Vertebrata PalAsiatica

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Abstract

Polyglyphanodontians are a group of squamates that flourished during the Late Cretaceous. They were widely distributed in Asia, North America, and other regions, and exhibited high diversity in genera, species, morphology, and ecology. Although polyglyphanodontians are known for numerous large herbivorous representatives, their major fossil localities have also yielded many small insectivorous species, including Funiusaurus luanchuanensis from the Upper Cretaceous Qiupa Formation of Henan, China. Funiusaurus was previously represented only by a nearly complete but relatively fragmented skull, which provided limited morphological information. Based on high-resolution CT data from a newly discovered complete skull and several other cranial and postcranial specimens, this study supplements extensive anatomical data for Funiusaurus, particularly for the palatal region, braincase, vertebral column, and limbs. These new data will help establish a more comprehensive morphological matrix for polyglyphanodontians, thereby enabling in-depth discussion of their evolutionary history, including changes in body size and diet.

Full Text

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Morphology of *Funiusaurus luanchuanensis* (Squamata, Polyglyphanodontia) based on new material

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Abstract Polyglyphanodontia is a successful clade of squamates thriving during the Late Cretaceous. They were widely distributed in Asia, North America and possibly some other regions, and are highly diverse in taxonomy, morphology and ecology. Although the clade is better known to have many large herbivores, quite a few small insectivorous species were described from all the main localities where polyglyphanodontian fossils were found. *Funiusaurus luanchuanensis* from the Upper Cretaceous Qiupa Formation of Henan Province, China is one of them. Previously, it was described based only on a nearly complete

but relatively fragmentary skull which therefore provided limited morphological information. Herein we add a great amount of anatomical data of this species based on high-resolution computerized tomography data of a new completely preserved skull and several other cranial and postcranial specimens, especially of the palate, braincase, vertebral column and limbs. The new data of *Funiusaurus* will help to build a more comprehensive phylogenetic data matrix of Polyglyphanodontia in the future, and further clarify the evolutionary history of body size or diet shift within the clade.

Key words Henan, Qiupa Formation, Late Cretaceous, *Funiusaurus*, Polyglyphanodontia

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1 Introduction

Polyglyphanodontia is a clade of squamates that thrived in Asia, North America and some other regions during the Late Cretaceous but went extinct at the end of Cretaceous (Jiang et al., 2025). Although there are doubts on some of the oldest representatives (*Kuwajimalla kagaensis* from Barremian–early Aptian of Japan, Evans and Manabe, 2008; *Cryptobicuspidon pachysymphysealis* from Aptian of Brazil, de Carvalho and Santucci, 2024), the clade was clearly distributed in North America and northern Africa during mid-Cretaceous, evidenced by *Bicuspidon* spp. from Utah (*B. numerosus*, *B. smikros*; Nydam and Cifelli, 2002; Nydam,

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2013a), and Morocco (*B. hogreli*; Vullo and Rage, 2018). There are only limited fossil records before the bloom of the clade during the Campanian and Maastrichtian in Asia and North America (Jiang et al., 2025).

During the last two stages of Late Cretaceous, Polyglyphanodontia reaches the highest in species richness and morphological disparity (Alifanov, 2000; Gao and Norell, 2000; Mo et al., 2010; Longrich et al., 2011; Nydam, 2013b; Xing et al., 2023), and therefore it is appealing to discuss its spatiotemporal diversification and the associated biotic and abiotic changes at the time (such as the flourishing of the angiosperm and the arising average temperature; Benton et al., 2022).

However, these topics are poorly studied and discussed due to the unstable phylogenetic position of Polyglyphanodontia among Squamata (Conrad, 2008; Gauthier et al., 2012; Reeder et al., 2015) and the inconsistent intrarelationship within the clade itself (Mo et al., 2010; Longrich et al., 2011; Fontana, 2014; Martinelli et al., 2021). Although the majority of Asian polyglyphanodontians are well represented by partial or nearly complete skull or skeleton and have provided a good amount of morphological data of the clade, their description was made before the prevalence of the high-resolution CT scanner in paleontological studies, limiting our understanding on some of their key features, such as those of braincase.

Funiusaurus luanchuanensis was named in 2014 (Xu et al., 2014) based on a nearly complete, although slightly fragmentary skull (HGM 41HIII-114). The morphology of the holotype is limited and sometime ambiguous by the preservation and the unavailability of the CT facility at that time. Herein we describe several new specimens of *Funiusaurus luanchuanensis*, including both cranial and postcranial skeleton, based on high-resolution CT scanned data. This work completes the morphology of this species, especially that of braincase, vertebral column and limbs. These data will help to build a more complete morphological dataset of Polyglyphanodontia and further clarify the interrelationship of polyglyphanodontian members.

2 Material and methods

All the new specimens studied herein were excavated in Qiupa locality during two field seasons of 2008 and 2021, and all deposited at the Henan Natural History Museum (previously Henan Geological Museum (HGM)). They were carefully mechanically prepared, and were photographed using a Nikon D850 to get high-resolution photos and an iPhone when it was difficult using the Nikon camera. One of the specimens (HGM L2021-1-8) was scanned at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP), using a Phoenix v|tome|x m300| CT scanner with a scan voltage of 120 kV and a flux of 140 μA. The obtained image stack of 1109 slices, with a voxel size of 6.896 μm, was processed in Avizo v9.1 to segment and visualize each bony element. Screenshots were taken of the surface renders of these elements in different views for use in the figures.

The anatomical terminology here follows Evans (2008), Russell and Bauer (2008) and Hoffstetter and Gasc (1969).

3 Systematic paleontology

Squamata Oppel, 1811

Polyglyphanodontia Alifanov, 2000

***Funiusaurus luanchuanensis* Xu et al., 2014**

Holotype HGM 41HIII-114, a nearly complete but slightly fragmentary skull.

Type locality and horizon Near Qiupa village, Luanchuan County, Henan Province; Qiupa Formation, Late Cretaceous.

Newly referred specimens HGM L2021-1-8, a nearly complete skull (Figs. 1, 2, 3, 4A); HGM L2021-1-2, posterior half of a skull (Fig. 4E); HGM L08-11-10, a fragmentary right maxilla (Fig. S1B); HGM L08-15, a partial skull with the left maxilla, jugal, lacrimal, prefrontal, palatine, ectopterygoid and the frontal (Fig. 4C); HGM 2021-1-6, a nearly left maxilla (Fig. S1C); HGM L2021-1-7, a partial skull with a premaxilla, a right maxilla, the paired partial mandible, and some postcranial elements, including one section of vertebral column with ribs in the pectoral region, and on section of sacral and anterior caudal vertebrae, a partial humerus, a ulna, and a nearly complete hindlimb with pelvic fragments (Fig. 5); HGM L2021-1-9, a pair of incomplete dentaries, a partial parietal and a fragmentary braincase (Figs. 4D, S1A); HGM 1137-2, middle section of a left lower jaw (Fig. 4B).

Amended diagnosis (revised from Xu et al., 2014) A small polyglyphanodontian lizard characterized by the following combination of derived features: 1) a heterodont dentition with a large caniniform tooth on the anterior maxillary dentition (the 3rd maxillary tooth) and barrel-shaped but tricuspid posterior teeth on both upper and lower jaws; 2) fused frontals with a frontoparietal width more than twice the interorbital width; 3) a robust jugal with a deep suborbital ramus and a prominent posterior process; 4) three processes on the posterior margin of the dentary; 5) a few pterygoid teeth at the junction of the anterior lamina and the posterior quadrate process; and 6) a postorbital with an extremely elongate posterior process.

