the palate, the specimen was scanned at the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences (KLVEHO, CAS) in Beijing,

using the Nano-CT system (Phoenix X-ray, GE Measurement & Control) at a pixel resolution of 8.166 μm . The scan employed a beam energy of 120 kV and a flux of 120 mA, using a 360° rotation with a step size of 1°. A total of 2233 image slices were obtained after cropping the regions without data. These slices were then processed in Avizo 9.1 (ThermoFisher Scientific Inc.) to segment the fossil out of the matrix virtually. When the surface models of the skull (Figs 2B, 2C) and isolated bones (Fig. 3) were rendered, snapshots were taken to make the figures for the paper. A reconstruction of the skull (right half, Supplemental

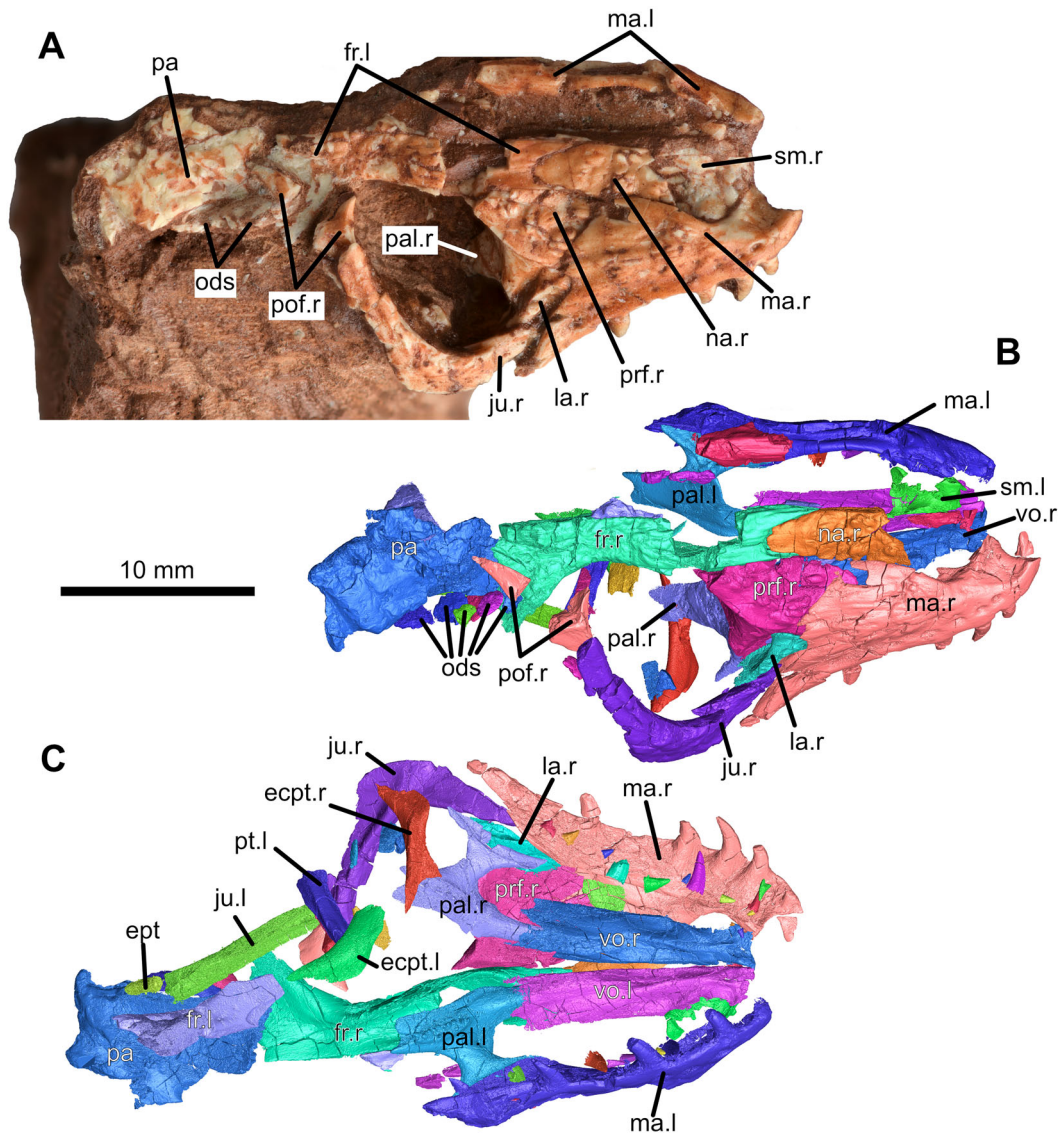


Figure 2. The holotype of *Zhongyuanxi jiai* gen. et sp. nov. HNHM 41HIII0727. **A**, Photograph in dorsolateral view; **B**, 3D reconstruction in the same view as in **A**; **C**, 3D reconstruction in ventral view. **Abbreviations:** *ecpt*, ectopterygoid; *ept*, epipterygoid; *fr*, frontal; *ju*, jugal; *la*, lacrimal; *ma*, maxilla; *na*, nasal; *ods*, osteoderms; *pa*, parietal; *pal*, palatine; *pof*, postfrontal; *prf*, prefrontal; *pt*, pterygoid; *sm*, septomaxilla; *vo*, vomer. The suffix after the abbreviation of bone elements, r and l, represent the right and left sides respectively.

material Fig. S1) was also made in Avizo 9.1 by manually articulating the bones to determine the bone connections.

To estimate the phylogenetic position of *Zhongyuanxi jiai*, we coded it into the matrix of Tałanda *et al.* (2022) (Supplemental material Datasets S1–7) which was modified from Bolet *et al.* (2021) (and originally from Gauthier *et al.*, 2012). We revised the matrix according to Meyer *et al.* (2023) and Brownstein *et al.* (2022), which followed Simões, Caldwell, *et al.* (2015) and Simões, Wilner, *et al.* (2015); we also revised the codings of *Parmeosaurus scutatus* according to Dong *et al.* (2018) and those of *Aiolosaurus oriens* (IGM 3/171, Gao & Norell, 2000) based on new reconstructions from original CT data downloaded from Morphosource (see Supplemental material Fig. S2). See Supplemental material Text S1 for the detailed changes of the matrix, Gauthier *et al.* (2012) for character descriptions, and Supplemental material Datasets S1–7 for the codings of *Zhongyuanxi jiai* and *Aiolosaurus oriens*.