Remarks The new cranial material is referred to *Funiusaurus luanchuanensis* mainly on the basis of a similarly small size to the holotype, a high facial process of the maxilla, a deep suborbital ramus of the jugal, deeply waisted frontals, and incipient tricuspid posterior teeth on both maxilla and dentary. *Funiusaurus* is regarded as a polyglyphanodontian based on a large facial process of maxilla, a broad suborbital ramus of jugal, vomer-pterygoid contact, palatine-ectopterygoid contact, a large splenial, and a heterodont dentition.

Description The description of the skull is based on HGM L2021-1-8 and that of the postcranial skeleton is based on HGM L2021-1-7, otherwise mentioned.

Skull The skull is robustly built although small (estimated skull lengths of all cranial

material are about 30 mm). The external naris is large, elongated in an anteroventral to posterodorsal direction, enclosed by the premaxilla, maxilla, and nasal.

The premaxilla is single with a long nasal process (Fig. 2B). The nasal process is tapering posteriorly, and might lose its posterior most tip, and a prominent ventral midline keel is present on the nasal process. It is possible that the

Fig. 1 The newly referred specimen of *Funiusaurus luanchuanensis* (HGM L2021-1-8) from the Upper Cretaceous Qiupa Formation of Luanchuan, Henan, China. A. photograph of the specimen in dorsolateral view; B. 3D rendering of the specimen in the same view

Figure 1: Fig. 1 The newly referred specimen of *Funiusaurus luanchuanensis* (HGM L2021-1-8) from the Upper Cretaceous Qiupa Formation of Luanchuan, Henan, China. A. photograph of the specimen in dorsolateral view; B. 3D rendering of the specimen in the same view

Fig. 2 3D rendering of isolated bones in *Funiusaurus luanchuanensis*

Figure 2: Fig. 2 3D rendering of isolated bones in *Funiusaurus luanchuanensis*

posterior portion of the nasal process had inserted between the nasals, but how far it went is difficult to estimate. The lateral maxillary process is short, curves posteriorly, and therefore the snout is pointed anteriorly. The end of the lateral process is embraced by the forked anterior premaxillary process of maxilla, bearing a deep V-shaped facet for the maxilla laterally (therefore the lateral process looks forked as described in Xu et al., 2014) and a larger facet at the base of and posterior to the nasal process

Fig. 1 The newly referred specimen of *Funiusaurus luanchuanensis* (HGM L2021-1-8) from the Upper Cretaceous Qiupa Formation of Luanchuan, Henan, China
A. photograph of the specimen in dorsolateral view; B. 3D rendering of the specimen in the same view
Abbreviations: an. angular; ar. articular; bo. basioccipital; bs. basisphenoid; co. coronoid; de. dentary; ept. epipterygoid; fr. frontal; ju. jugal; l. left; la. lacrimal; ma. maxilla; na. nasal; ot-op. otic-occipital; pa. parietal; pal. palatine; pocc. paroccipital process; pm. premaxilla; pof?. possible postfrontal; prf. prefrontal; pt. pterygoid; qu. quadrate; r. right; san. surangular; sm. septomaxilla; so. supraoccipital

on the palatal shelf of the premaxilla. Therefore, although the anterior end of the maxilla is forked, there is no premaxilla-maxillary aperture present. In ventral view, the palatal shelf is developed.

Fig. 2 3D rendering of isolated bones in *Funiusaurus luanchuanensis* (HGM L2021-1-8) from the Upper Cretaceous Qiupa Formation of Luanchuan, Henan, China

A. right maxilla in labial (A1), medial (A2) and dorsal (A3) views and one isolated maxillary tooth (A4) showing the tricuspid nature; the red box in A1 shows where the isolated tooth is from; B. premaxilla in right lateral view; C. frontal in dorsal (C1), left lateral (C2) and ventral (C3) views; D. quadrate in posterior view; E. left jugal in lateral (E1) and medial (E2) views; F. the palate in ventral view (F1), and the vomer (F2), palatine (F3) and pterygoid (F4) in

dorsal view; G. anterior portion of the right dentary in labial (G1) and lingual (G2) views; H. left mandible in labial (H1) and lingual (H2) views

Abbreviations: a.i.a.f. anterior interior alveolar foramen; a.s.f. anterior surangular foramen; an. angular; ar.co. articular condyle; bs.ft. basisphenoid facet; ce.co. cephalic condyle; co. coronoid; cr.cr. crista cranii; de. dentary; ecpt. ectopterygoid; ecpt.ft. ectopterygoid facet; fa.pr. facial process; fo.col. fossa columellae; io.ca. infraorbital canal; ju.ft. jugal facet; la.ft. lacrimal facet; ma.ft. maxilla facet; man.co. mandible condyle; med.rd. medial ridge; na.ft. nasal facet; na.pr. nasal process; p.m.f. posterior mylohyoid foramen; p.pr. posterior process; p.s.f. posterior surangular foramen; pa.f. parietal foramen; pa.lp. parietal lappet; pal. palatine; pal.ft. palatine facet; pal.sf. palatal shelf; pal.ss. palatine sinus; par. prearticular; pob.rm. postorbital ramus; pof.ft. postfrontal facet; prf.ft. prefrontal facet; pt. pterygoid; pt.lp. pterygoid lappet; pt.t. pterygoid teeth; rap. retroarticular process; rd. ridge; sac. opening of superior alveolar canal; san. surangular; sd.rd. subdental ridge; sm.ft. septomaxilla facet; spl. splenial; sob.rm. suborbital ramus; sym. symphysis; ty.cr. tympanic crest; vo. vomer; vo.f. vomerine foramen

Both the maxillae are preserved, with the left one more complete. The bone is large, and triangular in lateral view. There is a short anterior process, a broad facial process, and a relatively long posterior process. The anterior process is forked anteriorly with a lateral ramus and a larger medial ramus (Fig. 1B). The lateral ramus fits into the deep facet on the lateral process of the premaxilla, and the medial ramus curves medially to reach its counterpart and overlaps the palatal shelf of the premaxilla. Shortly after the bifurcation the facial process arises steeply from the premaxillary process and then deflects medially to contribute a small portion of the skull roof where it meets the nasal in an abutting style and the frontal to a small degree. The anterior margin of the facial process is thickened, and at its ventral base there is a small foramen (likely for the maxillary nerve and artery) medially (Fig. 2A3). Laterally there are five foramina roughly in a straight line parallel to the alveolar margin and there is an additional foramen above the first foramen. The posterior margin of the facial process is much sloping. The posterior process is about half the maxillary length, posteriorly exceeding the midpoint of the orbit, and bears a short edentulous portion at the posterior tip. The palatal shelf is well developed, and becomes broader where the palatine articulates, and tapers to a tip posteriorly. In the medial view, the most notable feature is a prominent ridge, running posterodorsally from the palatal shelf at the level of the third or fourth maxillary tooth, and parallel to the anterior margin of the facial process. The ridge divides the facial process into an anterior region and a posterior area. The anterior region is featured by two small depressions by a weak and broad ridge which originates from the small foramen on the anterior margin of the facial process. And the posterior area is characterized by a deep anterior fossa. Anterior to the ridge is the septomaxilla facet. At the middle length and roughly at the level of the last mental foramen, the superior alveola canal opens posteriorly. A distinct ridge is originated just posterior to the infraorbital canal opening for superior

alveolar canal (sense Evans, 2008), and strengthened posteriorly to form, with the lateral wall of the maxilla, a deep groove where the jugal ventral margin fits into. Lateral to the ridge is the ectopterygoid facet.