The analyses using Bayesian inference were conducted in MrBayes 3.2.7a with the same prior (a fossilized birth-death tree prior), model (a relaxed clock transition model) and other parameters as in Tałanda *et al.* (2022), except that (1) we set up a wider prior of root node age and (2) we updated all the fossil calibrations according to the new studies (see Supplemental material Table S1 for detailed information). The individual analyses were run unconstrained or constrained with a molecular backbone as in Tałanda *et al.* (2022) which is set up by a constraint tree. The constraint tree was reconstructed by firstly constructing a consensus higher-level tree of Squamata (Gekkota Dibamidae ((Scincidae Cordyloidea Xantusiidae) ((Teiidae (Lacertidae Amphisbaenia)) (Anguimorpha Iguania Serpentes)))) based on the molecular phylogenetic studies (Burbrink *et al.*, 2020; Pyron *et al.*, 2013; Zheng & Wiens, 2016) and secondly selecting one or two primitive/iconic taxa within each higher-level group. However, to allow for a lack of agreement as to the positions of *Heloderma* and *Shinisaurus* (Pyron, 2017), the constrained analyses were run with alternative constraints for these taxa, namely: (a) *Varanus* (*Xenosaurus*, *Heloderma*); (b) *Varanus* (*Heloderma*, *Shinisaurus*); (c) *Varanus* (*Shinisaurus*, *Xenosaurus*); (d) (*Varanus*, *Shinisaurus*) (*Heloderma*, *Xenosaurus*) (Supplemental material Fig. S3). The constrained and unconstrained analyses ran until reaching convergence (<0.05). The full resulting trees shown in Supplemental material Figs S4–8 and Fig. 4 focus on the anguimorph lineage of the constrained analysis, version (d), to show the detailed position of *Zhongyuanxi jiai*.

Phylogenetic analyses under unconstrained and constrained (version d) settings using maximum parsimony were also conducted in the software TNT v. 1.5 (Goloboff & Catalano, 2016). All the other terminal taxa were set as floating. We employed the New Technology search option with sectorial search, ratchet, drift and fusion options activated (default settings), and set a minimum length tree to be found in 20 replicates. The strict consensus tree is shown in Supplemental material Figs S9–10).

The synapomorphies at the node Neoanguimorpha and the node of *Zhongyuanxi jiai*+*Aiolosaurus* (see Supplemental material Text S1) under the Bayesian constrained topology were obtained in Mesquite using the ‘Trace Character History’ function after reading the resulting constrained tree and the character matrix into the software.

Systematic palaeontology

Order **Squamata** Oppel, 1811

Suborder **Anguimorpha** Fürbringer, 1900

Genus ***Zhongyuanxi*** gen. nov.

Type and only species. *Zhongyuanxi jiai* sp. nov.

Derivation of name. ‘Zhongyuan’ is the name for the central region of China whose core area is Henan Province where the holotype locality is found. ‘xi’ refers to ‘蜥’ in Chinese, which means a lizard.

Diagnosis. As for the type species.

Zhongyuanxi jiai sp. nov.

(Figs 2, 3)

Derivation of name. The species name honours Mr Jia Songhai of the Henan Natural History Museum for his great contributions to the excavation and research of vertebrate fossils and the popularization of vertebrate palaeontology in Henan Province, China.

Diagnosis. This new taxon is an anguimorph characterized by the presence of elongated vomers bearing vomerine teeth, in combination with external nares that are not extended posteriorly; palaeochoanate palate; discontinuous tubercular cranial sculpture and thickened, round-to-subrectangular non-imbricating cranial osteoderms; maxillary dentition restricted to the preorbital region; a few recurved, compressed and acuminate marginal teeth with basal plicidentine, and anterior and posterior carinae; a single but large lacrimal foramen. It differs from members of Varanidae (*Varanus*, *Saniwa*,