The left septomaxilla is preserved but may not be complete (Fig. 1B). The preserved part is small and roughly saddle-shaped, with a well-defined lateral maxillary facet. The dorsal surface looks smooth and ventrally the bone accommodates Jacobson' s organ.

The nasals are paired, but neither of them is well preserved (Fig. 1B). The preserved part suggests the posterior end is triangular and pointed posteriorly based on the left nasal and the facet of the right one on the frontal. The nasal widens anteriorly and meets the medial margin of the maxilla, but not of the prefrontal. The nasals would likely have been in contact along the midline.

The frontal is single and hourglass-shaped (Fig. 2C). The bone is narrowest at the level slightly posterior to its midlength and widened anteriorly to be twice of the minimal width, and posteriorly to be nearly three times of the minimal width. There is a prominent ridge

along the midline up to the level of the postfrontal facet. The lateral orbital margins are also deflected upwards to form robust ridges, and therefore two longitudinal depressions are present between the midline and lateral ridges. The surface of the depression is sculptured with short ridges, and the sculpture gets weaker around the parietal foramen which is located along the frontoparietal suture. Along the posterior margin of the frontal, the parietal foramen invades into the frontal more than into the parietal, and laterally the frontal bears developed parietal lappets to support the parietal. The crista cranii is moderately developed, to a greater degree anteriorly where the crest curves medially but does not meet its contralateral one. The crest gets weaker and becomes a low, wide ridge from the midlength of the frontal. Laterally the prefrontal and postfrontal facets are clearly present, although the connections are all lost. The prefrontal facet is large, extending posterior nearly to the midlength of the frontal, and the much smaller postfrontal facet is far away from the prefrontal facet, leaving the frontal lateral margin contribute to the orbit.

The parietal (Fig. 1B) is incompletely preserved with the supratemporal processes missing. The parietal table is short and wide. The suture with the frontal is not complete, and the right corner preserves the facet with the parietal lappet of the frontal. The table becomes narrows posteriorly nearly to its posterior end, i.e., the table is constricted at a posterior level where the supratemporal process originates. The table extends laterally to a small extent to overhang the lateral embayment, and therefore is separated from the latter by a ridge. The adductor muscles therefore originate below the table rather than dorsally on the table. In the midlength of the descending shelf there is a small but distinct alar process present. Posteriorly the nuchal crest is developed, and in the middle the pit for the ascending process of the supraoccipital is developed. The crest may meet the braincase. The parietal table extends posteriorly as laterally and

therefore forms two relatively deep fossae by the side of the pit. The ventral surface of the bone features two concavities lateral to a weakly developed midline swelling. The complete parietal in HGM L2021-1-2 (Fig. 4E) shows the wide parietal table continues posteriorly with two long supratemporal processes. The supratemporal processes are longer than the table and diverge at an angle of ~60 degrees. The process is roughly triangular at the base, but becomes more laminar posteriorly vertical to the horizon. The lateral surface of the supratemporal process preserves the supratemporal facet which goes anteriorly more than three fourths of the process length. In HGM L2021-1-8 by the side of the posterior quadrate process of the right pterygoid is a small, elongated bone which may be a supratemporal bone (Fig. 4A).

The left prefrontal (Fig. 1B) is better preserved although the frontal process is totally missing. The prefrontal boss is prominently present, represented by thickening of the anterior orbital margin. The thickening turns anteriorly and terminates at the suture with the maxilla. There is a concavity on the top of the prefrontal, enclosed by the thickening. The orbitonasal

flange is complete, ventrally articulating with the palatine, and laterally enclosing the lacrimal foramen with the lacrimal bone. The medial margin of the orbitonasal flange is nearly vertical, bordering the olfactory canal. The anterior laminal is extensively overlapped by the maxilla. The frontal process is well developed, based on the length of the prefrontal facet on the frontal.

The lacrimal is preserved only on the left side in HGM L2021-1-8 (Fig. 1B). It may have been greatly obscured by the maxilla, but partially exposed due to the breakage of the maxilla. The bone is best preserved in HGM L08-15 (Fig. 4C). As exposed, the bone is elongated along the posterior margin of the facial process of the maxilla, dorsally meeting the prefrontal at the point lower than the prefrontal boss, and ventrally articulating with the prefrontal and jugal medially and maxilla laterally. The posterior margin is slightly flaring laterally, being the anteroventral margin of the orbit. A large lacrimal foramen is between the lacrimal and prefrontal.

The jugal, nearly complete and in situ on the left side (Figs. 1B, 2E), is robust with a deep, laminar suborbital ramus and a narrow, columnar postorbital ramus. The two rami form an angle of 120 degrees although it looks the angle is nearly 90 degrees due the presence of a distinct triangular posterior process along the ventral margin of the suborbital ramus (also see in HGM L2021-1-2; Fig. 4E). Anteriorly the jugal is sandwiched between the medial prefrontal and the lateral lacrimal and maxilla. But whether the jugal meets the palatine is difficult to know due to the slight displacement of these bones. The suborbital ramus is overlapped by the maxilla extensively for nearly half the depth of the ramus. The postorbital ramus tapers dorsally, but not completely preserved in all the specimens, and therefore its connection with the postfrontal, postorbital, or squamosal is unknown. The medial ridge of jugal is prominent, located ventrally on the suborbital ramus and slightly anteriorly on the postorbital process, which is the plesiomorphic configuration for Squamata (Čerňanský et al., 2014).

The ridges meet at the junction where develops a pointed, pyramid-shape protuberance, which may meet the ectopterygoid. This protuberance, together with ectopterygoid restrains the movement of the coronoid anteriorly.

A fragmentary arched bone lateral to the left mandible is probably part of the left postfrontal (Figs. 1, 4A) considering the morphology from the holotype (Xu et al., 2014). It is the medial part embracing the frontoparietal suture. The anterior ramus is shorter than the posterior ramus, corresponding to the postfrontal facet on the frontal and parietal. Squamosal bones are not recognized in any specimens.

The left quadrate is preserved and complete in HGM L2021-1-8 (Figs. 1B, 2D), but preserved within the orbit in HGM L2021-1-2 (Fig. 4E). The central pillar is curved dorsally, ending posteriorly as a dorsal condyle, and the lateral conch is developed with a weakly developed tympanic crest. Between top of the crest and the dorsal condyle there is a notch to receive the squamosal peg. Medially the quadrate bears a moderately developed lamina

which develops a small pterygoid lappet ventrally. The mandibular condyle is mediolaterally elongated.

The palate is completely preserved and more or less in situ in HGM L2021-1-8. The suborbital fenestra is restricted by the ectopterygoid meeting the palatine (Figs. 2F, 4A).