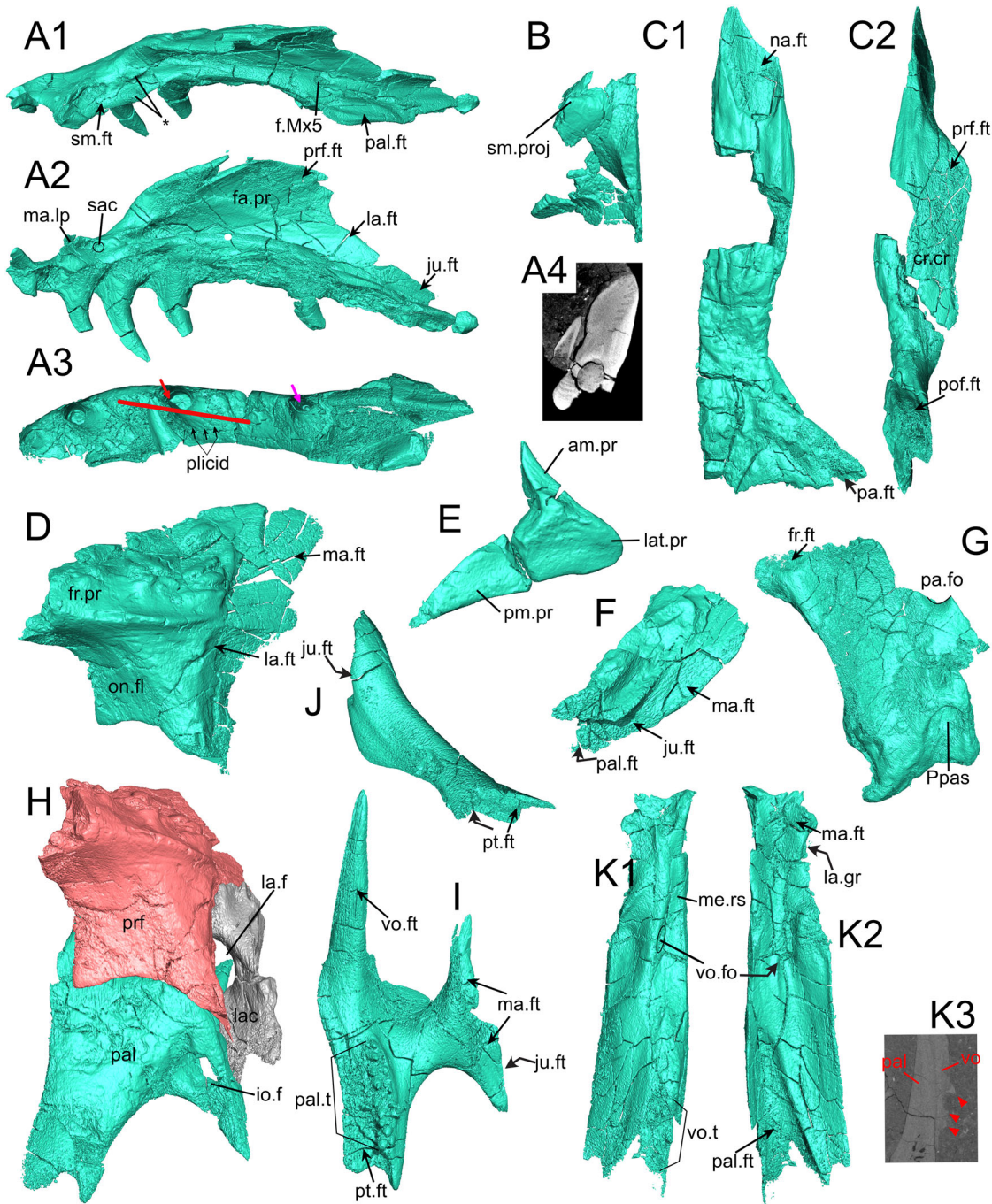


Figure 3. Virtually isolated bones of the *Zhongyuanxi jiai* holotype. **A**, maxillae: right bone in dorsal (A1) and medial (A2) views, left bone in ventral (A3) view showing anterior teeth with only anterior carinae (red arrow), but posterior teeth with both anterior and posterior carinae (purple arrow), and CT-scan section (A4) showing the plicidentine structure at the tooth base. The red line in A3 indicates the position of the section (A4); **B**, left septomaxilla in dorsal view; **C**, right frontal in dorsal (C1) and lateral (C2) views; **D**, right prefrontal in posterolateral view; **E**, right postfrontal in dorsal view; **F**, right lacrimal in lateral view; **G**, parietal in ventral view; **H**, reconstructed right antorbital region (prefrontal, lacrimal and palatine in articulation) in posterolateral view; **I**, left palatine in ventral view; **J**, right ectopterygoid in ventral view; **K**, right vomer in ventral (K1) and dorsal (K2) views, K3 showing a slice with vomerine teeth (red arrows). Black arrows point to facets on bones, and black lines point to structural details on the bone. **Abbreviations:** am.pr, anteromedial process; cr.cr, crista cranii; fa.pr, facial process; f.Mx5, foramen for maxillary division of CN5; fr.ft, frontal facet; io.f, infraorbital foramen; ju.ft, jugal facet; lac, lacrimal; la.f, lacrimal foramen; la.ft, lacrimal facet; la.gr, lacrimal groove; lat.pr, lateral process; ma.ft, maxilla facet; ma.lp, maxillary lappet; me.rs, median recess for palatal sinus of vomer; na.ft, nasal facet; on.fl, orbitonasal flange; pa.fo, parietal foramen; pa.ft, parietal facet; pal, palatine; pal.ft, palatine facet; pal.t, palatine, teeth; plicid, plicidentine; pm.pr, posteromedial process; pof.ft, postfrontal facet; Ppas, pit for processus ascendens; prf, prefrontal; prf.ft, prefrontal facet; pt.ft, pterygoid facet; pt.t, pterygoid teeth; sac, opening of superior alveolar canal; sm.ft, septomaxilla facet; sm.proj, septomaxilla projection; vo, vomer; vo.fo, vomerine foramen; vo.ft, vomer facet; vo.t, vomerine teeth.

Archaeovaranus, *Lanthanotus*) and its relatives (*Telmasaurus*, *Cherminotus*, *Aiolosaurus*) in having external nares that are not posteriorly extended, palaeochoanate palate, a single lacrimal foramen, thickened round-to-subrectangular cranial osteoderms; from *Heloderma* and its relatives (*Paraderma*, *Primaderma*) in having vomerine teeth, retaining a parietal foramen, and lacking venom grooves on the teeth.

Holotype. HNHM 41HIII0727, a partial skull preserved in reddish mudstone, but the posterior parts of the skull (braincase, temporal bones) are mostly missing (Fig. 2).

Type locality and horizon. Haoping site, Qiupa Village, Henan Province, China (Fig. 1); Qiupa Formation, Upper Cretaceous (?Maastrichtian).

Description

The skull is estimated to be about 30 mm in length from the tip of the maxilla to the posterior end of the parietal table. The skull roof (maxilla, nasal, prefrontal, frontal and parietal), as well as the jugal and lacrimal, is sculptured. The sculpture is irregular with a patchy distribution of tubercles that are scattered rather than continuous. Isolated osteoderms are preserved towards the back of the skull. The moderate development of sculpture and the presence of isolated osteoderms suggest that the individual was probably a subadult and not fully grown.

Maxilla. The right maxilla (~14.7 mm long) is nearly complete (Figs 2, 3A). The premaxillary process is moderately long and notched anteriorly, with the long lateral ramus curved medially to create a rounded muzzle. The medial ramus is relatively short, even allowing for possible breakage, and probably did not meet the contralateral maxilla behind the premaxilla. There is a pronounced emargination or notch between the medial and lateral rami, suggesting that there may have been a premaxillary-maxillary fenestra. A subtriangular depression posterior to the notch is bordered medially by a thin but deep ridge (ma.lp, Fig. 3A2), which is similar to the maxillary lappet in *Elgaria* and *Gerrhonotus* (Ledesma et al., 2021). Medial to the ridge, the palatal shelf is well developed to support the septomaxilla and flares ventrally (sm.ft, Fig. 3A1). Just anterior to the narial margin of the facial process, and at the junction between the ridge and the palatal shelf, there is the anterior opening of superior alveolar canal (sac, Fig. 3A2). Posterior to this foramen and medial to the narial margin of the facial process there are two processes which constrain the articulation between the maxilla and the septomaxilla (*, Fig. 3A1), and a similar structure is also present in *Heloderma* (TNHC 62767, Morphosource). The maxilla met the

vomer at the anterior tip of the palatal shelf, but it did not meet the vomer posteriorly to separate the vomeronasal opening from the choana (i.e. palaeochoanate palate). At the level of the third tooth position from the end of the tooth row and the posterior margin of the facial process, the maxillary palatal shelf expands to meet the palatine. The entry foramen for the maxillary ramus of the trigeminal nerve (f.Mx5, Fig. 3A1) is single and large. In lateral view (Fig. 2B), the facial process is large and generally triangular with a moderately inclined anterior margin and a slightly steeper posterior margin. The dorsal margin folds slightly medially and makes a small contribution to the skull roof, suggesting the skull, or at least the snout, was not shallow (Supplemental material Fig. S1). Laterally the facial process overlaps the prefrontal extensively and also the lacrimal to a much smaller extent. The posterior margin of the facial process bears a small spur at the junction between prefrontal and lacrimal facets. Seven nutrient foramina pierce the lateral surface of the maxilla in a line parallel to the alveolar margin (Supplemental material Fig. S1). Of these, the first three are closely positioned, whereas the sixth and seventh foramina are well-separated from the fourth and fifth ones. The posterior jugal process is relatively long and articulates dorsally and medially with the jugal. Posteriorly the maxilla extends beyond the anterior margin of the orbit for a short distance and the last tooth position lies at the anterior orbital margin (Supplemental material Fig. S1).

There are 9–10 maxillary tooth positions with the largest located anteriorly (probably the fourth tooth below the anterior margin of the facial process) (Fig. 3A, Supplemental material Fig. S1). The teeth are long, recurved, pointed, highly pleurodont, and widely spaced. They are also laterally compressed with an increasing degree of compression posteriorward along the tooth row (Fig. 3A3). The first five teeth bear only anterior carinae and a smooth, more or less rounded, posterior margin, whereas the posterior teeth have both anterior and posterior carinae (clearer on the left maxilla, Fig. 3A3). Several replacement teeth are preserved and display a similar morphology to their corresponding functional teeth (Fig. 2C). The carinae are not set off from the tooth shaft so as to form a flange. Whether there is serration along the carinae is hard to ascertain due to the preservation, but no venom groove is present. Plicidentine is present at the expanded tooth base but extends upward only for less than one-third of the tooth height (Figs 3A2–4). There are at least two generations of replacement teeth preserved for individual tooth positions (e.g. at the base of the second functional tooth on the right maxilla, Fig. 2C) but no resorption pits,

demonstrating that the replacement mode was of varanid type (i.e. new tooth distolingual to old).

Septomaxilla. The septomaxillae are preserved on both sides (Figs 2B, 3B). However, due to the thin bone, and therefore poor resolution of the CT scanning, it is impossible to reconstruct the detailed morphology of the septomaxillae. The posteriorly concave dorsal surface has an anterolateral projection (sm.proj, Fig. 3B) (Ledesma et al., 2021), and there is a midline ridge that should have accommodated the canal for the medial ethmoidal branch of the ophthalmic and ethmoidal nerves. However, due to low scan resolution in this region it is not possible to determine whether the canal was open or closed.

Nasal. The nasals were paired and met in the midline with a long suture. The preserved right nasal (preserved length ~5.9 mm) is broken anteriorly, making it difficult to estimate its original length (Fig. 2B). However, the preserved part suggests the nasal may have been long. The nasal was roughly constant in width for most of its preserved length in dorsal view and therefore the lateral and medial margins of the nasal are parallel to one another. Although the nasal is broken anteriorly, it is clear that the nasal, together with the maxilla, formed the posterior margin of the external naris, excluding the prefrontal. Thus the external narial openings were not extended posteriorly as they are in *Varanus* and *Heloderma*. Laterally the nasal met the maxilla in a non-overlapping suture. The nasal also has an extensive lateral suture with the prefrontal, excluding the frontal from contact with the maxilla. Posteriorly, the nasal overlaps the frontal, narrowing into a rounded end. The ventral surface of the nasal is concave longitudinally as the medial and lateral margins are thickened.

Frontal. The frontals (14.5 mm long) are long and paired (Figs 2B, 3C). The right bone is nearly complete and preserved in situ whereas the left frontal was broken into several pieces. The posterior half of the left frontal lies below the parietal as two closely positioned fragments, and there are two smaller fragments in situ articulating with the mid-section of the right frontal. Anteriorly, the right frontal bears a medial process between which is the facet for the nasal (na.ft, Fig. 3C1), and a rudimentary lateral process. The frontal is of roughly constant width in the anterior three quarters of its length. It then widens posteriorly where it articulates with the postfrontal, reaching its maximum width at the frontoparietal suture, as roughly twice the interorbital width. The well-developed crista cranii (subolfactory processes) (cr.cr, Fig. 3C2) show very little medial curvature, leaving a broad gap between them in ventral view. Laterally, the facet for the prefrontal is large, invading the dorsal surface slightly

and extending along the anterior two thirds of the frontal. In contrast, the postfrontal facet is small only on the expanded part of the frontal (i.e. the posterior quarter). The prefrontal and postfrontal do not meet each other in the orbital margin, but entry of the frontal into that margin is restricted. The medial, sutural, margin of the frontal is thickened. The frontoparietal suture is transverse with little evidence of interdigitation, except for a small faceted tab (pa.ft, Fig. 3C2) that supported the parietal at its lateral edge.

Parietal. The parietal (Figs 2B, 3G) was unpaired, and the preserved portion of the parietal table suggests it was large and sculptured. There is a small but distinct lateral ridge above the shallow descending flange, indicating that the adductor muscles probably originated lateral and ventral to the parietal, instead of on the dorsal surface. On the anterior part of the descending flange, there is a distinct facet for the postfrontal, but this may be incomplete. In ventral view, the pit for the ascending process of the supraoccipital (Ppas, Fig. 3G) is deep and opens posteriorly. Anterior to the pit, the posterior margin of the parietal foramen is preserved (pa.fo, Fig. 3G), indicating that the foramen was placed in the anterior part of the bone. A distinct nuchal surface appears to be absent and there is no trace of the supratemporal (post-parietal) processes if originally present.

Prefrontal. The prefrontal (Figs 2B, 3D) is large and triangular in dorsal view. It meets the nasal and frontal medially and is extensively overlapped by the maxilla laterally. The frontal process is not complete but, based on the corresponding facet on the frontal, was originally long and extended posteriorly along two-thirds of the orbital border of the frontal, as described above. The orbital margin of the prefrontal bears a weak ridge which approaches the suture with the maxilla and therefore roofed the orbit to a small extent. The orbitonasal flange is well developed and wide (on.fl, Fig. 3D). Its vertical medial margin forms most of the lateral border of the olfactory canal. The lateral margin is smooth and vertical, and with the lacrimal encloses the lacrimal foramen. Ventrally the orbitonasal flange meets the palatine along an extensive curved suture (Fig. 3H), and its long ventrolateral process meets the lacrimal, but not the jugal. Anteriorly the prefrontal has a large lamina that is overlapped extensively by the facial process of the maxilla (ma.ft, Fig. 3D). In ventromedial view the dorsomedial margin of the lamina bears a longitudinal groove at its junction with the orbitonasal flange.

Lacrimal. The lacrimal (Figs 2B, 3F) is elongate and obliquely positioned in lateral view, fitting into the notch along the posterior margin of the maxillary facial process and separating the prefrontal from the jugal.

The lacrimal was overlapped by the maxilla anteriorly and ventrally and articulated with the prefrontal at its dorsal extremity and with the palatine at its ventral extremity via large facets (la.ft in Fig. 3D; pal.ft in Fig. 3F). The single large lacrimal foramen was enclosed between the lacrimal and prefrontal (la.f, Fig. 3H). There is a grooved facet on the ventral surface of the lacrimal (lacrimal notch in Ledesma *et al.*, 2021) (ju.ft, Fig. 3F) which, when articulated, rests on the jugal and partially on the dorsal margin of the maxillary posterior process.

Jugal. The jugal (Fig. 2, Supplemental material Fig. S1) is slender and there is an angle of about 120° between the suborbital ramus and the much longer postorbital ramus. The anterior tip of the suborbital ramus articulates with the lacrimal dorsally and with the maxilla ventrally. The facet for the maxilla is an inverted 'V'-shape in cross-section, and the jugal lies on the vertical lamina of the posterior tip of the maxilla for two fifths of the length of the suborbital ramus (see ju.ft, Fig. 3A2). Medially the jugal meets the lacrimal (ju.ft, Fig. 3F) and the posterolateral end of the maxillary process of the palatine. The suborbital process widens posteriorly up to the junction with the postorbital process. A posterior jugal spur (or posterior process) is absent. Medially the bone would have articulated with the ectopterygoid, but a facet is not obvious. The bone is thickened dorsally and becomes laminar ventrally in the suborbital ramus, whereas the postorbital ramus is thickened anteriorly and laminar posteriorly. Foramina are present on the lateral surface of the bone (Supplemental material Fig. S1). Although the dorsal tip of postorbital ramus is broken, the preserved end lies close to the postfrontal bone. There was clearly a postorbital bar, but we cannot determine whether there was a bony (sutural) or ligamentous contact between the jugal and the dorsal orbital elements.

Postfrontal. The triradiate postfrontal (Fig. 3E) is broken into two parts. The anteromedial process met the frontal but is probably incomplete as it is shorter than its facet on the frontal. The posteromedial process met the parietal, and the medial two rami embraced the frontoparietal suture (Supplemental material Fig. S1). The short lateral process is rounded at its tip. The anterodorsal surface of the anteromedial process bears a depression, which might be the articulation with the jugal. There is no obvious postorbital facet and no potential postorbital or squamosal is preserved. The presence or absence of a complete upper temporal bar is therefore uncertain.