The vomers (Fig. 2F1–2) are paired and meet along the midline for most of their length. The vomer is moderately long, anteriorly and posteriorly narrow but broad for the middle half of the bone. The broad part does not meet the palatal shelf of the maxilla based on the lack of the facet on the vomer, but it is unknown how close the two are. It is also difficult to determine whether the vomer meet the premaxilla anteriorly due to the displacement of these bones. On the ventral surface of the bone and close to the medial margin, a low and short ridge originates where the bone begins to broaden, and together with the contralateral ridge encloses a small recess for the palatal sinus (Fig. 2F1). At the posterior end of the ridge, a vomerine foramen is developed at the base. The widened middle part of the bone has the lateral margin curling up dorsally and continues in frontal of the vomerine foramen medially, supporting the vomeronasal organ (Fig. 2F2). The posterior one forth narrows abruptly to only half the width and tapers to a posterior tip. It also thickens along the medial margin to form ridge, and it articulates with the palatine probably in an overlapping style and posteriorly meets the pterygoid.

The palatine (Fig. 2F1, F3) is roughly trapezium-shaped, anteriorly wider. The choana conch is weakly developed, whose anterior margin arches dorsally to suture with the prefrontal (Fig. 2F3), and the anterior margin is grooved anteriorly into a deep canal which goes laterally into the infraorbital foramen which is probably open laterally (i.e., not a complete foramen) (Fig. 2F1). Just behind the level of the prefrontal articulation, the maxillary process expands laterally to a moderate degree, especially anteriorly to form the maxillary facet.

The palatine sutures with the ectopterygoid extensively, excluding the maxilla from the suborbital fenestra, but the suture between the palatine and maxilla is difficult to follow. Posteriorly, the palatine narrows as choana conch shallows with the suborbital margin (lateral margin) slightly thicken and rounded. The palatine articulation with the pterygoid is extensively and probably simply overlapping along medial part of the palatine. The palatine is excluded from the interpterygoid vacuity as the pterygoid meets the vomer.

The pterygoids (Fig. 2F1, F4) are typically Y-shaped, and probably meet each other at their anteromost tips where they meet the vomers, and therefore the interpterygoid vacuity extends anteriorly between the pterygoid, but not further anteriorly. The palatine process (anteromedial process) is laminar, tapering to a tip, and long enough (over one third of the pterygoid length) to reach the vomer. The lateral process is much shorter but stout. A dorsal ridge runs dorsally in the middle of the lateral process to the end which is expanded to form a triangular cross section. The anterior apex of this triangular looks to meet the jugal, possibly

due to the deformation during preservation. The lateral process articulates with the bifurcated posteromedial process of the ectopterygoid ventrally and anterodorsally to the dorsal ridge. Together with the thickened ventral ramus of the posteromedial process of the ectopterygoid, the lateral end restrains the movement of the coronoid medially. The lamina connecting the palatine and lateral processes is slightly concave in the ventral view, as the posterior margin of the lateral process raises up. There are three or four small teeth at the apex of the lamina where the palatine and lateral processes converge. Afterwards a short neck connects the expanded and laminar quadrate process (posterior process). A deep fossa columellae is located where the quadrate process starts to expand, as well as the medially facing basipterygoid facet. The dorsal ridge from the lateral process continues posteriorly and passes by the fossa columellae and becomes the dorsal margin of the quadrate process. The laminar process is deeply concave medially and meets the quadrate at its posterior end based on the presence of the pterygoid lappet on the quadrate, although the articulation is lost.

The ectopterygoid (Fig. 2F1) is a relatively large bone, generally anteroposteriorly elongated, with a bifurcated posteromedial and an expanded anterolateral process. The neck between the two processes is short. As described above, the bifurcated posteromedial process articulates with the pterygoid dorsally and posteriorly and forms a thick although not deep pterygoid flange to restrain the medial movement of the coronoid. The anterolateral process meets the palatine and its lateral margin articulates extensively with the maxilla ventrally and the jugal dorsally.

The epipterygoids are columnar and slender with the ends slightly expanded. The two bones are slightly curved.

The braincase is mostly preserved, although its elements are slightly displaced

Fig. 3. 3D rendering of the braincase in *Funiusaurus luanchuanensis*

Figure 3: Fig. 3. 3D rendering of the braincase in *Funiusaurus luanchuanensis*

from each other in HGM L2021-1-8 (Figs. 3, 4A).

The basisphenoid and the basioccipital are best preserved among the braincase elements in HGM L2021-1-8. The basisphenoid is large compared to the basioccipital (Fig. 3D). The basisphenoid floor narrows posterior to the basipterygoid process and becomes thin where it overlaps the basioccipital, and together with the flattened lateral wall, sutures with the basioccipital in a wide inverted-V suture (Fig. 3E). The posterolateral end slope onto the basal tubercle. The lateral wall of the basisphenoid is deep anteriorly but gets flattened posteriorly. Anteriorly, the basipterygoid process (Fig. 3D, E) has a broad base and only its very distal end is expanded to form a large pterygoid facet. The two basipterygoid processes diverge at an angle of 120 degrees, and between the two is the broad base of the parasphenoid process. Posteriorly sits the pituitary fossa (hypophysial fossa) where the internal carotid foramina open (Fig. 3C). The floor of the pituitary fossa is featured by two anteriorly converging ridges which may represent the ossified part of the trabeculae cranii. At the posterior ends of the ridges are the internal carotid foramina (Fig. 3D). These foramina are not clearly delimited

due to the poor CT image quality. The anterior and posterior openings of the vidian canal are not discernible, but the right abducens foramina (CN VI) is clearly at the junction of the alar process and the dorsum sella and dorsolateral to the internal carotid foramina (Fig. 3C). The dorsum sellae is deep although it inclines posteriorly due to the compression of the braincase. Laterally from the dorsum sellae developed a prominent alar process which bears a thickened lateral ridge connecting ventrally the basipterygoid process, therefore hiding the laterally opening recessus vena jugularis from the anterior view. The basioccipital miss its condyle. The basal tubercle is developed, pointing ventrally rather than lateroventrally (Fig. 3E). The occipital recess is well delimited and deep, therefore the tubercle crest is well developed although not well preserved (Fig. 3B).

Fig. 3 3D rendering of the braincase in *Funiusaurus luanchuanensis* (HGM L2021-1-8), from the Upper Cretaceous Qiupa Formation of Luanchuan, Henan, China, in posterior (A) and left lateral (B) views, and restored basisphenoid and basioccipital in anterior (C), dorsal (D) and ventral (E) views. Abbreviations: al.pr. alar process; b.tb. basal tubercle; bpt.pr. basipterygoid process; CN6. opening of cranial nerve abducens; ds. dorsum sellae; f.mg. foramen magnum; f.o. foramen ovalis; icf. internal carotid foramen; lrst. lateral opening of recessus scalae tympani; oc.re. occipital recess; pocc. paroccipital process; psp. parasphenoid; so. supraoccipital

The supraoccipital, prootic and otooccipital are not well preserved in HGM

Fig. 4

Figure 4: Fig. 4

L2021-1-8 (Fig. 3), but partially exposed in HGM L2021-1-2 (Fig. 4E). Their sutures are difficult to recognize. There is a week midline ridge on the supraoccipital, and the ascending process is not ossified beyond the anterior margin in HGM L2021-1-8 (Fig. 3A), but the median ridge is stronger and the ascending process is more developed in HGM L2021-1-2 (Fig. 4E). The posterior margin is a smooth rather than angulated curve (Fig. 3A). The prootic bears a broad

and probably rectangular alar process anteriorly (also see HGM L2021-1-2) (Fig. 3B), and the prootic crest seems not developed. The facial foramen is not recognized, but the foramen ovalis and the lateral opening of the recessus scala tympani are well preserved (Fig. 3B). The paroccipital process is long but not dilated distally (also see HGM L2021-1-2) (Fig. 3A). The process extends laterally rather than posteriorly. Other features are not discernible.