Vomer. The vomers (9.9 mm long) are elongate and relatively narrow (Figs 2C, 3K). They meet along the

midline for most of their length but diverge slightly at their posterior tips. Anteriorly each vomer narrows slightly to create a vomeronasal fenestra, and along the posterior margin of the fenestra the bone bears a lacrimal groove (la.gr, Fig. 3K2). The ventral surface of the bone bears a low lateral crest along its anterior half and, together with the crest on the contralateral bone, encloses a ventral recess for the palatal sinus (me.rs, Fig. 3K1; median palatal sinus in Klembara *et al.*, 2017). Anterior to the crest, there is a round depression. Vomerine teeth are present along the posterior one fifth of the medial margin. The teeth are small and pointed (vo.t, Fig. 3K1; arrowheads, Fig. 3K3) and are arranged roughly in two rows. The presence of vomerine teeth is rare among crown-group squamates, other known examples being the living *Pseudopus apodus* (Klembara *et al.*, 2017), and the extinct *Eosaniwa koehni* (Rieppel *et al.*, 2007), *Melanosaurus maximus* (Gilmore, 1928), and *Paranecrosaurus feisti* (Smith & Habersetzer, 2021). In dorsal view, the lateral and medial margins of the vomer curve dorsally to form a wide and shallow gutter (supravomerine canal) along the length of the bone. In the centre, as seen on the left bone, there is a single vomerine foramen (vo.fo, Fig. 3K). In the posterior one third of this dorsal surface and on the medial half, there is a deep dorsal facet for the palatine (pal.ft, Fig. 3K2). The posterior end of the vomer is double notched with a lateral notch like that in *Pseudopus*. The whole vomer-palatine articulation is of an overlapping type and allowed the dorsoventral movement of the palatine relative to the vomer.

Palatine. The palatine (9.3 mm long when isolated) sutures firmly with the prefrontal dorsally and the maxilla laterally (Fig. 3H, I). The bone is triradiate with only a short deep choanal fossa between the anterior and lateral processes. The anterior process forms half the length of the palatine and its tapered end slots into the dorsal gutter (supravomerine canal) of the vomer. The lateral maxillary process is greatly expanded, with the anterior ramus being slightly longer than the posterior one. At the base of the process is a large infraorbital foramen/canal (io.f, Fig. 3H). Laterally the process has an extensive ventral articulation with the maxilla and a dorsal articulation with the jugal and lacrimal. The posterior end of this lateral process approaches or nearly reaches the posterior tip of the maxilla and meets the ectopterygoid posteriorly, thereby excluding the maxilla from the suborbital fenestra (Supplemental material Fig. S1). The posterior process forms a relatively broad lamina which is shorter than the anterior process and narrows slightly posteriorward. There is an elevated region stretching from the base of the anterior process to the posterolateral corner of the posterior process. Palatine

teeth are implanted on this elevated region and arranged roughly in two rows. Posteromedial to the palatine teeth there is a triangular facet for the anterior process of the pterygoid. The posterior margin is notched, but there is no hint of facet for the pterygoid on the dorsal surface of the bone, indicating that the articulation between the palatine and pterygoid was not an interlocking joint, but a simple overlapping joint as in *Heloderma*. Similarly, there is no facet along the medial margin of the palatine, indicating that the palatine fully entered the margins of the interpterygoid vacuity. In general, the palatine of *Zhongyuanxi jiai* is similar to that of *Heloderma* except that the posterior process is slightly longer and bears teeth, and the maxillary process is expanded to a greater extent with a large infraorbital foramen.

Pterygoid. Only the posterior quadrate process of the left pterygoid (Fig. 2B) is preserved, showing a general columnar shape with a medial longitudinal concavity. No other features can be seen.

Ectopterygoid. The right ectopterygoid (Figs 2C, 3J) is incomplete with its posteromedial ramus (particularly its dorsal process) broken, whereas the left bone has lost its posteromedial ramus completely. The ectopterygoid is gently curved rather than angulate. The anterolateral ramus articulated with the jugal and probably had a small contact with the maxilla and the palatine, based on the relative positions of the maxillary and ectopterygoid facets on the jugal, confirming that the maxilla was excluded from the suborbital fenestra (Supplemental material Fig. S1). The posteromedial head articulated with the pterygoid medially and dorsally.

Epipterygoid. The middle portion of an epipterygoid was preserved (Fig. 2C), but as the middle portion is featureless it is impossible to know whether it is from the left or right side. No other characters can be determined, except that the middle portion is columnar.

Osteoderm. Some osteoderms (ods, Fig. 2B) are preserved along the parietal lateral margin or below the jugal. They are rounded or sub-rectangular in shape and quite thick.

Phylogenetic position of *Zhongyuanxi jiai*

The fossil record of anguimorphs can be traced back to the Late Jurassic and Early Cretaceous (e.g. *Dorsetisaurus* from Guimarota in Portugal; Broschinski, 2000; Seiffert, 1973; the Morrison Formation of North America, Prothero & Estes, 1980; and the Purbeck Limestone Group of Britain, Hoffstetter, 1967). In a recent paper, Whiteside et al. (2022) described a new

reptile taxon (*Cryptovaranoides*) from the Upper Triassic of Britain, attributing it to Anguimorpha, but this placement is controversial (Brownstein et al. 2023; Whiteside et al. 2024).

Anguimorpha is consistently recovered as a monophyletic group in phylogenetic analyses using both morphological and molecular data (Conrad, 2008; Gauthier et al., 2012; Pyron et al., 2013; Reeder et al., 2015). However, the intergeneric relationships within the clade remain incompletely resolved. Analyses based solely on morphological data typically recover two clades: Varanoidea (or Platynota, Conrad, 2008) composed of *Heloderma*, *Varanus*, *Lanthanotus* and their close fossil relatives, and a group combining Anguidae, *Xenosaurus*, and usually *Shinisaurus* (Conrad, 2008; Estes et al., 1988; Gauthier et al., 2012). In contrast, molecular phylogenetic analyses, and combined (morphology + molecules) evidence analyses recover two different lineages, Neoanguimorpha with *Heloderma*, Anguioidea, *Xenosaurus* and their related fossil taxa, and Palaeoanguimorpha with *Varanus*, *Lanthanotus* and *Shinisaurus*, as well as related fossil taxa (Burbrink et al., 2020; Conrad, Ast, et al., 2011; Pyron et al., 2013; Wiens et al., 2012).

There are many morphological similarities supporting the grouping of *Heloderma*, *Varanus* and *Lanthanotus*, including the posteriorly extended external narial openings, elongated vomers, a maxilla that is short in relation to the orbit, well-developed frontal subolfactory processes extending toward the midline, low marginal tooth number with basal plicidentine, varanid mode of tooth replacement, and a potentially mobile intramandibular joint (Conrad, 2008; Estes et al., 1988; Gauthier et al., 2012). However, most of these would be considered as convergent characters within the frame of the molecular or combined evidence phylogeny of Anguimorpha. Therefore, the distribution of these characters among early anguimorph fossils could be useful in understanding how these characters evolved.