Fig. 4 Additional cranial anatomy of *Funiusaurus luanchuanensis* from the Upper Cretaceous Qiupa Formation of Luanchuan, Henan, China

A. HGM L2021-1-8: 3D rendering of the skull in ventral view after removing the mandibles; B. HGM 1137-2: the middle section of a left mandible in lingual view; C. HGM L08-15: a partial skull in lateral view; D. HGM L2021-1-9: a right dentary in labial view (D1) and a left dentary in lingual view (D2), arrows in D1 point to the mental foramina; E. HGM L2021-1-2: the skull in lateroposterior view

Abbreviations: a.i.a.f. anterior interior alveolar foramen; an. angular; ar. articular; at.n?. possible atlas neural arch; bc. braincase; bo. basioccipital; bs. basisphenoid; co. coronoid; co.ft. coronoid facet; de. dentary; ecpt. ectopterygoid; fr. frontal; i.m.f. inferior myhyoid foramen; ju. jugal; l. left; la. lacrimal; ma. maxilla; Mk. Meckelian canal; pa. parietal; pal. palatine; pm. premaxilla; pocc. paroccipital process; pof?. possible postfrontal; prf. prefrontal; pt. pterygoid; qu. quadrate; r. right; san. surangular; scl. scleral ossicles; sd.rd. subdental ridge; sm. septomaxilla; spl. splenial; spl.ft. splenial facet; st?. possible supratemporal bone; sym. symphysis; vo. vomer

Mandible The dentary is robustly built, almost reaching the level of the coronoid dorsal process (clear in HGM L2021-1-2; Fig. 4E). The bone becomes deeper from the symphysis gradually, and its posterior margin has two notches with a dorsal surangular ramus, a medial ramus of a similar length, and a longer ventral angular ramus (Fig. 4E). The ventral margin curls medially to floor the Meckel' s canal and therefore the canal opens medially (clear in HGM L2021-1-9; Fig. 4D2). The lateral surface of the bone is convex, and penetrated by six mental foramina in a straight line parallel to the alveolar margin, which are closely spaced in the anterior half of the dentary (clear in HGM L2021-1-9; Fig. 4D1). In the medial view, the symphysis is limited to the anterior tip and invaded by

the Meckel' s canal (Figs. 2G2, 4D2). The subdental ridge is well developed and forms a shallow but distinct subdental sulcus medial to the teeth. The ridge is of a constant depth until the level of the posterior sixth tooth where it starts to narrow gradually to a tip. The dentary is overlapped medially at the last tooth level, and then ridden dorsally by the coronoid bone. The ventral margin of the subdental ridge and the curling up ventral margin of the dentary suture with the splenial firmly (clear in HGM 1137-2; Fig. 4B). The splenial facet on the subdental ridge of the dentary is also seen in the left dentary of the specimen HGM L2021-1-9 (Fig. 4D2), suggesting the splenial goes anteriorly to the sixth tooth position.

The splenial is large, anteriorly extending at least the posterior twelfth tooth (Fig. 4D2). The posterior extremity is difficult to discern but at least reaches the level of the anteromedial process of the coronoid bone. The anterior inferior alveolar foramen seems to be enclosed within the splenial at the level of the posterior sixth/seventh tooth (Fig. 2H2). The middle section of the mandible (HGM 1137-2) also shows the anterior inferior alveolar foramen is within the splenial and the inferior mylohyoid foramen is located anterior and ventral to the anterior inferior alveolar foramen (1–2 tooth position away) (Fig. 4B).

The coronoid is a triangular bone in general (Fig. 2H). The dorsal process is high, inclines posteriorly to a small degree, and terminates in a blunt end. The labial process is barely developed. There is a small but deep triangular depression for the muscle insertion (muscle sulcus in Klembara et al., 2014). Medially the coronoid bears a short anteromedial process overlapping the dentary, a posteromedial process extending rather ventrally and reaching the angular, and a small posterior process (Fig. 2H2). A prominent and sharp ridge runs from the dorsal end of the coronoid bone down to the ventral end of the posteromedial process. The posteromedial and the posterior processes border the adductor fossa anteriorly.

The surangular is massive and its anterior end is overlapped by the dentary. The anterior surangular foramen is, located below the coronoid at the level of the posterior margin of the coronoid, within the surangular, but the dentary does not contribute to this foramen (clear in HGM L2021-1-2; Fig. 4E). There is an additional large foramen penetrating the surangular lower than the anterior surangular foramen at the origin of a lateroventral ridge in HGM

L2021-1-2 (Fig. 4E). The lateral surface spreads ventrally and laterally to be concave, and then deflected medially along a lateroventral ridge to form the lateral half of the wide adductor fossa floor (Figs. 2H1, 4E). The dorsal margin only slightly thickened anteriorly. The ventral surface of the surangular is mostly overlapped by the angular. The posterior surangular foramen is shortly in front of the mandibular fossa on the lateroventral ridge (Fig. 2H1; also seen in HGM L2021-1-2, Fig. 4E). Medially the surangular encloses the large and deep adductor fossa together with the prearticular.

The angular is relatively long from at least the level of the posterior third

tooth anteriorly, to the level slightly short from the articular condyle (Fig. 2H). Anteriorly the angular extends onto the floor of dentary, being as wide as the floor and exposed as a long strip (Fig. 2H2). Posteriorly beyond the posterior mylohyoid foramen at the level of the posteromedial process of the coronoid bone, the angular becomes even wider, with a width as the floor of the adductor fossa.

The articular bears a long prearticular portion which goes beyond the posteromedial process of the coronoid bone (Fig. 2H2). The prearticular portion bears a very thick mediodorsal margin which is the ventral margin of the adductor fossa, and from which the bone becomes thinner and curls laterally to form the medial half of the adductor fossa floor. The articular condyle is roughly square, facing posteriorly. The retroarticular process is well developed, and tapering to a knot-shaped tip, and its dorsal surface is concave (Fig. 2H).

Dentition The teeth are present on premaxilla, maxilla, dentary and pterygoid. The marginal teeth are pleurodont, closely spaced (Fig. 4C, D, E). There is quite a large amount of cement at the base, demonstrated in the specimen HGM 1137-2 (Fig. 4B). Both the posterior dentary and maxillary teeth are barrel shaped with a slightly bulged belly in the lingual and labial views.