All the resulting phylogenetic trees in this study suggest that *Zhongyuanxi jiai* is a member of Anguimorpha, grouped with *Aiolosaurus oriens* and closer to *Varanus* and its relatives. The Bayesian analyses also placed *Estesia mongoliensis* on the stem of Varanidae (the clade of *Varanus* + *Lanthanotus*, within Neoanguimorpha clade) within Anguimorpha, but the placement of *Gobiderma pulchrum* varies in different analyses (Fig. 4, Supplemental material Figs S4–8). The unconstrained analysis grouped *Heloderma* with *Varanus* and *Lanthanotus* as in previous unconstrained analyses (for example, Talanda et al., 2022) (Supplemental material Fig. S8). The strict consensus tree from the constrained analyses using maximum

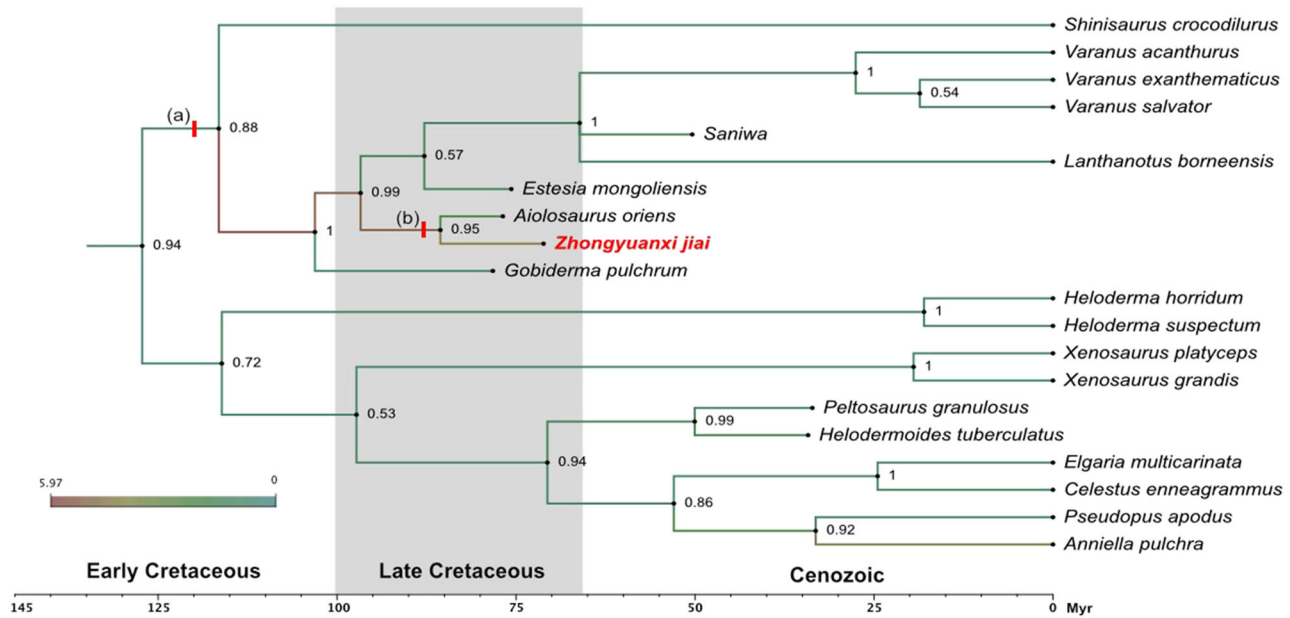


Figure 4. Anguimorph lineage showing the phylogenetic position of *Zhongyuanxi jiai*. See [Supplemental Figure S4](#) for the full tree.

parsimony does not recover a clade of Anguimorpha, but the *Zhongyuanxi-Aiolosaurus* lineage is still closer to the clade Varanidae ([Supplemental material Fig. S9](#)).

The morphology of *Zhongyuanxi jiai* resembles ‘varanoids’ like *Varanus* and *Lanthanotus*, but also *Heloderma* and its close fossil relatives in the combination of the following features: low tooth number, presence of basal plicidentine on the teeth, narrow and elongated vomers, presence of cranial sculpture and osteoderms, and an anterior ramus of the palatine that is much longer than posterior one (Estes et al., 1988). The grouping of *Zhongyuanxi jiai* and *Aiolosaurus oriens* is supported by only one unambiguous character (the presence of premaxillary-maxillary fenestra) (see [Supplemental material Text S1](#)). This support is weak, as this character is variable even within a single species (i.e. *Varanus*). This again suggests a complex evolution of morphological characters in Anguimorpha.

Comparisons with other anguimorphs

Considering the unresolved intrarelationships of Anguimorpha, we compare *Zhongyuanxi jiai* with ‘varanoid’ anguimorphs below.

Zhongyuanxi jiai differs from members of the Varanidae, including *Varanus* spp., *Saniwa* (North America, Early Eocene, Rieppel & Grande, 2007), and *Archaeovaranus* (China, Early Eocene, Dong et al.,

2022) and those Late Cretaceous Mongolian genera consistently recovered as closer to Varanidae than to Helodermatidae and Anguidae (e.g. *Telmasaurus*, *Ovoo*, *Cherminotus*, *Aiolosaurus*, Conrad, 2008; Dong et al., 2022; Ivanov et al., 2017) in having a relatively short snout, external narial openings that are not posteriorly extended (nasal and maxilla forming the posterior margin of the narial opening), sculptured skull roof, single lacrimal foramen, and palaeochoanate palate. *Zhongyuanxi jiai* further differs from *Varanus* in having palatal teeth and lacking a closed subolfactory canal. *Zhongyuanxi jiai* further differs from *Telmasaurus grangeri* (Gilmore, 1943) in having more weakly developed subolfactory process of the frontals (vs well-developed subolfactory processes approaching the midline but not meeting each other), two rows of palatine teeth (rather than numerous but irregularly arranged palatine teeth); from *Ovoo gurvel* (Norell et al., 2007) in having relatively anteriorly positioned naris (although the nasal meets the maxilla in both), greater extent of cranial sculpture, and fewer maxillary teeth; and from *Cherminotus longifrons* (Borsuk-Białynicka, 1984) in having the prefrontal and postfrontal widely separated from each other (vs the two bones approaching to meet), and a relatively deeper facial process of the maxilla. In particular, *Zhongyuanxi jiai* differs from its sister taxon *Aiolosaurus oriens* (Gao & Norell, 2000) in having a relatively short snout, external narial openings that are not posteriorly extended, a relatively deeper facial process, a sculptured skull roof with cranial osteoderms, a

single lacrimal foramen, vomerine teeth and a palaeochoanate palate.

Zhongyuanxi jiai is also different from other approximately contemporaneous anguimorphs from the Gobi Desert. *Zhongyuanxi jiai* differs from *Estesia mongoliensis* (Norell et al., 1992; Yi & Norell, 2013) in being smaller, having tuberculate sculpture on the skull (vs smooth skull roof), retaining extensive contact between the maxilla and the nasal (vs small contact), lacking a contact between the prefrontal and jugal, and having marginal teeth lacking anterior and posterior grooves; from *Parviderma inexacta* (Borsuk-Białynicka, 1984) in having two rows of palatine teeth (vs one row), paired frontals (vs single), a rectangular nasal (vs hooked or 'J'-shaped); from *Paravaranus* (Borsuk-Białynicka, 1984) in having paired frontals and nasals (vs single nasal and single frontal with strong constriction), a transverse frontoparietal suture (vs sinuous), a triradiate postfrontal (vs 'X'-shaped); from *Proplatynotia* (Borsuk-Białynicka, 1984) in having a palaeochoanate palate (vs neochoanate), fewer marginal teeth with plicidentine (10 vs 15 maxillary teeth), in lacking a maxilla-frontal contact, and a prominent prefrontal notch on the posterior margin of the facial process; and from *Saniwides* (Borsuk-Białynicka, 1984) in having fewer large, recurved maxillary teeth (10 vs 16), a single lacrimal foramen between prefrontal and lacrimal (vs one within the lacrimal), an angulate jugal (vs slight lateral curvature), and two rows of palatal teeth (vs numerous small teeth irregularly arranged).

Although *Zhongyuanxi jiai* is much smaller, its morphology resembles that of *Gobiderma pulchra* (Borsuk-Białynicka, 1984; Conrad, Rieppel, et al., 2011) in having a similar cranial sculpture (especially compared with less mature *Gobiderma* individuals; Conrad, Rieppel, et al., 2011), external narial openings that are not posteriorly extended, paired frontals, a medially bifurcate 'V'-shaped postfrontal, and a similar number of maxillary teeth. The differences include the palatine dentition, with two rows of teeth in *Zhongyuanxi jiai* but an elongate patch of dense small teeth in *Gobiderma*; a single lacrimal foramen between prefrontal and lacrimal in *Zhongyuanxi jiai* but within the lacrimal in *Gobiderma*; and a postfrontal with a much longer parietal process than frontal process in *Zhongyuanxi jiai* but with elongate processes of similar length in *Gobiderma*. This combination of differences renders it unlikely that *Zhongyuanxi jiai* could be a juvenile of *Gobiderma*.

Among the monstersaurians (*sensu* Norell & Gao, 1997), *Zhongyuanxi jiai* is different from *Heloderma* in retaining the parietal foramen, and in lacking a closed subolfactory canal and venom grooves on the teeth. *Zhongyuanxi jiai* also differs from the South China

Chianghsia nankangensis (Mo et al., 2012) in being much smaller and having tubercular sculpture on the skull roof (vs pitted sculpture) although their teeth are similar, being recurved, labiolingually compressed with plicidentine at base, and anterior and posterior carinae. *Zhongyuanxi jiai* differs from the other Asian monstersaurian *Asprosaurus bibongriensis* (Park et al., 2015) in the shape of the jugal (suborbital ramus wider than the postorbital ramus in *Zhongyuanxi jiai*, vs the opposite in *Asprosaurus*). There are no overlapping bones between *Zhongyuanxi jiai* and the Japanese *Morohasaurus kamitakiensis* (Ikeda et al., 2021), and therefore it is impossible to compare the two.

Several taxa from Upper Cretaceous of North America have also been regarded as members of the Monstersauria, including *Palaeosaniwa canadensis* (Balsai, 2001; Gilmore, 1928; Gao & Fox, 1996), *Paraderma bogerti* (Estes, 1964; Gao & Fox, 1996; Longrich et al., 2012), *Parasaniwa wyomingensis* (Estes, 1964; Gilmore, 1928; Gao & Fox, 1996; Longrich et al., 2012), *Primaderma nessovi* (Nydam, 2000), *Labrodioctes montanensis* (Gao & Fox, 1996), and *Cemeteryus monstrosus* (Longrich et al., 2012).

Zhongyuanxi jiai differs from these North American taxa in the pattern of its cranial sculpture (pitted tuberosities scattered on the dermal bones). The North American taxa bear ornament more similar to that of *Heloderma*, with rectangular, pentagonal, or hexagonal osteoderms fused on to the maxilla. However, this difference should be treated with caution as sculpture can change during ontogeny and osteoderms usually develop later than the underlying cranial bones (e.g. see Conrad, Rieppel, et al., 2011 for *Gobiderma*). *Zhongyuanxi jiai* differs from *Paraderma* and *Primaderma* in having no projecting blade along the anterior and posterior carinae of the tooth. *Zhongyuanxi jiai* further differs from *Primaderma* in having a palaeochoanate palate (vs neochoanate), and a broader maxillary supradental shelf, from *Labrodioctes* in the absence of venom grooves and the tuberculate cranial sculpture (vs thick, polygonal osteoderms), from *Cemeteryus* in the ventrolateral attachment for adductor muscles on the parietal (vs dorsolateral attachment), from *Parasaniwa* in lacking the projecting blade along the anterior and posterior carinae of the tooth, and from *Palaeosaniwa* in presence of a parietal foramen (vs none).

The Mesozoic history of anguimorphs in eastern Asia

The Upper Cretaceous deposits of eastern Asia, especially the Gobi Desert (Gao & Norell, 2000; Mo et al., 2012; Park et al., 2015), have yielded some of the most

important three-dimensionally preserved anguimorph fossils. However, many of these specimens were described prior to the widespread availability of high-resolution micro-computerized tomography, and their restudy, as well as that of newly recovered anguimorph fossils, using both modern imaging techniques, will help to understand anguimorph evolution. Moreover, these Late Cretaceous taxa seem to represent almost all of the major living anguimorph clades including xenosaurs/anguids (*Carusia* and its relatives), helodermatids (within the larger monstersaur clade, e.g. *Estesia*), lanthanotids (e.g. *Cherminotus*) and stem varanids (e.g. *Telmasaurus*) (e.g. Conrad, Ast, et al., 2011). This raises questions as to their origins and early history, including any connections with North America, but the eastern Asian lizard record for the Jurassic and Early Cretaceous is currently rather uninformative.

Lizard fossils are known from the Jurassic (e.g. Daohugou, China) and Early Cretaceous of East Asia (e.g. Barremian, Jehol Biota, China; Aptian-Albian, Höövör locality, Mongolia). To date, none of the Jurassic lizard taxa (e.g. *Hongshanxi*, Dong et al., 2019) has been allocated with confidence to a major squamate clade, and there are similar problems with most taxa from the Lower Cretaceous Jehol Biota and its equivalents in China (e.g. *Yabeinosaurus*, *Liushusaurus*). The Jehol *Dalinghosaurus* has been linked to shinisaurs (e.g. Conrad, 2008; Conrad, Ast, et al., 2011; Evans & Wang, 2005), placed within Lacertoidea (e.g. Brownstein et al., 2023; Simões et al., 2018, 2020), or related to iguanians (e.g. Dong et al., 2023; Tałanda et al., 2022), and its position is highly debatable. A more recently described specimen (*Indrasaurus wangi*, O'Connor et al., 2019), recovered as a dinosaurian gut content, shows some similarities in the dentition with Euramerican dorsetisaur, stem-anguimorphs, and further material of this taxon would be valuable. Alifanov (2019) also reported jaws of dorsetisaur, as well as xenosaurs, from the Aptian-Albian Mongolian locality of Höövör, but more detailed analysis of this important, but fragmentary, material is needed. More broadly within Asia, possible anguimorph remains have also been reported from central and southern localities including the Lower Cretaceous of Uzbekistan (Albian, ?xenosaur, Gao & Nesson, 1998), Thailand (Barremian eggs with embryos, Fernandez et al., 2015) and Myanmar (*Barlochersaurus*, amber specimen, Daza et al., 2018). There is clearly much more work to be done.

Presence of vomerine teeth in squamates

Palatal teeth are commonly present in vertebrates, and are thought to facilitate the prehension, intra-oral

transport and swallowing of food items during feeding (Schwenk, 2000). However, the presence, distribution, morphology, and arrangement of the palatal teeth are highly variable, both within and between species (e.g. Skawiński et al., 2017).