There are probably seven premaxillary teeth (contra four in Xu et al., 2014) based on the three preserved teeth and the space between them (there are also seven premaxillary teeth in HGM L2021-1-7; Fig. 5E) and the premaxillary teeth are small and probably simple, but due to the poor preservation the detail crown morphology is not known. In HGM L2021-1-8, the maxillary teeth consist of one or two small anterior teeth, one large caniniform tooth, and 12 post-caniniform teeth, totaling to 14–15 maxillary teeth (Fig. 4A). At both maxillae, the caniniform tooth is at the eruption or attachment stage and not fully functional. Most post-caniniform teeth are not preserved, except the first one and last several teeth on the right side and the last one on the left (Fig. 4A). Many replacement teeth are preserved mostly near the jaws. The tooth positions are separated by moderately developed interdental ridges (Fig. 4A) and based on the sizes of the tooth positions, the teeth become gradually larger and wider posterowards probably except the last two teeth which become slightly narrower but higher compared to the last third one. The first post-caniniform tooth is unicuspid, but

remaining post-caniniform teeth are probably tricuspid, evidenced by nearly all the preserved replacement teeth, with the central cusp is prominent and the mesial and distal cusps are much lower, rudimentary and separated from the central cusp by very shallow grooves (Fig. 2A4). Although more dentary teeth are preserved in situ, the preservation is poorer. The anterior teeth are probably conical and simple (Fig. 2G), and the last two teeth on the left dentary (probably smaller than their previous tooth based on the size of the tooth position) are clearly tricuspid, similar to the posterior maxillary teeth (Fig. 2H). The interdental ridges are also developed (Fig. 2H2).

The maxillary teeth are better preserved in specimen HGM L08-15 with one large caniniform tooth and 13 post-caniniform teeth are preserved although the caniniform and first post-caniniform teeth are broken (Fig. 4C). The crown tips of all other teeth are eroded to different degrees. The second and third post-caniniform teeth, as well as the last eight teeth show some degree of tricuspid morphology. The dentary teeth are better preserved in the specimen HGM L2021-1-9 (Fig. 4D). There are about 18 dentary teeth, with the first several ones simple and peg-like, and the ones from the eighth are tricuspid.

There are no resorption pits present in these specimens where the lingual sides of the teeth are seen (HGM L2021-1-8, L08-15, L2021-1-9), but the numerous replacement teeth and the erupting caniniform tooth in the specimen HGM L2021-1-8, and a complete set of teeth in the larger specimens HGM L08-15 and L2021-1-9 suggest tooth replacement occurred in *Funiusaurus* but the replacement rate considerably decreased in older individuals.

On the palate, only pterygoid teeth, three or four small teeth in a very restrained area where the palatal and lateral processes converge ahead of the neck (Fig. 2F1).

Scleral ossicles There are several thin, laminar, bony elements preserved below the parietal (Fig. 4A). These elements are roughly rectangular, thicker in the center but thin on the periphery, and in a similar size (2.0×2.5 mm^2 for ossicle (b)). They are probably scleral ossicles, and some of them look irregular in shape because several ossicles overlap together and difficult to separate in CT scan data (Fig. S2).

Vertebral column The preserved vertebral column, with some dorsal vertebrae, two sacral vertebrae and the following anterior section of the tail. All the vertebrae are clearly procoelous (Fig. 5).

The section of four vertebrae is badly preserved, and therefore difficult to know whether these vertebrae are cervical or dorsal ones. They are associated with ribs, and therefore they are surely not the first several cervical (Fig. 5D).

The section of six vertebrae, preserved by the side of the skull, are part of the dorsal section displaying their ventral view (Fig. 5C). The centrum is triangular in general, clearly longer than wide. Based on the spherical shape of the condyle, the centrum is at least not strongly compressed. A well developed and wide ventral ridge extends along the midline of

the whole centrum, and therefore there are two concavities at the side of the ridge (arrows, Fig. 5C). The synapophysis is just posterior to the margin of the cotyle at the base of the neural arches. The zygopophyses are large, horizontally expanded. The neural spine is long along the whole neural arch and exceeds the level of the central condyle posteriorly. The spine is low anteriorly and becomes taller posteriorly.

The posterior section of the vertebral column consists of the last dorsal vertebrae, the two sacrals, and the first eight caudals (Fig. 5B). The last dorsal

Fig. 5

Figure 5: Fig. 5

has already became shorter than the anterior dorsals but bears a higher and more rectangular spine (Fig. 5B1, B2). The two sacrals are even shorter with much narrower spines (Fig. 5B3). The second sacral preserves a complete left transverse processes, showing its long, wide, and robust nature, which

Fig. 5 A referred specimen of *Funiusaurus luanchuanensis* (HGM L2021-1-7) from the Upper Cretaceous Qiupa Formation of Luanchuan, Henan, China
A. the photo of the specimen with rectangles indicating the positions of other subfigures; B. the sacral and anterior caudal vertebral section with the right hind limb in different views; C. the articulated dorsal vertebrae in ventrolateral view; D. four cervical or dorsal vertebrae in lateral view; E. the partial skull in ventral view
Abbreviations: ac. astragalocalcaneum; con. condyle; cV. caudal vertebra; de. dentary; dt. distal tarsal; dV. dorsal vertebra; fe. femur; fi. fibula; hm. haemal arch; isc. ischium; ma. maxilla; mt. metatarsal; ns. neural spine; pm. premaxilla; pu. pubis; sV. sacral vertebra; syn. synapophysis; ti. tibia; tp. transverse process; ul. ulna; zyg. zygopophysis

presumably had articulated with the ilium. The articulation facet is seen on the lateral end of the left transverse process (Fig. 5B2).

The first caudal is of a similar length of the sacrals, but the following caudals become longer and longer (Fig. 5B2, B3). The transverse process of the first caudal is as long as the sacral diapophysis, but narrower, and it protrudes posterolaterally rather than laterally. The processes of the following caudals becomes shorter and slenderer, and up to the fourth or fifth caudal the processes become a small triangular protrusion. The neural spine of the caudals become narrower and longer, inclining posteriorly. And the zygopophyses become smaller and smaller. From the fourth caudal, the haemal arches are preserved associated with the vertebrate (Fig. 5B1, B3). They are positioned between the two caudal, Y-shaped with a long ventral lamina (longer than the dorsal bifurcated part).

Pectoral girdle and forelimb The humerus and ulna (possible from the left side) are preserved articulated between the dorsal column and the skull. No detail is seen from the humerus, and it is seen that the ulna bears a prominent olecranon process (Fig. 5C). There are some more fragmentary slender long bones, but it is difficult to recognize them.

Pelvis and hindlimb The right pubis and ischium preserve the acetabulum and articulate with the femur (Fig. 5B1, B2). Not much could be told from the pubis due to the incompleteness. Although the medial margin looks broken, the ischium seems to bear a small ischiadic tuberosity.

The hindlimb is slender in general. The femur (20.0 mm) bears a well-developed femoral condyle which is well divided from the internal trochanter (Fig. 5B1). A ridge originates from the trochanter, extends distally and diminishes at the one third of the bone. At the distal end, the two epicondyles are recognizable, as well as the intercondylar groove (Fig. 5B1). The fossa (popliteal fossa in Russell and Bauer, 2008) in front of the condyles is not well developed.

The tibia and fibula (17.5 mm) are in articulation, but the fibular proximal end is obscured by the haemal arch of the fourth caudal. The proximal end of the tibia is anteroposteriorly wide, and the ventral crest is well developed from this end (Fig. 5B1). The distal end is much smaller. The fibula is slender and consistent proximodistally.