An extensive palatal dentition is plesiomorphic for amniotes with an evolutionary reduction in most major lineages (Matsumoto & Evans, 2017), including Squamata. Estes et al. (1988) suggested that the presence of teeth on each palatal bone might be the result of a single developmental field, and that the absence of teeth on the anterior palatal elements in many species could therefore result from an anterior truncation in the expression of this field (Mahler & Kearney, 2006). As an example, the fossil record of turtles suggests palatal teeth, although surviving long after the disappearance of the marginal teeth, were lost on the vomers and palatines first, then later on the pterygoid (Davit-Béal et al., 2009; Lainoff et al., 2015).

A similar pattern of posteriorward reduction seems to have occurred in squamates (vomer, palatine, pterygoid in order). Gauthier et al. (1988) hypothesized that the presence of vomerine teeth was likely the ancestral condition for lepidosauromorphs and this is supported by stem lepidosaurs such as *Paliguana* (Ford et al., 2021). Within Lepidosauria as a whole, vomerine teeth were commonly present in Rhynchocephalia including *Gephyrosaurus*, *Diphydontosaurus* and *Clevosaurus* (Matsumoto & Evans, 2017), *Opisthiamimus gregori* (DeMar et al., 2022), and variably in the extant *Sphenodon* (Evans, 2008). In extant non-ophidian squamates, however, palatal teeth are most commonly present on the pterygoid (e.g. lacertids, iguanians) and occasionally on the palatine (e.g. some *Lanthanotus* and *Heloderma*, some iguanians; Evans, 2008). Vomerine teeth are, however, extremely rare and among extant squamates occur only in the limb-reduced lizard *Pseudopus* (Evans, 2008; Klembara et al., 2017). Consequently, the absence of vomerine teeth was regarded as one of synapomorphies of Squamata (Estes et al., 1988) or pan-Squamata (Tałanda et al., 2022), with occasional reversals like that of *Pseudopus*. Estes et al. (1988) considered that the loss of vomerine teeth occurred early in the origin of squamates from stem lepidosaurs, but fossils representing this stage of squamate evolution are rare and preservation of the vomer, usually a thin flat bone, is rarer still. More recent finds suggest the history of vomerine teeth in squamates is not straightforward (also see Brownstein et al., 2022). Vomerine teeth have been reported in three early (possible) pan-squamates, *Cryptovaranoides microlanius* from Upper Triassic of Britain (Whiteside et al., 2022), *Eoscincus ornatus* from the Upper Jurassic of the USA

(Brownstein et al., 2022) and an unnamed mid-Jurassic specimen from China (Conrad et al., 2013), whereas the late surviving (mid-Cretaceous) stem squamate *Oculudentavis* (Bolet et al., 2021) does not have vomerine teeth. As for the ophidian squamates, with the loss of the limbs, and the development of macrostomatan feeding strategies (e.g. pterygoid walk), most snakes display an extensive palatal dentition, with absence of palatal teeth apparently correlated with specialized feeding strategy (e.g. in most scolecophidians).

The arrangement pattern of vomerine teeth is variable among the squamate species in which they are recorded. In the controversial *Cryptovaranoidea microlanius*, the teeth seem to be arranged in partial medial and lateral rows (Whiteside et al., 2022, fig. 7A), whereas *Eoscincus* has least two rows of teeth toward the posterior end of the vomer. Unusually, these vomerine teeth are larger than those on the palatine or pterygoid. In the Eocene anguimorph *Eosaniwa koehni* the vomerine teeth form a straight, single row along almost the entire length of the extremely elongate vomer; in *Paranecrosaurus feisti*, there are only a few small teeth at the posterior tip of the vomer; and in *Melanosaurus maximus* (Gilmore, 1928), small vomerine teeth form a patch on the posterior part of the vomer. In the extant *Pseudopus apodus*, the vomerine teeth are arranged in a row along a ventral crest on the posterior-most part of the vomer (in larger specimens, there can be an irregular medial row). In *Zhongyuanxi jiai*, the arrangement of the vomerine teeth is most similar to that of *Eoscincus*, with two rows diverging posteriorly, but to a lesser degree and with fewer teeth compared to *Eoscincus*. In addition, the vomerine teeth of *Zhongyuanxi jiai* are located more medially. This arrangement, with two diverging tooth rows on the posterior portion of the vomer also occurs in the stem lepidosaur *Paliguana* (Ford et al., 2021).

Crown squamates with vomerine teeth are mostly anguimorphs. In addition to the extant *Pseudopus*, this includes three taxa from the Eocene – *Eosaniwa koehni* (Rieppel et al., 2007), *Paranecrosaurus feisti* (Smith & Habersetzer, 2021) and *Melanosaurus maximus* (Gilmore, 1928). *Zhongyuanxi jiai* thus adds to this list and is the first Cretaceous anguimorph reported with vomerine teeth. It is possible, therefore, that anguimorphs may have retained the capacity to redevelop vomerine teeth to a greater degree than other lizards.

The loss and regain of structures through deep time is now more fully understood in terms of the long-term conservation, but variable suppression, of developmental pathways (e.g. Sadier et al., 2022). These have been particularly well-studied for teeth. One striking example of this is the re-development of mandibular teeth in the

frog *Gastrotheca guentheri* (Paluh, Dillard, et al., 2021; Paluh, Riddell, et al., 2021; Wiens, 2011), despite these teeth being lost in most frogs more than 200 million years ago. In contrast to the marginal dentition, however, very few studies have been conducted on the development of palatal teeth, and most of these have focused on amphibians (Soukup et al., 2008, 2021). Buchtová et al. (2008) studied the development and molecular signalling of palatal tooth formation in snakes, and found it to be similar to that of the marginal dentition (maxillary and dentary teeth), but a separate study on turtles concluded that the induction of the marginal and the palatal dentition was controlled by different developmental programs (Lainoff et al., 2015). There is clearly potential for further work on palatal tooth development to uncover the factors underlying the variation in tooth distribution across squamates and to understand the functional and/or phylogenetic implications of that variation.

Conclusions

A new lizard, *Zhongyuanxi jiai*, is named and described from the Upper Cretaceous (?Maastrichtian) Qiupa Formation of China. It is characterized by a combination of the following features: presence of vomerine teeth, a palaeochoanate palate, a single but large lacrimal foramen, cranial sculpture and osteoderms, and a few recurved, compressed and acuminate marginal teeth with basal plicidentine and with anterior and posterior carinae. Phylogenetic analysis places it within Anguimorpha as a sister taxon to the Mongolian *Aiolosaurus oriens* on the varanid stem. This adds one more taxon to the diversity of East Asian anguimorphs. The character distribution, such as the plicidentine, the retreated external naris and the elongate vomers, among the Upper Cretaceous fossil anguimorphs are complex, and the Upper Cretaceous anguimorphs previously from the Gobi Desert need to be restudied with high-resolution micro-computerized tomography to clarify the character evolutionary history. We also expect new anguimorph fossils from the Upper Cretaceous as well as the Upper Jurassic and Lower Cretaceous of East Asia to help resolve the conflict between the morphological and molecular phylogenetic hypotheses and to clarify the evolutionary scenario of the Anguimorpha clade. One of the more unusual features of *Zhongyuanxi jiai* is the presence of vomerine teeth, adding one more taxon with this character in Anguimorpha and being the first one from the Cretaceous in addition to the Jurassic, Cenozoic and extant examples.

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Disclosure statement

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

Supplemental material

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