The astragalocalcaneum is firmly fused without any discernible suture (Fig. 5B1). It is elongate with a lateral process. The tibial and fibular facets on the proximal ends are separate by a low ridge. Distally it should have articulated with the distal tarsals, of which only one is preserved and probably distal tarsal II. The anterodistal and posterior distal notches are clear, and the oblique ridge is not clear due to the ventral view of the bone.

The first four metatarsals (mt I-IV) are preserved (Fig. 5B1), and Metatarsal IV is the longest, about twice the length of Metatarsal I. The second digit is complete, with three phalanges, but the other digits are not complete.

3 Comparison with other polyglyphanodontians

Funiusaurus clearly differs from large-bodied polyglyphanodontians, such as *Gilmoreteius*, *Tianyusaurus*, *Yechilacerta*, *Polyglyphanodon* and *Paraglyphanodon* (Gilmore, 1940, 1942, 1943a; Sulimski, 1975; Mo et al., 2010; Xing et al., 2023), and medium-bodied taxa such as *Darchansaurus*, *Erdentesaurus* and *Cherminsaurus* (Sulimski, 1975) by its small size (skull length about 30 mm whereas the latter with skull length more than 50 mm; Table 1) and tricuspid posterior teeth (vs. laterally compressed or transverse widened teeth with denticle along the top margin).

Among the Gobi taxa, there are many polyglyphanodontians with a similar size as *Funiusaurus*, the majority of which were put under the clade of 'Mongolochamopsidae' (Table 1). Most of mongolochamopsids (*Gobinatus*, *Gurvansaurus*, *Barungoia*, etc.; Alifanov, 2000), although some lack sufficient description and illustrations and therefore need restudy and validation, are different from *Funiusaurus* in unicuspid posterior teeth (vs. tricuspid). Four species, *Tchingisaurus*, *Pyramicephalosaurus*, *Mongolochamops* and *Altanteius*, were reported to have tricuspid teeth (Gao and Norell, 2000). The latter two *Mongolochamops* and *Altanteius* are not well preserved or described to compare but based on the figures in Alifanov (1988), *Mongolochamops* has a slender jugal without a posterior process. *Funiusaurus* differs from *Tchingisaurus* and *Pyramicephalosaurus* by a more robust build of the skull, a prominent posterior process of the jugal (vs. very week if any), a single frontal (vs. clearly paired), a

parietal foramen on the frontoparietal suture (vs. within the parietal), a more prominent caniniform teeth in the anterior part of the dentition, and presence of the pterygoid teeth. Moreover, *Funiusaurus* is further different from *Pyramicephalosaurus* in tricuspid tooth morphology: in *Funiusaurus*, the tooth is barrel-like, and the lateral cusps are incipient and not well separated from the central cusp, whereas in *Pyramicephalosaurus*, the tooth is slightly fan-shaped with the top wider than the bottom, and the lateral cusps are prominent in height (only slightly shorter than the central cusp), and well separated from the central cusp by distinct grooves although much narrower. The teeth of *Funiusaurus* are more similar to those of *Tchingisaurus multivagus*, in a barrel shape and incipient lateral cusps. The two taxa further differ in the position of the two foramina in the splenial, more specifically, inferior mylohyoid foramen is anterior to the anterior inferior alveolar foramen in *Funiusaurus*, but the former just ventral to the latter in *Tchingisaurus*.

Caninosaurus ganzhouensis from the Late Cretaceous of Ganzhou Basin in South China (Wang et al. 2025) also has a similar size to *Funiusaurus*, and a possibly similar dentition. There are more maxillary teeth and the caniniform tooth is much stronger in *Caninosaurus*, but otherwise, there are only differences in the premaxilla and frontals as preserved. The posterior teeth, only observable so far on maxilla, have their crown tips broken or eroded, and

Table 1 Polyglyphanodontian taxa with at least a nearly complete or partial skull preserved: the skull and/or mandible length (when skull not available) of the largest specimen, the tooth type and their diet

Region	Taxa	Specimen	Skull length	Mandible length	Tooth type (most complex)	Diet	Reference
North America	*Polyglyphanodon sternbergi*	USNM 15477	81.5		IV	Herbivorous	Gilmore, 1940
Ganzhou	*Xenodontosaurus fangi*	GMPB20180206	~107		II	Omnivorous	Jiang et al., 2026
Ganzhou	*Yechilacerta yinglianjia*	YLSNHM01794	~105		I	Herbivorous	Xing et al., 2023
Ganzhou	*Tianyusaurus* sp.	NHMG8502	87.4		I	Herbivorous	Mo et al., 2010
Ganzhou	*Caninosaurus ganzhouensis*	GUGW-VH110	~30		III	Insectivorous	Wang et al., 2025

Region	Taxa	Specimen	Skull length	Mandible length	Tooth type (most complex)	Diet	Reference
Gobi	*Gilmoreteius ferrugenous*	AMNH 6520	~115		I	Herbivorous	Gilmore, 1943a
Gobi	*Gilmoreteius chulsanensis*	ZPAL MgR-I/18	80		I	Herbivorous	Sulimski, 1975
Gobi	*Cherminsaurus kozlowskii*	ZPAL MgR-III/24	65		I	Herbivorous	Sulimski, 1975
Gobi	*Erdenetesaurus robinsonae*	ZPAL MgR-III/19	55		I	Herbivorous	Sulimski, 1975
Gobi	*Darchansaurus estesi*	ZPAL MgR-III/6	56		I	Herbivorous	Sulimski, 1975
Gobi	*Tubercephalosaurus pompabilis*	PIN No. 3124/328	85	75	I	Herbivorous	Alifanov, 2000
Gobi	*Alprisaurus bidentatus*	PIN No. 3142/302	~55		I	Herbivorous	Alifanov, 2000
Gobi	*Campedosaurus sulcularis*	PIN No. 3142/341	~50.5		I	Herbivorous	Alifanov, 2000
Gobi	*Gobinatalis arenosus*	IGM 3/126	35.2		III, unicuspid	Insectivorous	Gao and Norell, 2000
Gobi	*Tchingisaurus multivagus*	IGM 3/129	34		III, tricuspid	Insectivorous	Gao and Norell, 2000
Gobi	*Pyramicephalosaurus chermini-cus*	IGM 3/130	~20.9		III, tricuspid	Insectivorous	Gao and Norell, 2000
Gobi	*Conicodontosaurus djadochtaensis*	IVPP V10051	~25		III, unicuspid	Insectivorous	Gilmore, 1943b

Region	Taxa	Specimen	Skull length	Mandible length	Tooth type (most complex)	Diet	Reference
Gobi	*Mongolochampsops reshetovi*	PIN No. 3142/304	~43		III, tricuspid	Insectivorous	Alifanov, 1988
Gobi	*Altanteius facilis*	PIN No. 3142/306	~39		III, tricuspid	Insectivorous	Alifanov, 1993
Gobi	*Barungoia vasta*	PIN No. 4487/2	~24	~23	III, unicuspid	Insectivorous	Alifanov, 1993
Gobi	*Gurvansaurus potissimus*	PIN No. 3143/104		35	III, unicuspid	Insectivorous	Alifanov, 1993
Gobi	*Parameiva oculea*	PIN no. 3142/310		~20	III, unicuspid	Insectivorous	Alifanov, 1993
Gobi	*Prodenieria minima*	PIN No. 3142/324		~18	III, unicuspid	Insectivorous	Alifanov, 1993
Gobi	*Dzhadochtosaurus giganteus*	PIN No. 3143/103	69	53	III, unicuspid	Insectivorous	Alifanov, 1993
Gobi	*Cyclurasia multidentata*	PIN No. 3142/336	~35		III, ?	Insectivorous	Alifanov, 2000
Gobi	*Adamisaurus magnidentatus*	IGM 3/117	32.2		III, unicuspid	Insectivorous	Gao and Norell, 2000
Qiupa	*Funiusaurus luanchuanensis*	HGM 41HIII-14	~30		III, tricuspid	Insectivorous	Xu et al., 2014

Notes: Type I, "leaf-shaped" or "chisel-like" tooth, laterally compressed with linear multiple denticles on the top margin; Type II, transversely widened tooth with isolated cusps on the occlusal surface; Type III, "conical" or "peg-shaped" tooth, unicuspid or tricuspid; Type IV, transversely widened tooth with linear multiple denticles on the top margin.

AMNH, American Museum of Natural History, New York, USA; CUGW, Chinese University of Geosciences, Wuhan, China; CVEB, Centre for Evolution

of Vertebrate Biology, Yunnan University, Kunming, China; HGM, Henan Geological Museum, Zhengzhou, China (now Henan Natural History Museum); IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NHMG, Ganzhou Natural History Museum, Ganzhou, China; PIN, Paleontological Institute of Sciences, Moscow, Russia; USNM, United States National Museum, Washington, USA; YLSNHM, Yingliang Stone Natural History Museum, Shuitou, China; ZPAL, Paleozoological Institute of the Polish Academy of Sciences, Warsaw, Poland.

therefore it is difficult to know the exact crown morphology. However, based on the relatively compressed crowns which are as wide as the shaft, it is more likely that the posterior teeth in *Caninosaurus* is bicuspid or tricuspid.

Most of the chamopsiids from North America (*Chamops*, *Leptochamops*, *Tripennaculus*, *Socognathus*, etc.) are also small lizards that bears tricuspid posterior teeth. However, their preservation is very fragmentary, usually with only jaw elements or teeth preserved, and therefore the phylogenetic position of chamopsiids is highly debated, partially related to the debate whether Polyglyphanodontia is under or close to Teiidae (Gao and Fox, 1991, 1996; Denton and O' Neill, 1995; Longrich et al., 2010; Nydam et al., 2010; Fontana, 2014).

4 Discussions

The new material of *Funiusaurus* add the morphology of some cranial elements which are not preserved or badly preserved in the holotype HGM 41HIII-114, including the lacrimal bone (elongated small bone restricted to the anteroventral corner of the orbit), parietal (relatively short table with long supratemporal processes), quadrate (moderately developed medial lamina with a small pterygoid lappet), palate (vomer-pterygoid contact, anteroposteriorly oriented ectopterygoid reaching the palatine, presence of pterygoid teeth), braincase (robust basipterygoid process, long paroccipital process, broad alar process of prootic, etc.), as well as many postcranial elements (vertebrae, pelvis and hindlimb). Some of the previously reported anatomical features are clarified here too. For example, the posterior maxillary and dentary teeth are clearly tricuspid; the maxilla contacts the nasal and frontal; the lacrimal foramen is positioned between the prefrontal and lacrimal bone; the posterior process of the jugal is well developed as a triangular protuberance but not elongated to form the lower temporal bar; the two nasals meet along the midline; the frontal has moderately developed cristae cranii; the parietal foramen is located on the frontoparietal suture. A few features are also revised, such as there are seven premaxillary teeth (rather than four); the frontals are fused (rather than paired); the surangular and angular is separated (rather than fused).

The new anatomical information confirms *Funiusaurus* is a member of Polyglyphanodontia, based on the combination of following characters: a large facial process of maxilla, a broad suborbital ramus of jugal, vomer-pterygoid con-

tact, palatine-ectopterygoid contact, a large splenial, and a heterodont dentition (Jiang et al., 2025). Additionally, the presence of scleral ossicles in a Polyglyphanodontian taxon has not been reported before. The shape and the size of these scleral ossicles suggest that *Funiusaurus* had generalized, fairly flat scleral ring.

Polyglyphanodontia is well known to have many large-bodied and herbivorous members, such as *Polyglyphanodon* and *Gilmoreteius* (Table 1). These species lived in late Late Cretaceous where many herbivorous species of dinosaurs and crocodiles thrived (Melstrom and Irmis, 2019; Benton, 2025) and the forest-living amphibians started to doom (Roelants

et al., 2007). This may be related to the Cretaceous Terrestrial Revolution or Angiosperm Terrestrial Revolution (Lloyd et al., 2008; Benton et al., 2022). Meanwhile there are also many small polyglyphanodontians, including *Adamisaurus*, *Gobinatus*, *Tchingisaurus*, *Pyramicephalosaurus*, *Caninosaurus*, as well as *Funiusaurus* studied herein, which bear a generalized dentition (with the exception of Adamisaurus), conical teeth with one to three cusps, and probably ate insects. If the numerous species named by Alifanov (1988, 1993, 2000) are valid, or chamopsiids from North America is confirmed to be polyglyphanodontians, it is common and probably ancestral to be small and insectivorous to Polyglyphanodontia.

The evolution of the body size or the diet shift in Polyglyphanodontia and how the two aspects were interacting are currently unclear due to the uncertain phylogenetic relationship within the clade. For example, Pyron (2017) obtained a topology with a large-sized clade and a small-sized clade, the latter of which is closely related to teiids (Tupinambinae, Teiinae, Gymnophthalmidae), but other phylogenetic results did not (e.g., Simões et al., 2016). A more comprehensive phylogenetic study on the intrarelationship of Polyglyphanodontia is strongly needed to solve the evolutionary history of the clade, including the body size evolution and its mechanism, and the detailed anatomy of *Funiusaurus luanchuanensis* herein will help to build this new phylogenetic work.

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Morphological Study of New Material of *Funiusaurus* (Squamata, Teiioidea) from Luanchuan

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Abstract: Teiioids are a group of squamates that flourished in the Late Cretaceous. They were widely distributed in Asia, North America, and some other regions, and exhibit a high degree of diversity in generic composition, morphology, and ecology. Although teiioids are best known for their many large herbivorous representatives, their principal fossil localities have also yielded many small insectivorous forms. *Funiusaurus luanchuanensis* from the Qiupa Formation of the Upper Cretaceous of Henan, China, is one of these. Prior to *Funiusaurus*, only a single, nearly complete but relatively fragmentary skull was known; consequently, the morphological information available for it was limited. On the basis of high-resolution CT data from a newly discovered complete skull and other specimens of several skulls and postcranial bones, this study supplements a large amount of anatomical information for *Funiusaurus*, especially concerning the palatal region, braincase, vertebrae, and limb elements. These new data will help establish a more complete morphological matrix for teiioids and thereby allow more in-depth discussion of the evolutionary history of body size and dietary transitions in teiioids.

Keywords: Henan; Qiupa Formation; Late Cretaceous; *Funiusaurus*; Teiioidea

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Note: Figure translations are in progress. See original paper for figures.